ASSESSING CONSERVATION MEASURES FOR FIVE SOUTHERN AFRICAN ENDEMIC SHARK SPECIES

by

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Abstract

The South African coast has one of the greatest diversity of Chondrichthyan species in the world with more than 190 species recorded, including 111 species of sharks. Many of these species are endemic to southern Africa (defined as the coastlines of Namibia, South Africa and Mozambique) but are poorly studied, despite their classifications of concern according to the International Union for the Conservation of Nature (IUCN) Red List. However, South Africa continues its efforts to protect the marine environment with a network of 42 Marine Protected Areas established; the Second National Plan for the Protection of Sharks was published in 2022. Sharks, which are characterized by slow growth and maturity at an advanced age, have undergone a rapid decrease in population sizes due to overfishing and habitat loss since the 1970s. To help fill the knowledge gap on endemic shark species, I used long-term datasets to study movement ecology and behaviour in marine protected areas. Study species are dark shyshark *Haploblapharus pictus*, puffadder shyshark *Haploblepharus edwardsii*, pyjama shark *Poroderma africanum*, leopard catshark *Poroderma pantherinum* and spotted gully shark *Triakis megalopterus*. Datasets were composed of non-lethal sampling comprised of mark-recapture, baited remote underwater videos (BRUVs) and acoustic telemetry. Results are then used to assess current protection status of those species and give advice to adapt management policies.

The analysis of capture-recapture data made it possible to determine the distribution areas of each species in the study area as well as the differences in the size and location of these areas between different sexes and maturities. The efficacy of an MPA was discussed for the protection of those species, especially relevant for the puffadder shyshark, classified as “Endangered” on the IUCN Red List. Furthermore, a comparison between growth rate of wild and captive pyjama sharks helped assessing if captive data can be transposed to wild population in order to study endangered species.

Study of the movements of *T. megalopterus* along the coasts of the Western Cape revealed that this species does not specifically use marine protected areas, regardless of sex or sexual maturity. This characteristic suggests that in the future, if the population declines, which is a potential consequence of being caught as bycatch in

longline fisheries, it would be difficult for this population to recover. We also attempted to classify the different areas used by spotted gully sharks in order to identified priority areas for conservation such as nursery areas.

The analysis of the BRUVs revealed that the classic analysis techniques were sometimes not adequate to study the relationships between species. The majority of published analyzes are based on MaxN, an estimate of the abundance of each species, often to estimate the effectiveness of marine protected areas and sometimes by extrapolating on the relationships between species within the food chain. During this project, we tested a new alternative metric (visual co-occurrence) that could be included in future analyzes of this type of video, the goal being to obtain a more refined view of reality and potentially increase knowledge about the role that a specific species plays within the ecosystem.

Overall, the combination of the databases analysed during this project made it possible to increase knowledge on five endemic species of South Africa and southern Africa, specifically on their movement and differences between sexes in habitat use. The protection measures in place remain effective in maintaining these populations but, like *H. edwardsii*, do not allow these species to grow in abundance and thus change their IUCN status. In addition, a potential future decline for these populations due to global warming or anthropogenic impact, causing habitat loss, could be fatal for these species without specific protection measures for each species. Since 2022, several projects aim to increase the area of coastal zone covered by marine protected areas in South Africa, so the results of this study have a direct impact on future conservation and management measures for these species.

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CHAPTER ONE : General Introduction

1. Chondrichthyans

Chondrichthyes include sharks, rays and chimaeras, and are characterized by a skeleton made of tough, flexible cartilage and multiple gill openings (Ebert *et al.* 2021). This particularity happens to be advantageous compared to Osteichthyes, the bony fishes, because cartilage is lighter than bones, helping those species move more efficiently within the water column than fishes with bone-based skeletons (Ebert *et al.* 2021). Based on fossil records, cartilaginous fishes appeared 430 million years ago and have continued evolving, while surviving five mass extinctions (*i.e.* Late Ordovician, late Devonian, permo-triassic, Triassic-jurassic and cretaceous-paleogene). Due to advances in taxonomy and new areas, that were not accessible before, being sampled, additional species are being described regularly (*e.g. Bathyraja chapmani n. sp.* and *Galeus friedrichi* discovered late 2022; Ebert *et al.* 2022a; Ebert & Jang 2022b). The chondrichthyan class is composed of two subclasses, elasmobranchii, including sharks and batoid fishes, and holocephali, representing chimaeras (Figure 1). The major difference between the two subclasses is that holocephali possesses only one gill slit compared to elasmobranchii which possesses five to seven gill slits. Elasmobranchii skin is composed of dermal denticles, scales shaped like teeth unique to each species (Figure 2), while chimaeras have smooth and naked skin. Within the elasmobranchii subclass, there are eight orders of shark species and four orders of ray species. Shark species include more than 500 species; in fact, 540 species are listed on the International Union for the Conservation of Nature (IUCN) Red List.

Shark species are diverse morphologically; they exhibit different numbers of gill slits and dorsal fins, along with different body sizes, ranging from 20 cm (*i.e.* dwarf lanternshark *Etmopterus perryi*) to 18 m (*i.e.* whale shark *Rhincodon typus*), so that adults of the largest shark species is 90 times longer than those of the smallest. Most sharks have a cylindrical shape, but variations exist depending on lifestyle. Some benthic species such as the wobbegong sharks (family Orectolobidae) have a flat body due to their lifestyle, resting on the benthos, and limited movements, using ambush as a feeding strategy. Flat-bodied sharks are distinguished from rays by their pectoral fins, which are small and on each side of the body, similar to other sharks species whereas rays have bigger pectoral fins fused to their heads, giving a different shape (*e.g.* round or diamond shape). Moreover, gill slits are on the upper side of the body for sharks whereas they are located on the ventral side for rays. Due to differences in fin shapes and body structure between species, sharks exhibit three principal types of movements (*i.e.* anguilliform, carangiform and thunniform, Figure 3), these are more or less efficient and adapted to the distance covered by the shark along with its predatory behavior.

Sharks are different to most bony fishes because they use internal fertilization to reproduce. Mature males always possess two claspers and females two uteri. They exhibit three types of reproduction: oviparity where the females lay eggs called mermaid purses, in which embryos are feeding on a yolk sac (Figure 4A);
Yolk-sac viviparity where embryo feeds on a yolk-sac during development and sharks give birth to a live young (Figure 4B); and placental viviparity where embryos firstly feed on yolk-sac until emptied, then the yolk-sac attach to the uterine wall, forming a placenta (Figure 4C). Those different types of reproduction are each advantageous in their own way, but many sharks are K-selected species (slow growth rate and late

maturity) which makes them sensitive to over-exploitation because it takes a long time for the population to grow (Dulvy *et al.* 2014).

Furthermore, shark species are present in many marine habitats, from the ocean floor to coastal waters and also in freshwater environments (*e.g.* bull shark *Carcharinus leucas*) making them an essential taxa in global marine ecosystems (Heithaus *et al*. 2008). Also, species occupy diverse roles within the food web, going from apex predators on top of the food chain, responsible for maintaining a healthy ecosystem by removing weak individuals, to the mesopredator at low trophic levels; thus, sharks are deeply embedded in the well-being of ocean food webs (Heithaus et al. 2008, Roff et al. 2016). In addition to basic senses, such as taste and smell, sharks possess a lateral line, which detects movements in the water column, along with gel filled cells called “ampullae of Lorenzini”, located around their head and mouth that can detect changes in pressure and electric fields. Using electric fields made by living animal help sharks detect and locate prey but they can also detect earth’s magnetic field which help them during migration (Meyer *et al.* 2005; Ebert *et al.* 2021).

Of the c. 540 species of sharks, 168 are listed on the IUCN Red List of endangered species as “Vulnerable”, “Endangered”, or “Critically Endangered”, equivalent to 37% of all shark species listed (IUCN 2022-2). In fact, Chondrichthyes is the most threatened vertebrate class after amphibians (Dulvy *et al.* 2014; Dulvy *et al.* 2021, Figure 5). Moreover, within the 372 species remaining, 50 are listed as “Near-Threatened” meaning that, if the population continues decreasing, they can be facing extinction in the near future. There is thus a need for adequate conservation policies to protect shark species because many populations are decreasing rapidly (Dulvy *et al.* 2021; Pacoureau *et al.* 2021; Jorgensen *et al.* 2022). Shark populations are facing multiple threats, from climate change leading to a loss of habitat, to anthropogenic impacts linked with fisheries and water quality. From 1970 to 2020, the world's pelagic sharks population decreased by more than 70% due to increasing fishing pressure (Pacoureau *et al.* 2021); sharks are not only being caught by targeted fisheries but mostly as bycatch because most fishing methods are not species-specific (*e.g.* gillnets and pelagic longlines, da Silva *et al.* 2015). Many species urgently need protection because, in addition to having their population decreasing, they are also endemic to a specific region of the world, such as Australia where more than 70 species of sharks are endemic. By definition, an endemic species is unique to a distinct geographical region (Oxley 2017) which increases the susceptibility of being threatened, especially due to climate change and habitat loss (Arthington *et al.* 2016). As the population declines, sightings of the species decrease leading to a classification as "Critically Endangered (Possibly Extinct)" that could potentially lead to a global extinction if appropriate species-specific management policies are not implemented (Arthington *et al.* 2016).

2. Study area

One of the most diverse places in terms of chondrichthyan species is South Africa, which ranks 5th, Australia being the most diverse area with 329 species (Ebert *et al.* 2021). South Africa is the home of 191 species of chondrichthyans comprising 111 species of sharks (Ebert *et al.* 2021). Eighteen shark species are endemic to southern Africa (Namibia, South Africa and Mozambique; Table 1) with eight species being endemic to South Africa (Table 1; Ebert *et al.* 2021). Within those endemic species, four are listed as "Vulnerable" and one as "Endangered"; the main threat is exploitation, mainly fishing for human consumption along with habitat loss and degradation (Dulvy *et al.* 2021). Despite current threats to endemic species, a large proportion of research is conducted towards charismatic species such as the great white shark *Carcharodon carcharias* (*e.g.* Bowlby *et al.* 2022; Kock *et al.* 2022; Reinero *et al.* 2022; Towner *et al.* 2022) and the bull shark (Daly *et al.* 2021; Lubitz *et al.* 2023), with few studies focusing on smaller and endemic species (Osgood *et al.* 2019; Albano *et al.* 2021).

South Africa, due to its geographic position between the Atlantic Ocean and the Indian Ocean, has a unique marine biodiversity and ecosystems. The west coast of South Africa has the Benguela Upwelling System providing cold water, one of the four major eastern boundary upwelling systems of the world starting around Cape Point traveling up to Angola in the North. The current brings upwelling of nutrient-rich deep water along the coastline. The warm Agulhas Current follows down the east coast of Africa and gets close to the continental shelf from Maputo to the Agulhas Bank, in the Western Cape of South Africa. The current retroflects after colliding with the Antarctic Circumpolar current and join back the Indian Ocean Gyre. The Benguela and Agulhas currents collide near Cape Agulhas, at the southern tip of Africa, and there is a complex mixing zone extending further west to Cape Point (Teske *et al.* 2011, Figure 6), Due to the two currents, their mixing, and the multiple upwelling sites along the coastline, 150 marine ecosystems have been identified in South Africa (Skowno *et al.* 2019). Along this coastline, six "hope spots” were defined as marine areas of ecological and biodiversity significance by Dr Sylvia Earle (Mission Blue, 2014, https://missionblue.org/). The Cape Whale Coast is one of those hope spots providing habitat for, for example, great white sharks, African penguins *Spheniscus demersus* and southern right whales *Eubalaena australis*. This shows the ecological importance of the area and the need of further studies to increase the knowledge on those ecosystems and assess the need to add protection measures.

This study focuses firstly on the Walker Bay area (Figure 7), part of the Cape Whale Coast Hope Spot, where more than 60 species of elasmobranch are found of which seven are endemic to South Africa. In the west, Walker Bay has Hermanus, known worldwide for whale watching, and Gansbaai known for great white shark cage diving, in the east. The bay is a seasonal marine protected area (MPA) called the whale sanctuary; therefore, it is closed to all fishing activity during whale season from July to November and a restricted area for the rest of the year.

Chapters 2 and 3 focus entirely on species within the Walker Bay; Chapter 4 and 5 go beyond Walker Bay and follows the species of interest along the Western Cape coastline.

3. Species of interest

Dark shyshark Haploblepharus pictus

The dark shyshark or pretty happy shark *Haploblepharus pictus* belongs to the Pentanchidae family, also known as deepsea catsharks (Figure 8A). The body is characterized by a stocky broad head with large nostrils along with nasal flaps reaching the mouth. The colour of the body ranges from light brown to dark with dorsal saddles, can be sparsely dotted with large white spots and a white ventral side. This species is endemic to the southern African region (*i.e.* from Namibia to South Africa) and listed as “Least Concern” on the IUCN Red List (Pollom *et al.* 2019). Dark shysharks can be found in different habitat types (*e.g.* kelp forest, rocky reef and sand) from the surface to 35 m depths. They use the anguilliform swimming method (Figure 3), which is known to be the least efficient (Ebert *et al.* 2021), thus this species is not known to move long distances. This species is oviparous, laying dark coloured egg cases measuring around 6 cm (Figure 9A), with newborn measuring around 11 cm at birth. Adults reach up to 70 cm with males usually bigger than females and maturity reached around 40 cm and 36 cm for males and females respectively. As the dark shyshark is a small-bodied shark with small teeth (approximately 2mm), it feeds on small species such as sea snails, small bony fishes, cephalopods, crustaceans, polychaetes and echinoderms (Ebert *et al*. 2021).

Puffadder shyshark Haploblepharus edwardsii

The puffadder shyshark or happy eddie *Haploblepharus edwardsii* belongs to the Pentanchidae family and is endemic to South Africa (Figure 8B). The body is slender with a stocky broad head. Nostrils are large with expanded nasal flaps reaching mouth. The colour ranges between pale to dark brown, saddles are reddish with darker brown margin, numerous white spots are present, and the ventral side is white. This species is listed as "Endangered" on the IUCN Red List (Pollom *et al.* 2020c) and can be found in similar habitat than the dark shyshark (*i.e.* kelp forest, rocky reef and sand) while the depth range is different, from the surface to 288 m. This species also uses the same anguilliform swimming method as the dark shyshark (Figure 3). Puffadder shyshark also lay egg cases measuring approximately 3.5 cm, orange colour with horizontal stripes (Figure 9B), newborn measure around 8cm at birth. Adults can reach up to 64 cm TL with individuals reaching maturity between 35 and 40 cm. Misidentification between puffadder shyshark and dark shyshark often occurs as the dark shyshark can take different colouration patterns ranging from brown-beige to dark brown with slightly orange saddles. The species possess similar teeth as the dark shyshark (approximately 2mm), thus, feeds on similar species such as small bony fishes, crustaceans, cephalopods and polychaetes (Ebert *et al.* 2021).

Leopard catshark Poroderma pantherinum

The leopard catshark *Poroderma pantherinum* belongs the Scyliorhinidae family and is endemic to South Africa (Figure 8C). The head is characterized by long nasal barbels that reach the mouth, also the body can be recognized by dorsal fin set far back with the first dorsal being much larger than the second. The colour can be pale to almost black with leopard-like rosettes of dark spots. Variations to this pattern exists with spots sizes ranging from very small to very large with partial stripes. This species is listed as "Least Concern" on the IUCN Red List (Pollom *et al.* 2020b) and can be found from the surface to a maximum depth of 274 m. Similar to other catshark species, it uses the anguilliform swimming method (Figure 3). Leopard catsharks lay yellow coloured egg cases measuring approximately 8 cm (Figure 9C) and newborn measure around 11 cm at birth. Adults reach 77 cm with males maturing around 61 cm and female around 51 cm. The leopard catshark possesses small teeth with a size of approximately 2 mm and feeds on small bony fishes and invertebrates (Ebert *et al.* 2021).

Pyjama shark Poroderma africanum

The pyjama shark or striped catshark *Poroderma africanum* belongs to the Scyliorhinidae family and is endemic to South Africa (Figure 8D). The body is easily recognized due to dark longitudinal stripes with a greyish to dark coloured body. Head has prominent short nasal barbel and dorsal fins are set far back on the body. This species is listed as "Least Concern" on the IUCN Red List (Pollom *et al.* 2020a) and can be found from the surface to 100 m. Pyjama sharks lay dark-coloured eggs measuring approximately 12 cm (Figure 9D) and newborns measure between 14 and 17 cm at birth. Adults reach around 120 cm with males maturing at 72 cm and females at 78 cm, which represents the biggest catshark species of interest in this study. This species uses the anguilliform swimming method and feed on relatively bigger species, compared to other species of interest, with a diet composed of bony fish, small sharks (*e.g.* dark shyshark), invertebrates and sixgill hagfish (*Eptatretus hexatrema*; Ebert *et al.* 2021).

Spotted gully shark Triakis megalopterus

The spotted gully shark *Triakis megalopterus* belongs to the Triakidae family also known as houndsharks (Figure 10). The body is characterized by a grey-bronze colour with a white ventral side and numerous small black spots. They possess large broad fins with the first dorsal being almost vertical. It has a broad blunt snout with widely separated small nasal flaps that do not reach the mouth. This species is endemic to southern Africa and is listed as “Least Concern” on the IUCN Red List (Pollom *et al.* 2020d). Spotted gully sharks can be found from the surfline to 50 m depths in sandy or rocky habitats. This species uses the carangiform swimming method (Figure 3) where only the posterior half of the body is undulating making the swimming more efficient as spotted gully sharks are known to swim long distances but also resting on the bottom. They are viviparous with no placenta producing 5 to 15 pups per litter measuring 40 to 45 cm at birth. Adults measure up to 152 cm for males and 208 cm for females and reach maturity around 130 cm and 145 cm respectively. This species possesses small teeth of approximately 4 mm and feeds on crabs, small sharks, bony fishes, and crustaceans (Ebert *et al.* 2021).

4. Methods

Mark-recapture

Mark-recapture methods are commonly used in ecology to assess the abundance of a specific species, when counting all the individuals at the same time is impossible, without the need of lethal sampling. The method is used as much for terrestrial species as for marine species, but recapture rate is smaller in marine environment since study areas are often open, sampling is more difficult, and individuals can move long distances. To make sure the recapture rate is high enough to have significant results, mark-recapture monitoring are usually long-term studies to make sure enough time is given to possible recapture of individuals.

In the marine environment, marking of an individual can be done through tagging but also using photo identification such as unique dorsal fin patterns for blacktip reef sharks *Carcharhinus melanopterus* (Mourier *et al.* 2012) or unique white dot patterns on the backs of whale sharks *Rhyncodon typus* (Davies *et al.* 2012). Usual tagging materials comprise spaghetti tags (or dart tags; Dunlop *et al.* 2013), sheep ear tags (Brevé *et al.* 2016) or passive integrated transponder tags (PIT tags; Sato *et al.* 2013). Types of tags differ between studies due to differences in species morphology and ecology (Dunlop *et al.* 2013).

Depending on the species and the area studied, different information can be obtained from this type of study. Data collected give insight on individual movements (Daly *et al.* 2022), site fidelity (Anderson *et al.* 2011), social structure (Mourier *et al.* 2012), growth rate and age estimate (Dureuil *et al.* 2022), population parameters such as abundance and mortality (Rowat *et al.* 2009). Around the world, different collaborative programs started to provide bigger datasets on species, biggest programmes in terms of number of members is the Cooperative Tagging Centre of the

National Marine Fisheries Service, USA, and the programme that tagged the most animals was the Australian National Sportfishing Association Tagging Project (Dunlop *et al.* 2013). South Africa possesses a tagging programme operated by the Oceanographic Research Institute (ORI) called the Co-operative Fish Tagging Project (CFTP) started in 1984. For this project, dart tags of different sizes are used depending on the species, principally A and D tags. Tags are inserted using a tag applicator under the first dorsal fin for sharks, next to the tail for stingrays and skates, and under the dorsal fin for teleost (Dunlop *et al.* 2013; Figure 11).

Baited Remote Underwater Video (BRUV)

Baited Remote Underwater Videos (BRUVs) are commonly used worldwide to assess marine biodiversity. Compared to other monitoring techniques such as mark-recapture, this technique remains non-invasive for the species and non-destructive for the habitat, enabling researchers to gather data on multiple species at the same time. Originally, observing marine wildlife without disturbing the species was done through underwater visual census where a diver counts individuals, then, it evolved to remote underwater video (RUV), allowing screening by multiple scientists, reducing the number of double counts and individuals missed by the observer.

Recently, bait was added to RUVs creating BRUVs, different types of bait were tested, attracting different types of fish but usually bait is standardized with one kilogram of crushed sardines allowing a wide range of species to be attracted. The biggest difference between RUVs and BRUVs is the fish assemblage, greater abundance is found on BRUVs mostly dominated by carnivorous species. Typically, BRUVs comprise one camera facing a bait cannister, separated by 1 m, the BRUV rig can be plastic or metal depending on the study (Figure 12). Deployment can be horizontal or vertical, horizontal sits on the bottom, recording demersal species while vertical setting allows the observation of pelagic species. Another recent technique developed is stereo-BRUVs (Figure 13); whereas the traditional BRUV comprised one camera, stereo-BRUV have two, allowing the measurement of individuals in the footage. This is advantageous in order to separate juvenile individuals from adults in studies and compare abundance of the two categories.

BRUVs are deployed for a duration of 66 minutes, with six minutes allocated to bait dispersal and 60 minutes of footage are used for analysis. Data recorded during video analysis are the species names, MaxN and time of MaxN. MaxN represents the maximum number of individuals of a species observed in the same frame of a video, acting as an estimate of abundance (Cappo 2010; Whitmarsh *et al.* 2016). MaxN is traditionally used in BRUV studies in order to eliminate double counting, each appearance of a species cannot be considered as a different individual, and therefore, lower the chance of overestimating the abundance. Overtime, MaxN was proven to underestimate the abundance of species (Kilfoil *et al.* 2017; Sherman *et al.* 2018) and other technics were investigated such as time in – time out (TITO), mean count, time of first arrival and maxIND. Mean Count records the number of individuals in a frame at a given interval (*e.g.* 5, 10, 20s; Cappo *et al.* 2011), but increases the risk of missing a species that appears in between those time interval. TITO records the time of entry and exit of each individual, increasing the time of analysis, usually used for behavioral studies (Schobernd *et al.* 2014). Time of first arrival notes the time where a species is appearing in the video for the first time, allowing the estimation of how far the species was from the system (Campbell *et al.* 2015). MaxIND is used when unique marking can be observed on individuals such as stingrays (Sherman *et al.* 2018) or white sharks (Harasti *et al.* 2016).

Acoustic telemetry

Acoustic telemetry is one of the techniques used to track fish movement using high frequency sounds, generally 69kHz, picked up by fixed underwater receivers. It is commonly used on small species (Donaldson *et al.* 2014) or species that are not undergoing broad-scale migrations (Matley *et al.* 2022). Other techniques such as radio telemetry is usually used in freshwater systems as radio signal in marine water are limiting, and satellite telemetry is used on large individuals that undergo broad-scale movements as data is collected from anywhere when the tag breach the surface sending data to a satellite.

Acoustic tags can be implanted surgically in the abdomen of the individual in the case of a small tag or attached externally for bigger individuals. Tags can be equipped with various sensors such as temperature and pressure, but battery life will be shorter. Battery life range from 119 days for a small tag to 3650 days for bigger models. A nominal delay between emission of high frequency sound by the tag is set depending on researchers need and tag model. The sound is then picked up by receivers, attached to the sea floor, when the fish is swimming close. Range of signal detection depends on the power of the tag, turbidity of the water and potentially biofouling on the receiver (Huveneers *et al.* 2016). Data are collected by retrieving the receivers and downloading the data, receivers are also cleaned up of potential biofouling and batteries are changed.

Data collected using acoustic telemetry provides information on species movements and site fidelity (Elston *et al.* 2022), small-scale migration (Furey *et al.* 2020), identifying reproduction/ spawning events through specific migration events (Ingram & Peterson 2016; Danylchuk *et al.* 2019), anthropogenic impact

(Hammerschlag *et al.* 2022), effects of protected areas (Albano *et al.* 2021) and fisheries (Morfin *et al.* 2019). Locations of receivers are essential and differ from one type of study to another. Receivers can be placed in arrays delimiting areas, such as a river divided in multiple areas to monitor juvenile salmonid movements and migration (McMichael *et al.* 2010; Weiland *et al.* 2011). They can also be placed in different locations of interest such as estuaries or protected areas and give insight on habitat use (Espinoza *et al.* 2015; Matley *et al.* 2022).

In South Africa, the Acoustic Tracking Array Platform (ATAP) was created in 2011 after a partnership agreement between the Ocean Tracking Network (OTN), based in Canada, and the South African Institute for Aquatic Biodiversity (SAIAB; Murray *et al.* 2022). The ATAP is a collaborative program, managing receivers along the coastline, collecting, and maintaining data on various marine and freshwater species. The array comprises a mean of 179 receivers per year (± 43) along the coastline of South Africa with some receivers located in southern Mozambique (Murray *et al.* 2022; Figure 14). Equipment used by ATAP is manufactured by Innovasea (Nova Scotia, Canada), comprising VR2W acoustic receivers and coded 69kHz transmitters (Figure 15).

5. Management policies in South Africa

Marine Protected Areas (MPAs) have been implemented in South Africa over a century ago after the Fish Protection act of 1890 (Sowman *et al.* 2011). A MPA represents “any confined area within of adjacent to the marine environment, together with its overlying waters and associated flora, fauna, and historical and cultural features, which has been reserved by legislation or other effective means, including custom, with the effect that its marine and/or coastal biodiversity enjoys a higher level of protection than its surroundings” (CBD 2004). Up to 1940, MPAs in South Africa were a marine manifestation of an existing terrestrial reserve or protecting local resources, thus, low priority was given to fishery management (Sowman *et al.* 2011). Between 1940 and 1970, control of MPAs was transferred from the Cape Province to the Nation state (van Sittert 2002), efforts were made toward fishery industrialization after the war, leading to fishing shifting offshore and coastal MPAs becoming obsolete (van Sittert 1993). In the 1950s, a fall in commercial lobster catches led to the implementation of lobster reserves (Melville-Smith and van Sittert 2005), but those reserves were focused on small-scale and recreational fisheries to maintain exportation industry’s monopoly (van Sittert 2001). The oldest MPA created in South Africa and recognized by marine scientist was established in 1964 in Tsitsikamma, but its proclamation did not involve a full process of consultation with stakeholders, thus, the ”no-take” status has been challenged multiple times over the years (Lombard *et al.* 2020). Since 1970, MPAs have been serving the purpose of protecting marine resources with management and policies made based on scientific findings (Sowman *et al.* 2011). South Africa now possesses a network of MPAs comprising 42 MPAs protecting 5% of the territorial waters (Figure 16).

In 2013, the first South African National Plan of Action for Sharks (NPOA-sharks) was created, helping assess the current status of chondrichthyan species along with guidelines about management, especially fisheries (DFFE 2013). NPOA-sharks I was reviewed in 2020 by an international panel of experts to help improve the plan and identify solutions for the future. South Africa’s Second National Plan for the Conservation and Management of Sharks (NPOA-sharks II) was published in 2022 with a new action table for the next five years (2022-2027). Future research should both be focused on prioritized species such as threatened species but also on endemic species and Data Deficient species on the IUCN Red List. A key action is also to develop shark-specific observer regulations across fisheries, regulate species catch in fisheries along with applying anti-finning legislation (DFFE 2022).

Other programs are aiming at increasing the protection of South Africa's oceans such as the Marine Protected Area Expansion Project by the Wildland Conservation Trust aiming at increasing the area covered by existing MPAs in order to overlap with distribution range of endemic and threatened species occurring in South Africa (Faure-Beaulieu *et al.* 2023).

Concerning species of interest in this thesis, all species are not commercially exploited (dark shyshark, puffadder shyshark, leopard catshark, pyjama shark and spotted gully shark) but all are often caught by recreational anglers with the spotted gully shark increasingly being targeted because of its size (Booth *et al.* 2011). The spotted gully shark is also part of the bycatch of commercial fisheries because of misidentification with other Triakidae species (*e.g.* Soupfin shark *Galeorhinus galeus* and common smoothhoud shark *Mustelus mustelus*; da Silva *et al.* 2015).

6. Thesis aim and outlines

Using multiple long-term datasets from the South African Shark Conservancy (mark-recapture, BRUV and acoustic telemetry), this study aims at filling the knowledge gap on endemic shark species of southern Africa, and to use results to determine if conservation measures are effective for those species, providing more adequate management recommendations if necessary.

Chapter 1 provides a general introduction on the taxa studied, the study area, along with field methods used for this project.

Chapter 2 focuses on long term mark-recapture data collected by SASC and the Oceanographic Research Institute (ORI) from 2014 to 2023. The chapter describes distribution areas and movement patterns of four endemic catshark species within Walker Bay (*i.e.* dark shyshark, puffadder shyshark, pyjama shark and leopard catshark).

Chapter 3 uses mark recapture data from Walker Bay combined with captivity data from the Aquarium of Osaka (Japan) on the pyjama shark in order to investigate differences in growth and development between captive and wild populations. The goal is to assess if information on captive species can give insights on wild populations.

Chapter 4 focuses on the spotted gully shark, endemic to southern Africa, using acoustic telemetry. This chapter uses data collected by ATAP between 2019 and 2022 on individuals tagged in the Western Cape province by SASC, ATAP and the University of Miami. The chapter provides an analysis of the movement ecology of this species, specifically differences in area use (*i.e.* MPA and exploited areas) between sexes using network analysis.

Chapter 5 is using ATAP data between 2016 and 2022, investigating a potential ontogenetic shift in movement of the spotted gully shark. The goal is to highlight potential important areas, especially for juveniles, in the Western Cape that would benefit from adequate management policies in order to conserve the species.

Chapter 6 comprises a theoretical study using BRUV. Taking the example of shark species, we test new analytical approaches to BRUV data in order to improve results accuracy compared to traditional method of analysis (*i.e.* MaxN). The chapter explores co-occurrence between species, highlighting potential predator-prey interactions.

Chapter 7 combines results from Chapters 2 to 6 giving general conclusions about management and conservation of five endemic species of southern Africa.

7. Status of published chapters in this thesis

Chapter 2: Johnson TL, de Bresser JC, **Cottrant E**, Drobniewska NJ, Paulet TG, Underhill LG (2024) Distribution and site fidelity of four endemic catshark species in Walker Bay, South Africa. *African Journal of Marine Science* 46(1): 1-10. Doi: 10.2989/1814232X.2023.2278620.

TLJ: Conceptualization, Methodology, Formal Analysis, Writing – original draft, Visualization; JCdB: Conceptualization, Methodology, Formal Analysis, Writing – original draft, Visualization; **EC:** Investigation, Conceptualization, Methodology, Writing – original draft, Visualization, Supervision; NJD: Resources, Writing - review and editing, Project administration; TGP: Resources, Writing - review and editing, Project administration; LGU: Writing – review and editing, Supervision.

Chapter 3: Kiyatake I, Johnson TL, **Cottrant E**, Kitadani Y, Onda K, Murata M, Drobniewska NJ, Paulet TG, Nishida K (2023) A comparison of the growth and development of pyjama sharks (*Poroderma africanum*) in wild and captive populations. *Journal of Fish Biology*. Doi: 10.1111/jfb.15555

IK: Investigation, Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization; TLJ: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization; **EC:** Investigation, Conceptualization, Methodology, Writing - original draft, Visualization, Supervision; YK: Investigation, Project administration, Writing - review and editing; KO: Investigation, Writing - review and editing; MM: Formal analysis, Writing - review and editing; NJD: Resources, Writing - review and editing, Project administration; TGP: Resources, Writing - review and editing, Project administration; KN: Supervision, Resources, Writing - review and editing.

Chapter 4: Cottrant E, Drobniewska NJ, Johnson TL, Underhil LG, Murray TS, Hammerschlag N, Albano PS, Elston C, McCord ME, Cowley PD, Fallows C, Paulet TG (2023) Network analysis of the endemic spotted gully shark (*Triakis megalopterus*) reveals spatial vulnerability to exploitation in the Western Cape, South Africa. *African Journal of Marine Science* 45(4): 273-283. Doi: 10.2989/181423X.2023.2271959

EC: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization; NJD: Investigation, Resources, Writing - review and editing, Project administration; TLJ: Formal analysis, Writing - review and editing; LGU: Supervision, Writing - review and editing; TSM: Writing - review and editing, Data curation; NH: Writing - review and editing, Resources, Funding acquisition; PSA: Writing - review and editing, Investigation; CE: Writing – review and editing; MEM: Resources, Investigation, Funding acquisition; PDC: Investigation, Resources, Funding acquisition; CF: Writing - review and editing, Resources, Investigation; TGP: Investigation, Resources, Writing - review and editing, Supervision.

Chapter 5: Cottrant E, Morrison JH, Elston C, Murray TS, Watson RGA, Drobniewska NJ, Underhill LG, Hammerschlag N, Albano PS, McCord ME, Cowley PD, Fallows C, Paulet TG. Movement and site fidelity of the spotted gully shark *Triakis megalopterus* in the Western Cape, South Africa.

EC: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization; JHM: Conceptualization, Formal Analysis, Writing – review and editing, Visualization; CE: Conceptualization, Methodology, Writing – review and editing; TSM: Conceptualization, Methodology, Writing - review and editing, Data curation; RGAW: Software, Methodology, Writing – review and editing; NJD: Investigation, Resources, Writing - review and editing, Project administration; LGU: Supervision, Writing - review and editing; NH: Writing - review and editing, Resources, Funding acquisition; PSA: Writing - review and editing, Investigation; MEM: Resources, Investigation, Funding acquisition; PDC: Investigation, Resources, Funding acquisition; CF: Writing - review and editing, Resources, Investigation; TGP: Investigation, Resources, Writing - review and editing, Supervision.

Chapter 6: Cottrant E, Underhill LG, Drobniewska NJ, Paulet TG. An alternative theoretical approach to the interpretation of Baited Remote Underwater Video data.

EC: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization; LGU: Conceptualization, Supervision, Writing – review and editing; NJD: Investigation, Resources, Writing - review and editing, Project administration; TGP: Investigation, Resources, Writing - review and editing, Project administration.

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9. Figures

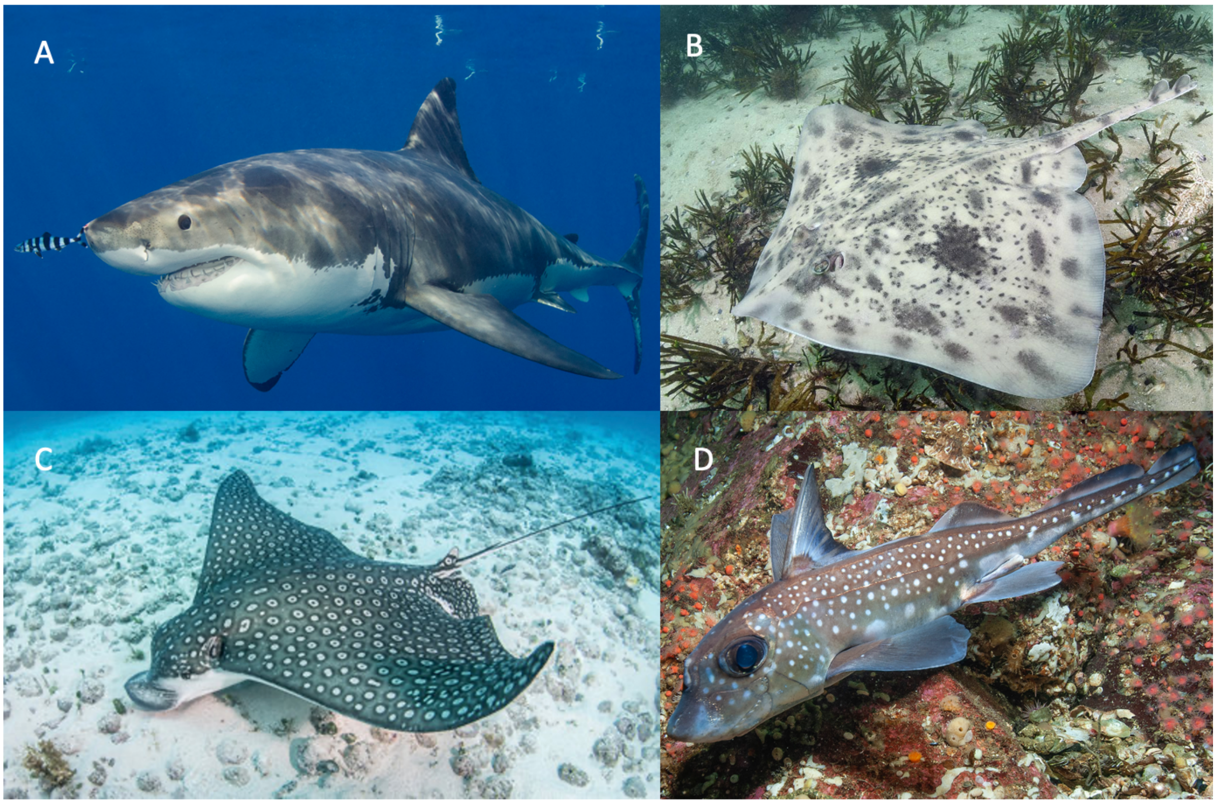

Figure 1: Class Chondrichthyes: (A) sharks, (B) skates, (C) rays and (D) chimaeras (Photo ©Andy Murch).

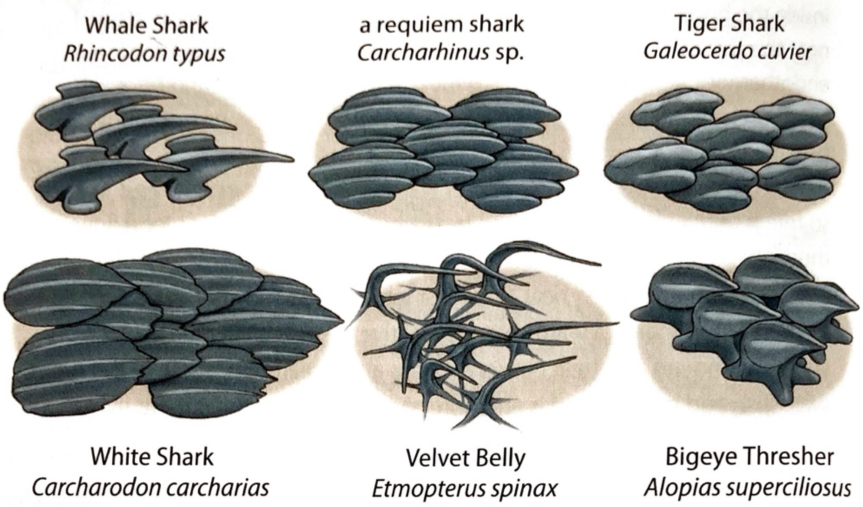

Figure 2: Variation in morphology of dermal denticles from different shark species (from Ebert *et al.* 2021).

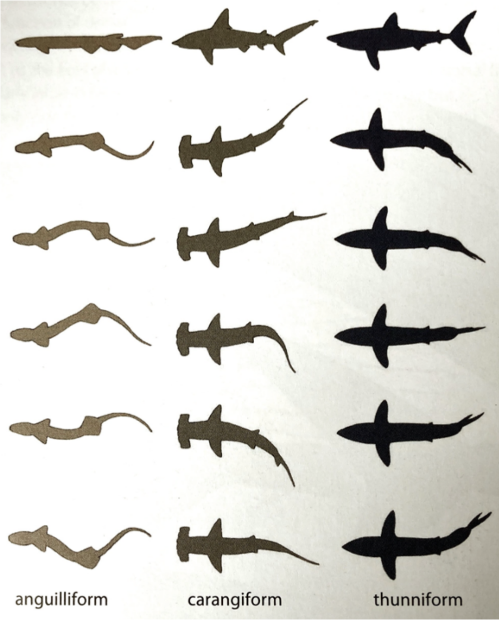

Figure 3: The three major swimming methods of sharks, seen from above (from Ebert *et al.* 2021).

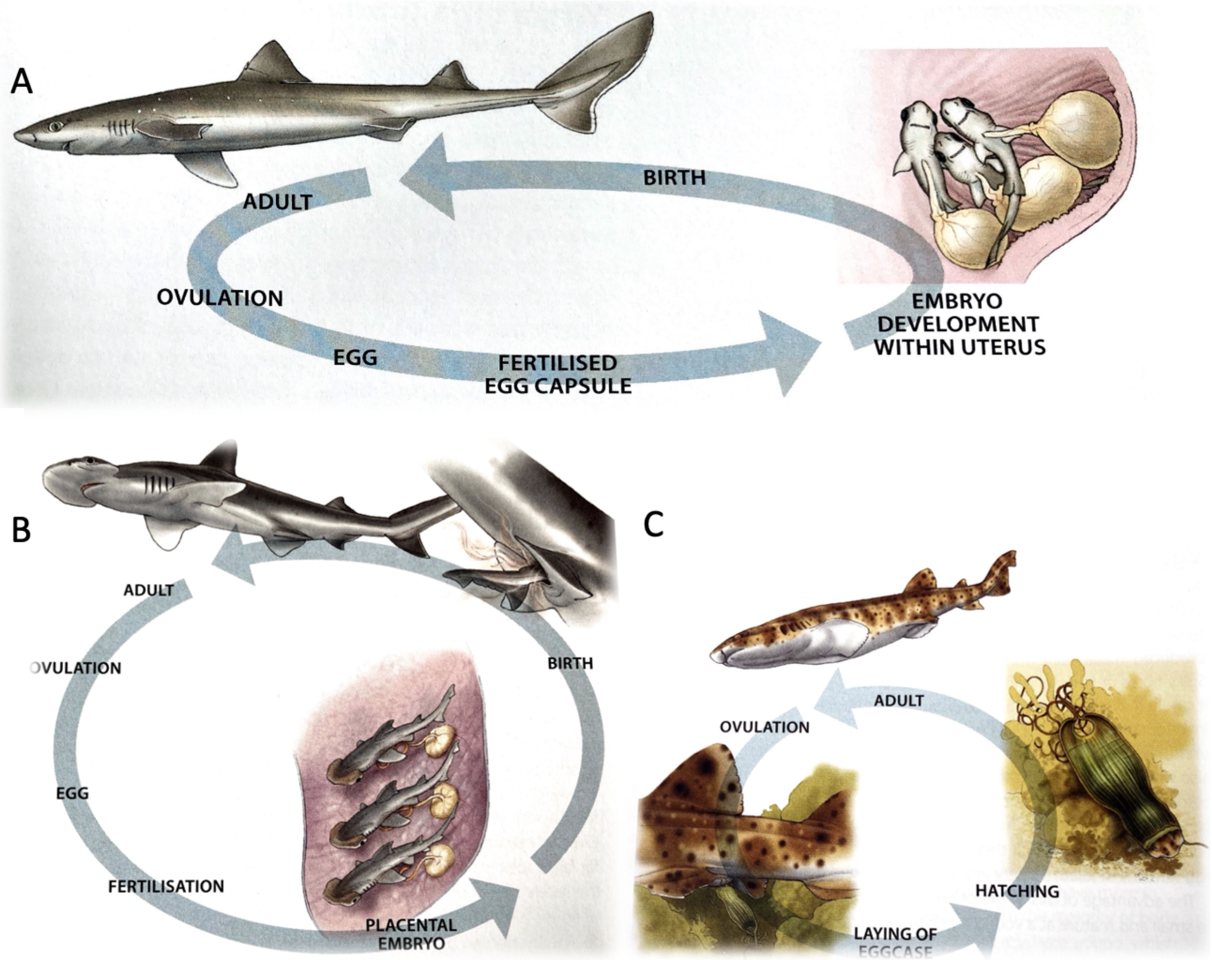

Figure 4: Shark reproduction types: (A) Yolk-sac viviparity, (B) Placental viviparity and (C) Oviparity (from Ebert *et al.* 2021).

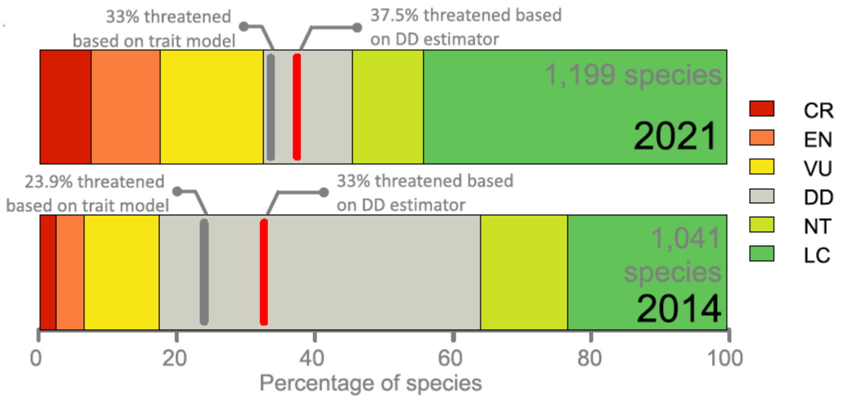

Figure 5: Difference in IUCN Red List status between 2021 (upper bar) and the first assessment (lower bar, 2014). This current threat is much greater (37.5%, estimated range 32.6%–45.6%, red line in upper bar), based on the observed number of threatened species combined with the estimated number of Data Deficient (DD) species that are likely to be threatened, than the 24% estimated using a trait-based model in 2014 (gray line in lower bar) and more similar to the estimate from the IUCN DD estimator (red line in lower bar, 33%, range 17%–64%; from Dulvy *et al.* 2021).

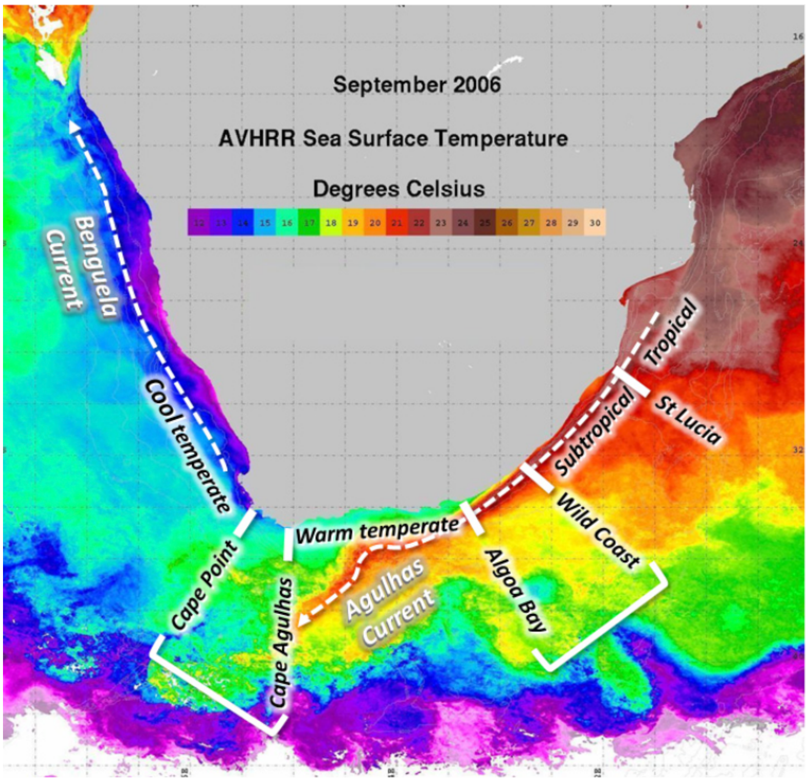

Figure 6: Location of south african currents and phylogeographic breaks (from Teske *et al.* 2011).

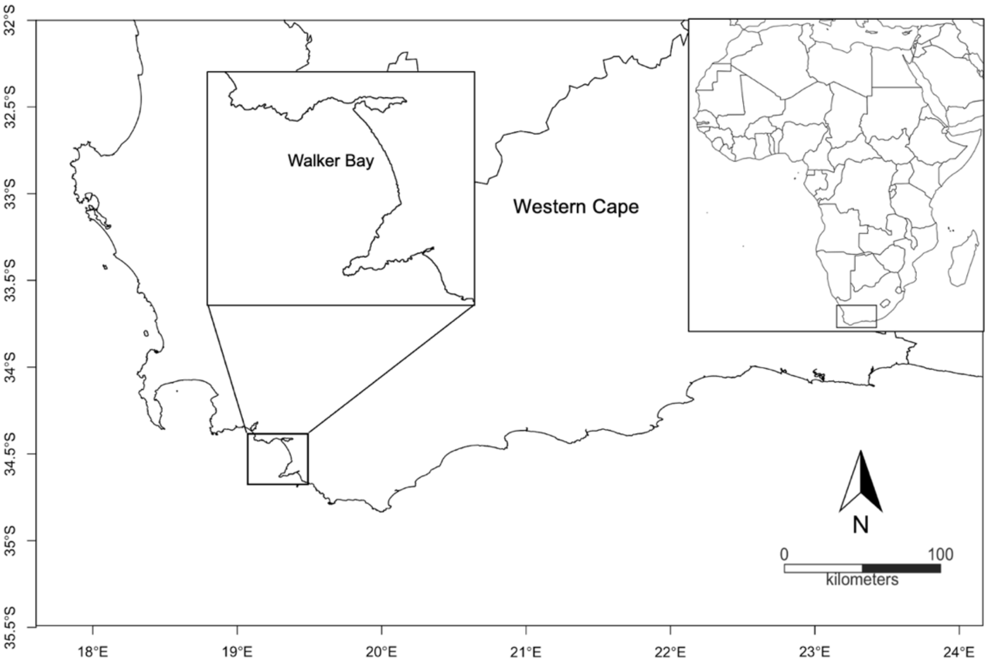

Figure 7: Map of the South African coastline with Walker Bay, the principal research area.

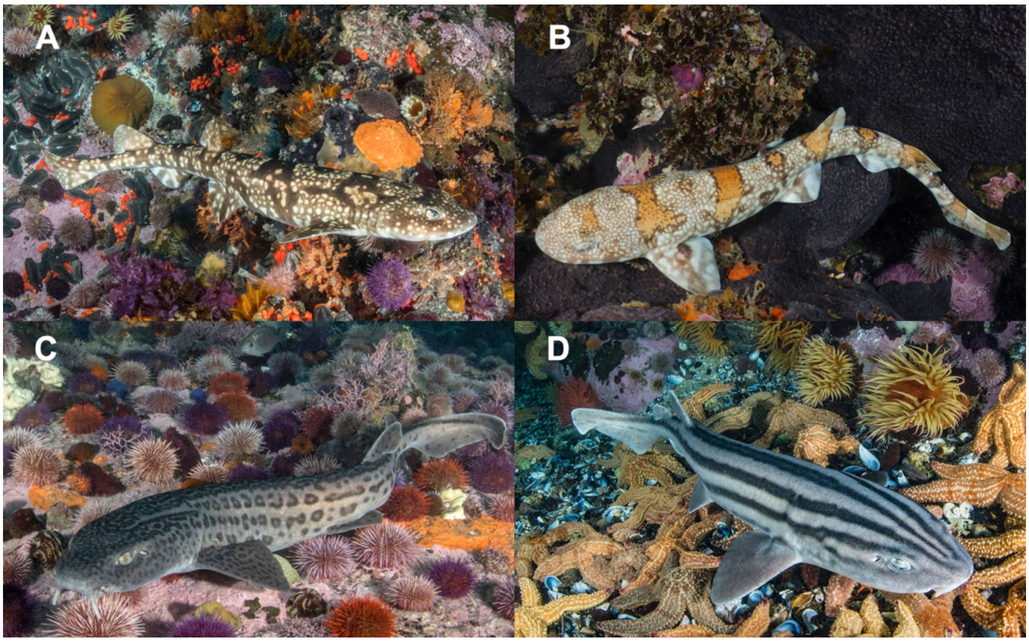

Figure 8: Species of interest belonging to the Pentanchidae and Scyliorhinidae family: (A) Dark shyshark, (B) Puffadder shyshark, (C) Leopard catshark, (D) Pyjama shark. (Photo ©Andy Murch).

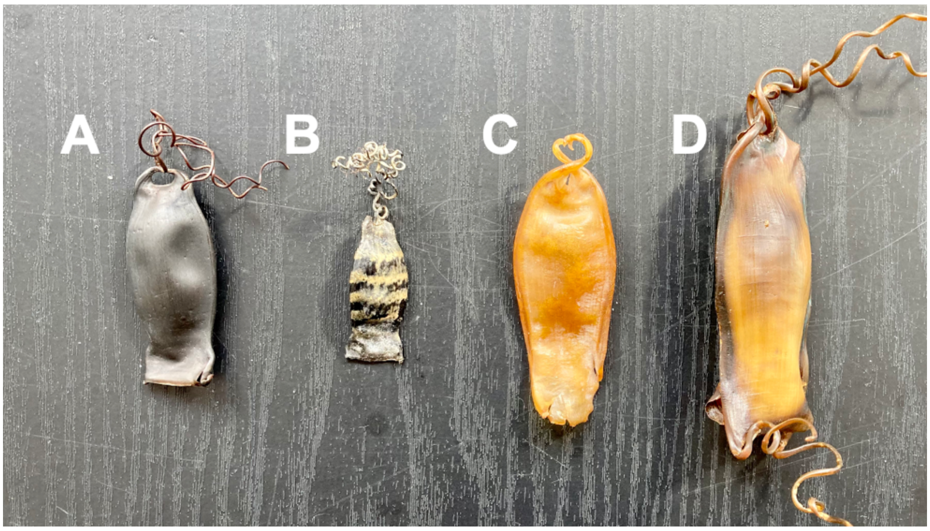

Figure 9: Dried egg cases of Pentanchidae and Scyliorhinidae species: (A) Dark shyshark, (B) puffadder shyshark, (C) leopard catshark, (D) pyjama shark.

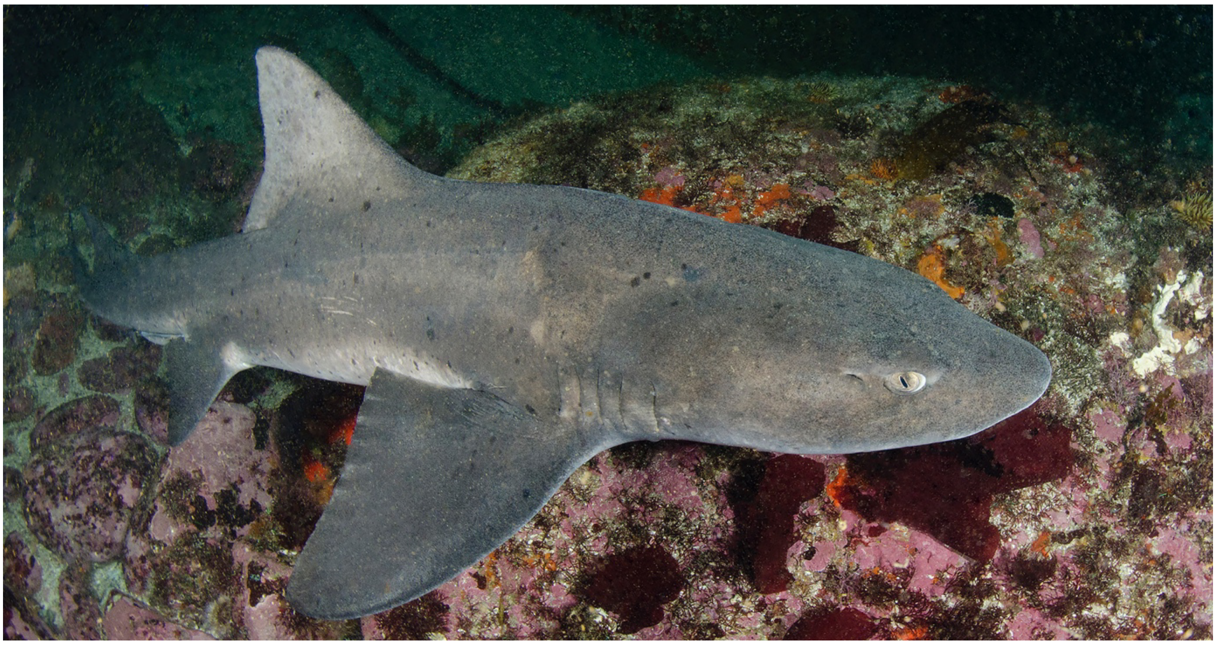

Figure 10: Spotted gully shark (Photo ©Andy Murch).

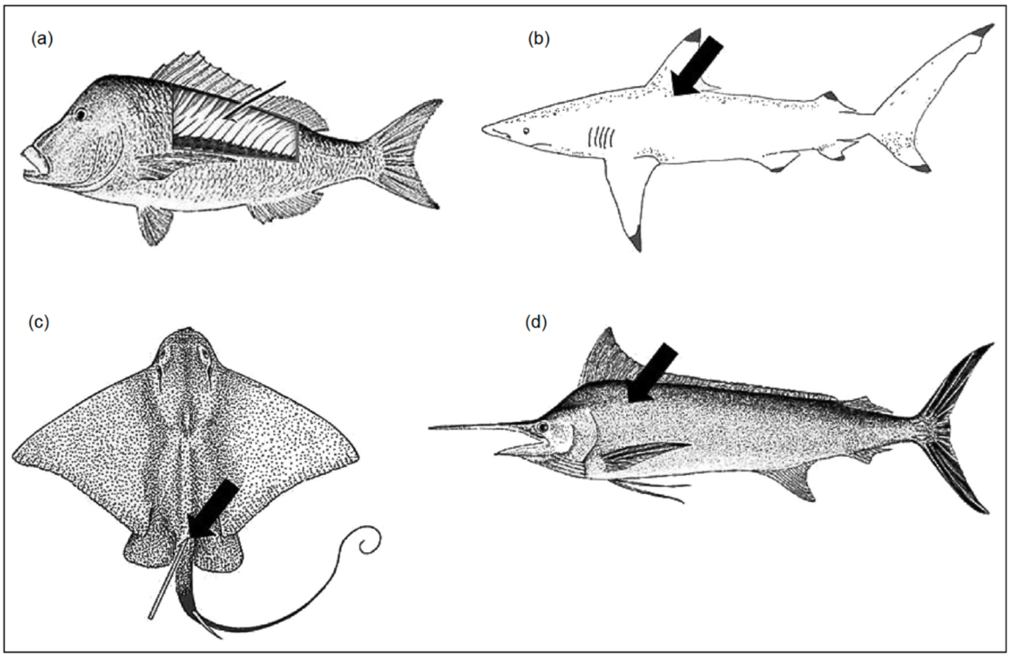

Figure 11: Tagging positions for (a) teleosts, (b) sharks, (c) skates and rays, and (d) billfish (from Dunlop *et al.* 2013).

Figure 12: Baited remote underwater video equipment with the camera facing the bait canister, attached to a steal rig.

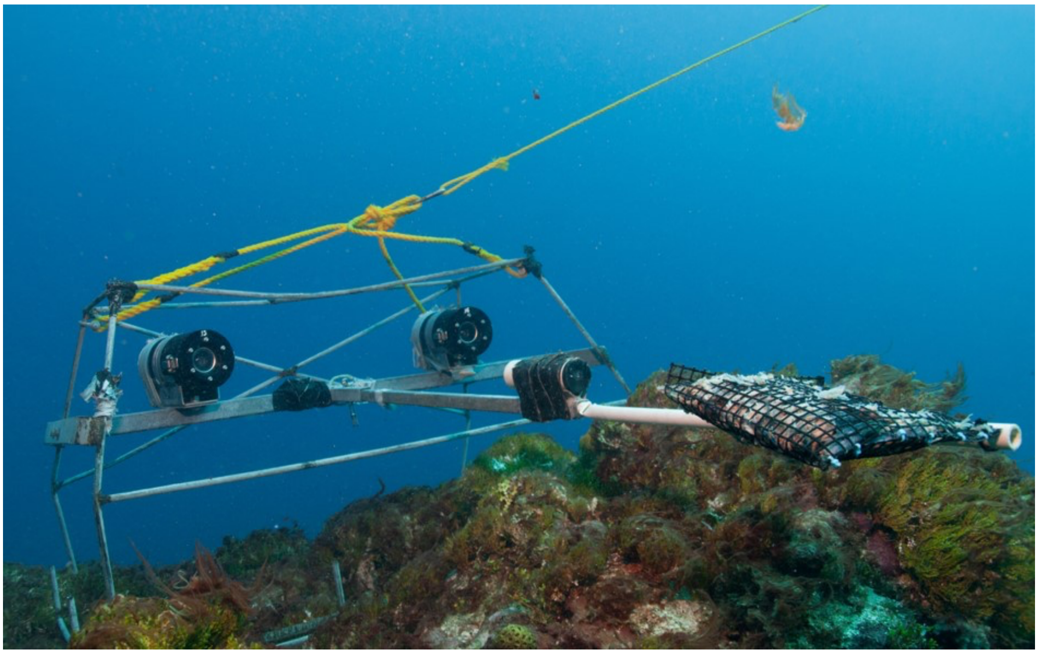

Figure 13: Stereo baited remote underwater video setting using two cameras.

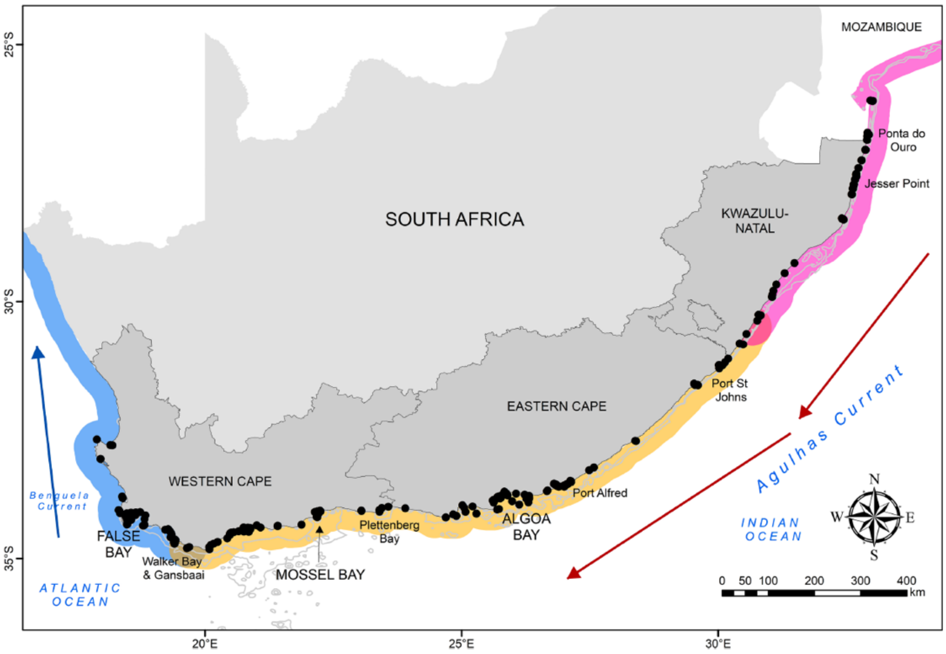

Figure 14: Locations of acoustic receivers along the South African coastline and southern Mozambique from the Acoustic Tracking Array Platform (from Murray *et al.* 2022).

Acoustic receiver

Acoustic transmitters

Figure 15: VR2W acoustic receiver and coded 69kHz transmitters used during this project manufactured by Innovasea, Nova Scotia, Canada.

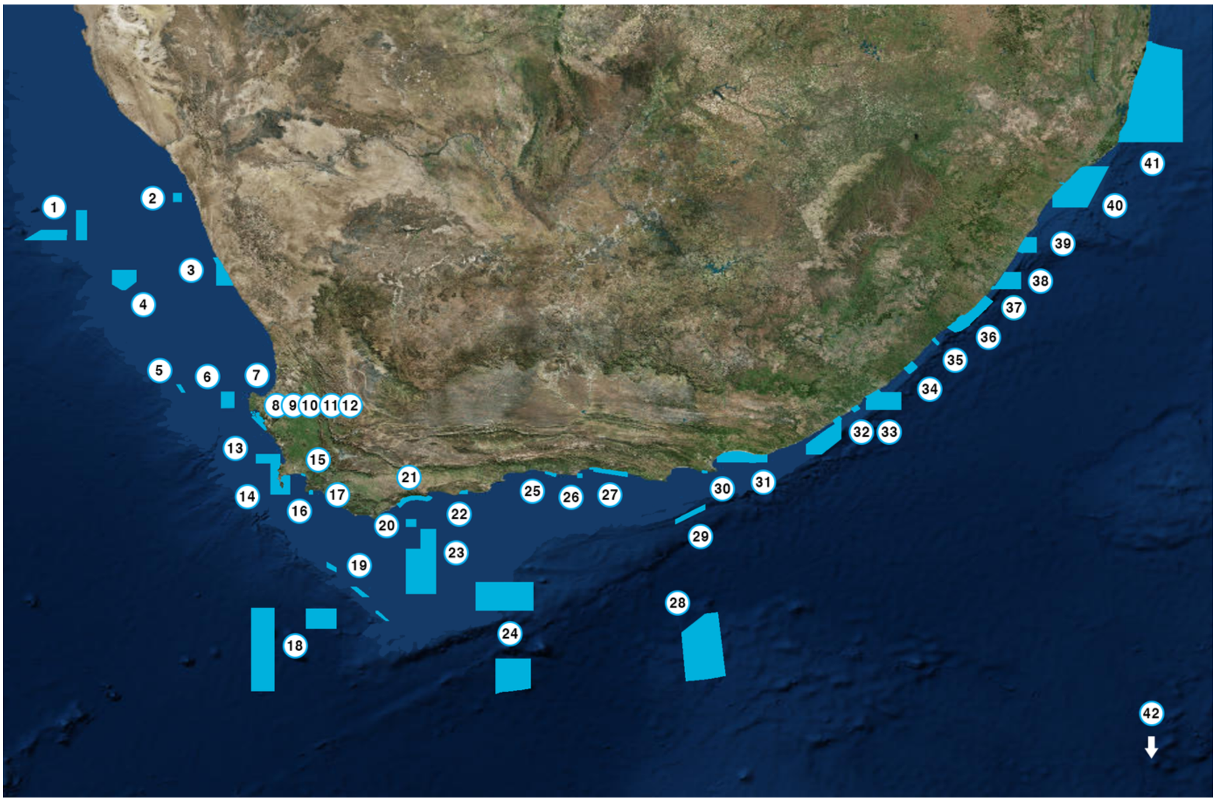

Figure 16: Locations of 41 marine protected areas in South Africa with one remaining area located in the Southern Ocean.

10.Tables

Table 1: List of shark species endemic to southern Africa (Namibia, South Africa and Mozambique). Species of interest in this thesis are shown in bold.

Order	Family	Common name	Scientific name	Conservation status (year assessed)
Carcharhiniformes	Hemigaleidae	Whitetip weasel shark	*Paragaleus leucolomatus*	Vulnerable (2020)
Carcharhiniformes	Pentanchidae	Brown shyshark	*Haploblepharus fuscus*	Vulnerable (2020)
Carcharhiniformes	**Pentanchidae**	**Dark shyshark**	***Haploblepharus pictus***	**Least Concern (2019)**
Carcharhiniformes	Pentanchidae	Eastern shyshark	*Haploblepharus kistnasamyi*	Vulnerable (2019)
Carcharhiniformes	Pentanchidae	Honeycomb izak catshark	*Holohalaelurus favus*	Endangered (2020)
Carcharhiniformes	Pentanchidae	Izak catshark	*Holohalaelurus regani*	Least Concern (2020)
Carcharhiniformes	**Pentanchidae**	**Puffadder shyshark**	***Haploblepharus edwardsii***	**Endangered (2020)**
Carcharhiniformes	Pentanchidae	Saldanha catshark	*Apristurus saldanha*	Least Concern (2019)
Carcharhiniformes	Pentanchidae	Tiger catshark	*Halaelurus natalensis*	Vulnerable (2020)
Carcharhiniformes	**Scyliorhinidae**	**Leopard catshark**	***Poroderma pantherinum***	**Least Concern (2020)**
Carcharhiniformes	**Scyliorhinidae**	**Pyjama shark**	***Poroderma africanum***	**Least Concern (2020)**
Carcharhiniformes	Scyliorhinidae	Yellowspotted catshark	*Scyliorhinus capensis*	Near Threatened (2019)
Carcharhiniformes	Triakidae	Flapnose houndshark	*Scylliogaleus quecketti*	Vulnerable (2019)
Carcharhiniformes	**Triakidae**	**Spotted gully shark**	***Triakis megalopterus***	**Least Concern (2020)**
Carcharhiniformes	Triakidae	White spotted houndshark	*Mustelus palumbes*	Least Concern (2020)
Hexanchiformes	Hexanchidae	Southern african frilled shark	*Chlamydose lachus africana*	Least Concern (2019)
Squaliformes	Squalidae	Long-snouted African dogfish	*Squalus bassi*	Least Concern (2020)
Squatiniformes	Pristiophoridae	Sixgill sawshark	*Pliotrema warreni*	Least Concern (2020)

CHAPTER TWO: An exploration of distribution and site fidelity of four endemic catshark species in Walker Bay, South Africa

1. Introduction

In both terrestrial and marine ecosystems, apex predators have undergone large population decreases, often resulting in them being classified into the greater threat categories (Stier *et al*. 2016). As a by-product, research has been focused on "charismatic" apex predators, at the expense of mesopredators (Prugh *et al.* 2009; Tambling *et al.* 2018). This pattern is also true for the elasmobranchs, with apex predator sharks being extensively researched (Gallagher and Klimley 2018; Huveneers *et al.* 2018; Gausmann 2021). Catsharks are mesopredators (Caut *et al.* 2013; Navarro *et al.* 2016; Osgood *et al.* 2019) and are underrepresented in ecological research, apart from a small number of exceptions such as the small-spotted catshark *Scyliorhinus canicula* (Aydın 2023; Falco *et al.* 2023; Reneiro *et al.* 2023). South Africa is a hotspot for catshark species, with five genera and 13 species of deepwater catshark (Pentanchidae) and three genera and four species of catshark (Scyliorhinidae) (Ebert *et al*. 2021a). Thirteen catshark species are endemic to southern Africa (Namibia, South Africa and Mozambique) and are thus at considerable risk from localised depletion and habitat degradation (Ebert *et al*. 2021a; IUCN Species Survival Commission 2012).

The puffadder shyshark *Haploblepharus edwardsii*, dark shyshark *Haploblepharus pictus*, leopard catshark *Poroderma pantherinum* and the pyjama catshark *Poroderma africanum* are endemic to the southern African region. The latter three species fall under the threat classification of Least Concern on the International Union for

Conservation of Nature Red List (IUCN) (Pollom *et al.* 2019, 2020a, 2020b), while the puffadder shyshark is classified as Endangered due to a significant population decline (Pollom *et al.* 2020c). All four species are oviparous and have a broad diet including small fish and invertebrates and are also known to be cannibalistic. *H. edwardsii* and *H. pictus* grow to a similar maximum length of 64 cm and 69 cm respectively, while *P. pantherinum* and *P. africanum* have greater variation in size, growing to 77 cm and 109 cm respectively (Ebert 2021b). There is a significant data gap concerning the movement ecology of these four endemic catsharks, with only one study using mark-recapture in the Eastern Cape, South Africa, on the movement patterns of *H. edwardsii, P. pantherinum, P. africanum,* as well as the brown shyshark *Haploblepharus fuscus* (Escobar-Porras 2009). In that study, the catshark species showed large levels of site fidelity and large travel distances of > 150 km across the study region, a pattern reflected in other catshark species such as *S. canicula* (Sims 2003; Jacoby *et al.* 2012) and the nursehound shark *Scyliorhinus stellaris* (Compagno 1984).

This study aims to build on the research of Escobar-Porras (2009) on endemic catshark ecology. At the time of that publication, *H. edwardsii* was listed under the classification Near-Threatened (Escobar-Porras 2009). The species was subsequently reevaluated to Endangered therefore increasing the importance for providing new data to aid in conservation. We describe the distribution area of each species, as well as the site fidelity and travel distances of each species across different regions of Walker Bay, Western Cape, South Africa. The results of this study will help in the development of well-substantiated management strategies which are beneficial for the four studied species themselves and their respective ecosystems.

2. Methods.

Data collection and study area

Data were collected over eight years (January 2014–June 2022), in all months of each year. Primary data were collected by the South African Shark Conservancy (SASC), supplemented by data submitted to the Oceanographic Research Institute by anglers from 2014 to 2022 (Jordaan and Mann 2021, 2022). Sampling was weather-dependent and no sampling was conducted between March 2020 and January 2021 due to the COVID-19 pandemic. A total of 27 named fishing locations were sampled in Walker Bay [34°30'S, 19°20'E], in addition to a further 23 unnamed fishing locations (Figure 1). Sharks recaptured outside of the sampling area were also included to calculate travelling distance. Research was conducted under research permit numbers RES2014-35, RES2016-23, RES2017-31, RES2018-59, RES2019-61, RES2020-16 and RES2022-67 issued by the Department of Forestry, Fisheries and the Environment of South Africa and ethics clearance 2021/V15/LU issued by the Faculty of Science Animal Ethics Committee of the University of Cape Town.

Walker Bay is characterised by three distinct habitat types: rocky reefs, kelp forests and sand. It is a biodiversity hotspot due to the nearby mixing of the cold Benguela Upwelling System and warm Agulhas Current which meet at the Cape of Good Hope, about 80 km northwest of the bay (Osgood *et al.* 2019). A small region of Walker Bay (45 km^2) has been designated as a seasonal Marine Protected Area (MPA) since 2001 (1 July–30 November), to protect the cetacean population and the remaining 60 km^2 of Walker Bay is designated as a restricted area (Government Gazette 22335 2001). The most sampled sites were Old Harbour, New Harbour and Rietfontein (Figure 1). Old Harbour and Rietfontein are characterised as a shallow (< 10 m) kelp forest with significant cover of sea bamboo *Ecklonia maxima* and patches of upright wrack

Bifurcariopsis capensis, New Harbour is characterised as a shallow (< 10 m) sandy habitat.

Mark-recapture

Sharks were caught either by fishing (handline, rod and reel, or longline) or by hand while snorkelling. Handlines comprised of 1.2-mm nylon monofilament line and de-barbed circle hooks ranging in size from 6’0 to 12’0 to target various shark species and sizes. Hooks were baited with sardine *Sardinops sagax,* Pacific saury *Cololabis saira*, common octopus *Octopus vulgaris*, or Cape Hope squid *Loligo reynaudii*. Bait canisters containing 1 kg of defrosted, crushed sardine were also deployed to attract specimens. For longline fishing, a demersal longline 300 m in length was deployed. The longline had a weight of 10 kg attached to each end which served as an anchor and a surface buoy. Twenty gangions with circle hooks (sizes 8–12’0) were attached 15 m apart along the main line and baited with the same bait as used for handlines. Longlines were set for 1.5 to 2 hours. Hand capture while freediving was conducted in water < 8 m deep. Captured sharks were held underwater in a soft mesh cage (30-mm mesh size, 600 mm diameter and 250 mm depth) for the duration of the dive session (~1 hour). Retention in the mesh cage was deemed ethically suitable as catsharks are buccal pumpers and thus lack of movement does not cause metabolic stress (Ebert *et al.* 2021b). Sharks with a lateral span smaller than the mesh size were taken directly to the laboratory to prevent escape and held in tanks until processing after the dive session.

Captured sharks were placed on a measuring mat and had their eyes covered with a wet cloth to minimise stress. The total length (TL in cm) was recorded and sex was determined by the presence or absence of claspers.

Individuals were tagged using external dart tags (Dunlop *et al.* 2013). The tag number of recaptured and newly tagged individuals was recorded with morphometric data. Animals less than 30 cm TL were not tagged due to their small size.

Recapture rate (R) for each species was calculated using the equation:

$$R = \frac{r}{N}$$

Where r is the total number of sharks recaptured and N is the total number of individuals captured.

Data analysis

All analyses were conducted using RStudio with R version 4.2.0 (RStudio Team 2022). All statistical analyses were performed using non-parametric tests due to a non-normal distribution of data (Shapiro-Wilk: $p < 0.05$).

Minimum convex polygons

All single capture and recapture locations of individuals were used to determine catshark distributions. For the analysis of the distributions of the four catshark species, Minimum Convex Polygons (MCP) were constructed using the R package *adehabitatHR* (Calenge 2006) and illustrated through maps with the packages *ggmap* (Kahle and Wickham 2013) and *rstudioapi* (Ushey *et al.* 2020). 95% polygons were used to account for any data collection errors, as well as the bias associated with MCPs (Burgman and Fox 2003; Nilsen *et al.* 2008). Nevertheless, the outer 5% of the capture points were shown as well for additional information and interpretation. MCPs were constructed for each species to analyse their general distribution across Walker Bay and were also separated by sex.

The area of each polygon was calculated and then corrected to exclude landmass using the polygon tool in Google Earth Pro (v7.3.4.8642, 2022).

Using polygon areas, the percentage overlap between sex or species was derived according to the formula described by Attwood and Weeks Jr (2003):

$$(\frac{\text{area}_{\alpha\beta}}{\text{distribution area}_{\alpha}} \times \frac{\text{area}_{\alpha\beta}}{\text{distribution area}_{\beta}})^{0.5}$$

where $\text{area}_{\alpha\beta}$ is the shared area of both groups or species, $\text{distribution area}_{\alpha}$ and $\text{distribution area}_{\beta}$ are the individual polygon areas of sex/species α and β, respectively.

Site fidelity and travel distance

Site fidelity (*SF*) was calculated as per the methods described by Tschopp *et al.* (2018) from species permanence (*IT*) and species periodicity (*It*):

$$IT = \frac{F_i}{F}$$

$$It = (\frac{F_i}{\sum_{j=1}^{T} c_{ij-1}})$$

$$SF = \frac{2}{\frac{1}{IT} + \frac{1}{It}}$$

where F_i is the proportion of time in the study area given by the time between the first and last capture (days), *F* is the length of the sampling period (days), *c* is a binary value indicating capture (1) or no capture (0) of an individual *i* on sampling occasion *j* and *T* is the number of sampling occasions. If recapture did not occur, *IT, It* and thus

SF were set to 0. SF was measured on a scale of 0-1 where 0 was no fidelity and 1 is absolute fidelity. All values were calculated for every individual tag number, and the mean and standard error were further calculated for each species per location and sex to provide a population average. For further details on the method refer to Tschopp *et al*. (2018). Only Old Harbour, New Harbour and Rietfontein (Figure 1) were used in this analysis to provide a baseline for site fidelity over a suitable sample size. Because of heavy zero-weighting from single captures (Tweedie 1984), each index was compared per location and sex using a Tweedie General Linear Model (GLM) with log link (T) produced using the "tweedie" function from the *statmod* package (Dunn 2022). The Tweedie distribution is a special case of regular distributions with a cluster at zero which helps fit the data better. In our study, the Tweedie GLM was advantageous compared to a regular GLM because of the high number of zeros contained in our dataset due to low recapture rates.

To determine straight line travelling distances of individual sharks, the Haversine formula was used to calculate distances between capture sites (Robusto 1957). Distance was obtained using the formula from Van Brummelen 2013:

$$hav\left(\frac{d}{r}\right) = hav(\varphi_2 - \varphi_1) + \cos(\varphi_1) * \cos(\varphi_2) * hav(\lambda_2 - \lambda_1)$$

where: hav is the Haversine function $hav(\theta) = sin^2\left(\frac{\theta}{2}\right)$; θ represents the central angle between two points on a sphere; r is the mean radius of the earth ($r = 6{,}371$km); φ_1 and φ_2 are the latitudes of the locations 1 and 2 in radians; λ_1 and λ_2 are the longitudes in radians.

The maximum and mean travel distances were then recorded for each species and sex, for individuals that exhibited movement. Mann-Whitney tests were used for each species to determine any significant differences in travel distance between sexes.

3. Results

Dataset overview

The dataset contained 2,461 capture events, representing 1,950 individual sharks. The most common shark to be captured was *H. pictus* with 1295 capture events representing 1023 individuals with 172 sharks recaptured (Males: *C* = 599, *N* = 448; Females: *C* = 591, *N* = 473; Unknown sex: *C* = 105, *N* = 102), followed by *P. africanum* with 580 capture events representing 505 individuals with 58 sharks recaptured (Males: *C* = 274, *N* = 242; Females: *C* = 289, *N* = 246; Unknown sex: *C* = 17, *N* = 17), *P. pantherinum* with 515 capture events representing 357 individuals with 84 sharks recaptured (Males: *C* = 197, *N* = 125; Females: *C* = 241, *N* = 156; Unknown sex: *C* = 77, *N* = 76) and finally *H. edwardsii* with 71 capture events representing 64 individuals (Males: *C* = 43, *N* = 37; Females: *C* = 21, *N* = 20; Unknown sex: *C* = 7, *N* = 7). *P. pantherinum* had the greatest recapture rate (*R* = 0.24), followed by *H. pictus* (*R* = 0.17), *P. africanum* (*R* = 0.11) and finally *H. edwardsii* did not get any recapture (*R* = 0).

Distribution area

Overall species distribution

When considering all individuals of each species, the 95% MCP showed that *H. pictus* had the largest estimated overall distribution range across Walker Bay at 133.1 km^2 when corrected for landmass (Figure 3). The second largest distribution was represented by *P. pantherinum* with 114.5 km^2, followed by *H. edwardsii* with 98.0 km^2. The smallest estimated distribution range was shown by *P. africanum* with 61.2 km^2.

Inspecting the overlap between the four shark species showed an area which included the four distributions. This area of overlap was measured to be 46.7 km^2. *H. pictus* enveloped *P. pantherinum* and *P. africanum* completely in the distribution area with a calculated shared overlap of 92% and 67% respectively. In turn, *P. pantherinum* enveloped *P. africanum* completely in the distribution with a calculated shared overlap of 73%. The lowest shared percentage overlap was found between *P. pantherinum* and *H. edwardsii* with 44% overlap. Furthermore, *H. edwardsii* shared their distribution area with *H. pictus* with 61% overlap and *P. africanum* with an overlap of 62%. Directional overlap is summarised in Supplementary Table S1.

Sex distribution

For *H. pictus* and *H. edwardsii,* the females (*H. pictus* = 49.4 km^2, *H. edwardsii* = 85.2 km^2) showed a larger 95% distribution compared to males (*H. pictus* = 15.0 km^2, *H. edwardsii* = 5.6 km^2). In contrast, for *P. africanum* and *P. pantherinum* the males (*P. africanum* = 47.6 km^2*, P. pantherinum* = 46.6 km^2) showed a larger distribution compared to the females (*P. africanum* = 40.8 km^2, *P. pantherinum* = 31.1 km^2). The difference between males and females was notably smaller for *P. africanum* and *P. pantherinum* compared to *H. pictus* and *H. edwardsii.*

Overlap between groups based on sex showed that three of the four shark species (*H. pictus, P. pantherinum, P. africanum*) had the smaller distributed group be completely enveloped by the larger distributed group. Specifically, *H. pictus* male*, P.*

pantherinum female and *P. africanum* female were completely enveloped by their male or female counterparts. The largest level of shared overlap between males and females was found in *P. africanum* with 93% followed by *P. pantherinum* with 82% overlap and *H. pictus* with an overlap of 55%. *H. edwardsii* showed the smallest level of overlap with 21% shared area between males and females. Directional overlap between males and females per species is summarised in Supplementary Table S2.

Inspecting all capture points, showed that the group with the largest 95% distribution area was not consistent with farthest capture/recapture coordinates for each species. Specifically, *H. pictus* females represented the largest 95% distribution while males were represented in the most outer points of overall distribution. A similar situation was seen in *P. africanum,* yet the males represented the largest 95% distribution while females would show the largest overall distribution in Walker Bay. For *P. pantherinum,* there are no noticeable differences in total distribution between males and females while males showed a larger 95% distribution. Finally, *H. edwardsii* did show a clear larger 95% distribution for females which was still present in the overall distribution yet less extreme.

Site fidelity

A total of 1,740 capture events representing 1,284 individual sharks from Old Harbour, New Harbour and Rietfontein were used for *SF* analysis (*H. edwardsii*: C = 30, N = 25; *H. pictus*: C = 966, N = 718; *P. pantherinum*: C = 357, N = 211; *P. africanum*: C = 387, N = 330). Mean *SF* was universally low for all three indices ($<$ 0.005; figure 4).

With respect to all four shark species, no significant interaction models were found using the Tweedie GLM ($p > 0.05$), thus both sexes and all locations could be combined into a single model for each species.

H. edwardsii expressed no significant difference in *SF* between males and females (T = 0.38, p = 0.71) and no significant differences were found between any of the three sites (Old Harbour:New Harbour: T = 0.30, p = 0.77; Old Harbour:Rietfontein: T = 0.35, p = 0.73; New Harbour:Rietfontein: T = 0.13, p = 0.90).

H. pictus expressed significantly greater *SF* in males compared to females (T = 3.38, $p < 0.01$) and was also significantly greater at Old Harbour compared to the other sites (Old Harbour:New Harbour: T = 5.70, $p < 0.01$; Old Harbour:Rietfontein: T = 3.61, $p < 0.01$). No significant difference was noted in *SF* between New Harbour and Rietfontein (T = 0.33, p = 0.74).

P. pantherinum expressed no significant difference in *SF* between males and females (T = 0.19, p = 0.85) and also expressed no significant difference in *SF* between New Harbour and the other sites (Old Harbour:New Harbour: T = 1.73, p = 0.09; New Harbour:Rietfontein: T = 1.80, p = 0.07). *SF* was significantly greater at Old Harbour compared to New Harbour (T = 3.18, $p < 0.01$).

P. africanum expressed no significant difference in *SF* between males and females (T = 0.55, p = 0.58) and no significant differences were found between any of the three sites (Old Harbour:New Harbour: T = 0.68, p = 0.50; Old Harbour:Rietfontein: T = 0.88, p = 0.38; New Harbour:Rietfontein: T = 0.30, p = 0.77).

Travel distance

Of the 318 individuals that were recaptured at least once, only 93 instances of travel were recorded from 83 individual sharks as other individuals remained in the same location. They included 34 *H. pictus*, 23 *P. pantherinum* and 26 *P. africanum* individuals. None of the tagged *H. edwardsii* were recaptured at a different location. Female *P. africanum* were found to travel the furthest, with a maximum recorded travelling distance at 38.55km (Table 1). There were no significant differences in the mean travel distance (km) between males and females of any species ($p > 0.05$ in all instances).

4. Discussion

H. pictus dominated the majority of captures of the four target species, contributing to more than 50% of all captures, which has previously been reflected in BRUV occurrence analysis (Osgood *et al*. 2019). Recapture rate for *P. pantherinum* and *P. africanum* exceeded previous study by Escobar-Porras (2009) with 0.24 and 0.11 in our study compared to a mean of 0.08 and 0.07 respectively (two datasets were used), but a high recapture rate was found in Escobar-Porras (2009) for *H. edwardsii* with a mean of 0.09 while no recapture event occurred during this study. As datasets used in both studies were of great length (more than 10 years), this cannot be the factor influencing recapture rate, nevertheless, the method could be of significance, as both studies used data from a nationwide tagging program (with fishing effort no specifically targeting catsharks), this study was supplemented by more than 10 years of data where fishing efforts were made towards catsharks. Considering that most fishing took place inshore, a shallow topography was expected. This was especially prevalent at the most common fishing sites, Old Harbour, New Harbour and Rietfontein, which did not surpass 10 m in depth. Therefore, it was likely that depth preference played a major role in the number of captures since *H. pictus* is rarely found deeper than 35 m depth (Pollom *et al*. 2019a; Ebert *et al.* 2021b), whilst the remaining three species can be found in depths exceeding 100 m (Pollom *et al.* 2020a, 2020b, 2020c). While this reasoning is also likely consistent when considering the small number of overall captures for *H. edwardsii*, it should also be considered that the Endangered status of this species played a credible role in its rarity (Pollom *et al*. 2020c). Specifically, if the endangerment of *H. edwardsii* did not play a role, the large difference in capture numbers compared to *P. pantherinum* and *P. africanum* would not have been observed considering all three species are found across a similar depth gradient (Pollom *et al.* 2020a, 2020b, 2020c).

All four species demonstrated moderate to high levels of overlap with each other (>40%), suggesting significant levels of co-occurrence and spatial interaction. Evidence provided by both Compagno (1984) and Escobar-Porras (2009) suggests levels of microhabitat separation between *H. edwardsii*, *P. pantherinum, P. africanum*, as well as the brown shyshark *Haploblepharus fuscus*, which has a similar habitat preference to *H. pictus* (Human 2007; Ebert *et al.* 2021b). This could suggest that, while the species in this study have spatial interaction at the coarse level, they likely segregate across microhabitats depending on behaviour, ecological requirements such as food preference, or potential territoriality and intraspecific competition (Papastamatiou *et al*. 2018). The lowest level of overlap with other species was expressed by *H. edwardsii*, ranging from 44–62%. While the species' low capture numbers likely impacted this result (Pollom *et al*. 2020c), it could be considered that *H. edwardsii* may be outcompeted by the other species of interest and thus seeks refuge in regions across greater distances. Therefore, it is likely that interspecific competition, alongside other factors such as bycatch and habitat degradation are driving *H. edwardsii* to extinction (Attwood *et al*. 2000, 2011), but further data on this species are needed to confirm.

When considering potential sexual segregation, results of this study do not align with previous research of other catsharks (Richardson *et al*. 2000; Wearmouth and Sims 2008; Wearmouth *et* al. 2012; Riesgo *et al.* 2019; Vásquez-Castillo *et al.* 2021). Often, sexual segregation is initiated due to the harassment of females by males (Wearmouth *et al*. 2012). This would mean that harassment is less present for the catsharks in this study. An exception to this was *H. edwardsii* which did show great difference between male and female distribution with only 21% overlap. The most probable explanation includes the low number of individuals of *H. edwardsii* and therefore less weight of the MCP was pulled towards the three main fishing locations (Burgman and Fox 2003; Nilsen *et al.* 2008). Sexual segregation has been observed in other catshark species where females resided in shallower areas to avoid male harassment, limit energy-costly mating or stay close to their eggs in shallower water (Sims *et al.* 2001). Next to possibly fewer mating events, sexual segregation could impact the fitness of *H. edwardsii*, as females would be more susceptible to be included as bycatch in area focused fisheries (Wearmouth *et al*. 2012). Lower fitness due to sexual segregation would explain why *H. edwardsii* is less abundant and more susceptible for disturbance than ecological similar species such as *H. pictus.*

This study acknowledges the potential for over or under estimation of MCP size, as a result of sample size and effort bias (Burgman and Fox 2003; Nilsen *et al.* 2008). Nevertheless, most of the possible limitations are buffered by focussing on 95% of the data while still including the total distribution in the results. This way, the illustrated area can be used with greater confidence for possible management strategies as the

MCPs show the area where most catshark species were observed. Sample size sensitivity did not play a role in the MCPs made for *H. pictus, P. africanum* and *P. pantherinum* while the same cannot be said for *H. edwardsii* which future research should be mindful of. Nevertheless, not much is known about this threatened species and MCPs are still of great importance for possible conservation in highlighted areas as it shows which areas play a greater role in their distribution and might need further protection. Overall *SF* was minimal in all species, failing to surpass a mean value of 0.006 in any instance. Overall small *SF* does not align with the results of Escobar-Porras (2009) which suggested strong levels of *SF*. While this could suggest large levels of variance in *SF* between different catshark sub-populations, the method of calculation was unclear in the study and was also likely impacted by the small sample size. It is unlikely that *SF* was underestimated in our study due to capture avoidance behaviour, as catsharks are considered opportunistic (Richardson *et al*. 2000; Laptikhovsky *et al*. 2001; Olaso *et al*. 2005). While this at first would appear contradictory to the small mean travel distances, as well as the small number of individuals recorded to have travelled, it is important to consider that travel distance measurements relied heavily on the probability of recapture which was small to moderate at most and was heavily weighted towards Old Harbour, New Harbour and Rietfontein. Thus, SF results form a baseline that could be confirmed by increasing the sample size, adding more sample sites and higher fishing effort. Moreover, this is supported by the previous study by Escobar-Porras (2009) that found higher distance travelled for *P. pantherinum* and *P. africanum* compared to this study, which shows that our results might be due to the lack of sampling sites, thus, the dataset could be missing recaptures that would record movement. The small *SF* values would suggest that every shark species travels more than the travel distances suggest. Catsharks are not strongly adapted to swimming due to their soft fin structure and a reliance on buccal pumping (Thomson and Simanek 1977; Ebert *et al*. 2021b) so the species of interest may rely on the energetic currents in the region to swim more efficiently (Boebel *et al*. 2003). This would aid in passive movement between the sample sites thus conserving energy. With small *SF* for the studied Catsharks, we can expect a large level of site interconnectivity, particularly between the three sites of interest.

Despite small levels of *SF,* it was apparent that *H. pictus* showed greater *SF* at Old Harbour compared to New Harbour and Rietfontein and similarly *P. pantherinum* showed greater *SF* at Old Harbour compared to New Harbour. Considering Old Harbour and Rietfontein share the same habitat type, it is unlikely that the presence of kelp played a key role in habitat preference to a major extent in the case of *H. pictus*. Kelp habitats are typically considered of greater suitability to catsharks compared to sand habitats since they provide a greater selection of prey and shelter from predators, but also provide suitable sites for egg deposition (Pretorius and Griffiths 2013; Osgood *et al*. 2019; E. Cottrant unpubl. data). While this could explain the greater *SF* for *P. pantherinum*, further consideration of other environmental factors should be considered for *H. pictus* such as food availability, intraspecific competition, or recreational fishing pressure. However, without quantification of these variables it is difficult to ascertain the reasoning behind the significant difference between Old Harbour and Rietfontein.

Future research should include more diverse fishing locations for capture data. This would not only avoid effort bias for MCP yet also provide more information on potential drivers such as depth distribution, habitats and anthropogenic disturbance. With the results of this study and complementing future data, more efficient management strategies can be formed. This will be beneficial for the conservation of all four catsharks and especially *H. edwardsii*.

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6. Figures

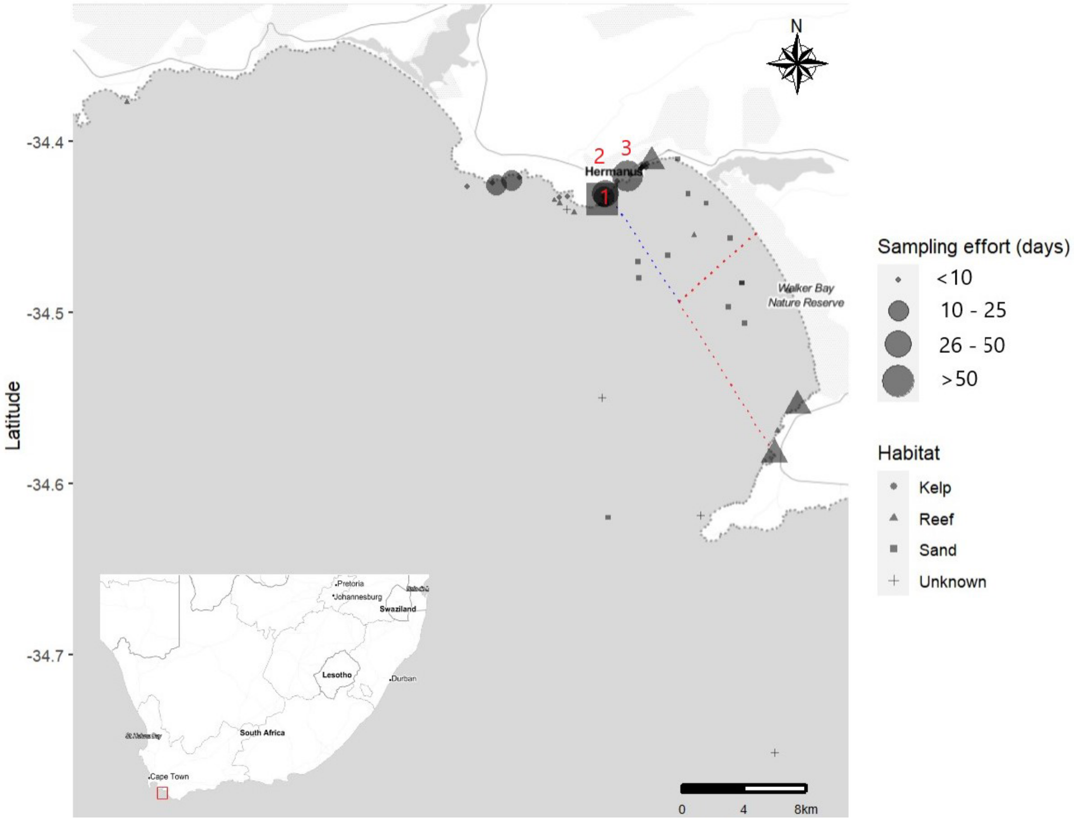

Figure 1: Sampling region across Walker Bay in the Western Cape, South Africa. Shapes represent the different marine habitats in Walker Bay (kelp, reef, sand and unknown). The size of the shapes represents the number of days of fishing at the location where at least one shark was caught. Number in the plot represent most fished location, Rietfontein (1, circle inside the square), New harbour (2, square), Old Harbour (3, circle) The area surrounded in the blue dotted line represents the Walker Bay Whale Sanctuary and the area surrounded in the red dotted line represents the Walker Bay restricted area.

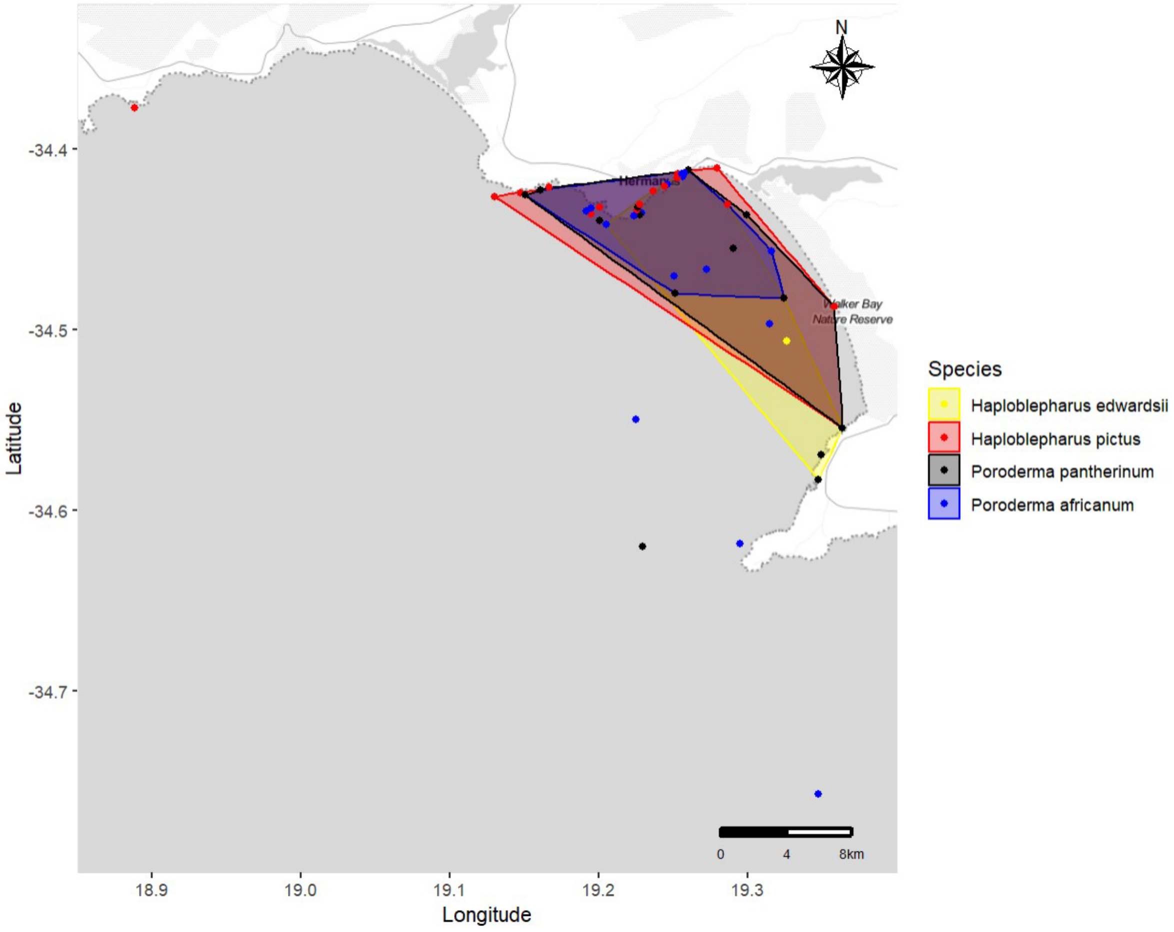

Figure 2: Total distribution of four endemic catsharks obtained from 95% minimum convex polygons in Walker Bay, South Africa. The distribution area of *Haploblepharus edwardsii* is depicted in yellow, *Haploblepharus pictus* in red, *Poroderma pantherinum* in black and *Poroderma africanum* in blue.

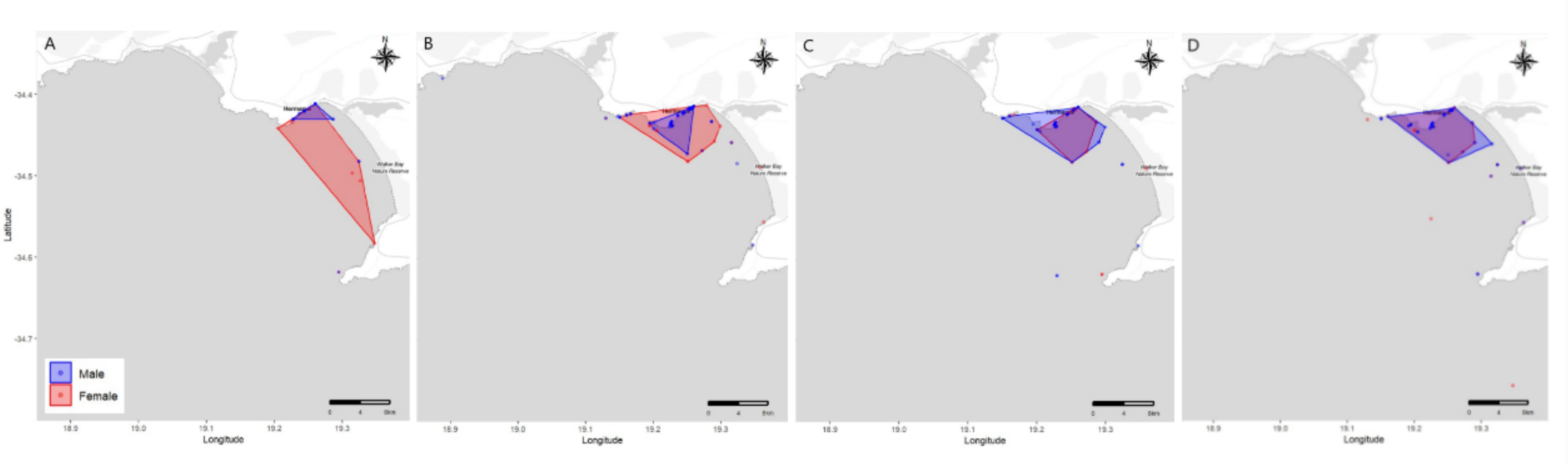

Figure 3: 95% distribution areas of *Haploblepharus edwardsii* (A), *Haploblepharus pictus* (B), *Poroderma pantherinum* (C) and Poroderma *africanum* (D) and in Walker Bay, South Africa based on sex variance. Females are represented in red and males in blue.

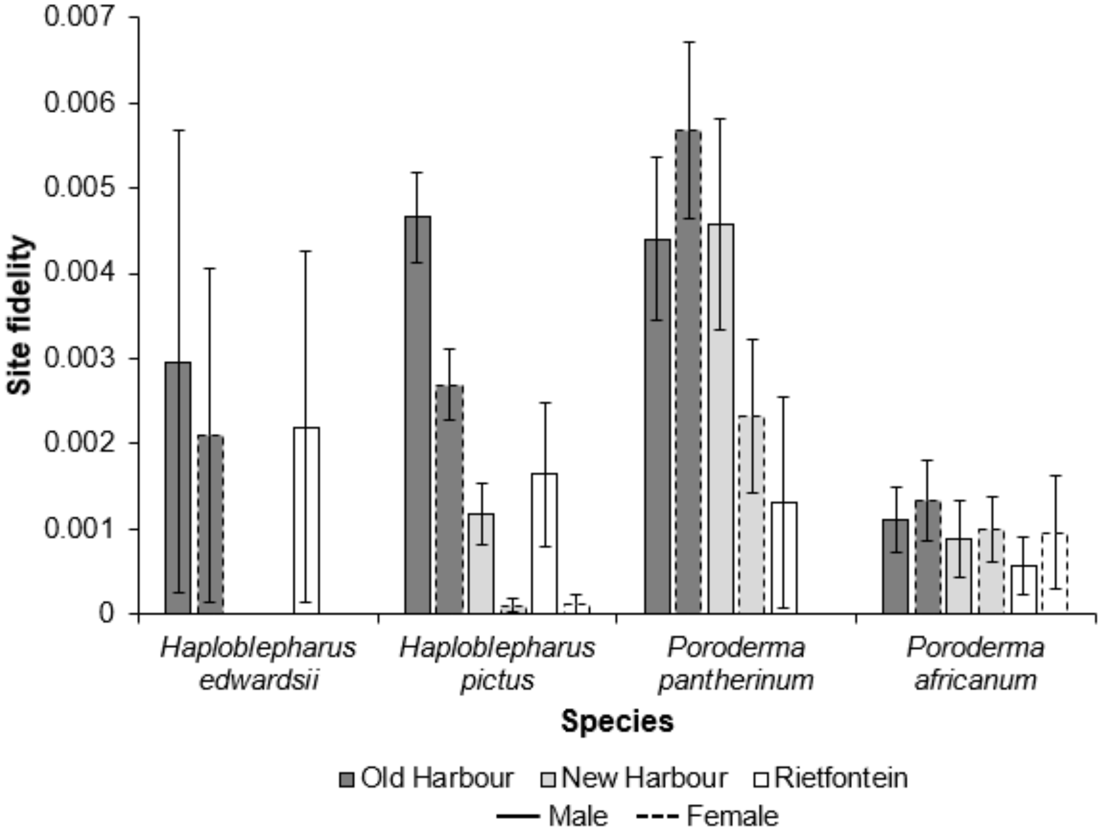

Figure 4: The mean site fidelity of male (solid bar) and female (dashed bar) *Haploblepharus edwardsii*, *Haploblepharus pictus*, *Poroderma pantherinum* and *Poroderma africanum* at Old Harbour (dark grey), New Harbour (light grey) and Rietfontein (white). Error bars represent standard error.

7. Tables

Table 1: The mean and maximum travel distance of recaptured individuals across Walker Bay. *Haploblepharus edwardsii* was excluded as no individual was found to travel between sites.

Species	Sex	Number of travelling individuals (n)	Mean travel distance (km) [±SE]	Maximum travel distance (km)
Haploblepharus pictus	Male	14	5.10 [±2.12]	33.00
	Female	20	3.47 [±0.75]	13.50
Poroderma pantherinum	Male	9	4.17 [±0.16]	12.83
	Female	14	3.52 [±1.02]	13.54
Poroderma africanum	Male	14	3.00 [±0.98]	13.54
	Female	12	3.86 [±2.69]	38.55

8. Supplementary material

Table 1. The percentage overlap of minimum convex polygons between the sexes of each shark species as per eq. 2. Each half of the equation is shortened to (A) and (B) in the final column for ease of reading.

Species	Total distribution area (km^2)		$\frac{area_{\alpha\beta}}{distribution\ area_{\alpha}}$(A) [%]	$\frac{area_{\alpha\beta}}{distribution\ area_{\beta}}$(B) [%]	(A x B)$^{0.5}$ [%]
	Males	Females			
Haploblepharus edwardsii	5.6	58.2	84	5	21
Haploblepharus pictus	15.0	49.4	100	30	55
Poroderma pantherinum	46.6	31.1	67	100	82
Poroderma africanum	47.6	40.8	86	100	93

Table 2. The percentage overlap of minimum convex polygons between each species as per eq. 2. Each half of the equation is shortened to (A) and (B) in the final column for ease of reading. Species are abbreviated to HE (*Haploblepharus edwardsii*), HP (*Haploblepharus pictus*), PP (*Poroderma pantherinum*), and PA (*Poroderma africanum*) for ease of reading.

	Total distribution area (km^2)	$\frac{area_{\alpha\beta}}{distribution\ area_{\alpha}}$(A) [%]				$\frac{area_{\alpha\beta}}{distribution\ area_{\beta}}$(B) [%]				(A x B)$^{0.5}$ [%]			
Species		HE	HP	PP	PA	HE	HP	PP	PA	HE	HP	PP	PA
HE	98.0	-	-	-	-	-	-	-	-	-	-	-	-
HP	133.1	53	-	-	-	72	-	-	-	61	-	-	-
PP	114.5	41	100	-	-	49	85	-	-	44	92	-	-
PA	61.2	79	100	100	-	48	46	54	-	62	67	73	-

CHAPTER THREE: A comparison of the growth and development of pyjama sharks *Poroderma africanum* in wild and captive populations

1. Introduction

Sharks have been successfully held in public aquariums around the world since 1864, with husbandry methods being increasingly more efficient and ethical over time (Smith *et al.* 2004). Numerous studies have been conducted, across taxa, investigating husbandry techniques (Matsumoto *et al.* 2017; Marin-Osorno *et al.* 2017), species biology (Ezcurra *et al.* 2017; Baylina *et al.* 2017), reproduction (Schaller, 2006) and physiology (Ueda *et al.* 2017). Captive breeding is especially important in the case of endangered or endemic species, offering solutions to population decline (Smith *et al.* 2004). Like many catshark species, the pyjama shark *Poroderma africanum* is known to survive well in captivity with multiple displays in public aquariums around the world (Koob, 2004; Montbach and Willis, 2017). However, only one study was conducted in captivity, investigating the learning capacity of the species for feeding purposes (Montbach and Willis, 2017).

The pyjama shark belongs to the family Scyliorhinidae and is endemic to South Africa, at depths shallower than 108 m (Ebert *et al.* 2021). It is distributed from Saldanha Bay in the Western Cape to just north of East London in the Eastern Cape across an assumed temperature gradient of 14-25ºC (Pollom *et al.* 2020; World sea temperatures, 2023). Currently listed as Least Concern on the IUCN Red List (Ibid 2020), this species is not of economic importance. Nevertheless, the population is impacted by by-catch in trawling and recreational fishing (Attwood *et al.* 2011; da Silva *et al.* 2015). Males reach sexual maturity at 75.0 - 91.0 cm and females at 75.0 - 93.0 cm in total length (L_t; Dainty, 2002; Ebert *et al.* 2021). Although distribution and abundance surveys have been conducted using mark-recapture and baited remote underwater videos (De Vos *et al.* 2015; Grusd *et al.* 2019, Johnson *et al.* 2024), little is known about the reproductive biology and growth of this species. As an oviparous species, the incubation period is 164 days after egg laying, and the L_t at hatching is estimated to be 14 cm (von Bonde, 1948; Ebert *et al.* 2021), but detailed information is lacking because only one fertilized egg was observed by von Bonde. While this species is not at risk of extinction, it is important to understand the underlying mechanisms of growth and development to improve the ecological knowledge of the species for future conservation and management practices (Prohaska *et al.* 2013).

This study aims to describe: (1) fertilization rate and incubation period of eggs in captive pyjama sharks; (2) age and size at maturity of captive female pyjama sharks (3) growth in wild and captive pyjama sharks. Despite its drawbacks, particularly owing to low recapture rates (Lee *et al.* 2014), mark-recapture has been successfully implemented into shark growth studies, including the pyjama shark (Meyer *et al.* 2014; Grusd *et al.* 2019; Dureuil *et al.* 2022). Therefore, the methods used in this study offer a robust comparison of wild and captive populations, despite using different methods of data collection. This is the first study to conduct analysis of growth between male and female pyjama sharks and is also the first study to consider differences in growth between wild and captive Scyliorhinidae. This study also benefits from a significantly larger sample size than previous studies, providing stronger analysis.

2. Materials and methods

Aquarium rearing

Data on captive pyjama sharks was collected at Osaka Aquarium Kaiyukan. One male and one female pyjama shark, caught in the waters around Port Elizabeth, South Africa, arrived at the Osaka Aquarium Kaiyukan from a fish supplier in Taiwan on 29/05/2005. They were kept in a tank of 230 x 95 x 70 cm (L x W x D), with a water volume of 1.2 m^3 and at a water temperature of 18°C. The male was 96.0 cm L_t, and the female was 88.0 cm L_t upon arrival. Animals were fed the day after arrival and were in apparent good health (healthy skin with no wounds and no abnormal swimming behaviour (Pogoreutz *et al.* 2019; Caballero *et al.* 2020)). They were fed three times a week until full, on a diet of capelin *Mallotus villosus*, Japanese horse mackerels *Trachurus japonicus*, black tiger prawn *Penaeus monodon* and neon flying squids *Ommastrephes bartamii*. Natural insemination occurred and egg laying occurred for the first time on the 04/06/2005 (seven day after the animals arrived at the aquarium) suggesting both individuals were mature and embryo development was confirmed 40 days after egg laying. Fertilized eggs and hatching pups were kept in cages in the same tank as the mature individuals. Neonates were fed daily from the day of hatching with Antarctic krill *Euphausia superba*, black tiger prawn without the shells, and neon flying squid filets. The pups were weighed (W_t; g) and measured for L_t (cm) on the day of hatching, and then at 10 to 30-day intervals.

Mark-Recapture

Data on wild pyjama sharks were collected by the South African Shark Conservancy (SASC) over nine years (January 2014 – February 2023) but no sampling was conducted between March 2020 and January 2021 due to the COVID-19 pandemic. Sampling was weather dependent, thus not occurring daily, across 50 sampling spots in the Walker Bay region, South Africa. Walker Bay is characterized by three distinct types of habitats (i.e., kelp, reef and sand) with sea surface temperatures ranging from 15 to 21 °C (SASC database, unpubl data). Sharks were caught either by fishing (handline or rod and reel) or by hand while snorkelling. Handlines comprised of 1.2 mm nylon monofilament line and de-barbed circle hooks ranging in size from 6’0 to 12’0 to target various shark sizes. Hooks were baited with sardine (*Sardinops sagax*), Pacific saury (*Cololabis saira*), common octopus (*Octopus vulgaris*), or Cape Hope squid (*Loligo reynaudii*). Bait canisters containing 1 kg of defrosted, crushed sardine were also deployed to attract specimens. Hand capture while free diving was conducted in water <8 m deep. Captured sharks were held underwater in a soft mesh cage (30 mm mesh size, 600 mm diameter and 250 mm depth) for the duration of the dive session (~1 hour). This was deemed ethically suitable as catsharks are buccal pumpers and thus lack of movement does not cause metabolic stress (Ebert *et al.* 2021; refer to section 8.5 of this study). All sharks were tagged using external dart tags (Dunlop *et al.* 2013). After capture, sex, L_t (cm) and W_t (g) were recorded.

Statistical analysis

All analysis was conducted using RStudio with R version 4.2.2 (R Core Team, 2022).

Fertilization rate and incubation period of eggs

Kruskal-Wallis tests (H) were performed to determine any significant differences between the mean number of overall eggs laid and the mean number of fertilized eggs laid between each month. Spearman rank correlation coefficients (r_s) were used to determine if there was any significant relationship between incubation period and L_t and W_t at birth. The sex ratio of offspring was compared using a chi-squared test (X^2).

Length-Weight relationship

The length-weight relationship was determined for each sex for wild and captive sharks, using the power function:

$$W_t = aL_t^b \quad (1)$$

where W_t is the total weight of the shark, L_t is the total length of the shark, and a and b are constants (King, 2013). Linear regressions were constructed for the natural log-transformed data and were analysed using a general linear model (GLM) to test for significance between the length-weight relationship of the sexes, as well as between aquarium reared and wild sharks. Furthermore, a GLM was used to test for significant differences between individuals of each sex in captive sharks. This was not done for wild sharks as there was not enough recapture data to produce length-weight curves for each individual.

A coefficient t-test was performed to test the null hypothesis of isometric growth in males and females using the equation:

$$t = \frac{b-3}{SE_b} \qquad (2)$$

where SE_b is the standard error of the slope (Morey *et al.* 2003). Isometric growth can be described as a growth in all bodily dimensions at an equal rate and follows a cubic relationship, therefore *b* is statistically equivalent to 3 (King 2013). Values above and below 3 equal positive and negative allometric growth respectively (Tesch, 1978).

Growth rate

Growth rates of the pyjama sharks were determined using the von Bertalanffy growth formula (VBG) shown below (von Bertalanffy, 1938):

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt} \qquad (3)$$

Where L_∞ is asymptotic length (cm), *k* is the growth coefficient, *t* is age (years), L_0 is L_t at birth (cm).

For aquarium reared sharks eq.3 was used to gain accurate estimations and the significance between the parameters of males and females, as well as between individuals of the same sex were compared using the Kimura Likelihood Ratio (X^2) (Kimura, 1980):

$$X^2 = -N * \ln \frac{ResSS_{no\ constraints}}{ResSS_{constrained}} \qquad (4)$$

Where *N* is the number of total measurements and *ResSS* is the residual sum of squares of each parameter. Constrained refers to the value of each parameter remaining unchanged from that of the values obtained from VBG of males and females or individuals combined. Only individuals that survived for at least 7 years were used to compare individual variation in growth to reduce the overestimation of L_∞ and underestimation of

k. L_t was used up to the 7-year cutoff after which, further L_t values were removed from analysis to maintain consistency between the sharks.

For wild caught sharks, an age estimate model was constructed using eq.3. As per the method described by Dureuil *et al.* (2022) a growth estimate simulation was conducted using the *TMB* and *tmbstan* packages (Kristensen *et al.* 2016; Monnahan and Kristensen 2018). The simulation used a Bayesian formulation of the Fabens method (Fabens, 1965; see Dureuil *et al.* 2022 for details) to determine true estimates for L_∞ and k. This required the L_t at each capture and the time at liberty (Δt) between each capture. Prior to running the simulation L_{max} was estimated as 106 cm as per Ebert *et al.* (2021) and L_∞ was estimated from its relationship to the maximum length (Froese and Binohlan 2000) using the equation:

$$\log L_\infty = 0.044 + 0.9841 * \log(L_{max}) \qquad (5)$$

Three negative growth rates were manually removed as outliers due to measurement error.

To compare the VBG growth parameters between captive and wild-caught sharks, an adapted version of the phi-Munro growth performance index was used (Munro and Pauly 1983):

$$\Phi' = \frac{(\log_{10} k_u + (2 * \log_{10} L_{\infty u})) + (\log_{10} k_l + (2 * \log_{10} L_{\infty l}))}{2} \qquad (6)$$

This adaptation took the upper and lower 95% confidence intervals of k and L_∞ into account for the calculation, reducing levels of bias. In this instance k_u and k_l are the upper and lower bounds of k respectively, while $L_{\infty u}$ and $L_{\infty l}$ are the upper and lower bounds of

L_∞. In this case, we can expect negative values since using the $\log_{10}$ on the lower bounds sometimes resulted in negative values.

3. Results

Fertilization rate and incubation period of eggs

During the study, egg laying was observed throughout the year, with the first female introduced to the aquaria laying 98 eggs between 2005 and 2007, and the three hatched females laying 221 eggs between 2013 and 2020 (Table 1). No health complications were noted during egg laying or gestation. Of the 319 eggs, embryonic development was confirmed in 60 eggs within 40 days of laying, and the fertilization rate was 18.8%. The number of eggs laid tended to be higher in March and November, and a greater proportion of eggs were fertilized between March and August (Figure 1) however these differences were not significant (H_{11} = 8.77, p = 0.46 and H_{11} = 2.63, p = 0.85 respectively). A total of 24 out of 60 fertilised eggs hatched, while the remaining 36 eggs ceased further development at varying stages and were considered deceased. The sexes of newly born individuals were 6 males and 21 females (Table 1). The mean incubation period (± standard error [SE]) was 239.47 ± 4.97 days, mean L_t of hatchlings (± SE) was 14.65 ± 0.24 cm, and the mean W_t (± SE) was 17.19 ± 0.75 g (Table 1). No correlation was observed between incubation period (days) and L_t at birth (cm) (r_s = 0.24, p = 0.26) or incubation period (days) and W_t at birth (g) (r_s = -0.03, p = 0.88). There was a significant difference between the observed (1 male:3.5 females) and expected (1 male:1 female) ratio of offspring (X^2_1 = 8.33, p < 0.01).

Age and size at maturity of females

Fertilized eggs had been observed since 2005, but no eggs were laid from 2008 to 2011 due to the death of the first mature female. Fertilized eggs were again laid from June 2013, though the female of origin was unknown since four females resided in the tank at the time. The four females were born between 2006 to 2008 (individual numbers 2, 3, 10, and 14 in Table 1) which suggests that the egg-laying female reached sexual maturity between approximately 1970 days (5.4 years old) and 2680 days (7.3 years old) after hatching. The sizes of those females ranged from 73.0 to 86.0 cm L_t and 2180 to 3800g W_t for weight, when the first egg was laid. Female 21 (Table 1) hatched on 14/01/2015, laid only empty egg cases from 27/05/2021, 2325 days after hatching (6.4 years old). This female started laying egg cases containing mature egg yolks on 29/08/2021, 2419 days after hatching (6.6 years old) suggesting that maturity was reached but the animal was likely not mating. The size at that time was 85.2 cm L_t and 3300g W_t.

Growth rates

With respects to the captive sharks, 1140 L_t measurements were collected from 27 different individuals. This included six males (292 measurements) and 21 females (848 measurements). Male sharks exhibited negative allometric growth (b = 2.89 [SE = 0.02], $t_{291} = -7.55$, $p < 0.01$) with the power function $W_t = 0.01L_t^{2.89}$ (Figure 2a; $r^2 = 0.99$, $p < 0.01$). Female sharks exhibited isometric growth (b = 2.99 [SE = 0.01], $t_{847} = -1.95$, $p = 0.05$) with the power function $W_t = 0.01L_t^{2.99}$ (Figure 2c; $r^2 = 0.99$, $p < 0.01$). The GLM revealed a significant difference between the regression slopes of each sex ($F_1 = 39.85$,

$p < 0.01$) as well as between individuals of each sex (Males: $F_1 = 10.24$, $p < 0.01$; Females: $F_1 = 10.07$, $p < 0.01$). The same number of measurements were used for VBG analysis as with length-weight analysis for captive sharks. Male sharks were represented by the growth function $L_t = 108.60 - (108.60 - 11.84)e^{-0.21t}$ and female sharks were represented by the growth function $L_t = 113.05 - (113.05 - 12.15)e^{-0.18t}$ (Figure 3). Kimura likelihood ratio analysis revealed no significant difference in L_∞ or L_0 between male and female sharks ($X^2_1 = 3.07$, $p = 0.08$ and $X^2_1 = 0.150$, $p = 0.70$ for L_∞ or L_0 respectively) though a significant difference was found between k values as well as the overall slope of the curves ($X^2_1 = 9.53$, $p < 0.01$ and $X^2_3 = 40.65$, $p < 0.01$ for k and all combined parameters respectively). Kimura likelihood ratio analysis also revealed a significant difference in all VBG parameters and the overall slope of the curves between males (L_∞: $X^2_1 = -13.53$, $p < 0.01$; L_0: $X^2_1 = -14.99$, $p < 0.01$; k: $X^2_1 = -6.92$, $p < 0.01$; Slope: $X^2_3 = 43.52$, $p < 0.01$) as well as females (L_∞: $X^2_1 = 264.04$, $p < 0.01$; L_0: $X^2_1 = 56.10$; k: $X^2_1 = 295.84$, $p < 0.01$; Slope: $X^2_3 = 602.36$, $p < 0.01$).

A total of 634 captures were made which also included recapture events. From these capture events, 550 individuals were tagged (273 males, 272 females and 5 sharks of unspecified sex) and 5 individuals were released without tagging due to size (3 male and 4 females). While L_t was recorded for all wild sharks caught, W_t was only recorded for a total of 99 wild-caught sharks and only two of these sharks were recaptured, giving a total of 101 different measurements. This included 54 males (56 measurements) and 45 females (45 measurements). As with captive sharks, males exhibited negative allometric growth ($b = 1.84$ [SE = 0.22], $t_{53} = -5.32$, $p < 0.01$) with the power function $W_t = 0.86L_t^{1.84}$ (Figure 2b; $r^2 = 0.56$, $p < 0.01$) and female sharks exhibited isometric growth ($b = 2.86$

[SE = 0.12], $t_{44} = -1.13$, $p = 0.26$) with the power function $W_t = 0.01L_t^{2.86}$ (Figure 2d; $r^2 = 0.92$, $p < 0.01$). The GLM also showed a significant difference between the regression slopes of each sex ($F_1 = 15.58$, $p < 0.01$) With respect to wild sharks, only 12 measurements of Δt were available for males and 22 measurements of Δt were available for females for the VBG due to a lack of recaptures. Male sharks were represented by the growth function $L_t = 106.02 - (106.02 - 14.00)e^{-0.13t}$ and female sharks were represented by the growth function $L_t = 106.05 - (106.05 - 14.00)e^{-0.07t}$ (Figure 3). Unfortunately, Kimura likelihood ratio analysis could not be used as age was estimated by rearranging eq.3 and thus gave false *ResSS* values when reanalysed using the methodology for captive individuals. However, there was a significant level of overlap with the 95% confidence intervals between wild and captive sharks for both L_∞ and k which suggested little difference between the curves (Figure 4).

A comparison of the length-weight relationship for captive and wild-caught male sharks revealed a significant difference between the regression slopes (Figure 2; $F_1 = 48.02$, $p < 0.01$), though no such difference was found with female sharks (Figure 2; $F_1 = 1.19$, $p = 0.28$). VBG could not be statistically compared between captive and wild-caught sharks as the age of wild-caught sharks was estimated. However, the growth performance index was lower in wild sharks and was also lower in females compared to males of their respective location (captive males: $\Phi' = 3.40$; wild males: $\Phi' = -0.69$; captive females: $\Phi' = 3.36$; wild females: $\Phi' = 0.42$). A lack of overlap between the 95% confidence intervals of both L_∞ and k between the captive and wild-caught female sharks suggested a difference between the curves (Figure 4). No such difference was found between the males.

4. Discussion

Fertilization rate and incubation period of eggs

This study aimed to analyse the breeding behaviour of pyjama sharks in captivity, based on the production of fertilised eggs. Results are consistent with a previous study on wild pyjama sharks (Dainty, 2002) which monitored gonad development in mature females. Ovarian follicles of varying size were present throughout the year suggesting that pyjama sharks can reproduce year-round. Sharks produced 2 to 3 egg per month which was representative of this species and the *Poroderma* genus as a whole (Ebert et al. 2021)

In the captive rearing study, the water temperature was kept at a constant 18°C and the mean incubation period for fertilized eggs was 239 days. This was 75 days longer than that described by von Bonde (1948). In the closely related leopard catshark *Poroderma pantherinum* the incubation period of fertilized eggs was found to decrease with increasing water temperature (Pretorius and Griffiths, 2013). As von Bonde (1948) did not record the temperature it could be inferred that there was a potential effect of temperature on this species' embryonic development. Similarly, Dainty (2002) observed a substantially longer incubation period (12 months) at 14℃ though this was based on a single observation, and it should be considered that the shark was trapped in the egg, likely subsisting on the yolk until being released manually. It should also be considered that oxygen concentration has been found to have a significant interactive effect with temperature on the development of small-spotted catshark *Scyliorhinus canicula* embryos (Musa *et al.* 2020). Therefore, it would be recommended that further studies should be performed to determine the effect of different environmental factors on pyjama shark embryonic development.

No correlation was found between *Lt* and *Wt* at birth with respect to the length of egg incubation period. This aspect of shark development is currently poorly studied, especially in catsharks, however, the oviparous grey bamboo shark *Chiloscyllium griseum* has also shown similar results with respect to the relationship between incubation period and size at birth (Jagadis and Ignatius, 2003). Several factors causing this can be speculated, such as an anti-predator response with respect to adult catsharks within the tank, or oxidative stress (Varela *et al*. 2023), though no evidence of the causative variable can be given without further study.

The offspring sex ratio significantly leaned towards female pups which has not been recorded in pyjama sharks to date. Previous studies suggest that reproductive biology with respect to sex selection is highly variable within Scyliorhinids, with a largely even offspring ratio recorded in the small-spotted catshark (Griffiths *et al.* 2012) and male leaning offspring production in the longhead catshark *Apristurus longicephalus* (Iglésias *et al.* 2005). Future studies should focus on potential environmental drivers of ontogenetic sexual selection but also life history drivers as having more females would be beneficial to grow a population faster.

Age and size at maturity of female

Regarding captive female maturity, the mature L_t of 73–89.5 cm in this study was consistent with Dainty (2002) and Ebert *et al.* (2021) who record L_t at maturity to be >82 cm and 78 cm, respectively. Considering that size at maturity is highly variable in many elasmobranch species, the large L_t range was expected (Ibid, 2021). Maturity was reached between 5.4 and 7.3 years in captivity, while it was estimated to be more than 24 years in the wild (Dainty, 2002). Considering that the growth performance and rate was faster in captive sharks, it can be assumed that maturity may be reached at an earlier age, as has been the case in other elasmobranch species. For example, the sand tiger shark (*Carcharias taurus*) has been found to reach sexual maturity at approximately 4.5 years in captivity, compared to approximately 9-10 years in the wild (Goldman, 2002). However, it has been reported that there is no difference in age at maturity between captive and wild individuals in the reef manta ray *Mobula alfredi* (Nozu *et al.* 2017). Therefore, it is necessary to consider that the age at maturity of captive and wild elasmobranchs may vary depending on the species and captive environment.

Growth rate

The overall trend for growth in pyjama sharks within this study suggested isometric growth for females and negative allometry for males regardless of being captive or wild-caught. Previous studies have suggested that small-bodied sharks that exhibit little movement typically follow an isometric growth pattern (Irschick and Hammerschlag, 2015; Ahnelt *et al.* 2020). Allometry in sharks is largely considered to be driven by habitat change (Gayford *et al.* 2023), therefore sexual segregation across habitat should be considered as a driver for differences in growth between sexes. However, recent findings from wild distribution analysis from Walker Bay has suggested no clear segregation between male and female pyjama sharks, sharing > 90% of their known habitat in the region (see Chapter 2). Therefore, there is a greater likelihood that sexual dimorphism is the primary driver for variances in growth between the sexes. Male-biased sexual size dimorphism is common in catsharks, with males developing longer and narrower heads to accommodate larger teeth (Erdoğan *et al*. 2004; Filiz and Taşkavak 2006; Colonello *et al*. 2020). This could possibly suggest why the pyjama sharks in this study increase in L_t at a greater rate than W_t, however further morphometrics should be recorded in future studies to confirm this hypothesis. Interestingly, wild-caught male sharks showed significantly greater negative allometry compared to captive male sharks, as well as much weaker correlation between length and weight increase. While the cause of this is currently unclear, it can be theorized that the captive males may be better adapted as they were born into a stabilized environment and a consistent feeding regime. Catsharks are considered as opportunistic scavengers (Richardson *et al.* 2000; Laptikhovsky *et al.* 2001; Olaso *et al.* 2005) often going for days without food in the wild, thus a significant impact on weight to length ratio would be expected.

Captive female sharks were found to express a significantly faster growth rate than captive male sharks although they did not attain a significantly greater asymptotic length. There is currently no literature available to corroborate differences between males and females of this species, though data from other Scyliorhinidae species suggests that this pattern is not universal within the family. For example, the blacktip sawtail catshark *Galeus sauteri* exhibits a greater growth coefficient in females (Liu *et al.* 2011), while the small-spotted catshark shows the opposite pattern (Ivory *et al.* 2004). However, without statistical analysis, it is difficult to ascertain whether these differences are significant. The growth performance index was somewhat lower in captive females compared to captive males, although the difference is minimal (0.037) suggesting little variance in growth performance. Currently there is a significant data gap concerning growth performance in catshark species between sexes, therefore it would be difficult to ascertain if growth performance would be expected to differ.

Observing the 95% confidence intervals for wild caught individuals would suggest no clear intersex difference between asymptotic length and the growth coefficients. However, the growth performance index was much greater in female sharks with a difference of 1.104. Munro and Pauly (1983) suggested that grouping asymptotic length and the growth coefficient is much more robust when analysing differences in growth. Therefore, we can assess that the growth performance was poor for wild male pyjama sharks, as was also reflected by the length-weight relationship. As previously discussed, this was likely a result of sexual size dimorphism (Erdoğan *et al*. 2004; Filiz and Taşkavak 2006; Colonello *et al*. 2020).

Both asymptotic length and the growth coefficients for males and females were larger in captive sharks, a pattern also reflected by a greater growth performance index in captive sharks. Other populations of wild sharks showed substantial variance in these parameters, with a slow growth rate (k = 0.036) in sharks from six sites in the Western Cape (Dainty, 2002) and a large asymptotic length (L_∞ = 117.8 cm) in sharks from Mossel Bay (Grusd *et al.* 2019). This suggests that growth parameters can significantly differ even within the same geographical region. However, it should be considered that the sexes were not split within these studies and thus likely affected the results. There is currently a large data gap concerning the difference in growth between wild and captive populations of catsharks, although studies involving other elasmobranch families often exhibit increased growth within captive individuals due to a stable feeding regime, and consistent temperature and dissolved oxygen levels (Wass, 1971; Carrier and Luer, 1990; Smith *et al.* 2004; Awruch *et al.* 2009). However, this pattern is not universal for all shark species (Branstetter, 1987; Parsons, 1993), thus it is recommended that further studies are conducted concerning the growth rate of other Scyliorhinidae between wild and captive populations to determine any patterns within the family.

Both length-weight analysis and VBG analysis showed significant variations between captive individuals of the same sex, though the drivers for these differences can only be speculated. Considering the sharks likely exhibited different behaviours, with respect to feeding and movement, as well as genetic and metabolic variance, it is likely that several factors influenced the variation in growth (Mohan *et al.* 2004). Individual differences in growth are poorly studied in most shark species, especially with respect to catsharks. However, dietary study in the blackmouth catshark *Galeus melastomus* has revealed interindividual differences in dietary selection within the same sub-population (Anastasopoulou *et al.* 2013) which could provide a potential answer for differences in growth between our captive individuals.

5. Conclusion

This study determined the incubation period, size and growth at hatching, age, and size at maturity of captive female pyjama sharks, which allowed for comparison of growth with wild populations. This is the first study to examine fertilized eggs, hatching, and growth in the same individual of this species, and the results, together with the growth and estimated age of the wild population, allow us to estimate these parameters more accurately for wild individuals in the future. At 18ºC, the incubation period for pyjama sharks was 239.46 ± 4.97 days, L_t at hatching was 14.65 ± 0.24 cm and W_t at hatching was 17.19 ± 0.75 g. The number of female offspring was significantly greater than males suggesting potential environmental drivers for ontogenetic sex selection. Females matured between 5.4 and 7.3 years in captivity which was significantly earlier than results found in previous studies. The captive reared individuals grew faster than wild individuals, exhibiting a greater growth performance, however, as with wild individuals, the growth patterns of reared individuals differed between sexes. This suggests that it is possible to infer the growth patterns of wild populations by following the growth of captive individuals of elasmobranchs. Stable reproduction of the species in captivity also provides evidence that *ex situ* rearing has the potential for biological and genetic conservation for this species, with potential for wild reintroduction programs if the species becomes threatened in the future. While the species is currently not endangered, this study provides a benchmark for informing conservation in the event of future population decline with respect to understanding growth, maturation, and fecundity.

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7. Figures

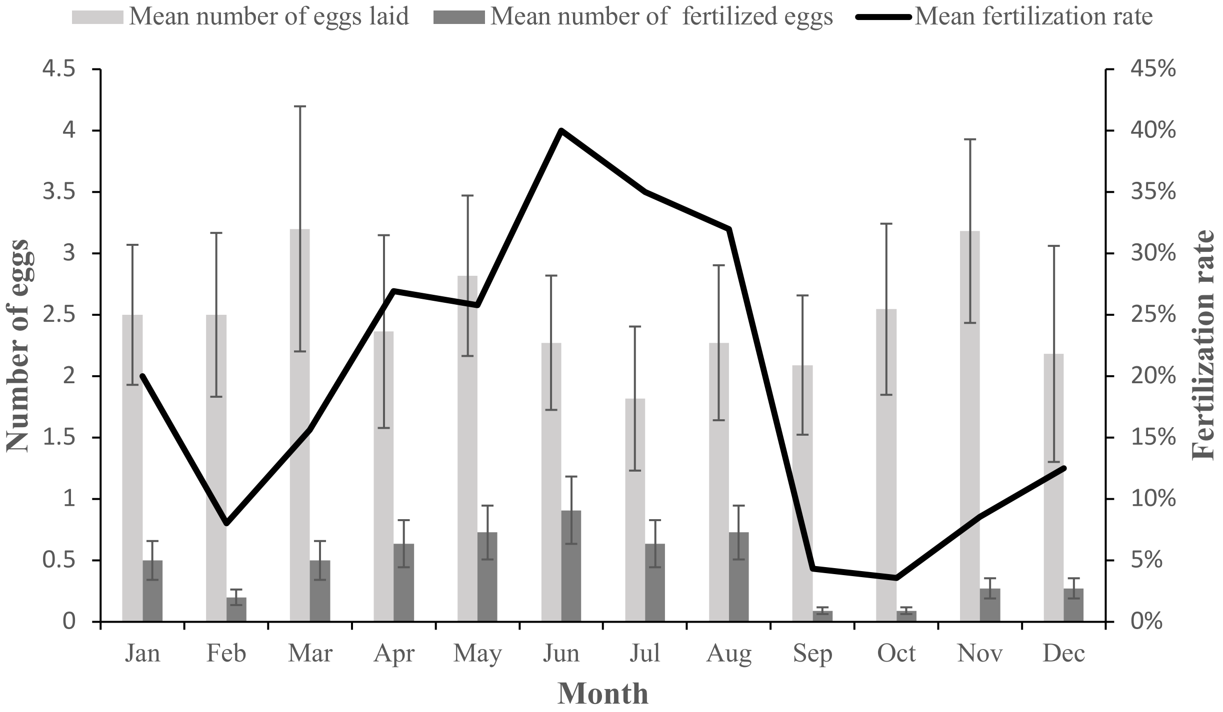

Figure 1: The mean number of eggs laid, mean number of fertilized eggs and mean fertilization rate per month in four female pyjama sharks from 2005 to 2020. Error bars represent standard error. No egg laying was noted between 2008 and 2011 due to the death of the mature female pyjama sharks.

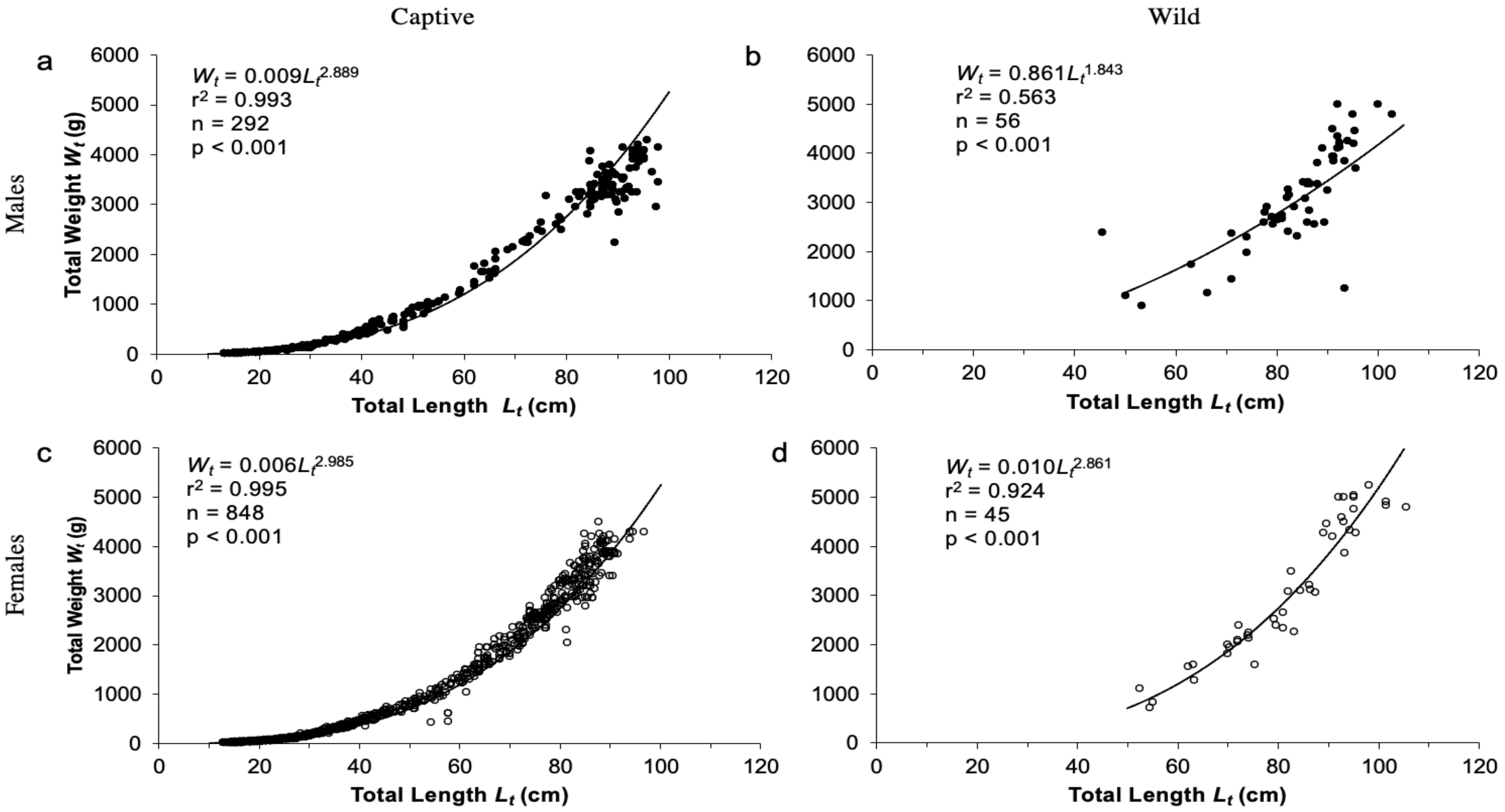

Figure 2: The length-weight relationship of captive male (a), wild male (b), captive females (c) and wild female (d) pyjama sharks *Poroderma africanum*.

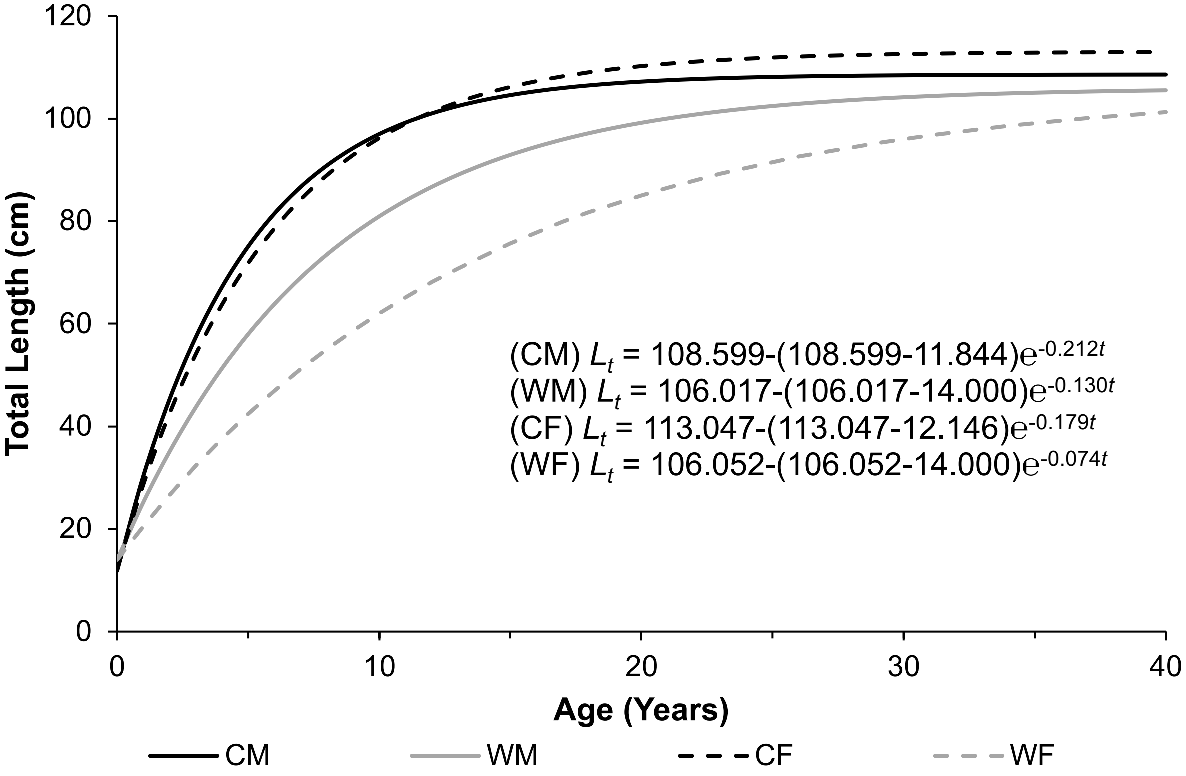

Figure 3 The length-at-age relationships for captive male (CM; solid black line), captive female (CF; dotted black line), wild male (WM; solid gray line) and wild female (WF; dotted gray line) pyjama sharks. von Bertalanffy growth equations are displayed using the abbreviations for each category.

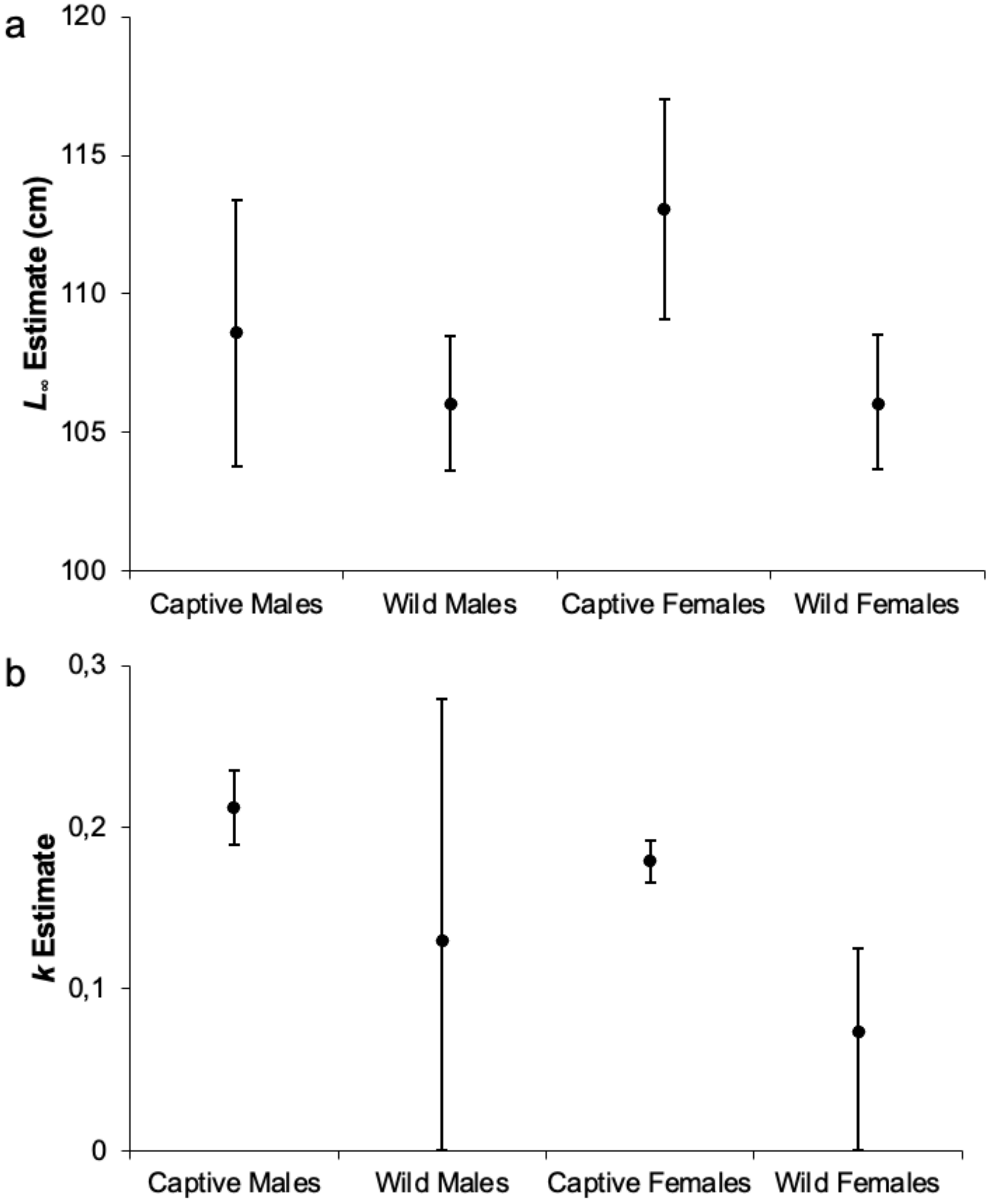

Figure 4: The asymptotic length (L_∞) (a) and growth coefficient (*k*) (b) for captive and wild-caught male and female pyjama sharks. Error bars represent the upper and lower 95% confidence intervals of the estimates.

8. Tables

Table 1 Fertilized eggs laid by captive pyjama sharks between 2005 to 2020. No egg laying was noted between 2008 and 2011 due to the death of the mature female pyjama shark.

No.	Egg laying date	Hatching date	Incubation period (days)	Total length at hatching (cm)	Body weight at hatching (g)	Sex
1*	15/07/2005	26/02/2006	226	15.8	27	M
2*	15/07/2005	28/02/2006	228	16.5	20	F
3*	01/07/2005	11/03/2006	253	16.0	22	F
4	25/07/2005	24/04/2006	273	16.8	24	F
5	26/08/2005	26/05/2006	273	15.6	20	M
6	11/10/2005	30/05/2006	231	16.5	22	F
7	25/08/2005	03/06/2006	282	15.0	13	M
8	11/10/2005	13/06/2006	245	16.0	19	F
9	20/11/2005	13/06/2006	205	15.4	16	F
10*	06/12/2005	24/07/2006	230	15.5	17	F
11	22/12/2005	21/08/2006	242	15.0	15	F
12	30/01/2006	13/11/2006	287	14.8	14	F
13	18/06/2006	18/02/2007	245	14.5	17	F
14*	07/06/2007	04/02/2008	242	14.7	16	F
15	-	14/11/2011	-	14.2	19	F
16	25/06/2013	12/02/2014	263	12.8	13	F
17	09/05/2014	11/12/2014	216	13.6	14	F
18*	24/05/2014	25/12/2014	215	13.2	14	M
19	24/05/2014	06/01/2015	227	13.2	15	F
20*	07/06/2014	06/01/2015	213	13.0	15	F
21*	07/06/2014	14/01/2015	221	12.8	14	F
22	20/04/2014	24/01/2015	279	13.2	12	M
23	24/01/2015	31/08/2015	219	13.3	13	F
24	24/01/2015	31/08/2015	219	13.3	13	M
25	-	22/11/2015	-	14.4	18	F
26	19/08/2018	20/03/2019	213	15.1	23	F
27	-	30/08/2021	-	15.4	19	F
		Mean ± SE	239.5 ± 5.0	14.7 ± 0.2	17.2 ± 0.7	Ratio: 1:3.5 (M:F)

*Individuals were kept for more than 7 years

CHAPTER FOUR: Network analysis of the endemic spotted gully shark *Triakis megalopterus* reveals spatial vulnerability to exploitation in the Western Cape, South Africa

1. Introduction

The protection of endemic elasmobranchs has been identified as a conservation priority to prevent local extinctions (Davidson and Dulvy 2017). The South African coastline is a hotspot for endemic coastal shark species, and has been identified as a priority region for conservation efforts (Davidson and Dulvy 2017). The spotted gully shark *Triakis megalopterus* is a mesopredatory species endemic to southern Africa (southern Angola, Namibia and South Africa; Figure 1A), feeding on benthic species such as teleosts, molluscs and crustaceans (Soekoe 2016). While currently listed as "Least Concern" on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Pollom *et al.* 2020), this species remains a target for recreational fishers, which increase the post release stress from catch and release practices (Cooke and Schramm 2007). This species is also indirectly targeted by commercial linefishers (Ebert *et al.* 2021), through misidentification with other Triakidae species (*e.g.* common smoothhound *Mustelus mustelus* and soupfin shark *Galeorhinus galeus*; Booth *et al.* 2011; da Silva *et al.* 2015). The proportion of chondrichthyans in the catches of recreational linefishers has increased over the years, with a notable decline in spotted gully sharks in False Bay, South Africa (Best *et al.* 2013). Given this species' endemicity, role in the food web, and potential susceptibility to fisheries in the region, the spotted gully shark is a conservation priority species of conservation concern (Booth *et al.* 2011). However, only a few studies, to date, have focused on this species ecology, with major findings being differences between populations from the Atlantic Ocean and the Indian Ocean, based on genetics (Soekoe 2016; Maduna *et al.* 2017) and stomach content analysis revealing a diet mostly composed of west coast rock lobster *Jasus lalandii* in the Western Cape (Soekoe 2016), but no study has been conducted regarding movement behaviour.

Identifying areas in which species aggregate is regularly used by managers to inform spatial planning initiatives, such as the development and use of marine protected areas (MPAs) to protect vulnerable and endangered populations (Espinoza *et al.* 2015; Cooke *et al.* 2022). In recent years, new approaches have been employed to monitor aggregation behaviours of animals, such as spatial and social network analyses (Jacoby *et al.* 2012; Stehfest *et al.* 2013; Mourier *et al.* 2018). A network represents a set of nodes and edges obtained using graph theory, allowing the study of pairwise interactions between nodes (Jacoby and Freeman 2016; Mourier *et al.* 2018). Network analysis can be conducted using various data collection techniques such as mark-recapture (Guttridge *et al.* 2011; Mourier *et al.* 2017), acoustic telemetry (Jacoby *et al.* 2016, 2021; Jacoby and Freeman 2016), or observation data (*e.g.* diving observations; Mourier *et al.* 2012; Mourier and Planes 2021). The result of a network analysis is an adjacency matrix giving the interaction between nodes, representing acoustic receivers in a spatial network, and tagged individuals in the case of a social network (Mourier *et al.* 2018). A network can be directed or not, showing the direction of a movement for a spatial network, and the impact of one individual on another in social network. Also, networks can be weighted or binary representing the strength of an association or simply its presence-absence, respectively. Spatial networks are often used to understand how species use MPAs by examining the frequency of movement between locations, and the relative importance of those locations within the study area (Stehfest *et al.* 2013; Espinoza *et al.* 2015). Social networks are frequently used to gain insights into species' population social structures, including aggregatory behaviour and sex segregation (Mourier *et al.* 2018; Jacoby *et al.* 2022; Villegas-Ríos *et al.* 2022).

To gain insights into the ecology and conservation needs of the spotted gully shark, this study employed passive acoustic tracking and subsequent spatial and social network analyses to study the behaviour and movement patterns of this species along the Western Cape coastline of South Africa. Accordingly, this study sought to address three primary questions: (1) Do spotted gully sharks exhibit non-random movements and aggregation patterns measured as associations between individuals? (2) If so, do spotted gully shark exhibit sexual segregation? and (3) How effective are existing MPAs in the Western Cape in protecting spotted gully sharks?

2. Methods

Study area and tagging procedure

This study took advantage of an array of 279 acoustic receiver stations (models VR2W and VR2AR; Innovasea, Halifax, Canada) deployed in coastal and estuarine environments along the South African coastline – the Acoustic Tracking Array Platform (ATAP, Murray *et al.* 2022). A total of 125 receivers were deployed in the marine environment of the Western Cape Province, and used during this study; 105 were active for the full study period (May 2019 to May 2022) and 20 were active for a portion of it (*i.e.* removed or first set during the study period; Figure 1). Range testing was previously performed for acoustic receiver located in False Bay (range of 1 200 m for n = 33; Kock *et al.* 2018), the De Hoop area (50% detection probability range of 200 m for n = 19; Albano *et al.* 2023) and Mossel Bay (800 m ± 200 m for n = 14; RG Watson, Marine Dynamics, pers. comm.). The performance of acoustic receivers is highly variable in the marine environment due to changing environmental conditions (Huveneers *et al.* 2016), therefore, a mean detection range of 500 m was used throughout this study.

Spotted gully sharks were caught between February 2016 and August 2021 in Walker Bay, De Hoop MPA, Mossel Bay and Wilderness (Figure 1) using handlines and rod and line equipped with circle hooks, or by hand (*e.g.* SCUBA diving or in rock pools). In all tagging instances, animals were put in tonic immobility and acoustic transmitters were surgically implanted inside the coelomic cavity as described in Hammerschlag *et al.* (2017). Tags used were V16s (V16-4L, 69 kHz, 16 mm diameter, 54 mm long, 24 g in air; Innovasea, Halifax, Canada) with varying battery life (mean = 2 468 days ± 1116 SD, Table 1) and a nominal delay of 60 to 120 seconds. Upon capture, the total length (TL) of the shark was measured (in cm), and sex was recorded.

Data organization

Data were downloaded from receivers at six to eight-month intervals and visually inspected to remove any false detections potentially resulting from tag collision (*i.e.* two tags pinging at the same time on the same receiver) or acoustic pollution (Simpfendorfer *et al.* 2015). Detections were deemed valid if two or more detections of an individual occurred on the same receiver within 30 minutes or single detections were corroborated by another receiver (*i.e.* located in the same area). This study used data collected from May 2019 to May 2022, representing three years of tracking. Only individuals detected by two or more receivers were considered. Analyses were conducted based on three datasets: all sharks, females, and males.

Spatial networks

Spatial network analysis was applied to identify differences in spatial use and high use areas between males and females (Stehfest *et al.* 2015). Receivers were categorised depending on the management level of the deployment area to quantify the potential benefit of protected areas (Espinoza *et al.* 2015). Categories included: (1) protected areas where any activity that can potentially alter the ecosystem is prohibited (*e.g.* fishing, destruction of any fauna and flora, discharging pollutants); and (2) exploited areas where commercial and recreational shark fishing is allowed. In spatial networks, nodes are the geographical locations – here acoustic receivers, and edges are movements between those receivers (Stehfest *et al.* 2013, 2015). All successive detections of an individual at the same receiver were grouped using a 30 minutes maximum blanking period and considered as one single visit, hereafter termed “detection event” (Jacoby *et al.* 2012; Mourier *et al.* 2021). A period of 30 minutes was chosen to reduce the number of detections due to immobile individuals that, given the nominal delay, could range from 15 to 30 detections per 30 minutes, and to keep information on high residency areas that would be lost with a bigger blanking period.

To test the influence of tagging location on individuals' space use, a general linear mixed model (GLMM) was used to test the impact of the distance to the tagging location on the amount of detection at a given receiver. GLMM was conducted using the 'glmer' function of the *lme4* package (Bates *et al.* 2015) with a poisson link function and individuals as a random effect.

Weighted matrices of directed movements between receivers were built for the two datasets (*i.e.* males and females), with a movement being recorded when an individual was detected on two different receiver a and b, regardless of how long the transition between a and b took. For the four resulting matrices, the weight of each edge, defined as the number of movements between each location, was computed to define which transitions between receivers were most common. Network metrics were calculated: Betweenness (B_i), representing the number of paths that pass through a specific node, from one node to another via the shortest path length; Centrality using In-degree (k_i^{in}) and Out-degree (k_i^{out}) to highlight entry and exit points in areas of interest or conservation concern; and edge density representing the percentage of actual edges present in the network (Jacoby *et al.* 2012). An area with high degree centrality could suggest strong site fidelity, high betweenness highlights the importance of specific locations, potentially providing access to a limited resource resulting in aggregatory areas, and edge density informs on non-random space use (Jacoby *et al.* 2012). Protection status at each receiver along with region (*i.e.* False Bay, Walker Bay, De Hoop and Mossel Bay) was added as a node attribute for each network (*i.e.* protected area and exploited area), thus network metrics were compared between attributes. The weight of each edge was calculated, with stronger edges representing more frequent movement between two receivers.

Effectiveness of protective areas was assessed by comparing network metrics between receivers located in protected areas and receivers located in exploited areas.

A null model representing random movements was created based on 10 000 permutations between pairs in the observed adjacency matrix of each network. Permutations were performed, for all receivers visited at least once during the study period, using the 'network.permuation' function of the *asnipe* package (Farine 2013). Two network metrics, diameter and average path length, were calculated for each network and compared between the observed network and the 10 000 random networks computed (Mourier *et al.* 2021). The diameter of a network represents the longest path between two receivers and gives and indication of the size of the network. Average path length gives an insight on the likelihood a transition between two receivers occurs.

Social networks

As movements were considered regardless of time, a social network approach was used to investigate co-occurrence patterns between individuals, linking results from spatial network to a temporal factor. Social networks describe associations between individuals where nodes are individuals and edges represent association. In this study, a gambit-of-the-group approach was used, describing the frequency with which two individuals were found in the same group (Cairns and Schwager 1987). Associations were proximity-based and defined as individuals detected at the same receivers within the same 5-minute interval (Aspillaga *et al.* 2021). Using the *spatsoc* package (Robitaille *et al.* 2019), the 'group_times' function was used to group detections per group of 5 minutes, then, the 'group_pts' function was used to group individuals, within time groups, that were detected on the same receiver by including receiver coordinates. The resulting group-by-individual matrix is a presence-absence matrix where, for each time interval, 1 represents individuals detected on the same receivers and 0, individuals that were not detected. Weighted networks were constructed accordingly, based on a simple ratio index (SRI) using the *asnipe* package (Farine 2013), illustrating strength of association between individuals. The SRI uses three assumptions: (1) detections are accurate; (2) the probability of identification of an individual is independent of whether the individual is associated or not; and (3) if an individual is detected, all its associates are also detected (Whitehead 2008).

Based on associations found by the social network for all individuals, additional networks were built for each area (*i.e.* False Bay, Walker Bay, De Hoop and Mossel Bay) for each year of the study (Y1: 01 May 2019 to 30 April 2020; Y2: 01 May 2020 to 30 April 2021; Y3: 01 May 2021 to 30 April 2022), to investigate location of aggregations, and the same methodology was followed.

Analyses were conducted using RStudio (version 2022.02.3+492) with R (version 4.2.1 GUI 1.79 High Sierra build, R Core Team 2022), and all networks were constructed using the *igraph* package (Csardi and Nepusz 2006).

Ethical note

Research was conducted under research permits RES2018-13, RES2018-59, RES2019-61 and RES2020-16 issued by the Department of Forestry, Fisheries and the Environment of South Africa and permit number CN32-31-5459 from CapeNature. Ethical clearance for individuals tagged by researchers from the South African Institute for

Aquatic Biodiversity (NRF-SAIAB) was obtained from the NRF-SAIAB Animal Ethics Committee #25/4/1/7/5_2017-08. All fishing, tagging and shark handling procedures were in accordance with established best practices (Murchie *et al.* 2012). No anaesthetic or analgesic was used during surgical procedures, instead, tonic immobility was induced by turning the shark on its dorsal side (Kessel and Hussey 2015). Fight time before the animal was put in tonic immobility was c. 5 minutes. An animal's head and gills were maintained in water at all times during surgery, allowing them to pump water through the gills, using spiracles, minimising stress. Gills were exposed to air for a few seconds only in the event of the shark being brought onto a boat for the tagging procedure (n = 4) and released. The incision measured c. 3.5 cm in the abdominal wall above the pelvic fins and was closed using three nylon sutures. Tagging was attempted only on animals larger than 70 cm TL and surgery procedure lasted approximately 3 minutes. Each animal was released in a healthy condition and observed swimming away strongly; no mortalities occurred during the tagging procedure.

3. Results

Dataset overview

A total of 25 individual spotted gully sharks were acoustically tagged in the Western Cape Province, with 22 (88%) being detected on at least two acoustic receivers. The data from these 22 individuals were used for analyses, representing 8 males and 14 females, with lengths ranging between 76 cm and 176 cm TL (mean = 134 cm TL ± 29 SD, Table 1). Among the individuals tagged, 13 (10 females and 3 males) were caught and released inside MPAs, and 9 (4 females and 5 males) were caught and released in exploited areas.

Of the 125 receivers used in this study, 67 (53.6%) receivers detected tagged spotted gully sharks, totaling 16 615 detections during the three-year sampling period (Table 1), excluding false detections (< 0.5%). Proximity to the tagging location had no effect on individual space use with no significant impact of the distance to tagging location on detections (GLMM: p = 0.18). All detections occurred on receivers located in the Western Cape, with only three detections recorded on receivers located in the Eastern Cape Province (Figure 1). A total of 32 (25.6%) receivers were located inside protected areas while 93 (74.4%) were located in exploited areas. Males represented a total of 9 756 detections (mean = 1 220 ± 1 577 SD), while females represented 6 859 detections (mean = 490 ± 1 029 SD). Detections occurred in two protected areas (Table Mountain National Park MPA and De Hoop MPA), two nature reserves located in Gansbaai (Dyer Island Provincial Nature Reserve and Geyser Island Provincial Nature Reserve), and the Whale Sanctuary seasonal MPA (Figure 1).

Spatial networks

After grouping detections according to the maximum blanking period (30 minutes), the spatial network dataset contained 4 705 detection events composed of 4 004 movements between receivers. Males represented 2 194 detection events (215 movements) and females represented 2 511 detection events (462 movements). Spatial networks indicated that despite movements being recorded along the entire Western Cape coastline, spotted gully sharks were often stationary, with most detection events (85.6%) displaying individuals detected on the same receiver numerous times (Figure 2).

The spatial networks for males showed that individuals were more active in Walker Bay and Gansbaai than in other areas, representing 71.5% of the detection events (Figure 2A). Male individuals were also detected more frequently in protected areas than in exploited areas with a higher amount of detection events in the Table Mountain National Park MPA (14.6%), De Hoop MPA (5.1%) and the Whale Sanctuary (68.6%), compared to the surrounding exploited areas. This was corroborated by the eigenvector centrality showing that the receiver most commonly visited was located in the Whale Sanctuary. Female individuals showed differing movement patterns with only a few detection events in the Table Mountain National Park MPA (1.6% of detections), but a higher amount of detection events in the De Hoop MPA (8.8%), when compared to male individuals (Figure 2B). While females also used the Whale Sanctuary (15.5% of total detections) and Gansbaai (2.1%), the most commonly used areas by females were the exploited areas along the Western Cape coastline (72.0%), and especially surrounding De Hoop MPA (65.7%; Figure 2B).

Male and female networks were found to be significantly different from the null model of random movement based on significant difference in diameter and average path length ($p < 0.001$ for both networks). For males, diameter of the observed network was 11 and a mean of 2.62 ± 0.008 for the null model, the average path length was 1.16 and 1.50 ± 0.003 for the observed network and null model respectively. For females, the diameter was 7 and a mean of 1.12 ± 0.003 for the observed network and null model respectively, the average path length for the observed network was 3.27 and a mean of 1.02 ± 0.001 for the null model.

Network metrics revealed that female individuals were using the acoustic array along the Western Cape to a greater extent than males as shown by the edge density (6.64% and 5.58%, respectively), also supported by the mean betweenness (B_i; 64.9 and 51.6, respectively; Table 2), but difference between male and female was not significant ($p = 0.5$). Betweenness also revealed that for both male and female individuals, protected areas were used to a greater extend than exploited areas, but differences were not significant for either males ($p = 0.31$) or females ($p = 0.53$) (Table 2). Furthermore, degree centrality was lower for protected areas than for exploited areas for both male and female networks, but differences were not significant ($p = 0.57$ and $p = 0.19$, respectively). Looking at differences between areas, males displayed strong site fidelity, with a high K_i, for Walker Bay compared to other areas (i.e. False Bay, De Hoop and Mossel Bay); differences in K_i were significant for all areas using a Kruskal-Wallis test ($p = 0.004$). Pairwise comparison between areas found significant differences only between False Bay and De Hoop ($p = 0.01$), Walker Bay and De Hoop ($p = 0.003$), De Hoop and Mossel Bay ($p = 0.01$). For females, based on degree centrality K_i, a high site fidelity was found for De Hoop compared to other areas, but no significant difference was found using a Kruskal-Wallis test ($p = 0.1$). Pairwise comparison found significant differences only between False Bay and Mossel Bay ($p = 0.03$), Walker Bay and Mossel Bay ($p = 0.01$), De Hoop and Mossel Bay ($p = 0.005$).

Social networks

For the social network including all individuals, a total of eight dyads (*i.e.* association between individuals) were identified from which four dyads represented associations between males, four dyads between males and females, and no dyads between females (Figure 3A). A total of seven sharks were found to be associating (four males and three females), all tagged prior or during the first year of the study period. After the first association was found in April 2020, at least eight months elapsed between the release date and the first associating event for all individuals. Co-occurrence between individuals occurred exclusively within Walker Bay, principally on one receiver (Figure 4). Therefore, only detections in Walker Bay were used to build the three social networks to investigate if co-occurrence patterns persited over time. Social network for Y1 showed four dyads with nine individuals detected, Y2 showed five dyads for five individuals detected and Y3 showed three dyads for eight individuals detected (Figure 3). Some dyads persisted over time, two dyads found in Y1 remained in Y2, and two other dyads remained between Y2 and Y3 (Figure 3). Interestingly, all associations occurred only during the winter season for Y1, Y2 and Y3 networks.

4. Discussion

Spatial network analysis revealed that tracked spotted gully sharks exhibited non-random movements along the Western Cape coastline. In addition, differences in space use between sexes suggested the potential for spatial segregation. Females showed higher use of the De Hoop region and males showed higher use of the Walker Bay region which could both be explained by the proximity with two important estuaries (Breede Estuary and Klein Estuary, respectively); both sexes also showed a high use of the False Bay area despite the fact that no individual was tagged in this area and no major estuary was present. Estuaries are often considered as key habitats for a variety of fish species, acting as nurseries and providing shelter for the growth of juveniles (Sheaves *et al.* 2014). Due to the increased abundance of small prey individuals, estuaries could be beneficial for a mesopredator such as the spotted gully shark, however, stomach content analysis on individuals from the Western Cape found the diet to be composed solely of crustaceans and molluscs, with the west coast rock lobster representing more than 98% of prey items found (Soekoe *et al.* 2022). The west coast rock lobster fishery is tightly regulated in South Africa due to a decreasing catch trend over the last decades, implementing size and bag limits along with a closed season (Holthuis 1991; Pollock *et al.* 2000). As such, with De Hoop and Walker Bay both containing MPAs (*i.e.* no-take zone), the abundance in those areas of the principal prey of spotted gully sharks could explain their usage of these areas. However, a previous study found no difference in abundance of west coast rock lobster inside compared to outside protected areas (Mayfield *et al.* 2005); thus, because food availability could be one of the factors explaining movements of this species towards those areas, other factors might also be of influence.

Co-occurrence patterns continued between years but solely in Walker Bay, principally between males, with no co-occurrence found between females. This corroborates spatial preferences of males along with potential sexual segregation. The fact that co-occurrences were only occurring during winter and persisting for multiple years is interesting; based on spatial network, those pairs might last longer than what was found in this study but occur outside of the receiver array. Another explanation could be that a certain resources are available during winter in Walker Bay and individuals are part of a bigger cohort that was not tagged. The difference in the amount of detection events after the blanking period (30 minutes) was applied showed differing behaviour between males and females, with males potentially more resident than females, which contradicts other studies on ground sharks (as no studies were found addressing differences in residency between sexes in Triakidae species) such as the blacktip reef shark *Carcharhinus melanopterus* (Schlaff *et al.* 2020) and the lemon shark *Negaprion acutidens* (Pillans *et al.* 2021), where females were more resident than males.

During this study, all spotted gully sharks were detected along the Western Cape coastline where the tagging occurred, except for three detection events along the Eastern Cape coastline. This lack of movement crossing the Western Cape border is consistent with the presence of multiple populations along their distribution range (*i.e.* southern Angola, Western Cape and Eastern Cape; Soekoe 2016), and in particular, a genetic divergence between the Western Cape and the Eastern Cape populations (Soekoe 2016). This could mean that this population of spotted gully sharks remains in the mixing zone, between the Agulhas and Benguela currents. This is supported by a lack of detection events beyond Cape Point and in the Eastern Cape, and also highlights the preference of the studied population for warm-temperate waters (Soekoe 2016).

The high use of the De Hoop region by females is interesting as it is essential to identify aggregatory areas of females, which may represent critical habitat for the species in the form of nursery and pupping areas (Heupel *et al.* 2007), previously described as crucial for their conservation in the region (FAO 1999; NPOA-Sharks II 2022). Juveniles from other species were previously found in the region showing that potentially the habitat is suitable as a nursery area and for multiple species (Albano *et al.* 2021). De Hoop could also potentially be a mating area, with untagged male individuals present but a previous study from Albano *et al.* (2023) found males not to be aggregating in the same area as females, showing that sex segregation might justify the aggregating patterns as opposed to mating behaviour. The fact that female spotted gully sharks are extensively using exploited areas is concerning in the event of a possible decrease in the population in the near future, thus, further investigation into their movement behavior should be considered along with increasing the protection covering their distribution range.

Considering the entire dataset, tagged spotted gully sharks exhibited high use of protected areas, but differences between protected and exploited area use was not significant showing that globally, protected areas are not effective for this species, based on space use. Locally, other studies using baited remote underwater videos (BRUVs) found a higher abundance of individuals from the Triakidae family inside the Whale Sanctuary MPA and De Hoop MPA, compared to adjacent exploited areas (Osgood *et al.* 2019; Albano *et al.* 2021). Protected areas were not specifically created for the conservation of spotted gully sharks, as their goal is to protect species that are endangered or are of economic importance (Attwood *et al.* 1997), and differing results from this study compared to previous findings shows the need for a bigger sample size. Indeed, this result needs to be taken with caution as this study includes only 25 individuals (of which data from 22 individuals was only used), and there is no information on the behaviour of untagged individuals. Detection range of receivers also needs to be taken into account when interpreting social networks, as potentially, individuals detected on the same receiver might not be close to each other. The spacing of receivers along the coastline was also inconsistent, which increased the probability of detections in specific areas compared to others (*e.g.* 12 receivers within the De Hoop MPA and no receivers between False Bay and Walker Bay), along with the probability that some aggregatory areas for this species could be outside of the detection range of receivers (*i.e.* very close inshore or in rocky gullies not suited to receiver deployment; Stehfest *et al.* 2015). Standardised catch-per-unit-effort data from the De Hoop MPA were previously used to assess the conservation status of the spotted gully shark (Pollom *et al.* 2020). While results showed that it is not the principal aggregatory area for this species, with more detection events occurring in the Whale Sanctuary area than De Hoop, an increase of the population in this region can hide a decrease in other areas.

5. Conclusion

This study revealed that tagged spotted gully sharks exhibited non-random movements with patterns of spatial segragation, along with co-occurrence between individuals. Movement data showed that future assessement of the population should not only be based on the De Hoop MPA (Pollom et al. 2020), but also include data from Walker Bay and False Bay. Existing MPAs located along the Western Cape coastline were commonly visited by spotted gully sharks, but results suggests that principal aggregation areas might not fall within MPA boundaries. Future research should combine acoustic telemetry with mark-recapture data as well as BRUVs across this species' entire distribution range in order to provide a more accurate assessment of spotted gully shark behaviour and social structure.

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7. Figures

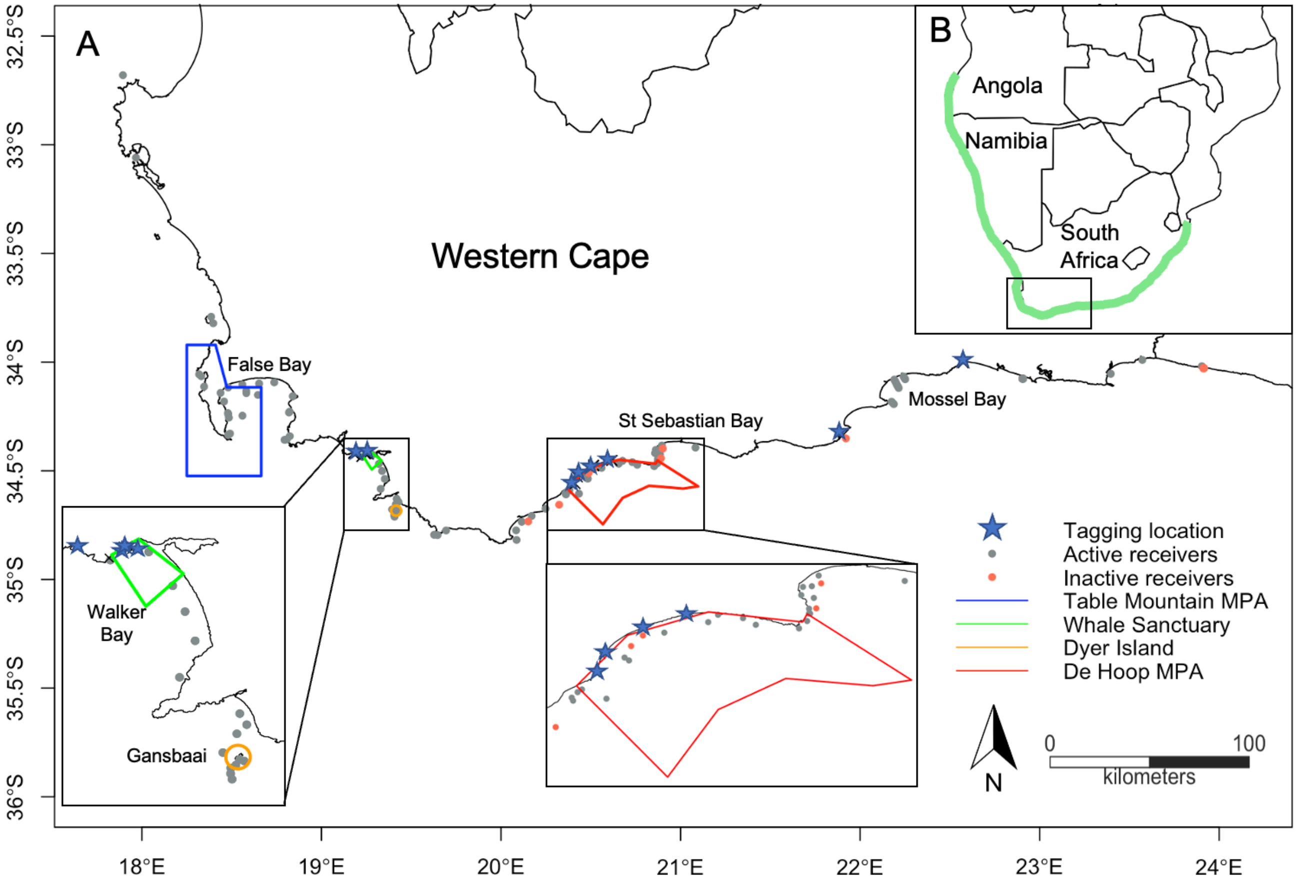

Figure 1: (A) Map of the Western Cape, South Africa, with locations of active receivers (grey dots) and receivers active for part of the study period (orange dots) along with (B) distribution range of Spotted gully shark within southern Africa. Blue stars indicate tagging locations, and different colour lines delimit protected areas

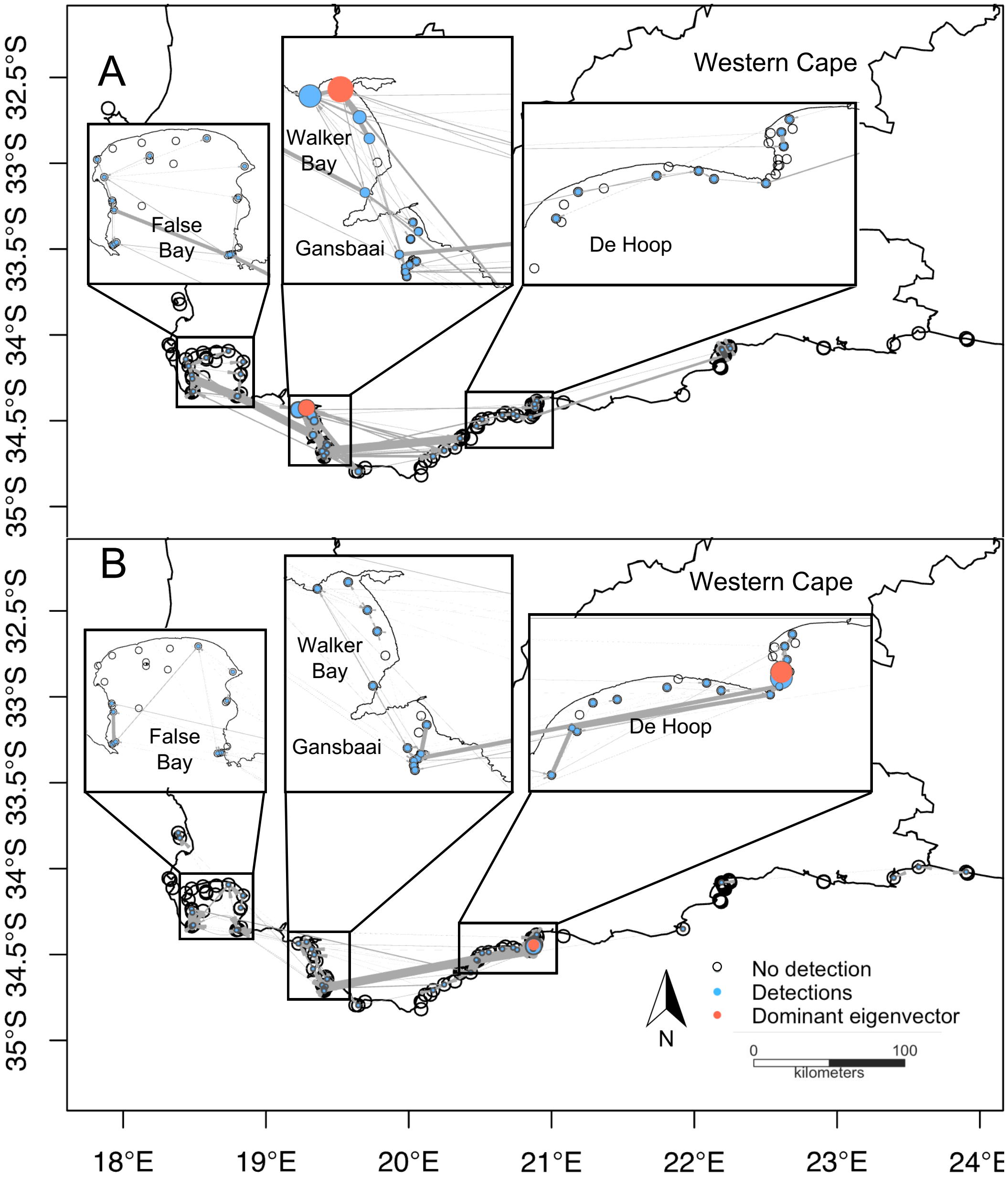

Figure 2: Spatial networks for (A) male spotted gully sharks and (B) females along the southern coast of South Africa; blue dots represent receivers on which detections were recorded, and white dots represent receivers on which no detections were recorded. For each network, the dominant eigenvector is represented by a red dot with size of each dots proportional to the eigenvector of each receiver, grey lines represents movement between two locations and lines thickness represents the number of time the transition was made.

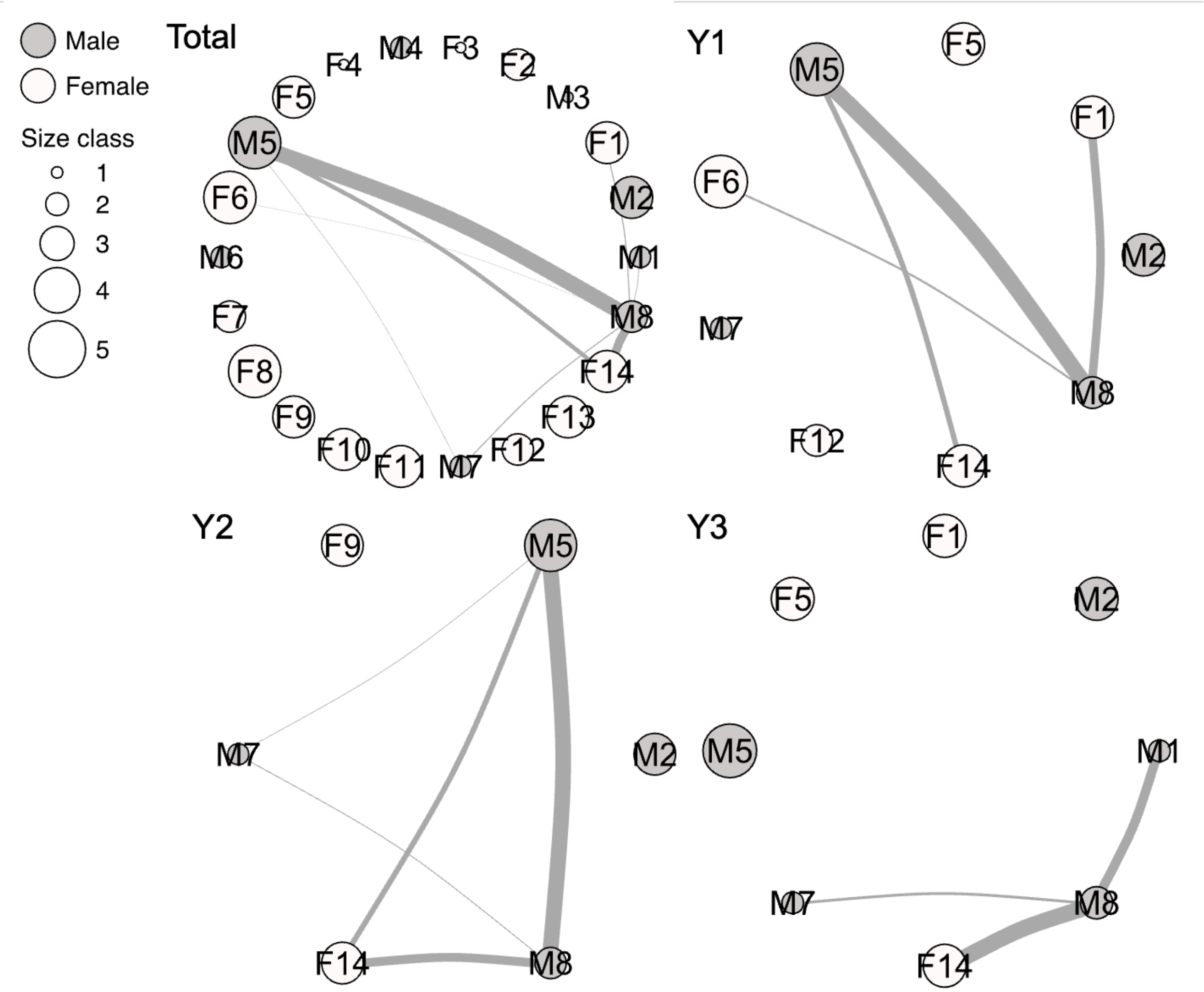

Figure 3: Observed social networks for spotted gully sharks for the full dataset, Y1, Y2, and Y3. Females are represented by purple circles while males are represented by green circles. Sizes of circles depend on the total length of the individual (larger circles represent larger individuals) and widths of edges depend on the edge weights.

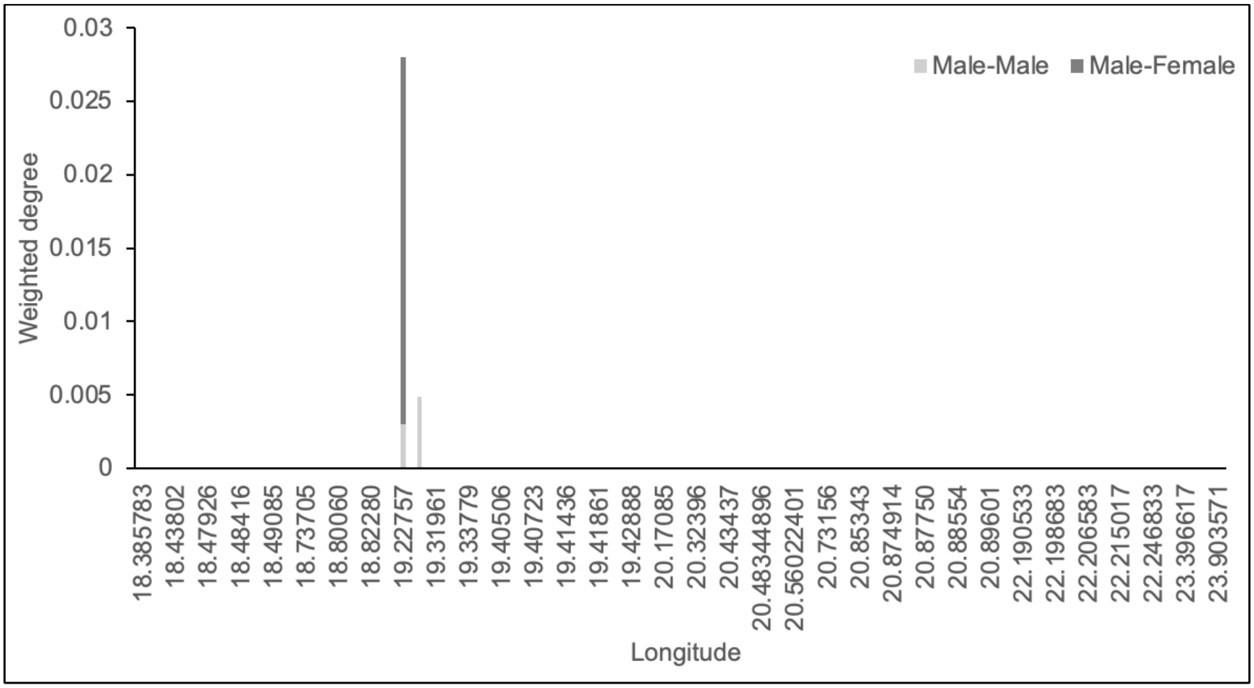

Figure 4: Location of co-occurrence between individuals along the Western Cape coastline.

8. Tables

Table 1: Tagging details and detection summary of spotted gully sharks tagged with acoustic transmitters in the Western Cape, South Africa and monitored between May 2019 and May 2022. Superscripts are indicative of tagging region (^{1} Mossel Bay area; ^{2} Walker Bay; ^{3} De Hoop)

ID code	Sex	Total length (cm)	Tagging date	Length of data series (days)	Tag life (days)	Capture location	Number of detections	Number of receivers
M6	M	108	2016-02-25	1897	3650	Wilderness	462	6
F7	F	124.6	2016-02-25	2101	3650	Wilderness	87	4
F10	F	153	2017-04-27	1814	3650	Kanon beach^1	25	4
M8	M	132	2018-02-09	1601	3197	Rietfontein^2	4 520	15
F14	F	146.4	2018-03-05	1480	2431	Old Harbour^2	1 893	17
M7	M	115	2018-03-20	1511	2466	Rietfontein^2	421	11
M3	M	76.1	2019-02-26	476	838	Koppie Alleen Beach^3	300	11
F2	F	132	2019-02-27	843	838	Koppie Alleen Beach^3	3 638	16
F5	F	158	2019-03-07	1148	3197	Roman Rock^2	146	8
F4	F	83	2019-04-25	399	838	Koppie Alleen Beach^3	5	2
F9	F	154	2019-04-25	840	838	Koppie Alleen Beach^3	119	12

M5	M	167	2019-06-02	1252	3197	Marine Pool Hermanus[2]	2 509	15
M1	M	118.2	2019-09-06	969	3197	Onrus Beach[2]	1 445	16
M2	M	148	2019-09-06	956	3197	Onrus Beach[2]	94	6
F1	F	152.4	2019-09-06	947	3197	Onrus Beach[2]	362	10
F8	F	175.6	2019-11-25	731	2907	Skipskop[3]	29	4
F12	F	139	2019-12-13	850	2503	Koppie Alleen Beach[3]	339	15
F13	F	155	2020-01-11	595	2377	Koppie Alleen Beach[3]	15	4
F6	F	174	2020-01-30	632	3197	Marine Pool Hermanus[2]	107	10
F3	F	94	2020-02-21	51	838	Skipskop[3]	71	8
M4	M	114	2020-02-24	419	838	Marker 33 Lekkerwater[3]	5	2
F11	F	152.4	2021-08-10	81	2546	Onrus Beach[2]	23	2

Table 2: Summary of metrics of spatial networks for female and male individuals along with summer and winter seasons (number of detections). Mean Betweenness (B_i), mean In-degree (K_i^{in}) and mean Out-degree (K_i^{out}) are represented for the overall network and for each network attribute. The mean network centralization (%) is also represented.

	Male (2194)			Female (2511)		
	B_i	K_i^{in}	K_i^{out}	B_i	K_i^{in}	K_i^{out}
Total	51.6	0.02 (32.6)	0.02 (32.6)	64.9	0.02 (37.8)	0.02 (37.3)
Open	46.2	0.02 (33.7)	0.02 (33.8)	53.5	0.02 (46.9)	0.02 (45.9)
Protected	64.3	0.01 (29.8)	0.01 (29.8)	93.7	0.01 (15.5)	0.01 (15.5)
False Bay	90.3	0.01 (22.7)	0.01 (22.7)	59.3	0.03 (8.1)	0.03 (7.5)
Walker Bay	87	0.05 (98.6)	0.05 (98.6)	89.6	0.01 (27.9)	0.01 (27.8)
De Hoop	10.8	0.003 (6.1)	0.003 (6.1)	89.3	0.04 (94.1)	0.04 (94.3)
Mossel Bay	35.9	0.01 (10.7)	0.01 (10.7)	4.5	0.001 (1.9)	0.001 (1.9)
Network centralisation (%)	5.58			6.64		

CHAPTER FIVE: Movement and site fidelity of the spotted gully shark *Triakis megalopterus* in the Western Cape, South Africa

1. Introduction

Movement of aquatic and marine species has been widely studied with various monitoring techniques such as mark-recapture (Johnson *et al.* 2024; Chapter 2), acoustic telemetry (Schlaff *et al.* 2020; Cottrant *et al.* 2023) and satellite tracking (Renshaw *et al.* 2023). Acoustic telemetry is advantageous compared to mark-recapture to study movement of coastal species due to the low recapture rates found in marine environment. Analyzing species movement gives insights on site fidelity to specific areas, that can be different between sexes or maturity stages (da Silva *et al.* 2021b), roaming behaviour thought the analysis of distance traveled (Schlaff *et al.* 2020), and habitat use and preference (Elston *et al.* 2023). Furthermore, aggregatory areas can also be derived from acoustic telemetry, and results can be different depending on life-history stages; thus, it is essential to understand a species' ecology for its conservation (Grubbs 2010; Knip *et al.* 2011; Matich and Heithaus 2015). For example, male and female sharks can aggregate in specific areas for mating purposes, extensively studied in the nurse shark (*Ginglymostoma cirratum*; Carrier and Pratt 1998, Afonso *et al.* 2016, Pratt *et al.* 2022). Alternatively, female sharks from other species can aggregate in different areas to give birth (Campana *et al.* 2010; Mourier and Planes 2012). Finally, juvenile sharks can aggregate in nursery areas depending on their energetic needs and presence of predators (Heupel *et al.* 2007, Knip *et al.* 2010, Heupel *et al.* 2018).

Research on endemic shark species has been identified as a global priority for conservation to prevent local extirpations (Davidson and Dulvy 2017). The spotted gully shark *Triakis megalopterus* is a medium-bodied shark species endemic to southern Africa, from southern Angola to the Wild (southeastern) Coast, South Africa (Ebert *et al*. 2021) (Figure 1), and is usually found in depths shallower than 30 m on rocky reefs (Smale and Goosen 1999), and in kelp forests (Ebert *et al.* 2021). This species has recently been reevaluated by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Pollom *et al*. 2020), and has been promoted from “Near Threatened” to “Least Concern”. Nevertheless, it is actively targeted by recreational fishers (Ebert *et al.* 2021), and could be susceptible to bycatch from commercial fisheries operating in shallower waters, which could result in post-release stress and mortality (Cooke and Schramm 2007). Previous studies investigated the diet of spotted gully shark across a range of sizes (Soekoe 2016), highlighting that it is a mesopredator, feeding on benthic species such as small teleosts, crustaceans and molluscs, while, in turn, the species is being preyed upon by various higher trophic species such as sevengill cowshark *Notorynchus cepedianus* (Ebert 1991) and orca (*Orcinus orca*; RGA Watson pers. obs.). While differences in diet have been found between different regions of its distribution range (*i.e.,* Angola, southwestern and southeastern coastlines of South Africa), with a higher prey diversity in the warmer regions of Angola and the Eastern Cape Province, South Africa, compared to the cooler water of the Western Cape Province (Smale and Goosen 1999; Soekoe 2016) (Figure 1), no significant ontogenetic shift in diet was found with an increase in size (Soekoe 2016).

Therefore, this study aimed to investigate movements patterns of the spotted gully shark from the Western Cape, South Africa. The goal was to assess site fidelity to different areas along the Western Cape coastline, distance travelled of individuals, with effect of sex, size and tagging location. Data collected with acoustic telemetry can be compared with findings using mark-recapture along the South African coastline (BQ Mann pers. comm.). Outcomes of this study will help identify important areas for spotted gully sharks that could be essential for their conservation and management.

2. Methods

Study area

South Africa is bordered by two oceans, namely the cool Atlantic Ocean on the west coast, and the warmer Indian Ocean on the east coast (Teske *et al.* 2011). The two oceans meet at Cape Agulhas, the most southern point of Africa, creating a mixing zone between Cape Agulhas and Cape Point, with warm-temperate waters specific to the Western Cape (Teske *et al.* 2011). A total of 150 different marine ecosystems have been identified along the South African coastline, representing a high diversity of marine species (Skowno *et al.* 2019). The movements of tagged sharks were monitored across the Acoustic Tracking Array Platform's (ATAP) receiver array (Murray *et al*. 2022; Figure 1). Only receivers deployed in the Western Cape (n = 125), which is located in the mixing zone between the Atlantic Ocean and Indian Ocean, were included for the purpose of this study. Receivers were grouped into seven main areas of interest (*i.e.* False Bay, Walker Bay, Gansbaai, Struisbaai, Breede, Mossel Bay and Plettenberg Bay; Figure 1). The most western acoustic detection was recorded on a receiver near Robben Island north of False

Bay, whereas the most eastern acoustic detection was recorded in Plettenberg Bay, in the Eastern Cape (Figure 1).

Tagging procedure

A total of 25 spotted gully sharks were acoustically tagged between 2016 and 2021 using acoustic transmitters (V16-4L; Innovasea, Halifax, Canada) with varying battery lives (mean = 2 433 days ± 1075 SD; Table 1). Sharks were caught in Walker Bay, De Hoop, Mossel Bay and Wilderness (Figure 1) using multiple gear types, including handlines (Walker Bay only), by hand when SCUBA diving (Walker Bay only), rod and reel equipped with circle hooks, or a seine net in the case of individuals trapped in rock pools, which occurred in 2020. Animals were handled in accordance with established best practices (Murchie *et al.* 2012), with gills submerged in the water at all times during the procedure to minimise stress. Individuals were put in tonic immobility, without the use of anaesthetic (Kessel and Hussey 2015), and acoustic transmitters were surgically implanted into the intracoelomic cavity. Incisions were approximately 1.5 cm in the abdominal wall, above the pelvic fins, and closed using three nylon sutures. Upon capture, total length (TL in cm) and sex of each individual was recorded. Based on size-at-50% maturity (Smale and Goosen 1999), males with a TL of less than 132 cm, and females less than 145 cm were classified as juveniles.

Research was conducted under research permits RES2018-13, RES2018-59, RES2019-61 and RES2020-16 issued by the Department of Forestry, Fisheries and the Environment of South Africa and permit number CN32-31-5459 from CapeNature. Ethical clearance for individuals tagged by researchers from the South African Institute for

Aquatic Biodiversity (NRF-SAIAB) was obtained from the NRF-SAIAB Animal Ethics Committee #25/4/1/7/5_2017-08.

Data organisation

Data were downloaded from receivers every six to eight months and visually inspected to remove any false detections potentially resulting from tag collision (*i.e.* two tags pinging at the same time on the same receiver) or acoustic pollution (Simpfendorfer *et al.* 2015). Detections were deemed valid if more than two detections of an individual occurred on the same receiver within 30 minutes or single detections were corroborated by another receiver (*i.e.* located in the same area).

Theoretical date of maturity was calculated for tagged juveniles spotted gully sharks to examine potential impact on results for individuals that became mature during the study period. Date was estimated based on the von Bertalanffy growth formula (VBG; von Bertalanffy 1938) with parameters from Booth *et al.* (2011) giving an estimated age at maturity of 10.9y for males and 15.3y for females. Age upon capture was calculated using the formula:

$$L_t = L_\infty(1 - e^{-k(t-t_0)})$$

Where L_t is the TL on the date of tagging, L_∞ is the theoretical maximum size obtained using VBG in Booth et al. (2011) ($L_\infty = 1667.89$mm for males and $L_\infty = 1738.93$ mm for females), k is the growth parameter ($k = 0.12$ for males and $k = 0.10$ for females) and t_0 is the theoretical age at zero length ($t_0 = -2.15$ for males and $t_0 = -2.67$ for females).

All analyses were performed using RStudio (version 2023.12.1+402; Posit team 2024) with R (version 4.3.3 GUI 1.80 Big Sur ARM build, R Core Team 2024).

Detection index

To investigate site fidelity of individuals to areas along the coastline, detection indices (DI) were calculated for all individuals (n = 25). Three DIs were calculated, one being array based (DI_a) which comprised all receivers in the study area (here WC), a second one being regional based where a DI was calculated per area of interest (DI_r; False Bay, Walker Bay, Gansbaai, Struisbaai, Breede, Mossel Bay and Plettenberg Bay), and a tagging location DI which comprised, for each individual, only receivers within their tagging area (DI_t). Comparison of those three DIs gave information on whether sharks exhibited site fidelity to their tagging location, to another defined area or if no clear pattern was observed along the coastline. DIs were calculated as the number of days detected divided by the number of days monitored, defined as the number of days between the tagging date and the last detection (Elston *et al.* 2023). Furthermore, to get an overview of the data, a roaming index (RI) was calculated as the number of receivers visited by an individuals divided by the total number of receivers in the study area, this index was then compared to DI_a (Schlaff *et al.* 2020).

A Generalized Linear Mixed Model (GLMM) was used to determine the effect of region, sex and TL (as a proxy for maturity) on individuals DI_r. Data were comprised between zero and one, with zeros resulting from a shark not being detected in one of the areas of interest during its time at liberty. Thus, a zero-inflated beta family with a “logit” link was used to match the continuous response variable and tag numbers were set as a random effect. A Generalized Additive Model (GAM) was used to assess the effect of sex, TL, and months (as a proxy for seasons) on spotted gully sharks amount of detection for each month. GAM was used as non-linear variations can occur between months, thus, it was set as a smooth term, individual tag numbers were set as random effect, and number of days in a month was set as an offset in order for the analysis to be done on DI_r. Data were non normally distributed, thus a poisson family was chosen with a log link as this model gave the lowest AIC compared to other link functions. GLMM was computed using the “glmer” function of the *lme4* package (Bates *et al.* 2015), and GAM was computed using the “gam” function of the *mgcv* package (Wood 2017).

Distance travelled

The total distance travelled was calculated for each shark from the release site and between each consecutive detection, until the last detection recorded. Only sharks that were detected on two or more receivers were included for analysis (n = 23; Table 1). The Haversine formula (Robusto 1957) modified by Van Brummelen (2013) was used to calculate the distance between locations by taking into account the curvature of the Earth. Calculations followed the formula:

$$hav\left(\frac{d}{r}\right) = hav(\varphi_2 - \varphi_1) + \cos(\varphi_1) * \cos(\varphi_2) * hav(\lambda_2 - \lambda_1)$$

Where hav is the Haversine function $hav(\theta) = sin^2(\frac{\theta}{2})$, θ represents the central angle between two points on a sphere, r is the mean radius of the Earth ($r =$ 6 371km), φ_1 and φ_2 are the latitudes of receivers in radians, λ_1 and λ_2 are the longitudes in radians. Due to the sparse setting of the receiver array, straight lines between receivers crossed land, thus, to prevent this, additional fictional receivers (n = 9) were added for calculation to keep sharks movements within the marine environment. Since all individuals have different time at liberty, distance travelled was divided by time at liberty to get a number of kilometres travelled per day, which was used in a Generalized Linear Model analysis (GLM). GLM was used to determine the influence of TL (as a proxy for maturity), sex and tagging area, on the total distance travelled by spotted gully sharks. Tagging area comprised Walker Bay (n = 11), Breede (n = 8), Wilderness (n = 2), and Kanon beach (n = 1), and a gaussian family with a "square root" link was set for the GLM since the data was normally distributed and the model using the "square root" link had the lowest AIC.

3. Results

Dataset overview

Tagged spotted gully sharks represented 15 females (five juveniles and 10 adults) and 10 males (six juveniles and four adults) with lengths ranging from 76 cm to 176 cm (mean = 131 cm TL ± 31 SD). Of the 125 receivers used in this study, 78 (62.4%) receivers detected spotted gully sharks, comprising 33 011 detections between 2016 and 2023. The majority of detections occurred on receivers located in the Western Cape, with detections found on only five receivers located in the Eastern Cape (Plettenberg Bay), close to the border of the Western Cape (0.01% of detection; Figure 2). A total of 33 (42.3%) receivers inside protected areas detected spotted gully sharks, while 45 (57.7%) were located in exploited areas. Areas of interest comprised False Bay with 17 receivers that detected individuals, Walker Bay with six receivers, Gansbaai with 11 receivers, Breede with 20 receivers, Struisbaai with three receivers, and Mossel Bay with 14 receivers. By comparing RI and DI_a, results showed that globally spotted gully sharks are not fully using the receiver array with RI comprised between 0 and 0.25 for all individuals, and this species is not resident to an area covered by receivers with DI_a comprised between 0 and 0.25 for all individuals (Figure 3).

Detection index

Individuals tagged in Breede (n = 10) comprised three individuals with proportion of detection in the tagging area above 0.90, three below 0.25 and four which had no detections in the tagged area (Table 2). Individuals tagged in Wilderness (n = 2) and the individual tagged in Kanon beach had proportions of detection over 0.90 in Mossel Bay, the closest bay to the respective tagging locations. Sharks tagged in Walker Bay (n = 12) comprised six individuals exhibiting proportion of detections within the tagging area over 0.75, two around 0.50, two under 0.10 and two sharks which were never detected in the Walker Bay despite being tagged there (Table 2). Overall, spotted gully sharks showed high fidelity to their tagging area with 12 individuals exhibiting proportion of detections in their respective tagging over 0.75 (Table 2). Furthermore, no significant influence of sex, TL and region was found on DI_t.

DI_r was almost identical for females and for males with a mean of 0.01 ± 0.004 SE for both (Figure 4). Differences were observed between regions with higher DI_r for Breede and Walker Bay with means of 0.02 ± 0.01 SE for both regions while the lowest DI_r for Struisbaai with a mean of 0.001 ± 0.0003 SE (Figure 4). No trend was observed by comparing DI_r depending on total length, thus maturity appeared to not influence which regions are preferred by sharks. Results were confirmed by the GLMM with no significative influence of sex, TL, and region on DI_r.

Months were found to have a significant influence on DI_r (p < 0.001) with positive influence meaning increased detections between February and May while a negative influence between October and December (Figure 5). Looking at DI_r for each month for each sex, females had a small positive impact on DI_r between March and May, and between August and October (p < 0.001). For males, a positive influence of months was found between December and June (Summer and Autumn seasons) while a negative influence was found between June and November (Winter and Spring seasons; p < 0.001). Regarding the shape of the global smoothing parameters compared to the parameter per sex, it was found that the males distribution matched closely the shape of the global smoothing parameter, compared to females (Figure 6). Months were found to have a significant influence on DI_r when comparing regions (p < 0.001), but influence could not be observed for Struisbaai and Gansbaai as the dataset was too small when looking at months. Breede was found to have similar DI_r throughout the year while a negative influence was found between May and August in False Bay, a negative influence was also found between April and August in Mossel Bay, and in Walker Bay, a positive influence was found throughout the year, except between September and December, where a negative influence was found (Figure 6).

Distance travelled

Distance travelled was calculated for 23 individuals that exhibited detection on at least two different receivers representing eight males and 15 females (mean TL = 1393.4 cm ± 53.5 SE; Table 3). The individual that exhibited the longest distance travelled was a juvenile female of 139 cm TL with 2 206.52 km travelled in 1 344 days, while the smallest distance was travelled by a juvenile male of 114 cm TL with 17.91 km travelled in 419 days. Individuals exhibited a mean distance travelled of 760 km ± 623 SD for a mean time at liberty of 1241 days ± 730 SD (Table 3). Looking at distance travelled per day, mean for all individuals was of 0.66 $km.day^{-1}$ ± 0.44 SD. Distance travelled per day was higher for females than for males with means of 0.75 $km.day^{-1}$ ± 0.45 and 0.49 $km.day^{-1}$ ± 0.40, respectively. Sex and TL did not significantly influence kilometers per day travelled by spotted gully sharks ($p > 0.05$ in all instances; Figure 7). Release area did not significantly influence the kilometres travelled by individuals but, Breede ($n = 8$) and Walker Bay ($n = 11$) had higher sample size than Wilderness ($n = 2$) and Kanon beach ($n = 1$). Furthermore, both areas had higher level of $km.day^{-1}$ (Figure 7), thus, an additional Student t-test was performed between Breede and Walker Bay, but no significant difference was observed.

4. Discussion

This study showed that, regionally, spotted gully sharks had low detection indices and roaming indices, thus, the receiver array is not fully covering their space use. In fact, receivers are located in relatively shallow coastal areas (mean depth of 21 m ± 8.3 SD, TS Murray, pers. comm.) showing that while spotted gully sharks are known to inhabit shallow waters (Ebert *et al.* 2021), it is possible that they use deeper areas more than expected. Comparing with mark-recapture, this species had higher catch rate between October and March on the entire South African coastline (BQ Mann, pers. comm.), also showing that individuals might not be using coastal areas throughout the year but coming seasonally for a specific purpose such as feeding, mating or parturition in nursery areas for females. Furthermore, distance travelled of individuals from this study also surpassed what is found using mark-recapture (BQ Mann, pers. comm.), showing the value of acoustic telemetry data for movement ecology, giving a finer scale insight on species behaviour. Our study also found that half of the tagged individuals remained within their tagging area with no significant influence of sex or sizes, thus, roaming behavior might be due to individual behaviour more than a specific need. Residency patterns might also be less identifiable due to the low sample size as previous studies found high residency patterns (Dunlop and Mann 2014) and a high number of individuals being recaptured within 5 km from their release sites (66.9%; BQ Mann, pers. comm.).

No difference was found in the receiver array use depending on the sex which was also found using network analysis in the Western Cape (Cottrant *et al.* 2023), but sexes were found to use the receiver array during different months of the year. For females, the positive influence of month on DI_r between March and May falls after the parturition period known for this species between February and March (Soekoe 2016). Indeed, this period is influenced by water temperature and occurs earlier in the year in the Western Cape compared to warmer waters in Angola and the Eastern Cape as individuals are growing slower (Soekoe 2016). This was also found for another Triakid species, the smoothhound shark *Mustelus mustelus*, where ovulation, mating and parturition periods were different between the different regions of its distribution range (e.g. South Africa, Senegal, Mauritania, Gulf of Tunis; da Silva *et al.* 2021a). This could show that parturition is not linked to a specific area covered by receivers or, parturition might occur throughout their distribution (Bass *et al.* 1975; BQ Mann, pers. comm.). Furthermore, gestation period of spotted gully shark is estimated to last between 19 to 21 months (Smale and Goosen

1999), thus, mating could occur between June and July which is a period where both sexes showed lower DI_r showing that the mating area of this species might fall outside of the receiver array. Data also showed a clear sexual segregation pattern with an increased DI_r for females between August and September while males were less detected during that period, matching previous findings of sexual segregation using network analysis (Cottrant *et al.* 2023).

Higher DI_r was found for Walker Bay and Breede, a pattern already observed using network analysis where females were found to use Breede more than males and the opposite for Walker Bay (Cottrant *et al.* 2023). The Breede area is located in the Indian Ocean, thus, the water temperature is warmer than found in Walker Bay, located in the Atlantic Ocean. Females could use Breede because of the warmer water temperature compared to Walker Bay because females are known to grow slower than males and reach maturity to a later age (Booth *et al.* 2011). A previous study by Soekoe (2016) also found two distinct populations, within the spotted gully shark southern African distribution, separated by Cape Agulhas, thus, our two study regions could have a different population. Nevertheless, no significant differences were found between regions regarding distance travelled by individuals, similar to findings using mark-recapture (BQ Mann, pers. comm.). Furthermore, while Breede and Walker Bay were used during different months of the year by spotted gully sharks, no differences was found between annual DI_r, thus, genetic differences and growth were found between populations separated by Cape Agulhas (Soekoe 2016), but our results suggest that movements and area use of this species are not impacted. Interestingly, a negative influence of months on DI_r was found in Walker Bay during spring months (between September and December), where the water temperature is warming, while spotted gully sharks are expected to come inshore to take advantage of warmer temperature, advantageous for their growth (Soekoe 2016). Study on the smoothhound shark found difference in temperature preferences between sexes (da Silva *et al.* 2021b), thus, as Walker Bay was previously found to be used more by males than females (Cottrant *et al.* 2023), water temperature in the bay might be exceeding the range supported by individuals. Nevertheless, due to the sparse setting of the receiver array, individuals might still be present in the bay but in different area or might be completely absent during that time of the year. More receivers would be needed, preferentially set linearly, to identify individuals entry to specific areas along the coastline and assess importance of specific areas.

Our study showed that spotted gully sharks are highly resident within their tagging area but also exhibit long distance movements. The sparse setting of the South African receiver array resulted in globally low detection indexes and roaming indexes, thus, to understand more about this species ecology, receivers should be set in important areas such as Breede and Walker Bay, that were shown to be extensively used by individuals. Results also showed that fine-scale movements, through acoustic telemetry could give different results than with mark-recapture (BQ Mann, pers. comm.), and genetic analysis (Soekoe 2016). Results from this study would benefit further sampling along the coastline to assess if site fidelity to tagging area is due to a resident behavior or if the use of those areas is due to another factor such as food availability, shelter from predator or environmental conditions.

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6. Figures

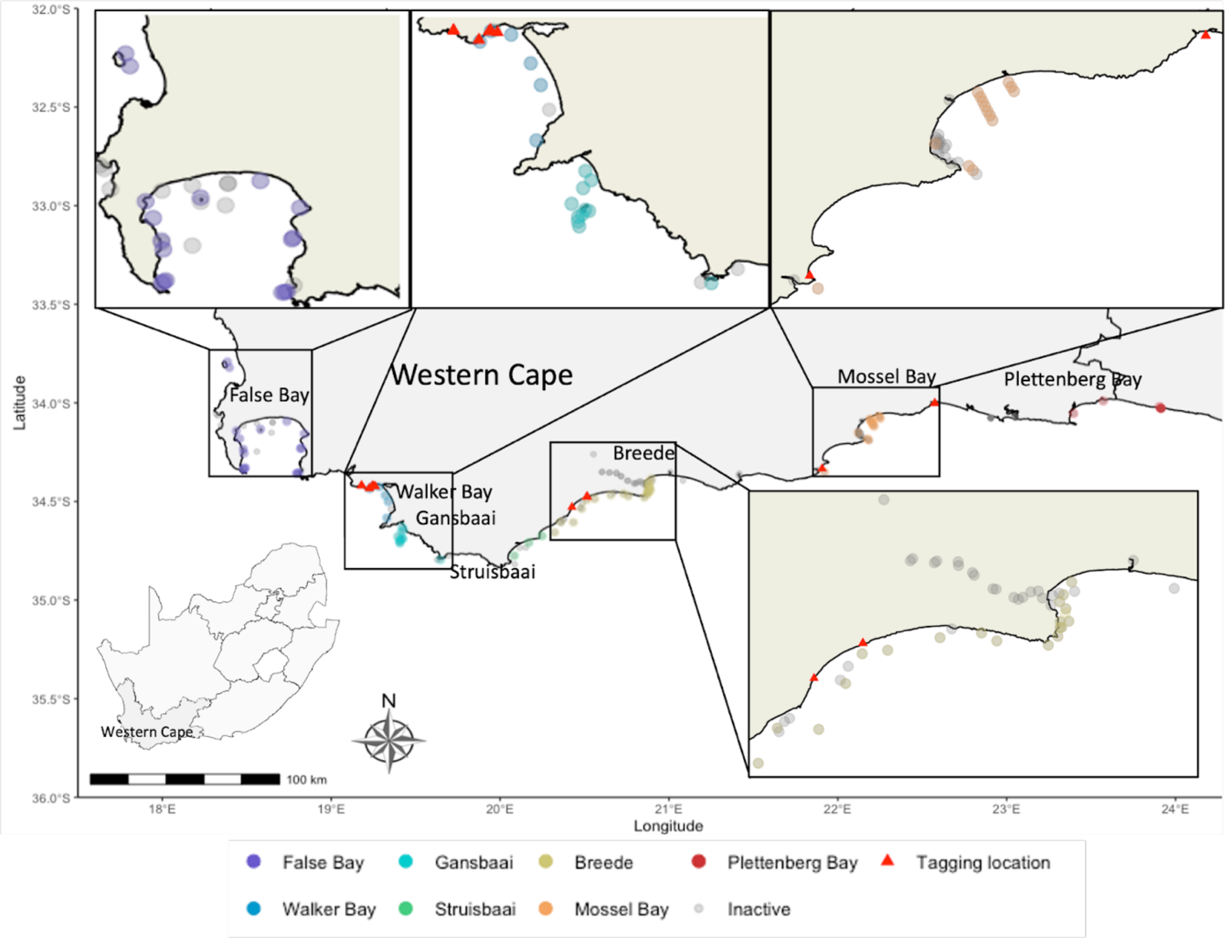

Figure 1: Acoustic receivers deployed in the Western Cape, South Africa with circles representing a receiver and red triangle a tagging location. The four main areas are highlighted with a zoomed-in map of the area in the area's designated colour.

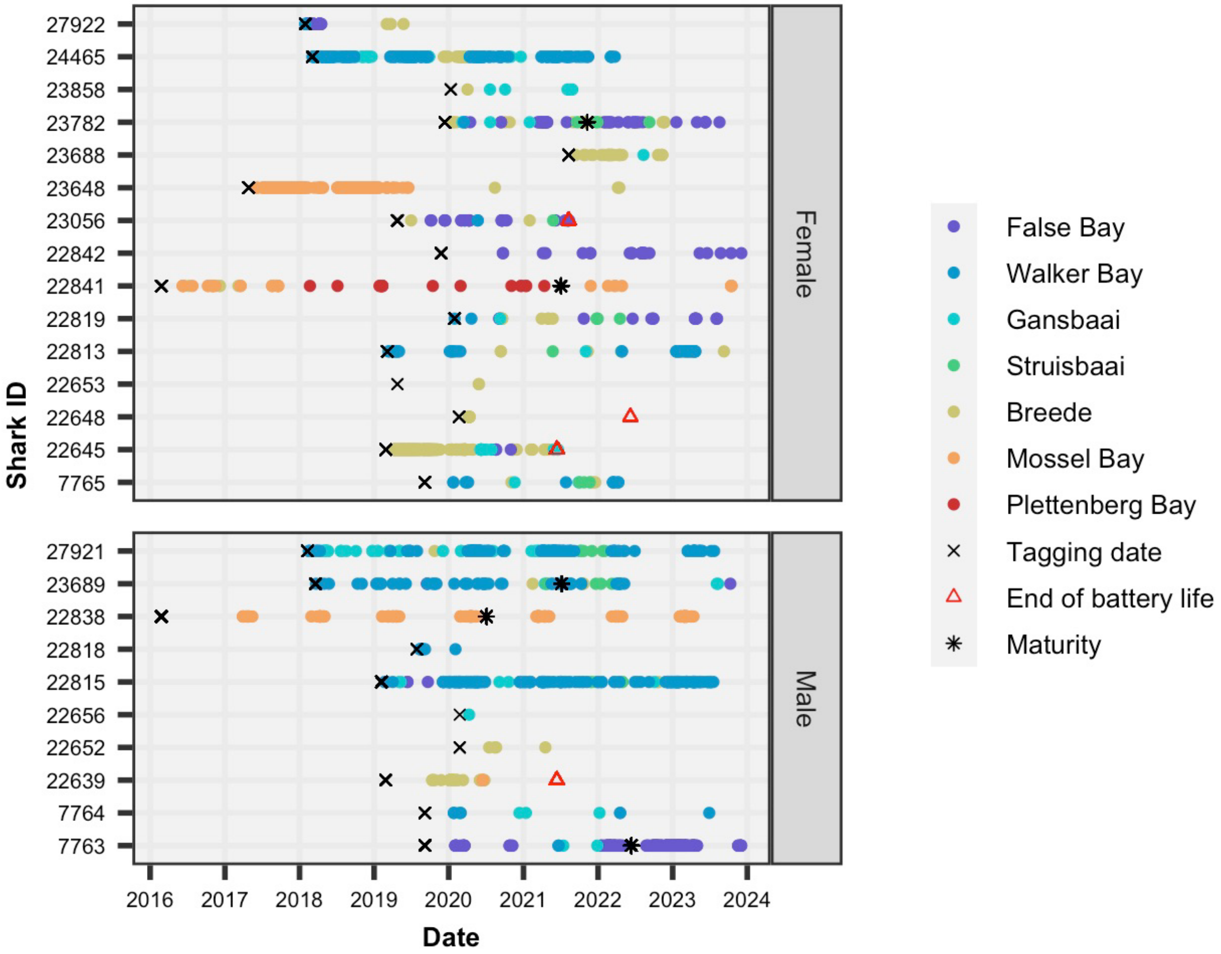

Figure 2: Abacus plot of detections of spotted gully sharks.

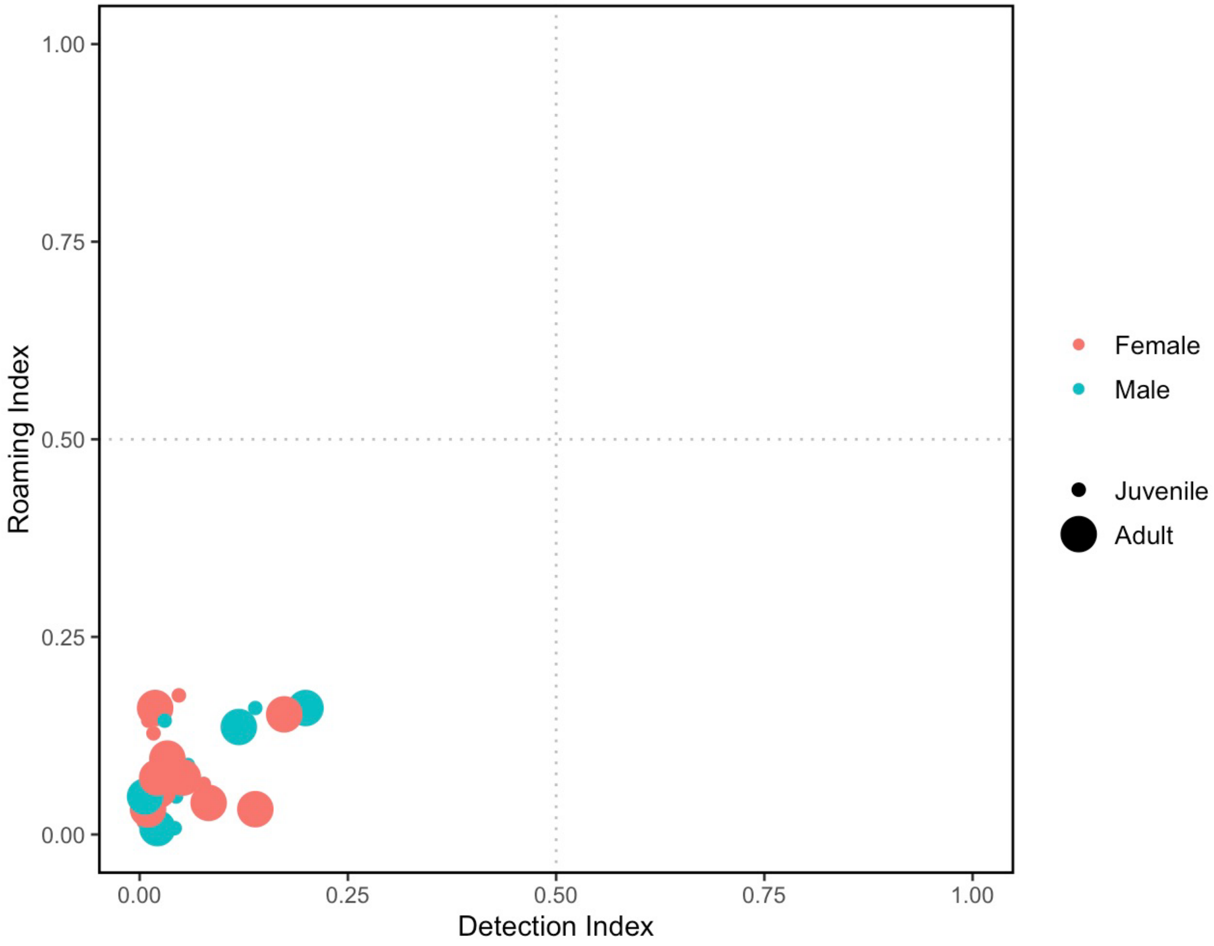

Figure 3: Roaming – Detection index analysis of spotted gully sharks, females are represented in red, males in blue, juveniles by small circles and adult are represented by big circles. Values are ranging from 0–1 representing low to high residency/roaming.

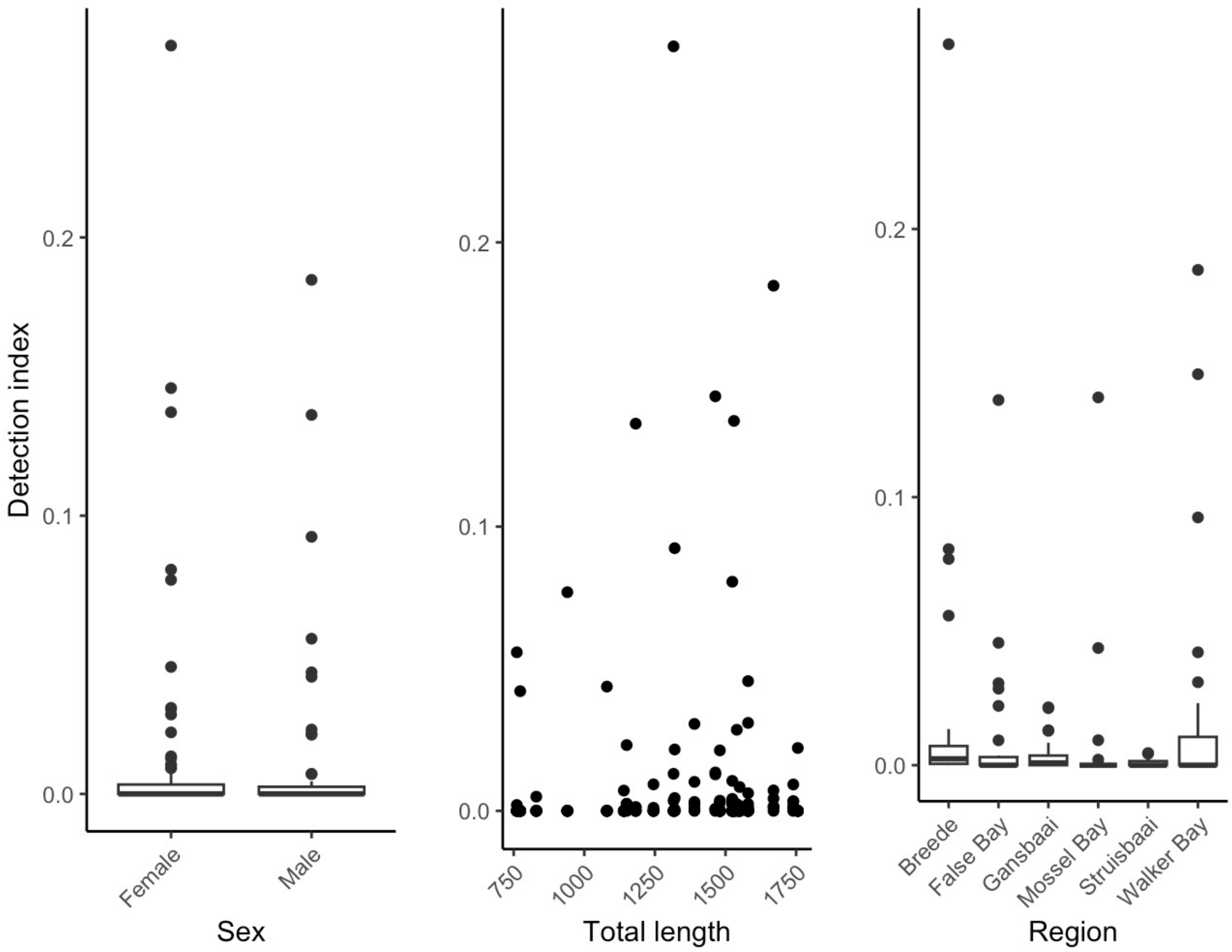

Figure 4: Detection index ($\mathrm{DI_r}$) of spotted gully sharks for each sex, total length and region.

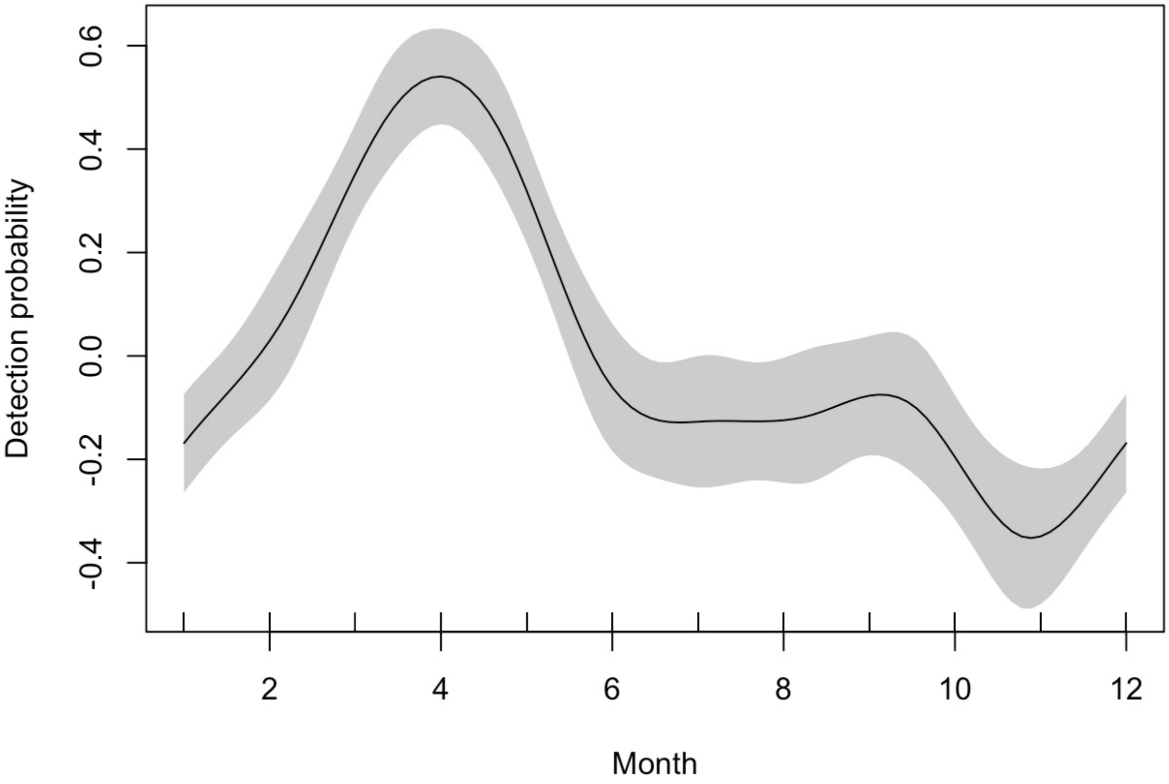

Figure 5: Detection probability of spotted gully shark on the entire acoustic array per months.

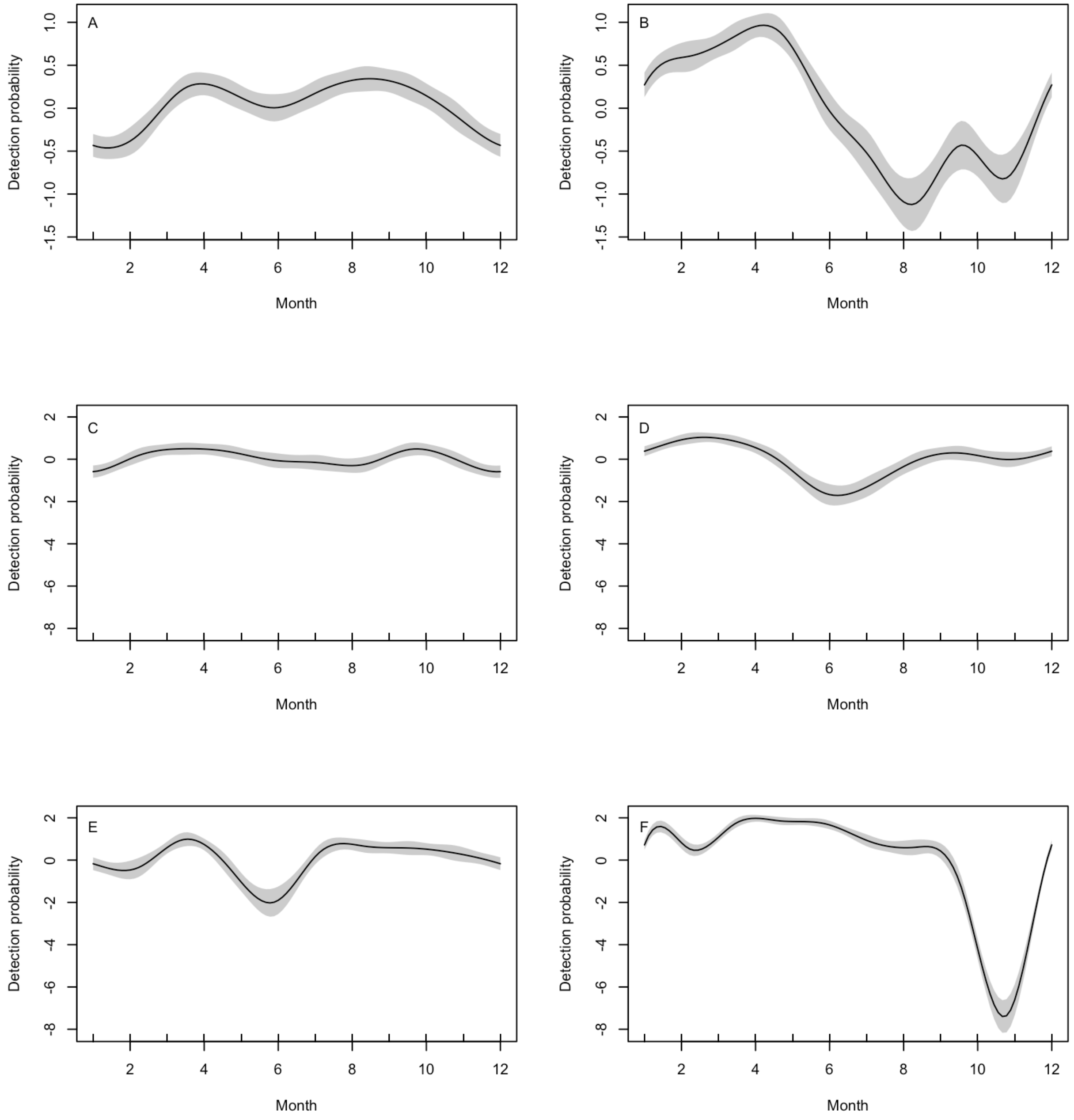

Figure 6: Probability of detection of spotted gully sharks between months for females (A), males (B), detections in Breede (C), False Bay (D), Mossel Bay (E), Walker Bay (F).

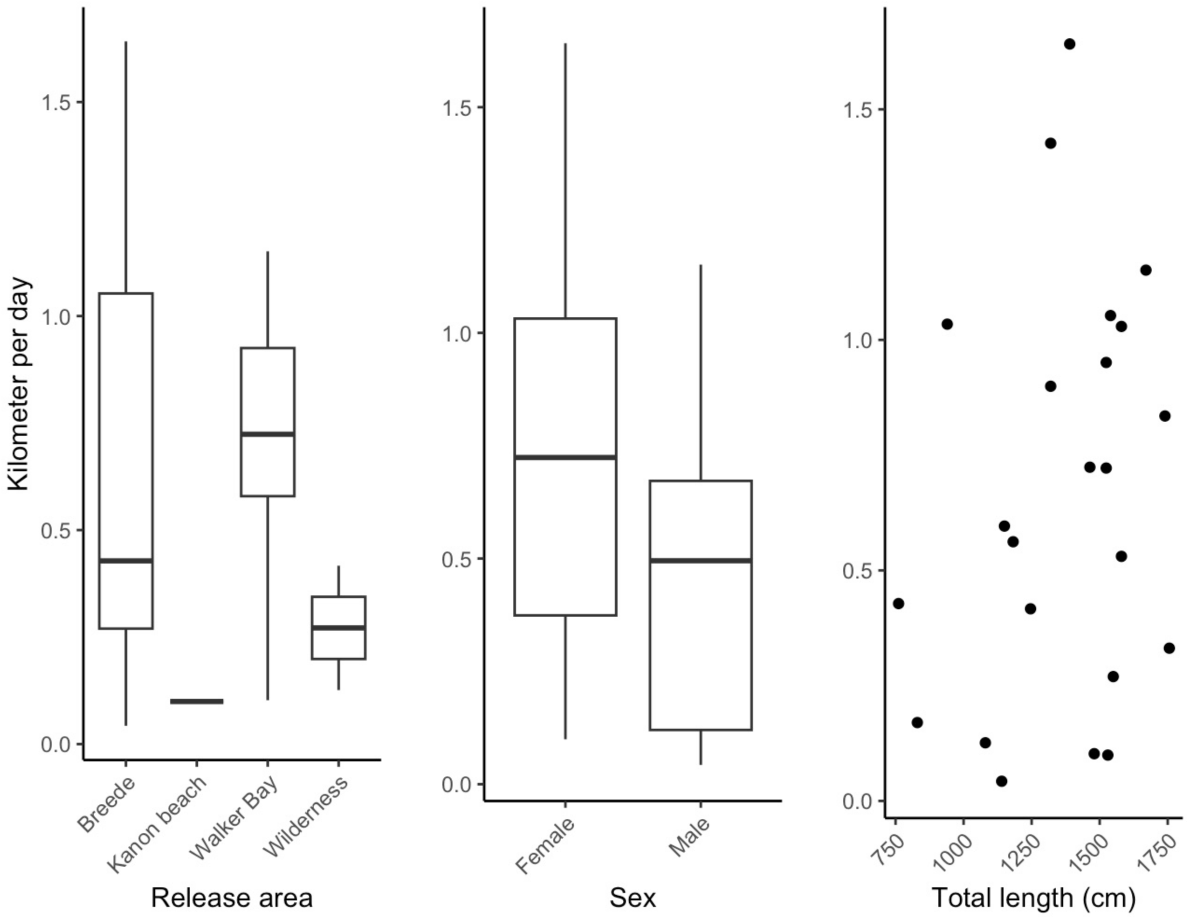

Figure 7: Kilometer per day travelled by each spotted gully shark per release area, sex and total length.

7. Tables

Table 1: Tagging details and detection summary of spotted gully sharks tagged with acoustic transmitters in the Western Cape, South Africa and monitored between June 2016 and December 2023.

ID code	Sex	Maturity	Total length (cm)	Tagging date	Tagging area	Tag life (days)	Length of data series (days)	Number of detections	Number of receivers
22838	M	Juvenile	108	2016-02-25	Wilderness	3650	2604	1123	6
22841	F	Juvenile	124.6	2016-02-25	Wilderness	3650	2790	548	18
23648	F	Adult	153	2017-04-27	Kanon Beach	3650	1814	3719	4
27922	F	Adult	158	2018-01-29	Walker Bay	3197	481	915	9
27921	M	Adult	132	2018-02-09	Walker Bay	3197	1990	5600	17
24465	F	Adult	146.4	2018-03-05	Walker Bay	2431	1480	2559	19
23689	M	Juvenile	115	2018-03-20	Walker Bay	2466	2030	521	18
22639	M	Juvenile	76.1	2019-02-26	Breede	838	483	300	11
22645	F	Juvenile	132	2019-02-27	Breede	838	843	4269	16
22813	F	Adult	158	2019-03-07	Walker Bay	3197	1647	621	9
23056	F	Adult	83	2019-04-25	Breede	838	840	130	12
22653	F	Juvenile	83	2019-04-25	Breede	838	400	5	2

22815	M	Adult	167	2019-06-02	Walker Bay	3197	1624	4676	20
22818	M	Juvenile	77.3	2019-07-29	Walker Bay	3197	190	43	1
7763	M	Juvenile	118.2	2019-09-06	Walker Bay	3197	1548	6162	20
7764	M	Adult	148	2019-09-06	Walker Bay	3197	1392	96	6
7765	F	Adult	152.4	2019-09-06	Walker Bay	3197	947	363	9
22842	F	Adult	175.6	2019-11-25	Breede	2907	1469	181	7
23782	F	Juvenile	139	2019-12-13	Breede	2503	1344	574	22
23858	F	Adult	155	2020-01-11	Breede	2377	595	15	4
22819	F	Adult	174	2020-01-30	Walker Bay	3197	1284	259	20
22648	F	Juvenile	94	2020-02-21	Breede	838	51	71	8
22652	M	Juvenile	114	2020-02-24	Breede	838	419	5	2
22656	M	Adult	148	2020-02-24	Breede	838	47	3	1
23688	F	Adult	152.4	2021-08-10	Walker Bay	2546	458	253	5

Table 2: Detection metrics for tagged spotted gully sharks with DD_t and DD_a representing days detected in the tagging area and across the entire receivers array, respectively. DI_t and DI_a represents detection indices within the tagging area and across the receivers array respectively, and proportion represents the number of days detected in the tagging area divided by the number of days detected in the array.

ID code	Sex	Total length (cm)	Tagging area	DD_t	DI_t	DD_a	DI_a	Proportion
22838	Male	108	Wilderness	112	0.04	112	0.04	1.00
22841	Female	124.5	Wilderness	26	0.01	29	0.01	0.90
23648	Female	153	Kanon beach	249	0.14	252	0.14	0.99
27922	Female	158	Walker Bay	0	0.00	25	0.05	0.00
27921	Male	132	Walker Bay	184	0.09	237	0.12	0.78
24465	Female	146.4	Walker Bay	216	0.15	257	0.17	0.84
23689	Male	115	Walker Bay	47	0.03	61	0.03	0.77
22639	Male	76.1	Breede	27	0.06	28	0.06	0.96
22645	Female	131.6	Breede	0	0.00	14	0.02	0.00
22813	Female	158	Walker Bay	51	0.03	58	0.04	0.88
23056	Female	154	Breede	2	0.00	28	0.03	0.07
22653	Female	83	Breede	2	0.01	2	0.01	1.00
22815	Male	167	Walker Bay	257	0.18	277	0.20	0.93
22818	Male	77.3	Walker Bay	8	0.04	8	0.04	1.00
7763	Male	118.2	Walker Bay	2	0.00	215	0.14	0.01
7764	Male	148	Walker Bay	4	0.00	9	0.01	0.44

7765	Female	152.4	Walker Bay	10	0.01	20	0.02	0.50
22842	Female	175.6	Breede	0	0.00	28	0.02	0.00
23782	Female	139	Breede	13	0.01	60	0.05	0.22
23858	Female	155	Breede	1	0.00	6	0.01	0.17
22819	Female	174	Walker Bay	2	0.00	22	0.02	0.09
22648	Female	153	Breede	249	0.14	252	0.14	0.99
22652	Male	114	Breede	0	0.00	3	0.01	0.00
22656	Male	148	Breede	0	0.00	1	0.02	0.00
23688	Female	152.4	Walker Bay	0	0.00	38	0.08	0.00

Table 3: Distance travelled caltulated for each spotted gully shark that were detected on two or more receivers between 2016 and 2023. Bold represents individuals where additional fictional receivers (n = 9) were used to calculate distance travelled.

ID code	Sex	Maturity	Total length (cm)	Release area	Length of data series (days)	Total distance travelled (km)	$Km.day^{-1}$
22838	Male	Juvenile	108	Wilderness	2604	328.36	0.13
22841	**Female**	**Juvenile**	**124.6**	**Wilderness**	**2790**	**1162.78**	**0.33**
23648	**Female**	**Adult**	**153**	**Kanon beach**	**1814**	**180.4**	**0.10**
27922	**Female**	**Adult**	**158**	**Walker Bay**	**481**	**495.03**	**1.03**
27921	**Male**	**Adult**	**132**	**Walker Bay**	**1990**	**1789.9**	**0.90**
24465	**Female**	**Adult**	**146.4**	**Walker Bay**	**1480**	**1071.29**	**0.72**
23689	**Male**	**Juvenile**	**115**	**Walker Bay**	**2030**	**1210.22**	**0.60**
22639	**Male**	**Juvenile**	**76.1**	**Breede**	**443**	**206.75**	**0.43**
22645	**Female**	**Juvenile**	**132**	**Breede**	**843**	**1202.53**	**1.43**
22813	**Female**	**Adult**	**167**	**Walker Bay**	**1647**	**873.74**	**0.53**
23056	**Female**	**Adult**	**154**	**Breede**	**840**	**884.33**	**1.05**
22653	Female	Juvenile	83	Breede	400	66.29	0.17
22815	**Male**	**Adult**	**167**	**Walker Bay**	**1624**	**1869.7**	**1.15**

7763	**Male**	**Juvenile**	**118.2**	**Walker Bay**	**1548**	**870.24**	**0.56**
7764	**Male**	**Adult**	**148**	**Walker Bay**	**1392**	**142.62**	**0.10**
7765	**Female**	**Adult**	**152.4**	**Walker Bay**	**947**	**683.72**	**0.72**
22842	Female	Adult	175.6	Breede	1469	486.69	0.33
23782	**Female**	**Juvenile**	**139**	**Breede**	**1344**	**2206.52**	**1.64**
23858	**Female**	**Adult**	**155**	**Breede**	**595**	**160.5**	**0.27**
22819	**Female**	**Adult**	**174**	**Walker Bay**	**1284**	**1072.1**	**0.83**
22648	Female	Juvenile	94	Breede	51	52.74	1.03
22652	**Male**	**Juvenile**	**114**	**Breede**	**419**	**17.91**	**0.04**
23688	**Female**	**Adult**	**152.4**	**Walker Bay**	**458**	**435.55**	**0.95**

CHAPTER SIX: An alternative theoretical approach to the interpretation of Baited Remote Underwater Video data

1. Introduction

Baited remote underwater videos (BRUVs) are commonly used to assess the abundance, diversity and structure of underwater communities (Brooks *et al.* 2011; White *et al.* 2013), along with underwater visual census (UVC) and fishery surveys (*e.g.* bag seine, beach seine, trawlers, hook-and-line; Baker *et al.* 2016, French *et al.* 2021). However, each method has limitations, for example, UVC can have biased counts due to the impact of the diver on fish behavior (*e.g.* attraction or repulsion; French *et al.* 2021). BRUVs do have the advantage of limiting sampling bias linked to habitat, depths and species selectivity due to hook or mesh size compared to fishery surveys (Cappo *et al.* 2006). It allows for studies in protected areas and of species of conservation concern (Cappo *et al.* 2003). BRUVs also offer reproducibility, whereby the same sites can be sampled multiple times, creating replicates and avoiding 'false negatives' (Tyre *et al.* 2003).

While BRUVs are being used worldwide, the methods to analyze the footage have not changed in the past decade, with MaxN being the primary analytical method (Cappo *et al.* 2006; Schobernd et al. 2013; Campbell *et al.* 2015). MaxN represents the maximum number of individuals of the same species counted in the same frame, avoiding multiple counts of the same individual (Ellis and DeMartini 1995; Cappo *et al.* 2003, 2004). MaxN is the basis of numerous BRUVs analysis such as co-occurrence between species, giving insight on species interactions and community structure (Hill *et al.* 2014; Sih *et al.* 2019; Osgood *et al.* 2020), along with species abundance and diversity (Whitmarsh *et al.* 2016). However, MaxN is known to underestimate abundance at high densities (Stobart *et al.* 2015; Kilfoil *et al.* 2017) as well as for individuals with identifiable characteristics (*e.g.* different spot patterns; Sherman *et al.* 2018). Therefore, this analytical metric might not be accurate when studying underwater communities, and may result in potential false information being used to build management and conservation policies. Previous studies evaluated the performance of MaxN compared to MeanCount, which represents the mean of counts of a species taken over different individual frames of the video. In some cases, MaxN was found to be more accurate for estimation of fish abundance (Campbell et al. 2015) while another study found that MaxN was not correlated to abundance and MeanCount was found to be more precise (Schobernd *et al.* 2013).

Co-occurrence patterns are often used in ecology to describe community structure and species interactions such as competition, mutualism, and predation (Tulloch *et al.* 2018). Understanding community structure is essential to predict potential anthropogenic impacts that could result in the disruption of the food web (Tulloch *et al.* 2018). Different methods can be used to derive co-occurrence, for example, BRUV using MaxN (Osgood *et al.* 2020), UVC using visual transects to count fishes (Sheppard *et al.* 2023), fish count using bottom-trawling survey (Wang *et al.* 2023), fish count using gill nets (Matich *et al.* 2017; Cottrant *et al.* 2021) and acoustic telemetry (Zemah-Shamir *et al.* 2022). All methods have limitations regarding temporal scale, for example, two individuals detected using acoustic detection by the same receiver could be hundreds of meters away from each other (Zemah-Shamir *et al.* 2022) and two individuals could be caught with the same gillnet more than an hour apart (Cottrant *et al.* 2021), thus not being in the same area at the same time.

In this study, MaxN was tested against a new approach to compare the results and to make recommendations for future studies. Co-occurrence resulting from visual observation was compared to patterns deduced from MaxN and were tested to describe fish community structure. The aim of this study was to identify which method would be the most precise for understanding fish species and community structure. Specifically with the greatest degree of accuracy and reproducibility, allowing for the development of appropriate conservation and management outcomes.

2. Methods

Study site and sampling design

Walker Bay in South Africa, was divided into six areas, comprising 20 sites (Figure 1). Sites were separated by a minimum of 500 meters, and included sites inside the Whale Sanctuary seasonal Marine Protected Area (MPA) and nearby restricted area (Figure 1). Sites were designed to ensure equal sampling of each habitat (*i.e.* Kelp forest, rocky reef and sand) across seasons, years and management level. Sampling was conducted from January 2018 to August 2019, with multiple replicates. BRUVs were deployed during daylight across all habitats. Rigs used for this study comprised a mild-steel cross-shaped base with 110cm between the bait canister and the camera. Upright posts supported the camera and the bait canister 20-30cm off the bottom and rigs were attached to a 1m chain and 60m rope to a buoy. Each bait canister was filled with one kilogram of chopped and crushed sardines (*Sardinops sagax*) and cameras used were GoPro® cameras (Hero 1, Hero 2, Hero 3, Silver edition and Hero+) set to 720p. All BRUVs were deployed for at least 66 minutes, allowing the bait to disperse (6 minutes) and the camera to record 60 minutes of footage. Only videos with a minimum duration of 50 minutes were analyzed and those samples with poor visibility

(< 1m) were discareded. Out of 153 videos recorded, a total of 121 videos were included in this study covering 70 different sites.

BRUV deployments were conducted under the authority of a research permit issued by the South African Department of Forestry, Fisheries and the Environment (RES2018-59 and RES2019-61).

Video analysis

All videos were analyzed using QuickTime Player version 10.5. For each video, species were identified using key features and identification books, and data was checked by another observer and validated. The time of first sighting was recorded for every species that entered the frame along with MaxN, which represented the maximum number of individuals present in the same frame (Ellis and DeMartini 1995; Cappo *et al.* 2003, 2004), and the time at MaxN. Co-occurrence between every shark species and any other species sighted was recorded (*e.g.* teleosts, crustacean, molluscs). Observed co-occurrence was defined as two species sighted in the same frame of a video, thus, two species were considered as co-occurring if they were sighted at least once together in the same frame of a BRUV. To assess co-occurrence patterns between species, traditionally, MaxN is used, meaning two species recorded in the same video are considered co-occurring species even if they were never observed in the same frame (Hill *et al.* 2014; Sih *et al.* 2019; Osgood *et al.* 2020). Here, co-occurrence patterns based on MaxN counts and on observed co-occurrence were compared using a presence-absence matrix, thus, two different temporal scales were compared.

Co-occurrence analysis

Overall co-occurrence, between a shark species and another species, was calculated using observed co-occurrence and co-occurrence derived from MaxN. For each species, the level of co-occurrence with a shark species was recorded when both species were observed in the same frame of the video for observed co-occurrence, and when both species were seen in the same video for co-occurrence derived from MaxN. Data obtained from both methods were compared using a Mann-Whitney U test to test for significance.

Differences in fish community structure between sites was analyzed by comparing co-occurrence patterns based on the occurrence of a shark species, resulting from both techniques (*i.e.* observed co-occurrence and co-occurrence derived from MaxN). Only co-occurrence between a shark species and other species was included in this study to simplify the analysis and focus on the method comparison. For each method, co-occurrence patterns resulted in a presence-absence matrix, for observed co-occurrence, when a shark species appear in the frame, the video was paused, and every other species present was recorded as present in the matrix. For co-occurrence derived from MaxN, when a shark species was present in a video, abundance data recorded with MaxN for every other species within the same video were turned into presence or absence data. A cluster analysis was performed on the presence-absence matrix using Bray-Curtis distance, linking sites with similar communities, resulting in a dendrogram. Dendrograms with MaxN and observed co-occurrence were compared, using the “cor_cophenetic” function from *dendextend* package (Galili 2015) with a pearson correlation, to obtain a similarity index. Based on the same presence-absence matrix, a general linear model (GLM) was generated for this matrix, using a binomial family with a logistic model, to assess the influence of each species on the occurrence of a shark species. Finally, GLMs resulting from both techniques were compared to quantify the difference between different BRUV analysis techniques. Akaike Information Criterion (AIC) was calculated to identify which model was most accurately fitting the data.

Analyses were conducted on R version 4.1.0 GUI 1.76 Big Sur ARM build (R Core Team 2022). Bray-Curtis distance was calculated using the *vegan* package (Oksanen *et al.* 2022) and *dendextend* package was used to build dendrograms (Galili 2015).

3. Results

Overall, 121 videos were analyzed for this study, resulting in 54 species identified including teleosts, chondrichthyans, crustaceans, cephalopods, myxinidae, birds and mammals. Among the chondrichthyans, 10 species of sharks were identified and were grouped in two categories to facilitate comparison between co-occurrence patterns obtained with MaxN and observed co-occurrence (*i.e.* Catsharks and other sharks; Table 1). Species that were sighted only once during the study were not considered for analysis as differences between MaxN and observed co-occurrence could not be considered as significant. Therefore, 10 species were excluded from analysis resulting in 34 species included (Table 2).

Co-occurrence between a catshark (Table 1) and another species (Table 2) resulted in 971 co-occurring events based on MaxN and 668 co-occurring events based on observed co-occurrence. Co-occurrence patterns based on MaxN were overestimated for all species ($p = 0.02$). Using MaxN, co-occurrence between two species of catsharks was overestimated by 41% and co-occurrence between a catshark and other shark was overestimated by 208%. Moreover, co-occurrence between a catshark and a crustacean was overestimated by 12% for West coast rock lobster *Jasus lalandii* and 27% for Cape rock crab *Plagusia chabrus*. Also, co-occurrence with the common octopus *Octopus vulgaris* was overestimated by 77% and 35% for the sixgill hagfish *Eptatretus hexatrema*. Among the teleosts, the most common species were not significantly overestimated (i.e. Panga *Pterogymnus laniarius* and Hottentot *Pachymetopon blochii*) but overestimation was found for small species (e.g. 123% for redfingers *Cheilodactylus fasciatus* and 50% for super klipfish *Clinus superciliosus*; Figure 2).

Co-occurrence between other sharks (Table 1) and another species (Table 2) resulted in 159 co-occurring events based on MaxN and 67 co-occurring events based on observed co-occurrence. Co-occurrence was overestimated for the majority of species using MaxN (*i.e.* only three species had the same level of co-occurring events with other sharks using both methods; $p < 0.001$). Co-occurrence between other sharks and a catshark species was overestimated by 179% using MaxN. A total of 14 species were considered co-occurring with other sharks using MaxN while *in situ* observation of co-occurrence showed that they were not. Indeed, batoids were predicted to co-occur with a large shark but were never observed together. Furthermore, redfinger and bluefin gurnard *Chelidonichthys kumu* were also predicted to co-occur with other sharks on multiple occasions but that was never confirmed by *in situ* observations. Catfish species co-occurrence with other sharks was overestimated, with 250% overestimation for black seacatfish *Galeichthys ater* and 200% for white sea catfish *Galeichthys feliceps* (Figure 3).

Bray-Curtis distances between sites were represented as dendrograms linking sites depending on the similarity between community structures. Dendrograms obtained using co-occurrence based on MaxN and observed co-occurrence were compared, linking similarity in community structure analysis using both methods (Figure 4). Correlation coefficient obtained between the two dendrograms was 0.66 indicating that community structure resulting from both methods were significantly different from one another (Figure 4).

Results from the GLM showed that, for both shark groups, St Joseph shark *Callorhinchus capensis* was assumed to be a co-occurring species but pairing was never observed in video analysis (Figures 5 & 6). Influence of another species occurrence on a catshark occurrence was different for 25 species between MaxN and observed co-occurrence, with 6 species switching between positive and negative influence (Figure 5). Moreover, AIC was lower for observed co-occurrence than MaxN with 122.81 and 125.68 respectively and a pseudo r^2 of 0.83 for both. Influence of species occurrence on other shark occurrence was different between co-occurrence based on MaxN and observed for 19 species with 3 species having their influence switch between positive and negative (Figure 6). AIC was lower for observed co-occurrence than MaxN with 92.27 and 96.56 respectively along with a pseudo r^2 of 0.86 and 0.84 respectively. Looking at commercially important or endangered species (Table 2), west coast rock lobster occurrence had relatively no impact on catshark occurrence with an estimated effect close to zero. The difference was larger for Red roman (*Chrysoblephus laticeps*) with the effect close to zero for MaxN but negative using observed co-occurrence (Figure 6). Furthermore, the effect of white stumpnose (*Rhabdosargus globiceps*) occurrence on catsharks' occurrence was positive using MaxN and negative using observed co-occurrence (Figure 6).

4. Discussion

The overestimation of co-occurrence patterns between shark species proved that MaxN poorly described fish communities along with predator-prey interactions. Fish communities described using MaxN and observed co-occurrence were significantly different, with a low correlation rate of 0.66, thus, the ecological role of species in the food web might be inaccurate depending on the method used. Sharks play different role in the food web, from small-bodied meso-predator (*i.e.* Catsharks) to top-predator (*i.e.* large sharks) and are often used as indicators of food web health (Osgood *et al.* 2020). Therefore, an incorrect interpretation of community structure analysis may result in inadequate management policies regarding these species, which could impact other species of conservation importance (Livernois *et al.* 2020; Osgood *et al.* 2020).

In the wild, small catshark species (*e.g.* Puffadder shyshark and Dark shyshark) form part of the diet of large sharks (*e.g.* Broadnose sevengill shark *Notorynchus cepedianus*; Ebert 1991) and other larger catshark species (*e.g.* Pyjama shark *Poroderma africanum*; Dainty 2002). Therefore, these species were only rarely observed co-occurring together. Catshark species studied possess similar diets, thus, findings using observed co-occurrence, which represent fine-scale space use, showed that these species exhibit non-aggressive co-existence by not using the area at the same time (Zemah-Shamir *et al.* 2022). Moreover, for co-occurrence patterns between a catshark and other species, a clear connection was found between the co-occurrence overestimation and the diet of catsharks (Dainty 2002). In fact, MaxN showed that prey and predators are found in the same BRUV footage, therefore in the same area, but observed co-occurrence showed they are not appearing at the same time. This can be explained by optimal foraging theory (*i.e.* a predator is going to stay relatively close to prey to use less energy hunting; MacArthur & Pianka 1966, Cottrant *et al.* 2021) as prey species are often alert of predators and swim away (Myers *et al.* 2007, Heithaus *et al.* 2008, Navia *et al.* 2010).

For species of conservation importance (*i.e.* threatened species or with economic value; Table 2), differences were also found in the influence of their occurrence on the occurrence of a shark species, depending on the method of analysis used. Differences such as a shift between a positive influence and a negative influence are crucial as it changes the interpretation made of fish assemblage and depends on the species position within the food web. Indeed, for large sharks, a negative influence would reflect a predator-prey interaction whereas a positive influence would reflect a competitive interaction between species and a null influence would mean that a species occurrence has a random effect on another (Astarloa *et al.* 2019). Therefore, management policies aiming at protecting more than one species as a community (*e.g.* MPAs) might be based on inaccurate information and might not be effective for species of concern.

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6. Tables

Table 1: Shark species observed in baited remote underwater videos (BRUVs) with the International Union for Conservation of Nature (IUCN) status. LC: least concerned; VU: vulnerable; EN: endangered; CR: critically endangered.

Family	Common name	Scientific name	IUCN
	Catsharks		
Scyliorhinidae	Dark shyshark	*Haploblepharus pictus*	LC
Scyliorhinidae	Leopard catshark	*Poroderma pantherinum*	LC
Scyliorhinidae	Puffader shyshark	*Haploblepharus edwardsii*	EN
Scyliorhinidae	Pyjama shark	*Poroderma africanum*	LC
Scyliorhinidae	Tiger catshark	*Halaelurus natalensis*	VU
	Other sharks (>1.2m total length)		
Sphyrnidae	Smooth hammerhead shark	*Sphyrna zygaena*	VU
Triakidae	Common smoothhound shark	*Mustelus mustelus*	EN
Triakidae	Soupfin shark	*Galeorhinus galeus*	CR
Triakidae	Spotted gully shark	*Triakis megalopterus*	LC
Hexanchidae	Broadnose sevengill shark	*Notorynchus cepedianus*	VU

Table 2: Species observed in Baited Remote Underwater Videos (BRUVs) ordered by taxon with International Union for the Conservation of Nature (IUCN) and South African Sustainable Seafood Initiative (SASSI) listings. NE: Not evaluated; LC: least concerned; NT: near threatened; VU: vulnerable; EN: endangered; CR: Critically endangered.

	Common name	Scientific name	IUCN	SASSI
Batoid	Short-tail stingray	*Bathytoshia brevicaudata*	LC	
	Eagle ray	*Myliobatis aquila*†	CR	
	Biscuit skate	*Raja straeleni**	NT	Red
	Spearnose skate	*Rostroraja alba*	EN	
Bird	White-breasted cormorant	*Phalacrocorax lucidus*†	NE	
Cephalopod	Chokka squid	*Loligo vulgaris reynaudii*†	LC	Orange
	Common octopus	*Octopus vulgaris*	LC	Orange
Chimaera	St Joseph shark	*Callorhinchus capensis**	LC	Red
Crustacean	Fat plough shell	*Bullia laevissima*	NE	
	Three spotted swimming crab	*Ovalipes trimaculatus*	NE	
	West coast rock lobster	*Jasus lalandii**	LC	Red
	Cape rock crab	*Plagusia chabrus*	NE	
	Masked crab	*Nautilocorystes ocellata*	NE	
Mammalia	Cape fur seal	*Arctocephalus pusillus pusillus*	LC	
Myxinid	Sixgill hagfish	*Eptatretus hexatrema*	LC	
Teleost	Black seacatfish	*Galeichthys ater*	NE	
	White seacatfish	*Galeichthys feliceps*	NE	
	Yellowback fusilier	*Caesio xanthonota*†	LC	
	Cape horse mackerel	*Trachurus capensis*	LC	Orange
	Yellowtail	*Seriola Lalandi*†	LC	Green
	Barred fingerfin	*Cheilodactylus pixi*	NE	
	Redfingers	*Cheilodactylus fasciatus*	LC	
	Twotone fingerfin	*Chirodactylus brachydactylus*	NE	
	Super klipfish	*Clinus superciliosus*	LC	
	Spinynose horsefish	*Congiopodus spinifer*†	LC	

Jutjaw	*Parascorpis typus*†	NE	
Bank steenbras	*Chirodactylus grandis*	NE	
Blacktail seabream	*Diplodus capensis**	LC	Red
Blue hottentot	*Pachymetopon aeneum*	LC	
Carpenter	*Argyrozona argyrozona**	NT	Orange
Fransmadam	*Boopsoidea inornata*	LC	
Hottentot	*Pachymetopon blochii*	LC	Green
Janbruin	*Gymnocrotaphus curvidens**	LC	Red
Panga	*Pterogymnus laniarius*	LC	Orange
Red roman	*Chrysoblephus laticeps**	NT	Orange
Red steenbras	*Petrus rupestris*†*	EN	Red
Red stumpnose	*Chrysoblephus gibbiceps**	EN	Red
Steentjie	*Spondyliosoma emarginatum*	LC	
Strepie	*Sarpa salpa*	LC	
White stumpnose	*Rhabdosargus globiceps**	VU	Red
Zebra	*Diplodus hottentotus**	LC	Red
Longsnout pipefish	*Syngnathus temminckii*†	LC	
Bluefin gurnard	*Chelidonichthys kumu*	LC	
Cape gurnard	*Chelidonichthys capensis*†	LC	Orange

†Species observed only once in a BRUV
* Species of conservation concern in South Africa

7. Figures

Figure 1: Baited remote underwater videos site locations within the Walker Bay, South Africa. Whale sanctuary seasonal marine protected area is highlighted in red, and the restricted area is highlighted in green.

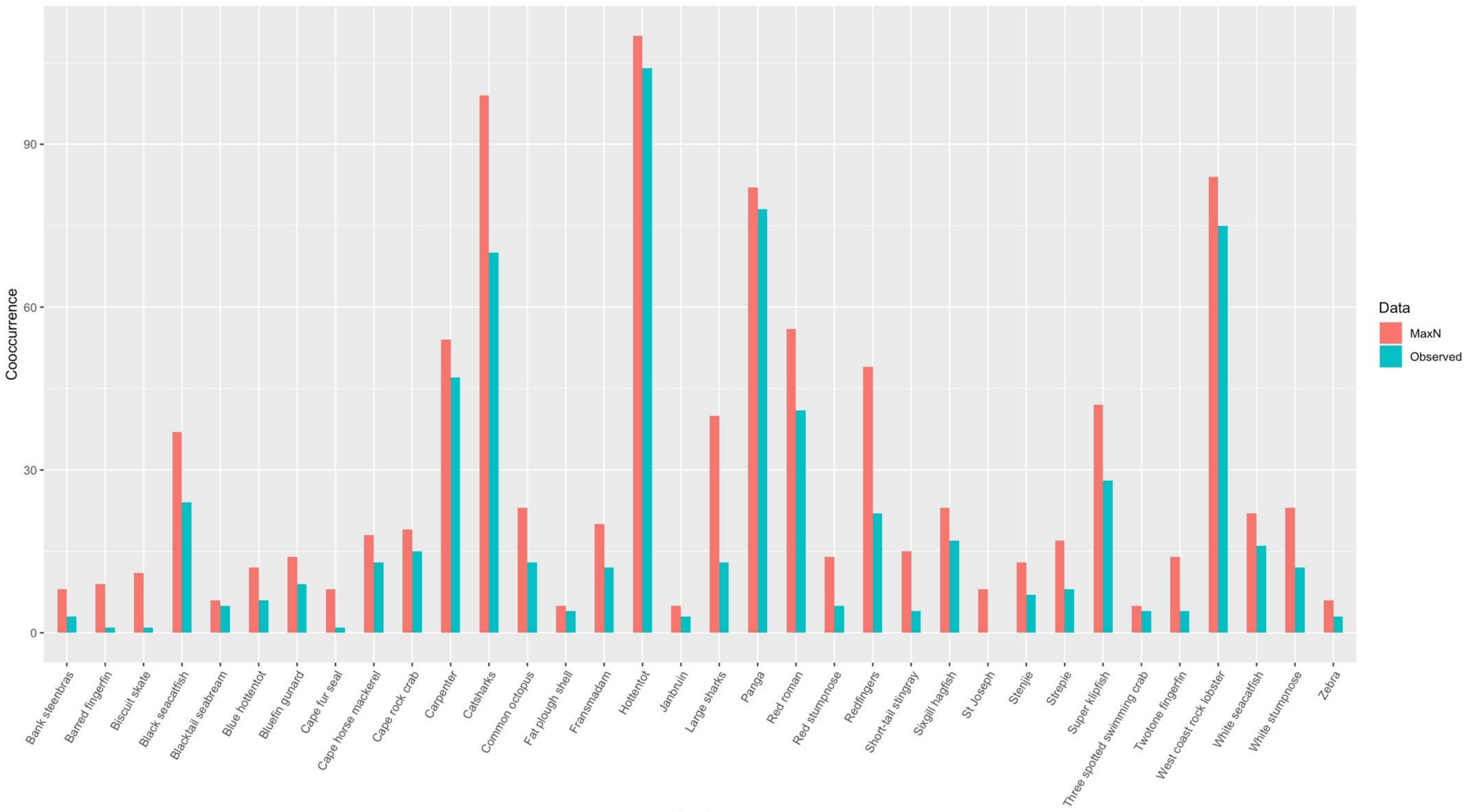

Figure 2: Counts of videos where co-occurrence between a catshark species and other species was observed (in blue) or estimated using MaxN (in red).

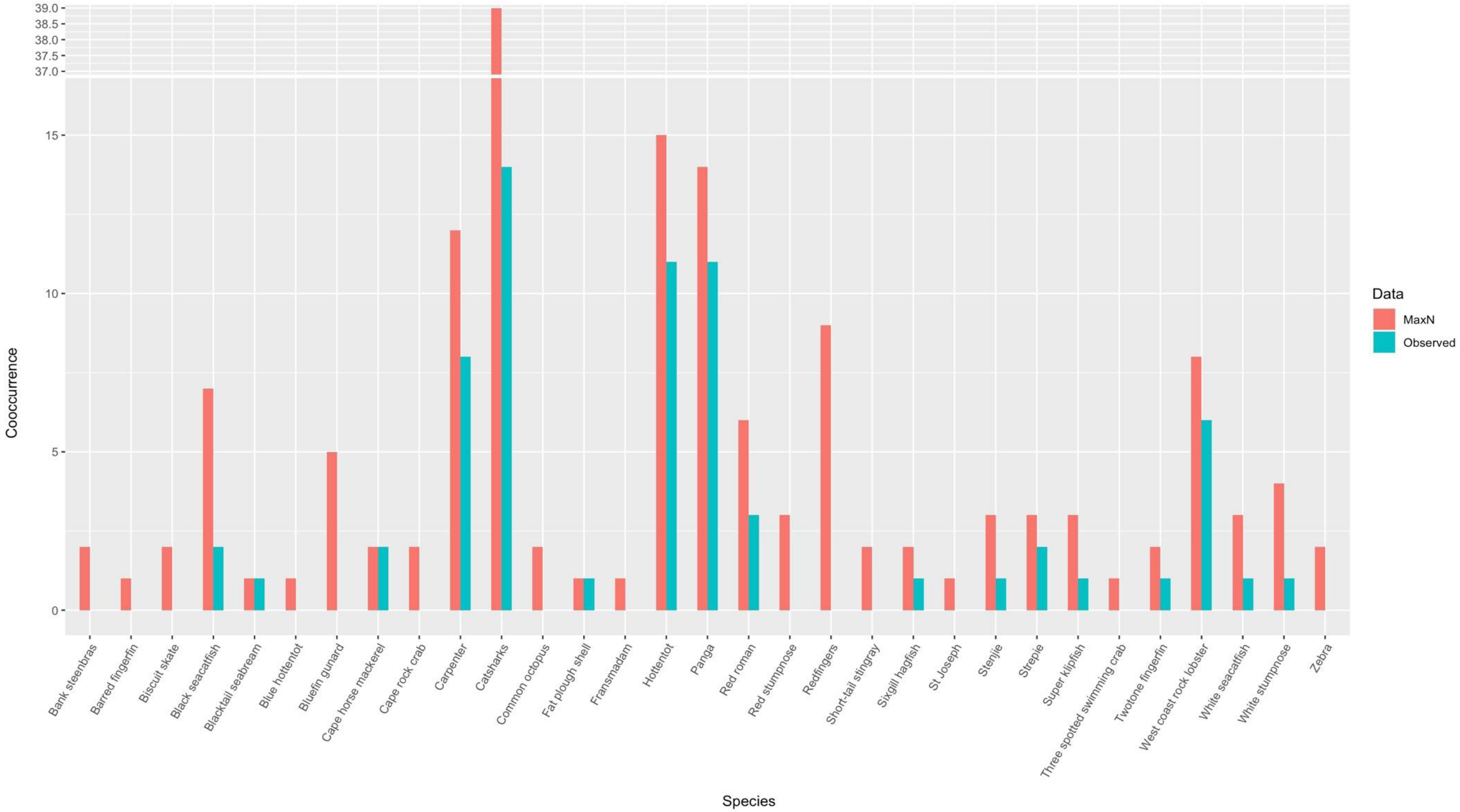

Figure 3: Counts of videos where co-occurrence between another species of shark and other species was observed (in blue) or estimated using MaxN (in red).

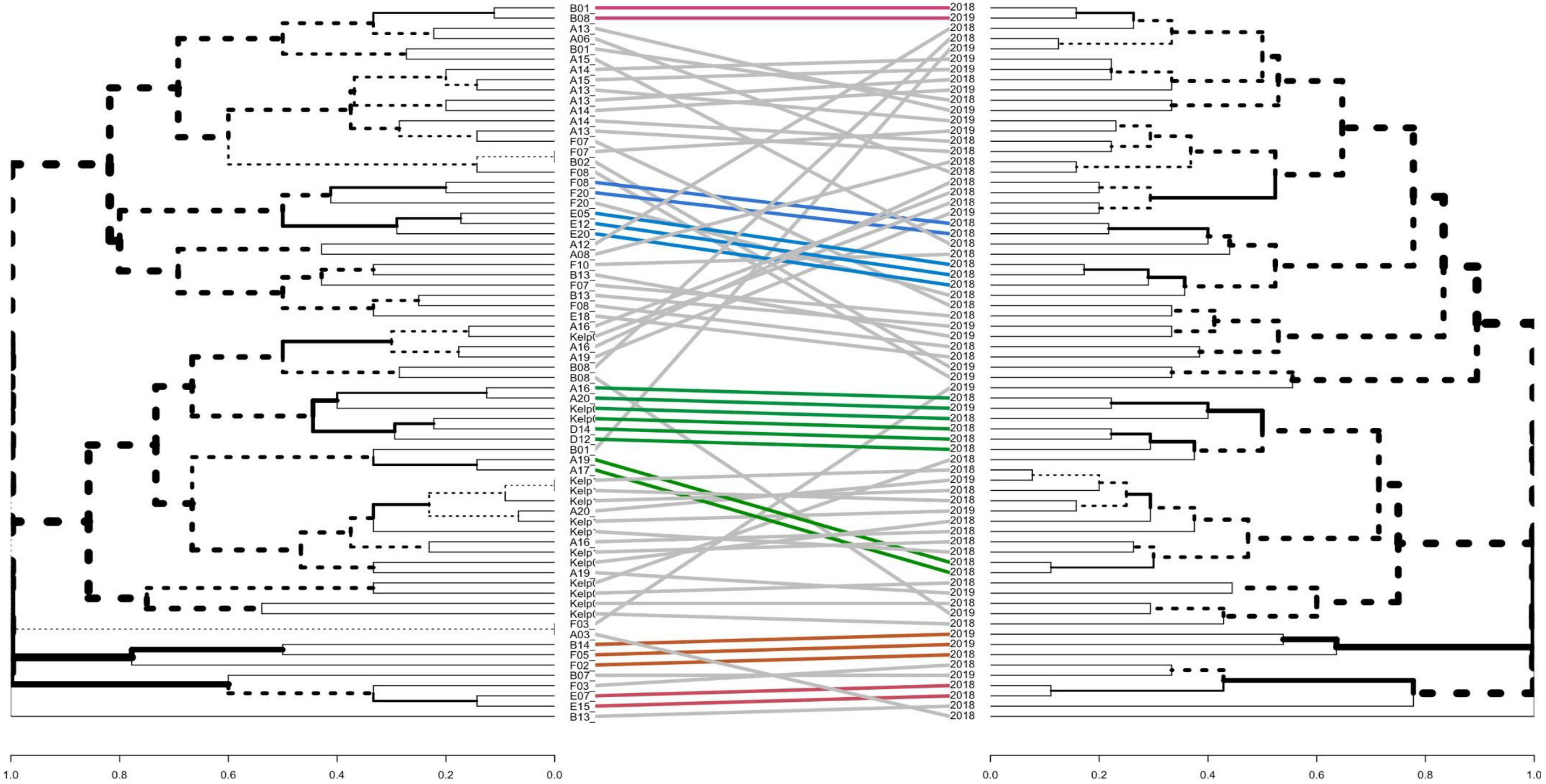

Figure 4: Dendrograms showing link between BRUV sites depending on similarities in the community structure using Bray-Curtis distance. Comparison between analysis using observed co-occurrence on the left and co-occurrence estimated using MaxN on the right.

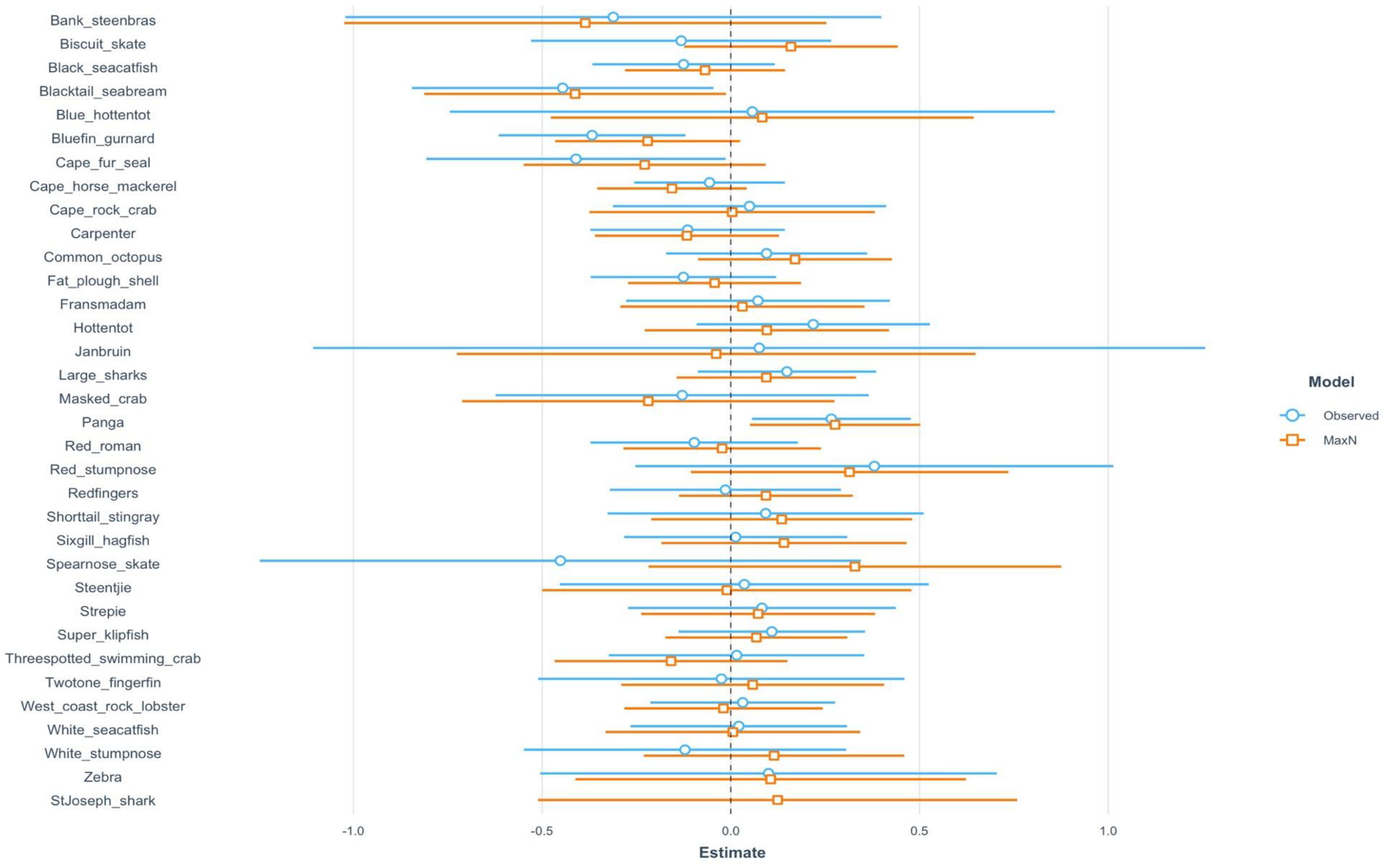

Figure 5: Difference in the general linear model (GLM) analysis using co-occurrence estimated using MaxN (in orange) and observed co-occurrence (in blue) for co-occurring event based on the presence of a catshark species.

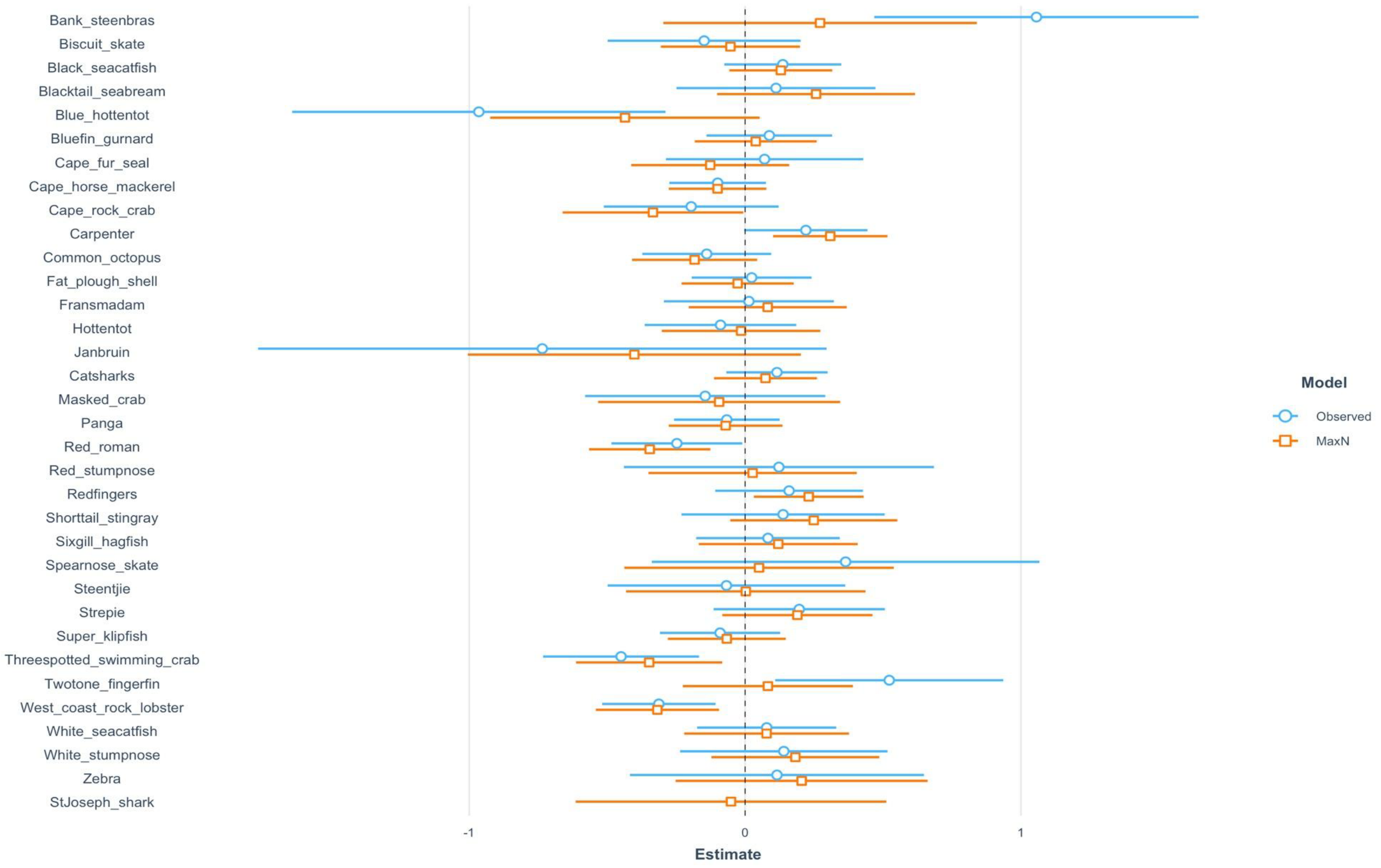

Figure 6: Difference in the general linear model (GLM) analysis using co-occurrence estimated using MaxN (in orange) and observed co-occurrence (in blue) for co-occurring event based on the presence of other sharks species

CHAPTER SEVEN: Conclusions about management status of five endemic southern African shark species

Shark conservation has been a global concern since the 1990s with several organizations developing management policies that all nations should follow such as, International Plans of Action for Conservation and Management of Sharks (IPOA-Sharks) established in 1999 (FAO 1999), inclusion of shark species in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2003 (CITES 2013), a Memorandum of Understanding on the Conservation of Migratory Sharks (CMS) first implemented in 2010 and signed by 49 countries along with the European Union as of 2018 (CMS 2018). Since about 2018, the conservation and management of Chondrichthyan species became more common in scientific articles with an increased number of studies published between 2020 and 2023 (Dulvy *et al.* 2021, Pacoureau *et al.* 2021, Sherman *et al.* 2023). Dulvy *et al.* (2021) showed that between 2014 and 2021, the number of chondrichthyan species threatened with extinction increased from 24% of the 1 199 species to 33%, mainly attributable to overfishing. Overfishing is also closely linked to other threats such as degradation of habitat, climate change, and pollution (Dulvy *et al.* 2021). Furthermore, a study on oceanic sharks population by Pacoureau *et al.* (2021) also showed that over the five decades from 1970 to 2020, the total population declined by 71%. A similar statement as of Pacoureau *et al.* (2021) was made by Sherman *et al.* (2023) regarding sharks and rays associated with coral reefs, with 59% of 134 species threatened with extinction. These studies also highlighted an increase in collaboration efforts between organisations and countries, which ensures results can be applied to a broader range of species and geographic areas. For this study, we used multiple long-term datasets (mark-recapture, acoustic telemetry and baited remote underwater videos) to increase the general knowledge about five endemic shark species of southern Africa, and to assess current protection measures in place.

Mark-recapture analysis for this thesis helped fill knowledge gaps for four endemic species (dark shyshark *Haploblepharus pictus*, puffadder shyshark *Haploblepharus edwardsii*, leopard catshark *Poroderma pantherinum* and pyjama shark *Poroderma africanum*). Based on the number of captures, the three species listed as “Least Concern” on the IUCN Red List (dark shyshark, leopard catshark and pyjama shark) (Pollom *et al.* 2019, 2020a, 2020b) dominated the captures; the “Endangered” puffadder shyshark remained rare and hard to study over the eight years of data (Pollom *et al.* 2020c). While results were biased by the fishing effort, focused more within the Whale Sanctuary Seasonal MPA than in other areas of Walker Bay, they nevertheless showed a habitat preference for kelp forest habitats. Species also showed an overlap in distribution ranges within Walker Bay. I found that the seldom captured puffadder shyshark might be rare because of a different depth use compared to other species and fishing sites. Recapture data showed that most individuals were not moving long distance thus the findings in Walker Bay represent a snapshot of patterns at the population level. While species seemed to be protected within the seasonal MPA, all species of the study were found to be inadequately protected along the South African coastline, based on the existing configuration of MPAs (Faure-Beaulieu *et al.* 2023).

Mark-recapture data also helped estimate the growth parameters for the pyjama shark; this is usually found by estimating the age of individuals using vertebrae, requiring lethal sampling (Cailliet and Goldman 2004). Here we showed that lethal sampling was not necessary for this type of study and data were compared between wild individuals in Walker Bay and captive individuals in the Osaka Aquarium, Japan. We found that the same growth pattern was indicated for both wild and captive individuals, with an isometric growth for females and a negative allometric growth pattern for males. This supported the idea that captive data can be useful when investigating wild populations, especially for rare species such as the endangered puffadder shyshark where captive data could be used to estimate growth patterns of the wild population.

Analysis of telemetry data was focused on the Western Cape Province with 25 individuals tagged by the South African Shark Conservancy, the South African Institute for Aquatic Biodiversity, and the University of Miami between 2016 and 2021. This illustrates the value of data sharing and collaboration in shark conservation initiatives. I used a novel approach to acoustic telemetry data, namely network analysis, to investigate differences in movement patterns between males and females and also the efficacy of existing MPAs to protect them. For this, a spatial network was employed and coupled with a social network investigating co-occurrence pattern between individuals. Spatial network analysis revealed that males and females were using the Western Cape coastline differently, highlighting potential sexual segregation. However, for both sexes of spotted gully sharks, there was no significantly greater use of MPAs compared to exploited areas. Results from the social network analysis revealed that some individuals were co-occurring together for multiple years in the same area (Walker Bay), during winter. This implies that the area could be an aggregatory area for the species during this period of the year. Globally, aggregatory areas for the spotted gully shark were found around MPAs but they were not included in the current protected area. Therefore, the species would benefit from an increase in coverage of those existing MPAs, as suggested by Faure-Beaulieu *et al.* (2023) with a 5% increase in area, instead of the creation of a new MPA. Pattern of sexual segregation was also confirmed by the general movement study, but detections on the receiver array were relatively low, highlighting the need of a better receiver coverage.

With regard to Baited Remote Underwater Videos (BRUVs), I decided to take a methodological approach for the analysis of this dataset in order to see if new information could be drawn from this type of data. I was particularly interested in information that is not usually recorded during video analysis. A typical BRUV study will use MaxN (the maximum number of individuals of the same species observed in the same frame of video) to estimate the abundance of a species, and diversity would be derived from the number of species observed in a footage. I looked at co-occurrence between individuals instead of using MaxN and recorded the species present in the same frame of a video in addition to our species of interest. By doing so, I could investigate patterns of co-occurrence between species, highlighting competition for resources and predation. This data is essential to understand the food web. BRUV studies are often conducted for multiple years and this method could make it easier to observe changes in the food web due to anthropogenic or climate change impacts. Interaction between individuals could explain a future decrease in the abundance of a species, due to a decrease in its prey for example, showing that to protect the species of interest, maybe it should be considered to protect its principal prey species.

In this thesis we exploited three long-term databases to increase knowledge of five endemic species of southern Africa and inform management. Results showed that each of the three sampling methods provided complementary insights related to the species of interest. Linked together, we learned that three species (dark shyshark, leopard catshark, and pyjama shark) seemed to be adequately protected within the Walker Bay area; however, across their distribution ranges, the current protection measures are insufficient (Faure-Beaulieu *et al.* 2023). These species are listed as "Least Concern" and, therefore, are not considered to be in urgent need of extensive protection measures; however, their management is essential because declines can be rapid. Given the slow growth rates of chondrichthyans, these declines might be hard to overcome, therefore, adequate conservation measures should be set beforehand. For the "Endangered" puffadder shyshark, management was difficult to assess due to its rarity in sampling, but a large number of observations were made during BRUV surveys. Thus, for an endangered species, combining multiple approaches can be beneficial to get a more accurate assessment of the population, essential for IUCN Red List listing. Indeed, the puffadder shyshark is not the only species with limited data, the brown shyshark *Haploblepharus fuscus* is also listed as "Vulnerable" (Pollom *et al.* 2020d) and, due to misidentification, mark-recapture data could not be confidently used. Osgood *et al.* (2020) showed that the dark shyshark and the puffadder shyshark had strong co-occurrence with other species and could be regarded as umbrella species for the conservation of threatened species. Thus, our studies showed that catshark species (namely dark shyshark, leopard catshark and pyjama sharks) are adequately managed within the Walker Bay, which could be similar for the puffadder shyshark and the brown shyshark. Further management perspectives would require characterization of the habitat use of those species, for example, estimating where egg laying is more important in order to prevent habitat loss. Indeed, those species often take advantage of kelp forest *Ecklonia maxima* to deposit eggs but, in the Walker Bay area, kelp is being used by Abalone *Haliotis midae* farms and is collected directly from the wild (Rothman *et al.* 2006; Troell *et al.* 2006), a pattern also known along the South African coastline (Troell *et al.* 2006). Kelp harvesting has not been found to impact kelp growth and recruitment (Rothman *et al.* 2006), but no link has been established between kelp harvesting and habitat loss for species such as catsharks. Thus, potentially, this activity could destroy the egg laying areas for catsharks. A citizen science program, ELMO Africa, collects egg case data comprising species name, egg case size and location along the South African coastline (C Elston, pers. comm.). This type of data could then be used to determine where an increased number of eggs of each species is found, and potentially, through current modelisation, estimate egg-laying areas. Those specific areas could then benefit from further protection such as quotas implemented for kelp collection to ensure the survival of the majority of eggs. Furthermore, based on the aquarium study with captive pyjama sharks, it is suggested that a similar study on captive puffadder shysharks could be undertaken to get growth information for the species. Lastly, a study of the water temperature and depth preferences of this species would help refine knowledge of the distribution range.

For the spotted gully shark, this thesis significantly increased the knowledge about the movement of this species along the coastline, highlighting areas that need further protection measures. The De Hoop MPA appeared to be an important area for the species, with an increased useage of the area by female individuals, but a lot of detections fall outside of the MPA. Thus, De Hoop would benefit from an increase in its size as other species such as juvenile smooth hammerhead sharks *Sphyrna* *zygaena* were found to be vulnerable, due to their extensive use of the surrounding area of the De Hoop MPA (Albano *et al.* 2023). The results of this thesis thus confirm the earlier descriptions of important areas for sharks within the Western Cape Province (Albano *et al.* 2021; Faure-Beaulieu *et al.* 2023) and the need to extend specific MPAs such as De Hoop MPA to increase protection on endemic and threatened shark species of southern Africa (Albano *et al.* 2023; Faure-Beaulieu *et al.* 2023).

While we showed that each method was contributing to filling the knowledge gap for endemic shark species of southern Africa, future studies should consider all three methods combined to have a complete understanding of species ecology and behaviour without the need for lethal sampling. Indeed, different spatial scales can be obtained through different sampling, from broad scale with mark-recapture, to finer scale movement using acoustic telemetry to define precise area use, to fine-scale species interactions using BRUVs. Thus, recommendation for future studies would be to increase collaboration between different research programs in South Africa, to combine data collected on the same species but in different regions and habitats.

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