African Journal of Marine Science 2026, 48(1): 115–125
Printed in South Africa — All rights reserved

AFRICAN JOURNAL OF
MARINE SCIENCE
ISSN 1814-232X EISSN 1814-2338
https://doi.org/10.2989/1814232X.2025.2605156

Residency, site affinity and coastal movements of the southern African endemic spotted gully shark *Triakis megalopterus*

E Cottrant[1,2,3]*, JH Morrison[1], C Elston[4,5], TS Murray[4,5], NJ Drobniewska[1], LG Underhill[2,6], N Hammerschlag[7,8], PS Albano[7,9], ME McCord[1,10], PD Cowley[4], C Fallows[11] and TG Paulet[1,5]

[1] South African Shark Conservancy, Hermanus, South Africa
[2] Department of Biological Sciences, University of Cape Town, Cape Town, South Africa
[3] Marine Biodiversity Exploitation and Conservation (MARBEC: University of Montpellier, IRD, CNRS, IFREMER), Montpellier, France
[4] South African Institute for Aquatic Biodiversity (SAIAB), Makhanda, South Africa
[5] Department of Ichthyology and Fisheries Science, Rhodes University, Makhanda, South Africa
[6] The Biodiversity and Development Institute, Cape Town, South Africa
[7] Rosenstiel School of Marine, Atmospheric, and Earth Science, University of Miami, Miami, Florida, United States
[8] Shark Research Foundation Inc., Boutliers Point, Nova Scotia, Canada
[9] NOAA Ocean Exploration, Silver Spring, Maryland, United States
[10] Central Coast Indigenous Resource Alliance, Campbell River, British Columbia, Canada
[11] Apex Shark Expeditions, Simonstown, South Africa
** Corresponding author, e-mail: emycottrant@gmail.com*

Rising global concern regarding the conservation and management of shark species makes it essential to identify key ecological species to guide conservation efforts, especially species with more restricted distributions such as endemic species. The southern African endemic spotted gully shark *Triakis megalopterus* is currently listed as Least Concern on the IUCN Red List of Threatened Species. Though not commercially exploited, increased catches of this species by recreational fishers and high misidentification with other species of Triakidae in commercial fisheries are bringing uncertainty regarding the future of the population. Although *T. megalopterus* is known for localised behaviour, the extent of its site fidelity and fine-scale movements remain largely unknown. Using passive acoustic telemetry, this study assessed the species' residency, site fidelity and movement patterns along the Western Cape coast of South Africa. Overall, the data revealed low detections, suggesting that individuals are using coastal areas not currently covered by receivers. Tagged *T. megalopterus* exhibited seasonal detection patterns within their zone of tagging, with increased detections during winter months. A high number of the detections occurred after the estimated parturition period; thus, the existing receiver array might not cover potential nursery areas for the species. The results also show that some individuals do undertake long-distance movements to other zones of the coastline, possibly driven by the need to locate reliable food sources. Finally, the species did not significantly use marine protected areas (MPAs), highlighting the importance of better receiver coverage and the need to expand existing MPAs.

Keywords: acoustic tagging, chondrichthyans, distance travelled, residency index, roaming index, seasonal movement, site fidelity, southeastern Atlantic

Online supplementary material: Detailed information on the 25 *Triakis megalopterus* tagged with acoustic transmitters (Table S1) and a summary of the calculated detection indices (Table S2) is available at https://doi.org/10.2989/1814232X.2025.2605156.

Introduction

Global concern has been raised regarding the future of shark and ray species because more than one-third of species are threatened owing to overfishing (Dulvy et al. 2024). The southwestern Indian Ocean (SWIO) is a known hotspot of shark and ray endemism, with 70 endemic species described (Pollom et al. 2024). However, a recent study found that overfishing and climate change significantly intensify the extinction risk of shark and ray species in the SWIO, which thus requires strengthened management of all species along with increased data collection (Pollom et al. 2024). To prevent chondrichthyan species extinctions, South Africa finalised the National Plan of Action for the Conservation and Management of Sharks II (NPOA-Sharks II) in 2022, with one of the required actions being to produce a list of priority species for research, assessment and management intervention (DFFE 2022). Based on multiple criteria, such as abundance trends, endemicity, levels of knowledge and relative exploitation, each shark species was attributed a score of relative importance, resulting in a list of prioritised coastal shark species, where the spotted gully shark (or sharptooth houndshark) *Triakis*

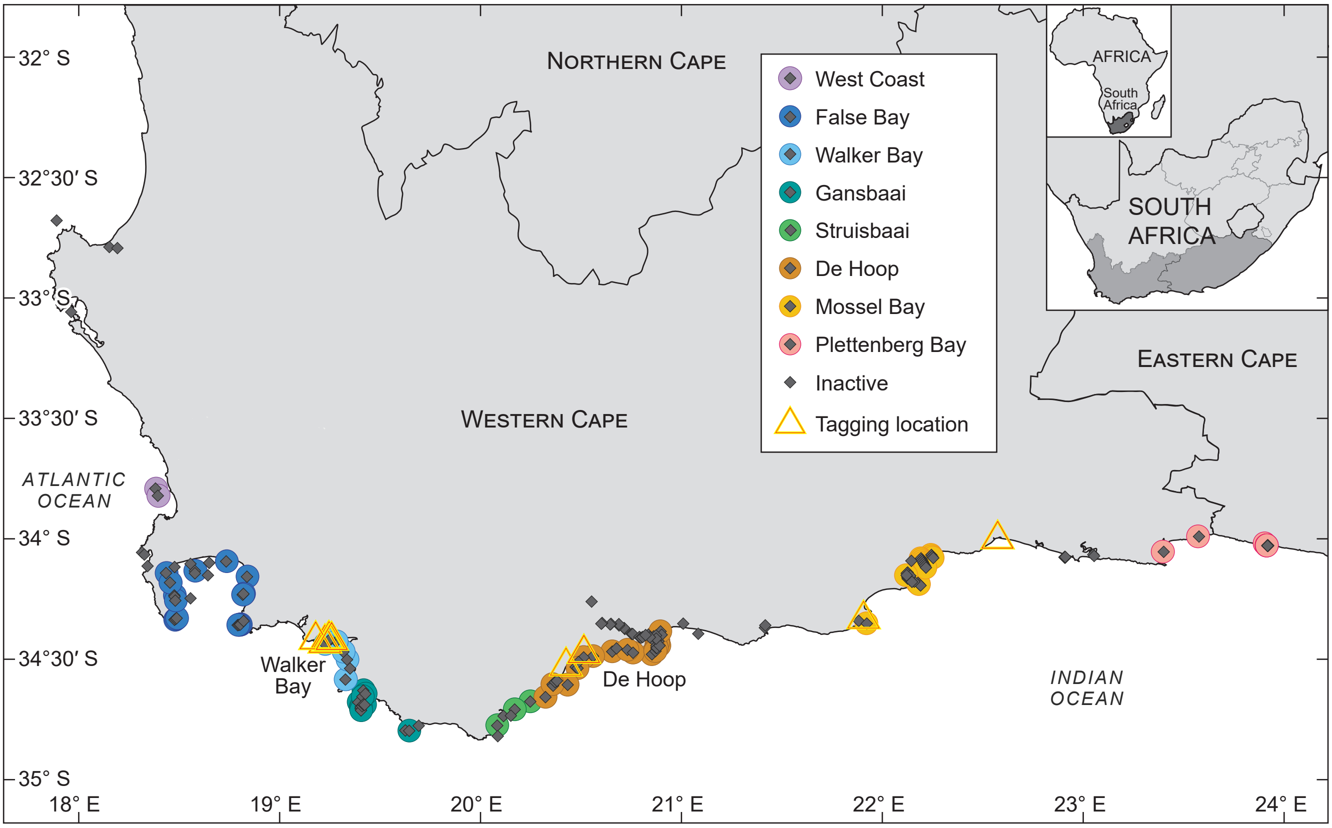

Figure 1: Map showing the acoustic receivers deployed along the coast of the Western Cape Province, South Africa. Receiver locations are coloured according to zones of interest, from west to east: West Coast, False Bay, Walker Bay, Gansbaai, Struisbaai, De Hoop, Mossel Bay and Plettenberg Bay; diamonds without colour denote inactive receivers

megalopterus appeared in the 16th position out of 22 shark species assessed (da Silva et al. 2023).

Triakis megalopterus is a medium-bodied shark species endemic to southern Africa, from southern Angola (Penrith 1978) to the Wild Coast on the southeastern coast of South Africa (Compagno 2005) (Figure 1), and is usually found at depths of <30 m on rocky reefs (Smale and Goosen 1999) and in kelp forests (Ebert et al. 2021). This species was recently re-evaluated by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Pollom et al. 2020) and was downgraded from Near Threatened to Least Concern largely due to a stable population trend, and because it is typically released by recreational fishers, with low post-release mortality (Ebert et al. 2021). However, the 2020 assessment focused solely on the De Hoop Marine Protected Area (MPA) on the South coast of South Africa, and though this work possibly approximated the trend of this species in this zone, broader consideration across its entire range might demonstrate a different population trend. *Triakis megalopterus* also remains a targeted species in the recreational fishing sector (Dicken et al. 2012; Ebert et al. 2021), and is susceptible to bycatch from commercial fisheries operating in shallower waters (Best et al. 2015; da Silva et al. 2023). This could result in post-release stress and mortality (Cooke and Schramm 2007), and hence even a small increase in fishing pressure (and associated mortality) could negatively impact the population (Booth et al. 2011).

While considerable work has been done on the genetics of the family Triakidae, including *T. megalopterus* (López et al. 2006; Maduna et al. 2017; Kiser et al. 2024; Winn et al. 2024), the species' movements have received less attention, with one acoustic telemetry study (Cottrant et al. 2023) and one mark-recapture study (Mann et al. 2024) to date. These studies indicated that *T. megalopterus* displays resident behaviour, with adults moving greater distances, on average, than juveniles (Mann et al. 2024), and there is some evidence of sexual segregation taking place at certain sites along the coast of South Africa (Cottrant et al. 2023). The studies of Cottrant et al. (2023) and Mann et al. (2024) both highlighted the importance of no-take MPAs with suitable habitat within their distribution range. Though *T. megalopterus* is relatively low on the list of priority shark species, frequent misidentification with other triakids may be masking the impact of fisheries on this species. Furthermore, since the previous assessment contributing to its current IUCN Red List listing was conducted within an MPA, there is a clear lack of data for exploited areas. Therefore, this study aimed to build on existing movement information by investigating the movements patterns of individuals tagged in waters of the Western Cape Province, South Africa. The goal was to assess site fidelity to different zones along the Western Cape coastline, distances travelled by individuals and residency to MPAs. The effects of sex, size and tagging area were also considered when investigating each aspect.

Materials and methods

Study area

The movements of tagged *T. megalopterus* were monitored along 750 km of the South African coastline using an array of coastal acoustic receivers forming part of the Acoustic Tracking Array Platform (ATAP) (Murray et al. 2022) (Figure 1). Because the westernmost acoustic detection was recorded on a receiver near Robben Island, north of False Bay, and the easternmost acoustic detection was recorded in Plettenberg Bay (Figure 1), data collected only on receivers deployed in the Western Cape Province (n = 125), which is located in the mixing zone between the cool-temperate and warm-temperate biogeographic provinces (Teske et al. 2011), were included for the purposes of this study. The receivers were grouped into eight main areas of interest, from west to east: West Coast, False Bay, Walker Bay, Gansbaai, Struisbaai, De Hoop (comprising receivers offshore of the Breede River estuary, as well as inside and around the De Hoop MPA), Mossel Bay and Plettenberg Bay (Figure 1).

Tagging procedure

From 2016 to 2021, 25 *T. megalopterus* were tagged with acoustic transmitters (V16-4L; Innovasea, Halifax, Canada) (Supplementary Table S1) with a varying battery life (mean ± standard deviation [SD] = 2 468 ± 1 116 days). The sharks were caught in Walker Bay (n = 12), De Hoop (n = 10), Mossel Bay (n = 1) and Wilderness (n = 2) (Figure 1) using multiple gear types, including handlines (Walker Bay only), by hand when SCUBA diving (Walker Bay only), rod and line using baited circle hooks, or a seine net in the case of individuals trapped in rock pools (at Hermanus, Walker Bay), which occurred in 2020. Animals were handled in accordance with established best practices (Murchie et al. 2012), with the gills kept submerged at all times during the tagging to minimise stress. The individual was placed in tonic immobility (Kessel and Hussey 2015) and an acoustic transmitter was surgically implanted into the intracoelomic cavity, following Hammerschlag et al. (2017). Incisions of ~1.5 cm in length were made in the abdominal wall, anterior to the pelvic fins, and closed using three nylon sutures. Upon capture, the total length (TL, cm) and sex of each individual were recorded. Based on size at 50% maturity (Smale and Goosen 1999), males of <132 cm TL and females of <145 cm TL 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 (DFFE), 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 6–8 months and visually inspected to remove any false detections potentially resulting from tag collision (i.e. two transmitters pinging at the same time on the same receiver) or acoustic pollution (Simpfendorfer et al. 2015). Detections were deemed valid if >2 detections of an individual occurred on the same receiver within 30 min or if single detections were corroborated by another receiver in the same area.

Theoretical dates of maturity were calculated for tagged juvenile sharks based on the von Bertalanffy growth (VBG) formula (von Bertalanffy 1938) with parameters from Booth et al. (2011), resulting in an estimated age at maturity of 10.9 years for males and 15.3 years for females. Age at tagging was calculated using the formula:

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

where L_t is the TL on the date of tagging, L_∞ is the theoretical maximum length that can be reached (obtained using VBG parameters in Booth et al. [2011]: (L_∞ = 1 667.89 mm TL for males, and L_∞ = 1 738.93 mm TL 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). After the age at tagging was estimated, we used the difference between the age at maturity and the age at tagging to obtain the number of days remaining to reach maturity.

All analyses were performed using R (R Core Team 2024) and RStudio (Posit Team 2024). For every model presented in the following sections, normality was assessed prior to analysis using a Shapiro–Wilk test.

Detection index: array-based, management-based, and tagging area-based

To investigate site fidelity of individuals to zones along the Western Cape coastline, detection indices (DI) were calculated for all individuals (n = 25). The DI was calculated as the number of days detected divided by the number of days monitored, with the latter defined as the number of days between the tagging date and the last detection of the individual (March et al. 2010; Zhang et al. 2015, 2020). In the case of maturity, for juveniles that became adults during the study period, the DI was calculated from the tagging date until the theoretical date of reaching adulthood, after which they were classified as adults and an additional DI value was calculated from the date of adulthood until the last detection. Three types of DIs were calculated: (i) an array-based DI (DI_a), which comprised all receivers in the study area; (ii) a management-based DI (DI_m), which calculated the DI separately from receiver data within MPAs ($\text{DI}_{\text{protected}}$) and from receiver data in exploited areas (DI_{open}); and (iii) a tagging area-based DI (DI_t), which for each individual comprised only receivers within its tagging area (e.g. all receivers present in the Walker Bay for individuals tagged in that zone). Using the three calculated DIs, we could assess the potential site fidelity to an individual's tagging area or other defined zone.

A generalised linear model (GLM) using the 'glm' function of the package *lme4* (Bates et al. 2015) was used to assess the effect of sex, maturity, TL and tagging area, on the DI_a, DI_m and DI_t. Families used were quasibinomial with a log link for all the DIs

$$\text{DI}_a = \textit{Maturity} + \textit{Sex} + \textit{TL} + \textit{Tagging area} \tag{2}$$

$$\text{DI}_m = \textit{Maturity} + \textit{Sex} + \textit{TL} + \textit{Tagging area} + \textit{Management type} \tag{3}$$

$$\mathrm{DI_t} = \mathit{Maturity} + \mathit{Sex} + \mathit{TL} + \mathit{Tagging\ area} \tag{4}$$

A generalised additive mixed model (GAMM) using the 'gam' function in the package *mgcv* (Wood 2017) was used to assess the effect of month (as a proxy for season) on the proportion of the $\mathrm{DI_t}$ for each month. A GAMM was used as nonlinear variations can occur between months, thus it was set as a smoothing term and individual tag numbers were set as a random effect. Data were non-normally distributed, and therefore a binomial family was chosen with a log link. Analyses were performed only on the individuals tagged in Walker Bay ($n = 12$) or in De Hoop ($n = 10$), as other tagging areas did not comprise enough individuals to exhibit significant results at the population level. Moreover, Walker Bay and De Hoop were also considered important zones for *T. megalopterus* as the highest number of captures were made in these zones based on the mark-recapture study (Mann et al. 2024).

$$\text{Monthly } \mathrm{DI_t} = s(ID, bs = \text{“re”}) + s(Month, by = ID, bs = \text{“re”}) + s(Month, bs = \text{“cc”}) \tag{5}$$

Furthermore, Mann–Whitney *U*-tests were performed to compare the values of $\mathrm{DI_a}$ and $\mathrm{DI_t}$ and accordingly to identify whether individuals were spending more time within their tagging area than in the rest of the receiver array. Tests were performed first on the entire dataset, and then only on individuals tagged in Walker Bay, and also only on individuals tagged in De Hoop, as the majority of individuals were tagged in these zones.

Space use

To evaluate the importance of the receiver array in elucidating space use by *T. megalopterus*, a roaming index (RI) was calculated as the number of receivers visited by an individual divided by the total number of receivers in the study area (Schlaff et al. 2020). Similar to the DI, a second RI was calculated for individuals that reached maturity during the study period to obtain an RI for juveniles and another RI for adults.

A GLM using the 'glm' function of the package *lme4* (Bates et al. 2015) was used to assess the effect of sex, maturity, TL and tagging area on the RI using a Gaussian family with a log link, whereby:

$$\mathrm{RI} = \mathit{Maturity} + \mathit{Sex} + \mathit{TL} + \mathit{Tagging\ area} \tag{6}$$

Furthermore, variability in use of the eight different zones covered by the acoustic array was assessed. The proportion of zones used by each tagged individual was calculated by dividing the number of zones visited by the total number of zones (i.e. eight). The correlation between the proportion of zones visited and the time at liberty was also tested using a Pearson correlation test. A GLM was performed using the 'glm' function of the package *lme4* (Bates et al. 2015) to investigate the influence of maturity, sex, TL and tagging area on the proportion of zones visited. Data were non-normally distributed, thus a quasibinomial family was used with a log link:

$$\text{Proportion of zones visited} = \mathit{Maturity} + \mathit{Sex} + \mathit{TL} + \mathit{Tagging\ area} \tag{7}$$

For each shark monitored, the total minimum distance travelled during the study period was calculated. This estimates the minimum distance travelled based on the fact that individuals might swim in zones that lack receivers between two consecutive detections; the distance was calculated as the sum of distances between the locations of consecutive detections with the first distance being between the tagging area and the location of the first detection. The Haversine formula (Robusto 1957) with a modification by Van Brummelen (2013) was used to calculate the distance by taking into account the curvature of the Earth, using the formula:

$$hav\left(\frac{d}{r}\right) = hav(\phi_2 - \phi_1) + \cos(\phi_1)*\cos(\phi_2)*hav(\lambda_2 - \lambda_1) \tag{8}$$

where *hav* is the Haversine function $hav(\theta) = \sin^2\left(\frac{\phi}{2}\right)$, 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 receivers 1 and 2 in radians; and λ_1 and λ_2 are longitudes in radians. Owing to the sparse setting of the receiver array, straight lines between certain pairs of the receivers cross land; to prevent this, nine additional fictional receivers were added for calculation to keep the approximated shark movements within the marine environment. A GLM was used to determine the influence of TL, sex, maturity and tagging area, on the total distance travelled by tagged sharks. Time at liberty was not included in the GLM analysis after a Pearson correlation test showed a significant correlation between time at liberty and distance travelled ($p < 0.05$). A Gaussian family with a square-root link was set for the GLM since the data were normally distributed.

$$\text{Distance travelled} = \mathit{Sex} + \mathit{Maturity} + \mathit{TL} + \mathit{Tagging\ area} \tag{9}$$

Results

Dataset overview

The tagged *T. megalopterus* represented 15 females (5 juveniles, 10 adults) and 10 males (6 juveniles, 4 adults) with a length range of 76.1–175.6 cm TL (mean ± SD: 137.2 ± 27.6 cm TL). Among the 11 juveniles tagged, 5 juveniles (2 females, 3 males) reached maturity during the study period (Figure 2). Of the 125 Western Cape receivers deployed for the duration of the study, 78 receivers (62.4%) detected *T. megalopterus*, comprising 33 011 detections between 2016 and 2023 (Figure 2). Of the receivers that detected tagged sharks, 33 (42.3%) were positioned inside protected areas.

Detection indices

The time at liberty for tagged individuals ranged from 47 to 2 791 days (1 122 ± 750.7 days) (Supplementary Table S2). The sharks displayed $\mathrm{DI_a}$ values in the range of 0.01–0.28 (mean 0.06), and no significant influence of TL, sex, maturity or tagging area were found ($p \geq 0.05$) (Supplementary Table S2; Figure 3).

The $\mathrm{DI_m}$ values for protected areas ($\mathrm{DI_{protected}}$) ranged from 0 to 0.17 (mean 0.03), and for exploited areas ($\mathrm{DI_{open}}$) it ranged from 0 to 0.23 (mean 0.04) (Figure 3). These $\mathrm{DI_m}$ values did not significantly vary with TL, sex, maturity or tagging area ($p \geq 0.05$ in all instances). Relative to the number of days detected on the receiver array, the mean proportion of days on which *T. megalopterus* were detected in protected areas (0.43 ± 0.36) was not significantly different from the mean proportion of days they were

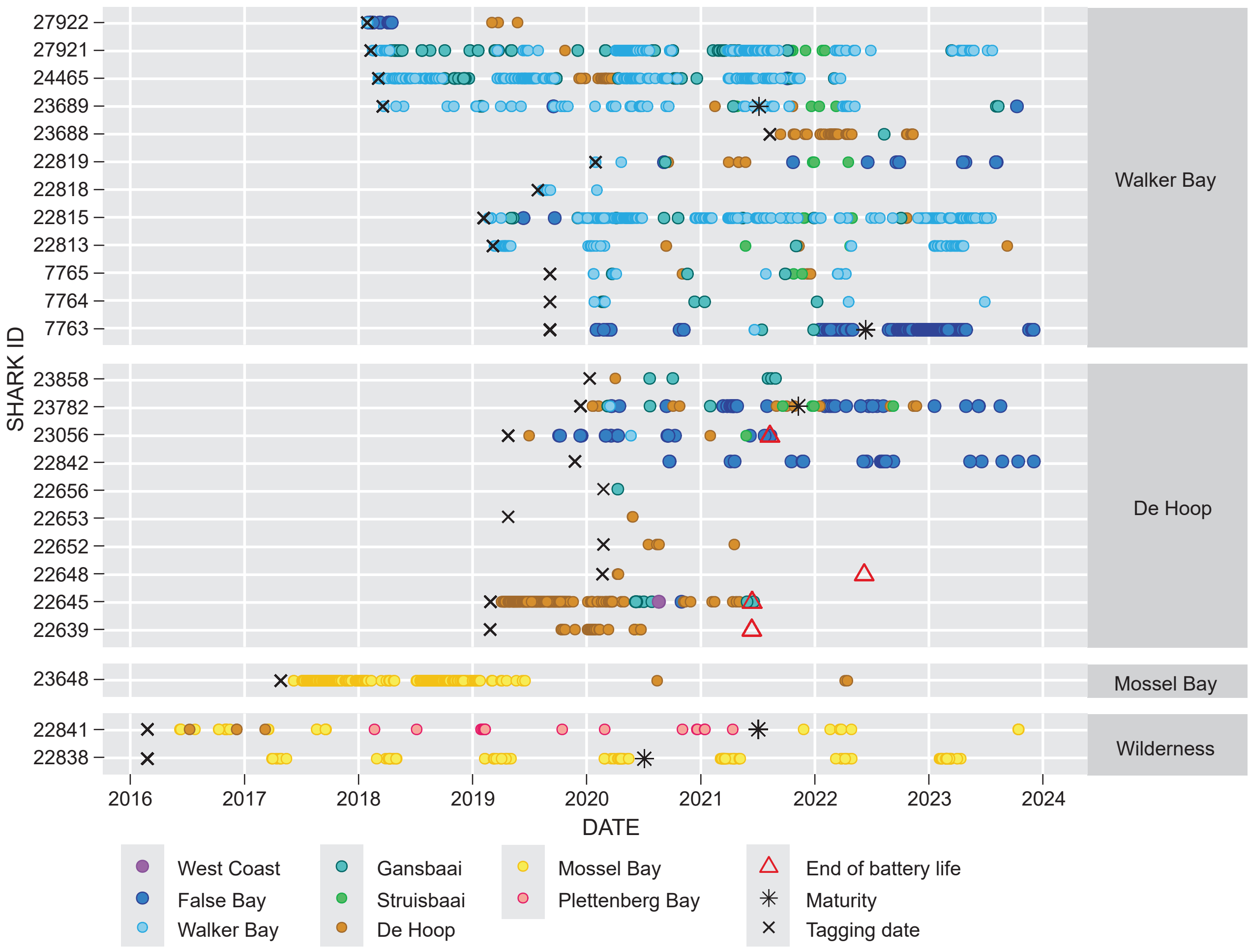

Figure 2: Daily detection plot for acoustically tagged *Triakis megalopterus* monitored along the Western Cape Province coastline, South Africa, between the start of 2016 and the end of 2023. Individuals were grouped by tagging area (see Figure 1)

detected in exploited areas (0.57 ± 0.36; Mann–Whitney *U*-test: $p = 0.17$).

The DI_t values ranged from 0 to 0.18 (mean 0.03), irrespective of the sharks' original tagging area (Supplementary Table S2; Figure 3). By tagging area, the range of the DI_t values was 0–0.08 (mean 0.01) for De Hoop sharks, 0.01–0.14 (mean 0.05) for Wilderness and Mossel Bay sharks, and 0–0.18 (mean 0.04) for Walker Bay sharks (Supplementary Table S2). Similar to the values of DI_a and DI_m, no significant influence of TL, maturity or sex was found on the values of DI_t ($p \geq 0.05$ in all instances). However, significance of the tagging area was found for the single shark tagged in Mossel Bay, which had a higher DI_t value compared with all other sharks from all other tagging areas (GLM: $F = 2.31$, $p = 0.04$).

The DI_a values were significantly higher than the DI_t values for all tests performed, specifically when using: (i) all individuals (DI_a range of 0.01–0.28, mean 0.07; DI_t range of 0 to 0.19, mean 0.03); (ii) Walker Bay-tagged individuals (DI_a range of 0.01–0.20, mean 0.08; DI_t range of 0–0.19, mean 0.04); and (iii) De Hoop-tagged individuals (DI_a range of 0.01–0.28, mean 0.06; DI_t range of 0–0.08, mean 0.02) ($p < 0.05$ in all instances). Proportions of days detected in the tagging area ranged from 0 to 0.90 for De Hoop-tagged sharks, 0.58 to 1.00 for individuals tagged at Wilderness and Mossel Bay, and 0 to 0.75 for sharks tagged at Walker Bay (Supplementary Table S2).

For *T. megalopterus* tagged in the Walker Bay zone, the probability of their detection was higher within this tagging area between March and September, and a lower probability of detection was found between September and December, with a strong decrease in detection probability between October and November ($p < 0.001$) (Figure 4a). Sharks tagged in the De Hoop and Walker Bay zones showed similar seasonal patterns of detection within their respective tagging area (Figure 4). De Hoop-tagged individuals were most likely to be detected in the De Hoop zone between April and November, with the detections peaking between September and October, whereas the probability of detection was low between November and April, and lowest in February ($p < 0.001$) (Figure 4b).

Space use patterns

The RI values ranged from 0.01 to 0.16 (mean ± SD: 0.08 ± 0.05), and were not significantly influenced by TL, sex, maturity or tagging area ($p \geq 0.05$ in all instances). The number of zones visited ranged from 1 to 5 of the total 8 zones

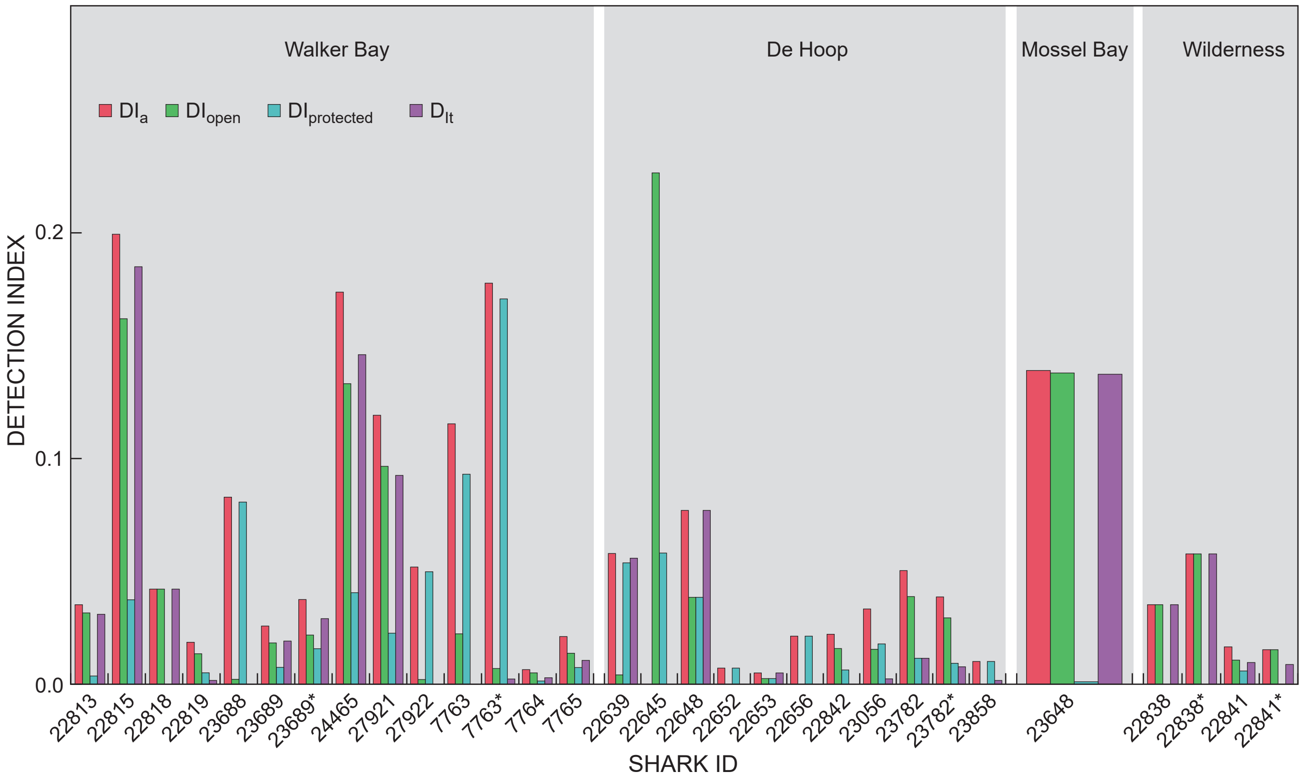

Figure 3: Detection indices for *Triakis megalopterus* tagged in South African waters, sorted by tagging area (from west to east) (see Figure 1). Detection index (DI) for: within the receiver array (DI_a), within the individual's tagging area (DI_t), in areas exposed to fishing (DI_{open}) or inside protected areas ($DI_{protected}$). An asterisk next to the shark ID represents results from the adult stage after the individual reached maturity during the study period

monitored (2.63 ± 1.47 zones), corresponding to proportions ranging from 0.14 to 0.71 (mean 0.37); no correlation with time at liberty was found, along with no significant influence of sex or maturity ($p \geq 0.05$ in all instances).

Results showed differences in the proportion of zones visited depending on the tagging area of individuals, with Walker Bay-tagged individuals visiting a greater proportion of zones (mean 0.41) than individuals tagged in any of the other areas (i.e. mean 0.27 for De Hoop, mean 0.25 for Mossel Bay, and mean 0.19 for Wilderness; GLM: $F = 0.48$, $p = 0.04$). The number of zones visited by an individual was also significantly influenced by TL, with larger individuals visiting more zones, meaning they displayed wider-ranging movements (GLM: $F = 0.001$, $p = 0.02$).

The minimum distance travelled was calculated for each of the 25 tagged sharks (Supplementary Table S2). An adult male (167.0 cm TL at tagging) exhibited the greatest minimum distance travelled, moving 1 870 km in 1 624 days monitored, while the smallest distance was by a juvenile male (77.3 cm TL at tagging) with 2.25 km travelled in 190 days. The tagged sharks exhibited a mean (±SD) minimum distance travelled of 594 ± 524 km for a mean (±SD) time at liberty of 930 ± 546 days (Supplementary Table S2). Juveniles exhibited a mean minimum distance travelled of 480 ± 493 km for a mean time at liberty of 804 ± 594 days, while adults had a higher mean minimum distance travelled of 664 ± 544 km for a mean time at liberty of 1 006 ± 416 days (Figure 5a). Distance travelled was significantly correlated to time at liberty, showing that larger sharks swim longer distances than smaller sharks ($p < 0.05$). Only three individuals had long-distance movements detected continuously towards the same direction along the coastline by multiple receivers: 1 juvenile male, 1 juvenile female and 1 adult female (average size 1 334.7 ± 164 SD cm TL). The largest movement record was in a southwestward direction between De Hoop and False Bay, with detections in Gansbaai and Walker Bay (minimum distance of 169 km).

Sex and life stage (juveniles vs adults) did not significantly influence the distance travelled by *T. megalopterus* ($p \geq 0.05$ in all instances) (Figure 5a,b). Similarly, tagging area did not significantly influence the distance travelled by individuals, but there were larger sample sizes in the De Hoop ($n = 10$) and Walker Bay ($n = 12$) zones than in Wilderness ($n = 2$) (Figure 5c). The minimum distance travelled by individuals was significantly influenced by TL, with larger individuals travelling farther (GLM: $F = 0.03$, $p = 0.04$). Indeed, individuals larger than 1 500 cm TL had a mean (±SD) minimum distance travelled of 714 ± 369 km, while individuals smaller than 1 200 cm TL had a mean minimum distance travelled of 256 ± 212 km.

Discussion

Two previous studies assessed the population of *T. megalopterus* for the IUCN (i.e. Booth et al. 2011; Pollom et al. 2020), but the study areas did not cover a

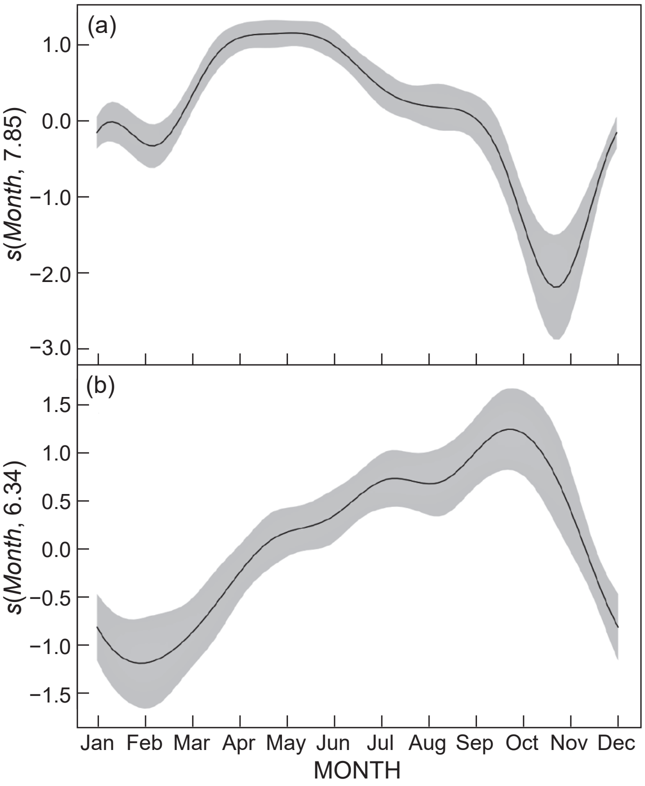

Figure 4: Effect plots for smooth terms in the generalised additive mixed models, highlighting how values of the tagging area-based detection index (DI_t) of *Triakis megalopterus* tagged at (a) Walker Bay and (b) De Hoop, South Africa, varied throughout the year

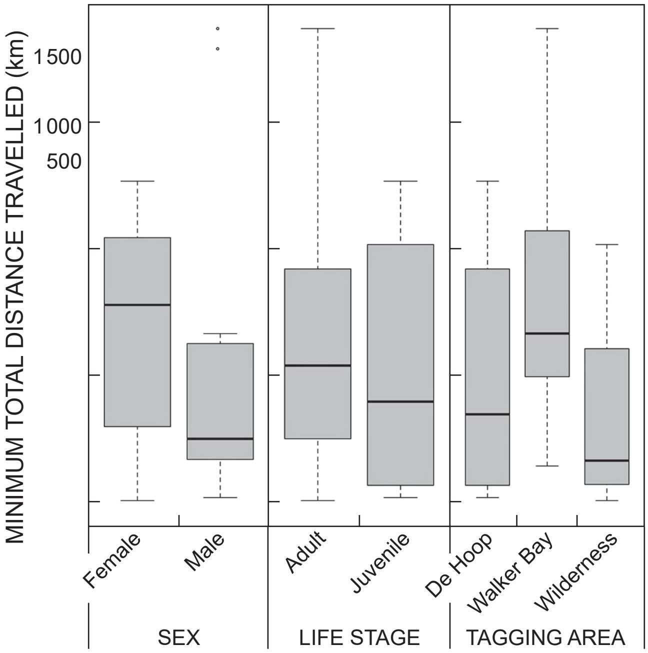

Figure 5: Minimum total distance travelled (km) for *Triakis megalopterus* tagged and released in specific areas along the Western Cape Province coastline, South Africa: (a) per sex, (b) per life stage (adult vs juvenile), and (c) per tagging area. Thick horizontal lines represent medians; grey boxes represent the first and third quantiles; whiskers represent the minimum and maximum

large proportion of their distribution range. The results of the current study revealed that *T. megalopterus* tagged and monitored in coastal waters of the Western Cape were generally resident to their respective tagging areas. However, low values of the detection indices and roaming index suggest that the receiver array was not fully capturing shark movement and residency patterns across their range. Comparatively higher roaming and detection indices have been found for other shark species, such as the blacktip reef shark *Carcharhinus melanopterus* (Schaff et al. 2020) and Caribbean reef shark *C. perezi* (Baremore et al. 2021). While those species are expected to be more mobile than *T. megalopterus* and occupy different habitats (i.e. reefs), given the higher detection rates obtained in those studies, we suggest that better receiver placement along the coast of the Western Cape could better capture the species' movements and residency.

Juveniles and adults of *T. megalopterus* prefer shallow waters <30 m deep (Goosen 1997; Smale and Goosen 1999; Ebert et al. 2021), where they feed on crustaceans, cephalopods and reef fishes (Smale and Goosen 1999). The majority of the ATAP receivers deployed in the Western Cape were positioned in relatively shallow coastal water, with a mean depth of 21 ± 8.3 m. As such, it was expected that these receivers would regularly detect the tagged individuals. However, low detection indices suggested that, regardless of the relatively shallow depths of the receivers, *T. megalopterus* might use shallower habitats than those covered by these receivers. In fact, this species is often observed in the surf zone, where receivers are usually not placed because of high wave action (EC pers. obs.; Velasco et al. 2023). Part of the Western Cape coastline comprises good reef structure along with numerous gullies forming ideal habitat for *T. megalopterus* (Skowno et al. 2019). The deployment locations of the acoustic receivers, in contrast, are generally sandy in nature, and set away from reef structures to reduce the impact of reef noise on the detection range of the receivers. As such, the low detection indices recorded here may be a result of the sharks traveling closer inshore coupled with the receivers not being deployed in optimal locations to detect this species. Indeed, the ATAP array was not designed or implemented in a way to detect any one species (Murray et al. 2022).

The tagged *T. megalopterus* exhibited a high proportion of days detected in their original tagging area, a pattern not influenced by sex, maturity or size. This result is consistent with other research on this species (e.g. Smale and Goosen 1999; Dunlop and Mann 2014; Mann et al. 2024). Nevertheless, the higher values of DI_a than DI_t showed that residency was not limited to the individual's tagging area, and while the individuals spent a high proportion of days within their tagging area, some individuals venture out and visited other zones along the coastline. Half of the tagged individuals remained within their tagging area irrespective of sex or size (i.e. no influence of either variable). Thus, roaming behaviour could be linked to individual variability in behaviour or physiological condition as opposed to driven by a specific need, such as feeding or mating. The results revealed marked differences in the proportion of zones visited depending on the individual's tagging area, with areas in which more individuals had been tagged having generally higher values compared with areas in which only a few individuals had been tagged. This is largely a result of sample sizes, and indicates a need to tag more individuals close to False Bay and Mossel Bay; accordingly, this also has implications for the layout of deployed receivers, since during the study many more receivers were deployed at Walker Bay and De Hoop than at Wilderness and Mossel Bay, which together had only 14 receivers out of the 125 in the study. Nonetheless, the high proportion of days that Walker Bay and De Hoop-tagged sharks spent in their original tagging areas could suggest that *T. megalopterus* in the Western Cape may be present in multiple discrete populations.

Previous genetic work on this species revealed two distinct populations within the South African distribution, separated at Cape Agulhas (Soekoe 2016). The De Hoop region is located in the Indian Ocean but near the mixing zone with the Atlantic Ocean, whereas Walker Bay is in the Atlantic Ocean, with each location falling on opposite sides of Cape Agulhas. Thus, water temperatures are generally lower in Walker Bay than in the Breede River mouth area of the De Hoop MPA (Teske et al. 2011), resulting in the presence of different prey species, which could potentially explain movements of *T. megalopterus* between zones that exhibit significant differences in water temperature. Indeed, individuals could be traveling across zones to seek food and then return back to the same area for reproductive purposes, which would explain how two genetically distinct populations could prevail. However, it could also mean that the previous cut-off proposed as a frontier separating the two populations might be farther east than previously considered. Indeed, the genetic differences were found based on individuals sampled in False Bay and Algoa Bay (Soekoe et al. 2022); therefore, it is possible that the limit is not Cape Agulhas, but (based on our results) could be around the Breede River mouth. The study of Soekoe et al. (2022) also found differences in the diet of *T. megalopterus* between the Western Cape and Eastern Cape; thus, it is possible that the population tagged at De Hoop is exhibiting similar behaviour than the Eastern Cape population that showed differences of diet between winter and summer (Soekoe et al. 2022). This could explain the movement of De Hoop-tagged individuals towards the colder waters of Walker Bay and False Bay, such as to forage for west coast rock lobsters *Jasus lalandii*.

Based on mark-recapture data, *T. megalopterus* has a generally higher catch rate between October and March (austral summer) along the entire South African coastline (Mann et al. 2024). This result differs from our findings, as tagged individuals used the two principal zones of interest (i.e. Walker Bay and De Hoop) to a greater extent during winter months, between March and September. Because mark-recapture is shore-based, this suggests that individuals might be using the closer inshore waters on a seasonal basis—for example, moving offshore for feeding and mating purposes, but shallower inshore areas for parturition and as nursery areas. Higher detections in winter in Walker Bay and De Hoop could be explained by an individual's life cycle (e.g. mating period, parturition) and seeking warmer or cooler temperatures in coastal areas at different times of the year. In fact, the greater probability of detection during winter aligns with after the parturition period for the species, estimated to be between February and March (Soekoe 2016). Indeed, this parturition period is influenced by water temperature and occurs earlier in the year in the Western Cape than in the warmer waters off Angola or in the Eastern Cape, which is thought to be the result of Western Cape individuals growing slower, a pattern generally observed in elasmobranch species which grow slower in cold than in warm waters (Economakis and Lobel 1998; Soekoe 2016). This was also found for another triakid species, the smoothhound shark *Mustelus mustelus*, where parturition periods were different across different zones of its distribution, occurring in spring and summer in the Northern Hemisphere (i.e. Senegal, Mauritania and Gulf of Tunis), and in October and November (austral spring) off South Africa (da Silva et al. 2021). This suggests that different parturition areas for *T. megalopterus* may be outside the zones covered by the receivers or else that there is no specific zone for parturition, which might occur throughout their distribution (Bass et al. 1975; Mann et al. 2024). Hence, this shows a need to increase the number of receivers close to the coastline as the current array might be missing key aggregation areas for the species.

Furthermore, the gestation period of *T. megalopterus* is estimated to last 19–21 months (Smale and Goosen 1999); thus, mating might occur between June and July. During that period, both sexes showed higher DI_t values, indicating that Walker Bay and De Hoop might be important aggregation sites for mating. A previous study using network analysis showed that co-occurrence patterns occurred only in Walker Bay during the winter months (Cottrant et al. 2023). Thus, aggregation in Walker Bay could be attributable to mating, as co-occurrences were found between males and females (Cottrant et al. 2023). Additionally, Walker Bay-tagged individuals displayed a pattern of returning to that same zone seasonally, which could suggest philopatric behaviour, which was also suggested by mark-recapture studies (Wagstaff 2023; Mann et al. 2024). Indeed, philopatry has been found in another triakid, the leopard shark *Triakis semifasciata* (Lewallen et al. 2007), thus this behaviour might also occur in *T. megalopterus*. Aggregation in the De Hoop area could be due to preferred food sources, especially for juveniles, as found previously for the smooth hammerhead shark *Sphyrna zygaena* (Albano et al. 2023). Our results showed that, regardless of the tagging area, individuals exhibited strong resident behaviour along with occasional long-distance movement. However, no significant influence of sex or maturity was found, which could indicate that either two genetically different populations occur but show similar temporal patterns, or that the previous geographic limit between the two population is inaccurate, suggesting that the sharks tagged in Walker Bay and De Hoop were from the same population.

The minimum distance travelled in the current study is greater than previously found with mark-recapture (Mann et al. 2024), which highlights the importance of additional information provided by acoustic telemetry. Even so, the limited scale of movement described by frequent detections of the tagged *T. megalopterus* in this study was consistent with mark-recapture findings, with movements linking De Hoop and False Bay. Furthermore, the distance travelled was found to be influenced solely by size, with no significant influence of sex or life stage, yet mark-recapture found the life stage to be a significant influence (Mann et al. 2024). This difference in findings might be explained by the lower sample size of acoustically tagged sharks, or, because telemetry reveals finer-scale movements, it could also mean that there is no clear ontogenetic shift in movements between adults and juveniles, but rather that individuals venture farther from their core site or that they expand their home range as they grow.

Detections were not higher in MPAs than in exploited areas, suggesting that the current placement of protected areas may not adequately protect *T. megalopterus* distributed along the Western Cape coast. This was likewise evidenced by network analysis that revealed the most-used areas fell outside MPAs (Cottrant et al. 2023), and spatial modelling found only a small proportion of the species' southern African distribution to be protected (Faure-Beaulieu et al. 2023). Considering a sparse receiver array, individuals might use MPAs more than what is shown by our data or use zones outside of MPAs. This is supported by a previous study using baited remote underwater videos (BRUVs) in the De Hoop area that found a significantly higher abundance of shark species (including *T. megalopterus*) inside the De Hoop MPA when compared with outside (Albano et al. 2021). Thus, to draw a conclusion on the efficiency of MPAs, more receivers would be needed, preferentially by setting multiple lines of receivers perpendicular to the coast, to identify individual entry to specific areas along the coastline, or as a grid inside existing MPAs, to assess the relative importance of specific areas. Together, these results (Albano et al. 2023; Cottrant et al. 2023) suggest that shark species would benefit from an extension of the De Hoop MPA. Furthermore, BRUVs have proven to be efficient to assess the use of an MPA by shark species, and could be used in zones of interest along the coast to highlight potential new zones of importance and in need of protection, not only for *T. megalopterus* but also for other endemic and endangered species.

Our results showed that *T. megalopterus* individuals spent a large proportion of time in their original tagging area, but also exhibited long-distance movements. The results suggest that this species aggregates in key areas, such as Walker Bay possibly for mating purposes, and De Hoop for feeding, thus indicating other zones along the coastline that could offer opportunities for increased spatial management. Moreover, there was some evidence of philopatry, but further sampling will be needed to confirm this. We speculate that the sparse setting of the South African receiver array and the specific locations of receivers are not optimal for detecting this species, which caused the low roaming and detection indices reported here. Therefore, to better understand this species' ecology, more receivers should be set in important zones shown to be extensively used by the tagged individuals, especially De Hoop and Walker Bay, to detect entry and exit from those areas and to provide more-detailed information on space use (e.g. Walker Bay has only four active receivers). More receivers are also required in shallower areas that are missed by the current setting. This study also highlights that fine-scale movement assessments through acoustic telemetry could give different results than mark-recapture study (i.e. Mann et al. 2024) or analysis of population genetics (i.e. Soekoe 2016). No factor assessed in this study was found to significantly influence the roaming behaviour of *T. megalopterus*; therefore, sampling of environmental conditions could be useful to determine whether the extent of roaming is due to individual behaviour or driven by key environmental variables.

Acknowledgements — The Acoustic Tracking Array Platform (ATAP) hosted by the National Research Foundation – South African Institute for Aquatic Biodiversity (NRF-SAIAB), the Ocean Tracking Network (OTN) headquartered at Dalhousie University, Canada, the Department of Science and Innovation-Shallow Marine and Coastal Research Infrastructure (DSI-SMCRI) programme and the National Research Foundation – South African Environmental Observation Network Elwandle Node (NRF-SAEON Elwandle Node) are thanked for providing acoustic telemetry hardware that facilitated data collection for this study. Furthermore, the Save Our Seas Foundation (SOSF) and the African Coelacanth Ecosystem Programme (ACEP) are acknowledged for funding to maintain the national ATAP. Funding for tagging and tracking of *T. megalopterus* in the De Hoop area was supported by the Shark Conservation Fund and OTN (grant to NH). For the Walker Bay region, 14 shark tags were obtained through a grant from ATAP and SOSF.

ORCID

Patricia Albano: https://orcid.org/0000-0002-2257-5441
Emy Cottrant: https://orcid.org/0000-0003-4449-0120
Paul Cowley: https://orcid.org/0000-0003-1246-4390
Natalia Drobniewska: https://orcid.org/0009-0003-4979-9917
Chantel Elston: https://orcid.org/0000-0002-5772-0098
Neil Hammerschlag: https://orcid.org/0000-0001-9002-9082
Meaghen McCord: https://orcid.org/0000-0001-7219-9176
Jessica Morisson: https://orcid.org/0009-0008-0082-9579
Taryn Murray: https://orcid.org/0000-0003-2694-7588
Timothy Guy Paulet: https://orcid.org/0000-0002-7722-0322
Les Underhill: https://orcid.org/0000-0002-8758-1527

References

Albano PS, Fallows C, Fallows M, Schuitema O, Bernard ATF, Sedgwick O, Hammerschlag N. 2021. Successful parks for sharks: no-take marine reserve provides conservation benefits to endemic and threatened sharks off South Africa. *Biological Conservation* 261: article 109302.

Albano PS, Fallows C, Fallows M, Williams LH, Murray T, Sedgwick O, Hammerschlag N. 2023. Acoustic tracking of a threatened juvenile shark species, the smooth hammerhead (*Sphyrna zygaena*), reveals vulnerability to exploitation at the boundary of a marine reserve. *Frontiers in Marine Science* 10: article 1082049.

Baremore IE, Graham RT, Burgess GH, Castellanos DW. 2021. Movement and residency of Caribbean reef sharks at a remote atoll in Belize, Central America. *Royal Society Open Science* 8: article 201036.

Bass AJ, D'Aubrey JD, Kistnasamy N. 1975. Sharks of the east coast of southern Africa. III. The families Carcharhinidae (excluding

Mustelus and *Carcharhinus*) and Sphyrnidae. *Investigational Report Oceanographic Research Institute* 38: 1–100.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.

Best LN, Attwood CG, da Silva C, Lamberth SJ. 2013. Chondrichthyan occurrence and abundance trends in False Bay, South Africa, spanning a century of catch and survey records. *African Zoology* 48: 201–227.

Booth AJ, Foulis AJ, Smale MJ. 2011. Age validation, growth, mortality, and demographic modeling of spotted gully shark (*Triakis megalopterus*) from the southeast coast of South Africa. *Fishery Bulletin* 109: 101–112.

Compagno LJV. 2005. Book review: *Coastal fishes of southern Africa*. *African Journal of Marine Science* 27: 343.

Cooke SJ, Schramm HL. 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. *Fisheries Management and Ecology* 14: 73–79.

Cottrant E, Drobniewska NJ, Johnson TL, Underhill LG, Murray TS, Hammerschlag N et al. 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: 273–283.

Daly-Engel TS, Seraphin KD, Holland KN, Coffey JP, Nance HA, Toonen RJ, Bowen BW. 2012. Global phylogeography with mixed-marker analysis reveals male-mediated dispersal in the Endangered scalloped hammerhead shark (*Sphyrna lewini*). *PLoS One* 7: e29986.

da Silva C, Attwood CG, Wintner SP, Wilke CG, Winker H, Smale MJ, Kerwath SE. 2021. Life history of *Mustelus mustelus* in the Langebaan Lagoon Marine Protected Area. *Marine and Freshwater Research* 72: 1142–1159.

da Silva C, Lamberth S, Kerwath S. 2023. Research prioritisation to manage sharks and rays in South African fisheries. In: IOTC Secretariat, *Report of the 19th Session of the IOTC Working Party on Ecosystems and Bycatch.* IOTC-2023-WPEB19-10. IOTC: La Saline-les-Bains, Reunion, France.

DFFE (Department of Forestry, Fisheries and the Environment). 2022. South Africa's second national plan of action for the conservation and management of sharks. Cape Town, South Africa: DFFE.

Dicken ML, Smale MJ, Booth AJ. 2012. Long-term catch and effort trends in Eastern Cape Angling Week competitions. *African Journal of Marine Science* 34: 259–268.

Dulvy NK, Pacoureau N, Matsushiba JH, Yan HF, van der Wright WJ, Rigby CL et al. 2024. Ecological erosion and expanding extinction risk of sharks and rays. *Science* 386: eadn1477.

Dunlop SW, Mann BQ. 2014. ORI Tagging Project: summary of tag and recapture data for spotted gully sharks *Triakis megalopterus* caught along the southern African coastline from January 1984 to December 2013. ORI Data Report 2014-3. Durban, South Africa: Oceanographic Research Institute.

Ebert DA, Dando M, Fowler S. 2021. *Sharks of the world: a complete guide*. Princeton, New Jersey: Princeton University Press.

Economakis AE, Lobel PS. 1998. Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. *Environmental Biology of Fishes* 51: 129–139.

Faure-Beaulieu N, Lombard AT, Olbers J, Goodall V, da Silva C, Daly R et al. 2023. A systematic conservation plan identifying critical areas for improved chondrichthyan protection in South Africa. *Biological Conservation* 284: article 110163.

Goosen AJJ. 1997. The reproduction, age and growth of the spotted gully shark, *Triakis megalopterus*, off the Eastern Cape coast. MSc thesis, University of Port Elizabeth, South Africa.

Hammerschlag N, Gutowsky LFG, Gallagher AJ, Matich P, Cooke SJ. 2017. Diel habitat use patterns of a marine apex predator (tiger shark, *Galeocerdo cuvier*) at a high-use area exposed to dive tourism. *Journal of Experimental Marine Biology and Ecology* 495: 24–34.

Kessel ST, Hussey NE. 2015. Tonic immobility as an anaesthetic for elasmobranchs during surgical implantation procedures. *Canadian Journal of Fisheries and Aquatic Sciences* 72: 1287–1291.

Kiser H, Skufca K, Bemis KE, Baeza JA. 2024. Comparative analysis of the mitochondrial genomes of smoothhound sharks provide insight into the phylogenetic relationships within the family Triakidae. *Gene Reports* 36: article 101957.

Lewallen EA, Anderson TW, Bohonak AJ. 2007. Genetic structure of leopard shark (*Triakis semifasciata*) populations in California waters. *Marine Biology* 152: 599–609.

López JA, Ryburn JA, Fedrigo O, Naylor GJP. 2006. Phylogeny of sharks of the family Triakidae (Carcharhiniformes) and its implications for the evolution of carcharhiniform placental viviparity. *Molecular Phylogenetics and Evolution* 40: 50–60.

Maduna SN, Rossouw C, da Silva C, Soekoe M, Bester-van der Merwe A. 2017. Specific identification and comparative population genetics of four coastal houndsharks based on novel NGS-mined microsatellites. *Ecology and Evolution* 7: 1462–1486.

Mann BQ, Jordaan GL, Dalton WN, Daly R, Soekoe M, Potts WM, Smale MJ, Swart L. 2024. Movement and growth of the spotted gully shark *Triakis megalopterus* (family Triakidae) in South African waters. *African Journal of Marine Science* 46: 109–123.

March D, Palmer M, Alós J, Grau A, Cardona F. 2010. Short-term residence, home range and diel patterns of the painted comber *Serranus scriba* in a temperate marine reserve. *Marine Ecology Progress Series* 400: 195–206.

Murchie KJ, Danylchuk AJ, Cooke SJ, O'Toole AC, Shultz A, Haak C et al. 2012. Considerations for tagging and tracking fish in tropical coastal habitats: lessons from bonefish, barracuda, and sharks tagged with acoustic transmitters. In: Adams NS, Beeman JW, Eiler JH (eds), *Telemetry techniques: a user guide for fisheries research*. Nashville, Tennessee: American Fisheries Society, Western Fisheries Research Center.

Murray TS, Elston C, Parkinson MC, Filmalter JD, Cowley PD. 2022. A decade of South Africa's Acoustic Tracking Array Platform: an example of a successful ocean stewardship programme. *Frontiers in Marine Science* 9: article 886554.

Penrith MJ. 1978. An annotated check-list of the inshore fishes of southern Angola. *Cimbebasia* 4: 179–190.

Pollom R, da Silva C, Gledhill K, McCord ME, Winker H. 2020. *Triakis megalopterus*. The IUCN Red List of Threatened Species 2020: e.T39362A124406649.

Pollom RA, Cheok J, Pacoureau N, Gledhill KS, Kyne PM, Ebert DA et al. 2024. Overfishing and climate change elevate extinction risk of endemic sharks and rays in the southwest Indian Ocean hotspot. *PLoS ONE* 19: e0306813.

Posit Team. 2024. *RStudio: integrated development environment for R*. Boston, Massachusetts: Posit Software, PBC.

R Core Team. 2024. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Robusto CC. 1957. The cosine–haversine formula. *The American Mathematical Monthly* 64: 38–40.

Schlaff AM, Heupel MR, Udyawer V, Simpfendorfer CA. 2020. Sex-based differences in movement and space use of the blacktip reef shark, *Carcharhinus melanopterus*. *PLoS ONE* 15: e0231142.

Simpfendorfer CA, Huveneers C, Steckenreuter A, Tattersall K, Hoenner X, Harcourt R, Heupel MR. 2015. Ghosts in the data: false detections in VEMCO pulse position modulation acoustic telemetry monitoring equipment. *Animal Biotelemetry* 3: article 55.

Skowno AL, Poole CJ, Raimondo DC, Sink KJ, van Deventer H, van Niekerk L et al. 2019. National Biodiversity Assessment

2018: the status of South Africa's ecosystems and biodiversity. Synthesis report. Pretoria, South Africa: South African National Biodiversity Institute.

Smale MJ, Goosen AJJ. 1999. Reproduction and feeding of spotted gully shark, *Triakis megalopterus*, off the Eastern Cape, South Africa. *Fishery Bulletin* 97: 987–998.

Soekoe M. 2016. Adaptations in allopatric populations of *Triakis megalopterus* isolated by the Benguela Current: steps towards understanding evolutionary processes affecting regional biodiversity. PhD thesis, Rhodes University, South Africa.

Soekoe M, Smale MJ, Potts WM. 2022. Highly conserved tooth morphology in allopatric elasmobranch populations despite contrasting diets – a case of *Triakis megalopterus* in southern Africa. *Environmental Biology of Fishes* 105: 821–850.

Teske PR, von der Heyden S, McQuaid CD, Barker NP. 2011. A review of marine phylogeography in southern Africa. *South African Journal of Science* 107: 1–11.

van Brummelen GR. 2013. *Heavenly mathematics: the forgotten art of spherical trigonometry*. Princeton, New Jersey: Princeton University Press.

Velasco E, Zubillaga J, Gonzalez M, Cottrant E. 2023. Spotted gully shark *Triakis megalopterus* at Robben Island, Table Bay, South Africa. *Biodiversity Observations* 13: 186–188.

von Bertalanffy. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology* 10: 181–213.

Wagstaff S. 2023. An intensive study of movement and population dynamics of *Triakis megalopterus* in the De Hoop Marine Protected Area, South Africa. MSc thesis, University of Cape Town, South Africa.

Winn JC, Maduna SN, Bester-van der Merwe A. 2024. A comprehensive phylogenomic study unveils evolutionary patterns and challenges in the mitochondrial genomes of Carcharhiniformes: a focus on Triakidae. *Genomics* 116: article 110771.

Wood SN. 2017. *Generalized additive models: an introduction with R* (2nd edn). London: Chapman and Hall/CRC.

Zhang Y, Xu Q, Alós J, Liu H, Xu Q, Yang H. 2015. Short-term fidelity, habitat use and vertical movement behaviour of the black rockfish *Sebastes schlegelii* as determined by acoustic telemetry. *PLoS ONE* 10: e0134381.

Zhang Y, Li Y, Zhang L, Wu Z, Zhu S, Li J, Li X. 2020. Site fidelity, habitat use, and movement patterns of the common carp during its breeding season in the Pearl River as determined by acoustic telemetry. *Water (Basel)* 12: article 2233.

Manuscript submitted May 2025 / revised September 2025 / accepted November 2025