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Distribution and movement of scalloped hammerhead *Sphryna lewini* and smooth hammerhead *Sphyrna zygaena* sharks along the east coast of southern Africa

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Knowledge of population distribution and movement is crucial for the conservation and management of shark species occurring in coastal waters. From 1984 to 2009, 641 scalloped hammerheads *Sphyrna lewini*, 1 342 smooth hammerheads *Sphyrna zygaena* and 1 352 unspecified hammerheads *Sphyrna* spp. were tagged and released along the east coast of South Africa, with recapture rates of 1.9%, 1.5%, and 0.7% respectively. Maximum and average distance moved was 629 km and 147.8 km (95% CI = 33.0–262.7 km) for *S. lewini* and 384 km and 141.8 km (95% CI = 99.1–184.5 km) for *S. Zygaena* respectively. The majority of sharks (68% *S. lewini*, 74.1% *S. zygaena* and 33.5% *Spyrna* spp.) were tagged in the Transkei region, with the largest number tagged in Port St Johns. Across regions, most tagged sharks were >50–100 cm precaudal length (PCL), except in Transkei where more sharks >100–150 cm PCL were tagged. In the Western Cape, Southern Cape and Eastern Cape, few sharks were tagged during the autumn/winter months, whereas in KwaZulu-Natal and Transkei sharks were tagged throughout the year. Large-scale directional movements observed may have been migrations in response to seasonal sea surface temperature changes. We identify coastal locations in Transkei that are of importance to juvenile and subadult hammerhead populations year-round.

Keywords: hammerhead sharks, migration, seasonality, tag recapture

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Introduction

Understanding the spatial and temporal occurrence of vulnerable and endangered shark species in coastal waters is essential for effective population conservation and management (Kohler and Turner 2001, Knipp et al. 2010, Speed et al. 2010). Delineating key aggregation sites, core activity areas and nursery habitat, and identifying seasonal movements, are important for defining habitat use and understanding the potential effects of coastal anthropogenic activities. Long-term tag-recapture datasets involving the species and area of interest provide an effective means through which population-level data can be obtained (Kohler and Turner 2001).

The scalloped hammerhead *Sphyrna lewini* (Griffith and Smith 1834), and smooth hammerhead *Sphyrna zygaena* (Linnaeus 1785) are large coastal and semi-oceanic pelagic sharks found in warm temperate and tropical waters worldwide, with *S. zygaena* occurring in more temperate waters (Compagno 1984). *Sphyrna lewini* is designated as Endangered by the IUCN Red List (Baum et al. 2007). In South Africa, catch rates of juvenile and adult *S. lewini* in protective gillnets off the coast of KwaZulu-Natal (KZN) declined by 64% between 1978 and 2003 (Dudley and Simpfendorfer 2006). In addition, newborn *S. lewini* were the most abundant elasmobranch bycatch taken by the Tugela Banks prawn fishery off KZN (Fennessy 1994). The mortality rate for *S. lewini* in this fishery was estimated to be 98% and a declining catch of newborn *S. lewini* was documented between 1989 and 1992 (Fennessy 1994). *Sphyrna lewini* is also taken as bycatch and targeted by commercial, recreational and artisanal fisheries in South Africa (de Bruyn et al. 2005) and neighbouring Mozambique (Sousa et al. 1997), as well as by illegally operating longline vessels along the western Indian Ocean coastline (IOTC 2005). Considering the Tugela Banks are thought to constitute a core nursery area for *S. lewini* in South Africa, coupled with low intrinsic rate of population growth and productivity for this species when compared with other sharks (Smith et al. 1998, Cortés 2002), regional species-specific management plans are required.

There are few data available regarding the biology and ecology of *S. zygaena*, particularly off southern Africa (Smale 1991). This species is currently listed as Vulnerable by the IUCN Red List (Casper et al. 2005) and, similar to

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S. lewini, is reportedly caught with a variety of fishing gear both as bycatch and as a target species (Compagno 1984). Found throughout much of the same range, *S. lewini* and *S. zygaena* have often been grouped together in catch records, making it difficult to obtain data on the two individual species (de Bruyn et al. 2005). As such, *Sphyrna* spp. grouped together in competition shore-angling catches decreased considerably within Transkei from 1977 to 2000 (Pradervand 2004).

The aims of this paper were to investigate the size range and spatial and temporal distribution of *S. lewini* and *S. zygaena* in coastal waters off the east coast of South Africa using a long-term, tag-recapture dataset (1984–2009). An additional aim was to examine coastal movement patterns to identify potential seasonal migrations/movements.

Material and methods

Study area

Tagging of target species was undertaken between the border of Mozambique-South Africa and Cape Point, South Africa, a 2 085 km stretch of coastline (Figure 1). The coastline was divided into five main regions according to Hussey et al. (2009), which form a sea surface temperature (SST) gradient moving south from tropical conditions in KZN to temperate conditions in the Western Cape. To examine the locations of tagged and recaptured animals, the coastline was further divided into 21 coastal sections, each 100 km long, according to Dicken et al. (2007) and Hussey et al. (2009).

Tagging

A voluntary tag-recapture programme was initiated by the Oceanographic Research Institute in 1983 to collect information on the movement and population structure of important linefish species in coastal waters. Throughout the programme, four different tags (A-, B-, C- and D-type) were applied to *Sphyrna* species, the tag-type depending on shark size/mass. Tags consisted of a monofilament vinyl streamer attached to a plastic barb (A- and D-tags) or stainless steel anchor (B-tags) (manufactured by Hallprint, Australia) that were inserted into the dorsal musculature. The majority of tags used were locally manufactured C-tags, which consisted of two interlocking plastic discs clipped together through a small hole in the base of the dorsal fin. These tags, however, were discontinued after 2001 due to resulting fin damage and excessive biofouling (Dicken et al. 2007). Upon first capture or recapture of a shark, programme participants recorded the date, tag code, tagging location and the precaudal length (PCL) of the shark.

Analysis of shark size range

Sphyrna species were divided into four size classes to examine the spatial and temporal size structure of the tagged sharks in the study area: 0–50 cm, >50–100 cm, >100–150 cm, and >150 cm. In certain instances, the total or fork length (TL and FL respectively) were recorded. For *S. lewini*, these were converted to PCL according to de Bruyn at al. (2005) and for *S. zygaena*, PCL was calculated using the conversion PCL = 75.5% of TL (77.2 ± 1.2) within the range 58–305 cm (Bass et al. 1975). Length of most recaptures was not recorded, because they were often caught by uninformed members of the public, thus limited sample size precluded growth calculations. Hereafter, all length measurements are given as PCL unless otherwise stated.

Analysis of spatial and temporal movement

From the reported recaptures we determined the number of days at liberty, minimum rate of movement between the tag-and-recapture location, and minimum displacement distance. Based on the minimum displacement distance, recaptured sharks were 'binned' into categories of 1–100 km, 101–200 km and >200 km. Recaptured sharks were classified as undertaking either northerly, southerly or no apparent movement. To examine spatial and seasonal movements, the displacements of sharks at liberty for ≤365 days were plotted by month and tag/recapture location, where tag/recapture location is the distance (km) from Kosi Bay at the northern border of the study area. As a result, the slope of the displacement line indicates the minimum rate of movement (km day^{-1}). Sharks at liberty for >365 days were excluded from the analysis because they could have undertaken multiple seasonal migrations.

Results

Scalloped hammerhead Sphyrna lewini

Spatial, temporal and size distribution

A total of 641 *S. lewini* was tagged and released between January 1984 and December 2009, of which 637 had length data at the time of initial capture (Figure 2). The mean (±SE) number of *S. lewini* tagged each year was 24.7 ± 4.3 (95% CI = 15.7–33.6) with a maximum of 103 sharks (16.1%) tagged in 1988 (Figure 3). The majority of *S. lewini* were tagged in the Transkei (Trans) region (436 or 68.0%), followed by 145 (22.6%) in KwaZulu-Natal (KZN), 28 (4.4%) in Eastern Cape (EC), 22 (3.4%) in Western Cape (WC) and 10 (1.6%) in Southern Cape (SC). The majority of *S. lewini* tagged were captured and released at only two locations within Trans: 194 or 30.3% of sharks were tagged at Port St Johns/Mzimvubu River and 134 or 20.9% were tagged 44 km north at Lupatana River. The numbers of *S. lewini* tagged by coastal section and geographical region are presented in Figure 4.

In terms of seasonal distribution, most *S. lewini* were captured and tagged in December (17.6%), whereas the smallest number tagged was in August (3.9%). In all regions, particularly south of Trans, a larger proportion was tagged in the spring and summer (October–March) than autumn and winter (April–September). This seasonal distribution, however, was less obvious in Trans where the numbers of *S. lewini* tagged each month were more evenly distributed throughout the seasons (Figure 1).

Most sharks tagged were >50 cm and ≤150 cm (>50–100 cm [46.5%], >100–150 cm [50%], with few newborns 0–50 cm [3.0%] and large >150 cm [0.6%]) sharks encountered. In all regions, there were more small (≤100 cm) than medium and large (>100 cm) *S.lewini* tagged, except in Trans where a larger proportion of sharks >100 cm were tagged and released (Figure 1).

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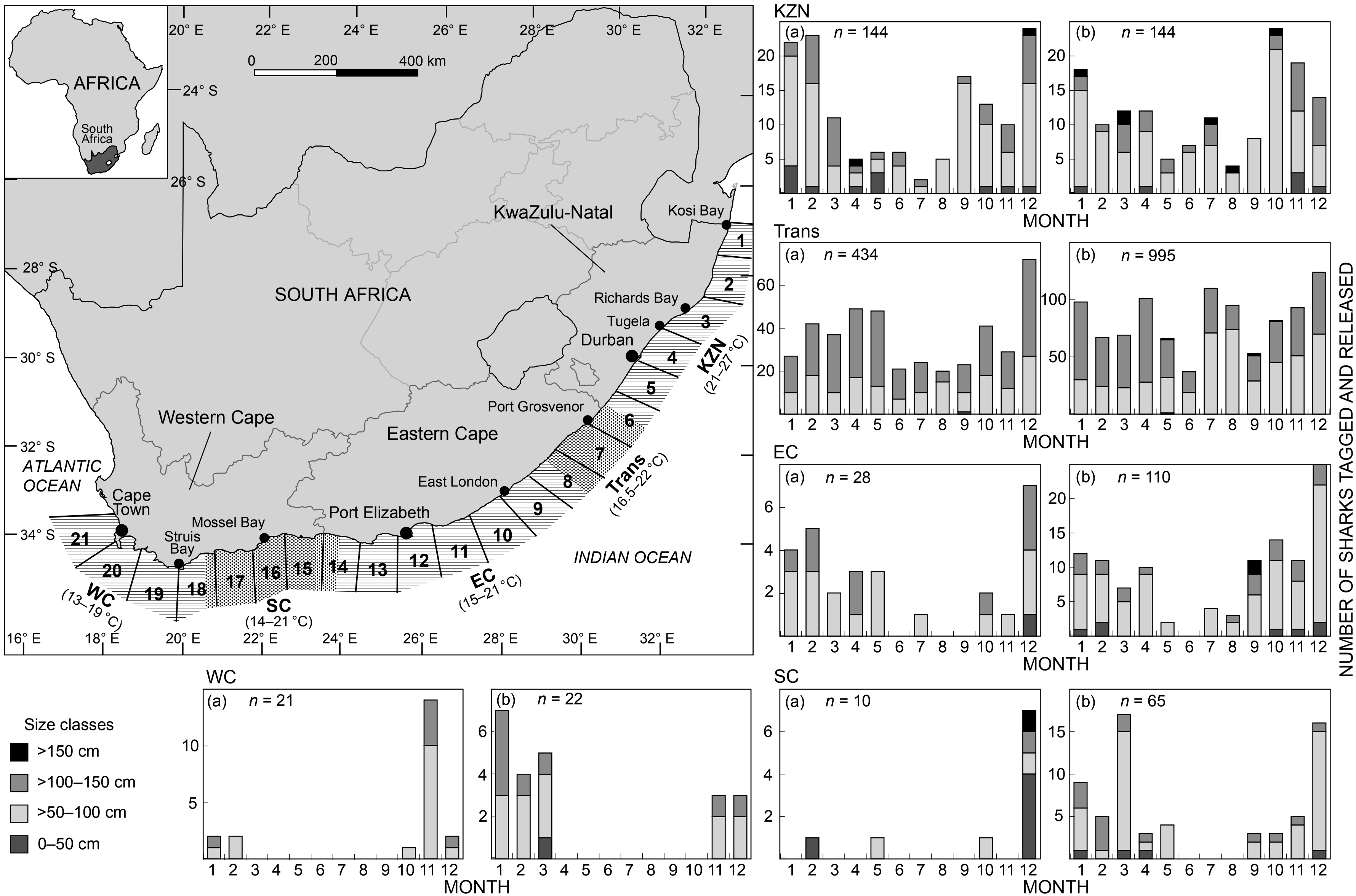

Figure 1: Map of study area in South Africa with the three geopolitical provinces (KwaZulu-Natal/KZN, Eastern Cape/EC, Western Cape/WC), five geographic regions (KZN, Transkei/Trans, EC, Southern Cape/SC, and WC), and 21 coastal sections each 100 km long. Temperature ranges for each region are presented according to van der Elst (1981), Bolton and Stegenga (1987) and Beckley and van Ballegooyen (1992), as in Hussey et al. (2009). Bar graphs show the number of (a) *S. lewini* and (b) *S. zygaena* tagged each month in each of the five geographic regions. Data are broken into four size classes (0–50 cm, >50–100 cm, >100–150 cm, >150 cm). Autumn/winter extends from April to September and spring/summer from October to March

Spatial and temporal analysis

Of the 641 *S. lewini* tagged and released, 12 (1.9%) were recaptured during the 25-year study period. The average distance moved (±SE) was 147.8 ± 52.2 km (95% CI = 33.0–262.7) and the average time at liberty was 224.6 ± 77.1 days (95% CI = 54.8–394.4). Grouped into displacement categories, two of those recaptured moved zero kilometres after one and two days at liberty, four moved 1–100 km from 29 to 832 days, two moved 100–200 km from 206 to 451 days and four moved >200 km from 24 to 550 days. The greatest minimum rate of movement was by a shark of 107 cm tagged in April in the Cintsa River area and recaptured 51 days later after moving 629 km north to Richards Bay at a speed of 12.3 km day^{-1}. Following release, the same shark was recaptured again 550 days later in December at Port St Johns, 421 km south of where it was first recaptured (Figure 5a).

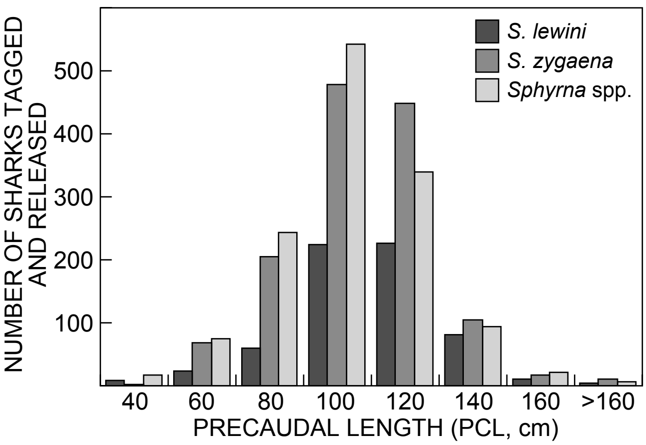

Figure 2: Precaudal length frequency distribution for *S. lewini*, *S. zygaena* and *Sphyrna* spp. tagged throughout the study area

Two of the 12 sharks recaptured were at liberty for over 365 days. Of these, one was recaptured after 832 days at liberty, having moved 42 km from Lupatana River to Agate Terrace, and the other was recaptured after 451 days, having moved 155 km from the Durban piers to TO Strand. Movements of the remaining 10 occurred within coastal sections 3–9 (Figure 5a). Of these, two sharks were recaptured at their initial tagging location (Lupatana River and Margate/Lucien Point) after one and two days at liberty respectively. Two *S. lewini* undertook southward movements: one was recaptured 15 km south of its tagging location (from Stibell's Rocks to Mzimkulu River) following a one month at liberty period in the summer, and the other was by a shark released in autumn and recaptured 421 km south (Richards Bay to Port St Johns) in the spring of the following year. The six remaining sharks undertook northward movements after being recaptured and released for the first time. One shark was displaced 6 km north (from Lupatana River to Port Grosvenor) over 123 days through autumn and winter, three sharks were tagged in spring/summer and were recaptured farther north in the subsequent autumn/winter season, one was tagged in the Cintsa River area during early autumn and was recaptured farther north in Richards Bay during late autumn, and one shark was tagged near Sandy Point in spring and recaptured a month later near Port Edward in summer.

Smooth hammerhead Sphyrna zygaena

Spatial, temporal and size distribution

In total, 1 342 *S. zygaena* were tagged during the 25-year study period, of which 1 336 were measured (PCL) at the

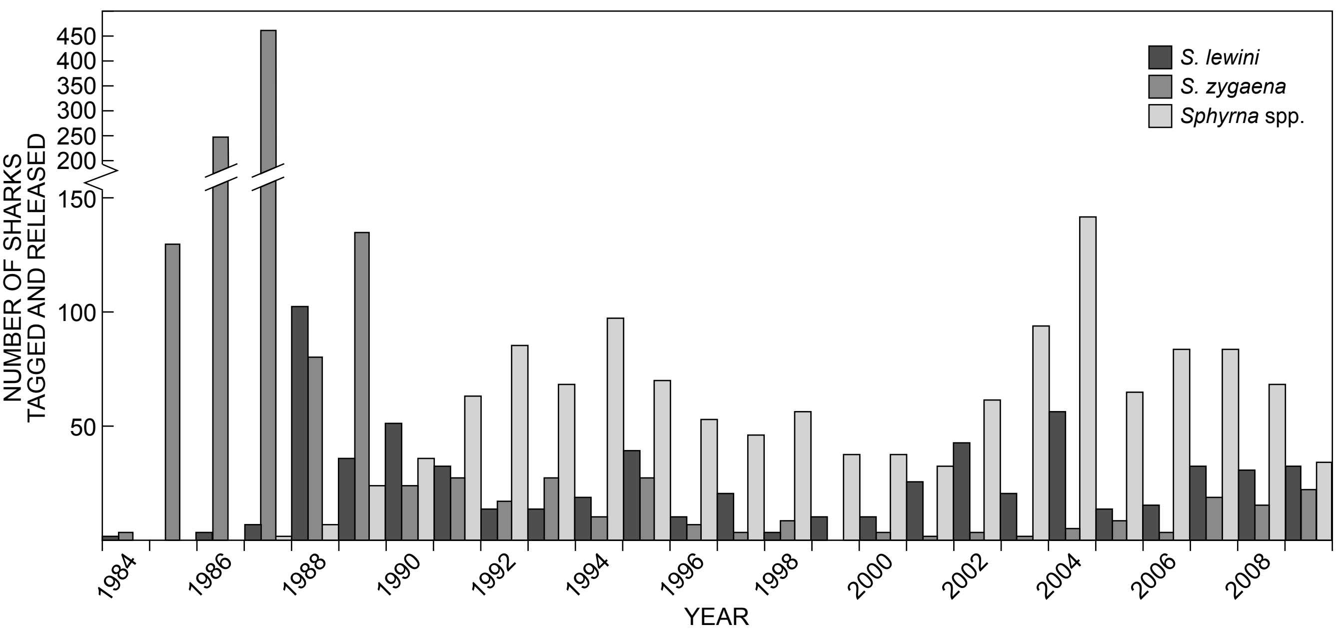

Figure 3: Number of *S. lewini*, *S. zygaena* and unspecified *Sphyrna* spp. tagged and released throughout the study area each year from 1984 to 2009. Note the broken *y*-axis

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time of initial capture (Figure 2). The mean number (±SE) of *S. zygaena* tagged each year was 51.6 ± 20.8 (95% CI = 8.9–94.4) with a maximum of 468 (34.9%) tagged in 1987 (Figure 3). Most *S. zygaena* were tagged in the Trans region (995 or 74.1% of total), followed by 150 (11.2%) in KZN, 110 (8.2%) in EC, 65 (4.8%) in SC and 22 (1.6%) in WC. The majority of *S. zygaena* were tagged at Port St Johns in Trans (857 or 63.9%), followed by Shark Point in Trans (24 or 1.8%) and Richards Bay in KZN (27 or 2.0%).

The greatest number of sharks were tagged in January (13.6%) and the lowest number in June (3.3%). The numbers of sharks tagged were more evenly distributed throughout the months in the northern regions of KZN and Trans, whereas in EC, SC and WC most sharks were tagged in the summer with few animals tagged in the winter.

Most *S. zygaena* tagged were >50 cm and ≤150 cm [>50–100 cm (55.0%), >100–150 cm (42.7%)], with few small [0–50 (1.4%)] and large [>150 cm (0.9%)] sharks encountered. In all regions, the majority of sharks were >50–100 cm PCL, except in Trans where the number of sharks of >50–100 and >100–150 cm PCL were almost equal, similar to the size distribution of *S. lewini* in the Trans region.

Spatial and temporal analysis

Of the 1 342 *S. zygaena* tagged during the study period, 20 (1.5%) were recaptured. The average distance moved (± SE) was 141.8 ± 20.4 km (95% CI = 99.1–184.5) and the average time at liberty was 603.5 ± 192.9 days (95% CI = 199.7–1 007.2). One shark was recaptured at its tagging location after 80 days at liberty. Six sharks moved 1–100 km over 293–3 075 days, nine sharks moved 101–200 km over 45–2 963 days, and four sharks moved >200 km over 52–601 days. The highest speed estimated was a minimum rate of movement of 5.1 km day^{-1}, undertaken by a smooth hammerhead (109 cm) that moved 384 km north from Port St Johns to Mtunzini in 75 days between September and December.

Of the 20 *S. zygaena* recaptured during the study period, 11 were within 365 days at liberty (Figure 5b). All of these sharks were tagged at Port St Johns and movements occurred within coastal sections 3–7. One shark was recaptured at Port St Johns after 80 days at liberty during spring/summer. The only southward movement was a 4 km displacement to Second Beach from August to May (293 days at liberty). The remaining nine sharks moved northward from Port St Johns, though movements were not as well defined as those of *S. lewini* in terms of directional movements related to seasonal SST changes (Figure 5b).

Sphyrna *spp.*

Spatial, temporal and size distribution

Of the 3 335 hammerhead sharks that were tagged, 1 352 (40.5%) were recorded as unspecified hammerheads (*Sphyrna* spp.) and may have either been *S. lewini* or *S. zygaena*, or potentially great hammerheads *S. mokarran*. Of these, 1 338 were measured at the time of initial capture (Figure 2). The mean number of unspecified hammerheads tagged each year (±SE) was 52.0 ± 7.0 (95% CI = 37.7–66.3) with a maximum number of 142 (10.5%) tagged in 2004. The distribution of *Sphyrna* spp. tagged across years was different to that of *S. lewini* and *S. zygaena*, which peaked in the mid- to late 1980s (Figure 3). Most *Sphyrna* spp. were tagged in the Trans region (453 or 33.5%), followed by SC (379 or 28.0%), KZN (300 or 22.2%), EC (161 or 11.9%) and WC (59 or 4.4%). The largest number of sharks tagged was at Port St Johns in Trans (201 or 14.9%), followed by Victoria Bay in Southern Cape (102 or 7.6%).

The largest number of tags was applied to *Sphyrna* spp. in December (256 or 18.9%) and the least number

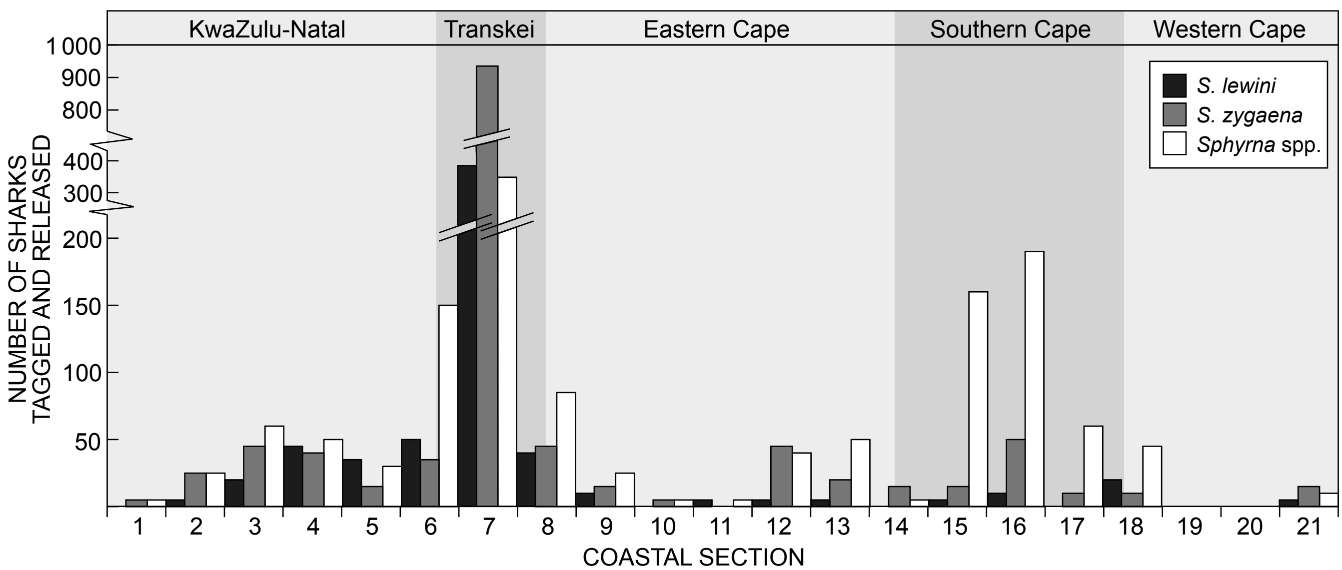

Figure 4: Geographic distribution of *S. lewini*, *S. zygaena* and unspecified *Sphyrna* spp. tagged across the 21 coastal sections from Kosi Bay (section 1) to Cape Point (section 21) in South Africa. Coastal sections are divided into the five geographical regions: KwaZulu-Natal, Transkei, Eastern Cape, Southern Cape and Western Cape. Note the broken *y*-axis

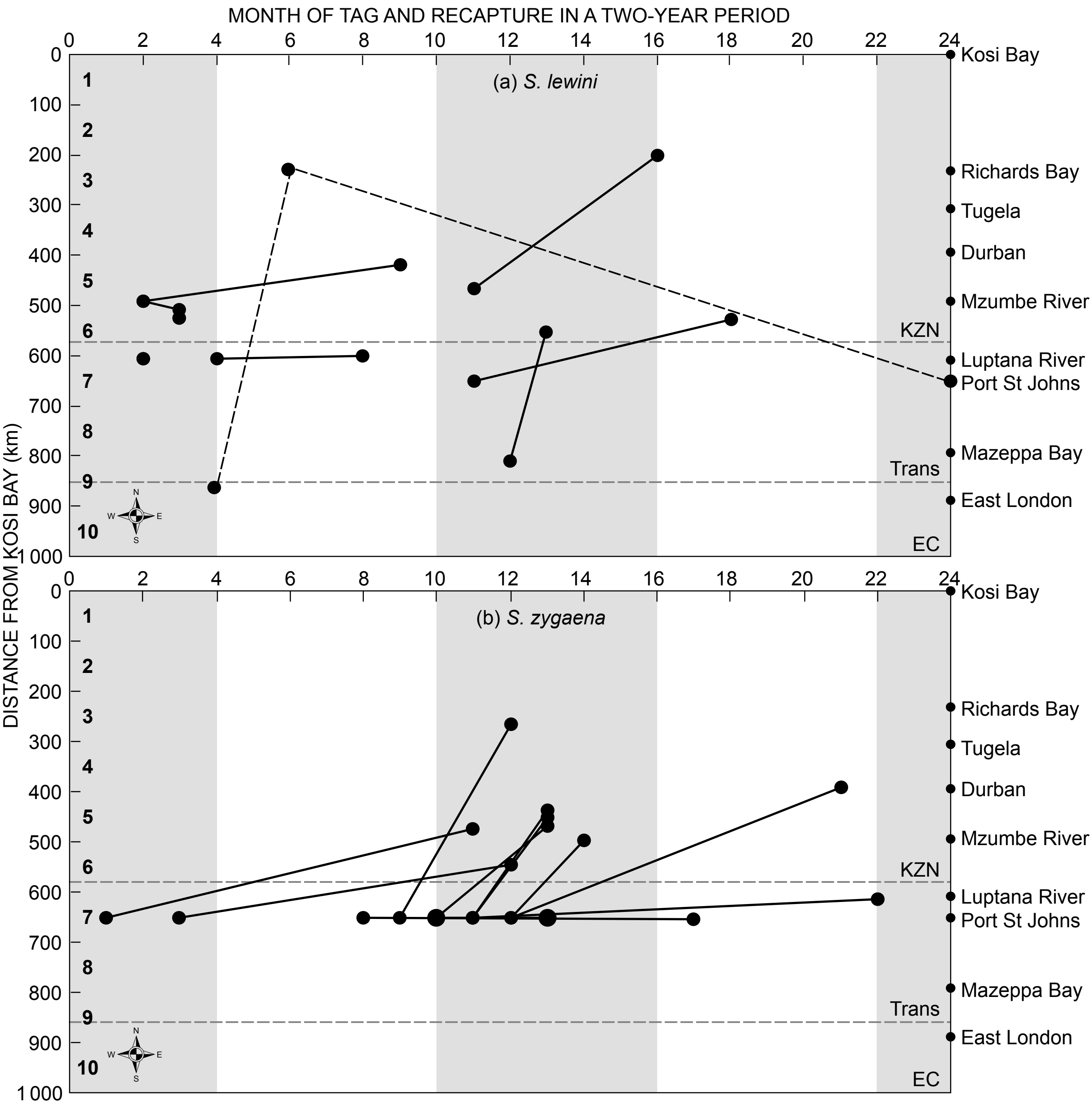

Figure 5: Displacement in location (kilometres from Kosi Bay) by month of tagging and month of recapture for all (a) *S. lewini* and (b) *S. zygaena* tagged and recaptured within a 365-day period during the 25-year study period. The numbers inside the *y*-axis denote the coastal section as defined on the map in Figure 1. The shaded areas represent spring and summer and the non-shaded areas autumn and winter. The angle of the displacement line between tag and recapture months indicates the minimum speed of travel (km day^{-1}). Horizontal lines indicate the borders between the geographical regions: KwaZulu-Natal (KZN), Transkei (Trans) and Eastern Cape (EC). The dashed line in plot (a) represents a *S. lewini* that was recaptured twice. This shark spent more than 365 days at liberty before the second recapture; however, it was still included to demonstrate repeated migrations of a single individual although more than one seasonal movement may have occurred during that time

of tags was applied in June (45 or 3.3%). The tagged *Sphyrna* spp. had a similar size distribution to *S. lewini* and *S. zygaena* (Figure 2) with the majority of sharks in each region being in the >50–100 cm size class, except for Trans which had a greater proportion of sharks >100–150 cm (data not shown). Of the 1 352 *Sphyrna* spp. tagged, 10 (0.7%) were recaptured, all occurring between coastal sections 2–17.

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Discussion

Tag recapture rates

Recapture rates were 1.9%, 1.5% and 0.7% for *S. lewini, S. zygaena* and unspecified *Sphyrna* spp. respectively. There are no comparable tag-recapture studies in South Africa for these species but there are from elsewhere. Recapture rates of *S. lewini* from eight studies reviewed by Kohler and Turner (2001) ranged between 0 and 18.5% (mean 4.0%, median 1.6%), and the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program in the Atlantic Ocean reported a recapture rate of 1.6% for this species (Kohler et al. 1998). Recapture rates of *S. zygaena* from four reviewed studies (Kohler and Turner 2001) ranged between 0 and 3.2% (mean 0.8%, median 0%) and was estimated to be 3.6% along the Atlantic coast by NMFS (Kohler et al. 1998).

Various factors may affect the recapture rates of hammerhead sharks, but movement and migration linked to life-stage is likely the most important. The vast majority of sharks tagged were <150 cm PCL and were therefore neonate, juvenile and/or subadult animals (Compagno 1984). Juvenile *S. lewini* are known to reside in nursery habitat for limited periods of time (Duncan and Holland 2006) and large *S. lewini* undertake ontogenetic movements to offshore waters with females reportedly moving earlier than males (Klimley 1987, Hussey et al. in press). Similarly, juvenile *S. zygaena* remain in coastal nursery habitats with adults found on deep reefs at the edge of the continental shelf (Smale 1991). Recapture rates may therefore be reduced because hammerhead sharks do not remain in coastal waters for prolonged periods of time with mature adults only moving inshore for reproductive purposes (Smale 1991, de Bruyn et al. 2005).

In addition, the low recapture rates of hammerhead sharks may be due to high mortality rates within the study region. Catches of *S. lewini* in beach protection nets are declining in KZN (Dudley and Simpfendorfer 2006) and there is a high mortality rate for neonate/juvenile *S. lewini* caught in the Tugela prawn fishery (Fennessy 1994). Furthermore, hammerhead sharks are known to be susceptible to capture and handling (Compagno 1984) and consequently field tagging by recreational anglers may have associated high mortality rates (Skomal 2007, McLoughlin and Eliason 2008).

Tag shedding may also affect recapture rates, and wounds resulting from tagging may contribute to mortality. C-type tags made up 54.3% and 87.9% of those used for *S. lewini* and *S. zygaena* respectively, but they were discontinued after 2001 due to fin damage and excessive biofouling (Dicken et al. 2007). However, within the same tagging programme and using the same tag types, dusky sharks *Carcharhinus obscurus* and raggedtooth sharks *Carcharias tauras* had higher recapture rates of 6.7% (*n* = 9 716) and 8.7% (*n* = 3 476) respectively (Dicken et al. 2007, Hussey et al. 2009), suggesting that tag retention and tagging-induced mortality are not major factors affecting recapture rates, although post-release survivorship may differ for *Sphyrna* spp.

Differences in fishing effort and recapture reporting across the study area could also affect recapture rates, as well as the absence of effort recorded north of the Mozambique–South Africa border where sharks may migrate beyond. Accepting possible bias as a result of the distribution of fishing effort, however, peak numbers of *S. lewini* and *S. zygaena* were tagged in the Transkei, while within the same tagging programme, dusky sharks were predominantly tagged in KZN (Hussey et al. 2009) and raggedtooth sharks were tagged mostly in the Eastern Cape (Dicken et al. 2007). Programme participants tagged all species caught and were distributed along the coast within the study area, indicating that tagging effort was not concentrated in the Transkei and actual species distributions are reflected in the numbers tagged. However, more localised bias may exist at popular fishing spots, particularly due to the beach-driving ban imposed on recreational vehicles in 2001, with further restrictions made in 2004 (Celliers et al. 2004) which made some fishing spots less accessible.

Spatial, temporal and size distribution

The seasonal tagging distribution of *S. lewini* was comparable to the catch rates of *S. lewini* in beach protection nets along the KZN coast, with the largest number of sharks caught and tagged during summer and the lowest in winter (de Bruyn et al. 2005). As beach protection nets are fixed installations and remain in the water over an annual cycle (with the exception of the period of annual sardine run which typically takes place in June and July; Dudley and Cliff 2010), these data are standardised and suggest that the observed seasonal tagging distributions accurately reflect seasonal animal abundance and are not a result of differences in seasonal fishing effort. This seasonal pattern was evident for both *S. lewini* and *S. zygaena* in all regions except for the Transkei where the numbers of sharks tagged on a monthly basis were more similar throughout the year. This may indicate that a large number of both *S. lewini* and *S. zygaena* reside in the Transkei throughout the winter, particularly in the Port St Johns region where the majority of sharks were tagged. One *S. lewini* moved only 6 km northward between April and August in the Lupatana River area of the Transkei, indicating that it likely remained in the region throughout the winter. Sharks were also tagged in KZN throughout the winter, but fewer animals were tagged and seasonality of capture was more defined, in agreement with de Bruyn et al. (2005). In the regions south of Transkei, almost no *S. lewini* or *S. zygaena* were tagged in the winter suggesting that lower SSTs may regulate the movement and residency of sharks at that time. It is important to note, however, that inferences on the seasonal distribution of sharks across regions may be biased by the actual fishing effort undertaken (Kohler and Turner 2001, Hussey et al. 2009).

There was a clear difference in the size distribution of both hammerhead species tagged in the Transkei relative to the other four regions; 61.3% and 49.8% of tagged *S. lewini* and *S. zygaena* respectively were >100–150 cm PCL in this region in contrast to 25.6% for *S. lewini* and 22.0% for *S. zygaena* in all other regions combined. These tagging data suggest that larger individuals of both species (>100–150 cm PCL) are present in the Transkei, particularly in the vicinity of Port St Johns. The comparable size distributions of hammerhead sharks in Port St Johns across years

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(data not shown) suggests that the mouth of the Mzimvubu River forms important coastal habitat for juvenile/subadult *S. lewini* and *S. zygaena* between neonates leaving nursery grounds and larger animals moving offshore. Hussey et al. (in press) reported that ontogenetic stable isotope profiles of male hammerhead sharks indicated animals of a similar size may be residing in the Eastern Cape/Transkei coastal waters for a period of time, in agreement with the tag recapture data. It is unknown whether the tagged *S. lewini* in this study were principally male sharks. We cannot rule out that misidentification of hammerhead shark species, however, may have led to the observed regional size distribution trends, but the recapture of a *S. lewini* in this region (after repeat recaptures and releases by different anglers) would suggest that the trends are real.

In contrast to the seasonal tagging distributions, the annual tagging distribution of *S. lewini* in KZN did not agree with shark catches in KZN protective gillnets from 1984 to 2003 (Dudley and Simpfendorfer 2006). Peak catch rates of *S. lewini* in beach protection nets occurred in 1985 and showed a significant decrease of approximately 64% over time until 2003, whereas the number of tags applied to *S. lewini* in KZN remained stable across years. This could relate to differences in the location of beach protection nets and fishing effort, or differences in fishing effort between years. In contrast, catch rates of *S. zygaena* in KZN gillnets reportedly remained stable from 1984 to 2003 (Dudley and Simpfendorfer 2006) whereas annual tagging rates of *S. zygaena* declined in KZN and all regions after a peak in 1987. This suggests that the numbers of *S. zygaena* off the east coast of South Africa decreased during the study period. However, possible misidentification of a large number of hammerhead sharks at the start of the tag-recapture programme should be considered. Contrary to the peak catch rate of *S. lewini* in beach protection nets in KZN in 1985, very few tags were applied to *S. lewini* in KZN or in any other region until 1988 when there was a sudden peak in the numbers of *S. lewini* tagged (103 tags applied; Figure 3). There was a similar trend for unspecified *Sphyrna* spp., with only one tag applied before 1988. Conversely, large numbers of *S. zygaena* were tagged between 1984 and 1987, with a peak in sharks tagged in 1987 (468 tags applied), after which the number of sharks caught and tagged declined. The general absence of *S. lewini* and unspecified *Sphyrna* spp. tags at the beginning of the study period and large numbers of *S. zygaena* during this time suggests that before 1988 *Sphyrna* spp. may have been grouped as *S. zygaena*. If so, this may have skewed the annual tagging distributions for *S. lewini* and *S. zygaena*.

Transkei was the peak tagging region for both *S. zygaena* (74.1%) and *S. lewini* (68.0%). Among the next most common regions, similar numbers of *S. zygaena* were tagged in KZN (150 or 11.2%) and EC (110 or 8.2%), whereas for *S. lewini*, a much larger proportion were tagged in KZN (145 or 22.6%) than EC (28 or 4.4%). This may highlight the difference in the distributions of these species, because *S. zygaena* have a more temperate distribution (Compagno 1984) with greater number of sharks tagged south of Transkei into cooler waters, while a nursery area for *S. lewini* is thought to exist in KZN (Fennessy 1994). During the study period, 1 342 *S. zygaena* and 641 *S. lewini* were tagged and released, indicating the greater abundance of *S. zygaena* in the study area.

South of Transkei there was an increase in the number of *S. zygaena* tagged from coastal sections 12–16 in the Eastern Cape and Southern Cape respectively (Figure 4), and coastal section 16 contained the second largest number of *S. zygaena* tagged (3.8%), after section 7 (69.8%; including Port St Johns). The large number of unspecified *Sphyrna* species tagged in coastal sections 12–18 and the general lack of *S. lewini* tagged in this region suggest that these unspecified hammerheads were actually *S. zygaena*, potentially making this region of greater importance to the species (Figure 4). Large schools of *S. zygaena* have been observed near Port Elizabeth in the Eastern Cape (Bass et al. 1975, Smale 1991) and the Southern Cape and Eastern Cape have been identified as nursery areas for *S. zygaena* (Smale 1991). Over the study period, a small number of *S. zygaena* <50 cm PCL (the size of newborn animals; Compagno 1984) were tagged between November and February in the Eastern Cape (Figure 1). Smale (1991) recorded neonatal *S. zygaena* with open umbilical scars in that region (coastal sections 12 and 13) between November and January. The overall size distribution of *S. zygaena* tagged in coastal waters of the Eastern Cape was similar to that of Smale (1991). Given that the distribution differences observed here between *S. lewini* and *S. zygaena* were similar to those previously described, suggests that the species were identified correctly in our study.

Spatial and temporal movement

The seasonal differences in both *S. lewini* and *S. zygaena* abundance along the east coast of South Africa suggest they exhibit migratory movements, possibly in association with seasonal changes in SST. Movement of *S. lewini* in response to an influx of cooler water in the Gulf of California was documented by Klimley and Butler (1988). Furthermore, although sample size is small, the majority of *S. lewini* tagged and recaptured demonstrated northward movements, providing further evidence that large directional movements are taking place in response to seasonal temperature changes. The multiple recaptures of a single *S. lewini* that moved northward between April and June at the greatest speed observed may indicate that this animal was tagged at the beginning of, or during, its northward winter migration (Figure 5a). Seasonal, regulated movements/migrations have been reported for dusky shark off southern Africa (Hussey et al. 2009) and for other shark species in the Atlantic Ocean (Castro 1996, Kohler et al. 1998, Pade et al. 2009). *Sphyrna zygaena* inhabit coastal nursery grounds in more temperate waters of the Eastern/Southern Cape region (Smale 1991), and large numbers of small individuals are caught in KZN protective gillnets (Dudley and Simpfendorfer 2006). Northern movements of tag-recaptured *S. zygaena* in our study confirm this movement, but the numbers of recaptures were limited and there were no obvious seasonal patterns. Overall, no movements of hammerhead sharks south of coastal section 9 were reported, so there are no examples of movement for either species in the southern half of the study area.

Although the numbers of *S. lewini* and *S. zygaena* tagged generally decreased moving south from KZN to

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cooler waters, Transkei constituted the core area where the largest numbers of both species of shark were caught. This increased presence in this region concurs with Pradervand (2004) who found that *Sphyrna* spp. were within the top three most common catches (11% by number or 31% by mass) between 1977 and 2000 from competition shore-angling data in the Transkei, but these species did not make up significant portions of the catch in KZN (Pradervand et al. 2007) or the Eastern Cape (Pradervand and Govender 2002) during this period. Consequently, there may be additional factors affecting *Sphyrna* spp. movement and habitat use, aside from SST, which places the Transkei as an important region to these species. The increased abundance of *Sphyrna* spp. in the Transkei, as well as the increased proportion of sharks in the >100–150 cm PCL size class, may relate to the continental shelf which is at its narrowest point in this region along the east coast of South Africa, and the close proximity of the fast-flowing Agulhas Current at Transkei (Lutjeharms 2006). Also, the rocky and deep-water areas along the Transkei coastline (e.g. Lupatana and the Gap, south of Port St Johns) makes fishing for sharks, particularly large ones, more accessible.

In conclusion, the number of *S. zygaena* tagged has declined since the mid-1980s in KZN and across all regions, contrary to Dudley and Simpfendorfer (2006) who reported stable catches of *S. zygaena* in KZN gillnets from 1978 to 2003. Although tagging of *S. lewini* does not appear to have decreased significantly over the study period, this should be viewed with caution as trends may be affected by species misidentification or annual changes in fishing effort. Catches of *S. lewini* in KZN beach nets have shown a significant decline between 1978 and 2003 (Dudley and Simpfendorfer 2006) and the Tugela Banks prawn fishery is known to have had a large impact on the juvenile *S. lewini* population (Fennessy 1994). Also, Pradervand (2004) showed a decreasing trend in catches of *Sphyrna* species (which overall dominated the catches by mass) in the Transkei from 1977 to 2000 based on competitive shore anglers' catches.

Anthropogenic activities such as coastal development, fishing (both commercial and recreational), and bycatch mortality can impact *k*-selected species, and understanding movement patterns as well as identifying key aggregation sites may be crucial for effective regional conservation and management strategies. This is of particular importance for the two species under study, considering that 51.2% of *S. lewini* were tagged at only two sites along the entire study area, Port St Johns (30.3%) and nearby Lupatana River (20.9%), and 63.9% of *S. zygaena* were tagged at Port St Johns alone. The large numbers of sharks tagged in this area suggests that these sites present a competitive advantage for both juvenile and adolescent *Sphyrna* species. In terms of regional shark management plans, it is therefore necessary that these sites be considered for protection as they constitute core coastal habitat for both *S. lewini* and *S. zygaena* populations along the east coast of South Africa. Fortunately, the region between the Lupatana River and the Mkozi River (a distance of approximately 9 km and known as Waterfall Bluff) was proclaimed a no-take zone for shore-angling within the Pondoland Marine Protected Area (MPA) in June 2004 (Mann et al. 2006). Furthermore, the area between the Sikombe River and Mboyti River (~40 km) and seaward to the 1 000 m depth contour (~10 km) is an offshore no-take zone (i.e. no fishing off a vessel) within the Pondoland MPA. These conservation measures should provide some protection to juvenile and adolescent hammerhead sharks while they are temporally resident in this core habitat.

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