The associative behaviour of silky sharks, *Carcharhinus falciformis*, with floating objects in the open ocean

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Abstract

The silky shark *Carcharhinus falciformis* forms the primary elasmobranch bycatch in tuna purse seine fisheries using fish aggregating devices (FADs) in all of the world's tropical oceans. Its life-history traits of slow growth, late maturation and low fecundity make it vulnerable to over exploitation, as is apparent from historical bycatch trends. Very little is known about the associative behaviour of this species with floating objects, information which is essential in formulating effective mitigation and management measures. This study aims to address this knowledge gap through the use of various electronic tagging techniques in conjunction with dietary analysis. Dietary data were collected from 323 silky sharks incidentally caught at FADs. Approximately 40% of the diet consisted of prey associated with FADs while the remaining 60% were non-associated species of crustaceans, cephalopods and fishes. These results suggest that the associative behaviour is not primarily driven by trophic enhancement, but is likely a combination of predator avoidance, social interactions and feeding. Fine-scale behavioural data from silky sharks associated with drifting FADs were collected through the use of acoustic telemetry techniques. Acoustic tags were implanted into 38 silky sharks (69-116 cm TL) at eight FADs. FADs were equipped with satellite linked acoustic receivers and abandoned to drift freely. Presence/absence and swimming depth data were telemetered via the Iridium satellite system. A total of 300 d of behavioural data were collected from 20 tagged individuals. Individuals remain associated with the same FAD for extended periods (min = 2.84 d, max = 30.60 d, mean = 15.69 d). Strong diel patterns were observed in both association and swimming depth. Typically individuals moved away from FADs after sunset and return later during the night, then remain closely associated until the following evening. Vertical behaviour also changed around sunset with sharks using fairly constant depths, within the upper 25 m, during the day and switching to rapid vertical movements during the night, with dives in excess of 250 m recoded. Broader scale movement behaviour was investigated using pop-up archival satellite tags (PSATs). Tags were deployed on 46 silky sharks (86-224.5 cm TL) for a total of 1495 d. Light data were used to calculate geolocation estimates and reconstruct the sharks' trajectories. Movement patterns differed between animals and according to deployment duration. Several extensive horizontal movements were observed, with an average track length of 3240 km during an average tag deployment of 44.02 d. Horizontal movement patterns were found to correlate very closely with drift patterns of FADs. Consequently, it appears that the movement behaviour of juvenile silky sharks is strongly influenced by the movement of drifting FADs in this region. Ghost fishing of silky sharks through entanglement in FADs was also investigated using data derived from PSATs as well as underwater visual censuses. Thirteen per cent of the tagged sharks became entangled in FADs and entangled sharks were observed in 35% of the 51 FADs surveyed. Using this information in conjunction with estimated time that sharks remained entangled in the FAD (from depth data from PSATs), and scaling up according to estimates of FAD numbers, it was found that between 480 000 and 960 000 silky sharks are killed annually in this manner in the Indian Ocean. Subsequent management measures in this region prevent the deployment of FADs with netting that could lead to entanglement. Overall, floating objects appear to play a significant role in the juvenile life stages of silky sharks in this region. While their association with floating objects is clearly advantageous in an evolutionary sense, under current tuna fishery trends, this behaviour is certainly detrimental for the population.

Acknowledgments

The voyage I have taken to reach here has, for me, been nothing short of amazing. It's origins can be traced back more than a decade, to my mother's excited suggestion that I apply for a Bachelors in Ichthyology & Fisheries Science at Rhodes University. Were it not for her maternal quest to find the most suitable path for her children's future, I do not believe I would have ever reached this point, and for that I am immensely grateful. My father's guidance onto and into the sea sparked a deep attachment that lingers in my earliest memories. His contagious passion for the life aquatic inspired me and doubtlessly set me on the trajectory that led me here. Thanks for it all Dad. Indeed, the unwavering support I received from my entire family along the way, George, Brenda, Lisa and Nick, has been immense. My wife, Nancy, has been the beacon guiding me through it all. Thank you for enduring the cumulative years of my expatriation and field work, your unfailing support and understanding have been nothing short of phenomenal. It has been the greatest pleasure to share this endeavor with you. Your constant and genuine excitement and enthusiasm with every new result and each progressive step toward the achievement of this goal have been an unprecedented motivator. Laurent Dagorn, I cannot thank you enough for imparting your encyclopedic knowledge of the world of FADs and tuna fisheries to me. Following you around the planet has been an incredible pleasure and honor. Your guidance and inspirational leadership are valued second only to your friendship. Paul Cowley, without you this PhD would never have been possible. Thank you for your belief in me and for the dedication, commitment, and friendship you have shown me over the years. Fabien Forget, my partner in crime across continents, islands and in the middle of oceans, thank you for your friendship throughout, and for your tireless support and contributions during all the fieldwork, lab work and office work. Robert Bauer, your programming wizardry and analytical assistance were greatly appreciated, thank you for all your help. Michel Potier and Fréd Ménard, thank you for your teachings and guidance and sharing your vast knowledge on the dietary analysis of pelagic predators. Similarly, I'd like to thank Malcolm Smale and Yves Cherel for their patient assistance with the identifications of cryptic cephalopod samples. Manuela Capello, your analytical prowess and refreshing approaches were greatly beneficial, thank you. My thanks also go out to all the staff and students of EME 212 in Sète, so many of you contributed in so many ways to the completion of this thesis. My sincere thanks also go to the staff of the Seychelles Fishing Authority, many of whom I am deeply indebted to for their assistance with the processing of dietary samples. I also thank Rhett Bennett, Greg Burke, Rodney Govinden, Jon Lopez and Marc Soria for their assistance during the various research cruises. My thanks also go to all the captains and crews of the many vessels from which my field work was conducted. Your friendly acceptance and willingness to collaborate and assist was greatly appreciated. I would also like to thank the International Seafood Sustainability Foundation for their financial support during my PhD and for facilitating much of the field work through vessel charter. Furthermore, I thank the commission of European Communities for their financial support through the FP 7, "Theme 2-Food, agriculture, fisheries and biotechnology" funded research project MADE, under which this research was conducted.

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Chapter 1

Thesis Introduction

1.1 General Introduction

This thesis explores the associative behaviour of the silky shark, *Carcharhinus falciformis* (Müller & Henle, 1839), with floating objects in the Indian Ocean. Through various methodological approaches, the motivations for, behaviour during, and consequences of these associations are investigated.

Floating objects in the open ocean, in the form of natural product (e.g. logs), artificial debris (flotsam) or purposely man-made objects (Fish Aggregating Devices, FADs) have the ability to attract a variety of fish species, which aggregate around these reference points (Hunter and Mitchell, 1967; Parin and Fedoryako, 1992; Freon and Dagorn, 2000; Castro *et al.*, 2002). In tropical and subtropical regions the communities that form around floating objects generally consist of similar species or families (Parin and Fedoryako, 1992). Often the bulk of the aggregated biomass is made up of three species of tuna: skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) (Fonteneau *et al.*, 2000). These species can form aggregations in excess of several hundred tons around a single floating object. The remainder of the aggregated community is often characterised by higher diversity and can include demersal, semi-pelagic and truly offshore pelagic species (Parin and Fedoryako, 1992; Taquet *et al.*, 2007b). In excess of 333 species have been found in association with floating objects in the open ocean (Castro *et al.*, 2002). The most common pelagic species include dorado (*Coryphaeana hippurus*), wahoo (*Acanthocybium solandri*), oceanic triggerfish *(Canthidermis maculata*), rainbow runner (*Elagatis bipinnulata*) and the silky shark. Investigations into the association of fish with floating objects began almost 50 years ago (Gooding and Magnuson, 1967; Hunter and Mitchell, 1967, 1968) and have developed into an important aspect of pelagic fisheries research (Dempster and Taquet, 2004), yet the reasons that drive this association remain poorly understood for many species (Freon and Dagorn, 2000). A multitude of hypotheses have been proposed to explain this behaviour, which likely reflects the variety of motivating forces that are specific to each species and involve complex interactions of multiple factors. Some examples of these hypotheses include predator avoidance, trophic benefits, a meeting point for the formation of larger schools, a schooling companion, negative phototropism or the indication of rich environments. Detailed reviews of this topic are provided by Freon and Dagorn (2000) and Castro *et al.* (2002).

The associative phenomenon has been exploited by fishers throughout recorded history (Jones, 1772 in Taquet *et al.*, 2007b), with the earliest record dating back to 200 AD by the Roman author Oppian (cited in Dempster and Taquet, 2004). Traditionally fishers would actively seek out drifting objects to capture the associated fishes, but over time they began to construct and deploy floating structures known as FADs, designed specifically for this purpose (Dempster and Taquet, 2004). Initially FADs were anchored near the coast such that fishers were provided with ready access to otherwise dispersed pelagic resources. Such FADs were generally used by small scale artisanal fleets in coastal or island nations. In the open ocean, large purse seine vessels targeting tropical tuna species would actively seek out drifting objects, usually logs, around which they would set their nets (hereafter referred to as 'sets') to catch the aggregated tunas (Hallier, 1985; Hilborn and Medley, 1989). Alternatively, these vessels would search for free swimming schools of tuna feeding at the surface, or those associated with marine mammals (Hall, 1992) or whale sharks (Silas and Pillai, 1982). In the early 1980s the development of radio tracking buoys allowed fishers to relocate drifting objects in the open ocean (Lopez *et al.*, 2014). At this time these purse seine vessels began to construct and deploy FADs, which they allowed to drift for months at a time. Using the attached radio tracking buoy, the FADs were relocated and the associated tunas captured. Drifting FADs typically consist of a small bamboo raft (1.5 m × 1.5 m) to which old netting is attached. This netting extends several meters below the surface, with weights at the lower end. The weighted net serves a dual purpose of providing a surface upon which marine life can flourish and to increase the drag of the FAD, causing it to move with the current rather than being blown by the wind. In the Indian Ocean, the design of FADs has changed little since they were first introduced in 1986 (Lopez *et al.*, 2014). However, the efficiency of the fishing method [90% of fishing sets result in a successful catch -(Fonteneau *et al.*, 2013)] along with advances in tracking buoy technology have seen the importance of this fishing tool grow steadily during the past three decades (Dagorn *et al.*, 2013). In 1997, the number of purse seine sets on FADs exceeded the number on free swimming schools of tuna in the Indian Ocean (Lopez *et al.*, 2014). Today catches from FADs represent more than 50% of the 2 million tons of tropical tuna caught globally each year (Fonteneau *et al.*, 2013) and in the Indian Ocean FAD sets produced almost 80% of the tuna catch in 2009 (Dagorn *et al.*, 2013). With the integration of GPS technology into the tracking buoys in 1996 (Lopez *et al.*, 2014) vessels were able to monitor many buoys simultaneously. Furthermore, in the late 1990's satellite transmitting echo-sounders were integrated into these buoys, which provided skippers with remotely derived indices of the aggregated biomass. Steady improvements in this technology have reduced the uncertainty of these indices, with certain buoy brands now providing skippers with reliable information which they use to determine their spatial fishing strategy. The exact number of FADs that each vessel has at its disposal at any point in time is a tightly guarded secret. As such, the number of FADs currently drifting in each ocean is unknown. Efforts have been made to improve this situation, initially through interviews with skippers, and more recently through the sharing of FAD tracking data between fleet owners and scientists in certain areas. In 2007, the number of FADs in use in the western Indian Ocean was estimated to be 2100 (Moreno *et al.*, 2007b). More recent estimates have put this number at approximately 5 700 (Maufroy *et al.*, 2014).

The widespread use of FADs in the purse seine fishery has raised concerns among scientists and fisheries managers for a number of reasons. Firstly, FAD fishing can potentially reduce the yield per recruit of the targeted tuna species as the vast majority of yellowfin and bigeye tuna captured are juveniles (Bromhead *et al.*, 2006), although the majority of tuna catches from FADs consist of adult skipjack tuna. Secondly, FAD fishing increases bycatch and could result in a disturbance to the balance of the pelagic ecosystem (Gilman, 2011; Morgan, 2011). The amount of bycatch is 2.8 - 6.7 times greater when purse seine nets are set on FADs compared to sets made on free schools of tuna (Dagorn *et al.*, 2013). Thirdly, FADs could potentially influence the normal movements patterns of the species associated with them (Marsac *et al.*, 2000; Hallier and Gaertner, 2008). It has also been suggested that the increased deployment of FADs over large areas of the ocean could result in an ecological trap for associated species as they may be taken to areas that are biologically inappropriate for feeding or through alterations to their natural migratory patterns, to breeding success (Wang *et al.*, 2014).

Aside from the direct impacts that FAD fishing has on tuna resources, the ecological impacts of this activity on non-target species is a major concern (Dagorn *et al.*, 2013). This is especially true for species that are sensitive to overexploitation, such as sharks and turtles. Five species of turtles have been recorded as bycatch in purse seine sets in the Indian Ocean and include loggerhead (*Ceretta ceretta*), green (*Chelonia mydas*), leatherback (*Dermochelys coriacea*), hawksbill (*Eretmochelys imbricata*) and olive ridley (*Lepidochelys olivacea*) turtles (Bourjea *et al.*, 2014). Turtles are generally found resting on top of the floating structure of the FAD and can become entangled in the netting that covers the raft. Overall the incidence of turtle capture is very low (0.019 - 0.022 individuals per set) and post release survival rates are believed to be high (Amandè *et al.*, 2010; Bourjea *et al.*, 2014). As such the impact of FAD fishing on turtles is believed to be minor (Bourjea *et al.*, 2014). Very few species of sharks are regularly encountered in association with drifting objects on a regular basis. The principle species are the oceanic whitetip shark (*C. longimanus*) and the silky shark (Roman-Verdesoto and Orozco-Zoller, 2005; Amandè *et al.*, 2008a; Gilman, 2011). In the Indian Ocean silky sharks are by far the most common elasmobranch species captured in the FAD-based fishery (González *et al.*, 2007; Amandè *et al.*, 2008a) and occur in 48% of the purse seine sets made on FADs (Amandè *et al.*, 2011). The number of silky sharks aggregated around a single floating object can reach several hundred (Taquet *et al.*, 2007b) and in sets on FADs where sharks are present an average of 11 are caught (Amandè *et al.*, 2011). The overall average capture rate at FADs is 2.02 individuals per set (Amandè *et al.*, 2008b). A large majority of captured silky sharks are early juveniles (Amandè *et al.*, 2008b). In the Indian Ocean the average size is approximately 1 m (González *et al.*, 2007; Amandè *et al.*, 2008a) with an age range of 0-5 years (Oshitani *et al.*, 2003; Rabehagasoa *et al.*, 2014). It is estimated that almost 200 000 silky sharks are taken as bycatch each year in all the FAD-based purse seine fisheries (Filmalter *et al.*, 2013). In the Indian Ocean alone, this figure is approximately 80 000 (Filmalter *et al.*, 2013). A

Study on the post release survival of silky sharks following capture in a purse seine nets has revealed that approximately 80% of the sharks die during the fishing process, when the best handling practices are followed (Poisson *et al.*, 2014).

1.2 Biology and ecology of the silky shark

Distribution

The silky shark is a large bodied member of the family carcharhinidae that has been described as one of the most common pelagic sharks (Compagno, 1984). It has a pan-tropical distribution, occurring in the tropics and subtropics of all the world's oceans. Silky sharks commonly inhabit insular and continental shelves, deep-water reefs, seamounts as well as the offshore pelagic environment (Bonfil, 2008), where juveniles are often found in association with drifting objects (Yoshimura and Kawasaki, 1985; Romanov, 2002; Anderson and Jauharee, 2009). In the western Atlantic Ocean neonates and early juveniles are believed to adopt a more demersal life-style, occupying nursery areas on the continental shelf (Springer, 1967; Branstetter, 1987; Bonfil, 1997). Branstetter (1987) suggested that juveniles in the Gulf of Mexico move offshore within one year of birth, to areas beyond the continental shelf where the occurrence of other large sharks is lower. Similar detailed information on the ontogenetic distribution patterns from other regions are largely lacking, primarily due to misidentification of silky sharks with other carcharhinid species (Bonfil, 2008). In the tropical eastern Pacific Ocean a large-scale shark identification program conducted during 2000 by the Inter-American Tropical Tuna Commission (IATTC) found that a significant proportion of silky sharks were previously identified as blacktip sharks (*Carcharhinus limbatus*) by observers on purse seine vessels (Roman-Verdesoto and Orozco-Zoller, 2005). Furthermore, in many large-scale fisheries, shark catches were seldom reported to the species level (Clarke *et al.*, 2006a; Bonfil, 2008). Historic longline catch data from the central Pacific Ocean suggested that silky sharks were more abundant near islands with catches decreasing with increasing distance from land (Strasburg, 1958). This author also noted a weak positive correlation between the size of silky sharks and the distance of the capture location from land. More recent work from the eastern Pacific Ocean found that silky shark catches on longlines increased further offshore of Costa Rica and Panama (Dapp *et al.*, 2013). Similarly, Watson *et al.* (2009) noted an increase in the abundance of juvenile and small silky sharks with increasing latitude north of the equator in the eastern Pacific Ocean, while larger individuals were more abundant south of the equator, based on observer data from purse seine vessels.

Biology

Silky sharks attain a maximum total length (TL) of approximately 3.3 m (Compagno, 1984). Joung *et al.* (2008) reported sexually dimorphic growth patterns in silky sharks from the western Pacific Ocean, with females growing larger than males. Other studies have failed to find the same results, reporting no difference in growth between the sexes (Bonfil *et al.*, 1993; Oshitani *et al.*, 2003; Rabehagasoa *et al.*, 2014). The species has a highly evolved reproductive style: placental viviparity. Following internal fertilization embryos develop during a 12 month gestation period. Litter size typically ranges between 6-12 pups with up to 16 individuals being reported at times (Bonfil, 2008). Both the size at maturity and the size at birth vary regionally, with almost all studies reporting slight differences in these parameters (Bonfil, 2008). The smallest size at maturity was reported from the eastern Pacific Ocean with both males and females maturing at 180 cm (Cadena-Cárdenas, 2001). Conversely, the largest size at maturity was reported from the southeastern Indian Ocean; 240 cm for males and 248-260 cm for females (Bass *et al.*, 1973). Estimates of size at birth range between 56-87 cm TL (Bonfil, 2008). Some age and growth studies have suggest that the maximum age is likely to be in excess of 20 years (Bonfil *et al.*, 1993; Rabehagasoa *et al.*, 2014), while others have reported shorter maximum ages with males attaining 8-14 years and females 11-13 years respectively (Oshitani *et al.*, 2003; Joung *et al.*, 2008). Comparisons of these life history parameters with other pelagic shark species have shown that silky sharks have productivity levels that are typical of carcharhinid sharks, which invest early in somatic growth, have delayed maturity, but live longer than many other shark species (Smith *et al.*, 1998).

Movement behaviour

Studies on silky shark movement patterns are limited and as a result very little is known about their movement behaviour throughout their distribution.

Clarke *et al.* (2011a) reported high levels of residency by adult silky sharks at provisioning sites on offshore reefs in the Red Sea. Mark-recapture studies have shown that silky sharks can display movements in excess of 1000 km (Kohler *et al.*, 1998). However, several individuals have been recaptured in close proximity to their tagging location (<200 km), after several months at liberty (Kato and Carvallo, 1967; Stevens, 1984b). Seasonal movement patterns have not been identified through these tagging efforts. The application of satellite tags to investigate the horizontal movements of silky sharks has been limited to the Pacific Ocean, and only in low numbers. Kohin *et al.* (2006) deployed seven pop-up satellite tags (PSATs) and three Smart Position Tags (SPOTs) on seven silky sharks in the eastern Pacific Ocean. Preliminary results showed that some individuals moved significant distances, with one shark traveling in excess of 2500 km in 10 months, moving from Costa Rica to the Gulf of California and back. Musyl *et al.* (2011a) deployed 10 PSATs on silky sharks in the central Pacific Ocean. They found no distinct pattern in the movements of the tagged sharks, with some moving north to south while others moved from south to north. The maximum linear displacements of these sharks ranged from 74 - 687 km during 12 - 145 days.

Exploitation and threats

Silky sharks are caught in artisanal and industrial fisheries that target pelagic sharks throughout their distribution range (Strasburg, 1958; Compagno, 1984; Bonfil *et al.*, 1993; Hazin *et al.*, 2007; Bonfil, 2008) but they also forms a major component of the bycatch incurred in both longline and tuna purse seine fisheries in all tropical oceans (Bane, 1966; Compagno, 1984; Santana *et al.*, 1998; Romanov, 2002; Roman-Verdesoto and Orozco-Zoller, 2005; Amandè *et al.*, 2008a; Watson *et al.*, 2009). Clarke *et al.* (2006a) suggested that silky sharks are the second most important species (after the blue shark, *Prionace glauca*) supporting the Honk Kong shark fin trade. There is convincing evidence to suggest that populations of this species have undergone large declines over the past five decades, as industrial pelagic fisheries (longline, gillnet and purse seine) have grown (Baum and Myers, 2004; Tavares and Arocha, 2008; Anderson and Jauharee, 2009; Clarke *et al.*, 2013). Clarke *et al.* (2013) revealed a decreasing trend in catch per unit effort (CPUE) and a decrease in the average size of silky sharks captured by both longline and purse seine gears in the western and central Pacific Ocean. Similarly, Dapp *et al.* (2013) noted a decline in the mean size of silky sharks caught in the longline fishery in equatorial east Pacific between 1999 and 2010. These trends in decreasing size suggests a reduction in adult abundance in the population. Baum and Myers (2004) showed a dramatic decline in the size of silky sharks in the Gulf of Mexico between the 1950s and the 1990s, where the average weight fell from 102.3 kg to 16.7 kg. The global annual catch of silky sharks was estimated to be between 400 000 and 2 million individuals (Clarke *et al.*, 2006b). In light of the widespread exploitation and incidental capture of this species the International Union for Conservation of Nature (IUCN) has designated it a global status of Near Threatened (Bonfil *et al.*, 2009). Further regional assessments have classified the species as vulnerable in the eastern central and southeast Pacific, vulnerable in the northwest and western central Atlantic, near threatened in the Indian Ocean and near threatened in the central Pacific (Bonfil *et al.*, 2009).

1.3 Thesis purpose and objective

Our understanding of several aspects of the biology and ecology of silky sharks in the Indian Ocean is extremely limited. In this region, very little is known about the reproductive biology of the species, specifically where breeding and parturition occur. Furthermore, no information exists on their large-scale horizontal movement behaviour, an aspect identified as a research priority by Bonfil (2008). Similarly, very little is known about the details of their feeding habits, as well as the motives and consequences of the association with floating objects. The purpose of this thesis was to address many of these gaps in our knowledge, with particular emphasis on silky shark association with FADs in the Indian Ocean. More specifically, the objectives of this study were to investigate (i) the diet of silky sharks associated with FADs, (ii) their fine scale behaviour while associated with FADs, (iii) their large-scale horizontal movement patterns, and (iv) in light of the wide spread use of FADs by tropical tuna purse seine fisheries, to quantify the mortality of silky sharks associated with FADs, through entanglement.

1.4 Thesis layout

This section serves to illustrate how this thesis forms a cohesive body of work, focused on improving our understanding of the association of silky sharks with floating objects and the role this behaviour plays in the ecology of the species. This thesis consists of a further six chapters each dealing with different aspects of the associative behaviour.

- Chapter 2 provides an overview of the study site and the methods used to address the various objectives of this thesis.
- Chapter 3 investigates the feeding ecology of silky sharks associated with floating objects, in an effort to assess whether trophic benefits drive associative behaviour.
- Chapter 4 characterises the fine scale behavioural patterns displayed by silky sharks when associated with drifting objects, through the use of electronic tags.
- Chapter 5 investigates the large scale horizontal movements of silky sharks, through satellite telemetry, in an attempt to understand how drifting FADs might influence their movements.
- Chapter 6 quantifies a previously unknown issue of unobserved mortality of silky sharks due to entanglement in the netting of FADs. This chapter was published in the journal Frontiers in Ecology and the Environment in 2013. (Reference: Filmalter, J. D., Capello, M., Deneubourg, J.-L., Cowley, P. D., and Dagorn, L. 2013. Looking behind the curtain: quantifying massive shark mortality in fish aggregating devices. Frontiers in Ecology and the Environment, 11: 291–296.)
- Chapter 7 provides a synthesis of the results of the thesis and ties them together in a general discussion, highlighting the implications of these finding in the context of the industrial tuna purse seine fishery.


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Chapter 2

Methods and Study Site

For the studies described in this thesis a variety of technologically advanced methods were employed to observe the behaviour of silky sharks (*Carcharhinus falciformis*) in the pelagic environment. This chapter outlines the methods used and explains their application in the various studies described in subsequent chapters. Furthermore, this chapter provides a general description of the area in which the studies were conducted.

2.1 Study site

The studies described within this thesis were conducted in two major areas of the western Indian Ocean, the Mozambique Channel and the Seychelles. The western Indian Ocean is characterised by two monsoon seasons with large scale alterations in wind regimes (Hastenrath and Greischar, 1991). These monsoon seasons are driven by the warming and cooling of the Asian subcontinent during the boreal summer and winter. Between November and March, the Northeast (NE) monsoon, air flows from southern Asia out over the Indian Ocean. In the Seychelles region winds primarily blow in a north westerly direction during this period. The Southwest (SW) monsoon occurs between May and September and in the Seychelles area the wind blows constantly from the south east. At lower latitudes the effects of the monsoons are less prevalent and winds tend to blow more consistently from the east for much of the year (Hastenrath and Greischar, 1991).

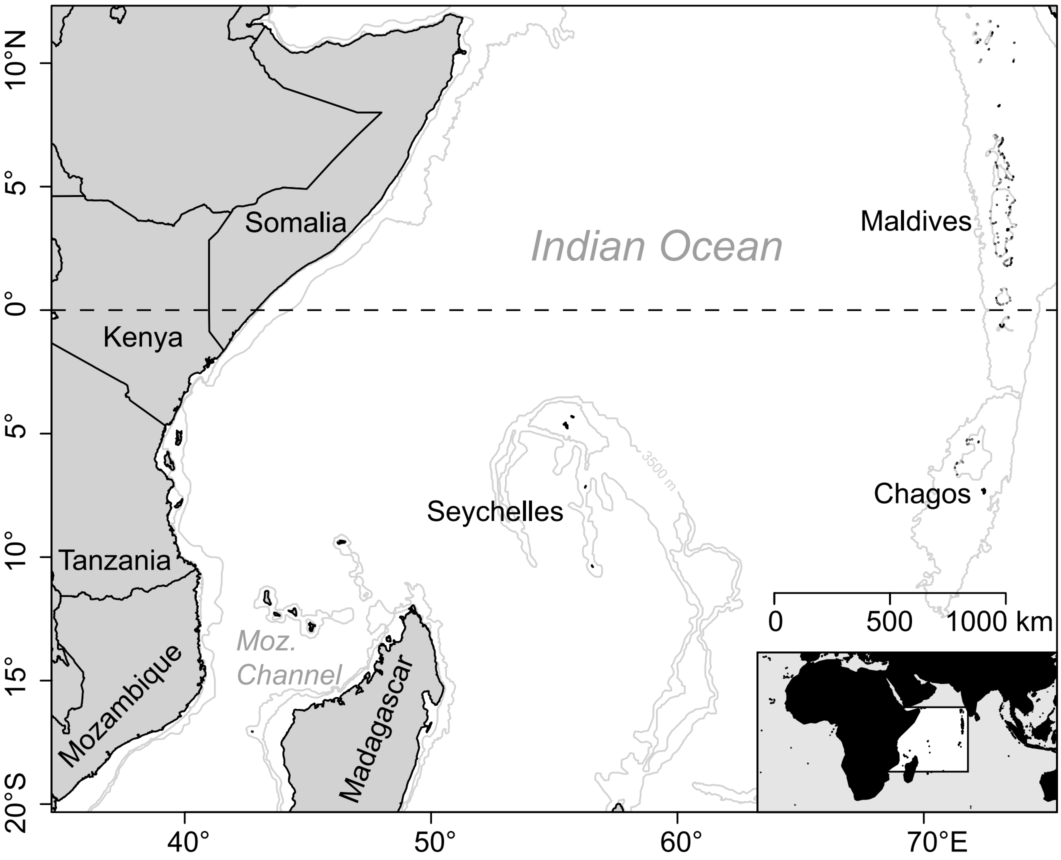

Figure 2.1 Location of the study site in the western Indian Ocean.

In terms of major oceanographic patterns, the monsoon variations have greatest effects in the northern hemisphere. Here, during the SW monsoon strong upwelling occurs off the Somalian coast with the formation of the near stationary cyclonic structure known as the Great Whirl (GW), which is absent during the NE monsoon (Schott *et al.*, 2002; Beal and Donohue, 2013). During the SW monsoon the Southwest Monsoon Current (SMC) flows from west to east between the GW and Maldives at latitudes of 5° - 10° N (Sikhakolli *et al.*, 2013). During the northwest monsoon this current reverses to produce the Northwest Monsoon Current (NMC). Throughout the year the Equatorial current flows from east to west along the equator with the Equatorial Counter-current (ECC) flowing from west to east at approximately 5° S. The South Equatorial Current (SEC) flows throughout the year from east to west at approximately 15° S. The SEC collides with northern Madagascar and the flow is split as it deflects to the north and to the south forming the East Madagascar Current (EMC). The northern flow crosses the top of the Mozambique Channel and again separates as some of the flow is directed south into the Channel while the remainder turns north in the East African Coastal Current (EACC).

The partial flow into the Channel generates highly complex cyclonic and anti-cyclonic structures that travel with a southerly trajectory down the Channel (de Ruijter *et al.*, 2002; Schott *et al.*, 2002; Schouten *et al.*, 2003).

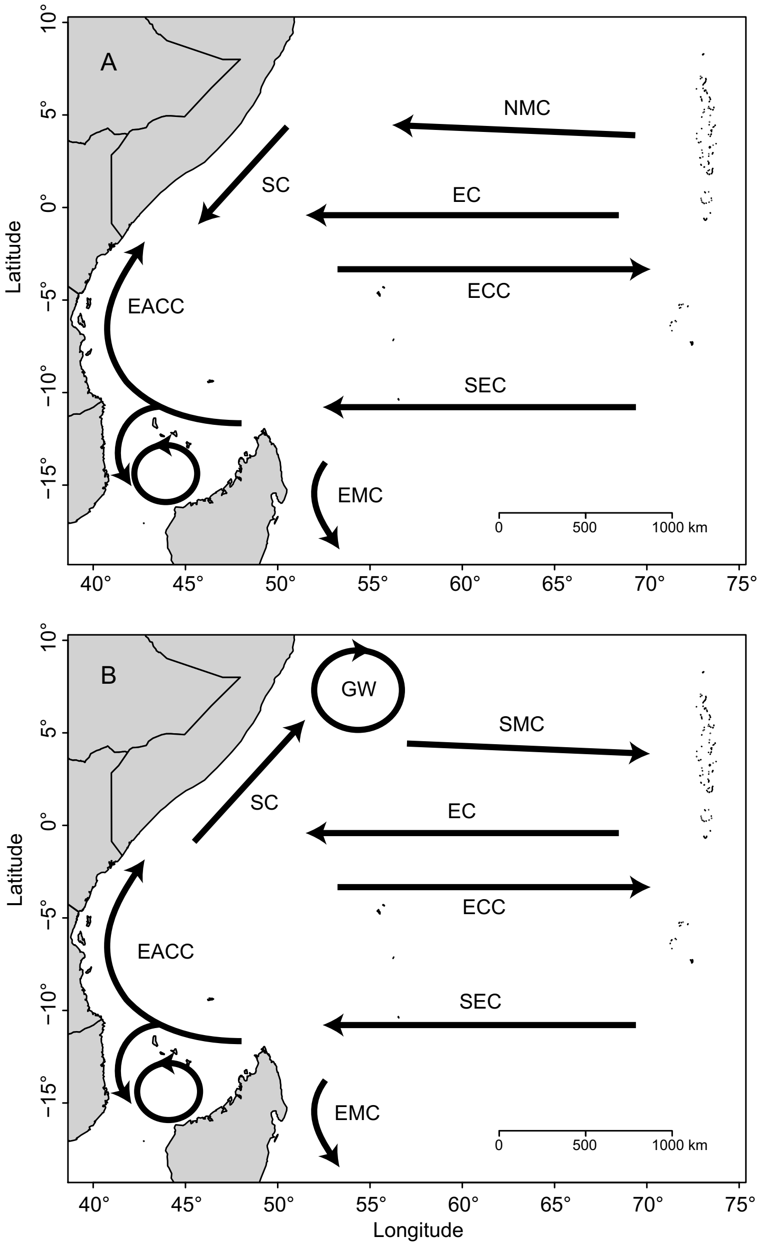

Figure 2.2 Schematic representation of the major current patterns during (A) the NE monsoon between November and March and (B) the SW monsoon between May and September. Current abbreviations: South Equatorial Current (SEC); East Madagascar Current (EMC); East African Coastal Current (EACC); Somali Current (SC); Equatorial Counter Current (ECC); Equatorial Current (EC); Northeast Monsoon Current (NMC); Southwest Monsoon Current (SMC). Redrawn from information in Sikhakolli *et al.* (2013) and Schott *et al.* (2002).

2.2 Tagging trips

Silky sharks were tagged at numerous drifting FADs in the western Indian Ocean between 2010 and 2012. Tagging was carried out during four research cruises on four different vessels Fig. 2.3. Two cruises were conducted in the Seychelles area and two in the Mozambique Channel 2.1. Two of the vessels (M/Y Inventive and M/V Dugong) were private vessels for charter, while the Mtwaro II and Torre Giulia were commercial longline and tuna purse seine fishing vessels respectively, chartered for research. Additionally, two trips were made onboard tuna purse seine vessels under normal commercial operation where silky sharks were tagged to study their post release survival. While some data from the latter two cruises were included in the horizontal movement analyses presented in Chapter 5 of this thesis, they were not specifically intended for the purpose of this study on the behaviour of silky sharks at FADs.

Table 2.1 Summary information of tagging cruises in the western Indian Ocean.

Vessel	Start date	End date	Duration (days)	Area
M/Y Inventive	04/03/10	17/3/10	13	Moz.
Mtwaro II	14/4/11	21/4/11	7	Moz.
M/V Maya's Dugong	16/6/11	27/6/11	11	Sey.
Torre Giulia	31/3/12	08/5/12	39	Sey.

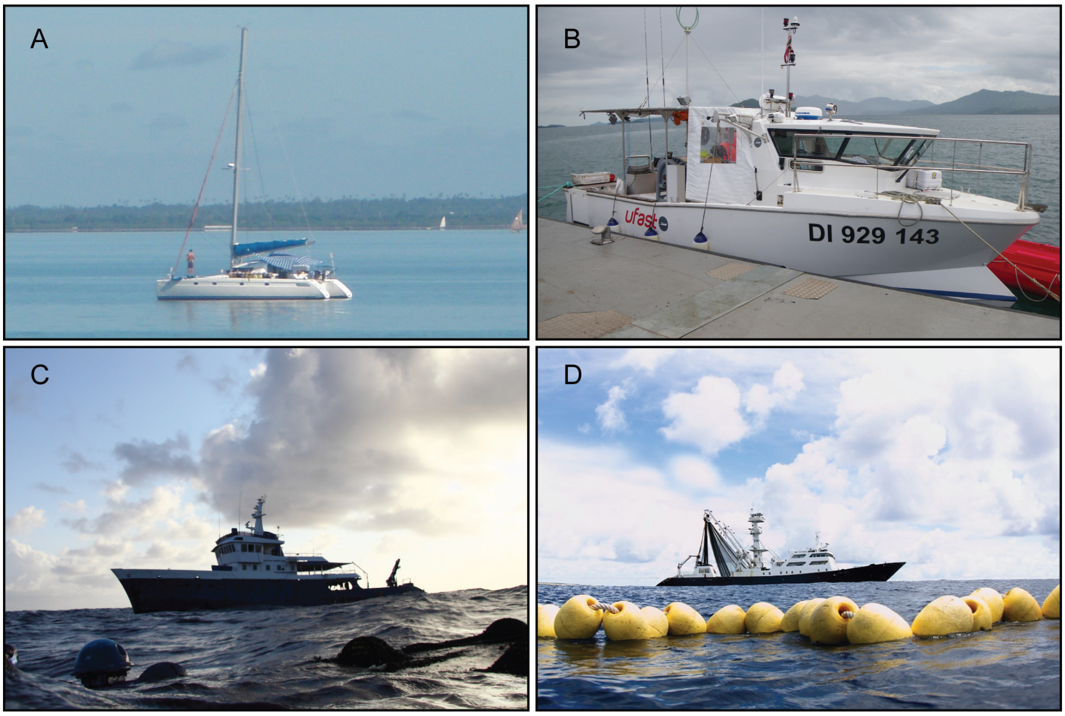

Figure 2.3 Vessels from which tagging of silky sharks at FADs in the western Indian Ocean was carried out. (A) M/Y Inventive, (B) F/V Mtwaro II, (C) M/Y Maya's Dugong and (D) F/V Torre Giulia.

2.3 Acoustic telemetry

The use of acoustic telemetry to study the behaviour of fishes has developed over the past 50 years and is now a technique widely accepted in the aquatic science community. The basic principle of acoustic telemetry relies on the use of a tag, attached to the study animal that emits an acoustic signal, and a receiver that can detect and decode the signal from some distance away. Early telemetry systems, developed for the study of salmonids, allowed the determination of the presence of a particular tagged individual in a confined area using an omnidirectional hydrophone (Trefethen, 1956). The tags were simple 'pingers', which would transmit an acoustic signal at a predetermined interval (usually milliseconds to seconds). Later, sensors were developed and integrated into the acoustic tags, which allowed additional information such as water temperature or the swimming depth of the fish to be telemetered from the tag to the receiver. Over time, further technological advances allowed these techniques to be successfully used to track the movements of highly mobile pelagic marine species such as skipjack tuna *Katsuwonus pelamis* (Yuen, 1970; Bard and Pincock, 1982; Levenez, 1982), albacore, *Thunnus alalunga*, (Laures *et al.*, 1977), yellowfin tuna, *T. albacares,* and bigeye tuna *T. obesus* (Holland *et al.*, 1990; Brill *et al.*, 1999; Dagorn *et al.*, 2000a). In these studies the acoustic receiver was equipped with a directional hydrophone, which allowed the tracking vessel to follow the movements of the fish, with an approximately constant distance maintained between the fish and vessel. Furthermore, these systems allowed the behaviour of fishes to be monitored from distances ranging between 200 and 2000 m (Yuen, 1970). From those early years, the popularity of acoustic telemetry methods to investigate the behaviour of a wide range fish species has increased substantially. This increase was largely due to the development of autonomous self contained acoustic receivers, capable of recording and storing large amounts of data over periods of several months (Klimley *et al.*, 1998; Kessel *et al.*, 2013), which significantly reduced experimental costs. With these systems, detections from tagged fishes were recorded in the non-volatile memory of the battery powered receiver which was then retrieved after several months and the data downloaded (Heupel *et al.*, 2006). While the study of free swimming pelagic animals remained largely restricted to active tracking methods (Holland *et al.*, 1985; Klimley *et al.*, 1988; Josse *et al.*, 1998; Brill *et al.*, 1999; Dagorn *et al.*, 2000b,a; Arnold and Dewar, 2001; Brill *et al.*, 2002; Klimley *et al.*, 2002), areas where these species aggregated, such as seamounts (Klimley *et al.*, 1988) or anchored fish aggregating devices (FADs) (Klimley and Holloway, 1999; Ohta and Kakuma, 2005; Dagorn *et al.*, 2007a; Taquet *et al.*, 2007a; Govinden *et al.*, 2013), allowed for the use of such autonomous passive systems. More recent developments in the field of acoustic telemetry have seen the advent of satellite linked receivers (Dagorn *et al.*, 2007b), which allow researchers to receive data from tagged fishes without the need to physically retrieve the receiver. Early prototypes of these receivers sent summaries of acoustic data logs via the ARGOS satellite system. Further development led to the production of an acoustic receiver (VR4-Global, Vemco, a division of Amirix) capable of recording and transmitting entire data logs, of every recorded detection, via the Iridium satellite system. These receivers are ideally suited for studying the behaviour of pelagic fishes associated with drifting objects in the open ocean environment. Previous studies of such aggregations required that a vessel revisit the floating object to retrieve the data (Matsumoto *et al.*, 2014) or that the fish be associated with a drifting vessel (Schaefer and Fuller, 2005). As such, the durations of observations was often limited. The use of satellite linked receivers allows for the longer-term monitoring of fishes

Figure 2.4 VR4-Global acoustic receiver (A) prior to deployment with hydrophone configuration and (B) deployed on a drifting FAD alongside a grey GPS echo-sounder buoy.

associated with drifting objects with limited costs, both financially and in terms of manpower, as receivers can be abandoned to drift freely around the open ocean. In the acoustic telemetry study presented in Chapter 4 of this thesis, VR4-Global satellite-linked acoustic receivers were deployed on drifting FADs to investigate the fine-scale behavioural patterns of tagged silky sharks with the equipped FAD. A single exception was the deployment of a conventional acoustic receiver (VR2W, Vemco) on a FAD that was revisited a month later and retrieved to download the data.

Tag specifications

As the principle focus of this study concerned behavioural patterns from extended observations, all sharks were tagged with coded tags. Coded tags emitted a train of eight acoustic pulses, within which the tag's ID was encoded. Transmission took approximately 3 seconds. Coded tags were 13 mm in diameter, and weighted 11 g in air and had an expected minimum battery life of 879 days. All coded tags had a 90 second nominal delay and transmitted at a frequency of 69 KHz. This nominal delay meant that acoustic emissions were separated by a time period that was randomly distributed between 50 and 130 seconds from the end of the previous emission, the mean of which was 90 seconds. The purpose of this randomised emission sequence was to reduce the probability of signals from different tags overlapping, and thus preventing correct identification by the receiver. Overlapping emissions, known as code collisions, resulted in either the detection not being logged at all, or a false detection where part of the signals from each tag was recorded by the receiver and a non-existent tag ID was logged. This problem is compounded as more tags are deployed and is especially relevant when the multiple tagged fish are simultaneously present around the same receiver, as is the case with an aggregation around a floating object. To mitigate this issue the number of fish tagged around any single floating object during the course of this study was limited to 25 individuals. A single active tracking experiment was conducted during the study, where one silky shark was tagged with a continuous pinger and tracked for approximately 2.5 hours. This tag, a V16P 3H, had a 1 second transmission frequency at 51KHz. The tag was 16 mm in diameter and weighed 16 g in air. All tags were surgically implanted into the peritoneal cavity of captured silky sharks. Specific details of the tagging and capture process are provided in the Materials and Methods section of Chapter 4.

Figure 2.5 Acoustic tags used during the study of silky sharks associated with drifting FADs in the western Indian Ocean. The upper tag is a coded V13, while the lower (red) tag is a continuous V16P tag.

Detection range

Understanding the distance at which acoustic tags can be detected by an acoustic receiver is critical for inferring information about the movements of the tagged fish (Heupel *et al.*, 2006; Kessel *et al.*, 2013). Detection range is known to depend on a multitude of factors including tag characteristic such as size and power output as well as environmental variables, such as sea state, presence of thermoclines and picnoclines, biological noise (especially in reef environments), physical noise, (such as in high energy surf zones or boat traffic) and physical barriers (e.g. high profile reefs or rocks) (Heupel *et al.*, 2006; Payne *et al.*, 2010; Kessel *et al.*, 2013). As several of these variables change with time, detection range is in a constant state of flux. Owing to the highly complex nature of this issue, it is common practise to adopt a single value for the functional detection range, which is typically specific to each study or study environment (Kessel *et al.*, 2013). In many studies range testing is carried out either prior to, or after, the study. These tests typically involve the deployment of tags at known distances from the receiver such that the relationship between distance and success of detection can be interpreted. Generally reception range has been tested around FADs in the open ocean by drifting away from the object (to which the receiver is attached) and measuring the distance and between the vessel (from which the tag is deployed) and the object. Following this method Taquet *et al.* (2007a) reported an average detection range of 360 m for coded V13 tags around anchored FADs on the Mahe plateau in the Seychelles. Dagorn *et al.* (2007a) reported detection ranges between 600 and 1000 m for V16 tags around FADs in Hawaii. Ideally range estimates should be obtained for all experiments and under as many different environmental conditions as possible, however, this is rarely feasible, especially when working in the open ocean. In the current study conducting comprehensive range tests was not possible due to the threat of piracy in the Indian Ocean. Consequently the detection range in this study was assumed to be similar to those reported in other studies of pelagic fish at FADs, where tags of equal specifications were used, i.e. 300 - 400 m reported in Taquet *et al.* (2007a). Additional estimates of range were obtained *a posteriori* based on detections from fishes tagged with coded tags recorded during the active tracking experiment which were then compared with the detections recorded by the VR4-Global receiver attached to the FAD. These results, detailed in Chapter 4, suggest that the detection range of V13 coded tags was approximately 400 m.

2.4 Archival tags

Archival tags record and store data from the surrounding environment. In this study two types of archival tags were deployed, internal archival tags (MK9, Wildlife Computers, Redmond, USA) and pop-up satellite archival tags (PSATs, Wildlife Computers, Redmond, USA). The model of PSAT tags used in this

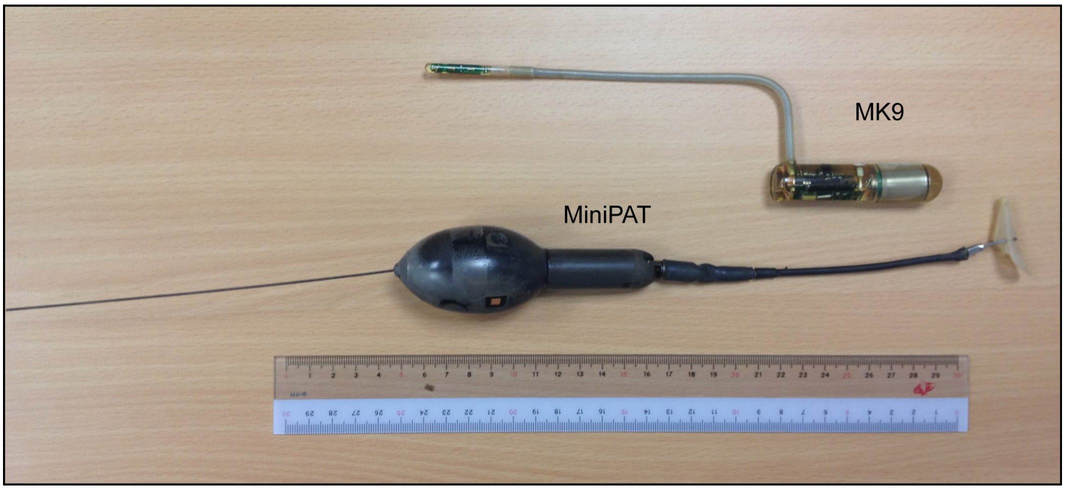

Figure 2.6 Archival tags used in this study. The upper tag is an MK9 internal archival and the lower is a MiniPAT pop-up satellite archival tag, with the tether and anchor configuration used in this study.

study were all miniPATs (Fig. 2.5). These tags were 12 cm in length, weighed 65 g in air and were positively buoyant. Both forms of archival tags collected the same types of data, with the principle difference between the two being that the internal archival tag (MK9) had to be retrieved from a recaptured shark to recover the data, while the PSAT (attached externally), transmitted data via the ARGOS satellite system after detaching from the animal.

Three data types were collected by the archival tags in this study included hydrostatic pressure (which provided depth information), temperature and light level, which were subsequently used to reconstruct the animal's approximate location. Owing to technological limitations, primarily in energy storage, PSATs are unable to transmit all archived data. Here, PSATs were programmed to archive all data streams at 5 second intervals. To overcome the limitations of power storage, while still maximising data output, PSATs summarise the data streams onboard, prior to transmission. As such, depth and temperature data were received at 5 minute intervals. Light level data were truncated using an internal algorithm, when a threshold rate of change in ambient light level was surpassed. In this way, only the light data, recorded at sunrise and sunset, were transmitted in the form of light curves. As the ARGOS satellite system does not allow for two-way communication, the tag has no way of detecting the presence of a satellite. As such, after PSATs popped up, data transmission was immediately initiated and only ceased once the tag's battery was depleted. As satellites tend to pass over any point on earth at a constant frequency, if the data were transmitted in an sequential manner, there is a probability that only certain portions of the data set will be received by the satellite. To overcome this potential problem, the data set is divided into discreet 'messages' containing portions of data from multiple streams. The PSATs would select and transmit these 'messages' at random from within the archive. In this way the same information may be received multiple time, but the probability of receiving data that is evenly dispersed across the deployment period is maximised. Nonetheless, owing to this data transmission procedure, gaps in the data series are inevitable and generally increase with the increasing deployment duration. The model of PSAT used here allowed the user to prioritise to the frequency with which messages from different data streams were transmitted. In this way the transmission of critical information, such as light levels for geolocation, could be optimised.

Light-based geolocation and model selection

Light data recorded by archival tags currently provides the most suitable method for obtaining positional estimates of free swimming animals below the sea surface (Hill and Braun, 2001). This method in it's simplest form can be explained as follows: The time of "sunrise" and "sunset" on a given day are obtained from light data recorded by the tag. The time of the mid-point between the rise and set or set and rise, local noon and local midnight, respectively, is then input into standard astronomical equations to produce an estimate of longitude. This is possible as the time of these events (local noon or midnight) vary in relation to Greenwich meridian time (GMT) with changing longitude. Latitude is estimated from the time difference between the sunrise and sunset events, as day length varies only with latitude. However, estimating latitude becomes difficult during equinox periods as day lengths becomes similar across all latitudes (Hill and Braun, 2001; Nielsen *et al.*, 2006). This global location sensing (GLS) geolocation method provides 'raw' position estimates with uncertainties that typically span multiple degrees of latitude and longitude (Nielsen *et al.*, 2006). Such large errors result from a multitude of factors including the tag's ability to accurately infer the time of sunrise and sunset, which is affected by the behaviour of the tagged animal such as diving during crepuscular periods, moving through waters of highly variable turbidity, or moving large distances within the same day (Hill and Braun, 2001). Several models have been developed to improve the accuracy of these raw estimates, of which perhaps the most widely used is the state-space Kalman-filter approach proposed by Sibert and Fournier (2001) and Sibert *et al.* (2003) and later adapted to incorporate environmental parameters such as sea surface temperature (SST) (Nielsen *et al.*, 2006) to further improve the accuracy of location estimates. Alternative state-space models used for the geolocation of marine organisms include Hidden Markov Models (HMM) (Thygesen *et al.*, 2009) and particle filters (Royer *et al.*, 2005). An alternative non-state-space modelling approach was proposed by Tremblay *et al.* (2009), which utilises a forward-particle filter, known as the IKNOS-WALK. Contrary to state-space models, in this method, no inferences are drawn from the unknown state of the animal, during the calculation of the following position (Tremblay *et al.*, 2009). Locations are instead calculated using a cloud of weighted particles, with the weighting manipulated according to constraining parameters such as maximum speed or avoidance of land. Furthermore, this model has the ability to handle data of varying accuracy, including ARGOS and GPS data and consider the specific error distributions of each data type. An additional benefit of this model is that in the presence of data gaps, the model outputs interpolated positions in a straight line, avoiding overfitting artefacts (Tremblay *et al.*, 2009). An assessment of the post-processing outputs of the Kalman-filter and IKNOS-WALK models was carried out to determine which best suited the GLS data received from the PSATs in this study. GLS data were obtained using the proprietary software from the tag manufacturer (GPE2, Wildlife Computers, Redmond, USA).

For comparative purposes, outputs from both models were plotted over a cloud of particles representing the uncertainty in the raw GLS data. For this exercise, 300 particles were generated for each location, obtained as output of the first step of the IKNOS-WALK model. SST data were not incorporated into either model as preliminary analysis showed that the often short deployment durations, and general homogeneity of the SST data in the region resulted in inadequate changes in observed SST during deployment to improve the track quality. Similarly, as the sharks were almost always in the open ocean, and seldom ventured beyond depths of a few hundred meters, the limitations in bathymetry were of no use and thus not included. Comparative plots (Fig. 2.7) suggested that the outputs of the IKNOS-WALK consistently represented the raw data more accurately. For some individuals (e.g. A and B in Fig. 2.7) both models produced very similar results, however, when the results differed (e.g. C and D in Fig. 2.7) these IKNOS-WALK tracks fell closer to the middle of the raw data cloud. Considering this apparent superiority, along with the intuitive nature and ability to include GPS data, the IKNOS-WALK model was selected and utilised for the analyses of horizontal movements of tagged silky sharks in Chapter 5.

While SST and bathymetry data were excluded from the model, it was important to include a maximum speed parameter in the IKNOS-WALK model. Typically, a single value of maximum speed is adopted for all animals of the same species in a study and bears some biological reflection of the animal's potential average rate of travel in its environment (Tremblay *et al.*, 2009). It is important to note that this maximum speed reflects the speed over ground, and does not incorporate situations where the animal may be involuntarily propelled over the surface of the earth, such as being driven by an ocean current. In the current study, the use of PSATs generally provided an independent assessment of the true location of the animal at the end of the deployment period, in the form of the tag's pop-up location. This location is provided by the ARGOS satellite system and is calculated using the Doppler Effect on transmission frequency of the signal when it is located by the satellites. Such locations have an accuracy that ranges between (<100 m - 1500 m). Using this known location, it was possible to evaluate the effect of the speed limit settings in the IKNOS-WALK model by comparing the end point of the model trajectory with the pop-up location when different speed limits were applied. While such a comparison could provide an idea of an appropriate speed limit, this was not always possible to do as on seven occasions the point at which the tag began to transmit did not match the time at which it detached from the shark. Consequently, the first known location of the tag was not always a true reflection of the last known location of the shark. There were several reasons for the occurrence of this temporal delay. Firstly, tags were programmed to initiate data transmission after two or three days at constant depth, had the scheduled release date not yet been reached. Therefore, when tags prematurely detached from the sharks, they reached the surface two to three days before initiating transmission and facilitating their remote location. Secondly, some tags were consumed by other predators and remained in their stomachs for several days before being regurgitated and floating to the surface. Thirdly, some sharks were captured and loaded onto vessels where the tags often failed to immediately transmit to the satellites, and thus the first location were likely a poor reflection of the shark's final position. In these situations it was difficult

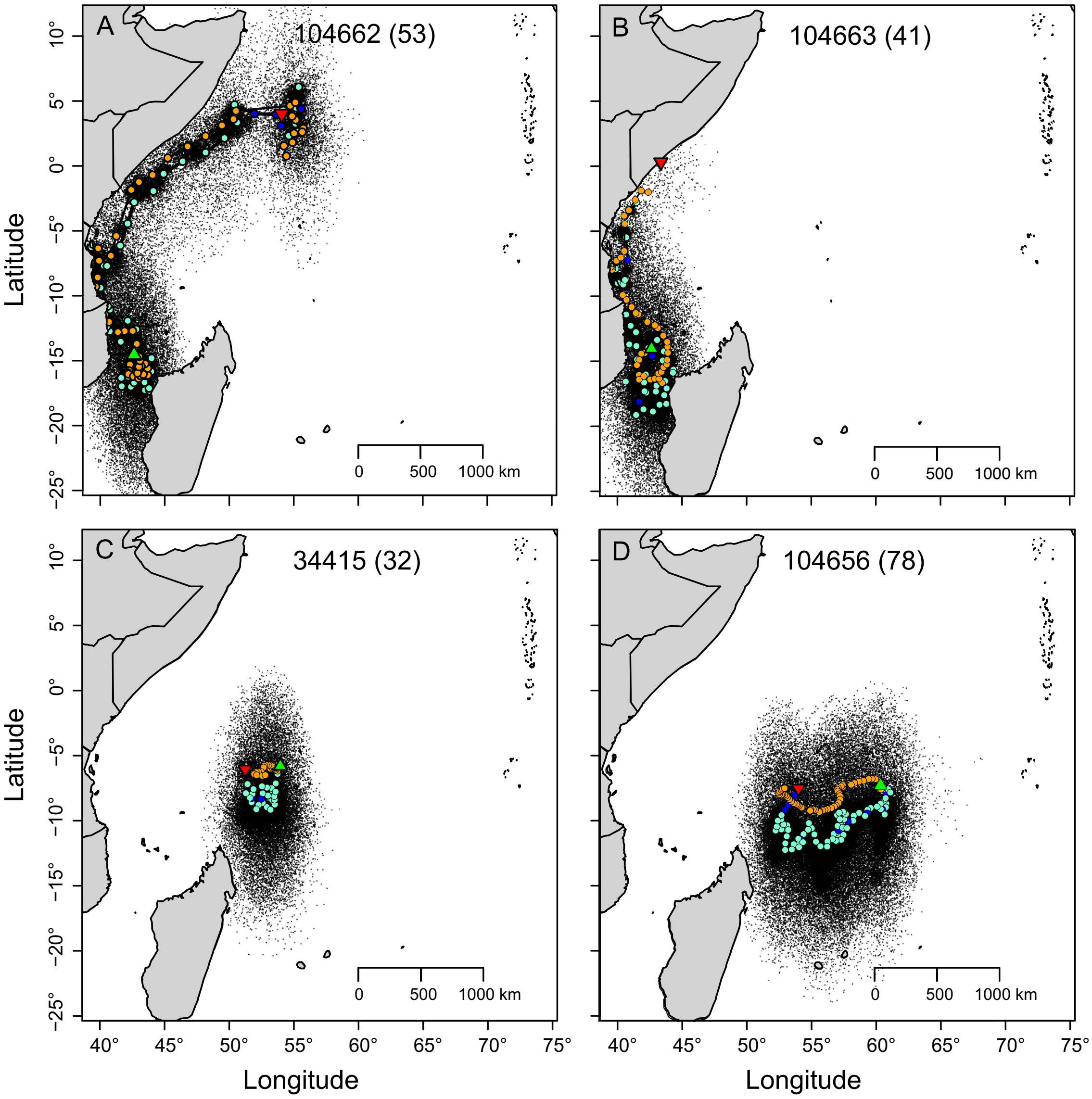

Figure 2.7 Maps showing the outputs of the models tested. Black clouds show the extent of the uncertainty in the un-modelled geolocation estimates. Orange circles represent the the Kalman-filter approach using the Trackit package in R (R Development Core Team, 2011). Light and dark blue circles show the output of the IKNOS model. Dark blue circles represent days where data were interpolated. Green and red triangles indicate tagging and pop-up locations respectively.

to assess the most appropriate speed limit.

Preliminary analysis of the data obtained from tags with known final locations indicated that appropriate speed limits differed greatly between individuals. Increasing the speed limit in situations where the animal moved slowly artificially generated larger movements with a more jagged track than was truly the case. Alternatively, restricting the speed of the model too greatly prevented the track from reaching the area where the tag popped up and thus artificially truncated the trajectory. Therefore, it was necessary to estimate a speed limit best suited to the behaviour of each tagged shark. To do this a method was developed that considered the errors inherent in the raw GLS locations, as provided by the manufactures geolocation software, GPE2. The method involved the following series of steps:

1. A cloud of particles, representing all raw location errors, was generated using the IKNOS-WALK model for each day that the shark was at liberty. Using this cloud a daily kernel density distribution was calculated with the MASS package in R (R Development Core Team, 2011) and truncated such that 90% of the data remained.

2. Density contours (50%, 95% and 99%) were then calculated for each kernel distribution, such that each contour bound the remaining percentage of the density distribution.

3. Data from each tag were then run through the IKNOS-WALK model at speeds ranging from 3 km.h^{-1} to 13 km.h^{-1} with an increment of 1 km.h^{-1}. At each time step the model output 50 potential locations (particles).

4. For each day of the trajectory, the portion of modelled particles that fell within the various density contours was then calculated.

5. Finally, the overall proportion of particles for the entire trajectory that fell within each contour was calculated. This overall proportion was then compared between all 11 speed limits and the lowest speed limit at which the highest proportion of data fell within the highest possible kernel density contour, was selected.

6. Additionally, when proportions within a contour were similar for multiple speeds, the lowest speed that allowed the trajectory to reach the known final location of the shark was selected.

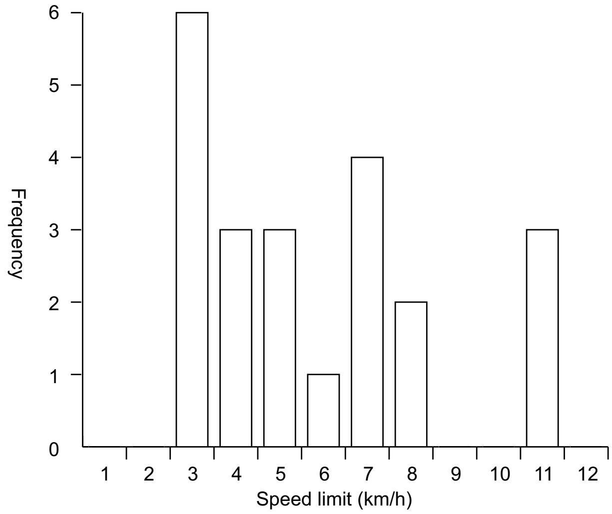

Figure 2.8 Frequency distribution of maximum speed parameter for the IKNOS-WALK light based geolocation model for individual silky sharks tagged with PSATs in the Indian Ocean.

Following these steps, the maximum speed assigned to each individual ranged between 3 and 11 km.h^{-1}(Fig. 2.8).

The detailed methods described in this chapter relate to telemetry and are thus applied in Chapter 4 on fine scale behaviour (acoustic telemetry) and Chapter 5 on large-scale horizontal behaviour (satellite telemetry). The specific methods use in the dietary analysis presented in Chapter 3 are dealt with in the Methods and Materials section within that chapter. Furthermore, as the study of silky shark entanglement mortality has been published, the methods are included in the form of the original manuscript.

F. Forget

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Chapter 3

Feeding ecology

3.1 Introduction

Several species of fish share the tendency to associate with objects drifting in the open ocean. The range of species that exhibit this trait spans several taxonomic groups and trophic levels. Furthermore, it is not a trait exclusive to pelagic fishes, with a variety of neritic species (generally juveniles) also regularly forming part of such aggregations (Castro *et al.*, 2002), despite their often vast distance from shore. A near equal diversity is shown in the range of hypotheses proposed to explain why some fish behave in this way (see Castro *et al.*, 2002; Dempster and Taquet, 2004, for reviews). However, to date, no clear consensus has been reached, and as such, the driving forces behind this behaviour remain largely unknown. Several proposed ideas are specific to certain types of fishes, often thought of as either predators or prey (Gooding and Magnuson, 1967; Freon and Dagorn, 2000) but as Freon and Dagorn (2000) suggest, they are not necessarily mutually exclusive and some, such as the 'meeting point' and 'indicator log' hypotheses, could apply to both groups. Early hypotheses centred around the idea that juvenile fish seek protection from predators (Hunter and Mitchell, 1967; Feigenbaum *et al.*, 1989; Rountree, 1989) by refuging close to drifting objects. *In situ* observations conducted by Gooding and Magnuson (1967) validated this hypothesis to some degree, when they observed juvenile drift fish, *Psenes cyanophrys*, and amberjack, *Seriola rivoliana*, avoiding predation from amberjack and dorado *Coryphaena hippurus* respectively. Conversely, the motivations for predatory species to aggregate appear to be far more complex, and to date remain largely unknown. Three species of tunas (skipjack tuna, *Katsuwonus pelamis*, yellowfin tuna, *Thunnus* *albacares*, and bigeye tuna, *T. obesus*) display a strong tendency to aggregate around floating objects. Considering that approximately half of the global catch of these three species come from such aggregations (Dagorn *et al.*, 2013) provides testimony of their propensity to associate with floating objects. In terms of biomass, these tunas often constitute more than 95% of an aggregation, which can, at times, reach several hundred tons in size (Dagorn *et al.*, 2012). In light of their economic and ecological importance, it is not surprising that the majority of hypotheses set forth to explain the aggregative phenomenon in recent years have focused on tunas (see review by Freon and Dagorn, 2000). The role that feeding plays in the associative behaviour of tunas has been investigated by several authors (Brock, 1985; Hunter and Mitchell, 1967; Ménard *et al.*, 2000a,b) and largely the findings have suggested that aggregated tunas derive little to no trophic enrichment through their association with floating objects. Given the extensive size of tuna aggregations and the lack of sufficient prey biomass within the total aggregation to feed so many tunas, these findings appear plausible. However, a 'feeding hypothesis' was proposed for predatory species that occur at lower densities, such as dorado (Kojima, 1956; Hunter and Mitchell, 1967), large tunas, sharks and billfishes (Ménard *et al.*, 2000b). To date, few studies on non-tuna species have investigated this relationship directly (Taquet, 2004). Two species of sharks regularly associate with drifting objects, the silky shark *Carcharhinus falciformis* and the oceanic whitetip shark *C. longimanus*. However, the silky shark is far more common, with the oceanic whitetip shark having undergone drastic declines in the past decade (Clarke *et al.*, 2013). Understanding the factors that drive the associative behaviour of silky sharks is an important component for investigating the impact that changing fisheries practices are having on this vulnerable species. As modern tuna purse seine fisheries continue to deploy increasing numbers of drifting objects (FADs) throughout the tropical oceans, the vulnerability of this species to fishery mortality continues to rise (Dagorn *et al.*, 2013). In addition, potential ecological impacts caused by altering the abundance of floating objects should be considered. Considering the high concentrations of potential prey, it seems valid to hypothesise that the associative behaviour of silky sharks could either be driven by, or linked to, their trophic requirements. Consequently, this study aimed to address the following question: Can the diet of silky sharks associated with drifting objects be used to explain/justify their motivation for associating? The simplest answer to this question (yes or no) will depend directly on the proportion of the diet that originates from species within the associated assemblage. As such, three possible outcomes are plausible:

1. A diet replete with associated prey would suggest that trophic benefits drive the associative behaviour.
2. A diet with a very low proportion of associated prey would imply feeding plays a minor role in the associative behaviour.
3. Any intermediate proportion of associated prey would preclude a definitive interpretation, and imply that either option may still be plausible.

Through the analysis of stomach contents of silky sharks caught at drifting objecting in the western Indian Ocean, the current study aimed to test whether trophic benefits explain the associative behaviour for this species.

3.2 Materials and Methods

Stomach content analysis

Silky sharks were captured by European tuna purse seine vessels while setting on FADs in the western Indian Ocean between 2001 and 2012. Between one and four sharks were randomly collected from selected fishing sets and either frozen dry in a blast freezer or in brine at -15° C with the tuna catch. On return to shore the sharks were defrosted in the laboratory, weighed to the nearest 0.1 kg, measured to the nearest mm fork length (FL), and the stomachs removed in a semi-frozen state. Once the stomachs were completely thawed, excess water was drained and five treatment steps followed, following the methods Potier *et al.* (2007a):

1. The total contents of each stomach was weighed to the nearest gram. Hard parts (i.e. squid beaks and fish otoliths) accumulated from fully digested prey items (no flesh attached) were removed and disregarded in the analysis to prevent over emphasis of certain prey types in the diet.
2. Contents were then divided into four broad categories (fishes, cephalopods, crustaceans and other) and weighed to obtain the wet-weight proportion of each category in the diet.

3. Single items within each category were then sorted, weighed and measured. Items were enumerated using identifiable fresh remains. For crustaceans counts were made using the highest number of either pairs of eyes, pairs of chelae or cephalo-thoraxes. For fishes, the number of parasphenoids, mandibles or greatest number of either left or right otoliths was used. For cephalopods the maximum number of either lower or upper beaks was used.

4. The items were then identified to the lowest possible taxonomic level using published identification keys and descriptions (Clark, 1986; Smith and Heemstra, 1986; Smale *et al.*, 1995) and a personal reference collection.

5. Specific measurements were then taken according to the type of each prey item. For crabs, the length of the propodus was measured (mm), for cephalopods the lower rostral length (LRL) (mm) was recorded and for fishes standard length (SL) (mm) was used. Additionally, when fish prey was partially digested, the lengths of hard structures (otoliths, paraphenoids or dentary) were measured and whole prey size estimated using species-specific regression equations between the structures length and SL.

Using the size of each prey item, whole weights were reconstituted using either published allometric equations (Clark, 1986; Smale *et al.*, 1995) or those developed with the help of M. Potier and F. Ménard, IRD, France. If no species-specific equation was available weights were calculated from closely related or morphologically similar species. Furthermore, when no measurement was obtainable from an identified prey item, the average size of that item from all stomachs was used. When items could not be identified to at least the family level, the measured wet weight was used.

Prey items were divided into broad ecological categories reflecting their known behavioural patterns and position in the water column. These categories were: epipelagic, mesopelagic and coastal. Epipelagic species constituted those found within the upper 200 m of the water column throughout the day and night. Mesopelagic organisms are those that undertake diel migrations during ephemeral periods, moving from depths greater than 200 m during the day to the surface layers during the night. Coastal species consisted of those known to primarily occur in coastal waters, at depths less than 100 m.

Furthermore, all prey items were also designated as either aggregative (i.e. known to occur at drifting objects in the Indian Ocean from Taquet *et al.* 2007b) or non-aggregative.

Data analysis

A Walsh two-sample t-test was performed to assess whether sharks displayed any temporal pattern in the consumption of associative and non-associative prey types. In order to assess the representativeness of the sampled stomachs in describing the diet of silky sharks, a cumulative prey curve was constructed following the methods of Ferry and Cailliet (1996). The order in which the stomachs were assessed was randomised 1000 times and the mean cumulative number and standard deviation of unique prey items calculated for each stomach assessed, following the equation:

$$S_n \int(n) ,$$

where S is the number of unique prey items observed in (n) stomachs analysed.

As silky sharks are known to predate on tunas and other fishes encircled within the purse seine net during the hauling of the net (Bane, 1966), all items that were very fresh were likely to have been consumed inside the net, and were thus removed and completely disregarded from the analyses. Four indices were used to describe the importance of each prey item and each broad category (cephalopods, crustaceans and teleosts) in the diet of silky sharks: 1) frequency of occurrence (O, the percentage occurrence in non-empty stomachs); 2) mean numerical proportion (MN); 3) mean proportion by reconstituted weight (MRW) and 4) index of relative importance (IRI). MN and MRW were calculated using the proportion that each species or category represented in each stomach and then calculating the mean proportion across all stomachs. In this way each individual silky shark was treated as the sampling unit, which facilitated the calculation of a standard deviation for each prey species or category. The IRI was calculated following the methods of Pinkas *et al.* (1971) and attempted to reconcile the frequency of occurrence index (O), the numerical frequency (N) and the size of the prey item (RW), such that a more holistic overview of the importance of various prey items could be compared. As such the IRI for prey item (*i*) was calculated as:

$$\mathrm{IRI}_i = (\%\mathrm{N}_i + \%\mathrm{RW}_i) \times \%\mathrm{O}_i ,$$

where $\%N_i$ is the numerical proportion of all sampled items represented by item *i*, calculated as: $\%N = \frac{n_i}{N_{tot}} \times 100$, where n_i is the total number of item *i* observed and N_{tot} is the total number of all items observed, $\%RW_i$ is the proportion of the total reconstituted weight represented by item *i,* calculated as: $\%RW = \frac{RWi}{RW_{tot}} \times 100$, RW_i is the total reconstituted weight of item *i* and RW_{tot} is the total reconstituted weight of all items observed and $\%O_i$ is the frequency of occurrence of item *i* calculated as the proportion of all stomachs that contained item *i*.

3.3 Results

A total of 323 (141 female, 127 male, 55 unknown) silky sharks were sampled for dietary analysis. Length measurements were collected for 296 individuals. Sizes ranged from 52 to 234 cm with a median fork length of 86.9 cm (Fig. 3.1). Samples were collected from an extensive geographic area that covered much of the central western Indian Ocean as well as the northern portion of the Mozambique Channel (Fig. 3.2). Of these sharks 82 (25.5%) had empty stomachs. Additionally, 35 (10.8%) sharks had only fishes ingested during the purse seine operation in their stomachs and were thus considered as being empty as well. Hence the total number of empty stomachs was 117 (36.2%). A further 23 individuals (7.1%) had only accumulated hard parts of digested prey. The remaining 183 (57.3%) stomachs were found to contain a variety of prey species including both epipelagic and mesopelagic organisms. The prey curve suggests that sufficient stomachs were sampled to characterise the diet of silky sharks in this environment. The decreasing standard deviation suggests that the curve is close to reaching an asymptotic value (Fig. 3.3).

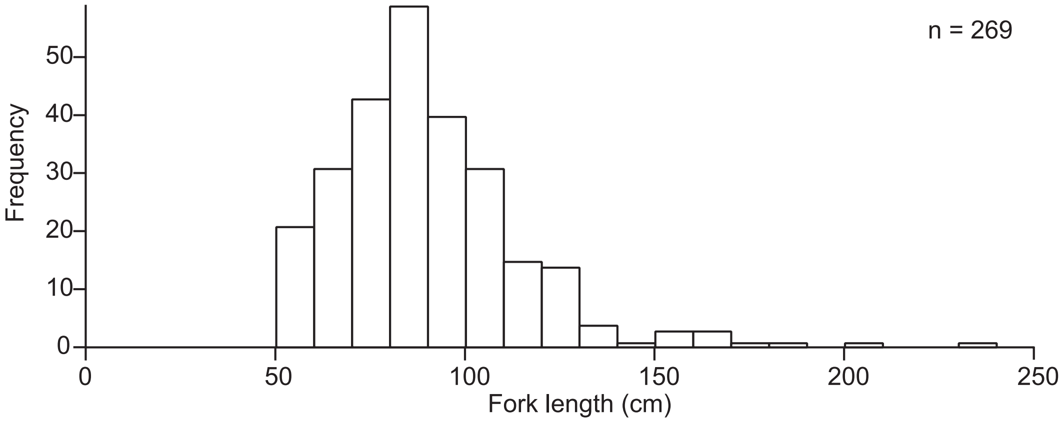


Figure 3.1 Length frequency of silky sharks caught at floating objects in the western Indian Ocean, sampled for dietary analysis.

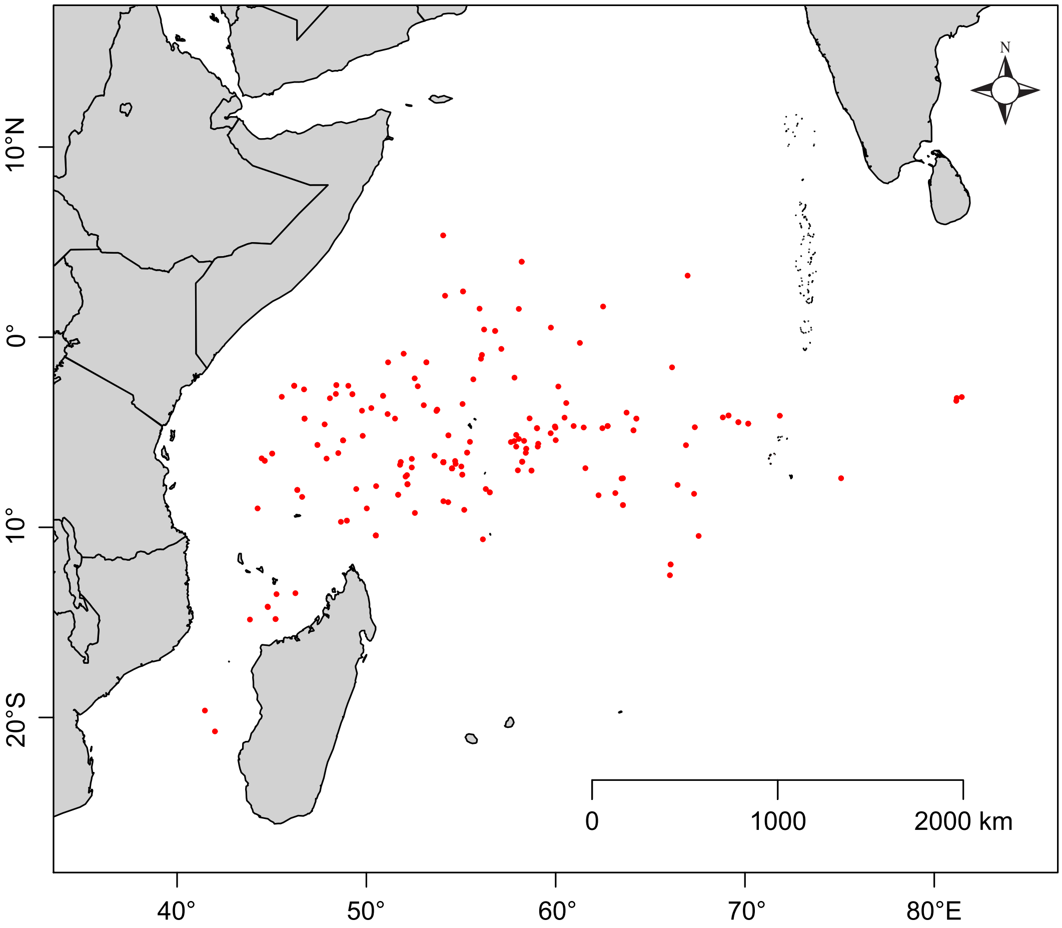


Figure 3.2 Spatial distribution of sampling of silky sharks caught at floating objects in the western Indian Ocean. Red dots indicate capture locations of one or more silky sharks.

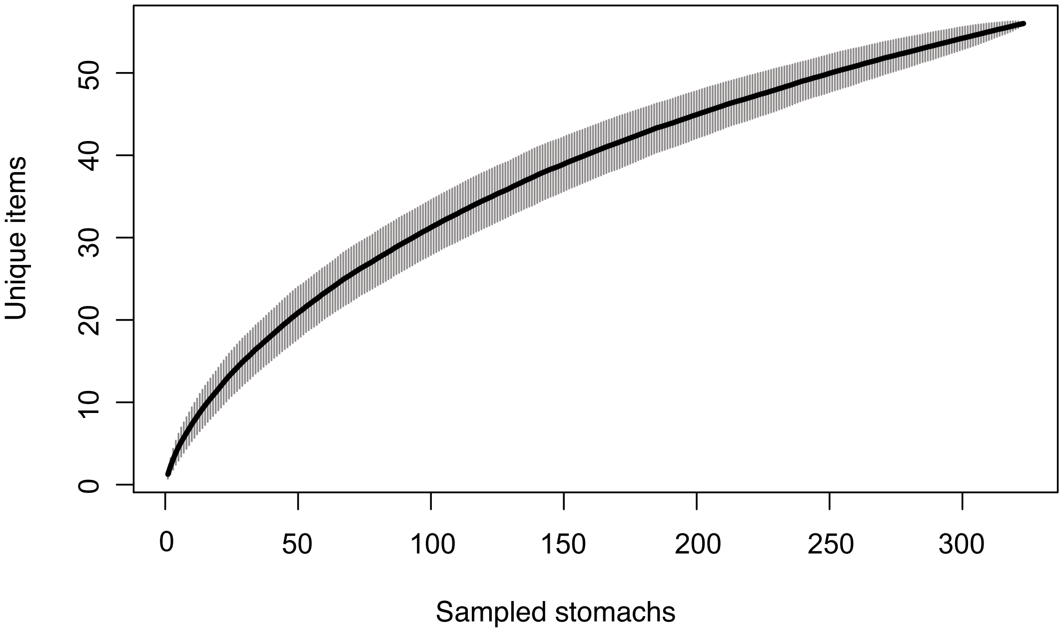


Figure 3.3 Cumulative prey curve showing the relationship between new unique prey items and the number of stomachs of silky sharks examined. Grey bars indicate standard deviations following 1000 randomisations of the order in which the stomachs were examined.

Diet composition

The mean reconstituted weight of stomach contents from all individuals was 198.6 g (range = 0 - 2655.3 g). Considering all prey items identified to the class level, teleosts formed the most important prey category across all indices (% MN, % MRW, % IRI), and were especially dominant in terms of % IRI (Fig. 3.4). Crustaceans were marginally less important in terms of % MN and % MRW than teleosts, but were significantly less prevalent in terms of % IRI. Cephalopods were consistently third in rank. Prey items from 43 categories including identification to, class, family and species were observed (Table 3.1). Diversity was lowest for crustaceans, with only two species identified, however, the swimming crab, *Charybdis smithii*, was the most common of all prey items and occurred in almost 40% of non-empty stomachs. While a large number of mantis shrimp, *Natosquilla investigatoris*, were also found, they were observed in few stomachs. A total of 11 cephalopod species from 10 families were found with fresh remains. Cephalopods were typically low in occurrence, with most species observed with fresh remains only once. The enoploteuthid, *Ancistrocheirus lesuerii*, was the most common cephalopod species recorded. While not considered in the calculation of dietary indices, the diversity of

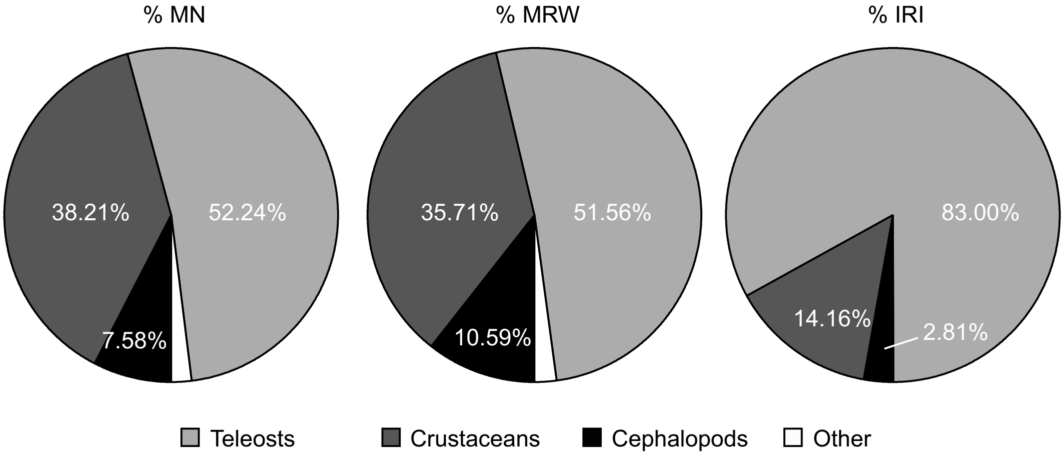


Figure 3.4 The relative proportion of each prey functional group for silky sharks, derived using three dietary indices.

cephalopod species was greater (17 species) when accumulated material was also considered (Table 3.2). Teleosts were the most diverse prey class. Fifteen species and 16 families were identified. Identified teleost were dominated by the scombrids and carangids, across all indices. Within these families, *Decapterus macarellus* and *K. pelamis* were the most important identified species.

Table 3.1 Summary information from fresh prey items identified from the stomach contents of silky sharks associated with floating objects in the western Indian Ocean. Occ. (n) is the numerical frequency of occurrence. Occ. (%) is the frequency of occurrence. % MN is the percentage in mean number and % MRW is the percentage in mean reconstituted weight. % IRI is the percentage in terms of the Index of Relative Importance and Eco. Cat. is the broad ecological category of the prey item.

Prey class	Prey family	Prey species	Occ. (n)	Occ.(%)	% MN	% MRW	% IRI	Associative	Eco. Cat.
Cephalopod			**28**	**13.66**	**7.58 ± 24.47**	**10.59 ± 28.64**	**2.81**		
	Alloposidae	*Haliphron atlanticus*	1	0.55	0.55 ± 7.39	0.55 ± 7.39	0.02	No	Mesopelagic
	Argonautidae	*Argonauta argo*	1	0.55	0.18 ± 2.46	0.00 ± 0.06	0.00	No	Epipelagic
	Cranchidae	*Taonius* sp.	1	0.55	0.18 ± 2.46	0.24 ± 3.26	0.00	No	Mesopelagic
	Enoploteuthidae	*Ancistrocheirus lesueurii*	7	3.83	2.14 ± 13.2	3.48 ± 17.71	0.97	No	Mesopelagic
	Histioteuthidae	*Histioteuthis hoylei*	1	0.55	0.08 ± 1.06	0.39 ± 5.30	0.01	No	Mesopelagic
	Mastigoteuthidae	*Mastigoteuthis* sp.	1	0.55	0.01 ± 0.07	0.41 ± 5.60	0.03	No	Mesopelagic
	Octopoteuthidae	*Octopoteuthis rugosa*	2	1.09	0.46 ± 4.43	0.63 ± 6.21	0.04	No	Epipelagic
	Ommastrephidae	*Ornithoteuthis volatilis*	1	0.55	0.55 ± 7.39	0.55 ± 7.39	0.00	No	Epipelagic
		Sthenoteuthis oualaniensis	2	1.09	0.55 ± 7.39	0.72 ± 7.75	0.03	No	Epipelagic
	Onychoteuthidae	*Callimachus rancureli*	1	0.55	0.02 ± 0.28	0.28 ± 3.74	0.01	No	Mesopelagic
		Unknown Onychoteuthid	1	0.55	0.02 ± 0.28	0.00 ± 0.01	0.00	No	Mesopelagic
	Tremoctopodidae	*Tremoctopus violaceus*	1	0.55	0.55 ± 7.39	0.55 ± 7.39	0.01	No	Epipelagic
	Unknown		8	4.37	2.30 ± 13.50	2.80 ± 14.94	0.31	No	
Crustacean			**701**	**44.81**	**38.21 ± 46.26**	**35.71 ± 45.52**	**14.16**		
	Portunidae	*Charybdis smithii*	329	39.89	34.13 ± 45.14	31.85 ± 44.28	59.81	No	Epipelagic
		Uknown portunid	2	1.09	0.13 ± 1.50	0.16 ± 2.07	0.01	No	Epipelagic
	Squillidae	*Natosquilla investigatoris*	360	3.28	3.22 ± 17.53	3.00 ± 16.7	4.17	No	Epipelagic
	Unknown		10	1.09	0.73 ± 7.78	0.70 ± 7.68	0.04	No	
Teleostei			**667**	**60.66**	**52.24 ± 47.02**	**51.56 ± 47.41**	**83.00**		
	Balistidae	Uknown balistid	3	1.64	1.00 ± 8.59	0.98 ± 8.70	0.08	Yes	Epipelagic
	Belonidae	Uknown belonid	5	1.64	0.84 ± 7.91	0.94 ± 8.60	0.09	Yes	Epipelagic
	Carangidae	*Decapterus macarellus*	90	2.73	2.23 ± 13.86	2.22 ± 13.85	1.05	Yes	Epipelagic
		Decapterus macrosoma	102	0.55	0.54 ± 7.32	0.13 ± 1.80	0.19	No	Epipelagic
		Decapterus sp.	28	3.28	2.38 ± 13.61	2.59 ± 15.21	0.63	Yes	Epipelagic
		Naucrates ductor	19	1.64	1.06 ± 10.08	1.12 ± 10.02	0.46	Yes	Epipelagic
		Unknown carangid	128	5.46	3.84 ± 18.23	3.62 ± 17.99	3.28	No	Epipelagic
	Chiasmodontidae	*Chiasmodon niger*	70	0.55	0.52 ± 6.99	0.14 ± 1.91	0.12	Yes	Mesopelagic
	Coryphaenidae	*Coryphaena equiselis*	2	0.55	0.27 ± 3.70	0.33 ± 4.43	0.03	Yes	Epipelagic
	Coryphaenidae	*Coryphaena hippurus*	3	1.09	1.09 ± 10.43	1.09 ± 10.43	0.31	Yes	Epipelagic
	Diodontidae	Unknown diodontid	1	0.55	0.55 ± 7.39	0.55 ± 7.39	0.01	Yes	Coastal
	Echeneidae	*Remora brachyptera*	2	1.09	0.25 ± 2.63	0.56 ± 6.26	0.03	No	Epipelagic
	Exocoetidae	*Exocoetus volitans*	2	0.55	0.55 ± 7.39	0.55 ± 7.39	0.01	No	Epipelagic
		Uknown Exocoetid	13	6.56	4.24 ± 18.75	4.71 ± 20.09	0.74	No	Epipelagic
	Gempylidae	*Gempylus serpens*	1	0.55	0.04 ± 0.49	0.05 ± 0.64	0.01	No	Mesopelagic
	Holocentridae	Unknown holocentrid	1	0.55	0.55 ± 7.39	0.55 ± 7.39	0.00	Yes	Coastal
	Kyphosidae	*Kyphosus* sp.	2	0.55	0.55 ± 7.39	0.55 ± 7.39	0.01	Yes	Coastal
	Lobotidae	*Lobotes surinamensis*	3	1.64	1.64 ± 12.73	1.64 ± 12.73	0.36	Yes	Coastal
	Monacanthidae	Unknown monacanthid	11	1.09	0.96 ± 9.22	0.64 ± 7.49	0.05	Yes	Coastal
	Scombridae	*Euthynnus affinis*	1	0.55	0.55 ± 7.39	0.55 ± 7.39	0.03	Yes	Epipelagic
		Katsuwonus pelamis	8	4.37	4.10 ± 19.53	4.13 ± 19.62	2.56	Yes	Epipelagic
		Thunnus albacares	1	0.55	0.55 ± 7.39	0.55 ± 7.39	0.06	Yes	Epipelagic
		Thunnus spp.	3	1.64	1.37 ± 11.03	1.63 ± 12.69	0.34	Yes	Epipelagic
		Unknown scombrid	38	12.02	8.57 ± 26.07	8.92 ± 26.95	9.04	Yes	Epipelagic
	Sphyraenidae	*Sphyraena barracuda*	1	0.55	0.55 ± 7.39	0.55 ± 7.39	0.04	Yes	Epipelagic
	Unknown		129	19.67	13.47 ± 31.47	12.30 ± 30.24	14.89		
Arthropod	Halobates	*Halobates* sp.	3	0.55	0.55 ± 7.39	0.55 ± 7.39	0.01		
plant	plant	macro algae	7	2.73	1.43 ± 10.78	1.58 ± 12.25	0.10		

Table 3.2 The diversity of cephalopods consumed by silky sharks associated with floating objects in the western Indian Ocean. Both fresh and accumulated prey items are included.

Species	n fresh	n accumulated	Total
Ancistrocheirus lesueurii	7	15	22
Argonauta argo	1		1
Callimachus rancureli	1	1	2
Chiroteuthis sp.		1	1
Cranchia scabra		2	2
Cycloteuthis akimushkini		3	3
Haliphron atlanticus	1		1
Histioteuthis dofleini		2	2
Histioteuthis hoylei	1	3	4
Mastigoteuthis sp.	1		1
Octopoteuthis rugosa	2	2	4
Onychoteuthis sp. 1		1	1
Onychoteuthis sp. 2		1	1
Ornithoteuthis volatilis	1		1
Sthenoteuthis oualaniensis	2	20	22
Taonius sp.	1	4	5
Tremoctopus violaceus	1		1

Eighty-eight percent of all fresh prey items were identified to the family level. The level of importance of each of the top three families, which constituted by far the majority of the diet, was consistent across all three indices (Table 3.3). Only flyingfishes (exocoetidae) were considered less important by the IRI than by the % MN and % MRW indices. The top ten families, according to the % IRI, consisted of four associative and six non-associative families. Based on the identified families, almost half of the diet ($\sim$ 43%) comprised organisms known to be associated with floating objects (Table 3.4). Furthermore, when prey items were characterised according to their ecological niche (epi- or mesopelagic), epipelagic items were found to strongly dominated the diet of silky sharks (Table 3.4). Prey items were found in a wide range of digestive states, from freshly consumed, to nearly entirely digested. Comparisons between the digestive state of associative and non-associative prey revealed that items from within the associated biomass were significantly more digested than non-associative prey items (Welsch two sample t-test, df = 968.8, p-value = 5.73×10^{-5}), Fig. 3.5.

Table 3.3 Comparisons between prey families consumed by silky sharks associated with floating objects in the western Indian Ocean. Families are ranked according to the index of relative importance.

Rank	Family	% IRI	% MRW	% MN	Associative
1	Portunidae	49.27	39.72 ± 47.82	41.85 ± 47.82	No
2	Scombridae	24.86	19.23 ± 38.75	18.76 ± 37.66	Yes
3	Carangidae	19.78	11.72 ± 30.63	12.61 ± 31.29	Yes
4	Squillidae	3.41	3.45 ± 17.88	3.79 ± 19.04	No
5	Enoploteuthidae	0.76	4.01 ± 18.98	2.94 ± 16.08	No
6	Exocoetidae	0.71	6.12 ± 22.82	5.72 ± 21.78	No
7	Coryphaenidae	0.42	1.87 ± 13.51	1.71 ± 12.44	Yes
8	Lobotidae	0.28	1.89 ± 13.65	1.92 ± 13.78	Yes
9	Chiasmodontidae	0.10	0.16 ± 2.05	0.61 ± 7.57	No
10	Belonidae	0.07	1.14 ± 9.44	1.12 ± 9.13	Yes
11	Balistidae	0.06	1.33 ± 10.03	1.28 ± 9.75	Yes
12	Ommastrephidae	0.04	1.46 ± 11.44	0.65 ± 8.01	No
13	Monacanthidae	0.04	0.74 ± 8.04	1.19 ± 10.51	Yes
14	Octopoteuthidae	0.03	0.89 ± 8.55	0.85 ± 8.42	No
15	Sphyraenidae	0.03	0.63 ± 7.93	0.64 ± 8.01	Yes
16	Mastigoteuthidae	0.02	0.48 ± 6.00	0.01 ± 0.08	No
17	Echeneidae	0.02	0.83 ± 7.61	0.41 ± 4.16	No
18	Alloposidae	0.01	0.63 ± 7.93	0.64 ± 8.01	No
19	Onychoteuthidae	0.01	0.32 ± 4.04	0.05 ± 0.64	No
20	Histioteuthidae	0.01	0.45 ± 5.68	0.09 ± 1.14	No
21	Gempylidae	0.01	0.05 ± 0.69	0.04 ± 0.53	No
22	Tremoctopodidae	0.01	0.63 ± 7.93	0.64 ± 8.01	No
23	Kyphosidae	0.01	0.63 ± 7.93	0.64 ± 8.01	Yes
24	Diodontidae	0.00	0.63 ± 7.93	0.64 ± 8.01	Yes
25	Holocentridae	0.00	0.63 ± 7.93	0.64 ± 8.01	Yes
26	Cranchidae	0.00	0.39 ± 4.92	0.32 ± 4.00	No
27	Argonautidae	0.00	0.01 ± 0.07	0.21 ± 2.67	No

Table 3.4 Proportion of the diet of silky sharks associated with floating objects in the western Indian Ocean as a function of the recognised associative state of the prey items as well as their ecological niche, derived from three dietary indices. % MN = Proportion by mean number, % MRW = Proportion by Mean Reconstituted Weight and % IRI = Proportion by Index of Relative importance.

Index	% Associative	% Non associative	% Mesopelagic	% Epipelagic
% MN	40.41	59.59	3.84	96.16
% MRW	41.16	58.84	5.54	94.46
% IRI	45.57	54.43	1.19	98.81

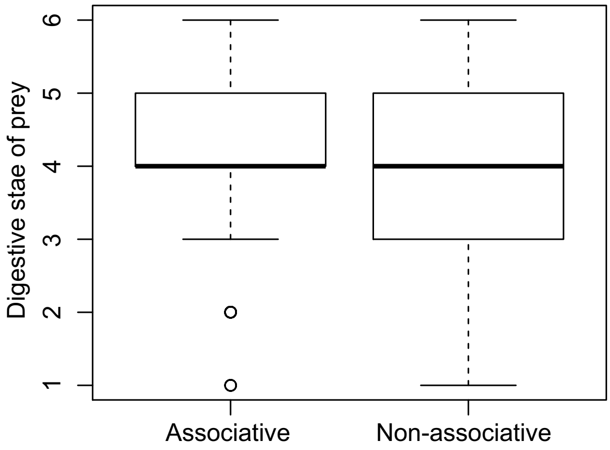


Figure 3.5 Box plot of the digestive state of associative and non-associative prey from silky sharks associated with floating objects in the western Indian Ocean. Circles represent outlying data points.

3.4 Discussion

This study provides the first detailed assessment of the diet of silky sharks associated with drifting objects, and is the most extensive for this species, in the Indian Ocean, conducted to date. The size range of sharks sampled (median FL = 87.6 cm, approx. TL = 108 cm) correlates well with the reported mode (100 cm) of the size range of silky sharks taken by the French tuna purse seine fleet in the Indian Ocean (Amandè *et al.*, 2008b) but is slightly smaller than that reported for the Spanish fleet which peaks between 110 – 119 cm TL (González *et al.*, 2007). The majority of individuals were early juveniles (Joung *et al.*, 2008) with only a few adults being captured. Amandè *et al.* (2008a) noted that large individuals were infrequently taken in the western Indian Ocean purse seine fishery. The broad geographic range from which samples were collected also extends over the majority of the area where fishing on floating objects typically occurs (Kaplan *et al.*, 2014).

Diet composition

The diet of silky sharks remains poorly studied throughout most of its cosmopolitan distribution, and in many areas information on the species' food habits stem from published reports based on the examination of few stomachs (Strasburg, 1958; Bane, 1966; Mearns *et al.*, 1981; Stevens, 1984a,b; Branstetter, 1987; Stevens and McLoughlin, 1991; Bowman *et al.*, 2000). General conclusions from these studies suggest that silky sharks are opportunistic feeders, ingesting a wide variety of prey types (Compagno, 1984; Bonfil, 2008). The functional group of prey that dominates the diet appears to be area specific and may reflect differential abundances of various prey types across the distribution of the species. For example, the comprehensive study conducted by Cabrera Chávez-Costa *et al.* (2010) found that the diet of silky sharks from two area in Baja California Sur were dominated by red crabs (% IRI = 83%), and jumbo squids (% IRI = 43%), respectively. Owing to the dominance of specific prey types in the diet, these authors considered that silky sharks in this region are selective predators. Other authors have described the silky shark as a generalist predator, feeding on various crustacean, cephalopod and fish species. The findings of this study confer with the latter as a high diversity of prey items from three main faunal groups were observed. However, the diet was dominated by teleosts, in terms of % MN, % MRW and % IRI. Teleosts were dominated by species known to aggregate around floating objects, principally members of the families scombridae and carangidae. The third family in terms of % MN and % MRW was exocoetidae. This family was also found to be an important component of the diet of dorado associated with floating objects in the Indian Ocean (Taquet, 2004).

Crustaceans were also important in the diet of the silky shark, but were dominated by two species, namely the isopods (*N. investigatoris*) and the decapods (*C. smithii*). Previously, Romanov *et al.* (2009) found a lower occurrence (%F = 11.8%) of *C. smithii* in a small sample of silky sharks (21 individuals) caught during tuna purse seine operations around floating objects in western Indian Ocean. However, they noted that the species was more common (% F = 28.2%) in the stomachs of silky sharks (n = 113) caught on longlines. These differences likely reflect the difference in sampling effort. In the current study, where substantially more sharks were sampled, the frequency of occurrence of *C. smithii* was higher (39.89%) than previously reported for either gear type. These authors suggested that this species represents an important prey resource for a multitude of pelagic predators within this region and was consistently the main prey of yellowfin tuna and lancet fish (*Alepisaurus ferox*). The isopod, *N. investigatoris* is known to undergo periodic cycles of abundance, which generally coincide with lower abundance of *C. smithii*. All observations of *N. investigatoris* recorded here, occurred during one such period of abundance between 2000-2005 (Potier *et al.*, 2007b).

Cephalopods formed the third most important functional group in the diet of silky sharks in this study. While this group only, contributed approximately 10% of the MRW and a frequency of occurrence of 13.66%, a wide variety of cephalopod species were identified. Ménard *et al.* (2013) reported a higher frequency of occurrence of cephalopods (20%) in the stomachs of silky sharks sampled from longlines and purse seine vessels in the same region. This difference may well be linked to the larger size of silky sharks typically caught on longlines, which would be expected to have a wider vertical niche (Grubbs, 2010), thus allowing them greater access to vertically migrating cephalopod resources. Interestingly these authors found that the epipelagic flying squid, *S. oulalaniensis* was by far the most common species in their sample, while only two individuals were observed in the fresh remains during the current study. However, when both fresh and accumulated items were considered, this species was observed 22 times, making it equally as common as the mesopelagic *A. lesueurii*. The observation of *Halobates* sp. and macro algae material in some stomachs are believed to reflect accidental consumption during feeding activity at the surface. Strasburg (1958) suggested the opportunistic feeding habits of many pelagic sharks often lead to them consuming items of little to no nutritive value. Similar items were observed in the stomachs of shortfin mako sharks *Isurus oxyrinchus* (Stillwell and Kohler, 1982; Maia *et al.*, 2006)

When compared with other dietary studies on fishes associated with FADs, the results suggest that silky sharks feed more actively at FADs than tunas. This is apparent form the high proportion of silky shark stomachs containing food compared to the generally empty stomach of tunas (Ménard *et al.*, 2000a). This difference may simply reflect higher metabolic and digestive rates of tunas (Magnuson, 1969; Olson and Boggs, 1986) which have been found to evacuate their stomachs completely in less than 24 h. However, when compared with other predators that occur at low densities around drifting objects (Taquet *et al.*, 2007b), results are more similar. Taquet (2004) found only 8.7% of stomachs of dorado associated with floating objects in the Indian Ocean to be empty. Dorado fed on a combination of associative and non-associative organisms, however, mesopelagic migrating species dominated the diet. Ménard *et al.* (2000b) observed a large proportion of scombrids in the diet of large yellowfin tuna from aggregations at floating objects and concluded that, for this size category, which generally represent a small percentage of the aggregated tunas, the abundance of small scombrids commonly associated with floating objects provides a trophic resource.

Feeding patterns

The percentage of empty stomachs observed (36%) was lower than all reports on the stomach contents of silky sharks with large sample sizes. Branstetter (1987) found 97% of silky shark stomachs to be empty in the gulf of Mexico from a sample of 114 individuals. Cabrera Chávez-Costa *et al.* (2010) reported 46% and 60% empty stomach from separate location in Baja California Sur with samples from 50 and 213 individuals, respectively. The major difference between the studies listed above and the current study is the use of an active rather than a passive fishing gear. Shark were all caught using longlines or gillnets in the previous studies. Wetherbee *et al.* (1990) suggested that longlines probably attract sharks with empty stomachs. Furthermore, passive gears may lead to higher rates of regurgitation owing to the longer soak times. In the current study, the time between the onset of panic and the landing of the sharks on the deck of the vessel is typically 10-40 minutes, depending on the size of the catch (personal observation). Furthermore, sharks were regularly observed feeding on tunas within the net, and were often landed with fresh juvenile tunas half swallowed and protruding from their mouths. As all fresh prey deemed to have be eaten within the seine were excluded, it is believed that the relatively low percentage of empty stomachs observed here, as compared to many other shark dietary studies (Wetherbee and Cortés, 2004), is an unbiased reflection of the feeding behaviour of silky sharks when associated with floating objects. Wetherbee and Cortés (2004) suggested that the general high frequency of empty stomachs and often few, well digested prey items, encountered in shark dietary studies, supports the view that the majority of sharks are intermittent feeders. As such, and considering the high percentage of empty stomachs reported elsewhere, the results of this study could suggest that juvenile silky sharks may feed more often when associated with floating objects, than when encountered away from FADs.

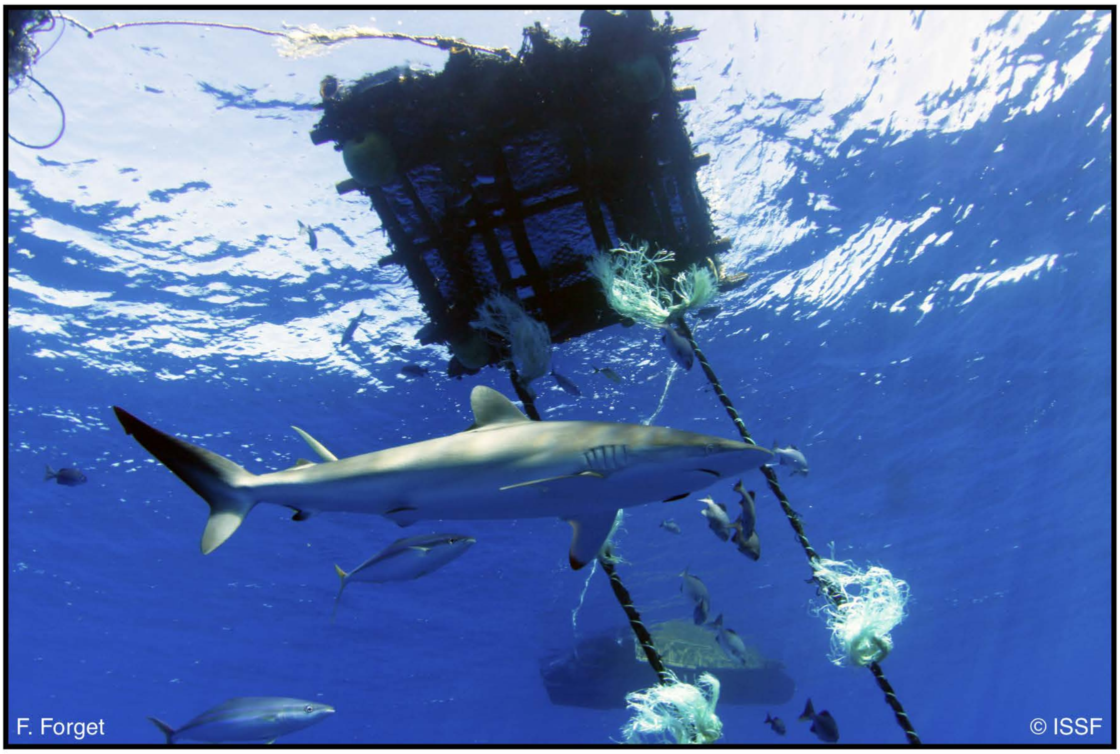
Using the digestive state of prey items in the stomachs, the percentage of empty stomachs and the weight of the prey items, it is possible to infer diel feeding chronology (Cortés, 1997). Furthermore, the presence of several food items of different digestive states in the same stomach indicate overlap in feeding activities (Maia *et al.*, 2006). However, to identify specific feeding chronology, knowledge of the rates of digestion of each different prey type and the development of a quantitative digestion scale is essential (Cortés, 1997). Generally such studies require the maintenance of the subject species in captivity, such that food items can be recovered at various times after ingestion. Owing to the significant constraints involved with the captive maintenance of pelagic sharks, such studies would be difficult to perform. However, Tricas (1979) held blue sharks in captivity and found that anchovies were digested twice as fast as squids and that the total gut evacuation time exceeded 24 hours. A summary of gut evacuation times in elasmobranchs presented by Wetherbee and Cortés (2004) suggest that the time required to completely digest a meal is generally longer than a day and often spans several days. While these authors reported on a wide range of shark species, the data set is devoid of tropical pelagic species. Considering the warm temperature of the waters that the silky sharks in this study inhabit (26-30°C), it is likely that the rate of digestion is slightly faster. A considerable constraint in the assessment of feeding chronology in the present study is a lack of details regarding the exact time at which the sharks were captured. It is known that a strong temporal pattern exists in the time at which sets on FADs are made, which usually corresponds to the time of sunrise (Forget et al., Submitted). As such, it is possible to assume that the majority of sharks in this sample were caught at the end of the night. The digestive state of prey items recovered here varied widely, from very recently ingested, to only accumulate otoliths and cephalopod beaks. A significantly higher digestive state was observed for associative prey than non-associative prey. This difference suggests that silky sharks may feed more regularly on associated prey in close proximity to a floating object during the day and switch to non-associative prey items at night. This finding corresponds well the occurrence of epipelagic and mesopelagic cephalopods and some mesopelagic fish species in the stomachs sampled here, which also suggest that the sharks actively feed at night, when these species migrate to the surface layers (Galván-Magaña *et al.*, 2013; Ménard *et al.*, 2013). Furthermore, Romanov *et al.* (2009) found that the swimming crab, *C. smithii*, which was a principle component of the diet of the sharks in this study, also undertake diel vertical migrations and are significantly more abundant in the upper 100 m of the water column between dusk and dawn than during the day. In total 43% of the diet (MRW) consisted of prey items that migrate into the surface layers during at night, illustrating that, at a minimum, almost half of the consumed food is eaten at night. Examination of the fine scale movement behaviour around floating objects described in the following chapter shows that silky sharks regularly undertake excursions away from the floating object at night and display rapid vertical oscillations, suggestive of foraging behaviour.

Feeding at FADs

The principle result of this study suggests that silky sharks associated with drifting objects do not feed exclusively, or even predominantly on other species from the associated assemblage. This result was consistent across all dietary indices. Taquet *et al.* (2007b) provided a detailed description of the fish community structures around floating objects in the Indian Ocean. While juvenile fish were commonly observed, the bulk of the aggregated (non-tuna) biomass consisted of a few species of larger individuals with high abundance (rainbow runners, oceanic triggerfish and dorado, each contributing 44.38%, 15.46% and 13.30% respectively). These species were rarely observed in the diet of silky sharks. Here, scombrids were the most common teleost family consumed and represented 19.23% of MRW. Owing to the difficulty in observing scombrids during underwater visual censuses, this family did not contribute greatly to the biomass reported by Taquet *et al.* (2007b). Nonetheless, considering the biomass of tunas is regularly several times, or even hundreds of times, greater than non-tunas, in such aggregations, this family is certainly the most abundant. Carangids constituted 11.72% of the diet (MRW), and were dominated by *Decapterus* species. Visual census show that this is the most abundant (non-tuna) family associated with drifting objects but is dominated by a high biomass of rainbow runners. Taquet *et al.* (2007b) reported that *D. macarellus* was observed at 72% of floating object surveyed, but their small size meant they formed a small portion of the biomass (Taquet *et al.*, 2007b). However, they appear to represent a more important food resource for silky sharks, probably reflecting their appropriate size for small sharks.

Taquet (2004) found that, in the Indian Ocean, dorado associated with drifting objects fed mostly on fishes, with approximately 27% of their diet (by weight) consisting of species from within the aggregation. By comparing the dietary composition of dorado caught in association with floating objects with that of individuals caught in the open ocean (on longlines) he concluded that feeding was not the principle component driving the associative behaviour of this species. Furthermore, he suggested that the aggregated biomass provided a reserve trophic resource for the dorado, should the availability of their preferred non-associated pelagic prey decline. Owing to the absences of dietary data on non-associated silky sharks, a similar comparison cannot be made here.

In the introduction to this chapter, three possible outcomes were described regarding the use of dietary information to determine the motivations the drive the associative behaviour. It was suggested that the dominance of associative prey would imply feeding was the main driver. Similarly a lack of associative prey would suggest feeding plays no role in the association. Finally, an intermediate amount of associative prey, would preclude the use of dietary information in the determination of a causal relationship. Following the results obtained it appears that the third scenario is most likely, but not conclusive, as, both activities (feeding and association) occur simultaneously and hence preclude the determination of a causation or correlation relationship. An essential step in answering this question is the comparative assessment of the diet of similar sized silky sharks associated with, and not associated with, drifting objects within the same area. However, owing to the widespread use of FADs in the tropical tuna fishery in the Indian Ocean, finding non-associated individuals will be challenging. The capture of non-associated sharks when targeting free swimming schools of tuna does occur, presenting a possible opportunity for such sampling. Additional information collected through electronic tagging (e.g. pH tags) to monitor feeding activity could also provide valuable information to better understand the aggregative phenomenon for this species.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Chapter 4

Fine-scale 3-dimensional movement behaviour

4.1 Introduction

Tuna purse seine vessels targeting tropical tuna species deploy large numbers of drifting fish aggregating devices (FADs) throughout the world's tropical and subtropical waters. Over time these FADs aggregate huge numbers of tunas as well as several non-tuna pelagic species. The principle species targeted through this practice are skipjack tuna *Katsuwonus pelamis*, yellowfin tuna *Thunnus albacares* and bigeye tuna *T. obesus*. Vessels will typically allow FADs to drift for several weeks or months before revisiting them to capture the aggregated fish biomass. While drifting around at sea, vessel will monitor their deployed FAD's position using a GPS buoy attached to the FAD. In recent years buoys with integrated echo-sounder technology have become increasingly popular and now provide the vessel with remote, real time, information on the size of the aggregation (Lopez *et al.*, 2014). While the vast majority (typically 95%) of the aggregated biomass consists of the targeted tuna species (Gilman, 2011; Dagorn *et al.*, 2013), several other species also aggregate around FADs and are thus taken as bycatch. These species include a variety of pelagic teleosts such as dorado, *Coryphaena hippurus*, rainbow runner, *Eligatis bipinnulata*, oceanic triggerfish, *Canthidermis maculata* and, wahoo, *Acanthocybium solandri*, as well as elasmobranchs, such as the silky shark, *Carcharhinus falciformis*, and the oceanic whitetip sharks, *Carcharhinus longimanus*.

The use of FADs as fishing tools has grown in popularity throughout the various fleets across all oceans in the past two decades. This practice now accounts for approximately 60% of the total tropical tuna (skipjack tuna, yellowfin tuna and bigeye tuna) purse seine catch and 40% of the global tropical tuna landings (Dagorn *et al.*, 2013). The growing popularity of FADs amongst fishers has led to concerns regarding, not only the over exploitation of tuna stock, but also the impact this practice has on bycatch species, such as elasmoranchs with life history traits poorly suited to high exploitation rates. Silky sharks are by far the most regularly caught elasmobranch species when fishing on FADs. They constitute approximately 90% of sharks caught in this fishery across all oceans (Gilman, 2011) and in the Indian Ocean specifically, represent at least 75% of the catch, by number (Amandè *et al.*, 2010). Data from observers onboard purse seine vessels collected between 2003-2007 in the Indian Ocean suggest that an average of 6 tons of silky sharks are caught per 1000 tons of tuna when fishing on FAD. Using this rate and the average number of reported FAD sets during that period, the annual catch of silky sharks in this ocean has been conservatively estimated at 82 000 individuals (Filmalter *et al.*, 2013). While vessels fishing in the Indian Ocean are mandated to discard all sharks at sea, Poisson *et al.* (2014) revealed that post-release survival rates were extremely low (approximately 19% of the released sharks survive). As the use of FADs continues to increase in this fishery (Dagorn *et al.*, 2013), there is a direct need to understand how these changing practices will influence the silky shark population.Understanding the details of the species' associative behaviour is a key step toward fulfilling this knowledge gap. This information can then be integrating into modelling approaches used to predict how changing FAD densities can affect populations, such as those recently described for tunas by Sempo *et al.* (2013).

To date two studies, Dagorn *et al.* (2007b) and Filmalter *et al.* (2011), have provided information on the behaviour of silky sharks associated with FADs. While both provided significant new insights into the behaviour of this species, more detailed information is essential for obtaining a better understanding of this associative behaviour. As such, the broad aim of this study was to investigate the fine-scale behaviour of silky sharks associated with drifting FADs in the western Indian Ocean using electronic tagging methods. The specific objectives were to 1) characterise the residence times of silky sharks at drifting FADs; 2) Assess temporal patterns in associative behaviour; 3) characterise vertical behaviour during periods of association and 4) investigate detailed horizontal and vertical movements around a FAD and within the aggregated community.

4.2 Materials and methods

Shark tagging

To address the specific objectives of the study various types of electronic tags were used to obtain a variety of information on species' behaviour. Juvenile silky sharks were caught using baited handlines at nine drifting FADs (Table 4.1) in the western Indian Ocean (Fig. 4.1) during four research cruises between 2010 and 2012. Each shark was surgically equipped (hereafter "tagged") with either V13 or V13P acoustic tags, (V13-1L-64K Vemco®, a division of Amirix Systems, Canada) transmitting at 69 kHz. The transmitters had a 90 s nominal delay (range: 50 to 130 s) and an expected minimum battery life of 879 days. Tagging was carried out following standard fish tag implantation techniques (Schaefer and Fuller, 2005; Dagorn *et al.*, 2007a). Briefly, sharks were landed using scoop net, placed in dorsal recumbency in a padded cradle, their eyes covered with a wet cloth and a hose pumping sea water was placed in the mouth to irrigate the gills. A small incision was then made, using a scalpel, along the ventral mid line, roughly 4 cm anterior to the anus. Once the peritoneal lining was penetrated the tag, which had been cleansed in ethanol and air dried, was inserted and the incision closed with two independent sutures.

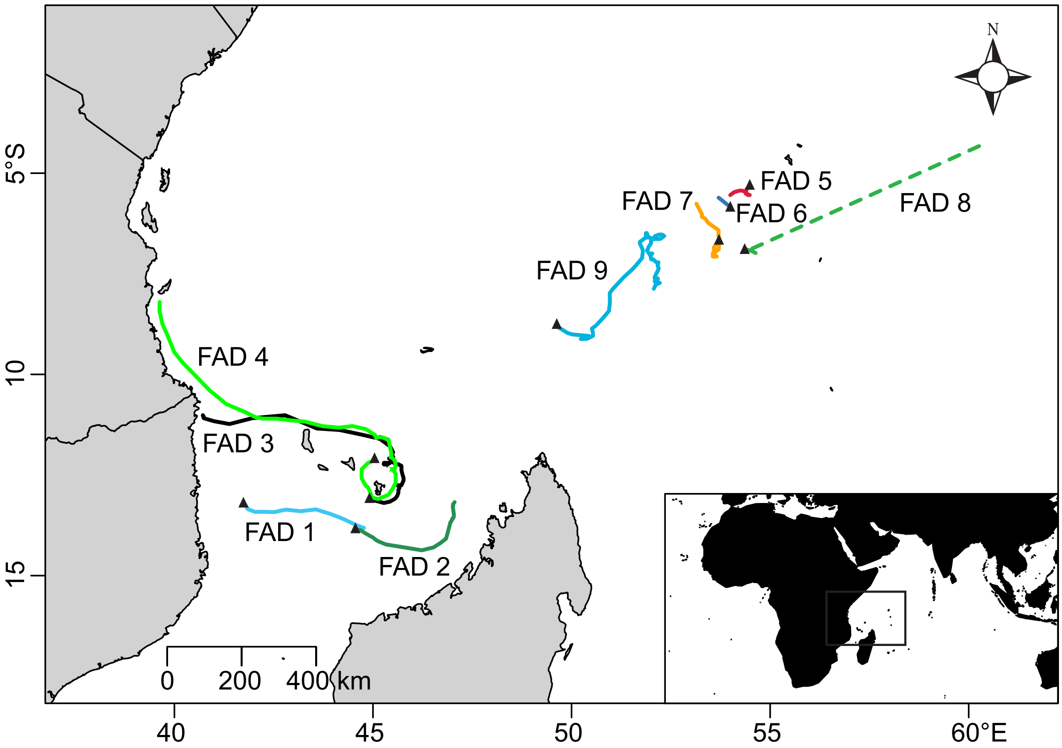


Figure 4.1 Location and drift trajectories of the 9 drifting FADs monitored during this study. Black triangles indicate start points. Dashed line indicates straight-line distance between deployment and retrieval of the VR2 receiver on FAD 8 where no positional estimates could be obtained.

A subsample of sharks was selected for double tagging. In addition to the internal acoustic tag, these individuals were also fitted with either an internal archival tag (MK 9, Wildlife Computers, Redmond, USA) or a pop-up satellite archival tag (PSAT, miniPAT, Wildlife Computers, Redmond, USA). The internal archival tags were inserted through the same incision as the acoustic tag prior to suturing, such that the light stalk with external thermistor protruded from the anterior end of the incision. Alternatively, MiniPATs were attached externally to the animal using two attachment techniques. Either the tag was tethered (using multi strand stainless steel wire coated with heat-shrink plastic) to a nylon anchor (36 mm Wilton dart, Wildlife Computers), which was inserted into the dorsal musculature of the shark at the base of the first dorsal fin, or the tag was mounted on the first dorsal fin. Fin mounting involved drilling a 4 mm hole through the posterior region of the dorsal fin through which a threaded nylon rod was passed. The end of the tag's tether was looped around this rod, between two stainless steel washers. These washers were then secured using stainless steel nuts on either side of the threaded rod and thus the fin. The selection of the attachment method used was based on the size of the individual and the availability of materials. Generally intramuscular darts were used on larger individuals. Before release, the total length (TL) of each shark was measured from the tip of the snout to the end of the dorsal lobe of the caudal fin, using a pair of callipers. The sex was then determined visually and the individual released directly adjacent to the FAD. The total tagging operation from capture to release lasted between 3 – 5 min.

Table 4.1 Metadata of FADs where silky sharks were captured and tagged in the western Indian Ocean.

FAD ID	Monitoring start date	Monitoring end date	Sharks tagged	Sharks detected	Drift distance (km)
FAD1	13/03/2010	24/03/2010	1	1	346
FAD2	15/03/2010	27/03/2010	4	4	365
FAD3	15/04/2011	08/05/2011	1	0	930
FAD4	20/04/2011	15/05/2011	3	1	1193
FAD5	18/06/2011	22/06/2011	7	3	87
FAD6	20/06/2011	20/06/2011	6	0	30
FAD7	22/06/2011	08/07/2011	1	1	268
FAD8	02/04/2012	04/05/2012	3	1	730
FAD9	13/04/2012	14/05/2012	13	10	854

Acoustic Receiver deployment

Prior to the commencement of fishing for sharks, a FAD was equipped with a satellite-linked acoustic receiver (VR4-GLOBAL, Vemco). This receiver automatically detected and stored data from the acoustic tags. The data was then transmitted via the Iridium satellite system on a daily basis. The information obtained from these receivers included the tag identification code and time of reception of each acoustic transmission that was detected. The data were not summarised as previous models of satellite linked acoustic receivers had done (Dagorn *et al.*, 2007b). Once tagging was completed, usually after one or two days, the FAD and receiver were abandoned to facilitate extended observation of the tagged individuals' behaviour. In addition to detection information, the receiver also provided a positional estimate, allowing the drift of the FAD to be monitored remotely. In one instance a conventional acoustic receiver (Vemco, VR2W) was attached to the FAD (FAD 8) instead of the satellite linked receiver. This receiver archived the information from the tagged animals and was later recovered and the data downloaded manually. No positional estimates were obtained for this FAD (FAD8 in Table 4.1).

Passive monitoring analysis

Several metrics were calculated to describe the behavioural patterns observed for tagged silky sharks, which facilitated comparisons with similar work on other FAD associated species. For all analyses, an individual was defined as present at the FAD if two or more detections were recorded within a single hour. As such, any single detections, separated by a gap of >1 h on either side, were removed from the dataset. This minimised the probability of including false detections. Total residence times spanned from the time of tagging until the last detection. Continuous residence times (CRTs) and continuous absence times (CATs) were calculated following (Ohta and Kakuma, 2005) and (Robert *et al.*, 2013) respectively, where continuous residency was considered when no temporal gap in detections >24 h occurred. The first CRT was considered to begin only after any effects of capture and tagging on normal behaviour were believed to have ended (see below). Fine-scale behaviour was assessed in a similar manner using 1 h as the minimum period to determine presence and absence, giving rise to fine-scale continuous residence times (FCRTs Govinden *et al.* 2013) and excursions.

Temporal behavioural patterns

The periodicity of temporal patterns in fine-scale behaviour was assessed by conducting a spectral analysis using a fast Fourier Transform (FFT). This analysis detects rhythms in the time series, the periodicity of which is visible in a power spectrum (Chatfield, 2004). The FFT was conducted using time series data of hourly detection frequencies generated from the start of the first CRT until the last recoded detection. This analysis was only conducted on individuals for which there were at least 3 days of data. The timing of excursions was assessed relative to the time of sunrise and sunset. As the FADs were constantly drifting, and tagging was conducted at different times of the year and in different areas of the ocean, using the timing of astronomical constants provided a more biologically significant reference point than simply comparing the start time of each excursion between individuals. As such, circular statistics were used to investigate whether the time differences between sunset and the start of an excursion were distributed uniformly through the night and day or whether the data displayed directionality. For this purpose, a Rayleigh Test with a significance level of 0.05 was performed. The distribution of arrival times (when a shark returned after an excursion) was assessed in the same manner. The time of local sunset was calculated using the position of the FAD and the calculation procedure available online from the U.S. National Oceanic and Atmospheric Administration (NOAA) (Cornwall *et al.*, 2014).

The duration of excursions was also compared across all individuals. As all excursions were shorter than 24 hours it was possible to again use circular statistical methods to assess their distribution, and thus a Rayleigh Test was performed to test for uniformity in their distribution.

Analysis of vertical behaviour

Depth distribution

Vertical behaviour was characterised using multiple comparisons corresponding to both temporal and horizontal changes in the tagged sharks' behaviour. Firstly, the behaviour between day and night was compared. This comparison facilitated the identification of possible diel changes in swimming depths or vertical movement patterns. Comparisons were performed using median swimming depths, during day and night. These comparisons were carried out using a Mann-Whitney U-test, as the data were found to not follow normal distributions (Shapiro-Wilks test). As with the horizontal analyses above, day and night data were separated using the time of sunrise and sunset on the day in question. The data used in these comparisons originated from individuals equipped with PSAT or archival tags and were restricted to their period of association with the FAD at which they were tagged. The reason for using this data rather than the depth data obtained from pressure sensitive acoustic tags in these and other silky sharks was that PSATs and archival tags provided vertical data when the shark was both within and outside of the reception range of the acoustic receiver. Furthermore, as the sharks were typically located outside of the reception range during the night, the acoustic depth dataset was severely skewed to daytime depths. While the number of shark with both acoustic and PSAT/archival tags was lower (n = 6) than those with pressure sensitive acoustic tags (n = 13), the smaller data set still provided a more complete view of the vertical behaviour of this species over a 24 hour period. Furthermore, depth data was generally more continuous from PSAT/archival tags, with samples recorded every 5 min as opposed to the more irregular sampling of the acoustic tags which depended upon both the distance between the shark and the receiver and the number of other tagged animals within the receiver's reception range.

Secondly, the vertical behaviour while the sharks were at the FAD and during excursions away from the FAD was assessed. This assessment was also conducted for the same six individuals that had been double tagged with either PSAT or archival tags. As such, the depth data from these tags were separated into time series representing depth during a FCRT or depth during an excursion. The start and end points of these time series sections were determined by the times of the first and last detections of the acoustic tag that was implanted within the same animal.

Active tracking

A previous study on the behaviour of silky sharks at FADs (Filmalter *et al.*, 2011) found that individuals often left the vicinity of the FAD directly after tagging, and at times only returned after several days. To investigate this behavioural phenomenon further, one individual was caught and tagged with a V16P 3H continuous pinger. This tag transmitted an acoustic signal once per second, which allowed the animal to be actively tracked. Tracking was conducted only during daylight hours from a small (5 m) auxiliary vessel from a commercial purse seine vessel. A portable Vemco VR100 receiver equipped with a uni-directional VH-110 hydrophone and set to detect the continuous tag at a frequency of 51 KHz was used. This receiver was also set to detect other fish and sharks that had been tagged with coded tags transmitting on 69KHz on a second reception channel. Owing to the use of the directional hydrophone, any detections recorded on this receiver during the active tracking were assumed to originate from animals behind the shark being tracked or alternatively, between the shark and the tracking vessel. Once the shark was released it was followed by the tracking vessel. The gain on the receiver was set to 0 throughout the experiment such that the distance between the vessel and the shark was minimised. As the exact location of the shark could never be truly known, the position of the tracking vessel was assumed to represent the position of the shark. The position of both the FAD and the vessel were monitored throughout the experiment using two hand held GPS units (Garmin E-Trex), one of which was placed in a water-proof container on the FAD and the second on the tracking vessel. These units were set to automatically record their location, accurate to 10 m, every 8-10 seconds.

To investigate the movement behaviour of this individual relative to the FAD, the distance between it and the FAD as well as it's bearing from the FAD, relative to the FADs heading, were calculated every minute. Girard *et al.* (2004) established a method for determining the distance from which a tracked fish displays directed orientate towards a FAD. This method involves the calculation of the reverse path length (starting from the time the fish returns to a FAD) and comparing it with the straight-line distance (backwards beeline) between the fish and the FAD throughout the course of the track (similarly calculated in reverse). They suggest that a linear relationship between these two variables is indicative of the late oriented stage of an animal seeking out a specific goal. Conversely, nonlinear relationships indicate random searching. The distance at which the relationship shifts from a linear to a non-linear function indicates the orientation distance. Here, the reverse path length and backwards beeline distance were calculated for the tracked silky shark using the location of the shark and the location of the FAD at 1 min intervals.

The study of the behaviour of silky sharks at FADs formed part of a larger project looking at the behaviour of tunas as well as bycatch species associated with floating objects in the Indian Ocean. As such, several other species of fishes were also tagged with acoustic tags at the same FADs and during the same time period as the silky sharks reported on here. These species included yellowfin tuna, bigeye tuna, skipjack tuna, rainbow runners and oceanic triggerfish. While the behaviour of these species is beyond the scope of the current study, the presence of tagged individuals of these species allowed for improved interpretation of the results obtained during the active tracking experiment. During the tracking process several of these other tagged species were also recorded. The distribution of distances from the FAD were compared between species using a Kruskal-Wallis rank sum test in the R software package (R Development Core Team, 2011) to assess whether species specific behaviours could be identified. Interactions between the tagged shark and other tagged species was examined through the development of a three dimensional graphic using the Igor Pro software package (Wavemetrics, Lake Oswego, OR, USA) incorporating several sources of information. This information included the position of the FAD, the horizontal and vertical position of the tracked shark and the horizontal and vertical positions of other tagged fishes around the same FAD. This information was integrated into a single figure to provide the first glance in the inter-specific spatio-temporal dynamics of a FAD aggregation.

Reception range testing

Assuming the position of the tracking vessel represented the position of the tagged fishes detected by the unidirectional hydrophone, it was possible to obtain a rough estimate of the reception range of the VR4 acoustic receiver attached to the FAD. This was achieved by comparing the detections recorded on the portable receiver on the tracking vessel with those recorded by the VR4 on the FAD and knowing the distance of the vessel from the FAD at the time of each detection.

4.3 Results

Sharks tagged

A total of 38 sharks were tagged with coded acoustic tags at 9 FADs, while one individual was tagged with a continuous pinger for active tracking. Seventeen of sharks these were also equipped with either an internal archival tag of a PSAT. Details of the tagging information and data collected are provided in Table 4.2.

Table 4.2 Meta data for silky sharks tagged with electronic tags at drifting FADs in the western Indian Ocean between 2010 and 2012 (CRT = continuous residence time, † denotes natural departures).

Tagging date	Tagging time	FAD ID	Size (cm TL)	Sex	Tag type	Acoustic tag ID	Total detections	Total association time	CRT	PSAT/Archival* tag ID
13/03/2010	16:50	FAD 1	88	F	V13P	64759	6210	10.44	8.72	34419
15/03/2010	17:17	FAD 2	109	M	V13P	64760	4273	11.56	11.03	34420
15/03/2010	18:17	FAD 2	77	F	V13P	64762	1740	6.36	6.36	-
16/03/2010	09:35	FAD 2	77	F	V13P	64798	2460	10.88	10.88	-
16/03/2010	10:47	FAD 2	81	F	V13P	64799	1099	6.31	6.31	-
15/04/2011	15:40	FAD 3	91	M	V13P	64772	0	0	0	34206
20/04/2011	16:54	FAD 4	103	F	V13P	64777	0	0	0	98719
20/04/2011	17:00	FAD 4	98.5	M	V13P	64778	0	0	0	34366
20/04/2011	22:57	FAD 4	80	F	V13P	64779	5422	16.81†	14.79	-
18/06/2011	11:07	FAD 5	98	F	V13P	64781	0	0	0	94261
18/06/2011	10:49	FAD 5	75.5	F	V13TP	64158	0	0	0	-
18/06/2011	11:30	FAD 5	73.5	F	V13	54269	0	0	0	-
18/06/2011	11:50	FAD 5	73	M	V13	54266	685	2.91	2.30	-
18/06/2011	13:00	FAD 5	78	M	V13	54267	0	0	0	-
18/06/2011	13:20	FAD 5	77	F	V13TP	64162	706	2.85	2.21	-
18/06/2011	13:30	FAD 5	73.5	F	V13	54268	625	2.84	2.35	-
20/06/2011	13:41	FAD 6	102	M	V13P	64785	0	0	0	94251
20/06/2011	14:00	FAD 6	69	F	V13	54271	0	0	0	-
20/06/2011	14:43	FAD 6	93	M	V13TP	64786	0	0	0	34415
20/06/2011	15:10	FAD 6	80.7	F	V13	54272	0	0	0	-
21/06/2011	11:55	FAD 6	72.3	M	V13	54274	0	0	0	-
21/06/2011	12:35	FAD 6	75	F	V13TP	64782	0	0	0	-
22/06/2011	11:45	FAD 7	77	F	V13	54275	2352	6.55†	6.52	-
02/04/2012	15:01	FAD 8	87.8	F	V13P	7099	4910	6.38	6.30	-
02/04/2012	15:11	FAD 8	79.7	M	V13	54236	0	0	0	-
03/04/2012	07:17	FAD 8	73.6	M	V13	54284	0	0	0	-
13/04/2012	15:09	FAD 9	102	F	V13P	7104	1435	30.60	26.95	-
13/04/2012	15:15	FAD 9	109	F	V13P	7105	2364	30.60	30.15	990030*
13/04/2012	15:30	FAD 9	106	F	V13	54280	7595	30.63	28.08	94260
13/04/2012	15:40	FAD 9	90	-	V13	54281	1548	10.09†	9.63	-
13/04/2012	15:50	FAD 9	93.3	M	V13P	7106	1495	10.14†	9.74	-
13/04/2012	16:50	FAD 9	103.3	F	V13P	7107	1137	13.12†	12.79	990036*
13/04/2012	17:19	FAD 9	111.8	F	V13P	7108	3559	30.58	30.23	990028*
13/04/2012	17:33	FAD 9	98.6	F	V13	54239	7479	30.55	30.07	104658
14/04/2012	09:35	FAD 9	111.3	-	V13	54240	7449	29.86	28.90	990026*
14/04/2012	11:50	FAD 9	116	-	V13P	7111	0	0	0	94253
14/04/2012	17:39	FAD 9	116	M	V13P	7113	0	0	0	94255
15/04/2012	07:54	FAD 9	100.6	M	V16P	31211	-	-	-	-

Twenty of the 38 tagged silky sharks were detected by the receivers, attached to the FADs. Six of the 18 sharks that were never detected were tagged at FAD 6 (Table 4.2) where the acoustic receiver malfunctioned resulting in no data collection. The remaining 12 sharks are believed to have permanently left the FAD where they were tagged soon after release. The possibility that they died cannot be excluded for four individuals, although data received from the PSATs also fitted to eight of these animals, indicated that they survived the tagging process. Consequently, data was only analysed for the 20 detected sharks. Total residence times ranged between 2.8 – 30.6 days, with an average of 15.7 (± 11.1 SD) days. In total the behaviour of silky sharks at drifting FADs was observed for 300 days. Of the 20 sharks detected, observational data on 12 individuals was truncated due to either equipment failure or a fishing vessel setting a net around the FAD, resulting in the removal of the acoustic receiver and hence termination of detection data. Observation on the remaining eight sharks were uninterrupted and departure from the FAD at which they were tagged was done on their own accord.

Post-tagging excursions

Directly after release 90% (n = 18) of the tagged sharks rapidly left the reception range of the acoustic receiver and stayed away from the FADs for > 7 hrs. These initial excursions lasted an average of 1.0 (± 0.9 SD) days and ranged between 7.4 hrs and 3.7 days. The majority of individuals (75%) returned to the FAD at night. Data from double tagged sharks suggested that once released the tagged shark immediately dived to depths of 60 – 100 m before slowly returning to the upper 40 m after 15 – 20 min.

Continuous residence times

Once the tagged sharks returned to the FAD the effects of the capture and tagging operation were assumed to have ended, and ‘normal’ behaviour resumed. After returning, none of the tagged shark left the detection range of a receiver for a period exceeding 24 hours over their respective monitoring periods.

Periodicity and Excursions

All sharks regularly undertook short excursions away from the FAD during their respective monitoring periods (Fig. 4.2). The typical behaviour consisted of presence at the FAD during the day and periods of absence during the night.

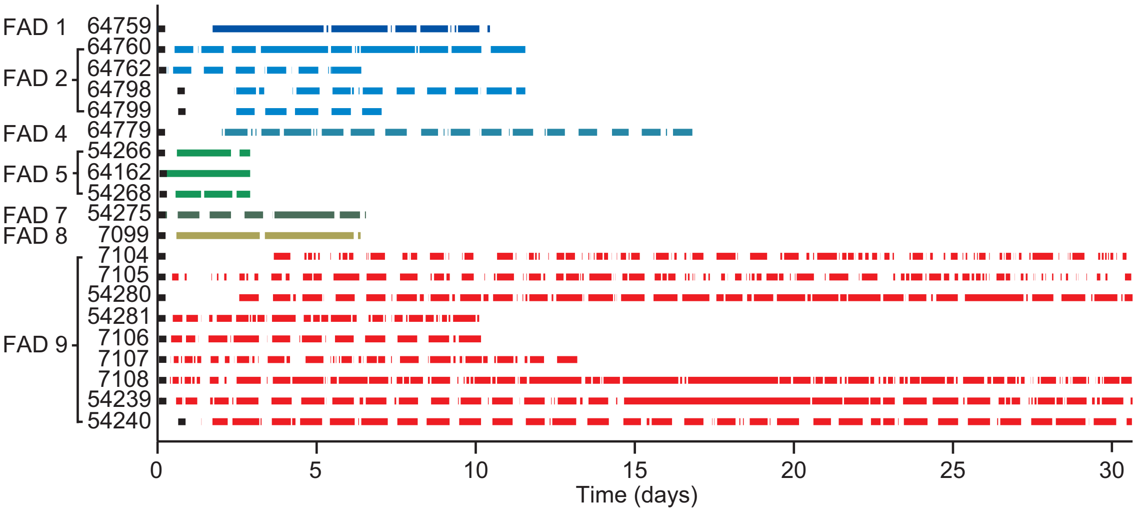


Figure 4.2 Residency of tagged silky sharks (n = 20) at drifting FADs in the western Indian Ocean. Tag ID is given on the y-axis and duration of observation on the x-axis. Each horizontal series shows the presence/absence of a shark at the FAD where it was tagged (colours indicate different FADs). Coloured areas depict presence while blank spaces indicate absence. Black squares represent the time at which each individual was tagged relative to the tagging time of the first individual at each FAD.

The duration of these presence periods (FCRTs) averaged 0.31 (± 0.43) days while excursions were generally shorter, averaging 0.15 (± 0.12) days. Spectral analysis using a FFT was performed on 17 individuals, that were present for >3 days. Results from this analysis revealed a marked peak at 24 hours in 82.4% of the individuals analysed, indicating a strong diel rhythm in associative behaviour. Examples of the spectral analysis results are shown in Fig. 4.3.

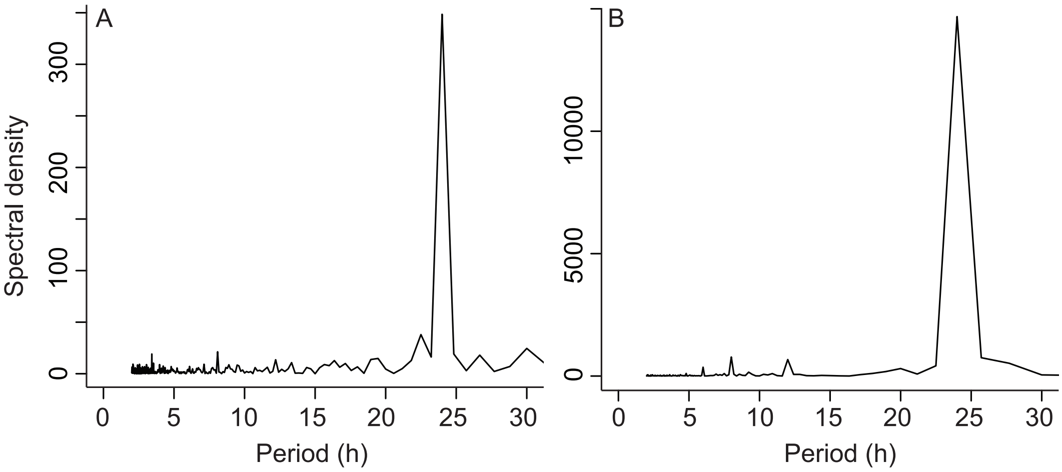


Figure 4.3 Examples of FFT showing the diel periodicity in the presence of two individuals at FADs in the western Indian Ocean, A is tag ID 64760 and B is tag ID 64779.

Timing of excursions

Circular analysis was performed on the distribution of the starting times of all excursions including final departures (non-truncated), relative to the time of local sunset on the day on which the excursion occurred (Fig. 4.4A). The data were found to be significantly clustered and not uniformly distributed over time (Rayleigh Test, Z = 50.875, $p < 10^{-12}$). The majority of excursions (74%) were initiated at night, while far fewer (26%) started between sunrise and sunset. The median start time was 95 min after sunset. A strong peak (22.9% of observations) in the start of excursions was observed in the first hour after sunset (Fig. 4.4A). The difference between sunset and the times that sharks returned to a FAD (Fig. 4.4B) showed less clustering, but were still significantly different from a uniform distribution (Rayleigh Test, Z = 77.545, $p < 10^{-12}$). The majority of excursions ended during the night, with a median return time of 9 h 23 min after sunset.

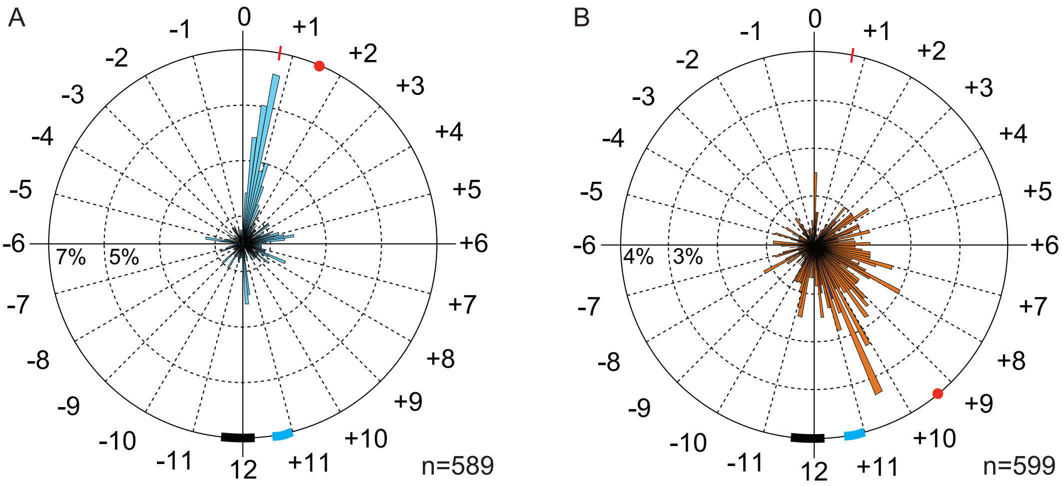


Figure 4.4 Radial plots showing the distribution of the time difference between A) the start and B) the end of all excursions and the time of local sunset (0) for silky sharks associated with drifting FADs in the western Indian Ocean. Red bars indicate nautical dusk. Red dots indicate median values. Thick blue bars indicate the range of times of nautical dawn. Thick black bars indicate the range of sunrise times during the study.

Within the first hour after sunset, the number of excursions initiated over 10 min intervals increased steadily until peaking 40 – 50 min after sunset. Comparison with *in situ* light data collected from an archival tag (9900026) revealed that this peak coincided with the time of complete darkness, as ambient light levels plateaued at a minimum (Fig. 4.5). This moment also corresponded exactly with time of nautical dusk, which is defined as the time when the disk of the sun reaches an angle of 8 degrees below the horizon. The frequency of departures decreased rapidly after this time, with minor increases occurring again roughly half way through the night and just prior to sunrise.

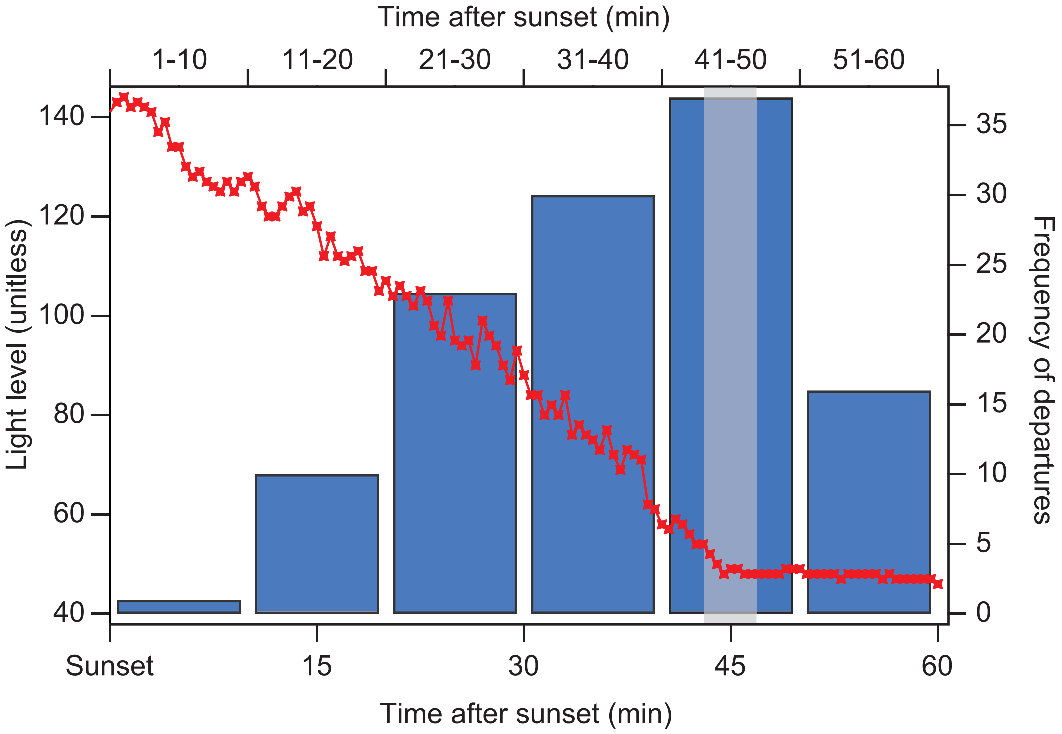


Figure 4.5 An example of decreasing ambient light in the hour following sunset (red line) recorded by an archival tag (990026) in a silky shark associated with FAD 9. Blue bars show the frequency of silky shark departures from all monitored FADs during the first hour after sunset. The grey bar indicates the time of nautical dusk, which occurred between 44 and 48 min after sunset over the entire study period.

The duration of excursions varied widely, ranging from 1 – 21.4 hours. The mean excursion duration was 3.7 hours (± 2.98 hours SD). No correlation was apparent between the start time relative to sunset and the excursion duration (Fig. 4.6A). Circular analysis of departure time and excursion duration revealed that excursions initiated within the first hour after sunset typically spanned either >4 – 8 hours or >8 – 12 hours. This suggested that the sharks returned to the FAD during the night (Fig. 4.6B).

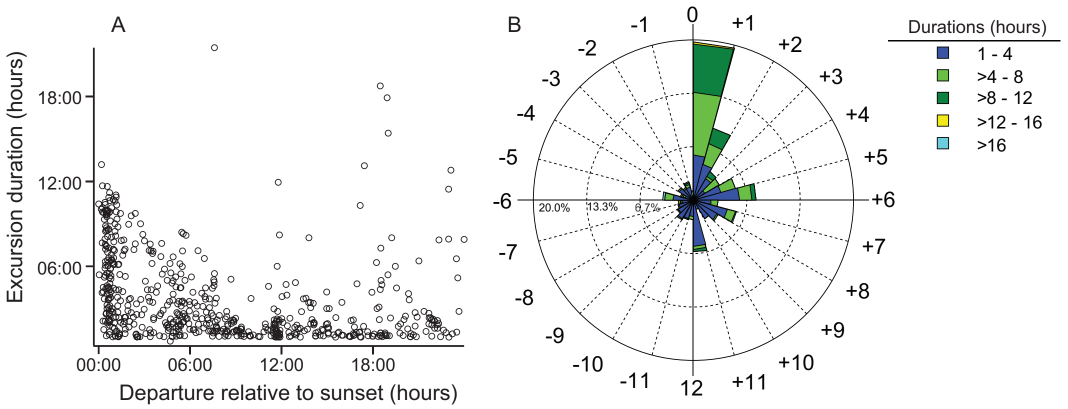


Figure 4.6 Excursion length and departure time relative to sunset of silky sharks associated with drifting FADs in the western Indian Ocean, B circular plot of departure time and duration.

Vertical behaviour

Diel changes in vertical behaviour were clearly visible in the time series data collected from the PSATs and archival tags. An extract of several days of such data from one individual is shown in Fig. 4.7. Generally sharks exhibited highly variable vertical behaviour during the night, moving rapidly up and down through the water column. Between these vertical excursions, the sharks were typically located close to the surface (<10 m). During the day vertical movements were more restricted. For several individuals a distinctive u-shaped pattern could be observed during the day. This shape was created by the shark remaining close to the surface at sunrise and then gradually moving deeper as midday approached, followed by a return movement to the surface as night approached (Fig. 4.7).

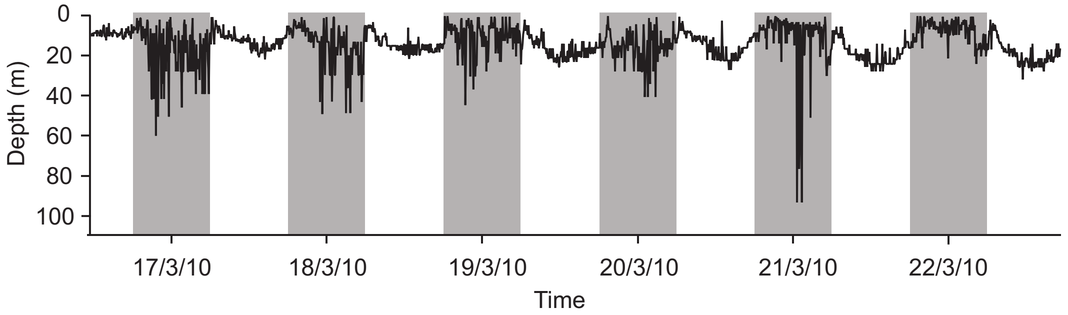


Figure 4.7 Example of diel behaviour changes in vertical time series data obtained from a PSAT (34419) on a silky shark at FAD 1. Grey bars indicate night. Distinctive u-shaped pattern is clearly visible during the day.

After performing FFTs on the uninterrupted time series data obtained from two recovered tags, the periodicity of this shift in behaviour was confirmed to be 24 hours (Fig. 4.8). The wide base of the 24 hour peak in the spectrograms indicate that, although the sharks regularly change their vertical behaviour, the exact time at which the change occurs differs from day to day.

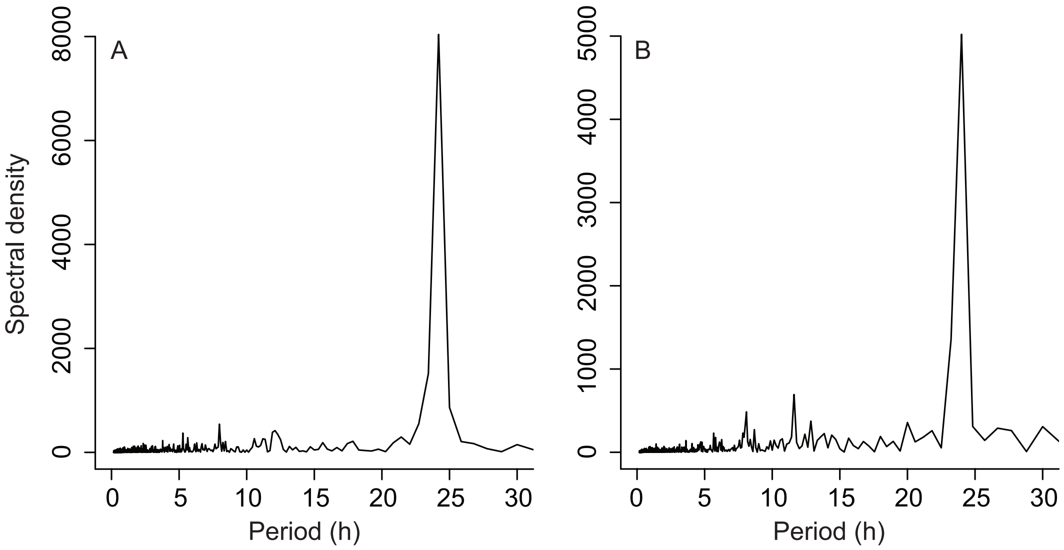


Figure 4.8 Fast Fourier transform of the vertical data collected from a recovered archival tag (990026) and PSAT (104674) in A and B respectively from silky sharks associated with drifting FADs in the western Indian Ocean. Peaks in periodicity at 24 hours indicate strong diel behavioural patterns.

Comparisons between day and night depths were conducted using data obtained from five PSATs and one archival tag. A series of Shapiro-Wilks tests for normality showed that none of the samples were normally distributed. As such day and night depth distributions were compared using a non-parametric Mann-Whitney U- test.

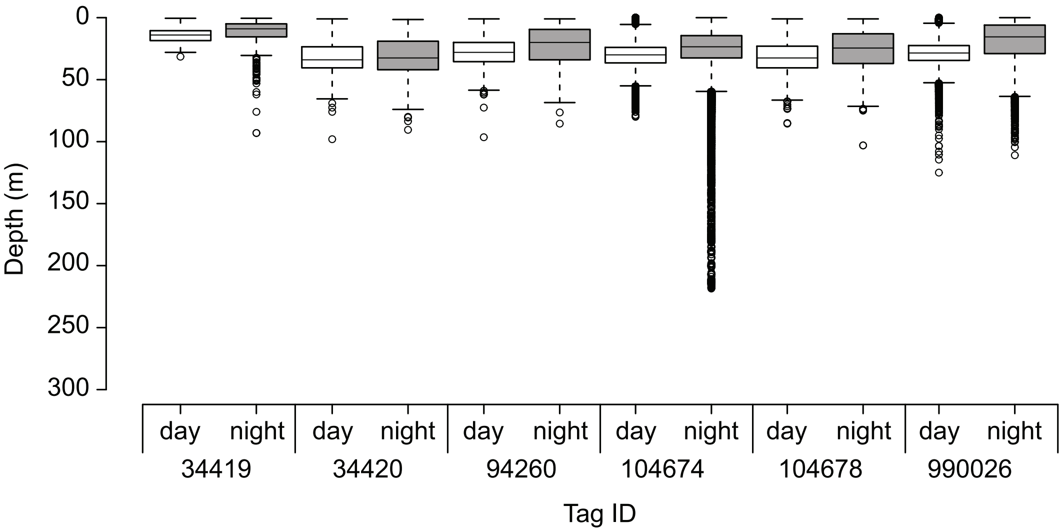


Figure 4.9 Boxplots of depth distributions during day and night obtained from PSAT and archival tags deployed on silky sharks at drifting FADs in the western Indian Ocean.

Significant differences in the median depth during day and night were found for all of the sharks, with median depths being consistently shallower at night than during the day (Fig. 4.9 and Table 4.3). Furthermore, the interquartile range (IQR) was always greater during the night, suggesting that the range of depths the sharks utilised during the night was wider (Fig. 4.9 and Table 4.3). For comparison with other studies day and night data were pooled across all individuals resulting in a median depth of 27 m and an IQR of 19-35 m.

Table 4.3 Summary statistics of vertical data from PSAT and archival tags deployed on silky sharks associated to drifting FADs in the western Indian Ocean.

	Median depth		IQR		
Tag ID	Day	Night	Day	Night	p-value
34419	14	9	8	11	<2.2e-16
34420	34	33	17	24	0.047
94260	28	20	16	25	<2.2e-16
104678	33	25	18	24	<2.2e-16
104674	30	24	13	18	<2.2e-16
990026	29	16	12	23	<2.2e-16

The average depth distribution during day and night from all six PSAT and archival tags is shown in Fig. 4.10A. Night time records are skewed towards shallower depths (<20 m) while day time depths are evenly distributed around a peak at approximately 30 m. Very similar patterns were observed in the depth distributions when the sharks were present at the FAD or on an excursion Fig.

4.10B. On average the sharks were shallower during excursions, with depths less than 15 m recorded most frequently. The depths occupied during periods of presence followed more of a normal bell-shaped distribution, with a peak at 30 – 39 m.

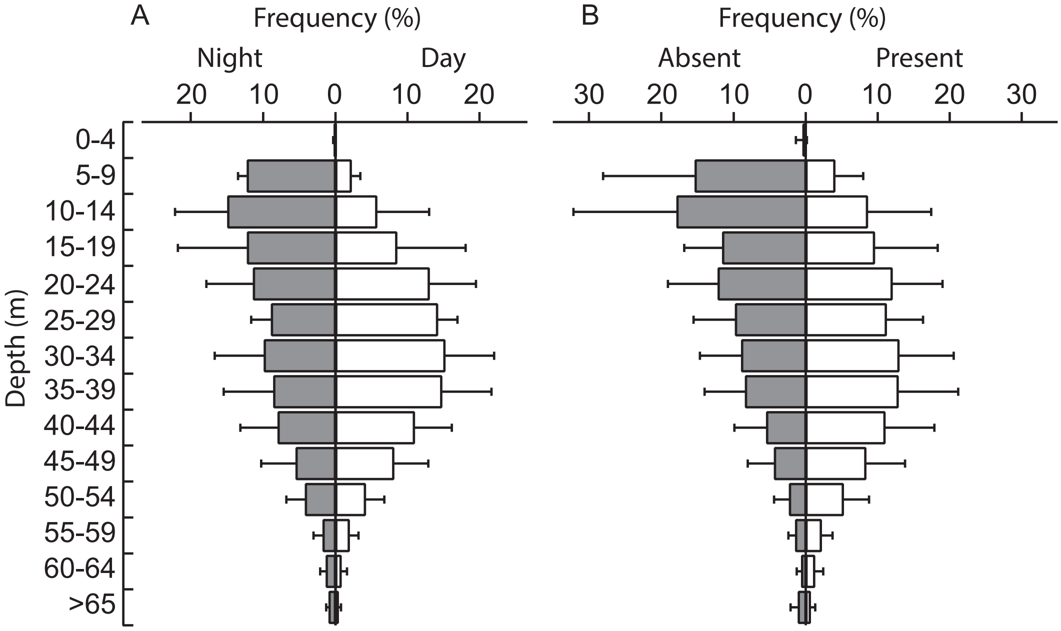


Figure 4.10 Averaged depth distribution from six silky sharks tagged PSATs and archival tags at drifting FADs in the western Indian Ocean. A) comparison between night and day and B) comparison between presence and absence at the FAD. Error bars represent standard deviations.

Active tracking

Tracking of the tagged shark (tag ID 31211) lasted 2h46min. Environmental conditions were excellent during the tracking period, with less than 5 knots of wind throughout the experiment. During this time the shark covered a total distance of 5788 m and the FAD drifted a distance of 2395 m. The average speed of the shark during the course of the track was 0.79 ms^{-1} (2.50 kmh^{-1}) or 0.75 bls^{-1} (body lengths per second). An overview of the shark and the FADs trajectory is shown in Fig. 4.11. After release at the FAD the shark moved around the FAD in a variety of directions for approximately 20 min. After which it moved ahead of the FAD's direction of drift (down current). The shark continued to move further away from the FAD, maintaining a fairly constant bearing relative to the bearing of the FAD's drift. After approximately 80 min, the drift of the FAD changed from SE to SW. Shortly after this change occurred, the shark changed direction and started swimming back towards the FAD.

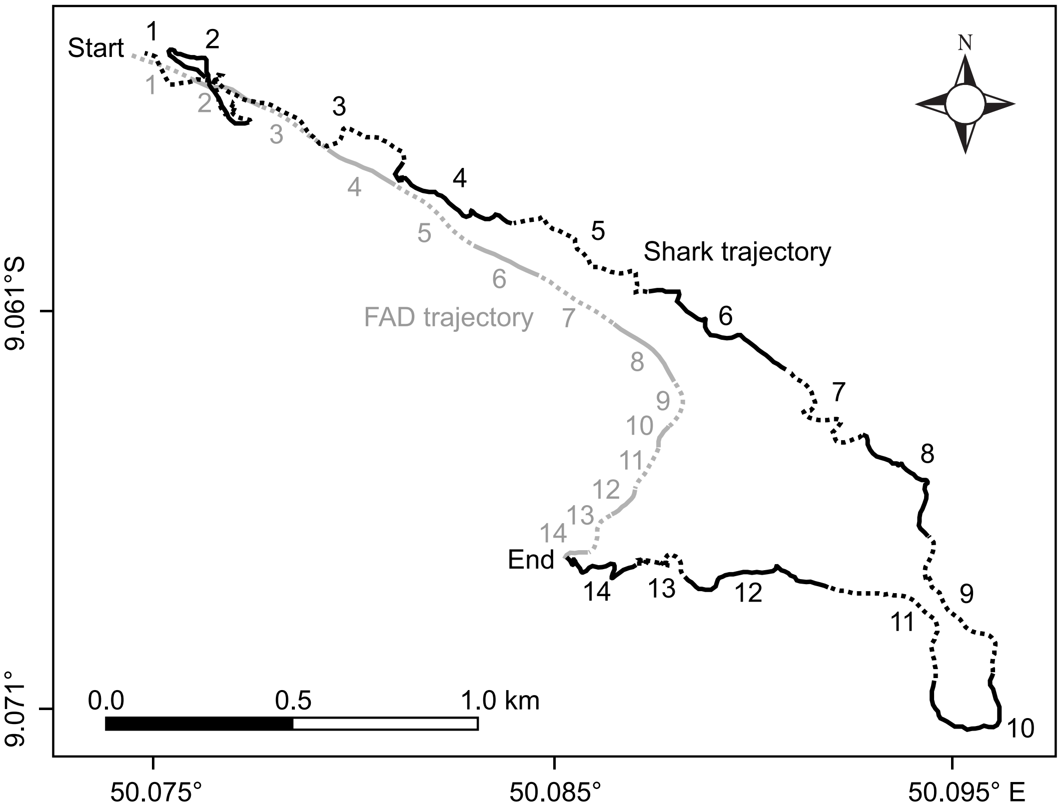


Figure 4.11 Horizontal movements of a silky shark associated with a drifting FAD in the Indian Ocean observed during a 2.3 h active tracking experiment. Black line indicates the shark's movements while the grey line shows the drift of the FAD. Solid and stippled portions indicate 10-minute periods while numbers show correspondence between 10 minute periods. For clarity, the 20-minute period after the shark returned to the FAD is not shown.

Using the reverse path length method described by Girard *et al.* (2004) it was possible to identify this point as the exact moment when the shark began a direct orientated movement towards the FAD (Fig. 4.12). This analysis indicates that the shark was able to detect the location of the FAD from 1200 m away and correct its trajectory constantly to compensate for the constantly changing position of the FAD, such that it would intercept it while covering the shortest possible distance.

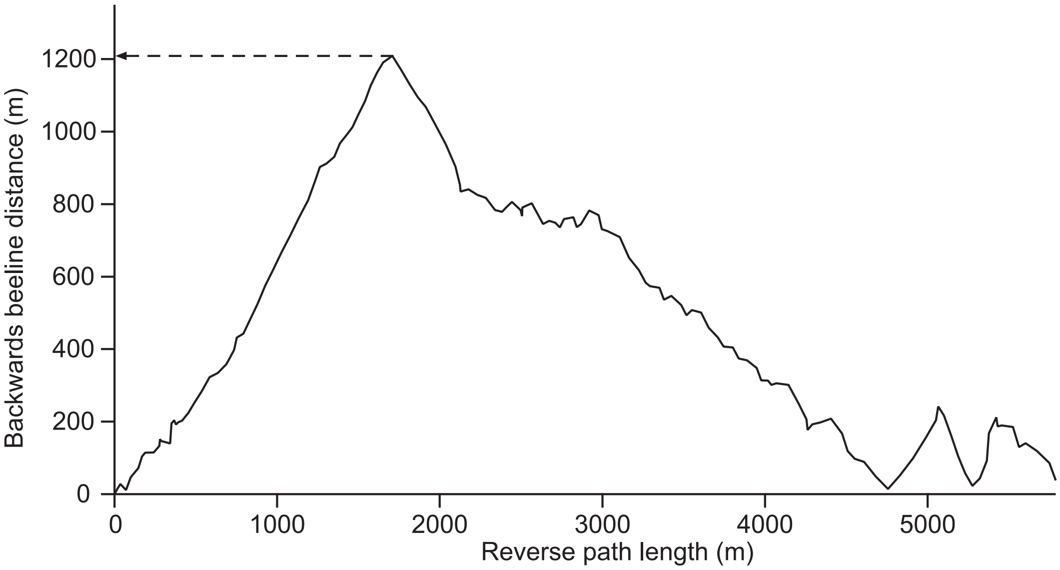


Figure 4.12 Assessment of the distance from which a tracked silky shark orientated to a drifting FAD in the western Indian Ocean, using the reverse path length and beeline distance method.

Assessment of the shark's position relative to the FAD indicated that it was most frequently within 10° of the FAD's heading, and thus largely down current from it (Fig. 4.13). As the FAD underwent a 90° alteration in heading during the tracking experiment, for the last 45 min of the experiment, the shark was located approximately 90° to the left of the FAD. The radical change in the FAD's trajectory was likely a result of the FAD reaching a current line and drifting accordingly. As a result of this directional shift the average bearing of the sharks from the FAD's heading was 310°. A Rayleigh's Z-test of the sharks bearing from the FAD throughout the experiment was significantly different from a uniform distribution ($Z = 52.114$, $p < 10^{-12}$).

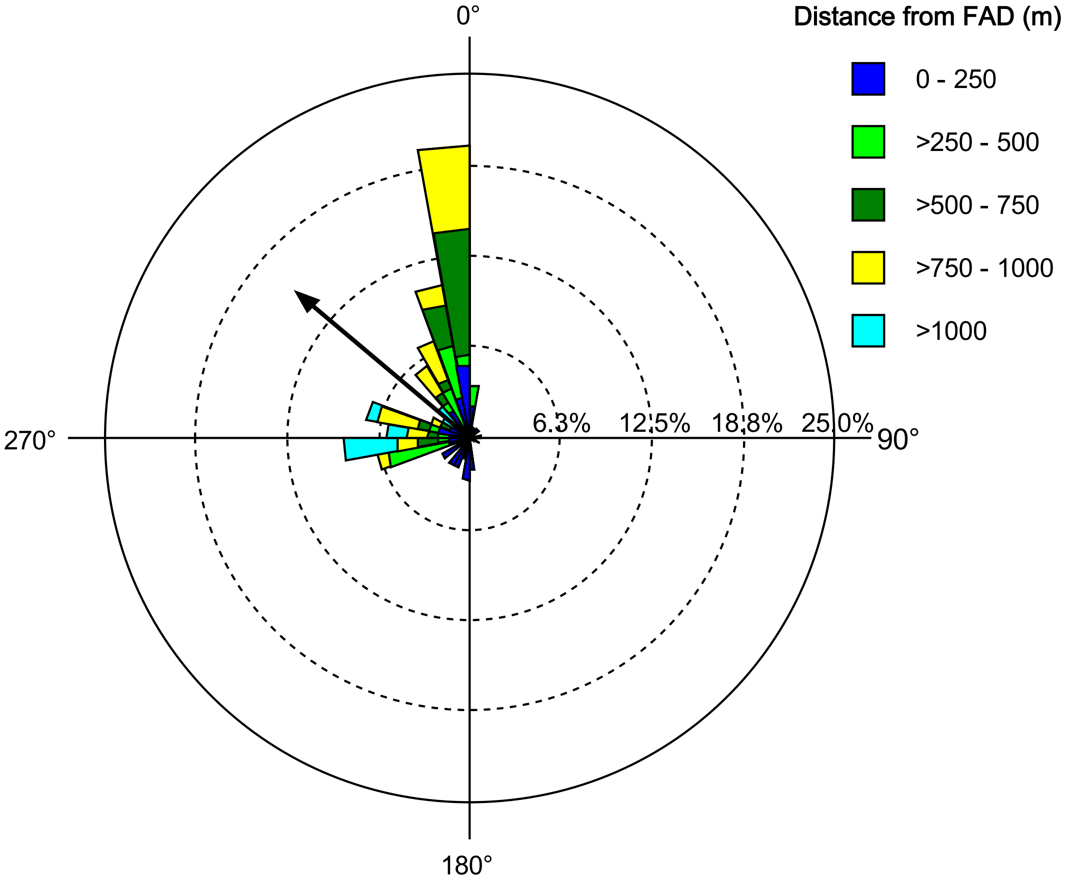


Figure 4.13 Circular plot showing the angular frequency and distribution of corresponding distances of a tracked silky relative to the drift direction of a drifting FAD in the western Indian Ocean.

Interactions with other species

During the course of the tracking experiment several other tagged species were detected by the uni-directional hydrophone. As the receiver's gain was set to zero, the position of these tagged individuals was assumed to be close to that of the shark being tracked. A summary of the detection results from these fishes is provided in Table 4.4. The frequency distribution of the distances at which the different species were detected showed that a clear spatial structure existed in the FAD associated community during the time of the tracking experiment (Fig. 4.14A). Rainbow runners and oceanic triggerfish were detected most frequently within 100 m of the FAD. Other silky sharks were detected most often within 100 m of the FAD, but also with regular consistency throughout the trajectory of the tracked shark. Yellowfin tuna were detected most frequently at 600 – 900 m from the FAD, but also at the furthest point reached from the FAD during the track, at 1209m (Fig. 4.14B).

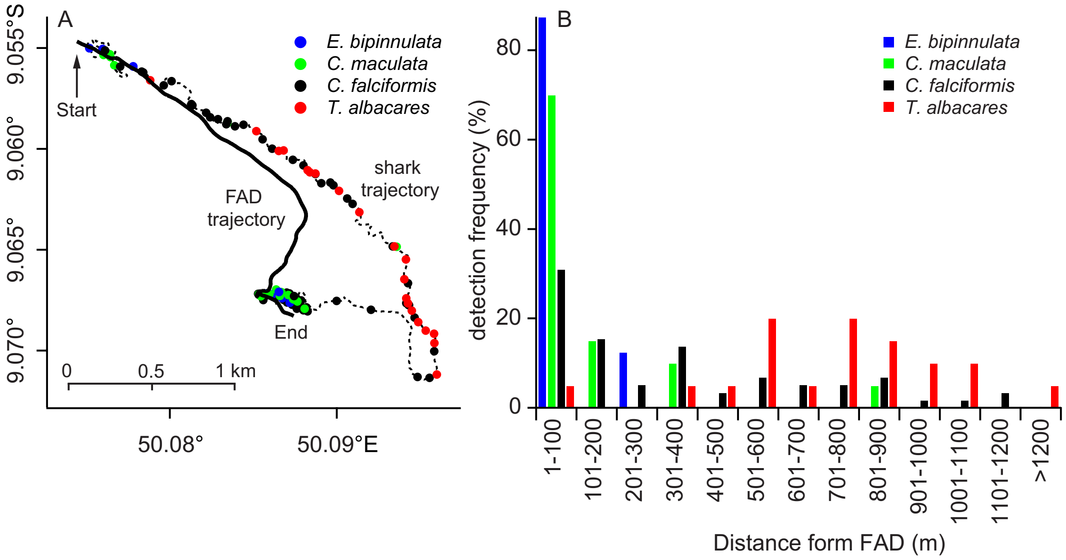


Figure 4.14 Detections recorded from other tagged fishes equipped with both pressure sensitive and sensor-less coded acoustic tags during the tracking of a silky shark around a drifting FAD in the western Indian Ocean. A) indicates the locations of detections during the track and B) shows the frequency distribution of the distances of the various species from the FAD.

Significant differences were found between the distances at which each species was detected (Kruskal-Wallis rank sum test, d.f. = 3, $p<0.01$). Rainbow runners and triggerfish had similar median distances, while silky sharks were detected further, but at an intermediate distance to yellowfin tuna (Table 4.4).

Table 4.4 Summary of spatial data collected from other tagged fishes around the drifting FAD during the active tracking of a silky shark.

Species	*E. bipinnulata*	*C. maculata*	*C. falciformis*	*T. albacares*
No. tagged	3	4	11	5
No. detected during track	3	3	8	2
Median distance (m ± SD)	76 ± 53	77 ± 179	302 ± 326	777 ± 273

A three dimensional examination of the depth and trajectory of the tracked sharks and other detected fishes revealed how the shark moved relative to these individuals (Fig. 4.15). As the details of this 3D visualisation are difficult to see when represented on a 2D plane, a video showing this plot from all sides can be viewed online at: `http://youtu.be/PBcbALU5pU0`. Directly after release, the shark rapidly descended to a depth of about 40 m. After approximately 20 min it made its way back to the surface where several other tagged triggerfish and rainbow runner were aggregated close to the FAD. The shark then started to move away from the FAD, heading down current. Along this trajectory it was often in close proximity to other tagged sharks, and detections from those with pressure sensitive tags show that it descended to similar depths as some of these individuals. As the shark moved further away from the FAD, it made its way towards a school of tuna, where several tagged yellowfin tuna were located. After approximately 1.5 hour of tracking the shark reached its furthest point from the FAD and dived down to roughly 60 m, where the tagged yellowfin tuna were situated.

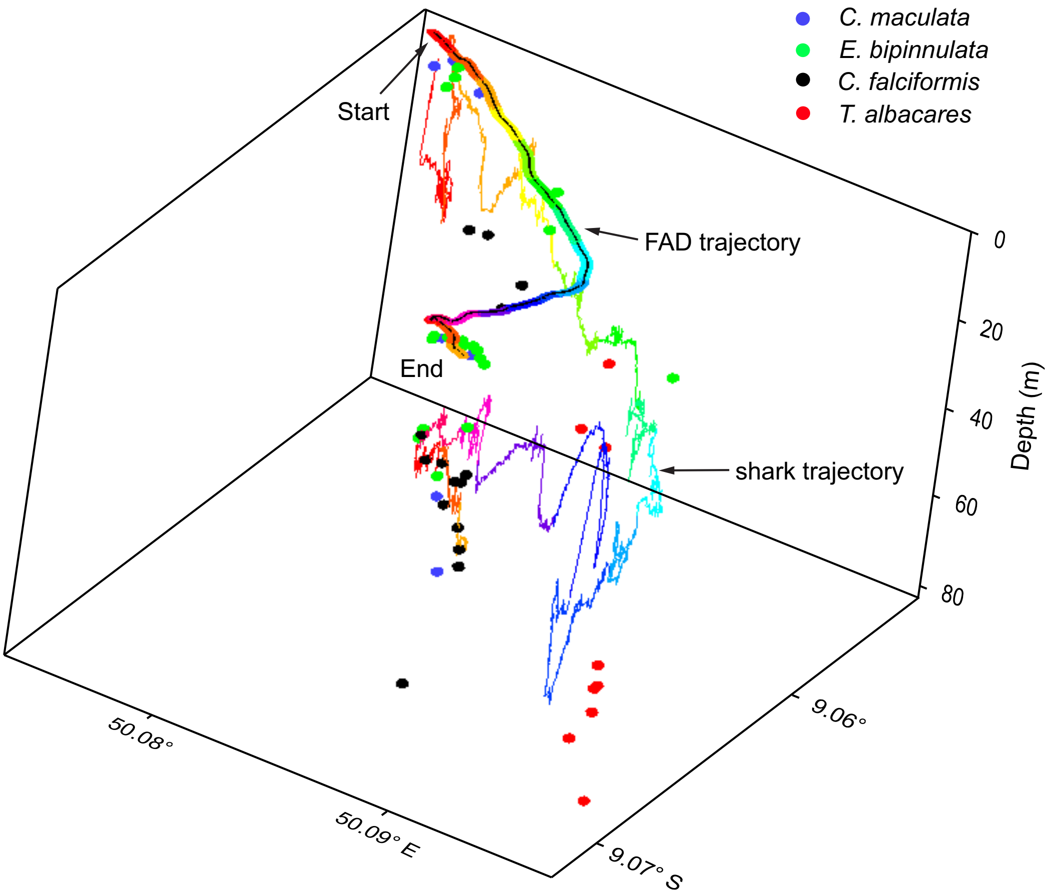


Figure 4.15 Three-dimensional plot showing the trajectory of a drifting FAD (broad coloured line) and the trajectory of an actively tracked silky shark (narrow coloured line) as well as positions of other FAD associated species equipped with pressure sensitive acoustic tags (coloured dots). Colours in the two trajectories indicate corresponding 10 minute periods.

It remained at this depth only briefly, before returning to the surface. At this time, the school of tuna were observed feeding at the surface around the tracking vessel. At about the same time, the FAD's drift changed by 90 degrees. After remaining close to the school of tuna for about 30 min, the tracked shark started to move back to the close proximity of the FAD. It encountered very few tagged fish during this portion of the track, and appeared to be focused on reaching the FAD. Once it arrived at the FAD, several other silky sharks, triggerfish and rainbow runner were again detected. The shark then remained close to the FAD for a further 20 min after which the tracking experiment was terminated.

Reception range assessment

A total of 106 detections were recorded from fishes tagged with coded tags by the tracking vessel during the experiment. Forty-two percent of these detections were recorded by the VR4 receiver on the FAD. The maximum distance at which a detection was simultaneously recoded was 803 m. Beyond 400 m from the FAD the percentage of detections simultaneously recorded by both receivers dropped significantly (Fig. 4.16). The reception range obtained here is similar to that reported by other studies using VR2 acoustic receiver attached to an anchored FADs (Ohta and Kakuma, 2005; Taquet *et al.*, 2007a).

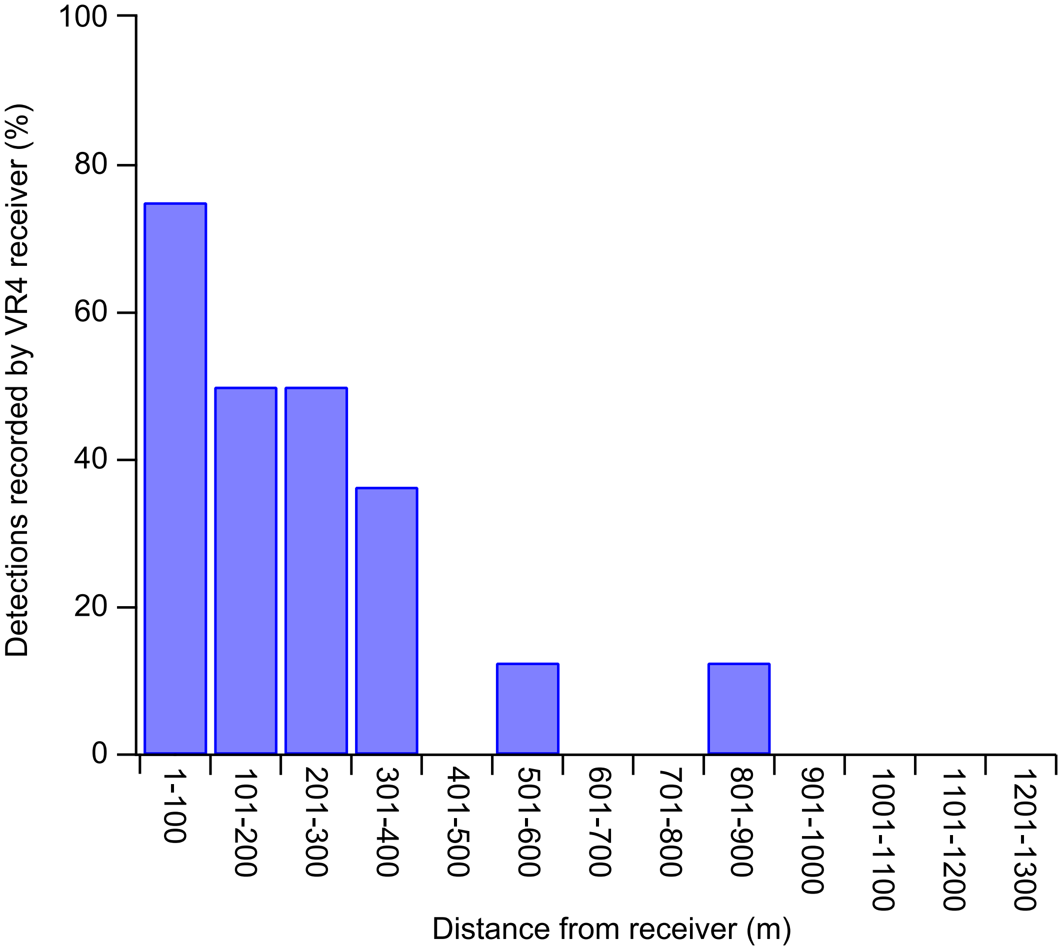


Figure 4.16 Percentage of detections recorded by the VR4 receiver on the FAD in relation to the number recorded by the VR100 on the tracking vessel.

4.4 Discussion

Effect of capture and tagging

The capture and tagging of silky sharks at FADs appears to impact their normal behaviour. This was evidenced by the high proportion of individuals (90%) that left the detection range of the acoustic receiver attached to the FAD shortly after they were released. Furthermore, 38% of tagged individuals never returned after these initial departures. Considering that after returning, not a single shark remained out of the detection range for more than 24 hours, it would appear that the stress associated with capture, handling and tagging has a significant effect on juvenile silky sharks. The duration of the "stressed" state averaged 1.04 (± 0.94) days, after which it was assumed that the returned shark resumed "normal" activity. Generally, studies using surgical tag implantation methods on pelagic fishes such as tunas (typically active tracking or archival tagging studies) have considered the effects of tagging on behaviour to be non-significant (Holland *et al.*, 1990; Musyl *et al.*, 2003; Dagorn *et al.*, 2007a; Matsumoto *et al.*, 2013, 2014) or have not examined them directly (Schaefer and Fuller, 2002). In active tracking studies in particular, the possibility to disregard the initial portion (hours) of an individual's behaviour is not a practical option as such tracks typically only span several hour or days (Holland *et al.*, 1990; Brill *et al.*, 1999; Dagorn *et al.*, 2000a; Matsumoto *et al.*, 2014). Furthermore, where passive acoustic techniques, such as those employed here, have been used, few have reported behavioural changes linked to tagging (Taquet *et al.*, 2007a; Filmalter *et al.*, 2011). Taquet *et al.* (2007a) considered dorado that left the monitored FAD within an hour of tagging to have been stressed or injured during the capture and tagging procedure and removed these animals from their study. However, this only occurred in 13% of the studied animals. Filmalter *et al.* (2011), in a previous study on silky shark behaviour at FADs, also observed that all individuals left the reception range of the receiver immediately after tagging, with a mean excursion duration of 0.94 days, which is similar to the average duration found in this study. That study also postulated the cause of this response to be the stress of capture and tagging. Interestingly, the probability of an individual returning to the FAD was lower when a PSAT was also attached to it (0.45), than when tags were only implanted internally (0.75). This result suggests that the additional stress associated with attaching external tag is often sufficient to break the shark's association with the FAD where it was caught.

Residency patterns

After tagged sharks returned to the FAD, all individuals showed very high residency, until they finally left, or when the experiment was prematurely terminated. The mean residence time found here, of almost 16 days, is three times longer than that reported in a previous study on silky shark behaviour at FADs of 5.19 days (Filmalter *et al.*, 2011). As both studies were influenced by premature termination of several experiments, they likely reflect an underestimation of the typical association time of silky sharks with floating object. When compared with other pelagic species known to aggregate at floating objects silky sharks are the most resident (Table 4.5).

Table 4.5 Comparison of reported residence times of various species of associated with FADs.

Species	Mean residence time (days)	Study	FAD type	Region/Area
Yellowfin tuna	1.04	Dagorn *et al.* (2007b)	Drifting	Indian Ocean
	7.9	Ohta and Kakuma (2005)	Anchored	Japan
	3-4	Mitsunaga *et al.* (2012)	Anchored	Philippines
	0.66	Govinden *et al.* (2013)	Anchored	Maldives
	8.0	Dagorn *et al.* (2007a)	Anchored	Hawaii
Bigeye tuna	1.43	Dagorn *et al.* (2007b)	Drifting	Indian Ocean
	7.0	Ohta and Kakuma (2005)	Anchored	Japan
	4.8	Dagorn *et al.* (2007a)	Anchored	Hawaii
Skipjack tuna	0.91	Dagorn *et al.* (2007b)	Drifting	Indian Ocean
	2.3	Matsumoto *et al.* (2014)	Drifting	Central Pacific Ocean
	0.2/3.5	Govinden *et al.* (2013)	Anchored	Maldives
Wahoo	1.57	Dagorn *et al.* (2007b)	Drifting	Indian Ocean
Oceanic triggerfish	12.49	Dagorn *et al.* (2007b)	Drifting	Indian Ocean
Dorado	3.96	Dagorn *et al.* (2007b)	Drifting	Indian Ocean
	6.25	Taquet *et al.* (2007a)	Drifting	Indian Ocean

While differing residence times between species do not necessarily reflect different motivations for associating with a floating object, they certainly do provide insight into the strength of the motivation to remain associated. The prolonged residence times of silky sharks suggest that the factors that cause other highly mobile pelagic teleost species, such as tunas, to break their association do not have as strong an influence on silky sharks. Ohta and Kakuma (2005) suggested that the internal state (hunger) and the local prey availability may be more important in determining when tunas leave FADs than external abiotic parameters. An obvious difference between tunas and silky sharks is their energetic requirements and associated feeding strategy. FAD associated yellowfin and bigeye tunas are generally small (40-65 cm)(Dagorn *et al.*, 2013). At this life history stage these tunas are growing at an exponential rate (Stequert *et al.*, 1996; Stequert and Conand, 2004), and as such have an extremely high energetic requirement. Furthermore, Ménard *et al.* (2000b) found that 85% of the stomachs of FAD associated tunas in the Atlantic Ocean were empty as opposed to just 26% for those caught in un-associated schools. As such, the short residence times of tunas is believed to reflect their need to find food (Ohta and Kakuma, 2005). Following this hypothesis, the long residence times of silky sharks may suggest that they are able to find sufficient food in the vicinity of the FAD to support their energetic requirements, which would certainly be lower than those of tunas. The fact that 64% of silky sharks caught at FADs had non-empty stomachs, as described in Chapter 3, lends further support to this hypothesis.

The strong diel patterns in presence and absence from the FADs were clearly visible through the 24 h peak in the spectral analysis. The typical pattern consisted of presence at the FAD during the day and excursions away during the night. Night time excursions have also been observed in tunas associated with FADs (Holland *et al.*, 1990; Ohta and Kakuma, 2005; Matsumoto *et al.*, 2014) while no distinct pattern in excursion time was found for FAD associated dorado (Taquet *et al.*, 2007a). In spite of these temporal differences between species, all studies have attributed excursion away from the FAD to foraging behaviour. The high regularity of departure events and their temporal precision following sunset suggests that sharks use the onset of darkness as the principle cue to initiate a switch in behavioural mode (association vs. excursion). This is further emphasised by the exact correlation of the strongest peak in departure frequency with the time at which ambient light levels reached a minimum. The duration of excursions was highly variable, with a mean of 3.7 hours (± 2.9 hours). However, nearly all excursions that started after dark ended before sunrise, with excursions that started later typically being shorter than those that started soon after sunset. These findings suggest that the behaviour adopted during the night (such a capturing prey) is either not as energetically efficient for the sharks during daylight hours or their prey is not available during this time. It is possible that the duration of the excursion is related to the feeding success, with shorter excursions indicating more successful feeding bouts, however, this hypothesis is not testable with the data obtained here, and will require simultaneous tracking and feeding observations as have been performed for other shark species (Sepulveda *et al.*, 2004).

Vertical behaviour

The FFT analysis of the complete time series of vertical data from recovered PSAT and archival tags clearly indicate a strong diel periodicity in the silky shark's vertical behaviour. A general pattern was evident across all individuals, where median depths were significantly shallower at night than during the day. However, the consistently larger IQR observed during the night suggest that in spite of a generally shallower distribution, the sharks also spent short periods of time descending to greater depths than those occupied during day light hours. Examination of the detailed time series data further illustrated this pattern. Further comparison of the day and night IQRs for each individual suggests that during the day the sharks exhibited a more stable vertical behaviour, seldom undertaking large vertical movements. Musyl *et al.* (2011a) also found significant differences between day and night depths of silky sharks tagged with PSATs in the Pacific Ocean and reported that overall, the sharks spent the majority of their time (95%) in the surface layers (above 120 m). Both the pooled median depth (32 m) and the IQR (11 – 48 m) of immature silky sharks in that study were similar to those found here (median = 27, IQR = 19 – 35 m). The general pattern of moving deeper at night and shallower during the day has been reported for other pelagic fish species that typically remain above the thermocline. These include dorado (Merten *et al.*, 2014) and the oceanic whitetip shark (Howey-Jordan *et al.*, 2013). However, the opposite pattern has been found for bigeye tuna (Holland *et al.*, 1990; Schaefer and Fuller, 2002), swordfish *Xiphias gladius* (Dewar *et al.*, 2011) and pelagic shark species with wider vertical ranges, such as the short fin mako *Isurus oxyrinchus* (Sepulveda *et al.*, 2004), common thresher *Alopias vulpinus* (Cartamil *et al.*, 2011), bigeye thresher *Alopia supercilliosus* (Weng and Block, 2004; Musyl *et al.*, 2011a) and blue shark *Prionace glauca* (Musyl *et al.*, 2011a). This behavioural pattern is believed to reflect the feeding strategy of these species, which involves feeding on meso-pelagic species in the deep scattering layer (DSL) at depth during the day and then tracking the diel migration of the DSL to the surface layers during the night (Holland *et al.*, 1990; Potier *et al.*, 2007a). While the depth range utilised by the silky sharks observed here is greater at night, it is still consistent with the shallow nocturnal depth range of pelagic species known to track the nocturnal migration of the DSL (Josse *et al.*, 1998; Dagorn *et al.*, 2000a; Schaefer and Fuller, 2002). The lack of large day time vertical oscillations generally associated with feeding activity further suggests that FAD-associated silky sharks feed primarily at night. Nonetheless, the results of the feeding study conducted in Chapter 3 revealed that only a small portion (5%) of the diet of FAD associated silky shark consists of mesopelagic prey species. Consequently, nocturnal feeding activity is more likely to reflect an improved efficiency in prey capture, rather than increased access to prey resources. Furthermore, as the majority of the sharks' diet consisted of species that do not associate with drifting objects, the pursuit and capture of these species would likely result in the sharks leaving the immediate vicinity of the FAD.

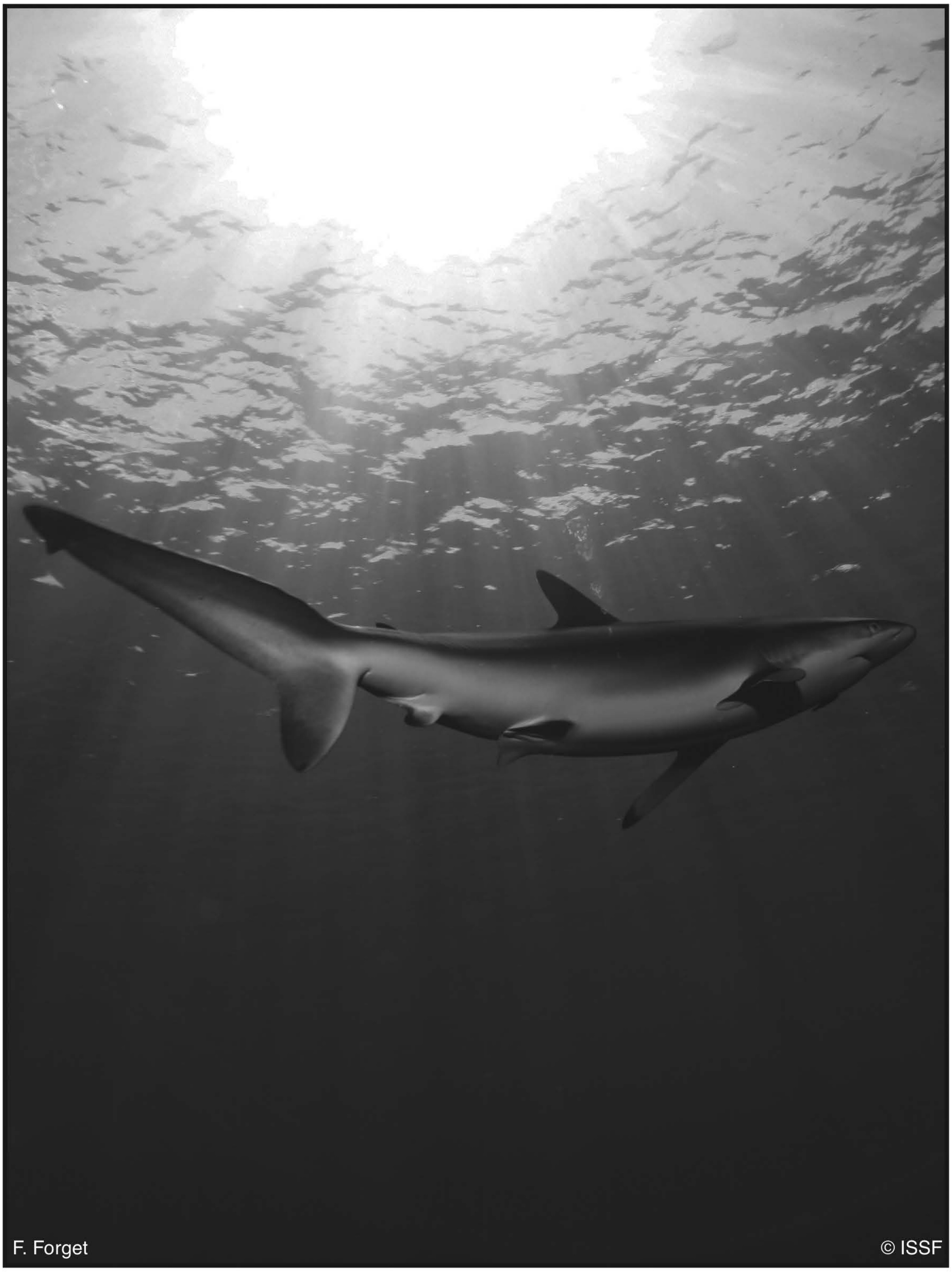
Active tracking

The active tracking experiment described here is the first of its kind on this species in the pelagic environment. While this experiment was initially designed to provide insight into the response of silky sharks to the stress of capture and tagging, it ultimately provided an unprecedented first glance into multiple forms of behavioural information. These included the shark's ability to home towards a FAD, the horizontal and vertical structure of the FAD-associated fish assemblage and how the shark interacted with this community.

The effect of capture and tagging on the tracked individual appeared consistent with other tagged silky sharks as it left the reception range of the receiver shortly after release. Interestingly this individual stayed away from the FAD for a far shorter time than the average obtained from other tagged sharks (slightly more than 2 h as opposed to the average of 24.9 hours). During its excursion away from the FAD the shark showed a clear pattern of remaining down current from the FAD. Furthermore it appeared to make orientated movements towards a school of tuna that was located approximately 1 km down current of the FAD. The position of the tuna school observed here is consistent with similar observations made by Schaefer and Fuller (2005), who found that tagged skipjack and bigeye tunas were consistently located down current of a drifting vessel in the eastern Pacific Ocean. While the reason for this apparent preference to remain down current remains unclear, a plausible hypothesis could be that, with the current flowing from the FAD towards the animals, the cues that they utilise to determine its location are detected most efficiently from this orientation. Alternatively, this behaviour may reflect the fishes' desire to be ahead of the FAD as it moves through the environment, which could enhance prey encounter rates. Both the trajectory of the shark and the reverse path length analysis clearly indicate that the shark was able to detect the position of the FAD from more than 1 km away. While results from a single tracked animal over a short period of time should certainly be considered preliminary, they do provide interesting insight into how the shark might perceive its environment. The lack of detections from other fishes during the shark's return leg to the FAD, followed by abundant detections of other silky sharks, trigger fish and rainbow runner once it arrives, suggest that the close proximity of these species to the FAD may aid the sharks ability to locate it. As such, the biomass of the intranatant and extranatant community as defined by Freon and Dagorn (2000) may play a significant role in detectability of a FAD by silky sharks. The distance reported here is similar to that obtained for dorado by Girard *et al.* (2007) at anchored FADs, but is significantly shorter than distances reported for tuna (7 - 10 km) (Girard *et al.*, 2004; Moreno *et al.*, 2007b). The significant spatial structure of the FAD aggregation is consistent with the definitions of extranatant and circumnatant species described by Freon and Dagorn (2000) and applied by Taquet *et al.* (2007b) to species at FADs in the western Indian Ocean.

Conclusion

The results obtained through this telemetry study suggest that tagging and handling influences the behaviour of silky sharks on a short term. After normal behaviour is resumed and they re-associate with the FAD, they display very regular spatio-temporal behavioural patterns. In general, they remain close to the FAD during the day, and undertake limited vertical movements. As darkness falls they leave the immediate vicinity of the FAD, and start to undertake rapid vertical oscillations, which likely reflect feeding activity. Then after a variable length of time, but still during the hours of darkness, the sharks return to the FAD. By the time the sun has risen they have settled back into a more stable vertical behavioural state. The long residence times observed here suggest that associating with drifting objects is an important behavioural strategy for juvenile silky sharks.


F. Forget

Chapter 5

Large-scale horizontal movement behaviour

5.1 Introduction

The silky shark, *Carcharhinus falciformis*, is important both commercially and as bycatch in fisheries throughout its pantropical distribution (Gilman, 2011). In the Indian Ocean it is captured by a multitude of gears (purse seine, longline and gillnets) (Murua *et al.*, 2013), primarily as a bycatch but in some cases also as a target catch. Owing to it's life history traits of slow growth, late maturation and low fecundity (Bonfil, 2008), when compared to the targeted co-occurring teleost species (principally tunas), silky sharks are vulnerable to over exploitation. Catch trends from other oceans have revealed strong population declines during the past decades (Baum and Myers, 2004; Clarke *et al.*, 2013), however comparable historic catch data are largely lacking in the Indian Ocean. Recent estimates of the total annual silky shark catch in the Indian Ocean suggest that close to 32 000 tons (Murua *et al.*, 2013) are caught each year, of which purse seine vessels reportedly catch approximately 1200 tons (Converted from bycatch to catch ratio in Dagorn *et al.*, 2013). Currently the only management measure in place that is specific to this species in the Indian Ocean applies to European purse seine vessels, which are not permitted to retain silky sharks (or any other shark) onboard. Data collected through onboard observers in the purse seine fishery have revealed that bycatch per unit effort for silky sharks are highest in the area east of Somalia (Amandè *et al.*, 2011). Currently there exists an area closure off Somalia for purse seine vessels during November (IOTC, 2010). However, as the peak in fishing activity in this area occurs between July and October, this measure is believed to be relatively ineffective (Amandè *et al.*, 2011; Kaplan *et al.*, 2014). Nonetheless, for a spatial measure such as this to be effective, information on the movements of both target and bycatch species in relation to the area is essential.

During the past two decades the use of fish aggregating devices (FADs) in tuna purse seine fisheries has increased considerably the world over (Dagorn *et al.*, 2013), with the same trend observed in the Indian Ocean (Dagorn *et al.*, 2013). In 2010 FADs contributed almost 80% of the total purse seine tuna catch in this ocean. As juvenile silky sharks are known to associate with drifting objects (Bonfil, 2008; Anderson and Jauharee, 2009; Filmalter *et al.*, 2011) the increase in fishing effort on floating objects has certainly increased the vulnerability of this species within purse seine fisheries, however, this alteration may have further indirect impacts on the species. In light of the associative behaviour the increased density of floating objects represents a significant human induced change in the habitat of this species (Dagorn *et al.*, 2013). While not asserted directly for silky sharks, several studies have hypothesised that this artificial habitat modification could adversely effect tuna populations through modifications in migratory patterns or retention in biologically inappropriate regions (Marsac *et al.*, 2000; Hallier and Gaertner, 2008). To date, no conclusive evidence has been provided to irrefutably validate these hypotheses and as such, there is an ongoing debate around this issue. Nonetheless, it remains an important consideration for the investigation of horizontal movement patterns of this species. Despite the wide distribution of the silky shark, knowledge on the horizontal movement behaviour of this species remains limited (Bonfil, 2008). This is particularly true in the Indian Ocean where almost nothing is known about it's movement patterns.

Considering the strong associative behaviour of juvenile silky sharks with drifting objects when observed at a fine spatio-temporal scale (Chapter 4), there is a clear need improve our understanding of the effects that FADs have on the behaviour of silky sharks at a larger scale. The increasing use of FADs and the declining trends in silky shark populations around the world suggest that the implementation of effective management measures are paramount for the conservation of this species. The aim of this study was to examine the large-scale horizontal movement behaviour of juvenile silky sharks using archival tagging techniques and to assess whether observed patterns correlated with drift patterns of FADs in the western Indian Ocean.

5.2 Materials and Methods

Tagging

Sharks were either caught during purse seine operations at FADs, or using baited handlines from a small vessel in the immediate vicinity of a FAD. When sharks were captured during purse seining, they were brought onboard and placed on a wet foam mattress while performing the tagging procedure. Similarly when captured from a small vessel they were brought onboard, placed in a padded cradle and a hose pumping clean slat water was places in their mouth to irrigate the gills. Pop-up Satellite Archival Tags (PSATs, model: miniPAT, Wildlife Computers, Redmond, USA) were attached to the sharks by inserting a plastic anchor, to which the tag was tethered, into the dorsal musculature of the shark. Initially a small puncture was made in the sharks skin such that the tag anchor could be inserted with ease. For some sharks, the tags were attached using a threaded nylon rod, which was passed through a hole drilled into the anterior base of the dorsal fin. Stainless sleet nuts and washers were used to secure the looped end of the tag tether to the rod. All tag tethers consisted of multi-strand stainless steel wire coated in heat-shrink plastic. When operating from small vessels, sharks were always double tagged with internal acoustic tags (V13 or V13P, Vemco). As an alternative to PSATs, some sharks caught from small vessels were tagged with internal archival tags (MK9, Wildlife Computers, Redmond, USA). All handline-caught sharks were released at the FAD where they were captured. In contrast, the sharks tagged directly from purse seine vessels were not double tagged and were typically released when the FAD was still attached to the vessel. Hence, the sharks were released after the aggregation was disturbed (i.e. largely non-existent) by the fishing operation and up to half an hour prior to the FAD being released and re-deployed. The entire tagging operation usually lasted approximately 3-5 min.

Tag Data Analysis

Only tags that remained attached to the animal for periods longer than five days were considered for the analysis of horizontal movements. When individuals were known to be associated with a FAD (obtained from the acoustic tag detection history) the GPS location of the FAD was used rather than the geolocation estimate from the PSAT or archival tag. Sharks tagged directly from purse seine vessels were primarily tagged to investigate their post-release survival and consequently short deployment durations were expected. Furthermore, several of the sharks were tagged close to the time of the equinox which produced considerable latitudinal uncertainty from light based geolocation methods as the difference in day length is almost equal at all latitudes (Hill and Braun, 2001). Positional data obtained from tags whose entire deployment spanned the weeks preceding and following the equinox were unusable. Hence only tags deployed outside of the equinox period or those that had significant portions of data after this period, were analysed.

Analytical methods

Geographic positions from PSATs were reconstructed using the archived light level data transmitted from the tags or downloaded from recovered tags. The geolocation (Global Location Sensing, GLS) was performed using the proprietary software from the tag manufacturer (WC-GPE2, Wildlife Computers, Redmond, USA). This software provides raw track information with associated latitudinal and longitudinal error estimates for each location, typically in the order of 10°- 20° latitude and 2°- 4° longitude, respectively. These GLS data and their associated errors were then modelled using the IKNOS-WALK model developed by Tremblay *et al.* (2009) and detailed in Chapter 2. Similarly, individual-specific maximum speeds were utilised as detailed in Chapter 2. Track uncertainty was estimated from the spatial distribution of 50 potential locations calculated at each time step. The time step utilised in this model was 24 hours, such that positions were estimated once a day.

FAD trajectories

Trajectories of drifting FADs were provided by the observer program "Observatoir thonier", obtained through a join project with the French purse seine fleet management association "Orthongel". Positional data were recorded by GPS tracking buoys attached to the FADs and transmitted via satellite. The temporal resolution of data varied between FADs and with time, and ranged from a location every 1 min to every 72 h with a median frequency of 12 hours. When more than one position was provided per day an average location was calculated for that day. As the data had GPS accuracy, errors were less than 100 m and hence assumed to be non-significant. Using a minimum and maximum speed filter of 1.85 (1 nm) and 92.6 km (50 nm), respectively, between subsequent tracking points, all tracks from buoys believed to have washed ashore or been onboard a vessel were removed. Furthermore, only FADs observed for at least six days (the minimum observation time of any shark) were considered.

Comparisons with FAD trajectories

As the inherent uncertainty of the shark locations was far greater than that of the FAD positions, direct comparison of daily shark vectors with those of FADs was impossible. Consequently, comparisons between movement patterns of sharks and FADs were carried out using a spatial retention approach. Using the tagging location of each shark as a reference, trajectories of FADs that drifted within a 185.2 km (100 nm) radius of each tagging location in a period starting seven days before and ending seven days after the tagging date were identified in the database. FAD trajectories were truncated on the last observation day of all sharks tagged in a given year. Using pre-defined zones in the Indian Ocean, the proportion of time that sharks tagged in each zone spent in that zone, as well all other zones, was calculated. Similarly, the proportion of time that FADs were observed in the zone where they were first encountered (i.e. within 100 nm of the tagging location of a shark) and all other zones was calculated. Comparisons were then made between corresponding sharks and FADs. Zones were defined in accordance with the sampling zones identified by European research program "Echantillonnage thonier" (Pianet *et al.*, 2000) and subsequently adopted by the Indian Ocean Tuna Commission (IOTC), Fig. 5.1.

5.3 Results

A total of four archival tags and 45 PSATs were deployed on silky sharks caught at FADs (Table 5.1). Twenty-five sharks were tagged in the northern Mozambique Channel, while 24 were tagged in the Seychelles area. The sex ratio of the tagged sample was nearly equal with 24 females and 22 males. Sex was not determined for three individuals. Of the 49 tags deployed, 41 PSATs reported data and one internal archival tag was recovered. Thirty-four of the PSATs remained attached to the shark for more than five days while 21 had usable light data outside of the equinox periods (Table 5.2). The deployment and pop-up/recapture locations of all 35 tags are displayed in Fig. 5.1. From these locations it is apparent that some sharks remained close to the area where they were tagged, while others undertook significant movements. Considering the EU sampling zones, 23% of the tags had pop-up/recovery locations in a zone other than that in which they were deployed, while 77% had deployment and pop-up locations in the same zone.

The majority of the individuals tagged in this study were juveniles. Only two sharks were of a size that would suggest they were sexually mature (Fig. 5.2)(Bonfil, 2008). The median total length of the tagged sharks was 114.9 cm (range: 91 - 235 cm).

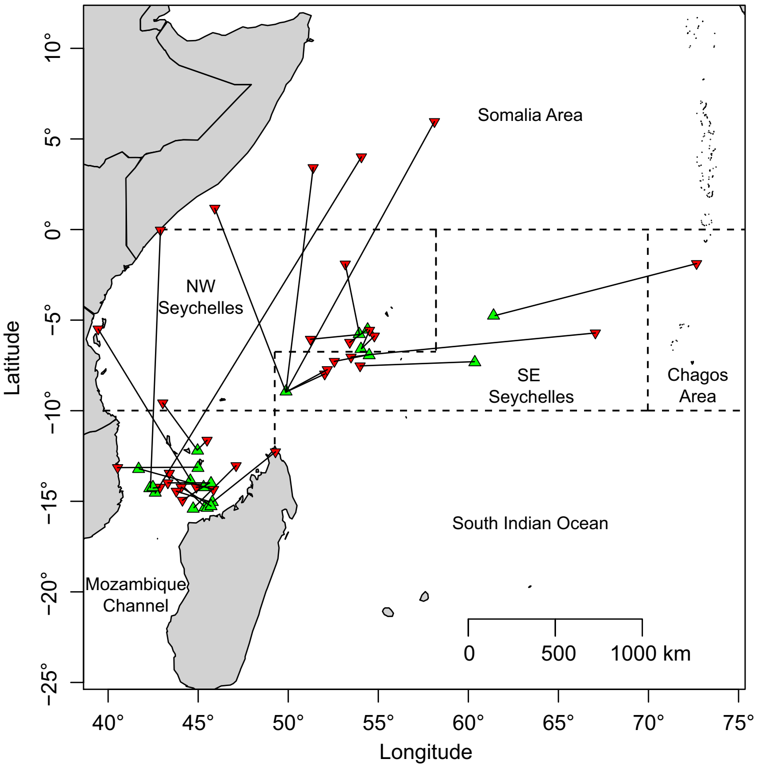


Figure 5.1 Deployment and pop-up/recapture locations of PSATs and internal archival tags attached to silky sharks caught at drifting FADs in the western Indian Ocean. Green triangles indicate tagging locations, red triangles indicate pop-up locations. Dashed lines denote the commonly utilised sampling zones for the EU fleet.

Only two of the 21 analysed PSATs remained deployed on the sharks for the entire programmed duration (Table 5.2) while the recovered internal archival tag was deployed for 141 d. The mean deployment duration of all tags was 53.4 (± 35.7) d. The median latitudinal and longitudinal uncertainty across all individuals was 1.2° and 1.3°, respectively. Consequently, the overall positional accuracy was approximately 130 km. Track lengths varied widely between individuals (range = 112 - 11023 km), with a mean track length of 4306 (±

Table 5.1 Summary information of all PSAT and archival tag (*) deployments on silky sharks caught at FADs in the western Indian Ocean.

Tag ID	TL (cm)	Sex	Area	Deployment Date	Pop-up Date	Release Date	Duration (d)
34419	88	F	Moz	13/03/2010	04/04/2010	01/04/2010	19
34420	109	M	Moz	15/03/2010	23/06/2010	23/06/2010	100
94249	86	F	Moz	24/03/2011	01/04/2011	29/03/2011	5
94248	140	M	Moz	24/03/2011	24/03/2011	24/03/2011	0
94246	112	M	Moz	26/03/2011	29/03/2011	26/03/2011	0
94244	127	F	Moz	26/03/2011	29/03/2011	26/03/2011	0
94247	132	M	Moz	27/03/2011	05/04/2011	02/04/2011	6
94255	137	F	Moz	28/03/2011	14/05/2011	11/05/2011	44
94245	137	F	Moz	28/03/2011	27/04/2011	24/04/2011	27
104660	100	F	Moz	29/03/2011	-	-	-
94256	138	F	Moz	29/03/2011	01/04/2011	29/03/2011	0
94257	87	F	Moz	31/03/2011	24/04/2011	15/04/2011	15
104661	138	M	Moz	01/04/2011	-	-	-
104659	116	F	Moz	01/04/2011	10/05/2011	07/05/2011	36
104658	87	M	Moz	01/04/2011	27/04/2011	22/04/2011	21
94259	90	M	Moz	01/04/2011	24/04/2011	18/04/2011	17
94258	98	F	Moz	01/04/2011	-	-	-
94254	155	M	Moz	02/04/2011	24/04/2011	15/04/2011	13
34206	91	M	Moz	15/04/2011	20/05/2011	12/05/2011	27
98719	103	F	Moz	20/04/2011	03/05/2011	02/05/2011	12
34366	99	M	Moz	20/04/2011	27/07/2011	27/07/2011	98
104663	119	F	Moz	25/05/2011	09/07/2011	05/07/2011	41
104662	122	F	Moz	25/05/2011	27/07/2011	17/07/2011	53
104655	150	M	Moz	25/05/2011	28/05/2011	25/05/2011	0
98717	235	M	Moz	27/05/2011	14/07/2011	11/07/2011	45
94261	98	F	Sey	18/06/2011	28/06/2011	24/06/2011	6
94251	102	M	Sey	20/06/2011	09/09/2011	03/09/2011	75
34415	93	M	Sey	20/06/2011	23/07/2011	23/07/2011	33
104665	104	M	Sey	02/04/2012	07/05/2012	01/05/2012	29
104664	114	F	Sey	02/04/2012	13/05/2012	13/05/2012	41
104667	132	M	Sey	03/04/2012	26/06/2012	20/06/2012	78
98724	155	M	Sey	03/04/2012	12/07/2012	12/07/2012	100
98723	130	F	Sey	03/04/2012	24/05/2012	16/05/2012	43
98719b	135	M	Sey	03/04/2012	17/04/2012	06/04/2012	3
990026*	99	F	Sey	13/04/2012	17/07/2012	01/09/2012	141
990030*	109	F	Sey	13/04/2012	-	-	-
990036*	103	F	Sey	13/04/2012	-	-	-
990028*	112	F	Sey	13/04/2012	-	-	-
104678	112	F	Sey	13/04/2012	15/05/2012	14/05/2012	31
94260	109	F	Sey	13/04/2012	12/08/2012	10/08/2012	119
104674	111	-	Sey	14/04/2012	14/05/2012	14/05/2012	30
94255	116	M	Sey	14/04/2012	19/04/2012	18/04/2012	4
94253	116	-	Sey	14/04/2012	15/06/2012	12/06/2012	59
98720	147	M	Sey	28/04/2012	-	-	-
98728	136	F	Sey	30/04/2012	01/05/2012	30/04/2012	0
98727	117	M	Sey	30/04/2012	01/05/2012	30/04/2012	0
104666	114	F	Sey	02/05/2012	02/05/2012	03/05/2012	1
98721	225	M	Sey	03/05/2012	18/06/2012	17/06/2012	45
104656	104	-	Sey	06/05/2012	24/07/2012	23/07/2012	78

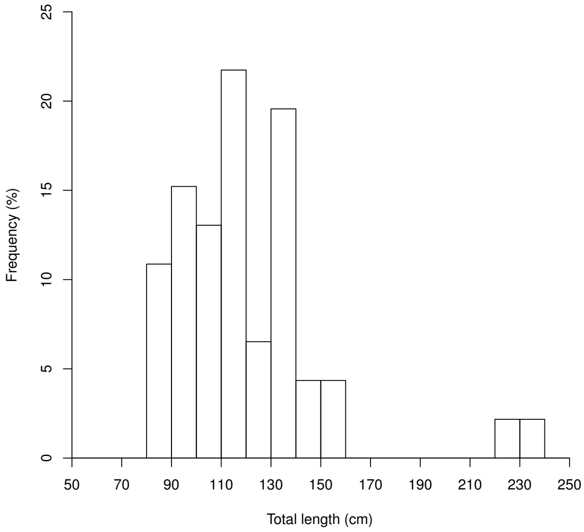
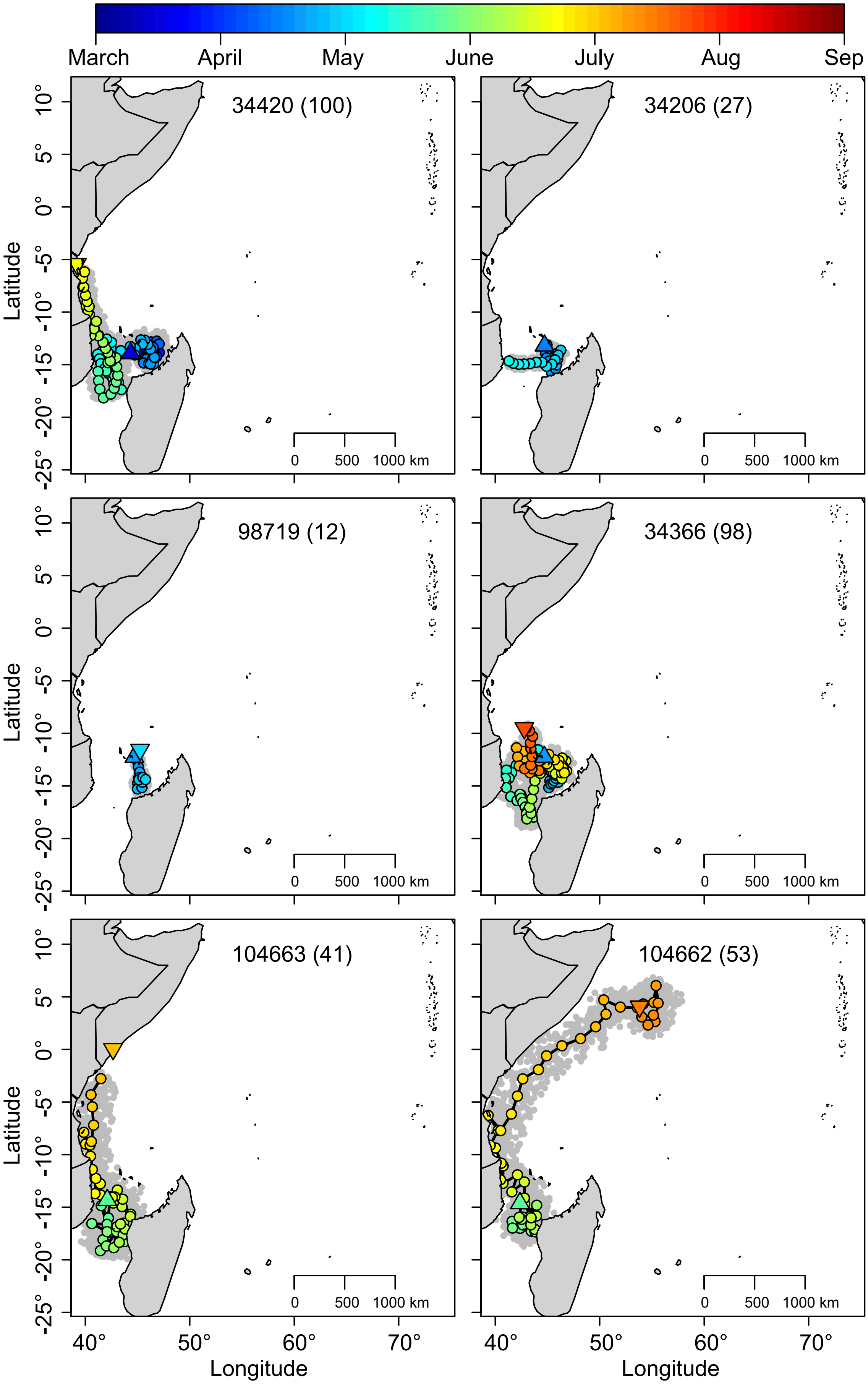


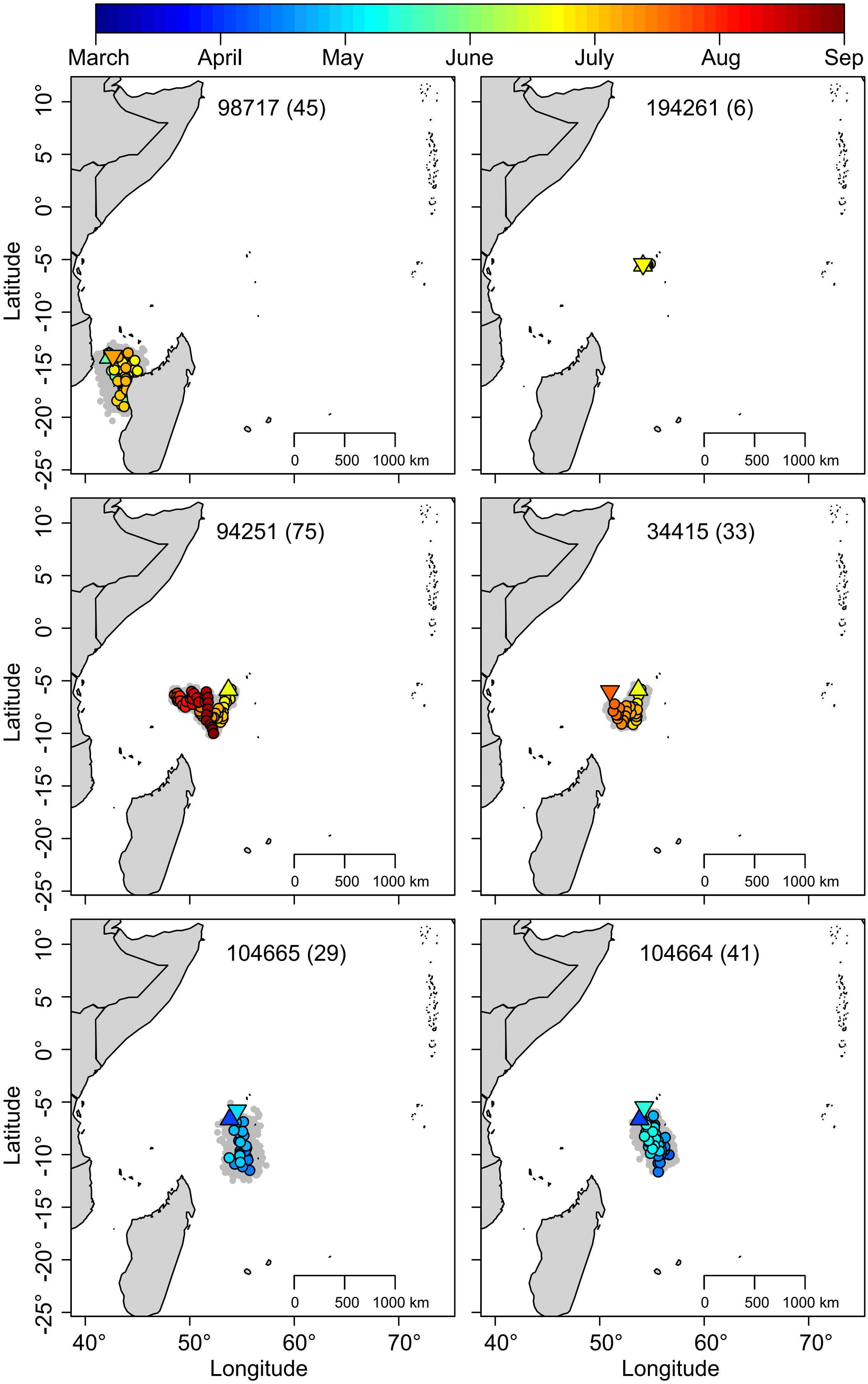
Figure 5.2 Length frequency distribution of silky sharks captured at FADs and equipped with PSATs and internal archival tags in the western Indian Ocean.

Table 5.2 Summary information of analysed PSAT and internal archival tags (*) deployed on silky sharks caught at FADs in the western Indian Ocean. SOG refers to speed over ground.

Tag ID	Duration (d)	Linear displacement (km)	Track length (km)	Speed Limit selected (km.h^{-1})	Average SOG (km.h^{-1})
34420	100	994	6735	5	2.81
34206	27	428	1395	3	2.23
98719	12	262	585	3	2.22
34366	98	367	7170	5	3.08
104663	41	1280	5714	11	5.81
104662	53	2453	8849	11	6.96
98717	45	70	5335	8	5.05
94261	6	11	112	3	0.78
94251	75	505	3447	3	1.94
34415	33	320	1792	4	2.33
104665	29	416	3255	8	4.84
104664	41	76	3707	6	3.77
104667	78	106	3839	4	2.25
98724	100	1393	4330	5	1.82
98723	43	408	2510	4	2.55
990026*	141	1384	4408	3	1.31
104678	31	292	1676	7	2.33
94260	119	1643	11023	7	3.86
104674	30	292	1676	7	2.33
94253	59	1137	8925	11	6.30
98721	45	1246	4474	7	4.24
104656	78	699	3789	3	2.02

2847 SD) km (Fig. 5.3). Three of the seven sharks tagged in the Mozambique Channel moved toward the Somalia area. One tag (ID 34420) released close to Zanzibar Island off northern Tanzania, while the shark with tag ID 104663 was apparently captured by local fishers in southern Somalia. This was evidenced by the direct trajectory and speed of the track after the tag began to transmit. Furthermore, the final ARGOS locations indicated that the tag was stationary in a small coastal village in southern Somalia. The remaining four individuals stayed within the Mozambique Channel throughout their observation periods. A second individual (Tag ID 34206) appeared to have been recaptured by local fishers, this time in northern Mozambique. Owing to the large uncertainty around the location estimates, the sharks' exact movements are unknown, but data from five of the seven sharks suggests that they undertook complex non-linear movements when in the northern portion of the Mozambique Channel. Sharks tagged in the Seychelles area showed more varied dispersal patterns. Three sharks (Tag IDs 990026, 94260 and 94253) moved to the Somalia area while nine remained within the Seychelles area throughout their observation periods. Only two sharks (Tag IDs 98724 and 98721) moved in an easterly direction. For both these individuals their movements were centred around the 5°S latitude. The track of one of these sharks (Tag ID 98721) ended close to the south of the Maldives while the other (Tag ID 98724) moved towards the Chagos archipelago before turning back east.


March
April
May
June
July
Aug
Sep
34420 (100)
34206 (27)
98719 (12)
34366 (98)
104663 (41)
104662 (53)
Latitude
Longitude
10°
5°
0°
-5°
-10°
-15°
-20°
-25°
40°
50°
60°
70°
0
500
1000 km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194261 (6)
94251 (75)
34415 (33)
104665 (29)
104664 (41)
Latitude
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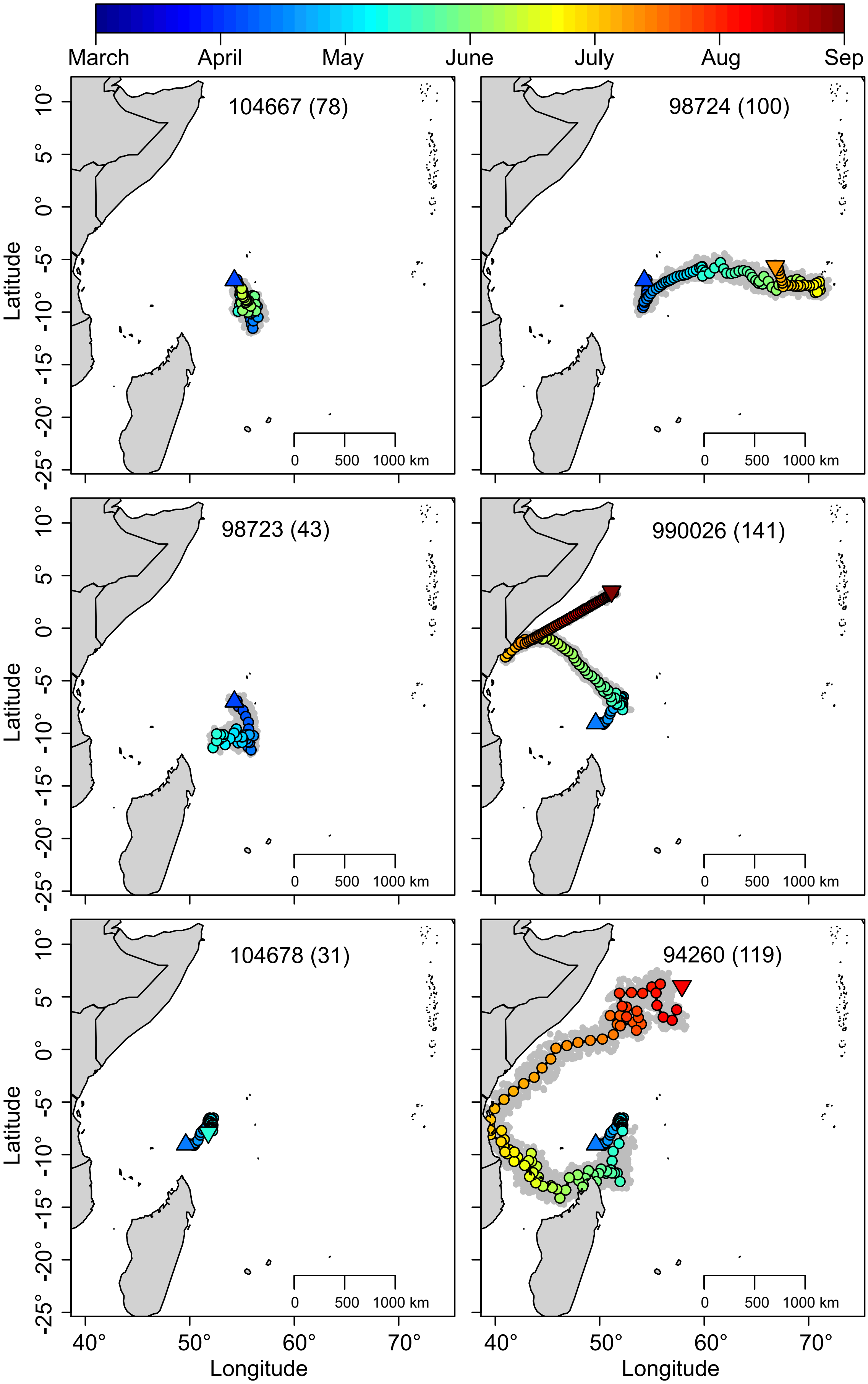
Longitude


March
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104667 (78)
98724 (100)
98723 (43)
990026 (141)
104678 (31)
94260 (119)
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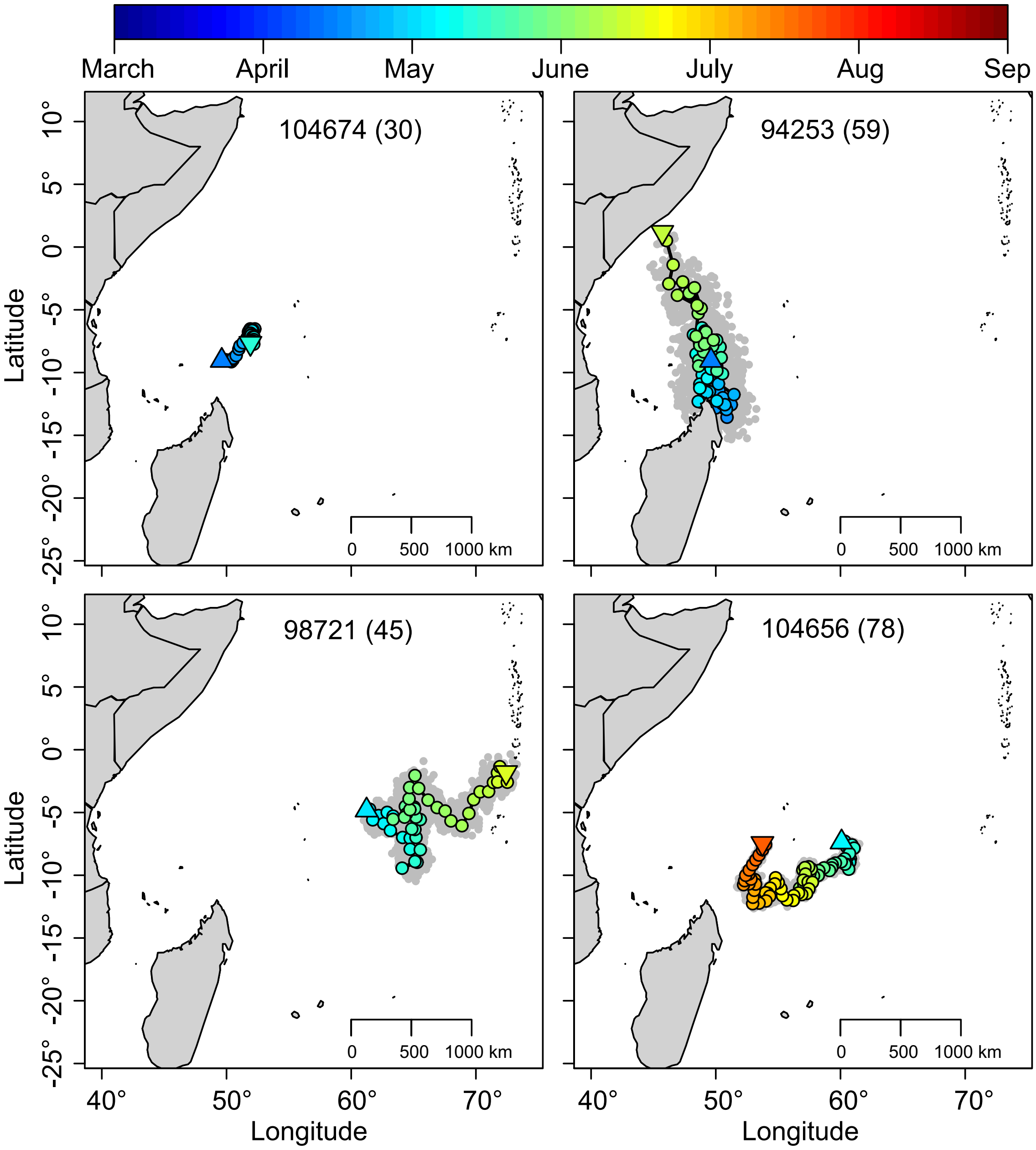


Figure 5.3 Horizontal trajectories of silky sharks equipped with PSAT and internal archival tags in the Indian Ocean. Upward pointing triangles indicate tagging locations, downward pointing triangles indicate locations where tags popped up or sharks were recaptured. Coloured circles indicate mean daily position and colours correspond to time as indicated by the colour bars. Grey clouds indicate model error. Labels indicate tag ID codes and deployment durations (in days) are given in brackets.

The median horizontal speed observed across all trajectories was 2.57 km.h^{-1} and ranged between 0.28 - 9.91 km.h^{-1}(Fig. 5.4A). The distribution of daily speeds varied greatly both within and between individuals (Fig. 5.4B), with the latter resulting from the differing maximum speeds limits input into the IKNOS-WALK model. Nonetheless, no individuals travelled at the maximum

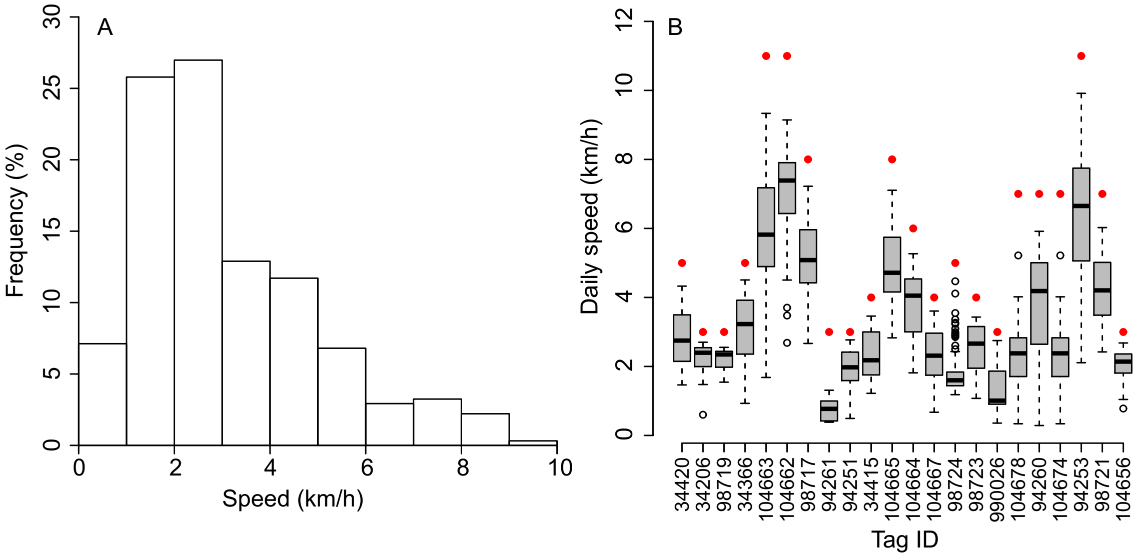


Figure 5.4 (A) Distribution of observed speeds of 22 silky sharks tagged with PSAT and archival tags. (B) Distributions of daily speeds of each tagged silky shark. Red dots indicate individual maximum speed limit criteria applied in the IKNOS-WALK model.

speed limit of the model and speeds were not constant throughout the tracks. This was particularly apparent for certain individuals, where portions of their track are very jagged, while other sections are smooth (e.g. Tag ID 104662). This jaggedness is a result of the model allowing the shark to move greater distances than it probably did, while the smoother portions are likely closer to the true speed at which the animal moved during that time. As a single speed is applied to the entire track, such artefacts are unavoidable.

Five silky sharks were tagged at the same FAD in the SW of the Seychelles between 13-14 April 2012 allowing for detailed comparative examination of individual movement behaviour as the observation of all five sharks started at the same point and all experienced the same environmental conditions. All five were double tagged with acoustic tags, and the FAD was equipped with a VR4-GLOBAL acoustic receiver. One shark (Tag ID 94253) immediately left the FAD after tagging. This individual appeared to initially move southwards towards Madagascar, before returning to the area where it was tagged and then continuing on towards the Somalia area in northwesterly direction, where it's tag released, two months after deployment (Fig. 5.5A). The four other individuals remained associated with the FAD for one month prior to being visited (and fished on) by a purse seine vessel. One tagged shark was recaptured during the set, while the PSAT of another released at the same time. The two remaining sharks avoided capture. Following the day of the set both these individuals

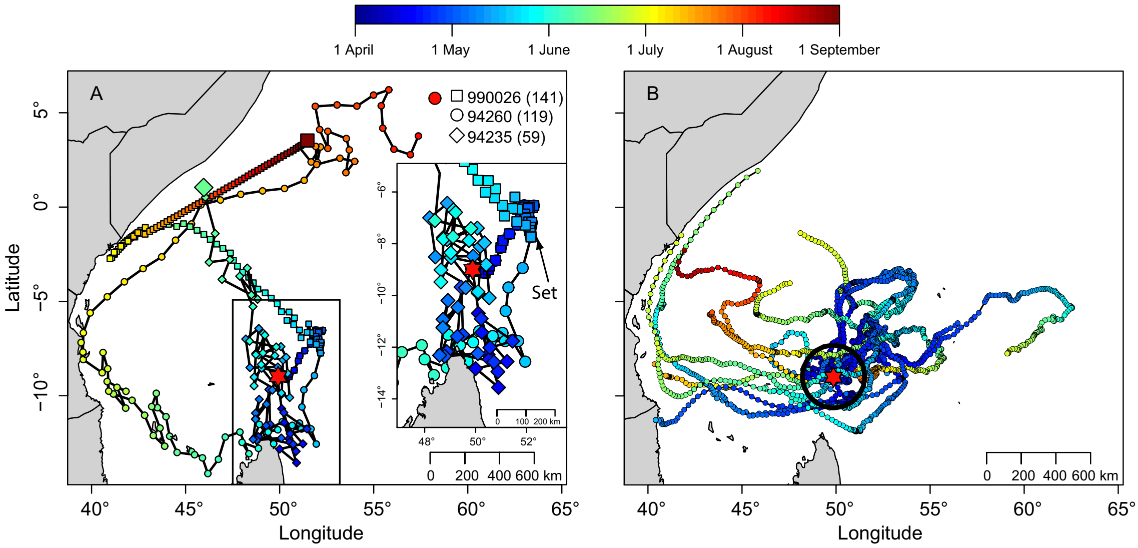


Figure 5.5 Comparison between (A) trajectories of three silky sharks tagged at the same FAD in two consecutive days, where red stars indicates release site and larger symbols indicate pop-up or recapture locations and (B) drifts of FADs within a 100 nm radius (black circle) of the tagging location (red star) for the period one week before to one week after the tagging date. Colours correspond to time (days), as indicated on the colour-bar.

(Tag IDs 990026 and 94260) left the area. One shark (Tag ID 94260) moved southwards, towards Madagascar, then crossed the north of the Mozambique Channel and moved up the African east coast, reaching the Somalia area by mid July. It remained in this area, moving northwards and then meandering between the equator and 5ºN until its tag released in mid-August. The second shark (Tag ID 990026) tagged with an internal archival tag, moved in a north westerly direction towards Somalia following a similar path to the individual that left the FAD immediately after tagging. This shark was recaptured at a FAD by a purse seine vessel off Somalia at the start of September. When the tag was recovered and the data downloaded it was clear the external stalk carrying the light sensor had been damaged 1.5 months prior to the end of the deployment. As such no light data were available for the last 1.5 months, resulting in this portion of the track being interpolated and thus appearing as a straight line.

Examination of the drifts of FADs (within 100 nm of the tagging location) over the same period when the sharks were at liberty, revealed that many of these FADs remained in the same general area (Fig. 5.5B). As the FADs are often visited or fished on, their trajectories are generally truncated when the tracking buoy was replaced or the FAD sinks. As such, few FADs were monitored for the entire duration of the shark monitoring period (April - September). Nonetheless, during this period the FADs appeared to turn in the Seychelles area before drifting towards the African coast. Some FADs drifted south and then crossed the top of the Mozambique Channel before heading north up the east African coast. Examination of the drift speed of individual FADs as they moved past Kenya, Tanzania and Somalia showed that in this area drift speed of up to 7.9 km.h^{-1}could be attained. FADs that did not travel south drifted around in the Seychelles area following no distinct path before moving west and northwest towards Kenya, Tanzania and Somalia. Overall the drift speed of the FADs ranged between (1.9 and 7.9 km.h^{-1}).

Examination of the drift trajectories of all FADs around each tagging location (Fig. 5.6) revealed several distinct patterns. The majority of FADs in the Mozambique Channel remained in this area throughout the period of observation, while a few drifted north along the African east coast. FADs were observed to follow spiralling trajectories and turn in a larger anti-clockwise rotation in the northern portion of the Channel. FADs in the Seychelles showed highly variable drift patterns. Some FADs appeared to be restricted between latitudes of 5°S and 10°S and longitudes of 50°E and 60°E. Alternatively, FADs close to the 5°S latitude in the SE Seychelles moved in an eastward direction before retroflecting between longitudes of 65°E and 75°E. Alternatively, FADs located at the SW border of the SE and NW Seychelles zones appeared to drift in a westerly or northwesterly direction towards the African continent and Somalia Area.

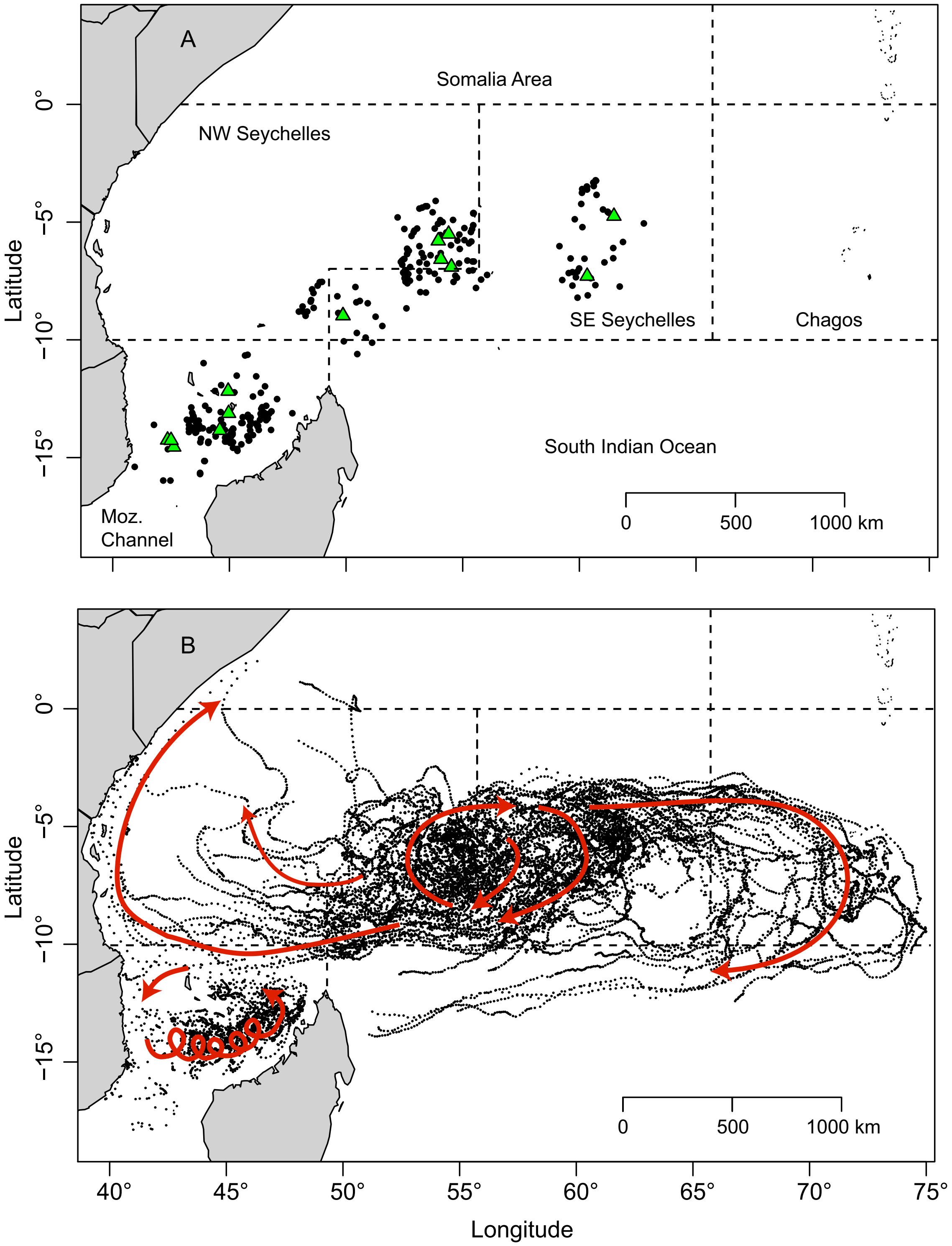


Figure 5.6 (A) Comparison between silky shark tagging locations (green triangles) and starting locations of FADs within 192.6 km (100 nm) of the tagging location over a period spanning seven days before and after the tagging date. (B) Drift trajectories of selected FADs between the time of tagging of sharks and the last observation of a tagged shark during the same year. Red arrows reflect schematic generalisations of drift patterns.

Comparison of the linear distances between the sharks' tagging locations and their daily locations throughout their observation periods provided information on their dispersal patterns (Fig. 5.7A). All sharks appeared to remain close to their tagging location initially (25 d), with most remaining within approximately 250 km. After which, there was no apparent relationship between time at liberty and distance from the tagging location, suggesting that tagging location had little effect on observed movement patterns. From this analysis it was clear that certain individuals, even when observed for extended periods, did not move far from the area where they were tagged, while others dispersed widely, with one individual (Tag ID 104652) moving approximately 2000 km away in 45 d.

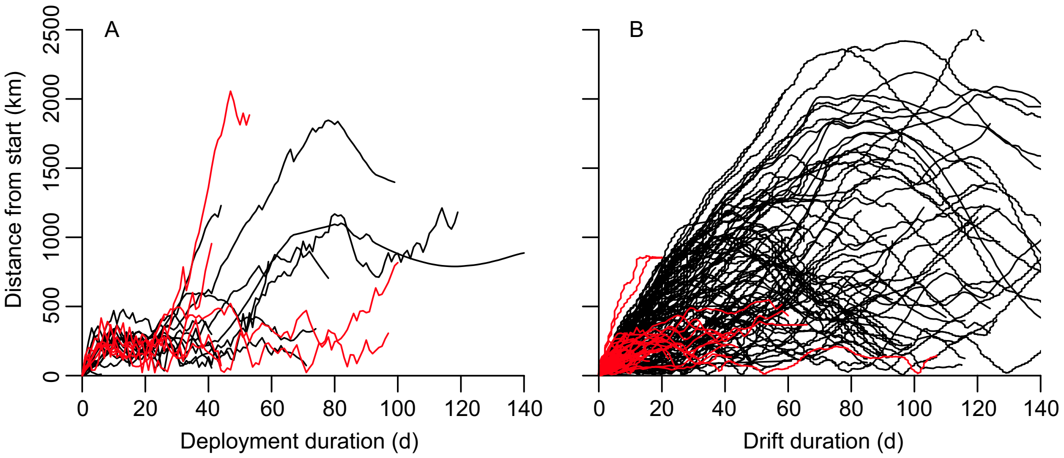


Figure 5.7 Dispersal of (A) silky sharks and (B) FADs over the observation period. Red lines indicate sharks or FADs from the Mozambique Channel and black lines indicate sharks or FADs from the Seychelles area.

The majority of tagged sharks in both areas showed little latitudinal dispersal, with most movements restricted to 10 degrees of latitude. However, some individuals from each area did undertake large latitudinal movements, generally in a northerly direction. The three individuals that headed north from the Mozambique Channel all did so June (Fig. 5.8A) while the two FADs that showed a similar dispersal pattern did so towards the end of April (Fig. 5.8B). Only one shark from the Mozambique Channel showed a significant longitudinal displacement, moving east towards the end of its track (Fig. 5.8A). No similar movements were observed from FADs originating from this area (Fig. 5.8B). Sharks tagged in the Seychelles area generally showed a similar pattern where some remained at the same latitude while others undertook significant latitudinal movements during their respective monitoring periods. Four of the 15 individuals monitored in this area made northward movements

Table 5.3 Dispersal of silky sharks and FADs from the Mozambique Channel and the Seychelles area in the western Indian Ocean.

Type	Start zone	Days observed	% Time (d)					
			Moz.	NW Sey.	Somalia	SE Sey.	Chagos	South I.O.
Sharks	Moz.	379	88.9	7.1	4.0	0	0	0
FADs	Moz.	1041	97.5	2.5	0	0	0	0
Sharks	NW Sey.	400	0	14	0	82.8	3.3	0
FADs	NW Sey.	3060	0.4	45.7	0.7	41.9	8.9	2.6
Sharks	SE Sey.	507	5.9	32.4	13.0	44.6	1.4	2.8
FADs	SE Sey.	6134	1.0	15.7	0.1	73.4	9.3	0.5

(Fig. 5.8C), with no apparent seasonal pattern. FADs from the same area generally remained within similar latitudes, however some moved in both northerly and southerly directions and again showed no clear seasonality (Fig. 5.8D). Great variability in longitudinal movements were apparent for sharks in the Seychelles (Fig. 5.8C). Some individuals moved east, some remained at their tagging longitude and still others moved west. A similar dispersion pattern was apparent in the longitudinal drifts of FADs (Fig. 5.8D) Soon after monitoring was initiated, FADs could be observed drifting east and west or alternatively remaining at a similar longitude.

The proportion of time that silky sharks occupied the various EU sampling zones was remarkably similar to drifting FADs in the area surrounding their tagging location (Table 5.3). Sharks tagged in the Mozambique Channel showed nearly 89% retention in this area, while the surrounding FADs were observed in the area for 97.5% of their time. During the remainder of the observation period, sharks from the Mozambique Channel were observed in both the NW Seychelles area and the Somalia zone. Sharks tagged in the NW Seychelles were located very close to the border of this zone and the SE Seychelles zone. For these sharks the majority of observation days (82.8%) were recorded in the SE Seychelles zone, principally due to the southward extension of most of their trajectories. Interestingly most of their pop-up locations occurred back in the NW Seychelles zone, suggesting that the southerly movements may simply be an artefact of the latitudinal geolocation uncertainty. FADs tracked from the NW Seychelles zone showed a similar proportion of observation days in both their original/tagging zone and the adjacent SE Seychelles zone (45.7% and 41.9% respectively). Some FADs were observed entering the Chagos area, but were recorded there for less than 10% of their observation days. Sharks tagged

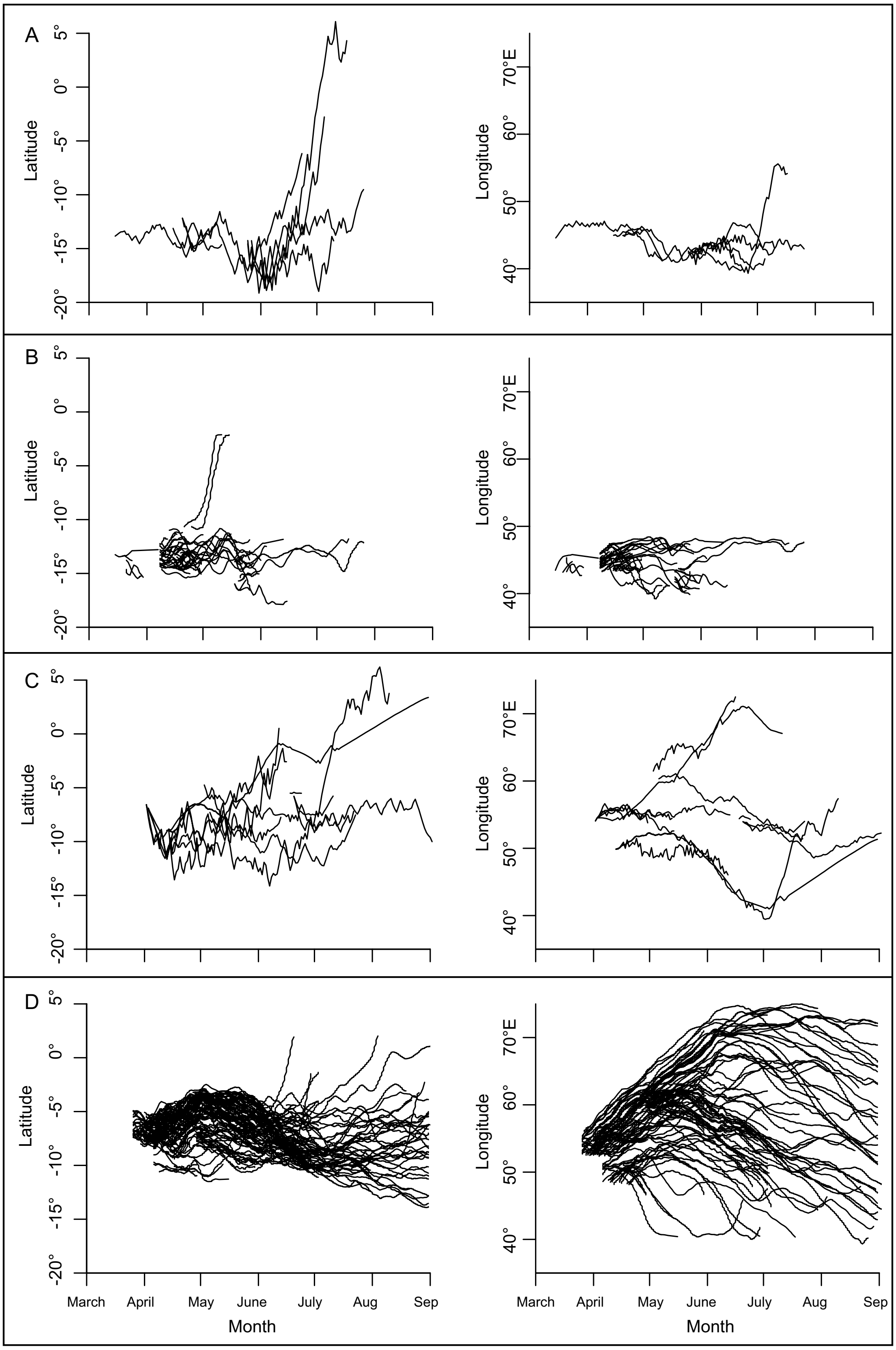


Figure 5.8 Monthly trends in latitudinal and longitudinal movements of (A) silky sharks tagged in northern Mozambique Channel, (B) FADs in the northern Mozambique Channel, (C) silky sharks tagged in the Seychelles area and (D) FADs in the Seychelles area. All FADs were within 192.6 km (100 nm) of the tagging location of a shark within seven days prior to and seven days after the tagging event.

in the SE Seychelles zone showed the greatest dispersal with some track days recorded in every zone. The highest proportion of observation days (44.6%) was still recorded in their original zone however records from the NW Seychelles were only marginally lower (32.4%). For these sharks some movements were observed in the Mozambique Channel area, as well as in the Somalia area. A similar pattern was observed for FADs in the SE Seychelles, where the majority of observations were made in the original zone and a smaller proportions observed in every other zone.

5.4 Discussion

Globally, the horizontal movements of silky sharks have received limited research attention. In the Pacific Ocean Kato and Carvallo (1967) tagged four silky sharks with conventional dart tags at the Revillagigedo Islands off the Mexican coast, of which one was recaptured very close (10-16 km) to where it was tagged. These authors conventionally tagged a further 119 silky sharks between southern California and Peru, of which four were recaptured. Three sharks travelled a minimum distance of between 104 and 152 km in four to five months while the fourth moved approximately 80 km in 3-4 d. Kohin *et al.* (2006) tagged six silky sharks with PSATs and three with SPOT tags off the coast of Costa Rica and reported preliminary results showing that one individual moved more than 2500 km during 10 months. More recently, Musyl *et al.* (2011a) reported linear displacements of 10 silky sharks (116 - 200 cm TL), tagged with PSATs in the central Pacific Ocean, ranging between 138.3 and 1272.6 km during deployments lasting 12 to 194 d. In the Atlantic Ocean Kohler *et al.* (1998) reported on the US National Marine Fisheries Service cooperative shark tagging program in which 819 silky sharks were tagged with dart tags between 1962 and 1993. A total of 54 silky sharks were recaptured with the maximum dispersal distance reported at 1339 km and a maximum travelling speed of 2.48 km.h^{-1}. While some of these tagging statistics suggest significant research effort, low recapture rates and a limited use of satellite tag technology have resulted in very little information on the spatio-temporal distribution or area use patterns of this species in either of these oceans. In the Indian Ocean, Stevens (1984b) tagged two large ($>$ 2 m) silky sharks adjacent to the Aldabra Atoll, and one was recaptured 11 km away after being at liberty for 140 d. In the current study 45 PSATs and 4 archival tags were deployed on silky sharks, with 22 tags providing useful horizontal movement data. Consequently, the results represent a significant advancement in the knowledge of the movement patterns of this species, both within this region and at a global scale. While the associative behaviour of silky sharks with drifting objects has been reported from all oceans (Bane, 1966; Yoshimura and Kawasaki, 1985; Dagorn *et al.*, 2007b; Watson *et al.*, 2009; Amandè *et al.*, 2010; Filmalter *et al.*, 2011), with exception of the current study, no work has been conducted to assess how this behaviour could affect horizontal movements in any other region.

The median total length of sharks tagged in this study (114.9 cm) was slightly larger than the mode reported from onboard observer data (100 cm) from purse seine vessels in the Indian Ocean (Amandè *et al.*, 2008b). This difference was due to the active selection of larger sharks that could carry the external PSATs. Of the 22 tags analysed here, only two remained attached to the shark for their programmed duration. This high shedding rate illustrates the difficulties of monitoring small sharks with PSATs however, premature tag shedding is common in most studies using PSATs (Musyl *et al.*, 2011b). There are several situations that could lead to tags becoming detached from a shark including mechanical failure in the corrosive pin or tether system, biofouling, tissue rejection of the anchor or predation of the tag by other organisms in the shark's environment (Musyl *et al.*, 2011b). On at least two occasions the tags in this study were believed to have been ingested by predators, witnessed through the temporary loss of light data and reduced changes in temperature despite continuing changes in depth, while the tag was in the stomach of the predator. Similar results have been observed for PSATs deployed on albacore tuna, *T. alalunga,* tagged in the north east Atlantic Ocean (Cosgrove *et al.*, 2015). Additionally, two tags that were physically recovered when sharks were recaptured, were found to have numerous bite marks on them suggesting that predatory attacks may be a common occurrence. Despite these restricted deployment durations, a total of 1284 d of movement data were collected during the study, providing a statistically robust sample to infer horizontal movement patterns.

Shark movement patterns

The dispersal patterns of tagged sharks during their respective monitoring periods were very similar to the observed drift patterns of FADs in the same vicinity. While no single relationship was evident for either, a broad range of trajectories were common to both data sets, suggesting that the movements of both are influenced by prevailing currents and drift patterns. Slight differences were evident when assessed on a regional basis, with both FADs and sharks generally remaining closer to their start location in the Mozambique Channel than in the Seychelles. This result most likely reflect the restrictive nature imposed by the land masses on either side of the Mozambique Channel, while the truly oceanic environment of the Seychelles region allowed for unrestricted drift patterns.

Movements in the Mozambique Channel

Most silky sharks tagged in the north of the Mozambique Channel displayed a circular movement in an anti-clockwise direction, which correlated well with the observed FAD drift patterns and general current patterns (see Fig. 2.2 in Chapter 2). The complex nature of the current patterns in this area is well documented (Schouten *et al.*, 2003) and characterised by anticyclonic eddies which meander southwards at a speed of approximately 6 km.d^{-1}. The lack of a similar southward movement by tagged sharks while they were within this area is possibly due to the limited time that they were observed there. Four sharks remained in this area for their entire observation periods, but three of them were only observed for 12-45 d. The fourth individual remained entirely in the northern region of the Channel before moving out of this area towards the very end of its 98 d track.

According to Kaplan *et al.* (2014) the purse seine fishing season for tunas in the Mozambique Channel typically spans from March to June. After this period catches rates generally decline and vessels tend to move out of the area. Kaplan *et al.* (2014) suggested that the movement of fishing fleets may reflect the movements of tunas, however they cautioned that this could also reflect spatio-temporal patterns in the availability of tunas to capture (i.e. close to the surface for purse seining). Indicative of a similar trend, three tagged silky sharks left the Mozambique Channel in June during two consecutive years. All three individuals followed similar trajectories after leaving the Channel, suggesting that they were moving with the East African Coastal Current (EACC). Both FADs that originated from the northern region of the Channel, and those that drifted into this area from the Seychelles zones, displayed similar drift patterns; turning north and following the flow of the

EACC past the Kenyan and Tanzanian coasts and into the Somalia Area. It is noteworthy that the highest recorded speed by sharks (9.9 km.h^{-1}) and FADs (7.9 km.h^{-1}) recorded during this study were both observed in this area, specifically as they approached the northerly flowing Somali Current.

Movements in the Seychelles Area

Sharks tagged in the Seychelles area displayed variable movement patterns. The general lack of coherence in both latitudinal and longitudinal movements of tagged sharks was mirrored by the multi-directional dispersion of FADs in this area. Interestingly, in the only other study to deploy satellite tags on marine fishes in the area to date, Rowat and Gore (2007) reported that three whale sharks tagged close to Mahe Island in the Seychelles also all moved out of the area in different directions. The retention analysis showed that the majority of sharks tagged in either of the Seychelles zones typically remained in these areas throughout their respective monitoring periods. While movements between the SE and the NW Seychelles zones were observed, this was to be expected as most individuals were tagged close to the border of the two zones. The eastward movement of two tagged individuals from the SE Seychelles zone followed the drift of FADs in the northern portion of this zone, around 5° S. Similarly, the reversal in direction of one shark (98724) near the 70^{o} E longitude was also observed in the drift of FADs that reached this area.

The divergent nature of the movement patterns in the SE Seychelles area was highlighted by three sharks tagged at the same FAD. Clear similarities between the sharks' movements and those of the surrounding FADs were observed. Although the routes taken differed between the individuals, they all finally reached the Somalia area. Similarly, FADs in this area followed different routes but ultimately moved towards the Somalia area, especially when they entered the EACC flow. It is also noteworthy that while two of the three sharks highlighted in this example remained associated with the same FAD for the one month during which it was monitored an additional four sharks (two with PSATs and acoustic tags and two with only acoustic tags) were also present at the same FAD for the entire month. This result suggests that the movements of FADs may strongly influence behaviour of juvenile silky sharks.

Influence of FADs on shark movements

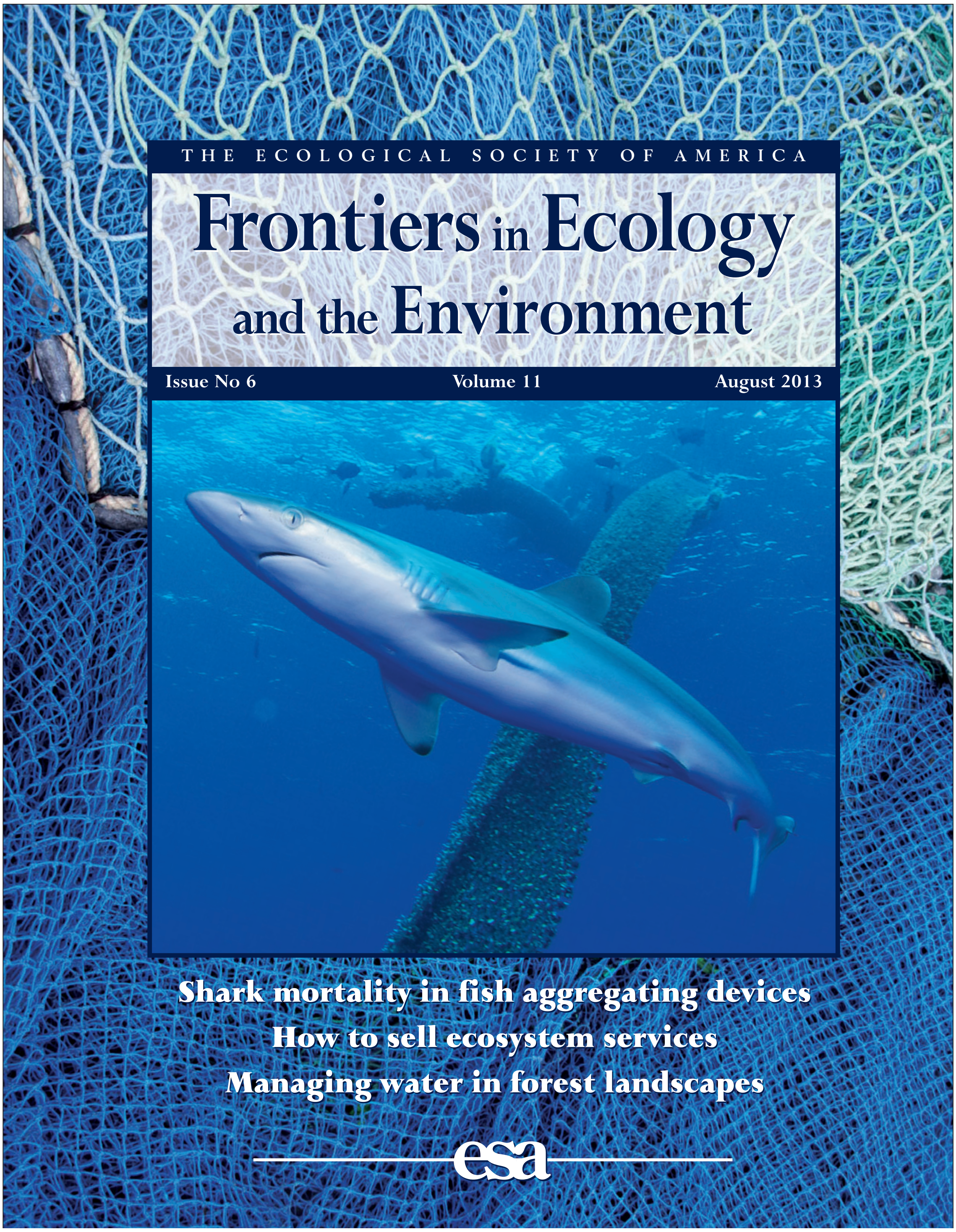
The findings of this study suggest that the large-scale movements of silky sharks in the western Indian Ocean mirrored those of drifting FADs. Unpublished analyses of FAD trajectories has revealed a strong correlation with ocean current patterns (L. Pascuali pers. comm.). Consequently, determining a cause and effect relationship between shark movements and FAD movements is impossible due to their confounding correlation with current patterns. To definitively demonstrate whether or not silky shark follow FADs around the ocean would require much finer resolution movement data as is typically provided through acoustic telemetry methods. However, owing to the limitations surrounding this method, including high costs and the need for the exhaustive deployment of acoustic receivers on FADs, this is currently not a viable option. As such, scaling up from short-term fine-scale movements collected through acoustic telemetry to broader-scale and longer-term movements from archival tags currently represents the best approach for addressing this question. The movement results obtained here align well with the short term acoustic telemetry results presented in Chapter 4, with the strong associative behaviour reported there appearing to continue at the larger scale. Therefore it is possible that FADs 'carry' silky sharks around the ocean, as hypothesised in Marsac *et al.* (2000) and Hallier and Gaertner (2008) for tunas. However, whether FADs represent an ecological trap for silky sharks, as these studies suggest they may for tunas, remains unclear, as it would depend whether their association negatively effects the fitness of the population. Further tagging effort that covers both monsoon seasons with deployments in other areas, such as the Somalia zone and the Chagos area, would greatly aid in determining the influence of currents and drift patterns at different times of the year. Furthermore, as this study focused on juveniles which are mostly associated with FADs, tagging of adults should also be a priority for the future, specifically to assess movements that could be linked to reproductive behaviour as well as the possible influence of FADs on the movements of larger individuals.

Management Implications

Currently two spatial management measures exist for the western Indian Ocean pelagic environment. Firstly, in 2010 the Chagos Archipelago EEZ was declared a no-take marine protected area (MPA) by the UK government.

This MPA covers an area of 650 000 km^2 and encompasses the entire British Indian Ocean Territory. Secondly, the IOTC implemented an annual one month closure for purse seine fishing, during November, over a large area off the east coast of Somalia (IOTC, 2010). The efficacy of these measures has been challenged by the scientific community in terms of both bycatch reduction and enhancement of tuna stocks (Kaplan *et al.*, 2014). The results of this study highlight the high mobility of silky sharks and thus further challenge the significance of these management measures for this species. Clearly if management measures aimed at protecting the silky shark are to be developed, they will need to focus on the general practice of fishing with FADs, rather than an area based approach. Such measure could include restrictions on the total allowable sets on FADs, the number of FADs deployed per year and the design of FADs.

Overall our understanding of the movements of pelagic fishes in the tropical Indian Ocean is extremely limited. Apart from this study, and that of Rowat and Gore (2007) on whale sharks, virtually no other horizontal movement data from satellite tagged fishes from this area have been published. In contrast, conventional tagging of tunas has been extensive, with over 120 thousand individuals of three species (skipjack, yellowfin and bigeye tunas) tagged with dart tags between 2005 and 2007, under the Regional Tuna Tagging Project (RTTP-IO) (Hallier and Fonteneau, 2014). However, published results yielded limited information on the movement patterns of tunas in the Indian Ocean (Hallier and Gaertner, 2008). While the current study addresses this knowledge gap, further efforts in this area are essential for both improved fisheries management and a better understanding of biological and ecosystem functioning.



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Shark mortality in fish aggregating devices
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Chapter 6

Quantifying unobserved mortality

6.1 Introduction

Human-induced impacts on marine populations are typically thought of in terms of the harvesting of resources, which is generally regarded as the largest direct anthropogenic effect on marine ecosystems. However, other, more complex issues – including global warming (Schmittner, 2005; Cheung *et al.*, 2010), ocean acidification (Caldeira and Wickett, 2003), trophic cascades due to the removal of entire ecosystem tiers (Jackson *et al.*, 2001; Myers *et al.*, 2007), marine pollution (Halpern *et al.*, 2008), and technological shifts in fishing practices – may ultimately have impacts equaling or even surpassing those caused by ongoing harvest-related exploitation; impacts associated with these processes are harder to quantify because they are not easily observable or go unobserved at short timescales. The current methodology used to assess marine population health often excludes such processes and instead relies almost entirely on a single parameter, the amount of biomass extracted, which has been observed and quantified for decades. Although the impacts of these processes are often complex and difficult to measure and remedy, their mitigation in some cases may be relatively simple. Here we quantify and provide solutions for a previously unknown impact of a technological shift in the global tuna purse-seine fishery, representing an extensive new source of mortality for a pelagic shark species already designated as Near Threatened by the International Union for Conservation of Nature (Bonfil *et al.*, 2009). During the past 20 years, the tropical tuna purse-seine fishery, operating throughout oceans worldwide, has changed its typical fishing practice. Traditionally, tuna schools were caught when feeding at the surface or when associated with marine mammals (Scott *et al.*, 2012) or drifting logs (Freon and Dagorn, 2000). More recently, the use of artificial fish aggregating devices (FADs) has become widespread. FADs work by taking advantage of the propensity of tropical tunas to aggregate around floating objects (Parrish and Edelstein-Keshet, 1999). Once deployed a FAD is left to drift freely in the open ocean for several months, with its spatial location monitored remotely via a satellite-tracked buoy (Dagorn *et al.*, 2013). The FADs are then revisited by the fishing vessels and the aggregated tuna and associated bycatch species captured. This fishery enhancement tool now accounts for >40% of all of the world's annual tropical tuna catch (4 million tons; Miyake *et al.* 2010). These FADs usually consist of bamboo poles bound with old netting, which extends to varying depths below the water's surface. The subsurface structure of a FAD is believed to aid in the attraction of small fish, and serves to increase drag, ensuring ocean currents rather than wind drive the direction of its drift. Many fishers consider FADs essential for the formation of tuna aggregations. This netting can entangle marine animals, but because of the difficulty involved in observing such mortality events, they have largely been ignored by marine scientists and resource managers. The popularity of FADs in tuna purse-seine fleets has led to global concerns over the increased capture of undesirable sized tunas and bycatch, which include vulnerable pelagic shark species (Gilman, 2011). The silky shark (*Carcharhinus falciformis*) constitutes up to 90% of the elasmobranch bycatch in this fishery (Gilman, 2011). Localised depletion is a concern in many parts of this shark's circumglobal distribution (Bonfil, 2008; Anderson and Jauharee, 2009; Bonfil *et al.*, 2009) because it is also captured in greater numbers by other fishing gears including longlines and gillnets (Bonfil, 2008; Gilman, 2011; Hall *et al.*, 2012). Juveniles of this species also regularly associate with drifting objects (Anderson and Jauharee, 2009; Filmalter *et al.*, 2011), accounting for their prevalence in FAD nets. This behaviour also results in their entanglement in the netting of the FADs themselves, a previously unknown source of mortality. The now widespread use of FADs could pose a major risk to silky shark populations and requires quantification. Currently no methods exist for investigating "ghost fishing" on the high seas. This work aims to provide the first quantitative results for evaluating the scale of this problem, in the Indian Ocean, as well as outlining new experimental and analytical approaches that can be used for future assessments in other fisheries or oceans.

6.2 Materials and Methods

Satellite tagging: estimating the average time before entanglement

A total of 43 silky sharks were captured and fitted with pop-up satellite archival tags (PSATs; product name "MiniPAT", Wildlife Computers, Redmond, WA) during six cruises conducted between 2010 and 2012 off shore of the Republic of Seychelles and in the northern Mozambique Channel (Fig. 6.1). Sharks were caught either by handline from research vessels (n = 13) or during purse-seine operations on commercial vessels (n = 30). Those caught from purse-seine vessels were tagged to investigate their post-release survival. Tags were attached either to a single threaded nylon rod secured through the first dorsal fin (n = 11) or by a nylon anchor, to which the tag was tethered, which was inserted into the dorsal musculature at the base of the first dorsal fin (n = 32). For the analysis presented here, only sharks that did not display direct post-release mortality (i.e. immediately sinking to a depth of >1600 m after release) were included, which led to a total of 29 individuals (Table C.1). Analysis of the detailed time-series depth profiles received from the tags clearly indicated that some of the individuals had succumbed as a result of FAD entanglement (Appendix A). The data series revealed an abrupt cessation of vertical movements followed by a constant depth reading close to the surface for extended periods (0.34–2.40 days) (Table D.1). After death by entanglement, the tagged sharks then sank to a depth >1600 m, causing the tag to automatically release and float to the surface (Fig. 6.1B).

Using the data from retrieved PSATs, we were able to estimate the daily probability of a silky shark becoming entangled in a FAD. To achieve this, we found that it was necessary to consider the observation duration of all tagged sharks, because this differed between individuals owing to the premature shedding of many tags. Considering $t = 0$ as the tagging time, we denote the total number of sharks that are still observed at time t as $N_{tot}(t)$. Because $N_{tot}(t)$ varies in time due either to tag shedding or to entanglement events, we can express its temporal variation through:

$$\frac{dN_{tot}(t)}{dt} = -\alpha_e N_{tot}(t) - \alpha_s N_{tot}(t) \tag{6.1}$$

where α_e denotes the probability of entanglement and α_s the probability of

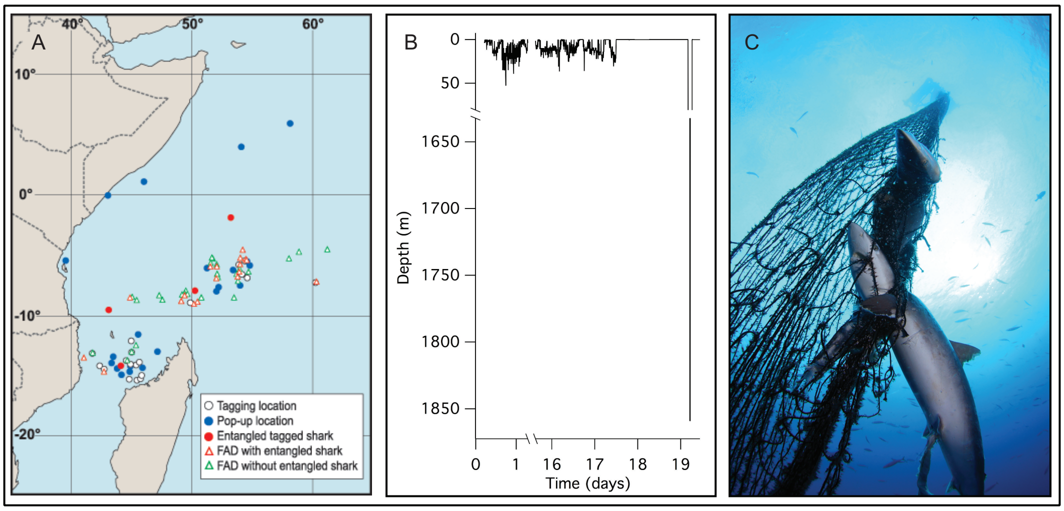

Figure 6.1 (A) Study area showing PSAT tagging and pop-up locations as well as locations of underwater observations at drifting FADs in the western Indian Ocean. (B) Typical depth profile received from a PSAT on a silky shark that became entangled. (C) Juvenile silky sharks entangled in the subsurface structure of a drifting FAD (F Forget, © ISSF).

tag shedding; both probabilities are assumed to be time-independent. From equation 6.1, we can express the number of sharks that are still observed at time t as:

$$N_{tot}(t) = N_{tot}(0)^{-(\alpha_e+\alpha_s)t} \tag{6.2}$$

where $N_{tot}(t)$ is the total number of sharks released after tagging. The total number of entangled sharks at time t, denoted by $N_e(t)$, then reads:

$$N_e(t) = \int_0^1 \alpha_e N_{tot}(t)dt = \alpha_e N_{tot}(0)\tfrac{(1-exp[-(\alpha_e+\alpha_s)t])}{\alpha_e+\alpha_s} \tag{6.3}$$

that, for large observation times $t\infty$, leads to the following expression for α_e:

$$\alpha_e = \tfrac{N_e(t_\infty)}{N_{tot}(0)}(\alpha_e+\alpha_s) \tag{6.4}$$

The value of the exponent $(\alpha_e+\alpha_s)$ was obtained through a survival curve analysis of the number of sharks still observed at time t (equation 6.2), fitting the cumulative distribution of $N_{tot}(t)$ with an exponential model. From Equation 6.4, the average time required for a silky shark swimming in an environment with FADs to become entangled was estimated as $\frac{1}{\alpha_e}$.

Underwater observations: estimating the daily probability of a FAD entangling a shark

In addition to the tagging data, underwater observations were conducted between 2010 and 2012 by divers at 51 FADs with subsurface netting (Fig. 6.1A and C). During these observations, the presence and number of entangled sharks was noted (Table E.1). Using a bootstrap resampling method (Efron and Tibshirani, 1993) run with 1000 iterations, we then estimated the average and standard error of the number of FADs with zero, one, and two entangled silky sharks. From this dataset, we could estimate the daily probability of a FAD entangling a shark, taking into account both the possibility that a single FAD could entangle multiple sharks and that sharks could remain entangled for several days. Given X_0 as the number of FADs with zero entangled sharks and X_j as the number of FADs with a non-zero number of entangled sharks j, we expressed their time dependence through the following system of differential equations:

$$\begin{cases} \frac{dX_0}{dt} = -\mu X_0 + \theta X_1 \\ \frac{dX_j}{dt} = -\theta j X_j - \mu X_j + \mu X_{(j-1)} + \theta (j+1) X_{(j+1)} \end{cases} \tag{6.5}$$

where μ is the probability of a FAD entangling a silky shark and θ is the probability of the entangled shark dropping out of the net. To adopt the most parsimonious model, we considered that the parameters μ and θ were constant for all FADs. For any value of entangled sharks per FAD j, Equation 6.5 leads to the stationary solutions:

$$X_j = \frac{1}{j!} \left(\frac{\mu}{\theta} \right)^j X_0 \tag{6.6}$$

Considering that the sum of the number of FADs with j entangled sharks must equal the total number of observed FADs (denoted as N_{FAD}), the estimated daily probability of a FAD entangling a shark μ is expressed as:

$$\mu = -\theta ln \left(\frac{X_0}{N_{FAD}} \right) \tag{6.7}$$

The factor θ was obtained from a survival curve analysis of the observed time individuals spent entangled (dead) in the net before sinking, from the PSAT dataset (Fig. A.3; D.1). For this purpose, we adopted the most parsimonious

Table 6.1 Time at liberty before entanglement for four individual silky sharks tagged with PSATs.

Shark ID	Time at liberty (days)
4	94
8	75
19	17
13	4

model for survival events - that is, a single exponential model of the form $f(t) = exp^{-\theta t}$ - and fitted this to the observed entanglement duration data.

Several factors may influence the time an entangled shark will remain in the netting of a FAD. Many species of fish – including the oceanic triggerfish (*Canthidermis maculata*) and rainbow runner (*Elagatis bipinnulata*) – commonly aggregate around FADs in the Indian Ocean. When a shark becomes entangled, these fish often feed on its carcass. Some entangled sharks were also observed with large portions of musculature removed, very likely by other, larger sharks. As the carcass is broken up due to this predation, it falls from the net and sinks. In addition, the manner in which sharks become entangled can vary greatly, from being strongly meshed behind the gills and around the head to simply being wrapping up with the net hooked on the jaw. These and other factors, such as the prevailing state of the sea, which will influence the jerking motion of the net, interact to determine how long the shark's carcass will remain in the net.

6.3 Results

Four of the 29 sharks tagged became entangled after 3.88–97.50 days at liberty (Table 6.1). The exponential model fitted to the tagging observation duration data produced an exponent of 0.024 (Fig. 6.2). Following Equation 1, the average time required for an individual silky shark swimming in an environment with FADs to become entangled was estimated as 300 ± 45 days. From growth models (Joung *et al.*, 2008) and catch size frequencies (Amandè *et al.*, 2010), we know that silky sharks found around FADs are generally in their first 3 years of life. Integrating the estimated average entanglement time of 300 days into an exponential survival model, we found that the entanglement mortality is 71% ± 4% after one year. Following this rate, the number of sharks avoiding entanglement after 3 years is only 2.6% ± 0.4% (Fig. 6.3A). Results from the

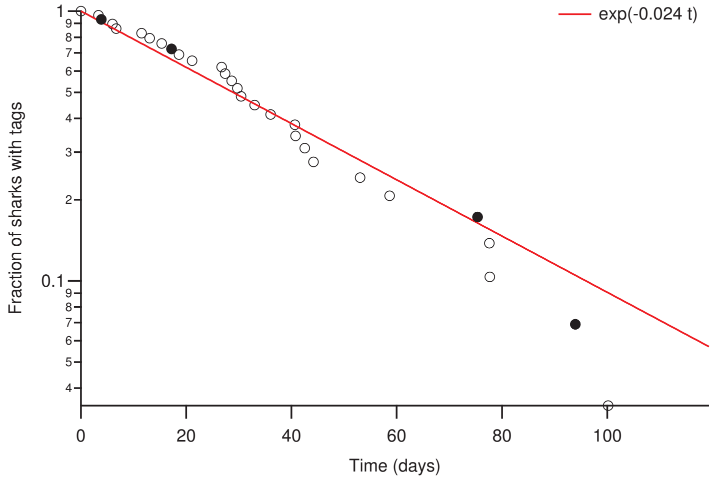

Figure 6.2 Semilog plot of the survival curve of the observation durations for silky sharks tagged with PSATs fitted with an exponential function of the form $f(t) = exp^{[-(\alpha_e+\alpha_s)t]}$. Solid black circles represent entangled individuals; open circles represent individuals that avoided entanglement.

Table 6.2 Number and frequency of FADs (with a net) found with 0, 1 and 2 entangled sharks from underwater observations.

Number of entangled sharks per FAD	Number of observations (± SE)	Frequency (± SE)
0	33 (± 3.5)	65% (± 7%)
1	14 (± 3.1)	27% (± 6%)
2	4 (± 2.0)	8% (± 4%)

underwater observation dataset revealed that 35% of FADs surveyed had at least one entangled silky shark (Table 6.2). The estimated value of θ was θ = 0.85 ± 0.1 days^{-1} (Fig. A.1), which led to an average time spent entangled in the net of approximately 1.2 ± 0.2 days. Integrating this result into Equation 6.7, we estimated the daily probability of a FAD entangling a shark as μ = 0.35 ± 0.08. To test the validity of our model (Equation 6.5), we performed a chi-square test of homogeneity between the theoretical Poisson distribution (Equation 6.6) and the experimental distribution of FADs with zero, one, and two entangled sharks (Table 6.2). The test indicates that we can accept the null hypothesis of homogeneity between the two distributions for values of μ between 0.25 (4 days) and 0.6 (2 days), which validates our model and results (Fig. A.2). To extrapolate our predictions to the ocean basin, we considered different numbers of FADs active per day in the Indian Ocean (Appendix B). Assuming the presence of between 3750 and 7500 active FADs (Fig. 6.3B), estimates of between 480 000 ± 110 000 and 960 000 ± 220 000 silky sharks are killed per year, respectively.

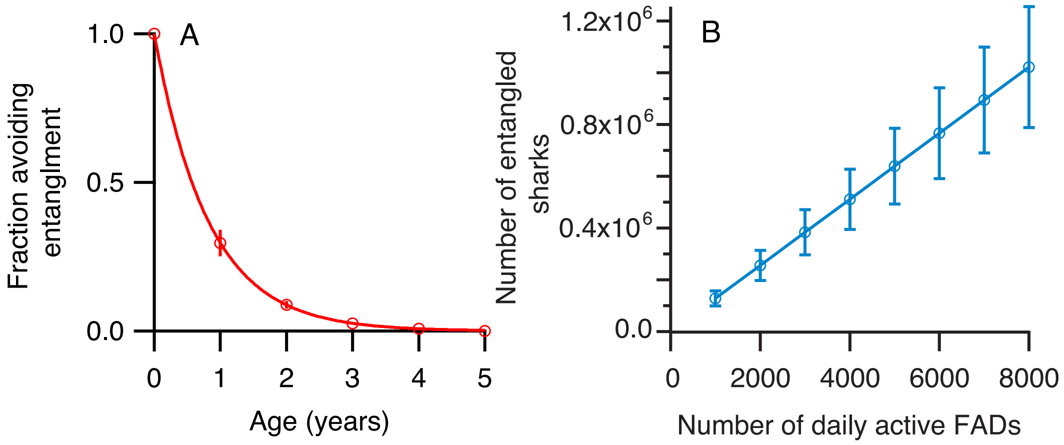

Figure 6.3 (A) Predicted survival curve of juvenile silky sharks due to entanglement, using an average time before entanglement of 300 days. The proportion of sharks surviving is 29% after one year, 9% after 2 years, and 3% after 3 years. (B) Estimated annual number of entangled sharks in the Indian Ocean as a function of the number of FADs active per day, from the estimated daily probability of a FAD entangling a shark of $\mu = 0.35$. Error bars in (A) and (B) indicate standard errors.

6.4 Discussion

The high frequency of entanglement events that we observed provides preliminary evidence that the impact of FADs is severe. Although uncertainty is inherent and unavoidable in this type of study (Piatt and Ford, 1996), this first quantitative estimate serves to highlight both the extent of this issue and the need for immediate attention. Our study is based on two approaches that are not typically used concomitantly: behavioural information (obtained through satellite tagging) and count statistics (generally used in population analyses, but novel here because they incorporate underwater observations from the pelagic realm). The fact that these two independent experimental protocols both signal high rates of entanglement reinforces our predictions. The mortality rates reported here are concerning, and lead directly to questions regarding their effects on populations. Owing to the absence of catch data from other types of fishing gear believed to substantially impact silky sharks in the Indian Ocean (gillnets and longlines), any attempt at assessing their population status in this region is impossible (Bonfil, 2008). However, the little information available suggests strong declines in recent decades (Anderson and Jauharee, 2009). The fact that juvenile silky sharks are still regularly encountered at FADs suggests that either a portion of the population may not be exposed to high FAD densities or the population effect of entanglement is delayed. Addressing the first hypothesis requires information on the spatial density distribution of juvenile silky sharks as well as FADs. However, these parameters are still unknown for the Indian Ocean. As for the second hypothesis, a delay in the population effect could be the result of several interacting factors. First, the individuals affected by entanglement are typically within the first 3 years of age. Second, silky sharks mature after approximately 10 years (Joung *et al.*, 2008) and females generally produce between six to 12 offspring every 2 years (Bonfil, 2008). Third, the use of FADs has recently increased greatly. As such, severe population impacts may only be observed in years to come. To contextualise our results in relation to the observed bycatch mortality of silky sharks from the tuna purse-seine fishery in the Indian Ocean, we used data reported in Dagorn *et al.* (2013) on the amount of silky sharks (tons) caught per 1000 tons of tuna (Table F.1). We then converted this to the number of individuals using the weight at 110 cm fork length, the peak of the observed bycatch length frequency (Amandè *et al.*, 2008a; Roman-Verdesoto and Orozco-Zoller, 2005), using published conversion factors (approximately 15 kg; (Joung *et al.*, 2008). This led to an average estimate of 82 000 silky sharks taken as bycatch in the Indian Ocean purse-seine fishery each year, an order of magnitude less than the mortality estimates presented here. Furthermore, following the same method, the global purse-seine fishery catches an average of 158 000 silky sharks annually (Dagorn *et al.*, 2013), which is still inferior to our lower estimate from the Indian Ocean. Our estimates are more comparable with the estimate of silky shark bycatch from longline vessels in the Central and South Pacific more than 20 years ago (900 000 individuals; (Bonfil, 1994) or the range of a more recent estimate from all of the world's fisheries combined, obtained from the shark fin trade in Southeast Asia (Fig. 6.4 ; Clarke *et al.* 2006b). Comparing our results with the situations in other oceans is currently impossible, because no similar data exist. Furthermore, we argue that extrapolation using regional FAD deployment figures alone should be avoided, given that entanglement probability is likely to vary between oceans due to both FAD design and silky shark abundance. We recognise that the sample sizes used in this study are limited and that increasing sample sizes would improve the accuracy of our extrapolations. However, while improving data collection through widespread monitoring is imperative, we argue that priority should be given to solving this issue. Despite these small sample sizes, both independent datasets suggest that FAD entanglement poses an immense threat to silky shark populations. Yet simple, cost-effective solutions exist that would promote the conservation of this species. Redesigning FADs by excluding meshed materials would eliminate this problem while sustaining the production of the fishery. Although these subsurface structures are of importance, the use of netting is not. Alternative materials that are biodegradable and provide zero chance of entanglement, such as sisal ropes, can offer effective substitutes. Although the findings of this study reflect the impacts of a technological change on a single species of shark, the problem identified here is of wider importance. Fisheries managers require more adaptive approaches. While efforts are currently underway to improve the monitoring of catches and bycatch, we have shown that this information is not always adequate for detecting all impacts of changing fishery practices. As marine resources become scarcer, the technologies used to maintain efficient economic extraction rates will continue to develop. It is the responsibility of scientists and managers to identify such changes, along with all of their possible impacts, as and when they occur. FADs have been used with increasing frequency worldwide for the past 20 to 30 years, but it is only now that the unexpected impact on silky shark populations in the Indian Ocean has been detected. Clearly, such retrospective approaches will not lead to long-term sustainability of fisheries. Anticipation is essential to mitigating negative human-induced impacts on ecosystems and as such should be a cornerstone of resource management in the future.

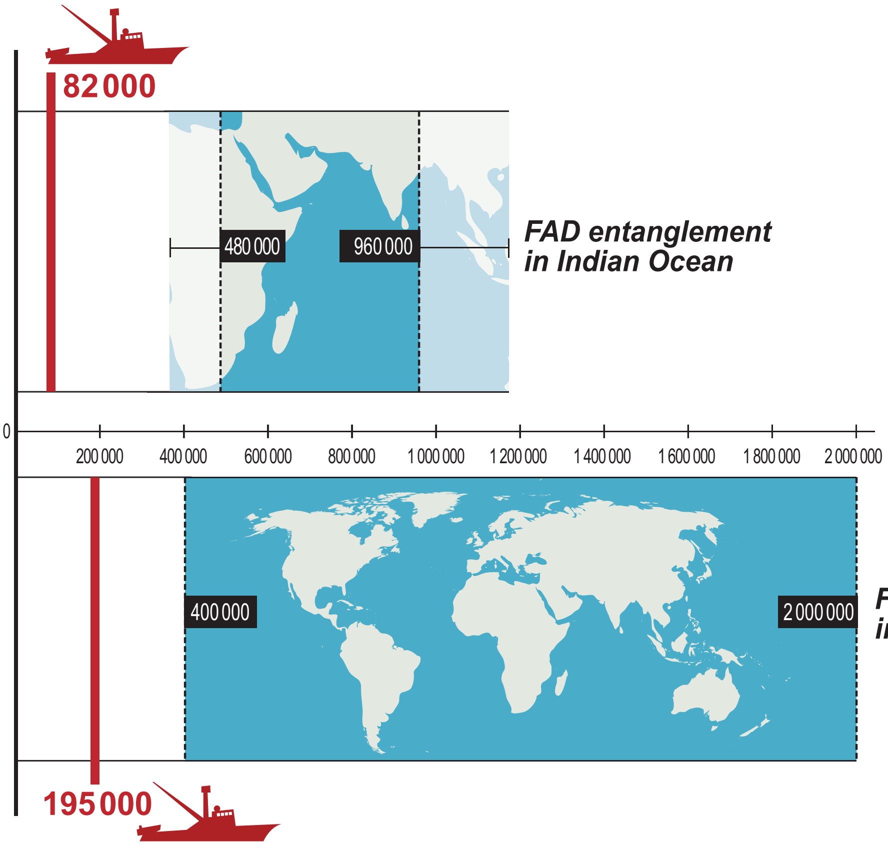

Figure 6.4 Estimated range of silky shark mortality due to FAD entanglement from the Indian Ocean (top) as compared with estimated silky shark mortality from all world fisheries from the shark fin trade in Hong Kong (bottom). Red lines indicate annual incidental capture in purse-seine fisheries at each scale.

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F. Forget

Chapter 7

General discussion

Pelagic animals inhabit a vast and seemingly homogenous environment where currents, fronts, and bathymetric features, such as seamounts appear to play an important function in their distribution and abundance (Fonteneau *et al.*, 2008; Tew Kai *et al.*, 2009; Morato *et al.*, 2010). In addition, the presence of floating objects, which occur at a minute scale in the oceanic environment, has been shown to have a profound influence on how pelagic animals are distributed in time and space (Hunter and Mitchell, 1967; Parrish and Edelstein-Keshet, 1999; Freon and Dagorn, 2000; Castro *et al.*, 2002). Floating objects can be of natural origin, such as tree trunks or branches, or debris from human activities, such as rope or lost fishing gear, or they may be specifically constructed and deployed for the exploitation of pelagic fishes and are known as fish aggregating devices (FADs). These objects provide a unique micro-habitat which selected pelagic inhabitants have evolved behaviours to exploit through direct association. Understanding this associative behaviour has been the focus of scientific investigation for decades, across all the world's oceans and many of its seas (Kojima, 1956; Hunter and Mitchell, 1967, 1968; Gooding and Magnuson, 1967). Nonetheless, despite significant focused research, the motives and benefits that make different fish species associate with floating objects remain largely unknown. A multitude of hypotheses have been proposed to explain this behaviour and were reviewed by Freon and Dagorn (2000) and Castro *et al.* (2002). These include but are not exclusive to: protection against predation; availability of food; reference point for fish; visual stimulus in an optic void; meeting point; schooling companion; substitute of the sea bed for species not adapted to pelagic life; negative phototropic response of fish to shadows; spawning substrate; cleaning station; resting area (Castro *et al.*, 2002). Some of these hypotheses are more applicable to certain species groups (such as juvenile reef fishes) than others (such as pelagic predators), which reflects the high diversity of species and functional groups that are known to associate with floating objects. The silky shark (*Carcharhinus falciformis*) is the most common elasmobranch species found in association with drifting objects in all of the world's tropical and sub-tropical oceans with early juveniles being the most abundant size class. The high frequency with which juvenile silky sharks are encountered at floating objects suggests that these structures play an important role in their early ecology. However, prior to this study, virtually nothing was known about why these sharks display such a behaviour or its significance in their life history as a whole.

Whilst improving our fundamental knowledge on why marine organisms behave the way they do is a critical component of marine research, undertaking applied research for the direct betterment of conservation and management strategies is equally important. Silky sharks are classified as Near Threatened by the IUCN (International Union for the Conservation of Nature) (Bonfil *et al.*, 2009). Although historic species-specific catch data are scarce, significant declines in abundance and average size have been reported over the past 2-5 decades (Baum and Myers, 2004; Anderson and Jauharee, 2009; Clarke *et al.*, 2011b, 2013). These declines are largely attributed to their common occurrence as bycatch in tuna fisheries, but also by targeted effort in certain regions (Gilman, 2011; Hall *et al.*, 2012; Dapp *et al.*, 2013). The associative behaviour displayed by juvenile silky sharks has both direct and potentially indirect consequences on their population. Direct impacts result from their incidental capture by purse seine vessels targeting tunas around drifting FADs. It is estimated that approximately 195 000 silky sharks are captured in purse seine sets on FADs across all oceans each year (Filmalter *et al.*, 2013). Recent work on the post release survival of silky sharks captured by purse seine vessels in the Indian Ocean found that, under current practices, a maximum of 19% of the sharks survive (Poisson *et al.*, 2014). Possible indirect population impacts resulting from the associative behaviour concern the creation of an "ecological trap", which could be a result of the artificial modification of the habitat of floating objects, due to the large-scale deployment of FADs (Marsac *et al.*, 2000).

The purpose of this study was to improve our knowledge on both the fundamental aspects of the associative behaviour of silky sharks with floating objects as well as obtaining information that is directly or indirectly applicable to the management and conservation of this species in light of this associative behaviour.

7.1 Why do silky sharks associate with floating objects?

The behavioural trait of associating with floating objects evolved across a diverse range of species, with each likely to derive specific benefits therefrom and ultimately providing a positive contribution to their fitness. Theoretical ecological models predict that animal turnover rates will decrease with increasing habitat quality (Griffen and Drake, 2008). As such, the duration of residence periods at a floating object may reflect the quality of the floating object mico-habitat for each species. In the case of silky sharks, periods of association with the same object can span several weeks to months, and thus their occurrence at floating objects is not fleeting or opportunistic. Being associated is clearly beneficial. The fact that most silky sharks at floating objects are juveniles, suggests that the benefits of association reduce as the sharks grow. Accordingly, silky sharks may become less dependent on floating objects with time (age). Under this assumption it would appear that protection from predation could play a role in driving the associative behaviour. Although silky sharks themselves are certainly predators, neonates and early juveniles could be preyed upon by larger sharks or teleosts such as marlin. Branstetter (1990) suggested that the reported rapid growth of silky sharks in their first year could be due to their small size at birth resulting in high predation risk for neonates. To date no reports of silky sharks occurring in the diet of marlins have been published (Brock, 1984; Júnior *et al.*, 2004; Abitia-Cardenas *et al.*, 1999; Rudershausen *et al.*, 2010) which could validate this hypothesis, however, personal observations of juvenile silky sharks displaying an escape response as a marlin approached a drifting FAD, lend support to this hypothesis. For small species of fish, predation avoidance may be achieved by using the structure of a floating object to interfere with the attack of a predator. However, this seems less likely for a silky shark as it would be too large to refuge between the branches of a floating log, or the within the netting of a FAD. Rather, the benefits of being part of a larger aggregation may serve this purpose (Parrish and Edelstein-Keshet, 1999), in a similar manner to shoaling behaviour. Again, personal observations of silky sharks occasionally schooling at FADs (with 60 or more individuals displaying polarised swimming patterns at times) credits this hypothesis. Although predation risk is likely to decrease with increasing size, ontogenetic shifts in feeding strategy or daily energy requirements may also result in a change in reliance on floating objects or the aggregations that accompany them. Changes in feeding strategy or energy requirement as size increases could be due to multiple factors including improved swimming efficiency (Schmidt-Neilsen, 1972), improved prey capture ability (Lucifora *et al.*, 2009), less energy required for growth (Smith *et al.*, 1998) or the ability to endure longer periods between meals (Schmidt-Neilsen, 1972). Examining the dietary habits of juvenile silky sharks associated with floating objects revealed that approximately 40% of their diet consisted of fishes from the aggregated biomass. The high frequency of non-empty stomachs observed compared with the much lower frequency observed in studies of larger (Strasburg, 1958; Bane, 1966; Branstetter, 1987; Stevens, 1984a,b; Cabrera Chávez-Costa *et al.*, 2010), non-associated silky sharks from other areas of its distribution, suggests that they feed more regularly when associated with a floating object. Consequently, the nutritional benefits obtained through the associative behaviour appear to play a role in driving this behaviour. While associated prey is not the dominant component of their diet, the aggregated biomass could represent an important reserve when prey abundance in the surrounding environment is limited. This reserve is likely to be a critical factor that allows the sharks to remain associated with a floating object for extended periods. Tunas associated with drifting objects typically display short residence times that span a few days (Ohta and Kakuma, 2005; Schaefer and Fuller, 2005; Dagorn *et al.*, 2007a; Govinden *et al.*, 2013; Matsumoto *et al.*, 2014). While a clear understanding of the factors that cause the tunas to disperse after such short periods remain unclear, several authors have suggested that it likely reflects changes in local environmental conditions, including prey availability (Ohta and Kakuma, 2005; Robert *et al.*, 2013). Furthermore, tunas associated with FADs are known to derive little nutritive benefit from the aggregated biomass (Ménard *et al.*, 2000b,a) suggesting that FADS clearly do not represent the same 'food reserve' for tunas as they do for silky sharks.

A major benefit of shoal formation is the improved ability to detect and capture prey (Pitcher and Parrish, 1993). By associating with drifting objects, silky sharks may derive such benefits from the large aggregations of tunas and other predators that often occur around the same object. Although tunas do not feed directly on associated prey, they are often observed feeding on free-swimming prey in close proximity to the floating object. In this way the sharks may benefit indirectly from the tuna schools, with the large number individuals resulting in a superior ability to search for and locate prey. By simply tracking the moving tuna schools in the vicinity of the FAD the sharks can feed with them once they find prey. This was the case during the active tracking experiment described in Chapter 4. Although this is only a single observation of a silky shark moving towards actively feeding tunas, on several occasions the silky sharks caught for the acoustic telemetry study were caught closer to tuna schools, detected on the tagging vessels echo-sounder or observed feeding at the surface, than to the FAD itself.

When considered holistically, there appear to be multiple factors that contribute to the associative behaviour displayed by silky sharks, all of which provide different, but complementary benefits. Although it remains inconclusive, it is hypothesised that the principle advantages include predator avoidance and trophic benefits derived from several sources, not just the aggregated biomass.

7.2 How vulnerable are silky sharks at FADs?

In the FAD-based tuna fishery, skippers estimate that deployed FADs have a lifespan of 1-6 months (Moreno *et al.*, 2007c). Over this period the same FAD may be visited, fished on and redeployed several times. Considering that silky sharks can remain associated with the same object for more than a month (see Chapter 4), it is proposed that they are highly vulnerable to capture. Furthermore, the average depth of a purse seine net is approximately 200 m (Ben-Yami, 1994), which is significantly deeper than the average depth occupied by silky sharks, during both the day (30 m) and night (<20 m). Although silky sharks display strong temporal patterns of close association during the day and excursions away from floating objects during the night, this behaviour does not reduce their vulnerability to capture as purse seine sets are typically carried out around sunrise. If mitigation measures were to be developed based on the time of lowest probability of silky shark presence, it would appear that fishing operations soon after dusk would be optimal. Unfortunately this period also coincides with the lowest probability of tuna presence at floating objects (Forget *et al.* in prep.) and hence the adoption of such a measure by fishers would seem very unlikely.

Although the incidental capture of silky sharks during purse seine operations is a major concern in this fishery, the unnoticed mortality due to entanglement in FADs appears to be a much greater issue. In the Indian Ocean alone estimates of FAD ghost fishing are almost 10 times higher than actual bycatch during fishing operations (see Chapter 6). Fortunately simple solutions to this problem have resulted in a rapid response from managers and fishers alike. Since the publication of the results described in Chapter 6 of this thesis (Filmalter *et al.*, 2013), the Indian Ocean Tuna Commission has passed a resolution stating that FADs should be designed in manner that minimises the entanglement of sharks and turtles . Furthermore, the management organisation of the French fleet in the Indian and Atlantic Oceans (Orthongel) has undertaken a project to develop and test various designs of FADs to avoid entanglement. Nonetheless, the development of monitoring and enforcement systems to assess the efficacy of these measures and efforts is paramount. Although onboard observers are present on some vessels, their ability to assess entanglement events is limited as they can not enter the water and FADs are seldom lifted onto the vessel in the Indian Ocean.

7.3 Do FADs represent an ecologic trap for silky sharks?

All marine scientists working on tropical tuna fisheries agree that FADs are fishing traps as they increase the catchability of all species that associate with them. However, apart from their direct impact of increased fishing mortality, additional indirect impacts on the ecology of FAD-associated species have been suggested due to the widespread deployment of thousands of FADs. The ecological trap hypothesis was first proposed by Marsac *et al.* (2000) and stemmed largely from the observation that FAD associated tunas generally had empty stomachs and skipjack tuna had smaller girths, while those caught in free swimming schools were found to have stomachs that contained prey items more frequently and skipjack tuna also had larger girths. Following these observations several authors have suggested that the associative behaviour of tunas, in conjunction with the mass deployment of FADs, may cause them to become 'trapped' in an array of drifting objects, in areas where environmental conditions are suboptimal (e.g. low prey abundance) thus leading to negative impacts on their condition (Marsac *et al.*, 2000). Furthermore it has been suggested that association with floating objects may alter the natural migration patterns of tunas and thus ultimately effect recruitment success following spawning in inappropriate areas (Ménard *et al.*, 2000a). Much debate surrounds these hypotheses, as the causation and correlation relationship remains poorly understood. In fact some authors have argued that the lower condition and empty stomachs of tunas at FADs may rather be the cause of the association as opposed to a result thereof (Robert *et al.*, 2014). Nonetheless, the critical aspect required to shed light on these hypotheses is the amount of time tunas spend at a given floating object, as well as in an array of floating objects. Fine-scale observations suggest that tunas have short residency times at floating objects (various studies report median residence times between 7.0 -7.9 days (Ohta and Kakuma, 2005) and means of 0.66 - 4.8 days across the three target species, Dagorn *et al.* 2007a; Govinden *et al.* 2013) , however, the large-scale movements of tunas relative to the drift patterns of arrays of FADs remain unknown. Silky sharks, on the other hand, remain associated for long periods (weeks/months) and there is now strong evidence to suggest that their movements are linked to the movements of FADs over large spatial scales (see Chapter 5). Consequently, the ecological trap hypothesis appears plausible, however, the most critical component, i.e. a negative impact on the fitness of the species, seems unlikely.

In the pelagic environment, it appears that juvenile silky sharks are most often found in association with floating objects or schools of tuna. Historically, smaller sharks were more common around floating objects, while larger individuals were found with free swimming tuna schools (Anderson and Jauharee, 2009), however, recent length frequency data from observers onboard purse seine vessels in the Indian Ocean do not indicate a large difference in size between the two behavioural modes (Amandè *et al.*, 2008a). Nonetheless, both associations may well be linked to trophic benefits.

The prey field in the epipelagic environment is known to be highly patchy (Romanov *et al.*, 2009). As silky sharks are limited to the epipelagic zone, their access to prey is inherently stochastic. Considering the limitations in the ability of a single individual in such an environment to locate patchy prey resources, there exists a strong selective pressure for developing behaviours that improve the probability of prey location. By following tuna schools, or associating with floating objects, silky sharks may receive benefits from the greater ability of the tuna school, or the entire aggregation, to locate patchy prey. Additionally, in the case of floating object, the aggregated biomass itself, is a valuable trophic resource. Under the current environmental conditions in the Indian Ocean (specifically the density of floating objects and the abundance of tuna schools), the likelihood of observing a silky shark is almost 10 fold higher at a floating object than with a free swimming school of tuna, based on bycatch data from the two fishing modes (Amandè *et al.*, 2011). However, this may not always have been the case. Before the start of industrial pelagic fisheries, the abundance of tuna was certainly greater than it is today. As such, it is fair to assume that the occurrence of free swimming schools of tuna was also more frequent. Early reports from tuna fishing activities (both pole and line and purse seine) suggest that silky sharks of all sizes were very common in tuna schools (Bane, 1966). Similarly, historic video footage of pole and line fishing from tuna vessels in the eastern Pacific Ocean show images of what appear to be silky sharks in large numbers between schools of feeding tuna `https://www.youtube.com/watch?v=lp_Rs75-5vI`. Similar scenes are very rare in the modern tuna fishery. Interpreting these results is complicated by the fact that these two major parameters in the ecology of silky sharks have undergone great changes during the intervening period; the number of tuna schools have decreased and the number of floating objects have increased. If only one of these variables had changed, any observed change in abundance or behaviour could be related to that change.

While it would appear that silky sharks were previously more abundant in free swimming schools of tuna, without information on the historic abundance at floating objects it is difficult to say that a behaviour shift has taken place. Nonetheless, if the role of both floating objects and tuna schools are considered as similar in terms of their contribution to the ecology of the species, it would appear that the deployment of large numbers of floating objects could in fact have a positive contribution for silky sharks. In the past, juvenile silky sharks may have been more likely to encounter a tuna school than to encounter a floating object. However, maintaining the association with a rapidly moving tuna school would be energetically expensive, yet the abundance of schools may have nullified this cost, as finding another school after losing one may not have taken much time. Conversely, today it may well be the case that a silky shark in the open ocean is more likely to encounter a floating object than a tuna school. Clearly, maintaining a close association with a drifting object has a much lower energy demand than keeping up with a tuna school, and the trophic benefits may be equal, if not greater.

As such, rather than trapping silky sharks, FADs may theoretically benefit them by increasing the availability of prey resources, increasing the probability of encountering highly efficient prey locators (tuna schools) and increasing survival through group formation and predator avoidance. The latter point is, of course, only applicable if their vulnerability to capture and FAD entanglement are mitigated.

7.4 Are silky sharks at a crossroads in the Indian Ocean?

Industrial pelagic fisheries started in the Indian Ocean in 1952 with the entrance of the Japanese longline fleet. By the early 1970's the Republic of China (Taiwan) and the Republic of Korea also had fleets in the fishery (Silas and Pillai, 1982). The Indian Ocean was the last ocean to develop an industrial tuna purse seine fishery, with French and Spanish vessels entering the region in 1981 and 1984 respectively (Miyake *et al.*, 2004). Prior to that a small number of Japanese vessels were purse seining for tuna in the Indian Ocean in 1978 (Miyake *et al.*, 2004). Although historic information on the pelagic gillnet fishery is scarce, tuna catch data suggests that this effort has increased steadily since 1980 (ISSF, 2014). Furthermore, catch data also suggest that fishing effort across all these gears has increased steadily over the past 30 years, with catches of the major tuna species peaking around 2005 (ISSF, 2014). Bycatch data from these early fisheries is extremely rare and information on the capture of sharks were often grouped into a 'pelagic sharks' category (Silas and Pillai, 1982). Reports from early longlining effort in the western Indian Ocean suggest that catch rates of pelagic sharks were high, contributing up to 70% of the catch in the Arabian Sea in the 1960s and '70s (Kawaguchi, 1967). Since then a significant decline have been observed and the proportion of pelagic sharks in catches from the same area was reported to be 16.09% in 2005-2006 (Varghese *et al.*, 2007). Similarly, hooking rates of pelagic sharks in this area were 1.0-3.5% in 1964-65 (Silas and Pillai, 1982), while rates of 0.1% were reported in 2005-2006 (Varghese *et al.*, 2007). Detailed historic data on shark catch rates at floating objects in the Indian Ocean are also extremely rare. A report from the Lakshadweep Islands in 1982-83 suggested that shark catches associated with flotsam in this area comprised 6.45% - 24.62% of the total weight of monthly catches landed by tuna pole and line vessels (Mohan, 1985). Recently, interviews with pole and line fishers in the near-by Maldives have suggested a drastic decrease in abundance of silky sharks associated with tuna schools and floating objects (Anderson and Jauharee, 2009).

Despite the increased fishing pressure on the pelagic ecosystem in the Indian Ocean and the clear declines in pelagic shark populations, the occurrence of silky sharks at floating objects in the western Indian Ocean remains common. For example, the ratio of sharks to tuna catch from FAD sets by purse seine vessels is three fold greater in this region than in any other area of the world (Dagorn *et al.*, 2013). Furthermore, during this study, silky sharks were encountered at 57% of the FADs surveyed. Considering the species′ inherent K-selected life-history traits it is an enigma as to how the observed abundance is maintained.

Data from observers onboard purse seine vessels suggest that encountering mature individuals is rare (Roman-Verdesoto and Orozco-Zoller, 2005; Amandè *et al.*, 2008a), both with free swimming schools of tuna and floating objects. Consequently, it is possible that adults are not vulnerable to purse seine activities, either due to their absence from the fishing zone or their behaviour when in the zone. Historically, silky sharks were classified as semi-pelagic as their abundance was found to decrease with increasing distance from land in the central Pacific Ocean (Strasburg, 1958). In the western Indian Ocean purse seine activities around the Seychelles islands are forbidden within 12 nautical miles of land. Although longliners do not have the same restrictions, most of their activity in this area occurs further offshore. Furthermore, off the Somalian coast, no industrial fishing occurs within the 200 mile EEZ.

It is possible that adult populations with high residency occur within these zones, where industrial fishing activities are limited or absent. An acoustic telemetry study of adult silky sharks in the Red Sea showed a high degree of residency at certain coastal reefs (Clarke *et al.*, 2011a). Similarly, Stevens (1984b) reported the recapture of a large silky shark 11 km from where it was tagged near the Aldabra Atoll in the southern Seychelles, 140 days after it was tagged. In parallel to the current study, five adult silky sharks (226-285 cm TL) were tagged with PSATs from longliners operating near islands and seamounts in the western Indian Ocean. Although the data received from these tags was of very poor quality 60% the tagging and pop-up locations were within 25 km of each other, over deployment periods ranging between 8 and 165 days.

These results suggest that adults are largely resident. Behavioural polymorphism is often observed in fish populations (Starr *et al.*, 2004; Meyer *et al.*, 2010), where a portion of the population displays nomadic behaviour, while the remaining portion are more resident. It is possible that the mobile portion of the adult population of silky sharks has been over-exploited through the activities of industrial fisheries in the pelagic environment and that the more coastal resident individuals contribute significantly to the persistence of the species. As such, in the modern pelagic ecosystem, juvenile silky sharks are far more abundant than adults. Their presence in these areas is likely a result of their association with drifting FADs that pass through the zones where the adult populations reside and possibly breed. If this is indeed the case, then locating and protecting such adult populations could be critical to the longterm survival of the species. Clearly deploying more PSATs on large adults in both the open ocean and coastal environments is essential to validate this hypothesis.

7.5 Directions for future research

Although the work described in the chapters of this thesis have provided new information on the ecology and behaviour of silky sharks associated with drifting objects, there are still gaps in our knowledge, which require specific research attention. In terms of the feeding ecology of this species, we still know very little about their feeding habits when not associated with a floating object. As such, collection of stomach content data from silky sharks of the same size caught away from FADs (either on longlines or with free swimming schools of tuna in purse seines) is a priority. Following a comparative approach with the data collected thus far, new insights into the factors that drive the associative behaviour could be elucidated.

The fine-scale behavioural data collected through the combination of acoustic telemetry and archival tagging techniques provided new insight into the temporal behavioural patterns of this species. Nonetheless, additional information obtained through tags equipped with new sensors, that could, for example, directly monitor feeding activity, would allow the hypotheses proposed in Chapter 4 (e.g. short term nocturnal excursions reflect foraging activity and the duration of the excursions are linked to feeding success) to be rigorously tested. Furthermore, developing and deploying sensors that can monitor associations between conspecifics or even between species (such as tunas and sharks, see Holland *et al.*, 2010) would provide information essential for examining how individuals or species interact (i.e. are sharks aided by tunas in their search for prey?) and again provide a deeper understanding of the associative behavioural phenomenon.

Through the deployment of PSAT tags we have learnt that small sharks can move great distances across the ocean, and that these movements are likely linked to the movements of FADs. Developing monitoring systems that could allow the presence of a tagged shark at any FAD to be recorded would be a vital step in validating this hypothesis. As drifting FADs are increasingly equipped with high-tech tracking buoys with integrated echo-sounders (Lopez *et al.*, 2014), there is clearly potential to integrate acoustic receivers into these buoys as well. Furthermore, if all drifting objects are simultaneously monitored, the time that sharks spend between periods of association can be obtained. This information can then be used to develop population indices (Sempo *et al.*, 2013), which are currently lacking for this species in the Indian Ocean.

7.6 Management implications

Despite the focus of this thesis being ecological, several of the results have clear implications for the improved management of silky sharks. Firstly, enforcing changes to the design of drifting FADs is an essential step towards the reduction of fishery associated mortality of silky sharks in the Indian Ocean. Although the IOTC and NGOs such as the ISSF have provided guidelines describing the best practices when constructing non-entangling FADs (such as removing all netting), how well these guidelines are being implemented and monitored by the various fleets remains poorly documented.

The large movements displayed by several sharks in this study indicate that area based management measures are likely to be ineffective for protecting juveniles of this species. Furthermore, these movements clearly demonstrate that should any management measure be put in place, they will need to be applied to the entire western Indian Ocean region, not just a portion thereof.

An important aspect of the results obtain here relied on the provision of the tracking buoy data from FADs. While some fleets provide this data to scientists (e.g. the French fleet), others do not. As such, our understanding of the total number of FADs active at any point in time remains limited. This information is vital for understanding the extent of the effects of FAD fishing, both on the ecology of associated species as well as the influence on their spatial behavioural patterns. Developing systems that will enhance the provision of such data is an essential step in managing the impacts of this fishery on the pelagic ecosystem.

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Appendices

A Determining entanglement events and longevity

To verify that the data from the tags represented an entanglement event and not the behaviour of the silky sharks, we developed a method based on the vertical behaviour displayed by each individual throughout tag deployment. In addition to sharks outfitted with pop-up satellite archival tags (PSATs) becoming entangled, one *C. falciformis* (77 cm total length) tagged with a pressure-sensitive acoustic tag (Vemco, Halifax, Canada), which had been surgically implanted inside the shark's peritoneal cavity, also became entangled. The time-series data from this tag were recorded and transmitted via a satellite-linked acoustic receiver (VR4-Global, Vemco), which was attached to the drifting fish aggregating device (FAD) where the shark had been tagged 5.42 days before. The data from this tag were included in the estimation of entanglement longevity.

Here we define the time t_e as the point at which the shark became entangled and the time t_s as the point at which the shark sank from the net, with the tag still attached (Fig. A.3). We considered the time interval $(t_s - t_e)$ as the "entanglement longevity". To distinguish the entanglement event from other periods of reduced vertical movements and to establish the temporal boundaries t_e and t_s of the time spent in the net, we developed the following approach. Time bins of 30 minutes were created, and average swimming depth Dj and its associated variance $\sigma^2 Dj$ were calculated. We then identified periods of low vertical movement (LVM) as time windows where the shark's swimming behaviour was characterised by a constant depth and very small vertical displacement within the temporal bin, based on two criteria:

1. The variance of the depth $\sigma^2 Dj$ of each bin constituting the LVM time window was smaller than 1 m.
2. For each bin j constituting the LVM time window, the consecutive bin

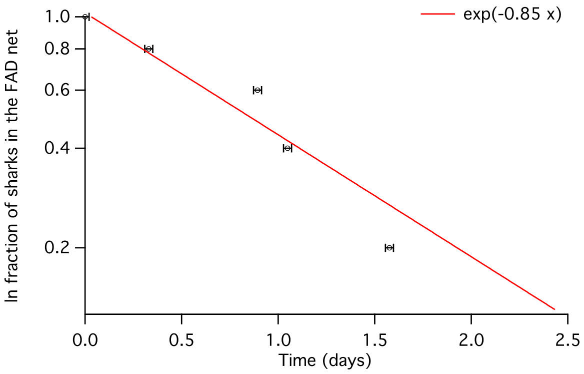

Figure A.1 Semi-log plot of the survival curve of entanglement durations from juvenile silky sharks tagged with pressure0sensitive electronic tags fitted with an exponential function of the form $f(t) = exp^{-\theta t}$.

> $j+1$ also constituted the same LVM time window if the relative difference among their depth was smaller than 2 m ($|Dj - Dj+1|$< 2 m).

These criteria were chosen according to the precision of the depth sensor of the tag (0.5 m). In this way, we identified several LVM time windows in the tagged sharks' behaviour. We calculated the distribution, average value, and standard deviation of these LVM time windows, apart from the last one recorded before sinking, which was a candidate for an entanglement event. If the tagged shark was not observed sinking from the net (n = 1), we considered the entanglement longevity to be the last recorded period at a constant depth, which was not at the surface (>3 m). Table D.1 shows the estimated entanglement times. The average LVM time window, other than the entanglement times, calculated for the entangled sharks corresponded to 0.64 ± 0.61 hours. The distribution of LVM time windows was highly skewed toward very short times $\leq$30 min (Fig. SA.4). Therefore, we could safely consider that the entanglement times in Table D.1 corresponded to true entanglement events, since their durations were several standard deviations away from the average LVM window length.

Certainty of entanglement event

There are several possible interpretations of the vertical pattern observed in the PSAT datasets; however, none explain the pattern as well as that of an entanglement event. Before considering the PSAT data, the interpretation of the acoustic tag data is equally as important and less complicated. This tag was internally implanted and is negatively buoyant. It can be detected only when within the range of the receiver, which is fixed to the FAD. The shark in

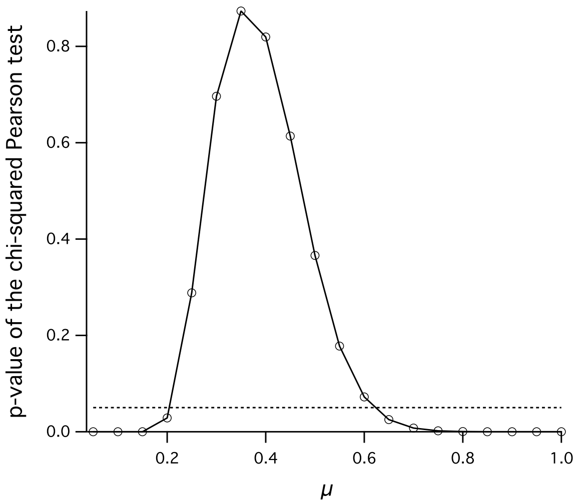

Figure A.2 P values of the comparison between underwater observation data of silky sharks entangled in FADs and the theoretical Poisson distribution calculated with different values of μ. The test of comparison was the chi-square test.

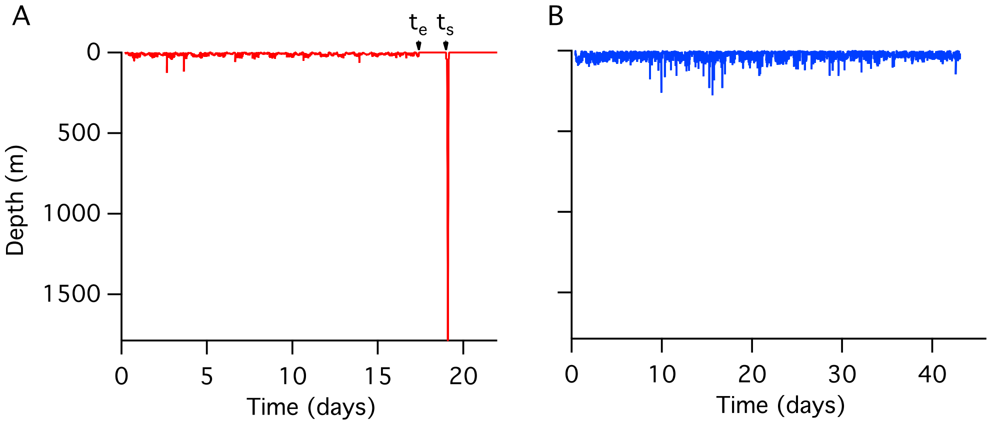

Figure A.3 (A) Typical depth profile of a tagged shark that became entangled during the monitoring period, from tagging to entanglement. Arrows labeled t_e and t_s indicate the entanglement time and sinking time, respectively. (B) Typical depth profile of a tagged shark that did not become entangled.

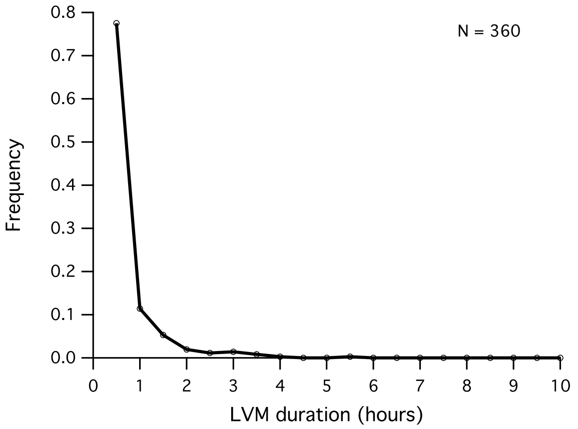

Figure A.4 Distribution of LVM times from the entangled sharks.

question ceased all vertical displacement after 5.42 days of "normal" behaviour, and was continuously detected for 21.43 hours. The tag then sank out of the reception range. At this particular FAD, there were three other silky sharks tagged with acoustic tags, none of which displayed any change in behaviour similar to the shark in question, suggesting that the receiver was functioning normally. Before these sharks were tagged, underwater observations were performed and the sharks and FAD-associated net were observed. Coupled with the regular observation of non-tagged sharks entangled in the nets of FADs, it is highly probable that this individual became entangled. After the 21.43 hours, either the shark fell from the net or the tag fell from its peritoneal cavity as other FAD-associated fish consumed its carcass.

The interpretation of PSAT data is more complicated given that these tags are buoyant and will float when deployment is terminated. There are several possible reasons for a tag deployment to be terminated, but again, none explain the observed vertical pattern as well as FAD entanglement. First, if a tag becomes detached prematurely, either by the anchor working out of the musculature, or the tag being pulled off by another animal, it will float at the surface. There is no reason for it to suddenly sink after several hours or days of floating. Second, if the tagged shark dies, it and the tag will sink, but then the observed constant depth prior to sinking is unlikely to occur.

The analysis above clearly demonstrates that this constant depth is not part of the shark's natural behaviour. If the shark was dying due to injuries from tagging or predation, it seems equally unlikely for it to be able to maintain a constant depth for such an extended period in the throes of death. The shark possibly became entangled in something other than the netting of a FAD, such as a drifting gillnet; however, there are several lines of evidence to suggest that this is less likely. First, we have shown, through underwater observations, that these sharks do become entangled in FADs, irrespective of whether they were tagged. Second, as these sharks associate with drifting objects for extended periods (at least several days at a time), they are constantly exposed to the possibility of entanglement. Finally, although poorly documented, the use of pelagic gillnets is known to be far less common in the equatorial western Indian Ocean, where the suspected entanglements occurred, than in waters north of 10°N. Conversely, the distribution of FADs encompasses the entire area where sharks were tagged and where suspected entanglements occurred. For all of these reasons, the possibility that something other than entanglement led to the consistent patterns observed in the four PSAT data series seems highly unlikely.

Species concerned

Only two species of elasmobranch regularly associate with drifting objects, the silky shark and the oceanic whitetip shark (*Carcharhinus longimanus*). Silky sharks are far more common, representing more than 90% of the elasmobranch catch in FAD sets. It is certainly the associative behaviour that leads to the entanglement of silky sharks. Furthermore, because those that associate are juveniles, they match the mesh size of the netting that is regularly used in FAD construction. As such, the potential for the net to act as a gillnet is almost optimised for this small size of shark. The juveniles of other common pelagic shark species, such as the blue shark (*Prionace glauca*), typically occur in more temperate waters beyond the bounds of the FAD fishing activity. The possibility that another species of shark can become entangled in a FAD cannot be denied but it is certainly far less likely.

B Estimating total FAD numbers in the Indian Ocean

Quantification of the number of *Carcharhinus falciformis* killed through entanglement annually in the Indian Ocean required the estimation of the number of FADs active on a daily basis. The fishery consists almost entirely of Spanish, Seychelles, and French flagged vessels. As information on FAD deployment is not readily available, we used fleet-specific data and trends. The Spanish fleet (13 vessels) reported the deployment of 3692 FADs with nets in 2010 to the Indian Ocean Tuna Commission (data from IOTC). Additionally, eight vessels, with Spanish skippers but flagged in Seychelles, did not report these data but were assumed to operate in the same manner, and as such, deploy 2272 FADs annually. The French fleet (13 vessels) has a self-imposed limit of 200 tracking buoys per vessel per year and consequently deploys a maximum of 2600. We know that 58% of these buoys are deployed on FADs (Moreno *et al.*, 2007a), leading to 1508 FADs annually. Adding these three figures gives an approximate estimate of 7500 FADs deployed annually that could entangle sharks. This estimate is probably only accurate in terms of the order of magnitude, due to poor data reporting since the emergence of the FAD fishery. As FADs undergo cycles of serial ownership, their absolute history and life span is masked. Some evidence suggests that FAD lifetime may be as long as one year (Moreno *et al.*, 2007b), whereas a more conservative estimate suggests 6 months. As such, we obtained estimates of 3750 and 7500 FADs active on a daily basis. This compares well with the estimated 2500 FADs active daily, obtained from interviews with skippers in 2004 and 2005 (Moreno *et al.*, 2007b).

C Meta data of tagged silky sharks

Table C.1 Meta data of juvenile silky sharks *Carcharhinus falciformis* tagged with PSAT tags at drifting FADs in the Indian Ocean. Sharks 1-13 formed part of behavioural studies while sharks 14 – 29 were tagged to study post-release survival. * denotes individuals that became entangled. Tags were programmed to release after 100 days except those marked with ‡, which were set for 150 days.

Identity	Tagging date	Total length (cm)	Sex	Observation time (days)
1	13/03/2010	88	F	18
2	15/03/2010	109	M	100
3	15/04/2011	91	M	26
4	20/04/2011	98.5	M	94*
5	20/04/2011	103	F	11
6	18/06/2011	98	F	6
7	20/06/2011	93	M	32
8	20/06/2011	102	M	75*
9	13/04/2012	109	F	119†
10	13/04/2012	111.8	F	30†
11	14/04/2012	111.3	-	29†
12	14/04/2012	116	-	58†
13	14/04/2012	116	M	4*†
14	26/03/2011	137	F	2
15	27/03/2011	127	F	6
16	28/03/2011	140	M	27
17	28/03/2011	86	F	44
18	31/03/2011	100	F	15
19	01/04/2011	87	F	17*
20	01/04/2011	98	F	21
21	01/04/2011	87	M	36
22	02/04/2011	155	-	13
23	25/05/2011	122	F	53
24	25/05/2011	150	M	40
25	02/04/2012	104	M	28
26	02/04/2012	113.6	F	40
27	03/04/2012	132	M	77
28	03/04/2012	155	M	42
29	06/05/2012	104	-	77†

D Entanglement duration

Table D.1 Entanglement times estimated for four sharks fitted with PSATs and one acoustically tagged* shark.

Identity code	Entanglement times (hours)
64*	21.43
4	7.92
8	54.42
19	37.83
13	25.17

E Underwater observations

Table E.1 Data from underwater observations at FADs with nets.

FAD	No. of sharks entangled	No. of free sharks Observed
1	1	0
2	2	0
3	0	2
4	0	6
5	0	0
6	0	0
7	1	0
8	1	25
9	1	15
10	0	10
11	0	10
12	1	1
13	2	4
14	0	3
15	1	2
16	0	2
17	2	1
18	0	5
19	0	1
20	0	3
21	1	5
22	0	0
23	0	3
24	1	0
25	0	7
26	0	0
27	0	0
28	0	0
29	1	0
30	0	0
31	0	0
32	0	0
33	1	0
34	0	0
35	0	0
36	0	0
37	0	3
38	0	0
39	1	3
40	0	1
41	0	0
42	1	1
43	1	0
44	2	1
45	0	0
46	0	2
47	0	1
48	0	2
49	0	2
50	1	2
51	0	7

F Silky shark bycatch per ocean

Table F.1 Data used to estimate silky shark bycatch in number of individuals from each ocean area, taken from Dagorn et al. (2012). EPO = eastern Pacific Ocean, AO = Atlantic Ocean, IO = Indian Ocean and WCPO = western and central Pacific Ocean. Data reported by species, BET = bigeye tuna (*Thunnus obesus*), SKJ = skipjack tuna (*Katsuwonus pelamis*) and YFT = yellowfin tuna (*T. albacares*).

	EPO	AO	IO	WCPO	Total
Tons of sharks/1000 t FAD tuna	1.9	1.8	6	1.1	10.8
Landed BET (t)	70000	15750	21000	47500	154250
Landed SKJ (t)	151680	80900	151590	857920	1242090
Landed YFT (t)	35700	14040	55590	178560	283890
Total tuna (t)	257380	110690	228180	1083980	1680230
Total sharks (t)	440.1198	179.3178	1232.172	1073.1402	2924.7498
No. of silky sharks	29341	11955	82145	71543	194983