An intensive study of movement and population dynamics of *Triakis megalopterus* in the De Hoop Marine Protected Area, South Africa

Samantha Wagstaff

Supervisor: Associate Professor Colin Attwood

Biological Sciences
University of Cape Town
Rondebosch 7701 South Africa

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Abstract

Coastal dwelling sharks are particularly at risk of decline due to the predicted rapid change in their environment and high incidences of accidental bycatch. Effective protection typically includes managing the fishing mortality and providing marine protected areas (MPAs) as refugia. To this effect, estimating natural mortality rates and home range size is vital. *Triakis megalopterus*, a commonly caught, endemic coastal shark of South Africa provides an excellent opportunity for this assessment. Mark-recapture data of 924 *T. megalopterus* caught at two sites in the De Hoop MPA from 1996 to 2020, a no-take reserve, were used to estimate home range size and natural mortality rates. Displacement frequencies were modelled to estimate home range size and space use within the MPA. Natural mortality rates for both sexes were estimated using two methods, one based on length data, combined with pre-established growth models, and another using the probability of recapture. *Triakis megalopterus* at De Hoop MPA displays a high level of philopatry. Individuals show consistent small movements over periods up to thirteen years. Multiple recaptures of the same sharks indicate frequent and repeated use of home ranges in the order of 1.0 km of coastline. The best fit model suggests a high degree of central tendency in space use. Skewed sex ratios towards females could be due to sex-specific longevity or mortality. The population had low mean natural mortality rates of 0.099/yr [95% C.I. 0.088/yr to 0.112/yr] for males and 0.072/yr [95% C.I. 0.062/yr to 0.082/yr] for females as estimated from the length data. These rates were close to published findings in other studies, which used models fitted to environmental and life-history data. Survivorship estimates for *T. megalopterus* based on tag-recapture probabilities were lower than expected compared to length-derived natural mortality rates, but still suggest a low natural mortality rate. The difference is likely caused by deflated length-based mortality estimation, caused by the high number of large female capture lengths, tag loss and predation. In conclusion, the small movements, philopatric tendencies, sex-specific movements, and rates, and small home range of *T. megalopterus* suggests that populations are highly susceptible to fishing and individuals are unlikely to radiate far and replenish diminished locations.

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Introduction

It is widely documented that many shark species are in decline (Jackson et al., 2001; Worm et al., 2013; Dulvy et al., 2014; Dulvy et al., 2021). Sharks are generally characterised by slow growth and low reproductive output, signifying a higher risk of extinction. Extinction risk can be accurately calculated by incorporating detailed demographic rates and spatial ranges (Agardy, 2000; Kohler & Turner, 2001; Field et al., 2009), which are also essential for conservation (Speed et al., 2011; Botsford et al., 2019; Hays et al., 2019) and fisheries management (FAO, 2021; Zhou et al., 2021). Mortality rates are trusted parameters for marine population demographics and health but are often estimated using indirect methods. Mortality can be directly calculated using tagging data from mark-recapture (Gruber et al., 2001; Kohler & Turner, 2001). Movement patterns drawn from mark-recapture can also provide an indicator of home range size and dispersal. Understanding individuals’ natural ranges and the movement therein informs both the identification of important areas within fisheries and the implementation of conservation efforts.

Triakids are ideal candidates for studies of movement and mortality rates because they are primarily coastal species commonly used in fisheries (Dent & Clark, 2015) and are often caught as bycatch. The coastal environment is predicted to undergo the most rapid change in the marine landscape over the next few years (Harley et al., 2006), so understanding the dynamics of Triakidae populations is important for better protection against anthropogenic impacts, including pollution and fishing. Thus, the Triakidae family is useful in studies to observe these changes and develop sustainable fishing or conservation practices.

Overview of the family Triakidae

Distribution

The Triakidae family is one of the largest and most widely distributed of the order Carcharhiniformes (Ground sharks), which includes the houndsharks, smooth-hounds, tope and whiskery sharks. Triakids are split into two subfamilies (Triakinae and Galeorhininae), nine genera and about 40 species (Compagno, 1984; Van Der Laan et al., 2014; Ebert et al., 2017). Triakids are found in all tropical and temperate coastal waters, where they frequent sandy and rocky habitats (Ebert et al., 2021).

Biology

Generally drab-coloured, triakids are small to moderate-sized demersal sharks. They are differentiated from other shark families by the combination of horizontally oval eyes, anterior nasal flaps, an anal fin, and two large-sized dorsal fins with the base of the first dorsal situated well ahead of the pelvic floor (Ebert et al., 2021). Triakids are further defined by high asymmetry in tail fin shape, i.e., the lower lobe of the tail ranges from absent to large, and dorsal fin size, i.e. the second dorsal fin is approximately half to two-thirds the size of the first. Upper and lower jaws have defined symphysial tooth rows filled with many small teeth (Ebert et al., 2021). Their teeth point towards the commissure and range in shape from rounded low molar-like teeth (e.g., *Mustelus spp.*) to more bladelike teeth (e.g., *Galeorhinus galeus*) (Herman et al., 1988; Perez et al., 2013). Ground sharks primarily consume benthic and littoral invertebrates and fish using long mouths that reach past the front of the eye (Ebert et al., 2021).

Reproduction

Though many demersal elasmobranchs exhibit oviparous (egg-laying) reproduction and pelagic species are generally viviparous (live-bearing) (Snelson Jr. et al., 2008), Triakids are actually live-bearing. Bearing live young is advantageous because females can invest resources to generate higher quality embryos and give birth to larger young. A larger size at birth increases a pup’s chances of survival by enhancing its predatory capacity and reducing its own predation risks (Awruch, 2018). Members of Triakidae utilise one of two reproductive modes, namely (a) viviparity with placenta (matrotrophy) and (b) aplacental viviparity, where embryos feed on either yolk or both yolk and uterine secretion (lecithotrophic and limited histotrophy, respectively) (Lopez et al., 2006; Ebert et al., 2021). Aplacental viviparity (the reproductive mode of *T. megalopterus)* is synonymous with ovoviviparity, a live birth in which the eggs hatch within the body of the mother and is often considered an intermediary between viviparity and oviparity. This variation in reproduction is unique since other families in Carcharhiniformes typically exhibit either placental viviparity or both yolk-sac viviparity and oviparity (Lopez et al., 2006).

Behaviour

Although Carcharhiniformes' reproductive strategies have been well-researched, little is known about triakid behaviours and movement patterns. Natural logistics have consistently limited research of shark behaviours, specifically, a) the difficulty in keeping large sharks in captivity and b) the difficulty in accurately observing behaviour under natural conditions (Martin et al., 2009). Compounding these difficulties are sharks' high mobility both vertically and horizontally, as well as the obscure nature of the marine environment. Behaviours of more than half (25 out of 45) of known Triakid species' are either completely unknown or unrecorded (data from Ebert et al., 2021). However, in terms of observed triakids, many swim close to the seafloor or mid-water and are generally considered slow swimmers (Ebert et al., 2021). Some species like the *G. galeus* are more active, moving from inshore shallows to offshore depths of up to 826 m (Thorburn et al., 2019) and up to 50 km a day (Weigmann, 2016). Some species show schooling behaviours (e.g., *M. lenticulatus*), but species more commonly segregate by sex or size (e.g., *Mustelus spp.*) (data from Ebert et al., 2021). There is need for further study on Triakid behaviours to improve management and the trade and use of these animals.

Occurrence in fisheries

Triakids' size and almost ubiquitous distribution cause them to feature strongly in coastal fisheries across the globe. Legally, commercial fisheries target some triakid (e.g., *Mustelus spp.*, *Hemitriakis spp.,* and *G. galeus*) species for meat, fins, liver oil, and fishmeal (Simpfendorfer et al., 2002; Dent & Clark, 2015). Illegally, triakids are often used as substitution 'fish' or mislabelled within seafood products, as has recently been discovered by DNA barcoding (Barbuto et al., 2010; Kuguru et al., 2018; Delpiani et al., 2020). Others are reputed to fare well in captivity and are more often collected and traded for aquaria (e.g., *Triakis spp.*) (Compagno, 1984; Carlisle et al., 2015; Buckley et al., 2018).

Of the two subfamilies in Triakidae (Triakinae and Galeorhininae), the subfamily Triakinae includes the genera *Mustelus, Scylliogaleus,* and *Triakis*, all of which are represented in South African waters. Species of *Mustelus* and *Triakis* feature strongly in coastal ecosystems and the landings by many South African fisheries (Mann, 2013).

Members of the genus *Triakis*

The characteristics that separate the genus *Triakis* from the rest of Triakidae, as defined by Bigelow and Schroeder (1948), are a lack of barbels, separate nostrils from the mouth, conspicuous labial furrows and spiracles, and compressed teeth with two or more pointed cusps, the axial being the longest. Members of *Triakis* have small, pointy teeth (approximately two mm), some with three cupsids (Ebert et al., 2021); thus, the genus's name, 'Tri', meaning three and 'acis', meaning pointed. Their teeth and mouth morphometrics denote a demersal generalist diet of invertebrates and bony fish with teeth suited better for crushing or grip retention rather than tearing or puncture (Moss, 1977; Motta & Huber, 2012; Soekoe et al., 2022).

Additional differentiating factors encompass their reproductive physiology and geographical distribution. *Triakis spp.* are ovoviviparous reproducers (i.e., aplacental viviparous) (Dulvy & Reynolds, 1997; Ebert et al., 2021). Some females' average litters of 9-10 pups (*T. scyllium* & *T. megalopterus*) after long gestation periods (>10 months), but not all species within *Triakis* have known reproductive cycles (Ebert et al., 2021). All are typically found in marine tropical and subtropical regions near the sea floor of continental shelves (Ebert et al., 2013).

There are five species of *Triakis,* four of which are confined to the Pacific. The most widely distributed is *T. maculata* (spotted houndshark, Kner & Steindachner, 1867), found in coastal waters of the eastern Pacific from the Galapagos to Northern Chile, but much is unknown about the species (Acuña-Marrero et al., 2018; Dulvy et al., 2020). Locally it is marketed along with *Mustelus spp.,* as 'tollo' (Gonzalez-Pestana et al., 2016). *Triakis scyllium* (banded houndshark, Müller & Henle, 1839) is found from Southern Siberia to Hong Kong in the western Pacific (Ebert et al., 2013), where locally, it is also consumed or traded for aquaria (Ishihara et al., 2019). *Triakis semifasciata* (leopard shark, Girard, 1855) is a common schooling shark found on the Western Coasts of the USA and Mexico, where it is caught chiefly for recreational fishing and aquaria but is occasionally eaten (Smith & Horeczko, 2006; Ebert et al., 2021). Uniquely, *T. semifasciata* will form mixed-species aggregations with smoothhounds, dogfish sharks, sevengill sharks, and bat rays (Smith & Horeczko, 2006). Triakis *acutipinna* (sharpfin hound shark, Kato, 1968) has the smallest known genus distribution and is found only in Manabi Province in Ecuadorian waters (Ebert et al., 2013). Although houndsharks are eaten unintentionally and purposely worldwide (Dent & Clark, 2015; Lopez de le lama et al., 2018), interviewed fishers suggested that *T. acutipinna* is challenging to process due to its tough skin and is generally discarded when caught with only occasional local consumption (Cevallos-Garcias et al., 2022).

What is known about *Triakis megalopterus*?

The spotted gully shark *Triakis megalopterus (*Smith, 1839) is the only member of the genus found outside the Pacific Ocean and one of seven Triakidae species found in South African waters (Ebert et al., 2013). Triakis *megalopterus* can be found from southern Angola to eastern South Africa (Smale & Goosen, 1999; Compagno, 2009; Booth et al., 2011). Triakis *megalopterus* occurs in subtidal waters (<50 m) off sandy beaches, rocky shores and in shallow bays, generally as a bottom-dweller (Compagno et al., 1989; Smale & Goosen, 1999). It is usually found in depths of less than 10 m (Ebert et al., 2013; Weigmann, 2016).

Like other *Triakis* species, *T. megalopterus* is also often captured in recreational line fisheries and occasionally as bycatch in beach seine, longline, and trawl fisheries (least common) (Pollom et al., 2020). They typically have a counter-shaded grey/brown colour, with small black freckle-like spots, all over the body (Compagno et al., 1989). Their preferred prey includes crabs, cephalopods, bony fish, and small sharks (Smale & Goosen, 1999; Soekoe et al., 2022). Because *T. megalopterus* can be caught from shore, more is known about them than other *Triakis* (e.g., *T. maculata* and *T. acutipinna*).

Reproduction

Triakis megalopterus have one of the most prolonged gestation periods (19 to 21-months) recorded in all sharks and, indeed, among all vertebrates (Ebert et al., 2013). Comparatively, gestation in the African elephant *Loxodonta africana* (the longest of mammals) lasts 22 months (Wittemyer et al., 2007). The spiny dogfish *Squalus acanthias* gestation is about 22-23 months, the longest among all sharks (Jones & Ugland, 2001; Chatzispyrou & Megalofonou, 2005). Embryonic life-history traits are increasingly relevant, as the length of the gestation period and the neonate mass have been linked in several taxa (Ricklefs, 2010). *Triakis megalopterus* produce an aplacental viviparous litter of 5–15 pups (average 8-10), each with an estimated total length (TL) at birth of 40 cm (Smale & Goosen, 1999; Ebert et al., 2013; Soekoe, 2016). After a long pregnancy and birthing large offspring females have a reproductive resting period of two to three years between pregnancies (Ebert et al., 2021), but there is some evidence that females may sometimes shorten this period to a couple of months (Smale & Goosen, 1999). Fertilisation occurs in the late spring, from October to December (Smale & Goosen, 1999). In the austral summer, they form schools, frequently with numerous pregnant females present (Ebert et al., 2013), like *T. semifasciata* (Nosal et al., 2013; 2014). Females only have a narrow reproduction window due to the estimated age at maturity being 15 years, a maximum lifespan between 25 to 30 years old (Booth et al., 2011; Soekoe, 2016) and an approximate generation length of 20 years (Booth et al., 2011).

Length

As is common in many large cartilaginous species, female *T. megalopterus* grow larger than males. Males mature at a smaller length of approximately 125 cm TL, whereas females mature at approximately 140 cm TL (Smale & Goosen, 1999; Ebert et al., 2013;

Weigmann, 2016). *Triakis megalopterus* maximum total length is approximately 200 cm. Their length at 50% maturity was estimated to be 132 cm and 145 cm TL for males and females, respectively (Smale & Goosen, 1999). Booth et al. (2011) conducted an age validation on *T. megalopterus,* counting vertebral bands on the outside of a florescent ring from an injected calcium-chelating fluorescent compound called tetracycline. From this, *T. megalopterus* age at 50% maturity for males was 10.9 years and for females, it was 15.3 years. Soekoe (2016) confirmed these estimates. Therefore, male *T. megalopterus* mature at an earlier age and generally are smaller than females.

Occurrence in fisheries

It is estimated that 1-10 tons of *T. meglopterus* were caught in 2010 between the South African commercial linefishery and the hake longline fishery, despite being on the prohibited species list for commercial set by South Africa’s National Plan of Action for Sharks (DAFF, 2013). Fishery catch data and consumer statistics show *T. megalopterus* is often a bycatch (Best et al., 2013) and likely a compensatory replacement fish for all-take marine fisheries (Stevens et al., 2000). It is often confused with *Mustelus mustelus* (the common smoothhound shark, Linnaeus, 1758), the principal shark species caught (commercially and recreationally) in the South African Linefishery (Goosen, 1997; Smale & Da Silva, 2012; Dicken et al., 2012; Maduna, 2019). Best et al. (2013) found *T. megalopterus* among the most prevalent shark species in South African commercial linefishing and recreational shore-angling catches. The primary fishery focused on harvesting *T. megalopterus* is the recreational shore fishery, with particular emphasis in its competitive sector, which actively pursues this species. While there exists a daily bag limit of 1 T. megalopterus per person per day (SAAMBR, 2023), the post-release survival rate is unknown as they are released alive. Nevertheless, T. megalopterus is found in target and bycatch fisheries like the demersal shark longline fishery and the inshore demersal trawl fishery, even though it is a well-protected and less desirable species (Da Silva et al., 2015). They and other smaller sharks are sold as biltong or mislabelled as different fish (Pollom et al., 2020) and are sometimes exported for international consumption to Asia, Europe, and Australia (Da Silva & Bürgener, 2007; Compagno, 2009).

Movement and space use

Previous studies have suggested a high degree of philopatry (sometimes also referred to as site fidelity), a tendency to remain in or return to a specific area (Mayr, 1963), in *T. megalopterus*. Some *T. megalopterus* in South African waters have been recaptured within 10 km after 15 or more years (Dunlop & Mann, 2014; Soekoe, 2016). Additionally, adults and juveniles did not typically travel further than 50 km between the initial capture site and subsequent recapture (Maggs et al., 2019). Within the aforementioned study, juveniles had consistently shorter trajectories eastward, suggesting a lack of juvenile dispersal. Despite the large numbers tagged and released (n=10234) and subsequently recaptured (n=719 [7%]) in the ORI Cooperative Fish Tagging Project (Jordaan et al., 2022), very few *T. megalopterus* have been reported travelling far distances (100 km+). Dunlop & Mann (2014) reported one shark that moved over 900 km, and another eight individuals, tagged by the Department of Forestry, Fisheries and the Environment (DFFE), were reported to have travelled distances of up to 200 km (*pers. Obs*). This further supports the findings of Maggs (2019) that *T. megalopterus* actually have a low probability of moving long distances and highlights the need to understand their smaller movements and space use within their home ranges.

T. megalopterus habitat preference and movements are likely underpinned by their feeding and breeding behaviours. Triakis *megalopterus* are slow-swimming sharks (Ebert et al., 2021) that prefer inshore rocky reef habitats (Smale & Goosen, 1999; Osgood et al., 2019). Albano et al., (2021) support a reef preference in *T. megalopterus*, having observed a greater abundance of individuals in reef habitats compared to sandy and rubble habitats. Despite the difficulty of conducting studies on foraging behaviour of sharks in a natural setting, in captivity *T. megalopterus* were observed actively patrolling the bottom or midwater, but were rarely in the open (Ebert et al., 2013; Osgood et al., 2019). This patrolling behaviour is likely reflective of its foraging mechanisms (suction) and the location of preferred prey. *Triakis megalopterus* is a trophic generalist hypothesised to use a suction-based feeding mechanism (Soekoe et al., 2022). Preferred prey of *T. megalopterus,* living along South Africa’s west coast, are rock lobsters (*Jasus lalandii,* Soekoe, 2016; Soekoe et al., 2022) followed by rock crabs (*Plagusia chabrus,* Smale & Goosen, 1999; Soekoe, 2016) which predominantly inhabit rocky reefs. Other explanations for *T. megalopterus* use of space should include pupping and breeding behaviour, which little is known about. Still, it’s hypothesized that they breed in shallow waters (<30 m) (Smale & Goosen, 1999) and that pupping occurs on the Southern Cape Coast (Bass et al., 1975). Small juveniles have been reported in the Transkei (Bass et al., 1975) and in high quantities near East London (Goosen, 1997). Therefore, foraging mechanisms, preferred prey, and pupping behaviours may likely shape the movement of *T. megalopterus* and their use of space in the water column.

Shark tagging

Tagging sharks can provide data on population dynamics including movement, space use, home ranges, mortality rates and catchability (Kohler & Turner, 2001). The tag type used can moderate operational costs and allow for citizen science involvement (Potts et al., 2021). For example, conventional external shark tags (spaghetti or dart tags) do not require special detection equipment and can be identified visually, facilitating recognition by recreational anglers. Spaghetti tags are economical, well-used, cause minimal damage to the animal (Heupel & Bennet, 1997) and do not depend upon a tagged shark coming close to data-logging devices, unlike Radio Frequency Identification (RFID) and acoustic tags (Chawla & Ha, 2007). This enables innate flexibility in sampling because samplers do not need to be in pre-set location A, but rather chance locations A, B, C, Z, etc. Conventional shark tags also allow for observation over the years (depending on tag shedding/retention rates), whereas other methods are typically limited to shorter periods. Due to the relative ease of samplingand the involvement of citizen scientists large sample sizes can be compiled over many years with conventional shark tags, which generally allow for robust analyses.

A population of tagged *T. megalopterus* within the De Hoop Marine Protected Area (MPA) on the southern coast of South Africa provided an ideal opportunity to assess questions surrounding movement behaviour and mortality rates of this species. Tagging has been implemented since 1984 with 924 individuals tagged. De Hoop is a highly protected MPA where the removal of any resources is prohibited (a ‘no-take’ MPA), situated near the core of *T. megalopterus*’ natural distribution. Additionally, their numbers and composition should be unaltered from a primarily natural baseline since the human impact is kept to a minimum in a ‘no-take’ MPA (assuming that they do not move outside the boundaries of the MPA). Areas with ‘no-take’ provide an opportunity to evaluate mortality rates without the compounding effects of fishing mortality (Edgar et al., 2014). Furthermore, recapture chances are likely higher in less mobile species and when fishing mortality is excluded, possibly increasing accuracy and precision of movement data.

De Hoop MPA fish survey

De Hoop MPA hosts a variety of fish species from both oceans, as well as many species endemic to the South African coast (Cape Nature & Marine and Coastal Management, 2006). To date, 43 species have been recorded in De Hoop shore angling samples (Solano-Fernandez et al., 2012). However, Turpie et al. (2000) predicted that this is approximately only 26% of the total number of teleost in De Hoop, based on expected species distributions (i.e. this includes non-angling species). Analyses of shore-angling samples show that this MPA hosts at least 17 chondrichthyan species, with representatives from five of the 13 extant chondrichthyan orders (Bennett & Attwood,1993, DFFE unpubl. Data). Triakis *megalopterus* made up approximately 50% of chondrichthyan shore-based catch in De Hoop, from 1995-2020 followed by *M. mustelus* (smooth hound shark) and *C. brachyurus* (Bronze whaler shark) at 19% each.

Knowledge gap

Albano et al. (2021) recommended that scientists working in MPAs should record the home ranges and primary habitat use of the species existing within them. Spatial management plans can then be made to suit the movements of the animals to be protected (e.g., Mann et al., 2016 - estimating optimum size for inshore no-take MPAs). Previous work on *T. megalopterus* has examined movement patterns (Dunlop & Mann, 2014; Maggs et al., 2019) and their abundance in areas inside or outside an MPA (Albano et al., 2021), but have lacked a systematic approach to estimate the home ranges of the species and the use of space within the home range size. This is likely because each study encompassed multiple species across large areas and were unable to focus on species-specific home range analyses. Population dynamics of *T. megalopterus* have been estimated and validated through life-history parameters by both Booth et al. (2011) and Soekoe (2016). However, in both cases, sampling was conducted in areas where fishing occurred, potentially distorting estimated natural mortality rates. As indicated by its high longevity, late maturity, and long gestation periods (Smale & Goosen, 1999; Booth et al., 2011), *T. megalopterus* is highly vulnerable to fishing induced mortality. Sustainable management of shark fisheries should ideally take the natural mortality rate into account. Furthermore, estimating the probability of survival is essential in creating relevant conservation plans. If a species is rarely caught, it can be inferred that the species is either does not encounter fishing gear or rare. If a species is regularly caught, it can be inferred that the species is either abundant, resident or has a propensity for being caught.

Study aims

This study aimed to improve upon previous mortality estimates for *T. megalopterus* by analysing a population within a ‘no-take’ MPA, thereby removing the confounding variables introduced by fishing pressure present in previous studies. MPA’s present a golden opportunity (often referred to as a benchmark) to separate out the effects of natural and fishing mortality on a provided population. Further, the study aimed to calculate the home range and space use of the population in this study for the first time, which can be used to ensure more effective management and conservation of the species.

Objectives

The objectives of this study were to conduct an intensive analysis of *T. megalopterus*' movement, space use and mortality rates using 26 years of morphometric and mark-recapture data from a population in the De Hoop MPA on the southern coast of South Africa. In this study,

- The frequency of total lengths of caught individuals were described.
- Recapture patterns in individuals with multiple recaptures were analysed.
- Time at liberty and distances moved between initial capture and subsequent recapture as support of home range analysis were presented.
- Models representing possible space use patterns were used to explore time spent in displacement .
- Finally, whether sex affects length-based mortality estimates and survivorship estimates based on recapture probabilities were explored.

Methods

Study site

The De Hoop Marine Protected Area (MPA) was established in 1985 on the southern Cape of South Africa (Figure 1). It covers 289 km^2 of coastal waters. All forms of fishing in the MPA have been prohibited since 1985. From 1995 to 2020 *T. megalopterus* were tagged near the centre of the MPA at two locations, 11.9 km apart: Koppie Alleen (34°28.65’S, 20°30.70’E) and Lekkerwater (34°26.92’S, 20°39.15’E) (Figure 1c). The shoreline length of each study site was 3.4 km, and the two Study Sites were 11.9 km apart.

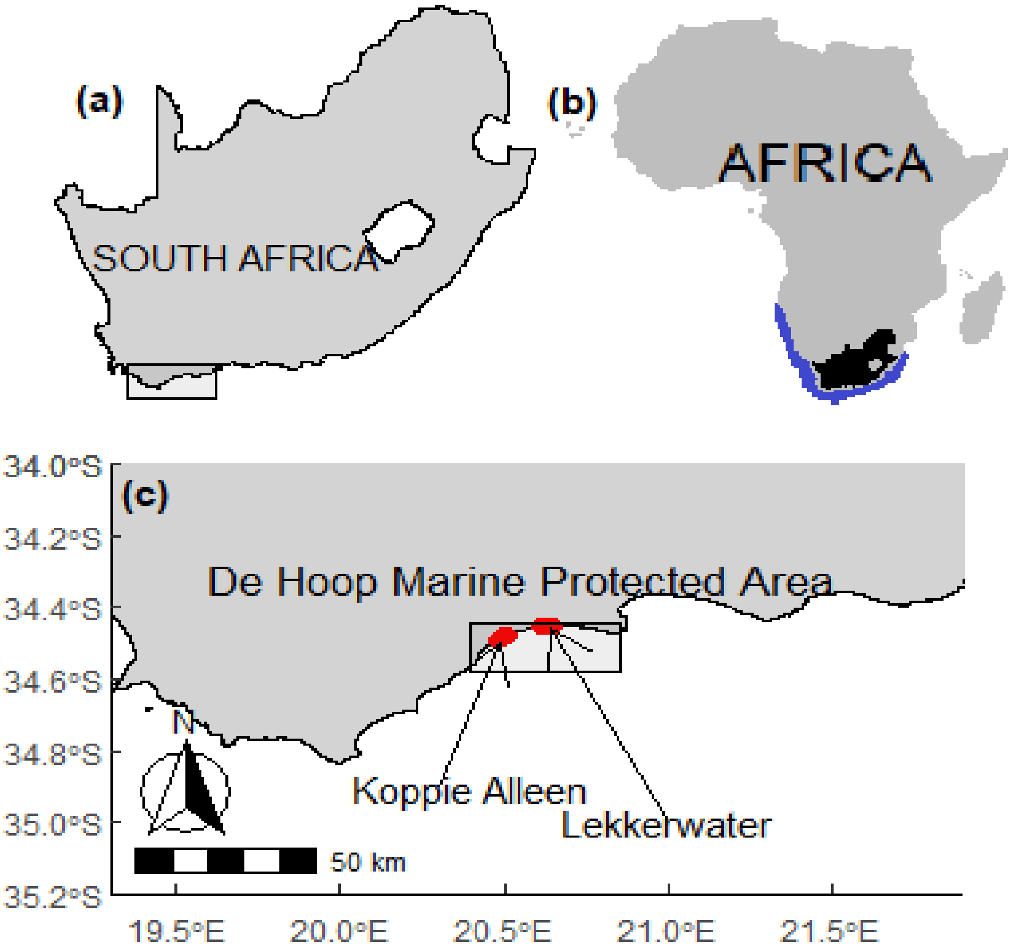

Figure 1. (a) A map of South Africa with inset showing the Western Cape area expanded in map c; b) The *T. megalopterus* species distribution is shown in blue; and c) The capture locations, Lekkerwater and Koppie Alleen in De Hoop Marine Protected Area indicated in red.

Abiotic elements

De Hoop is located at the intersection of the warm Indian Ocean and the cold South Atlantic Ocean. As a result, it has a warm temperate climate with sea temperatures that range between 12 and 20°C (Attwood, 2003). Both sites within the MPA constitute a high-energy coastline, where sandy beaches are interspersed with aeolianite sandstone rock platforms. High wave exposure and sand mobility have created spatiotemporal variation in rock coverage and the erosion of De Hoop's rock platforms into surf zone reefs. Some typically submerged platforms are only exposed during low and spring tides. The surf zone stretches 200 m from the beach and includes the reef zone. Reefs in the area are confined to water depths shallower than six meters (Attwood, 2003).

Mark-recapture data

Spatially referenced tag and recapture records of *T. megalopterus* were obtained from the South African Department of Forestry, Fisheries and the Environment (DFFE). The origin of these data are described below.

Fish sampling at De Hoop began in 1984 to monitor and study *Dichistius capensis* (commonly known as galjeon). Scientists were assisted by a small number of experienced volunteer anglers (citizen scientists) that visited Koppie Alleen every 4–8 weeks, 5-10 times per year. In 1987, the Lekkerwater site was added, and sampling alternated between both sites from then on. In addition to *D. capensis,* other teleosts were also tagged. The number of trips decreased to six per year, with three trips of four consecutive days in each site. From 1995 onwards, two anglers specifically targeted sharks on each trip, while the other anglers targeted either small teleosts or large teleosts, although all targeting methods landed sharks on occasion.

Anglers targeting sharks used squid and pilchard as standard bait. Upon capture, each shark was placed on a ruled wet stretcher, measured, sexed, tagged, and released. The sharks' total lengths (TL) were measured to the nearest mm. The capture location was georeferenced to the nearest 0.1 km, measured along the high-water mark. Each 0.1 km position was marked with a numbered flag. A towel soaked in seawater was placed over the shark's eyes and gills to calm the animal during the procedure. An external dart tag obtained from the Oceanographic Research Institute's Cooperative Fish Tagging Project (ORI-CFTP) (see Dunlop et al., 2013 for details) was inserted using a hollow stainless-steel applicator into the dorsal musculature of the shark directly beneath the first dorsal fin.The above procedure was repeated upon recapturing a tagged individual, except that the tag number was simply recorded. If the tag was damaged, it was replaced with a new tag. After the procedure, tagged individuals were returned to the water.

Statistical methods

Data format and extraction

DFFE stored the data as tables in MS Access (Microsoft Corporation, 2018). The following fields were retrieved: status (capture or recapture), site of capture (Lekkerwater/Koppie Alleen), information per capture (survey trip number, angler ID, species ID, implanted tag ID, location (flag) ID, total length, fork length, dorsal to dorsal length, and sex). Some *T.* megalopterus tagged in De Hoop were recaptured outside the reserve (eight individuals) were not included as a) their displacements (km moved) were substantially more than two standard deviations away from the mean displacement and b) they were not sampled at the same rate as those caught in the reserve. Thusly, they were deemed not to be clearly representative of the population (i.e., the exception to the rule) and to exhibit minimal residency. Although it is important to note that these individuals moved distances between 23 km and 236 km. A similar table for tagged teleosts and a habitat survey that included rock vs. sand percentage for each flag at Lekkerwater and Koppie Alleen were also retrieved. These habitat data consisted of rock and sand along a transect running perpendicular to the shore from the low water mark to back of the surf zone.

Length and sex distributions

The number of sharks caught at each site and lengths at initial capture were tested for normality using a QQ-plot, and Shapiro-Wilks test. Due to non-normality of all response variables, Mann-Whitney U tests were used (Mann & Whitney, 1947) to determine whether sample distributions were equal: (i) for the capture rate (measured as sharks caught per trip) at Lekkerwater and Koppie Alleen, (ii) for the length of females and males at initial capture and (iii) for the length of captured individuals at Lekkerwater and Koppie Alleen. The Mann-Whitney U test estimate along with both sample sizes and p-values are presented per analysis. In order to parse out location abundance, the count of tagged *T. megalopterus* and all other tagged fish (not separated by species) caught within the MPA were separated by the location (flag number) at which they were tagged (0.1 km resolution), then compared to the estimated rock cover percentage in the area also with a 0.1 km resolution. Teleost capture counts per flag were included to demonstrate if catch throughout the area was similar, irrespective of location, and to further demonstrate potential habitat hotspots. Subsequently, two Pearson correlation’s coefficient tests were conducted (Benesty et al.,

2009) to determine (i) whether the number of sharks captured at each flag correlated with rock coverage at said flag and (ii) whether the number of captured sharks correlated with overall teleost numbers captured at each flag. The correlation coefficient estimate, test statistic, sample size and p-values are presented per analysis.

Distribution and movement

Capture and recapture positions were used to calculate capture distributions and displacements. The frequency of capture of *T. megalopterus* and all fish (not separated by species) at each location (flag) were plotted in separate graphs. The percentage rock cover at each flag was also graphed. The displacement of each recapture was calculated as the distance between the original capture and recapture positions at Lekkerwater and Koppie Alleen. Only first recapture displacements were used for some analyses to avoid the pseudo-replication, as some sharks were caught on multiple (up to six) subsequent occasions. Nevertheless, these multiple recaptures were used separately in an analysis of space use. Records of individuals caught twice on the same day were excluded.

Displacement frequency data can be used to estimate home range size and the use of space within that range. To model home range size, three hypothetical displacement distributions were envisioned utilising a method developed by Attwood and Cowley (2005), namely: (i) difference of flat deviates (DFD) represents a flat or uniform distribution of space use, (ii) difference of normal deviates (DND) represents a gaussian process with a central tendency, and (iii) difference of gamma deviates (DGD) represents a more-flexible model of central tendency. DFD represents sharks spending equal time at every position in the home range. DND represents sharks spending the bulk of time at one location and progressively less time at ever-increasing distances from that location in accordance with a random-walk model. DGD is a more flexible distribution that allows for leptokurtic or platykurtic distributions of time spent at locations in the home range. Each distribution indicated the amount of time a shark spends in an area of size x (each displacement was rounded to 0.1 km of the coastline length to match the data resolution) at a random time of capture.

DFD: $$p(x) = 1/v \qquad (1)$$

DND: $$p(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{(x^2/2\sigma^2)} \qquad (2)$$

DGD: $$p(x) = \frac{x^{a-1}}{\beta^a \Gamma(a)} e^{(-x/\beta)^a} \qquad (3)$$

Where x is the coastline distance displacement, *p(x)* is the proportion of time spent in a coastline distance of x, v is total home-range size, σ standard deviation, α shape of the distribution, β inverse-scale of the distribution, and $\Gamma(\alpha)$ is the gamma function.

Theoretical displacement distributions were generated by drawing 10000 sets of two random positions for each model — representing capture and recapture positions — and then calculating the absolute difference in distance between each two in every set. The theoretical distributions were binned by applying the same resolution as the observed displacement data. The theoretical distributions were compared to the observed distributions, and the models were fitted by minimising the sum of squares of the residuals.

The flat deviation distribution used total home-range size v as the only free parameter, and the normal distribution used the standard deviation σ. The more flexible DGD model used α and β. The model that best matched the observed shark displacement data was selected as the most likely of the three. Home range size was equated to *v* for DFD, and values of x that correspond to p(x) of 0.8 (i.e., the coastline length that holds a shark for 80% of its time).

Mortality and age

Despite an already established non-linear regression of length compared to age (von Bertalanffy, 1957; Renner-Martin et al., 2018), the conversion of length to age is not possible algebraically. The von Bertalanffy relationship (VGBF) establishes an average length-to-age relationship, for which a size-at-infinite age is a critical parameter. There is much variation in the relationship and, in particular, the length attainable at an older age. For example, a shark of 200 cm length could be between 19 and 38 years old. Some of the sharks that were captured exceeded the length at infinity of the best-fit model, which meant that the formula could not be used to calculate age from length by simply applying it in reverse.

In addition to the above problem, the probability of a shark of a given length being a particular age is partly dependent on the mortality rate of sharks, as sharks of different ages are not in equal abundance. The estimation of an age distribution needs to consider the natural growth variation and the prevailing mortality rate. In other words, there is a probability distribution of age for any given length, but that probability distribution is influenced by the underlying age distribution in the population from which lengths are drawn.

A simulation procedure was used to generate sets of lengths of 100,000 sharks drawn from several hypothetical populations, each with a different prior mortality rate (and, therefore, age distribution). For each population, the probability density functions for age at length for both sexes were calculated. First, age distributions, were generated using the exponential function:

$$f(a) = 100000 * e^{-Ma}, \tag{4}$$

where $f(a)$ is the frequency of shark of age a in the statistical population with mortality rate M. To generate an age distribution, random deviates drawn between 0 and 1 were log-transformed and divided by M.

$$N_{(a)} = N_{(0)}e^{-Ma} \tag{5}$$

$$a = -ln(N_{(a)}/M) \tag{6}$$

$$L(a) = L\infty(1 - exp(-k(a - t_0))) \tag{7}$$

$L(a)$ is the length at age, $L\infty$ asymptotic (theoretical infinite) length, t_0 the theoretical age at zero, and k the growth rate.

The age distributions for both sexes were used to calculate length distributions. For each age in the distribution, a length was calculated by drawing the three VGBF parameters ($L\infty$, k, t_0) from normal distributions, whose means and standard deviations were estimated using vertebral tissue by Booth et al. (2011). In this way, an age-length key of 10,000 theoretical sharks was generated for each mortality rate for both sexes, using one-year age classes and 5 cm size classes.

The length data in the observed data set were also binned into 5 cm size classes. To assign an age for each observed shark, an age was drawn randomly from the distribution of ages of the hypothetical sharks in its length category. One set of estimated ages was drawn for each mortality rate. Mortality rates ranging from 0.025/yr to 0.25/yr were used. Linearised negative exponential models were fitted to the age-length data produced (Figure 2) to estimate mortality rates. This is an iterative process, which starts by choosing a mortality rate (input mortality rate) to generate age data, which are then used to estimate a mortality rate. The best estimate is assumed to be the one which corresponds with the input mortality rate.

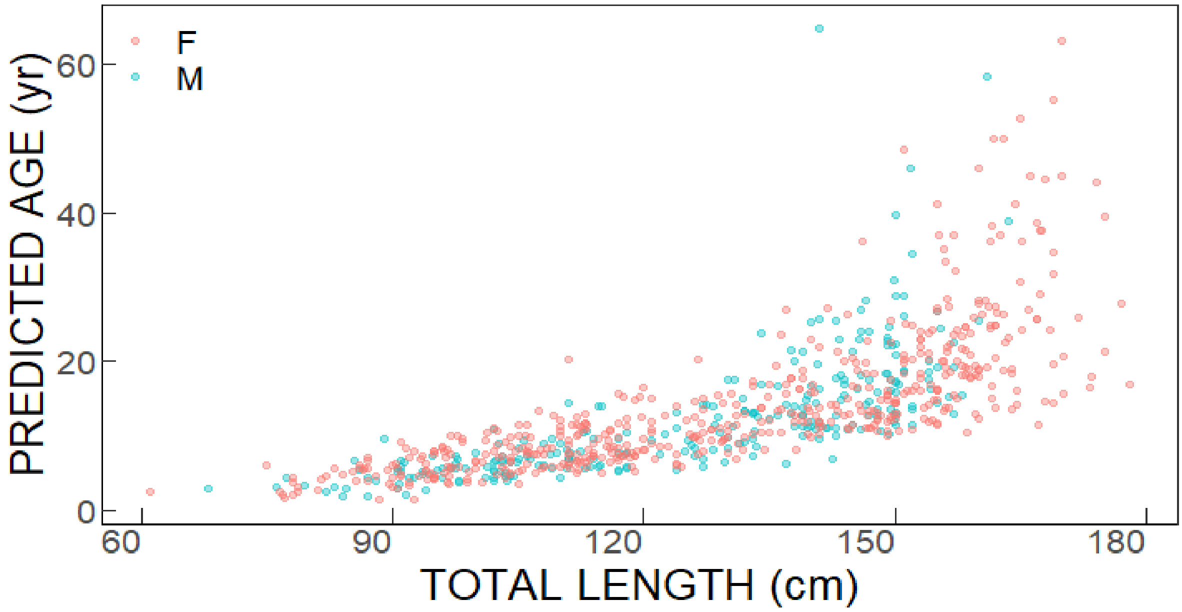

Figure 2. Female (F) and male (M) *Triakis megalopterus* ages (yr) were estimated by drawing randomly from theoretical age distributions based on the von Bertalanffy growth function applied to observed total lengths (cm) (n=526 females, 258 males). Shown above are the results of one of 100 simulations used to generate catch-at-age data from length data. In the example simulation shown here with an input mortality rate of 0.25/yr, estimated ages ranged from 1 to 32 years, with an average age for all sharks of 10.83 yr [SD ± 5.72 yr]. As an illustration of the sex difference, the average estimated age was 9.90 yr [SD ± 5.21 yr] for males and 11.30 yr [SD ± 5.91 yr] for females.

The age selection and model fitting procedure described in the paragraph above was repeated 100 times to generate 100 mortality estimates for each input mortality rate. The mean and 95% confidence intervals of the 100 mortality estimates were plotted against each input mortality rate. A 1:1 line was plotted on the graph of the mean estimated mortality rate versus the input mortality rate. The point at which the 1:1 line intersected the mean estimated mortality rate was taken as the best estimate of the mortality rate of *T. megalopterus*. At this point, the mortality rate indicated by the length data agreed with the mortality rate used to generate the ages. The corresponding upper and lower 95% confidence intervals were drawn from the estimated mortality distribution at the point of intersection.

Survivorship and the probability of recapture

Mark-recapture data can also be used to estimate mortality rates, or its opposite quantity, survivorship. A Cormack-Jolly-Seber model (CJS) of an open population was used to estimate the instantaneous annual survival rates for male and female *T. megalopterus*. The probability of recapturing a tagged shark is partly a function of (a) its survival rate and (b) the fishing effort to catch sharks.

The model used assumed that the probability of a tagged shark being recaptured in any of the years that follow its release is a function of the probability of it surviving to that year and the amount of fishing effort applied in that year. (It is important to note that a CJS model innately works on assumptions that all emigration is permanent and that tags are recorded correctly and not lost nor overlooked.) The model estimates two quantities, namely annual survivorship, and the probability of capturing a particular shark in one year, given a fixed amount of survey (fishing) effort. Because the fishing technique and fishing effort was standardised, the fishing mortality rate (F) was deemed not to vary among years, Based on established fisheries equations (Arreguin-Sanchez, 1996):

$$F = qE, \tag{8}$$

where q is catchability and E is the effort expenditure.

Annual survivorship *S* is related to annual instantaneous natural mortality rate (M) (as follows:

$$S = e^{-M} \ , \tag{9}$$

where *S* is the average probability of a shark surviving one year.

The probability of capturing a particular shark in one year I is therefore given by:

$$c = F * S^{t}, \tag{10}$$

where t is the number of years that elapsed since the tag was inserted (time at liberty).

Catchability and survivorship estimates were used to generate a matrix of capture probabilities for each tagged shark in each year (t) following its initial tagging. The observed set of capture-recapture events was used to estimate *q* and *s* with a likelihood model:

$$L_{ij} = \frac{{c_{ij}}^{f_{ij}}}{e^{c_{ij}}f_{ij}}, \tag{11}$$

where L_{ij} is the likelihood of shark *i* being capturing in year *j,* f_{ij} is the frequency of capture of shark *i* in year *j*, and c_{ij} is the expected probability of capture of shark *i* in year *j*.

Survivorship and catchability were estimated by finding the minimum of the sum of the negative log-likelihood (*SLL*) across all sharks and all years:

$$SLL = \min\left(\sum_i \sum_j lnL_{i,j}\right). \tag{12}$$

The most likely combination of survivorship and catchability was determined iteratively. *SLL* was calculated for 100 unique combinations of survivorship and catchability. The profile of *SLL* was contoured over the domains of survivorship and catchability. The lowest *SLL* provided the theoretically most likely combination of survivorship and catchability for each sex of *T. megalopterus*.

$$CI95 = \frac{2SLL+3.84}{2} \qquad (13)$$

Where $CI95$ is the upper 95% point of the chi-square distribution of one degree of freedom (3.84) of *SLL* values was used to estimate the 95% confidence intervals of survivorship and catchability (Lebreton et al., 1993).

Results

In total, 924 *Triakis megalopterus* were tagged at the Lekkerwater and Koppie Alleen study sites in De Hoop Marine Protected Area (MPA) from 1996 to 2020. Triakis *megalopterus* was the most frequently captured elasmobranch in the De Hoop MPA, making up 49.8% of the elasmobranch captures and 77.9% of their recaptures. Of the 924 individuals, 97 were caught twice in the MPA, and 36 were caught again for a third time. An average of 41 *T. megalopterus* [SD ± 22.8] were caught per year and on average 8 individuals [SD ± 5.31] were captured per four-day angling trip regardless of season.

Effort and capture distribution

More individuals were caught at Lekkerwater (n = 556) than at Koppie Alleen (n = 434) (Figure 3a left-side), and, correspondingly, the capture rate was higher at Lekkerwater than Koppie Alleen (measured as sharks caught per trip) at the two locations (Mann-Whitney U estimate = 2326.5, n1(Lekkerwater) = 60, n2(Koppie Alleen) = 64, p-value = 0.042). The majority of captures and recaptures were on the western side of Lekkerwater and eastern side of Koppie Alleen (Figure 3a).

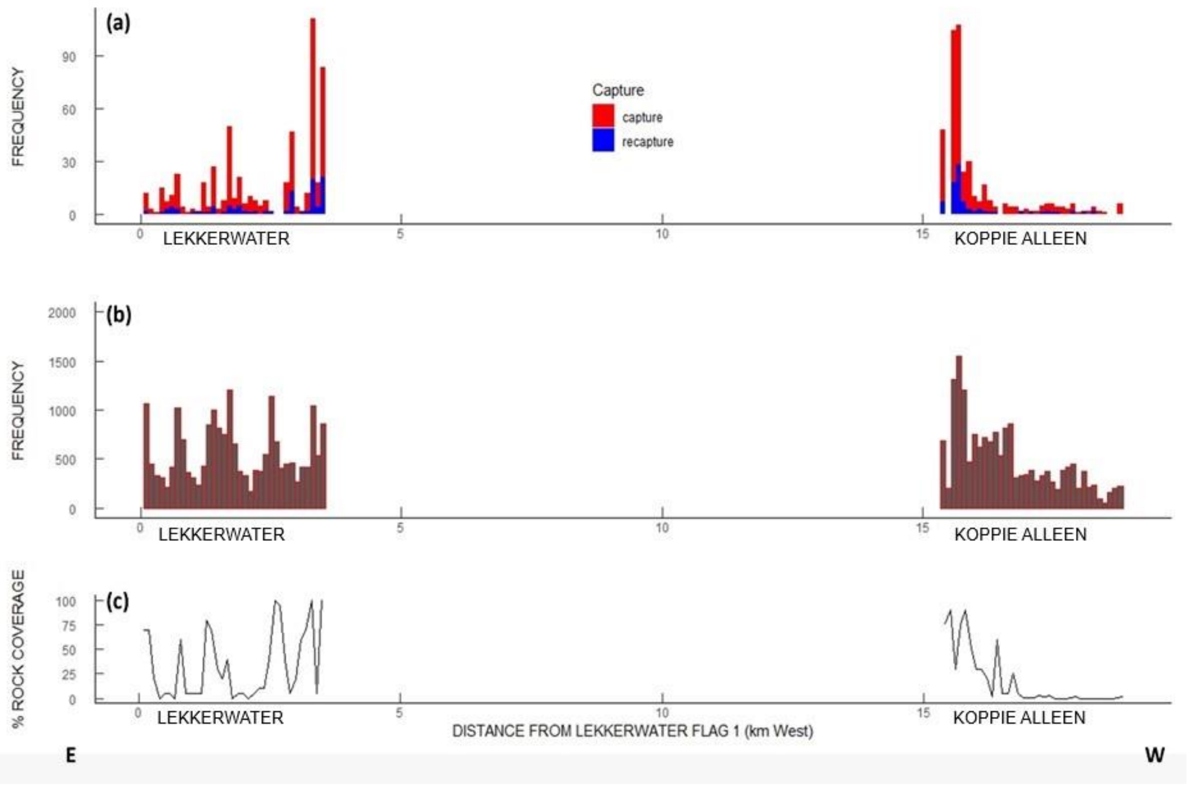

Figure 3. (a) Frequency distribution of *Triakis megalopterus* captured and recaptured (n=1022) in De Hoop MPA. (b) Frequency distribution of all teleost captured in De Hoop MPA. Each bin in (a) and (b) reflects a flagged capture location 0.1 km apart with positive values representing westward from Lekkerwater flag 1. (c) The estimated percentage of rock coverage at each flagged capture location.

Rock coverage at each flag was positively correlated with the number of sharks captured (Correlation estimate = 0.416, t = 3.772, df = 68, p-value = <0.005). Furthermore, the number of sharks caught at each flag were positively correlated with the number of fish caught (Correlation estimate= 0.629, t = 6.679, df = 68, p-value = <0.005).

Length and sex distributions

Tagged individuals ranged from 57.9 cm to 178 cm TL(mean 127 cm [SD ± 25 cm]). The sex ratio for all captured sharks was female skewed (2F:1M). Females were significantly longer at initial capture than males (Mann-Whitney U estimate = 47898, n1(Females)= 400, n2(Males)= 204, p-value = 0.001). Female total length averaged 132.9 cm [SD ± 25.6 cm] (Figure 4a) and males averaged a total length of 126.7 cm [SD ± 22.5 cm] (Figure 4b). The average length at first capture was 129.2 cm [SD ± 25.4 cm] (Figure 4c), and the average recapture length was 119 cm [SD ± 23.5 cm] (Figure 4d). There was also no cogent difference in the sex ratio (2.1F:1M Lekkerwater; 1.8F:1M Koppie Alleen) or length of captured individuals between the two sites (Mann-Whitney U estimate = 114096, n1(Lekkerwater) = 556, n2(Koppie Alleen) = 434, p-value = 0.142).

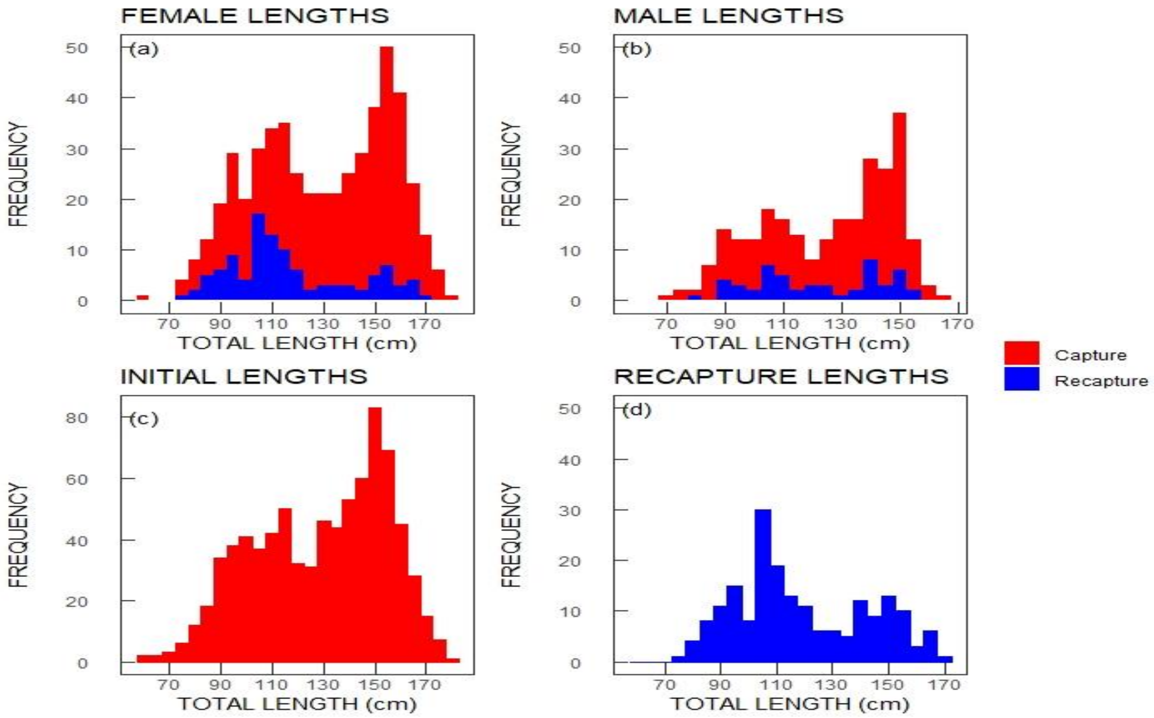

Figure 4. Frequency distributions of *Triakis megalopterus* total length (TL) in De Hoop MPA binned into 5 cm increments: a) TL for female capture (n=400) and recapture (n=106), b) TL for males capture (n=204) and recapture (n=52), c) TL at initial capture for all individuals (n=800) and d) TL at recapture for all individuals (n=190).

Time at liberty and distance moved

Recaptured individuals were caught at an average distance of 0.9 km from their original capture location (Figure 5b). Few recaptured individuals travelled distances that exceeded 10 km (15 individuals). A maximum movement of 16.6 km of those recaptured in the MPA, even though the maximum possible distance i.e., from the most western flag of Koppie Allen to the most eastern flag of Lekkerwater is 18.8 km. Of the 15 aforementioned individuals, eight were caught outside the reserve (which were not included in analyses as their movements were considerably more than two standard deviations away from the mean). Most sharks (n=97) were recaptured within 6 months of their first capture (58.16%), with a strong decrease in capture probability after the first year (Figure 6). Time at liberty ranged from a couple of days to 13 years (mean 1.95 yr [var 3.8 yr^2], Figure 5a).

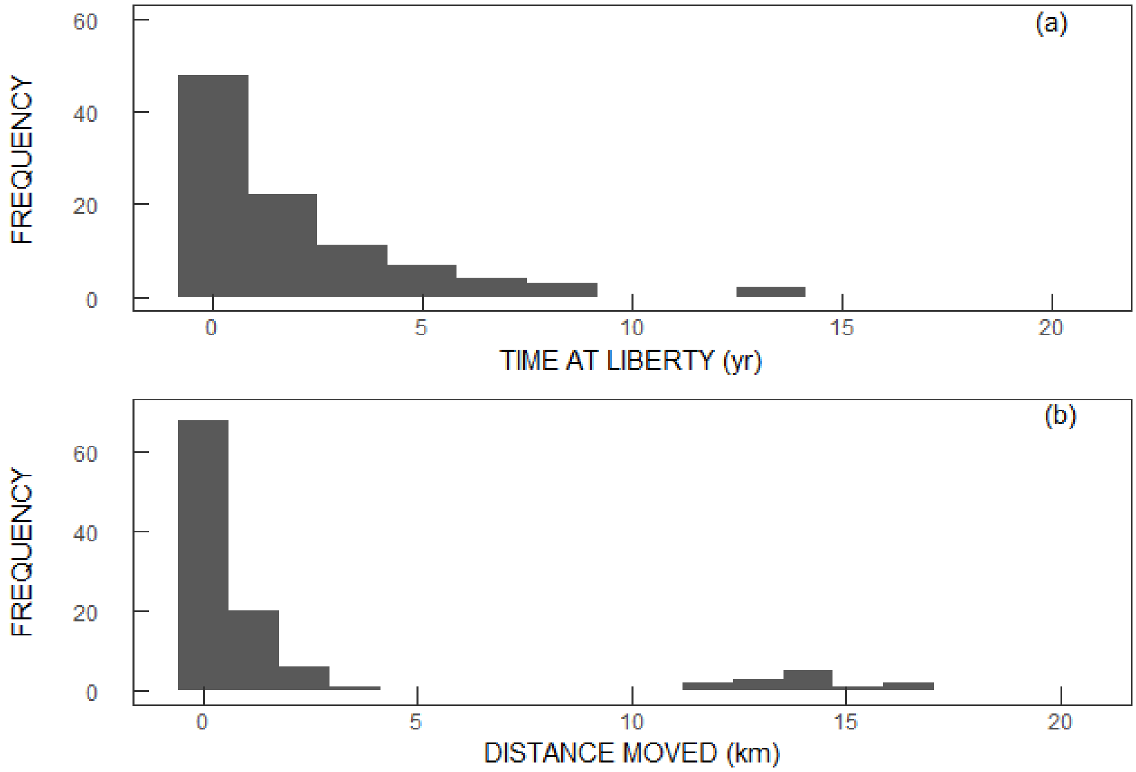

Figure 5. Frequency distribution to display the effect of a) time at liberty (yr) b) distance moved (km) since first recapture event of all recaptured *Triakis megalopterus* (n=97). Individuals recaptured on the same day as their first capture were not included. Time at liberty was binned into year increments.

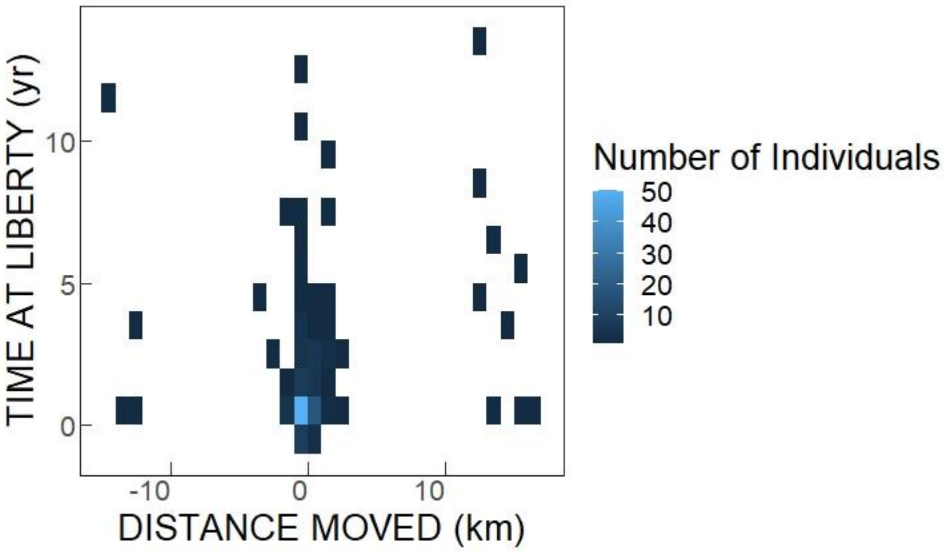

Figure 6. Frequency distribution to display the effect of relative time at liberty (yr) and distance travelled between captures (km) for all recaptured *Triakis megalopterus* (n=177), with negative and positive values representing eastward and westward movements, respectively.

Of the 97 recaptured sharks, 36 individuals (37.1%) were recaptured more than once (multiple recaptures). Most of these (73.81%) were recaptured within 1 km of their original capture location. Only three of the multiple recapture individuals were caught more than 15 km away and the other 33 multiple recapture individuals were captured repeatedly near their initial tagging location (Figure 7). Despite the maximum possible distance to be detected in MPA surveys being 18.8 km, the farthest moving individual, in the study, moved 16.6 km between captures.

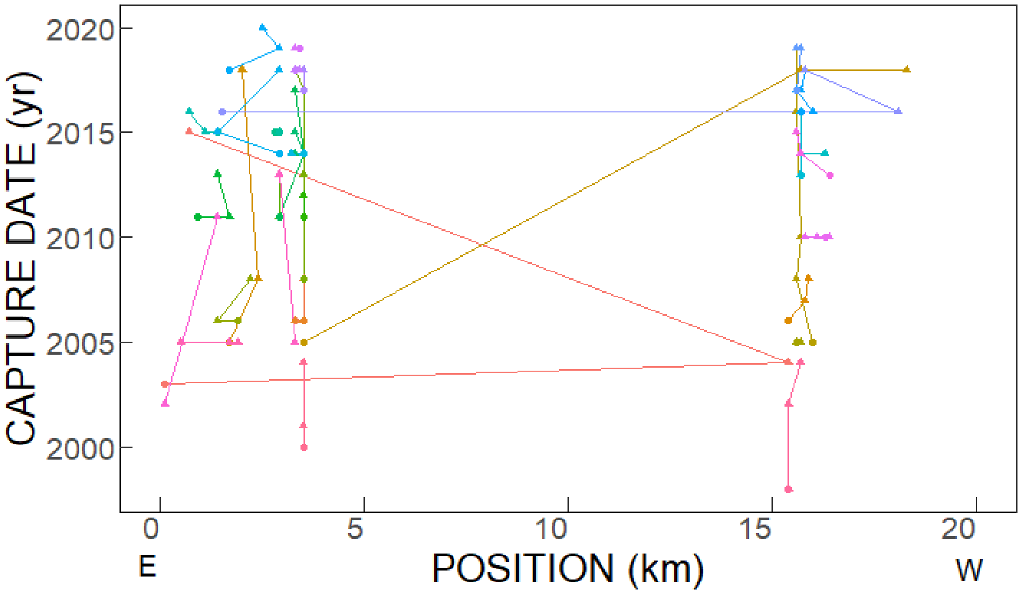

Figure 7. *Triakis megalopterus* multiple (three or more captures) recapture pattern over time and space (n=117 capture observations, 36 tagged individuals). Zero represents Lekkerwate"s first flag, and km increases westward towards Koppie Alleen. Individuals are indicated by different colours. Dots indicate the first capture and triangles indicate recapture events. Line connects subsequent recaptures.

Models of space use

None of the models perfectly explain the space-use within the home range of T. *megalopterus* (Figure 8). DND and DGD explained a similar fraction of the variation in the observed data and provided a better fit (RSS DND =0.045, RSS DGD = 0.030, RSS DFD=0.053) than the DFD. Based on these models *T. megalopterus* in De Hoop MPA have a home range estimated to be 0.9 km (Figure 8) as that is the coastline length that holds a shark for 80% of its time.

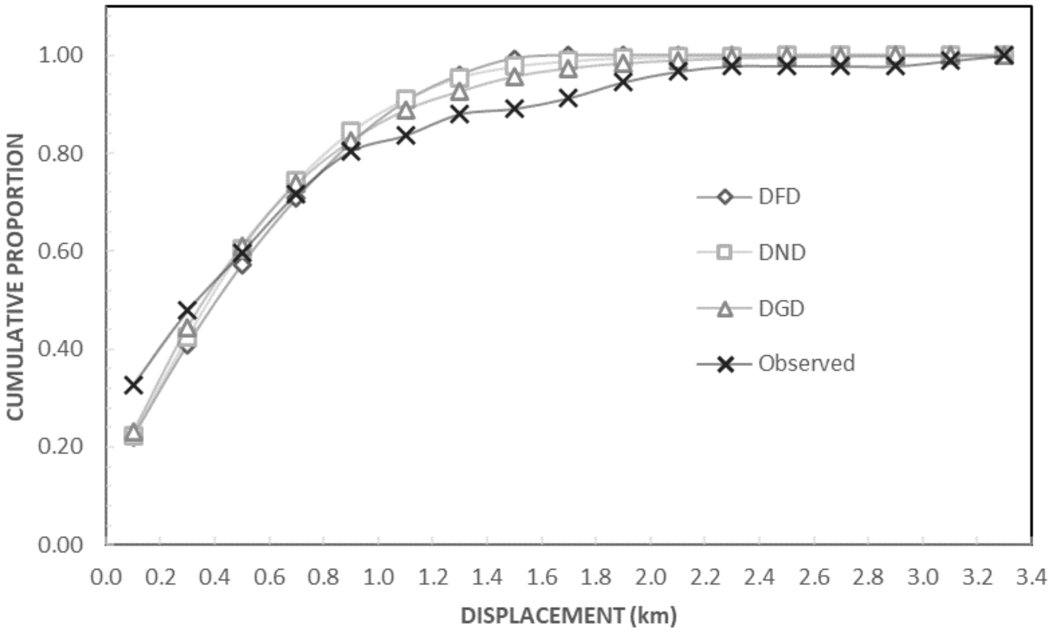

Figure 8. The observed and modelled cumulative proportion of recaptures plotted against increasing distances from the point of release (n=109 observations). Only an individual's first recapture was used. The three models (DFD, DND, DGD) were fitted to these data.

Mortality rate

Male *T. megalopterus* in the De Hoop MPA were estimated to have a higher mortality rate than female *T. megalopterus*. The average estimated male mortality rate was 0.099/yr [95% C.I. 0.088/yr to 0.112/yr] (Figure 9). Females had an estimated mortality rate of 0.072/yr [95% C.I. 0.062/yr to 0.082/yr] (Figure 9). The input mortality rate used for converting length to age did not have a large impact on the estimated mortality rate. Linear regressions of estimated mortality rates as a function of input mortality rates for both sex's yielded slopes of 0.148 for males and 0.227 for females, implying that the initial assumption affected the estimates by 14.8% and 22.7% respectively.

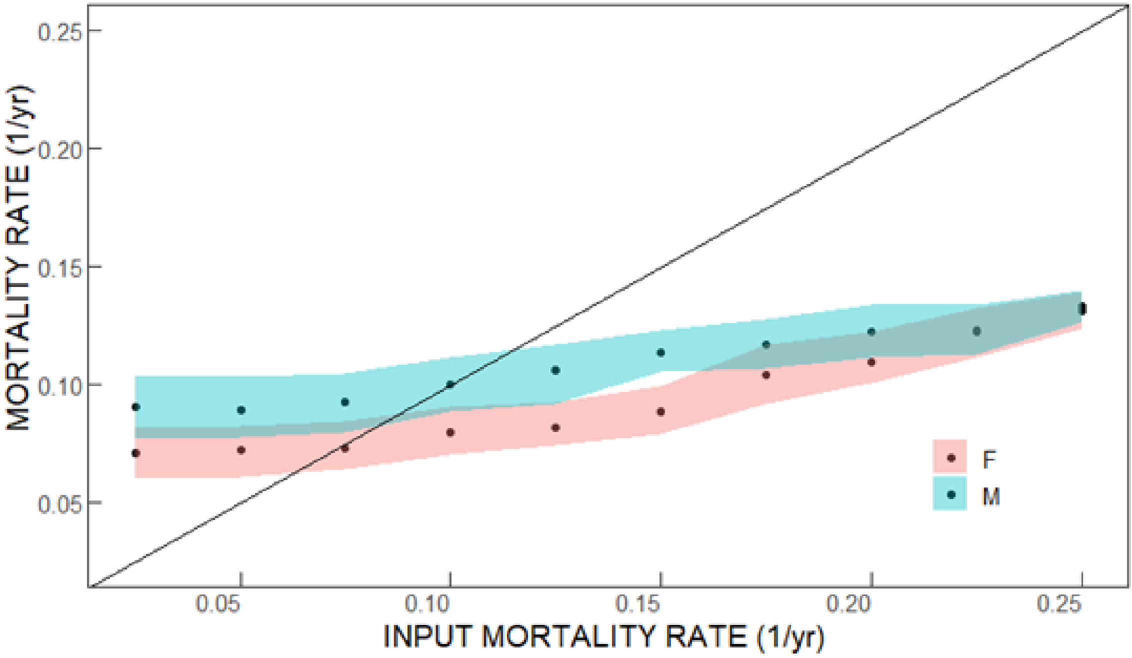

Figure 9. Mean estimated mortality rates (1/yr) of male (M) and female (F) *Triakis megalopterus* with 95% confidence intervals (shaded areas), over a range of initial input mortality rates (n=784; 526 Female, 258 Male). The 1:1 solid line is shown to isolate the rate at which the input and output rates are in agreement.

Survivorship and catchability estimates

The CJS model for survivorship and catchability estimates were negatively correlated (Figure 10). The lowest SLL for females was 313.5 and for males it was 146.1. The best estimates for female survivorship and catchability were 0.830/yr [95% C.I. 0.766/yr to 0.894/yr] and 0.048/yr [95% C.I. 0.034/yr to 0.069/yr] respectively (Figure 10a). The best estimates for male survivorship and catchability were 0.828/yr [95% C.I. 0.74/yr to 0.94/yr] and 0.042/yr [95% C.I. 0.026/yr to 0.072/yr] respectively (Figure 10b). Using equation 11 the survivorship was converted to mortality rate for males [0.189/yr] and for females [0.186/yr].

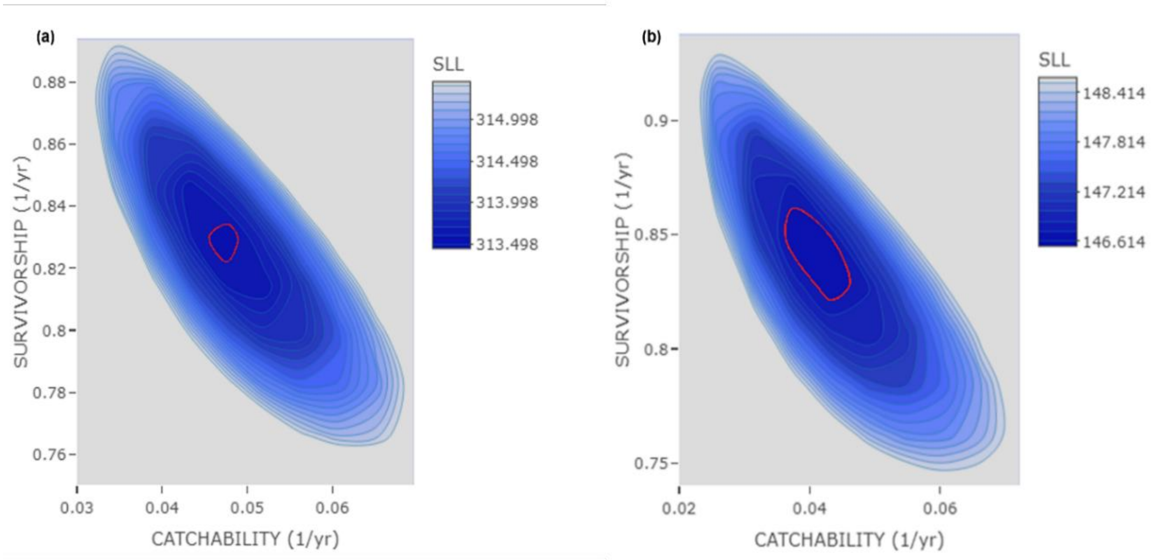

Figure 10. Contour plot of the sum of the negative log-likelihood (SLL) of the data for the CJS model with parameters catchability and survivorship, for (a) female (n=428) and (b) male (n=218) *Triakis megalopterus*. The parameter values of the model are represented by the centre of the ellipse circled in red, and the entire blue ellipse represents the 95% confidence interval of the parameter estimates.

Discussion

Mark-recapture data from 924 *Triakis megalopterus* in the De Hoop MPA provided insight into the population movement and dynamics of this species. The data set originates from a MPA where no fishing was allowed and for which all recaptures were recorded by the survey team. The research oversight of the data collection yielded a higher spatial resolution and more complete recording of recaptures than studies which relied solely on reporting by fishers (Booth et al., 2011; Soekoe, 2016). The higher resolution was put to good effect to estimate mortality rates and home range size and behaviour, which are useful for the management of coastal fishery species (Hueter et al., 2005; Hays et al., 2019). Recaptures made outside of the study area are usually not reported, which may compromise the results of studies into extensive movements. A previous long-term mark-recapture study of *T. megalopterus* movement (Maggs et al., 2019), used an extensive low-resolution data set from exploited areas which showed that long-distances movements are uncommon, but home range-behaviour and mortality rates could not be described.

The period of the study reported here was more than the 20-year generation time estimated by Booth et al., (2011), which implies that individuals from subsequent generations were sampled. The fact that more than one generation was sampled strengthens the accuracy of the mortality estimates. Perhaps more importantly, the estimates nominally represent natural mortality rates, because the data came from a no-fishing area. The separation of natural and fishing induced mortality rates is seldom achieved from fishery-dependent catch-at-age data, and typically only emerges from the fitting of fishery assessment models.

Philopatric behaviours in *T. megalopterus*

The population of *T. megalopterus* that was sampled at De Hoop has a strong tendency for philopatric behaviour, as evidenced by the prevalence of zero and small displacements, repeat usage of localities over periods of up to 13 years and long-term home range stability. Species that yield many recaptures with short capture-recapture distances, such as in this study, are universally associated with philopatry (Hueter et al., 2005; Chapman et al., 2015). Previous studies support philopatry in *T. megalopterus*, as roughly 80% of recaptured sharks were located within a 20-kilometer radius of their release site, regardless of time at liberty (Dunlop & Mann, 2014; Soekoe, 2016). Other studies showed that juvenile and adult *T. megalopterus* have a low (8-24%) likelihood of moving over long distances (>50km) along the southern and western South African coasts (Maggs et al., 2019).

The reported philopatric behaviour of *T. megalopterus* is not uncommon when compared to other coastal shark species. It is a well-documented behaviour in at least 31 shark species from six of the extant eight orders (Chapman et al., 2015). Neither phylogeny, ecology, nor size have been identified as clear underlying reasons for the commonality of philopatry in sharks (Hueter, 2005; Speed et al., 2010; Chapman et al., 2015). Even some large open ocean predators exhibit philopatry e.g., *Carcharodon carcharias* (Domeier et al., 2007), but reef-associated coastal species e.g., *Ginglymostoma cirratum* (Pratt & Carrier, 2001), *Sphyrna tiburo* (Heupel et al., 2006); *Stegostoma fasciatum* (Dudgeon et al., 2008; Dudgeon et al., 2013); Triaenodon obesus (Bond et al., 2012); *Carcharhinus melanopterus* (Stevens et al., 1984; Yates et al., 2016; Weideli et al., 2019) appear more likely to exhibit strong site fidelity.

Chapman et al. (2015) suggest that residency, philopatry and site fidelity may have a greater impact on the structure of coastal shark populations than their ability to disperse over long distances. These movement behaviours can act alone or together to create more distinct population patterns than would be predicted based solely on their potential for movement. Although it is true that home range sizes increase with body size (Kramer & Chapman, 1999) and some *T. megalopterus* (eight individuals) were recaptured outside of the reserve that ranged distances 23-236km, it is possible these individuals are exhibiting home range relocation (Kramer & Chapman, 1999; Attwood & Cowley, 2005) or dispersal rather than representative of the average. Big environmental changes could induce highly philopatric species (like *T. megalopterus*) to relocate. Therefore, the inquiry regarding *T. megalopterus* pertains not to their philopatric tendencies *per se*, but rather to the extent and underlying reasons for such behaviour, clarified through analyses of their home range magnitude and degree of site fidelity.

The high incidences of multiple recaptures of *T. megalopterus* in the De Hoop MPA reinforces evidence of high site fidelity in the species. Although the number of recaptures decreased significantly after one year of time at liberty, individuals captured more than three times were caught very close (<16km) to their initial capture site, suggesting long-term repeated use of sites. Maggs et al. (2019) specifically excluded multiple recaptures in their study and Soekoe et al. (2016) did not report any multiple recaptured *T. megalopterus* individuals and Booth et al. (2011) only mentions one. This disparity among these studies could be caused by the low recapture reporting rate in exploited areas. Soekoe (2016) drew largely on sharks tagged outside the MPA.

High numbers of *T. megalopterus* were consistently caught at Lekkerwater and Koppie Alleen although distributions of capture were not uniform. The distributions of the captures and recaptures peaked towards the western part of Lekkerwater and the eastern part of Koppie Alleen, which corresponded with the higher percentage of rock (relative to sand) present in those locations. Habitat preference could explain the observed abundance as Albano et al., (2021) suggests, however this would require analysis of specific habitat type composition at a micro-scale. The alternative explanation of the skewed distributions of capture positions, is that effort was unevenly applied at each site. Reef habitats are home to more teleosts and sharks, and fishermen like to fish there more frequently since they catch more fish there. Although this explanation should be considered with caution on the grounds that the peaks in the reported number of teleost caught mirror those of *T. megalopterus* across the sites, suggesting that habitat preference has the stronger effect than an uneven effort distribution.

Assuming sharks occupy well defined home ranges, the size of the home ranges can only be adequately estimated if the study sites are large enough to contain them. In the case of the teleost *Dichistius capensis* (also an invertebrate feeder), the home ranges were substantially smaller than the study sites (Attwood & Cowley, 2005). Nevertheless, the right-skewed distribution of *T. megalopterus* displacements had a peak that was vastly smaller than the size of a study site (3.4 km) between 0.9 km and 1.6 km. The cumulative distribution showed that the bulk (90%) of displacements were also contained in an area far smaller than length of study sites.

The model of movement that likely applies to *T. megalopterus* is a combination of frequent and long-term use of a small, circumscribed area, which may be called its home range, and infrequent, long-distance wanderings (Dunlop & Mann, 2014; Maggs et al., 2019). Model analysis of the displacement data suggests that space use is highly concentrated in a small area and that long-term home range size is in the order of 1 km of shore-line length. The offshore dimension is not likely too substantial as the reefs are mostly within the surf zone at the study sites. The practical interpretation of this finding is that an individual may spend 80% of its time in an area of this approximate size, for periods of a decade or more. Movements of *T. megalopterus* between Lekkerwater and Koppie Alleen are very rare (1.4%), despite the equal effort applied at each site, which implies that the home range size is less than 11.9 km distance between the two sites. For the purpose of detailed spatial management, such estimates should be useful as the paucity of large movements by *T. megalopterus* suggests that the population is susceptible to local depletion in areas of even moderate fishing.

The space-use models applied to the displacement data, are based on physical processes (e.g., random walk), and do not accurately represent the habits of sharks which seek out very specific habitat features (e.g., rocky reefs or areas sheltered from currents). As a result, the models do not fully reproduce the high frequency of zero displacements, yet the estimated small home range size for *T. megalopterus* agree with reports on other coastal demersal species of similar sizes and habits (Stevens, 1984; Heupel et al., 2006). In contrast to other coastal sharks which target shoaling fish as their main source of prey (e.g., *Carcharhinus brachyurus*, Lucifora et al., 2009), *T. megalopterus* likely can survive in such a relatively small home range as this coastal habitat has a sufficient supply of resident prey (Vianna et al., 2013; Heyns-Veale et al., 2019), such as molluscs, crustaceans, and teleosts. Additionally, this coastal habitat likely provides safety from larger predatory elasmobranchs and reproductive refugia (Sims et al., 2001).

The home range behaviours explored in the space use models and in particular the estimates of home range size can be in used marine spatial planning and the optimization of MPA design (Mann et al., 2016; Albano et al., 2021). Ecological research can also benefit from additional clarity regarding space use, as the size of an area frequented by an individual must hold sufficient resources for its subsistence. Variation in local abundance, particularly where abundance might be correlated with fishing pressure or other forms of disturbance, should also correspond to the size of home ranges. Small home ranges generally equate to high spatial variability in abundance, whereas wide ranging sharks tend not to exhibit consistent local variations.

The potential effect of sex ratio on estimates of mortality and movement

More females were caught than males at both study sites (2.1F:1M Lekkerwater; 1.8F:1M Koppie Alleen). Similarly, skewed sex ratios towards higher numbers of females were found in *T. megalopterus* by Booth et al. (2011) and in three other South African populations (Soekoe, 2016). Skewed sex ratios likely influence movement and sex-specific population dynamics. Unequal sex ratios are common in shark site fidelity and residency studies (Heithaus, 2001; Pratt & Carrier, 2001; Dudgeon et al., 2008; Brooks et al., 2013; Chapman, 2015; Lea et al., 2016; Swift & Portnoy, 2021), but Otway & Burke (2004) and Domeier et al., (2007) reported equal sex ratios in the shark species they studied.

There are many possible explanations for skewed sex ratios towards females. An uneven sex ratio at birth that remains uneven over time in the population is reported in various shark species (Wearmouth & Sims, 2010) (e.g., *Carcharhinus falciformis,* Varghese et al., 2016). Yet, *T. megalopterus* had an even (1:1) sex ratio when embryos were sampled by Smale & Goosen (1999), and so did similar species *Loxodon macrorhinus* (Gutteridge et al., 2013) and *T. semifasciata* (Nosal et al., 2013). Therefore, there is an apparent influence on the sex-ratio, after birth, in catches of adolescents and adults. For example, female *T. megalopterus* may be more aggressive and outcompete males for the bait and thus be caught more often. Additionally, sex-specific movement could lead to sexual segregation as is seen in some other Triakids (Nosal et al., 2014; Tagliafico et al., 2017). Males may move offshore out of anglers' reach, or females may move to limit mating opportunities and avoid harassment or injury (Sims et al., 2001), thus exhibiting sexual segregation.

Certain life history traits (e.g., gestation, growth rates, and lifespan) of female *T. megalopterus* may be another possible explanation for uneven observed sex ratios. The lengthy gestation period, combined with large offspring size at birth, could reinforce female-specific philopatry to shallow areas as seen in *Loxodon macrorhinus* by Gutteridge et al. (2013) contributing to the observed skewed sex ratios. Sex-specific growth rates and associated longevity could also cause the uneven observed sex ratios. Female sharks typically grow faster, larger, and longer than males. Despite varying growth rates between the sexes, the absence of a significant impact on the sex ratio was evident from the overlap between catchability and survivorship estimates, as well as a convergence in the average total length (TL) of individuals caught. Although, female *T. megalopterus* mortality rates were consistently estimated to be lower than male *T. megalopterus.* This difference may partly explain the skewed sex ratio, as females naturally live longer which increases their frequency in catches.

Mortality and survivorship rates

Estimates of natural mortality rate are used in fisheries science to assess the sustainability of harvesting, alongside rates of fishing mortality, longevity, and fecundity. Even though *T. megalopterus* is uncommonly used for food, it is often recreationally caught and released. Therefore, the current fishing pressures are low for *T. megalopterus*, but the potential vulnerability to fishing pressures are high. The fishing mortality rate for *T. megalopterus* that is predicted to cause a negative population growth is estimated at $F > 0.004$/yr (Booth et al., 2011). This low threshold fishing mortality rate is the result of a lengthy *K*-selected reproductive strategy and late maturity. By providing direct empirically derived, sex-specific annual mortality rates using two data sources; length data and recapture probabilities, this study was able to improve upon mortality estimates by Booth et al. (2011) and Soekoe (2016) who used models of mortality rate based on environmental and life history data (Gruber et al., 2001).

T. megalopterus length data yielded low natural mortality rate estimates of 0.099/yr [95% C.I. 0.088/yr to 0.112/yr] for males and 0.072/yr [95% C.I. 0.062/yr to 0.082/yr] for females. Booth et al. (2011) estimated combined sex natural mortality in *T. megalopterus* from a variety of models based on ambient environmental data and biological characteristics. The median was 0.15/yr, but these estimates do not take population data into account and typically carry a very wide confidence interval. Nevertheless, the median is only slightly higher than what was found from the length data. The difference might reflect the addition of fishing mortality, as Booth et al. (2011) sampled in exploited areas.

The mortality rate estimated from length data analyses also agrees with the range of combined sex estimates reported by Soekoe (2016), who estimated natural mortality of 0.07/yr to 0.14/yr in three South African populations of *T. megalopterus* using catch-at-age data. Soekoe's data were also collected in non-protected areas of southern Africa and their estimates were also not separated by sex because of low sample size. Soekoe's (2016) estimates were either equal to or higher than the natural mortality estimates from De Hoop MPA, but the deviations were not large. Length-based mortality rates may be inflated by the length of caught sharks. The von Bertlanaffy growth function is dependent upon the length/age of individuals included. Therefore, the high proportion of large sharks (above 1500mm) caught in De Hoop, could generate the lower estimated mortality rate. However, the empirical estimates generated by this study may lend some credibility to the models used by Booth et al. (2011) and Soeke (2016), despite the lack of current population data in these models.

The low mortality rates estimated from *T. megalopterus* at De Hoop in comparison to other areas indicate the MPAs success in conserving the species (Albano, et al., 2021). *Triakis megalopterus* is indeed long lived and can grow to relatively large sizes, which is consistent with low natural mortality. Despite its non-endangered IUCN status, harvesting of this species should continue to be limited by recreational fisheries and the fishing industries, as a low mortality rate indicates that a sustainable harvest rate will also be low. The mortality estimates and its confidence interval now also serves a useful benchmark to evaluate total mortality rates in other areas, and by difference, the fishing mortality rate. The new estimates can also serve as a benchmark to evaluate future changes in mortality in the De Hoop MPA.

Annual survivorship rates can be converted to annual mortality rates (equation 9), allowing comparison between both estimated rates. The recapture probability data generated slightly different annual survivorship estimates than what would have been expected based on the length-derived mortality rate estimates. After conversion to an annual mortality rate, the recapture-probability based estimates were lower than the length-based mortality rate estimates with a 0.089/yr difference in males and 0.114/yr difference in females. The greater female difference is driven by females having a lower length-based mortality and both sexes having similar survivability. Despite more females being caught than males (400:204) both sexes had similar probabilities of being recaught with overlapping catchability confidence intervals. The difference between the two types of mortality estimates could be exacerbated by a deflated length-based mortality estimation, caused by the high number of large female capture lengths.

There may be additional factors contributing to the discrepancy between the converted survivorship and the length-derived natural mortality rate, such as tag loss. Survivorship estimates include tag loss and are therefore not directly comparable to the natural mortality estimate based on length data (Minta & Mangel, 1989; Dudgeon et al., 2008; Gaertner & Hallier, 2015). Gaertner & Hallier (2015) found that tag loss in tuna may have caused 2–6% bias in the underestimation of mortality rate. Triakis *megalopterus* are often found bearing tag scars (C. Attwood, University of Cape Town, *Pers. obs*), which confirms that tags are lost. It is not known to what extent *T. megalopterus* experience tag loss. It is possible that tags are being snagged in nets (Govender & Birnie, 1997) or on rocks. As *T. megalopterus* has an affinity to rocky terrains, it may have increased opportunities to rub or scrape against surfaces, potentially increasing the risk of tag loss. However, the terrain may not be the main cause of tags lost or unread, it may be caused by the biofouling that often occurs around the tag (Dickens et al., 2006). No matter the cause of any tag loss and the indirect comparison between the converted survivorship and the length-derived mortality rate, both support a low natural mortality rate.

Post-release predation of tagged and released individuals may also inhibit tag detection. Anecdotally *T. megalopterus* is preyed upon by *Notorynchus cepedianus* (Ebert, 1991), and in another study it was found in the stomach contents of *Carcharias taurus* (Smale, 2005). It is also likely consumed by *Carcharodon carcharias*, which has a very diverse diet and is another opportunistic predator found in the area (Hussey et al., 2012). Although *T. megalopterus* may not be a primary target for larger predators it could influence the two reported mortality estimates. More research is required to understand how mortality estimates are affected by predation.

Conclusion

This study highlights, in conjunction with other studies, that *T. megalopterus* displays a high level of philopatry to De Hoop MPA. The observed philopatric behaviours (consistent capture rates, low individual movement, and multiple recaptures) indicate that these sharks likely frequent small home ranges throughout their lives. This is supported when compared to the identified possible low space-use distributions suggesting that individuals are highly concentrated in a small area (<3.4km) and spend approximately 80% of their time within this area. This study also reports a higher incidence of females than males and suggests that skewed sex ratios towards females could be due to sex-specific longevity or movement. Mortality rates were estimated to be low for both males and females, and survivorship estimates based on tag-recapture probabilities were lower than expected. Both imply long-life expectancy within an MPA. Triakis *megalopterus* populations outside MPA protection are likely very susceptible to negative effects of fishing due to the combination of small home ranges, reproductive life history characteristics, and demographic traits.

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