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

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The spotted gully shark *Triakis megalopterus* (Triakidae) is a mesopredatory species endemic to southern Africa. It is currently listed as Least Concern on the IUCN Red List in accordance with an estimated increase in population size, general release by recreational linefishers and incidental catches in the commercial linefisheries. Previous research suggests this species to be resident, and as such it is likely to receive protection in coastal marine protected areas (MPAs). However, its ecology and movement behaviour remain poorly studied. This study employed acoustic telemetry to provide information on the species' movements along the coast of the Western Cape Province, South Africa. We used network analyses to investigate movement randomness, associations between individuals, sexual segregation, and the effectiveness of MPAs. Our findings reveal nonrandom movements as well as patterns of co-occurrence between individuals. Spatial network analysis suggested sexual segregation, because areas of high use (Walker Bay and De Hoop) differed between males and females. Co-occurrences were observed exclusively in Walker Bay, chiefly between males, with no co-occurrence found between females. The tagged spotted gully sharks were not detected extensively within existing MPA boundaries, though there was no significant difference between their movements inside and outside protected areas for both sexes.

Keywords: acoustic tagging, aggregation, chondrichthyans, marine protected area, movement pattern, sharptooth houndshark, social preference, Triakidae

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* (also known as the sharptooth houndshark) in the family Triakidae 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 IUCN Red List of Threatened Species (Pollom et al. 2020), this species remains a target for recreational fishers, which leads to 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 triakid species (e.g. the common smooth-hound *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, and there has been a notable decline in spotted gully shark abundance in False Bay, South Africa (Best et al. 2013). Given this species' endemicity, role in the food web and vulnerability to fisheries in the region, the spotted gully shark is a priority species of conservation concern (Booth et al. 2011). However, only a few studies to date have focused on the ecology of this species, 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 on its movement behaviour.

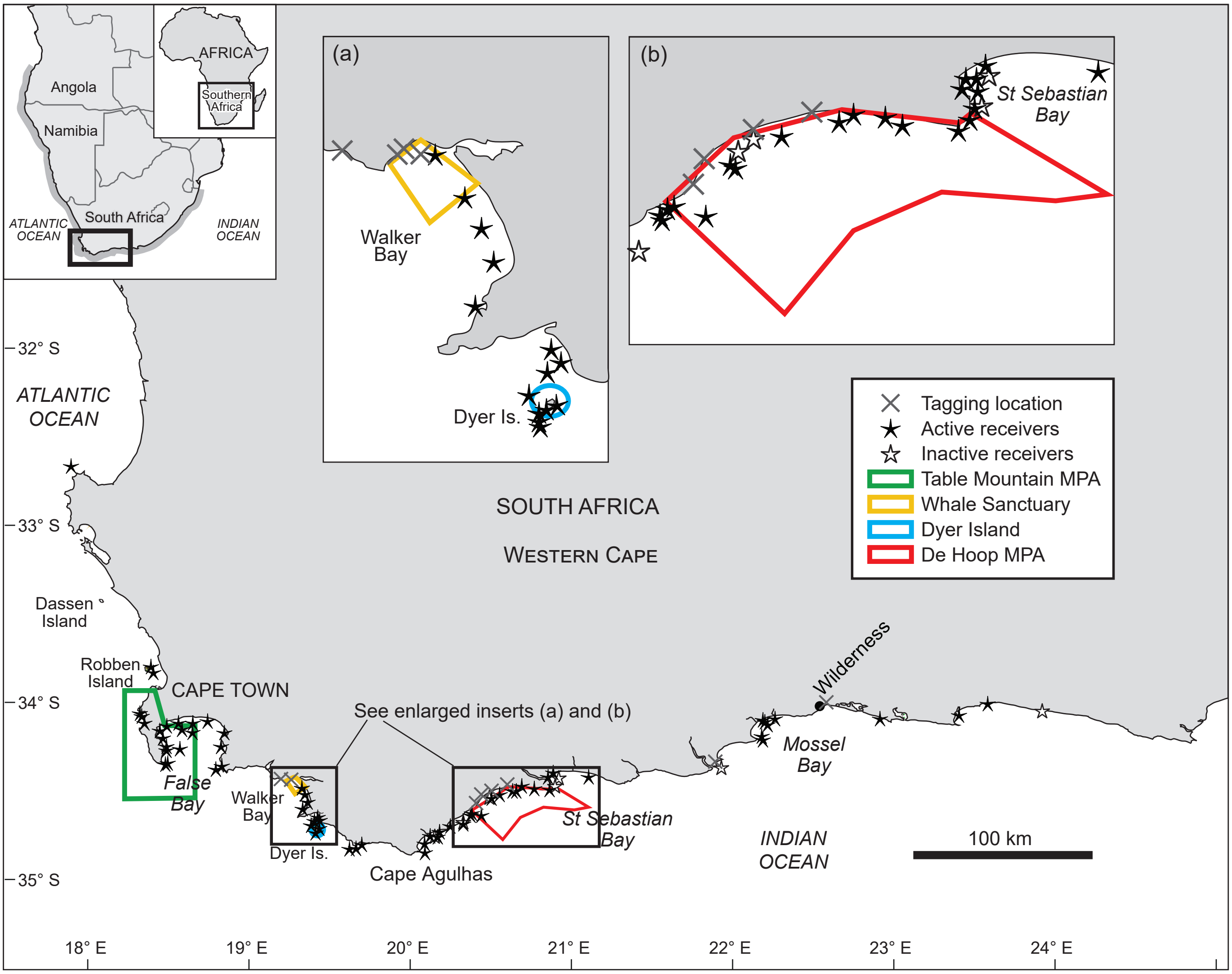

Figure 1: Map showing locations of the active acoustic receivers and inactive receivers (representing receivers that were active for only part of the study period), the tagging locations of spotted gully shark *Triakis megalopterus*, and various offshore protected areas on the coast of the Western Cape Province, South Africa. Enlarged insets show (a) the Walker Bay and Dyer Island area, and (b) the De Hoop area

Identifying areas in which species aggregate is a method regularly used by fisheries 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 the 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 and Freeman 2016; Jacoby et al. 2016, 2021) or observation (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 movement for a spatial network and the impact of one individual on another within a social network. Also, networks can be either 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 a study area (Stehfest et al. 2013; Espinoza et al. 2015). Social networks are also 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

Table 1: Tagging details and detection summary for spotted gully sharks *Triakis megalopterus* tagged with acoustic transmitters in the Western Cape Province, South Africa, and monitored between May 2019 and May 2022. Superscript numbers indicate the tagging areas: 1 = Mossel Bay; 2 = Walker Bay; 3 = De Hoop

ID code	Sex	Total length (cm)	Tagging date	Length of data series (days)	Tag life (days)	Capture location	No. of detections	No. of receivers
M6	M	108	25 Feb 2016	1 897	3 650	Wilderness	462	6
F7	F	124.6	25 Feb 2016	2 101	3 650	Wilderness	87	4
F10	F	153	27 Apr 2017	1 814	3 650	Kanon Beach[1]	25	4
M8	M	132	9 Feb 2018	1 601	3 197	Rietfontein[2]	4 520	15
F14	F	146.4	5 Mar 2018	1 480	2 431	Old Harbour[2]	1 893	17
M7	M	115	20 Mar 2018	1 511	2 466	Rietfontein[2]	421	11
M3	M	76.1	26 Feb 2019	476	838	Koppie Alleen Beach[3]	300	11
F2	F	132	27 Feb 2019	843	838	Koppie Alleen Beach[3]	3 638	16
F5	F	158	7 Mar 2019	1 148	3 197	Roman Rock[2]	146	8
F4	F	83	25 Apr 2019	399	838	Koppie Alleen Beach[3]	5	2
F9	F	154	25 Apr 2019	840	838	Koppie Alleen Beach[3]	119	12
M5	M	167	2 Jun 2019	1 252	3 197	Marine pool Hermanus[2]	2 509	15
M1	M	118.2	6 Sep 2019	969	3 197	Onrus Beach[2]	1 445	16
M2	M	148	6 Sep 2019	956	3 197	Onrus Beach[2]	94	6
F1	F	152.4	6 Sep 2019	947	3 197	Onrus Beach[2]	362	10
F8	F	175.6	25 Nov 2019	731	2 907	Skipskop[3]	29	4
F12	F	139	13 Dec 2019	850	2 503	Koppie Alleen Beach[3]	339	15
F13	F	155	11 Jan 2020	595	2 377	Koppie Alleen Beach[3]	15	4
F6	F	174	30 Jan 2020	632	3 197	Marine pool Hermanus[2]	107	10
F3	F	94	21 Feb 2020	51	838	Skipskop[3]	71	8
M4	M	114	24 Feb 2020	419	838	Marker 33 Lekkerwater[3]	5	2
F11	F	152.4	10 Aug 2021	81	2 546	Onrus Beach[2]	23	2

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 nonrandom movements and aggregation patterns measured as associations between individuals? (2) If so, do spotted gully sharks exhibit sexual segregation? (3) How effective are existing MPAs in the Western Cape in protecting spotted gully sharks?

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, known as 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–May 2022) and 20 were active for a portion of it (i.e. eventually removed or else first set during the study period) (Figure 1). Range testing was previously performed for acoustic receivers located in False Bay (within a range of 1 200 m, n = 33: Kock et al. 2018), the De Hoop area (50% detection probability within a range of 200 m, n = 19: Albano et al. 2023) and Mossel Bay (range of 800 m [SD 200 m], n = 14: RG Watson, Marine Dynamics, pers. comm.). The performance of acoustic receivers is highly variable in the marine environment owing to changing environmental conditions (Huveneers et al. 2016); therefore, a mean detection range of 500 m was considered throughout this study.

Spotted gully sharks were caught across the study areas (Walker Bay, De Hoop MPA, Mossel Bay and Wilderness) (Figure 1) between February 2016 and August 2021, either by using handlines or rod and line equipped with circle hooks, or by hand while SCUBA diving or in rock pools. In all tagging instances, the animal was put into tonic immobility and an acoustic transmitter was surgically implanted inside the intracoelomic cavity, as described in Hammerschlag et al. (2017). The tags used were V16s (V16-4L, 69 kHz, 16 mm diameter, 54 mm long, 24-g weight in air; Innovasea, Halifax, Canada) with varying battery life (mean 2 468 [SD 1 116] days) (Table 1) and a nominal delay of 60–120 seconds. Upon capture, the total length (TL, in cm) of the shark was measured and the sex recorded.

Data organisation

Data were downloaded from receivers at 6–8-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 min, or if 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 3 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). The receivers were categorised as either within a protected area, where any activity that can potentially alter the ecosystem is prohibited (e.g. fishing, destruction of any fauna and flora, discharging pollutants), or within an exploited area, 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-min maximum blanking period and considered as a single visit, hereafter termed 'detection event' (Jacoby et al. 2012; Mourier et al. 2021). A period of 30 min was chosen to reduce the number of detections as a result of immobile individuals that, given the nominal delay, could range from 15 to 30 detections per 30-min period, and to keep information on high-residency areas that would be lost with a longer 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 package 'lme4' (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 receivers, 'a' and 'b', regardless of how long the transition between receivers '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 nonrandom space use (Jacoby et al. 2012). Protection status at each receiver along with the area name (i.e. False Bay, Walker Bay, De Hoop and Mossel Bay) was added as a node attribute for each category of receiver network (i.e. protected area versus exploited area), and 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.permutation' function of the 'asnipe' package (Farine 2013). Two network metrics, namely 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 an indication of the size of the network. Average path length gives an insight on the likelihood that a transition between two receivers will occur.

Social networks

Because movements were considered regardless of time, a social-network approach was used to investigate co-occurrence patterns between individuals, linking results from spatial networks 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-min interval (Aspillaga et al. 2021). Using the package 'spatsoc' (Robitaille et al. 2019), the 'group_times' function was used to group detections per group of 5 min, and 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' denotes the individuals that were not detected. Weighted networks were constructed accordingly, based on a simple ratio index (SRI) using the package 'asnipe' (Farine 2013), illustrating the strength of the association between individuals. The SRI uses three assumptions: (i) detections are accurate; (ii) the probability of identification of an individual is independent of whether the individual is associated or not; and (iii) 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: 1 May 2019–30 April 2020; Y2: 1 May 2020–30 April 2021; Y3: 1 May 2021–30 April 2022), to investigate location of aggregations, and the same method was followed.

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

Ethical note

Research was conducted under research permits issued by the Department of Forestry, Fisheries and the Environment of South Africa (RES2018-13, RES2018-59, RES2019-61 and RES2020-16) and permit number CN32-31-5459 from CapeNature. Ethical clearance for researchers from the South African Institute for Aquatic Biodiversity (NRF-SAIAB) to tag individual sharks 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 rotating the shark to dorsal side down (Kessel and Hussey 2015). Fight-time before the animal was put into tonic immobility was ~5 min. Each animal's head and gills were maintained in the water at all times during surgery, allowing them to pump water through the spiracles to ventilate the gills, and thereby minimising stress. The 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 thereafter released. The incision measured ~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 the surgery procedure lasted ~3 min. Each animal was released in a healthy condition and was observed swimming away strongly; no mortalities occurred during the tagging procedure.

Results

Dataset overview

A total of 25 spotted gully sharks were acoustically tagged along the Western Cape Province, with 22 of the individuals (88%) being detected on at least two acoustic receivers. Thus, data from these 22 individuals were used for the analyses; they comprised 14 females and 8 males, with a length range of 76–176 cm TL (mean 134 [SD 29] cm TL) (Table 1). Of these tagged individuals, 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 fixed acoustic receivers monitored in this study, 67 receivers (53.6%) detected tagged spotted gully sharks, totalling 16 615 detections during the 3-year study 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 distance to tagging location on the detections (GLMM: p = 0.18). Nearly all detections occurred on receivers located in waters of the Western Cape Province (Figure 1), with only three detections recorded on receivers located in waters of the Eastern Cape Province. A total of 32 receivers (25.6%) were located inside protected areas, while 93 receivers (74.4%) were located in exploited areas. Male sharks represented a total of 9 756 detections (mean 1 220 [SD 1 577]), while female sharks represented 6 859 detections (mean 490 [SD 1 029]). Detections occurred in two protected areas (Table Mountain National Park MPA and De Hoop MPA), in two nature reserves in Gansbaai (Dyer Island Provincial Nature Reserve and Geyser Island Provincial Nature Reserve), and in the Walker Bay Whale Sanctuary which is a seasonal MPA (Figure 1).

Spatial network dataset

After grouping detections according to the maximum blanking period (30 min), 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, the 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 the other areas, representing 71.5% of the detection events (Figure 2a). Male individuals were also detected more frequently in a protected area than in an exploited area, 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%) when compared with the surrounding exploited areas. This was corroborated by the eigenvector centrality showing that the receiver most commonly passed was one located in the Whale Sanctuary. Female individuals showed different movement patterns, with only a few detection events in the Table Mountain National Park MPA (1.6% of detections) but more detection events in the De Hoop MPA (8.8%), when compared with male individuals (Figure 2b). Whereas 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 the De Hoop MPA (65.7%) (Figure 2b).

The male and female networks were found to be significantly different from the null model of random movement based on significant differences in the diameter of the network and their average path length (p < 0.001 for both networks). For males, the diameter of the observed network was 11, with a mean of 2.62 (SD 0.008) for the null model, and the average path length for the observed network was 1.16, and 1.50 (SD 0.003) for the null model, where the units for the network diameter and average path length is the number of edges. For females, the diameter of the observed network was 7, and a mean of 1.12 (SD 0.003) for the null model, and the average path length for the observed network was 3.27, with a mean of 1.02 (SD 0.001) for the null model.

Network metrics revealed that female individuals were using the acoustic array along the Western Cape coastline to a greater extent than males, as shown by edge density (6.64% and 5.58%, respectively) and also supported by the mean betweenness (B_i: 64.9 and 51.6, respectively) (Table 2), but the difference between males and females was not significant (p = 0.5). Betweenness also revealed that for both male and female individuals, protected areas were used to a greater extent than exploited areas, but the difference was not significant for either males (p = 0.31) or females (p = 0.53) (Table 2). Furthermore,

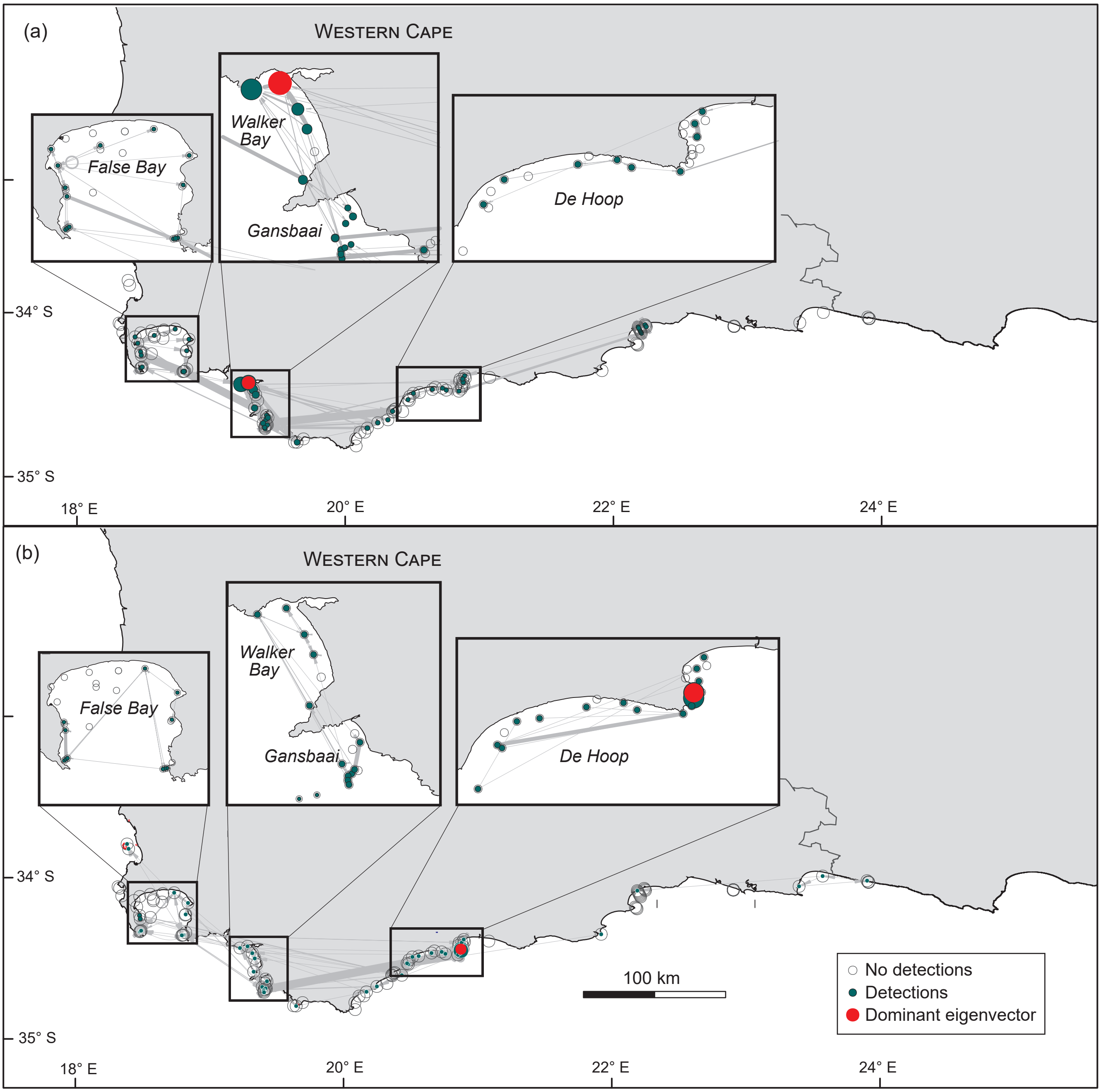

Figure 2: Spatial networks for (a) males and (b) females of tagged spotted gully sharks *Triakis megalopterus* along the southwestern coast of South Africa, showing acoustic receivers on which detections were recorded, and receivers on which no detections were recorded. For each network, the dominant eigenvector is represented by a red dot, with the size of each dot proportional to the eigenvector of each receiver. Grey lines represent movement between two locations, and thickness of the line represents the number of times the transition was made

degree centrality was lower for protected areas than for exploited areas for both the male and female networks, but the differences were not significant (p = 0.57 and p = 0.19, respectively). Looking at differences between areas, males displayed strong site fidelity (high K_i) at Walker Bay compared with the 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), and De Hoop and Mossel Bay (p = 0.01). For females, based on degree centrality (K_i), high site fidelity was found for De Hoop compared with the 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), and De Hoop and Mossel Bay (p = 0.005).

Table 2: Summary of metrics of spatial networks for female and male individuals of spotted gully sharks *Triakis megalopterus* tagged with acoustic transmitters along the Western Cape coastline, South Africa, and monitored between May 2019 and May 2022. 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 centralisation (%) is also represented

	Males (*n* = 2 194 detections)			Females (*n* = 2 511 detections)		
	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)
Edge density (%)	5.58			6.64		

Social network dyads

For the social network including all individuals, a total of eight dyads (i.e. associations between individuals) were identified, of which four dyads represented associations between males, four dyads between males and females, and no dyads between females (Figure 3). A total of seven sharks were found to be associating (four males and three females), all tagged prior to or during the first year of the study. 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, as detected principally on one receiver (Figure 4). Therefore, only detections in Walker Bay were used to build the three social network to investigate whether co-occurrence patterns persisted over time. The 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 the Y1, Y2 and Y3 networks.

Discussion

Spatial network analysis revealed that tracked spotted gully sharks exhibited nonrandom movements along the Western Cape coastline. In addition, differences in space use between the sexes demonstrated the potential for spatial segregation by sex. Females showed higher use of the De Hoop area, and males showed higher use of the Walker Bay area, which could be explained by the proximity to important estuaries (Breede Estuary and Klein Estuary, respectively). Both sexes also showed high use of the False Bay area despite the fact that no individual was tagged in this area and no major estuary is 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). Owing to increased abundance of small-sized prey, estuaries could be beneficial for a mesopredator such as the spotted gully shark. However, stomach content analysis on spotted gully sharks 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 because of a decreasing catch trend in recent decades, and includes size and bag limits along with a closed season (Holthuis 1991; DEFF 2020). As such, with the De Hoop and Walker Bay areas both containing MPAs (including no-take zones), the abundance of the principal prey of spotted gully sharks could explain their usage of these areas. However, a previous study found no difference in the abundance of west coast rock lobster inside and outside of protected areas (Mayfield et al. 2005); thus, because food availability could be just one of the factors explaining movements of this species towards those areas, other factors might 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 occurred only during winter and persisted for multiple years is interesting; based on the spatial network, those pairs might persist longer than was found in this study but might occur outside of the receiver array. Another explanation could be that certain resources are available during winter in Walker Bay and the individuals were part of a bigger cohort that was not tagged. The difference in the number of detection events after the blanking period (30 min) was applied showed differing behaviour between males and females, with males potentially more resident than females, which contradicts other studies on ground sharks (Carcharhiniformes) (as no studies were found addressing differences in residency between sexes in triakid species specifically), 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 the tagged spotted gully sharks were detected along the Western Cape coastline where the tagging occurred, except for three detection events along the Eastern Cape coastline. Lack of movement beyond waters of the Western Cape is consistent with the presence of multiple populations along their distribution range (i.e.

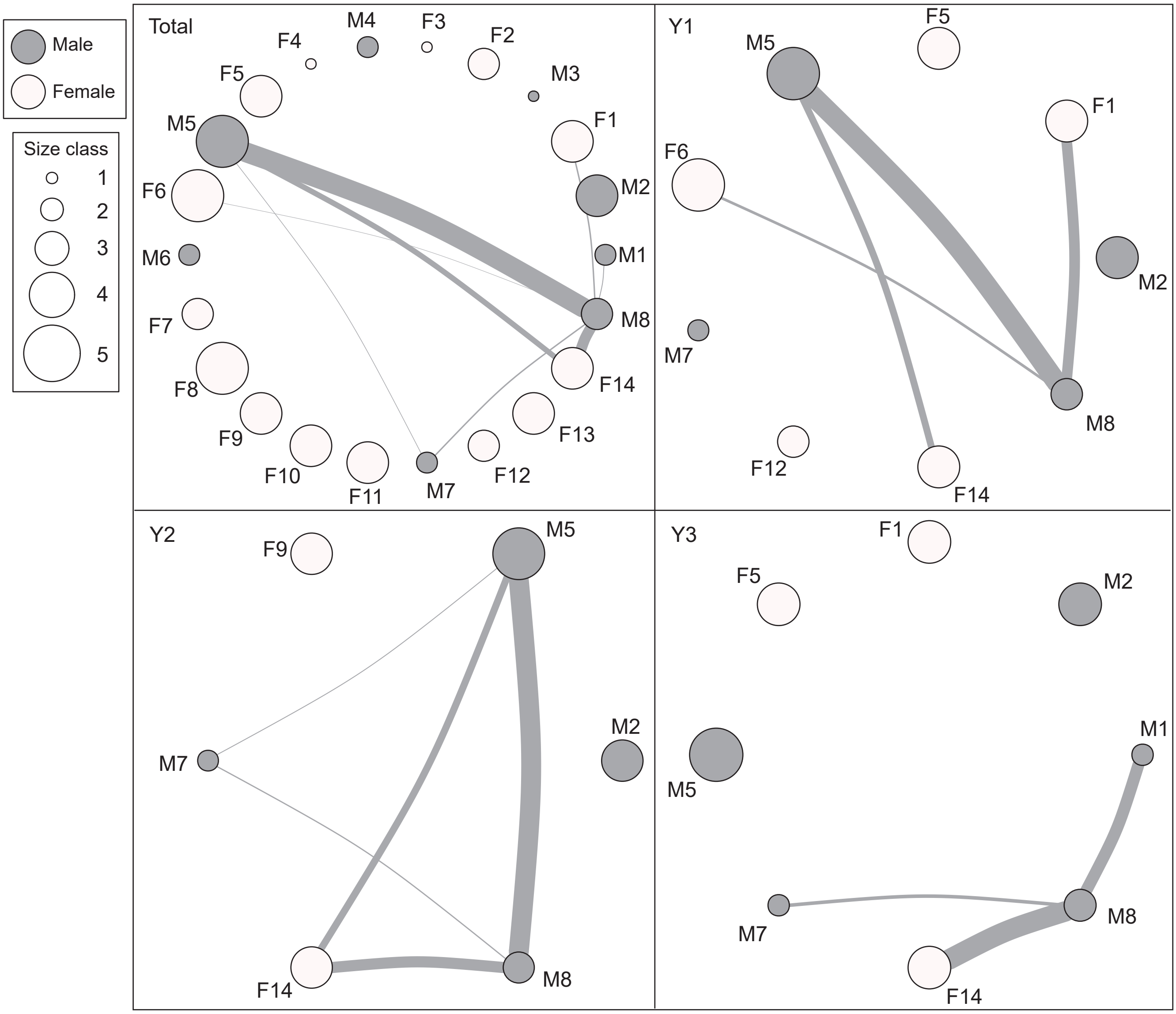

Figure 3: Observed social networks for spotted gully sharks *Triakis megalopterus* along the southwestern coast of South Africa for the full (total) 3-year dataset (Y1, Y2, Y3) for females (F) and males (M). Circle size reflects the total length of the individual (larger circles represent larger individuals), and widths of edges depend on the edge weights. Y1 = 1 May 2019–30 April 2020; Y2 = 1 May 2020–30 April 2021; Y3 = 1 May 2021–30 April 2022

southern Angola to the Western Cape and Eastern Cape, South Africa: Soekoe 2016), and in particular, a genetic divergence between the Western Cape and 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 to the west of Cape Point as well as in the Eastern Cape, and also highlights the preference of the studied population for warm-temperate waters (Soekoe 2016).

High use of the De Hoop area by females is interesting as it is essential to identify aggregation areas of females, which may represent critical habitat for the species in the form of nursery and pupping areas (Heupel et al. 2007). Indeed, nursery areas have been described as crucial for the conservation of chondrichthyans (FAO 1999; DFFE 2022). Juveniles of other species were previously found in the region, showing that the habitat is suitable as a nursery area for multiple species (Albano et al. 2021). De Hoop could possibly be a mating area, with untagged male individuals present, although a previous study (Albano et al. 2023) found males not to be aggregating in the same area as females, showing that sex segregation might explain 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 behaviour should be considered along with expanding protection across the species' full distribution range.

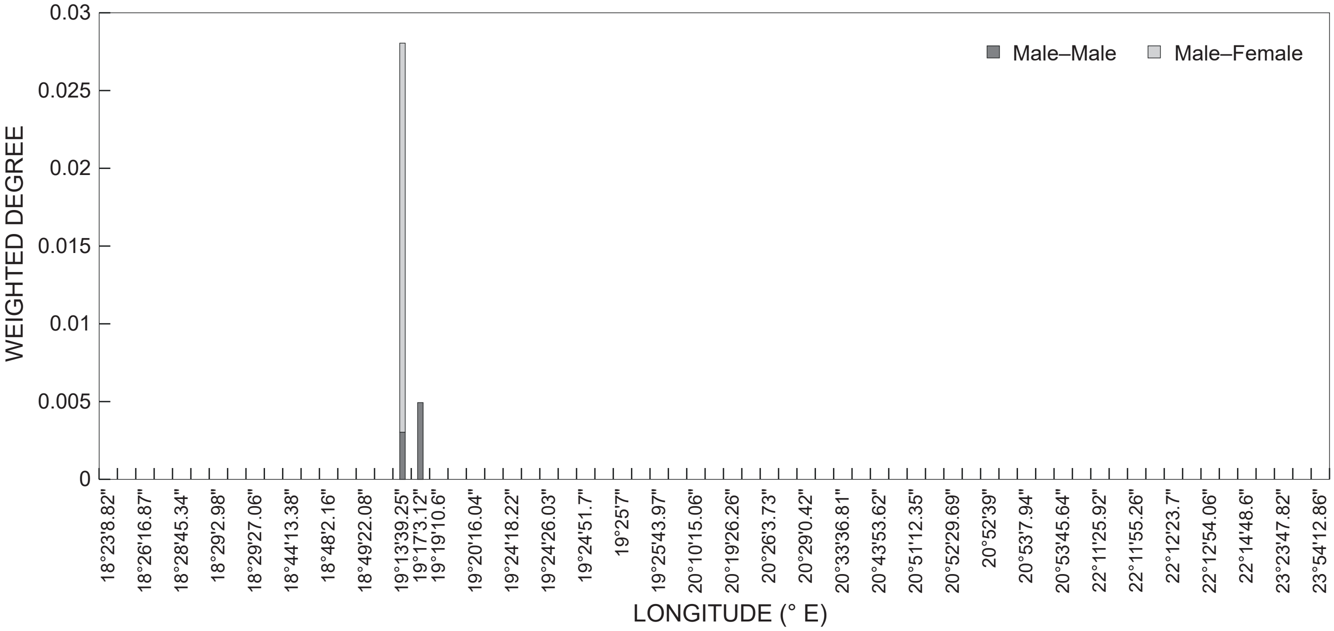

Figure 4: Location of co-occurrence events between tagged spotted gully shark *Triakis megalopterus* along the southwestern coast of South Africa

Considering the entire dataset, the tagged spotted gully sharks displayed high use of protected areas, but differences between the use of protected and exploited areas were not significant, suggesting that, globally, protected areas might not be 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 family Triakidae inside the Whale Sanctuary and De Hoop MPA compared with in adjacent exploited areas (Osgood et al. 2019; Albano et al. 2021). Local 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 with previous findings shows the need for a bigger sample size. Indeed, this result needs to be taken with caution as this study included only 25 individuals (of which data from only 22 individuals were used), and there is no information on the behaviour of untagged individuals. The detection range of receivers also needs to be taken into account 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 with in 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 aggregation 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 a principal aggregation area for this species, with more detection events occurring in the Whale Sanctuary area than at De Hoop, an increase of the population around De Hoop might mask a decrease in other areas.

Conclusions

This study revealed that tagged spotted gully sharks exhibited nonrandom movements with patterns of spatial segregation by sex, along with co-occurrence between individuals. Movement data showed that future assessment of the population should not be based only in the De Hoop MPA (Pollom et al. 2020), but should 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 the results suggest that principal aggregation areas might not fall within MPA boundaries. Future research should combine acoustic telemetry with mark-recapture data as well as information gleaned from BRUVs, across the species' entire distribution range, to provide a more accurate assessment of this shark's movement behaviour and social structure.

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