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Sharks caught in the KwaZulu-Natal bather protection programme, South Africa. 14. The smooth hammerhead shark *Sphyrna zygaena* (Linnaeus)

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The current study provides long-term catch-rate, biological and feeding data for smooth hammerhead sharks, *Sphyrna zygaena*, caught in South Africa's KwaZulu-Natal bather protection programme. In total, 2 512 *S. zygaena* were caught in net installations between 1978 and 2014, and 72 *S. zygaena* were caught on drumlines between 2007 and 2014. There was no significant log-linear year trend in the net catch rate over time (slope = 0.0054, *t* = 1.808, *p* = 0.07). However, there was a significant temporal increase in mean size of the captured sharks (slope = 0.0012, *t* = 3.502, *p* < 0.001). A quasi-Poisson generalised additive mixed model showed that increasing latitude, winter months, colder sea temperatures and the deployment of drumlines all had a significant positive effect on the catch rate of sharks in nets. The size frequency of the catch was unimodal, with significantly more females caught in the nets and more males on the drumlines. The majority (93.1%) of all sharks caught were immature and measured between 80 and 120 cm precaudal length. Teleosts and cephalopods dominated the sharks' diet in terms of all dietary indices. The prey species consumed indicate that immature *S. zygaena* are feeding primarily within the pelagic zone of shallow coastal habitats.

Keywords: CPUE, drumlines, generalised additive mixed model, length frequency, sex ratio, shark nets, stomach contents

Introduction

Adults of the smooth hammerhead *Sphyrna zygaena* are found worldwide in tropical and warm-temperate coastal and pelagic waters (Compagno 1984; Stevens 1984). In the western Indian Ocean (WIO), they occur from southern Mozambique to South Africa as well as in Indian and Sri Lankan waters (Compagno 1984; Ebert et al. 2013). In South Africa, *S. zygaena* juveniles are found primarily inshore, and adults farther offshore in the temperate waters off the Eastern Cape and Western Cape provinces (Bass et al. 1975; Smale 1991; Diemer et al. 2011; Dicken et al. 2012). The sharks are less common along the KwaZulu-Natal (KZN) coastline, where they are caught primarily in more southerly areas during the winter, when sea temperatures are cooler (Wallet 1973; Bass et al. 1975).

Although caught in a variety of commercial fisheries worldwide (Compagno 1984; Bonfil 1994; Clarke et al. 2006), *S. zygaena* is one of the least studied of all pelagic sharks. There are few data available for any aspects of its movement patterns, habitat use or population dynamics for any part of its distributional range. In an ecological risk assessment of pelagic sharks of the Atlantic Ocean, Cortés et al. (2010) stated that *S. zygaena* is a species for which better biological data are more urgently required to assess its relative risk of exploitation. This species was included

on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), effective from September 2014 (https://cites.org/eng/prog/shark/other_sharks.php), and is currently listed as Vulnerable on the IUCN Red List (Casper et al. 2005).

Hammerhead sharks are often targeted and killed for the trade in shark fins (Abercrombie et al. 2005; Clarke et al. 2006). As a result, they are likely to be heavily exploited in both artisanal and large-scale longline fisheries throughout the WIO (IOTC 2013). In South Africa, *S. zygaena* have historically been caught in a variety of commercial and recreational fisheries, both as a target species as well as bycatch (da Silva et al. 2015). Reported catches total less than 10 tonnes per year; however, these catches are likely underestimated as they do not account for unreported or discarded sharks (da Silva et al. 2015). In 2011, retention of all hammerhead species in South Africa was banned in the pelagic longline fishery, and in 2015 catches were further prohibited in all commercial fisheries except for the 'linefishery' (da Silva et al. 2015). The current commercial linefishery is defined by the use of a simple hook-and-line fishing system (excluding the use of longlines and drumlines), with a limit of 10 hooks per line (DAFF 2014). Despite being released in most fisheries, it is likely that hammerhead sharks will continue to be impacted

due to high levels of post-release mortality (Coelho et al. 2012; Gallagher et al. 2014). Another source of fishing mortality for *S. zygaena* is the KZN bather protection programme, where it is one of the 14 most commonly caught shark species (Dudley and Simpfendorfer 2006).

Little is known about the biology or ecology of *S. zygaena* in South Africa. This article presents an analysis of long-term spatial and temporal trends in the catch and biology of *S. zygaena* caught in the KZN bather protection programme. This information is essential to better understand its abundance, population structure and habitat use, which is necessary for its management. This report is the fourteenth in a series describing the general biology and catch statistics of the shark species commonly caught in this programme.

Materials and methods

Study site and fishing gear
The KZN bather protection programme currently uses shark nets, or a combination of nets and drumlines, at 37 beaches along the KZN coastline (Figure 1). Shark nets were originally installed at Durban in 1952 and at other beaches from the early 1960s. In December 2014, the total length of netting was 22.4 km. The majority of nets are 213.5 m long, 6.3 m deep, and have a stretched mesh of 51 cm. The exceptions are net installations at Durban and two nearby beaches, which are 304.8 m long, 7.6 m deep, and constructed from yellow, rather than black, polyethylene braid. All nets are set parallel to and approximately 300–500 m from the shore in a water depth of 10–14 m. Additional details on the netting operation are given by Cliff and Dudley (1992).

In an effort to reduce the bycatch of harmless sharks and other non-target species, including turtles, rays and cetaceans, there has been a gradual removal of nets and, at some beaches, partial replacement with drumlines (Figure 1; Cliff and Dudley 2011). Each drumline is anchored adjacent to the nets and consists of a single Mustad 4480DT 14/0 J hook (Gjøvik, Norway) suspended 4 m beneath a large float (Dudley et al. 1998; Cliff and Dudley 2011). The hooks are baited with either southern rover *Emmelichthys nitidus* or jacopever species (Scorpaenidae), which are bycatch species in the demersal trawl fishery for hake *Merluccius* spp. The 79 drumlines currently in operation were deployed at a replacement ratio of four drumlines to one net and have resulted in a cumulative net reduction of 4.1 km. Specifics of the drumline deployments are given in Dicken et al. (2016).

Both nets and drumlines are deployed in fixed locations throughout the year and serviced at first light approximately 18 to 20 times a month. Sea surface temperature (SST) was measured with an analogue thermometer, and vertical water clarity estimated using the depth of the net as a guide, from 1981 onwards. The catch and life-history data presented in this study were recorded between 1978 and 2014, as species-specific catch-and-effort data for sharks prior to 1978 are considered unreliable (Cliff and Dudley 1992).

Morphometrics
All shark measurements presented here (unless stated otherwise), including those cited from the literature, are of precaudal length (PCL). Precaudal length was measured (to the nearest mm) as the straight-line distance between perpendiculars to the snout and to the precaudal notch. Measurements were taken in the field as well as from laboratory-dissected sharks. Lengths measured in the field exceeded those measured in the laboratory by a mean of 35.1 mm (SD 40.9). To facilitate comparison with measurements cited in other studies the relationships provided below were calculated using laboratory lengths, which are more accurate than field lengths. Equations are presented for males and females separately only if a significant difference was found between the sexes (ANCOVA, $p < 0.05$).

For total length (TL, mm) as measured from the snout tip to the tip of the upper caudal-fin lobe with the caudal fin in its 'natural' position (visually estimated):

$$TL = 1.258 \times PCL + 72.326 \quad (n = 357; r^2 = 0.91, p < 0.001, \text{range } 540–1\,430 \text{ mm PCL}). \tag{1}$$

For TL where the tail was depressed to lie parallel to the body axis:

$$TL = 1.421 \times PCL - 21.989 \quad (n = 354; r^2 = 0.92, p < 0.001, \text{range } 540–1\,430 \text{ mm PCL}). \tag{2}$$

Upper caudal-lobe length (UCL) was measured as a straight line from the tip of the upper caudal-fin lobe to the precaudal notch. Assuming a linear relationship, the equation relating UCL to PCL is:

$$UCL = 0.384 \times PCL + 14.703 \quad (n = 1\,659; r^2 = 0.80, p < 0.001, \text{range } 481–1\,500 \text{ mm PCL}) \tag{3}$$

The following relationship was found between PCL and fork length (FL, mm):

$$FL = 0.972 \times PCL + 49.765 \quad (n = 1\,697; r^2 = 0.86, p < 0.001, \text{range } 481–1\,700 \text{ mm PCL}). \tag{4}$$

Mouth width (MW) was measured as the straight-line distance between the corners of the mouth. The equation relating MW to PCL is:

$$MW = 0.051 \times PCL + 26.484 \quad (n = 329; r^2 = 0.21, p < 0.001, \text{range } 674–1\,430 \text{ mm PCL}). \tag{5}$$

Girth (GIR) was measured at the third gill slit as:

$$GIR = 0.403 \times PCL - 7.397 \quad (n = 251; r^2 = 0.47, p < 0.001, \text{range } 800–1\,430 \text{ mm PCL}). \tag{6}$$

Females were found to be significantly heavier (*M*, kg) than males in relation to the PCL (ANCOVA, $F = 3309.873$, $p < 0.001$) (Figure 2):

$$\text{Females: } M = 1.0834 \times 10^{-8} \, PCL^{3.005} \quad (n = 894; r^2 = 0.91, p < 0.001, \text{range } 481–1\,430 \text{ mm PCL}) \tag{7}$$

$$\text{Males: } M = 2.1834 \times 10^{-8} \, PCL^{2.9011} \quad (n = 776; r^2 = 0.88, p < 0.001, \text{range } 540–1\,500 \text{ mm PCL}) \tag{8}$$

$$\text{Both sexes combined: } M = 1.4550 \times 10^{-8} \, PCL^{2.9614} \quad (n = 1\,674; r^2 = 0.90, p < 0.001, \text{range } 481–1\,500 \text{ mm PCL}). \tag{9}$$
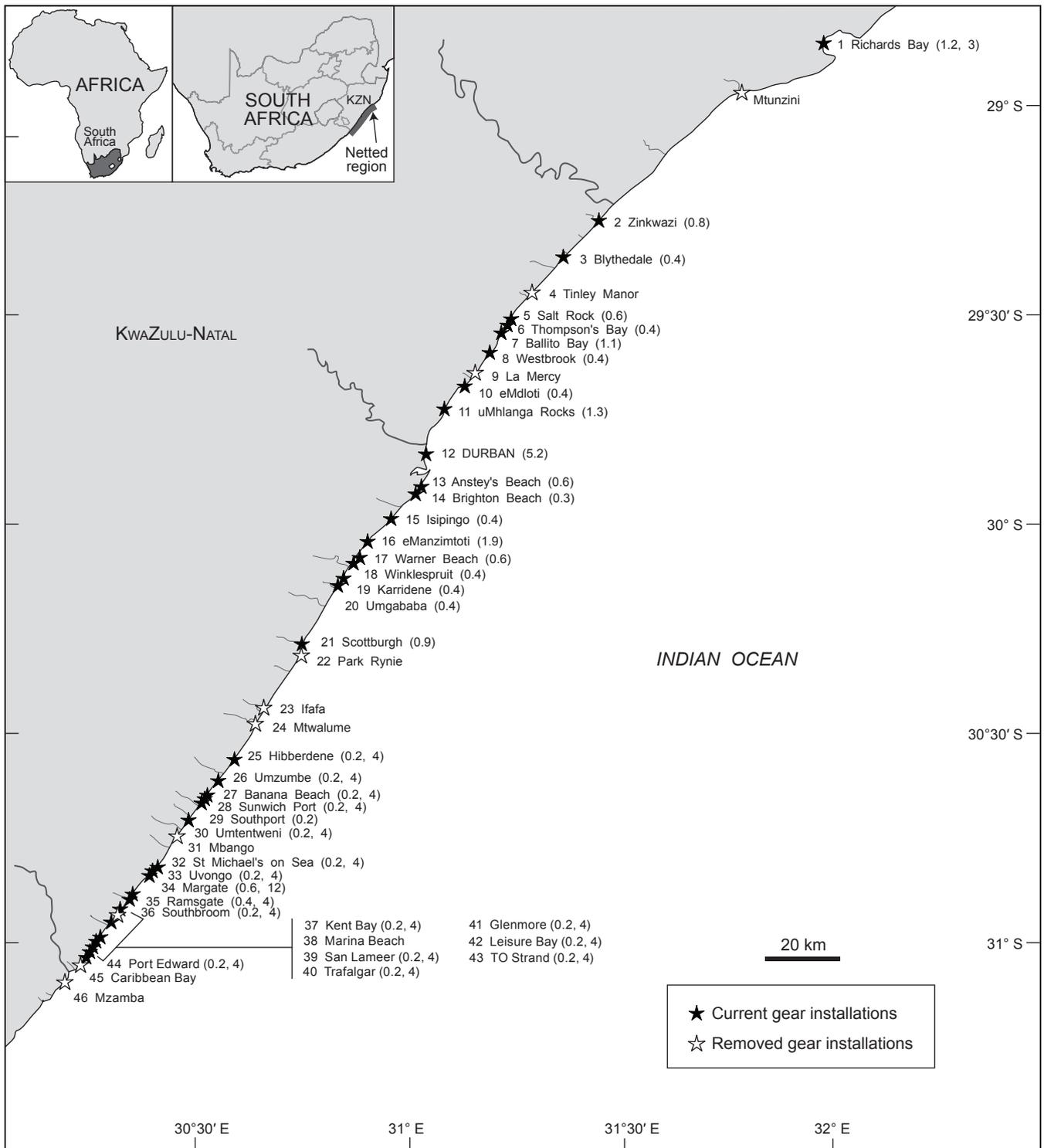
Figure 1: Beaches with bather protection gear on the coast of KwaZulu-Natal, South Africa; numbers in parentheses indicate lengths of the nets (km) and the number of drumlines (when present), in December 2014. White stars indicate installations that were permanently removed during the period of the study (1978–2014). Inset shows the locality of the netted region in relation to southern Africa
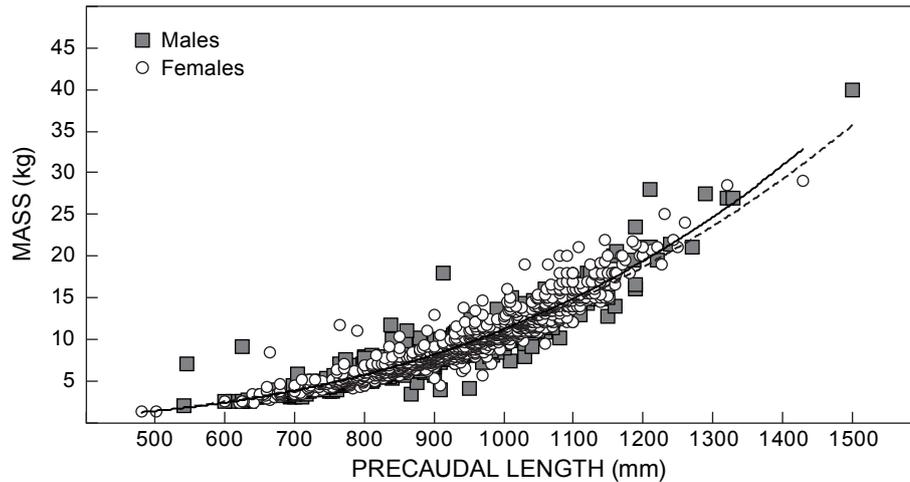
Figure 2: Length–mass relationship of males (dashed line) and females (solid line) of *Sphyrna zygaena* sampled in the study

Females were found to have significantly heavier livers (LM, kg) than males in relation to PCL (ANCOVA, $F = 6.300$, $p = 0.012$):

Females: $LM = 1.2787 \times 10^{-10} PCL^{3.2185}$ ($n = 405$; $r^2 = 0.56$, $p < 0.001$, range 665–1 430 mm PCL)   (10)

Males: $LM = 4.1841 \times 10^{-9} PCL^{2.7015}$ ($n = 383$; $r^2 = 0.46$, $p < 0.001$, range 545–1 500 mm PCL)   (11)

Both sexes combined: $LM = 5.8277 \times 10^{-10} PCL^{2.9941}$ ($n = 788$; $r^2 = 0.52$, $p < 0.001$, range 545–1 500 mm PCL).   (12)

The relationship between heart mass (H, g) and PCL was:

$H = 2.0760 \times 10^{-7} PCL^{2.6679}$ ($n = 538$; $r^2 = 0.72$, $p < 0.001$, range 680–1 430 mm PCL).   (13)

Catch and effort statistical analyses

When analysing relative abundance trends using yearly means of raw catch per unit effort (CPUE), there are several factors that can result in bias (Maunder and Punt 2004; Winker et al. 2014; Ono et al. 2015). These factors commonly include month, area, gear and other fisheries-specific effects, which can be used as covariates in regression models to control for their effect on the resulting abundance index (Campbell 2004; Maunder and Punt 2004). This model-based procedure is known as CPUE standardisation, and is typically seen as a prerequisite for inferring abundance trends from catch and effort data (Maunder and Punt 2004; Maunder et al. 2006). To account for variations in the length of netting used over time and between sites, CPUE was expressed as no. of sharks km-net^{-1} month^{-1}.

Gillnet CPUE was modelled using generalised additive mixed models (GAMMs) (Wood 2006). Beach was included as a random effect term, while month and latitude were modelled as non-linear predictor variables (Su et al. 2008; Winker et al. 2013; Dicken et al. 2016). Treating the variation among beaches as a random effect was important to account for the unbalanced and nested, fixed-station

(beach netting installation) sampling design (Zuur et al. 2009; Dicken et al. 2016). The introduction of drumlines was also considered as a fixed effect in the standardisation models to investigate whether the deployment of drumlines had any effect on gillnet CPUE.

SST (°C) was recorded at each netted beach from 1981 to 2014. To investigate how changes in SST affected shark catches during this period, it was included as a model variable in the form of monthly temperature residuals that were normalised by the mean monthly temperature across the available time-series (1981–2014). Thus, residuals were calculated as the difference between mean monthly SST for a specific year and mean monthly SST for the period 1981–2014. Monthly SST residuals were used as a model variable to avoid collinearity between SST and month. In initial trials, mean water visibility (clarity) was also tested as a potential predictor for *S. zygaena* CPUE; however, this covariate was dropped in the early model-selection phase due to poor model convergence.

During June and July each year, sardines *Sardinops sagax* move along the KZN coastline from the southwest in a phenomenon known as the sardine run (Armstrong et al. 1991; van der Lingen et al. 2010). Although S. *zygaena* are often caught during a similar time-period as the sardines, their spatial and temporal distribution patterns extend beyond those typically associated with the run (Dudley and Cliff 2010). Investigating the relationship between catches of *S. zygaena* and sardines is further complicated by the discretionary removal of fishing gear between June and July to prevent high catches of certain sharks and bycatch species associated with the sardine shoals (Cliff and Dudley 1992; Dudley et al. 2005; Dudley and Cliff 2010). These gear removals vary markedly between years, both in their location and duration. As a result, beach-seine landings or sightings of sardines rarely correspond with a high number of sharks caught in the nets (Dudley and Cliff 2010; van der Lingen et al. 2010). For these reasons, no adjustments to net (or drumline) catch rates were made to account for the sardine run (i.e. exclusion of June and July catches) or incorporated into the model structure.

To investigate a potential relationship between CPUE and *El Niño* and *La Niña* events, anomalous values (i.e. different from the mean) were highlighted from the CPUE time-series. A 3-month running mean was then applied to these anomalies, as per Rouault et al. (2010), to allow for a better comparison with the *Niño*-3.4 Index. The *Niño*-3.4 Index is a commonly used index to define *El Niño* and *La Niña* events. Either event can be said to occur when 5-month running means of SST anomalies in the *Niño*-3.4 region (5° N–5° S, 170°–120° W) are above or below 0.4 °C for six months or more (Bunge and Clarke 2009).

Using a simple linear model to compare the CPUE and *Niño*-3.4 values, the coefficient of determination (r^2) was found to be 0.00, indicating that no relationship existed. Rouault et al. (2010) demonstrated that the relationship between SSTs and *El Niño* events is strongest in the summer. As a result, the CPUE and *Niño*-3.4 values were split into 12 different time-series, one for each month. Simple linear models were then constructed to investigate any monthly relationships. The largest r^2 value generated was −0.04, indicating that the relationship between monthly CPUE values and *El Niño*–Southern Oscillation (ENSO) events were no stronger than for the time-series as a whole. As a result, neither *El Niño* nor *La Niña* events were included as covariates in the GAMMs.

The full GAMM included thin-plate regression splines for year, latitude and monthly temperature residuals (ΔSST) for the period 1981–2014, the categorical covariate drumline, and a cyclic cubic smoothing function for month, such that:

$$CPUE(nets) = e^{\beta_0 + s(year) + s(month) + s(lattitude) + s(\Delta SST) + drumline + \alpha_j}$$

(14)

where β_0 is the intercept term for the fixed effects, $s()$ denotes the smoothing functions, and α_j denotes the random effect for beach j (Zuur et al. 2009; Weltz et al. 2013). For the base-case models, including all covariates (1981–2014), year was fitted using the spline function. In addition, the final models were re-run for the entire time-series 1978–2014, with year treated as either a spline function or as a continuous variable to test for significance of an underlying log-linear trend. Both of these GAMMs excluded ΔSST as a predictor variable, as it was only collected from 1981 onwards. The resulting annual trends therefore represent the predicted CPUE under the historical temperature regime without removing the temperature effect from the abundance index.

The significance of the random-effects structure was supported for all sub-models by Akaike's information criterion (AIC). Sequential F-tests were used to determine the covariates that contributed significantly ($p < 0.05$) to the deviance explained. A quasi-Poisson error model with a log-link function was used to account for the moderate overdispersion in the CPUE data. Effort (length of netting) was treated as an offset term, and thus as a known denominator of the dependent variable catch (counts) (Zuur et al. 2009), to maintain the underlying count nature of the CPUE response. For the standardisation of catch data in this study, CPUE was modelled for a single combined dataset. Modelling components of the dataset separately (e.g. sex) resulted in models that were too complicated for the data available, and thus model overfitting.

Drumline CPUE was recorded as number of sharks per drumline per year (no. sharks drumline^{-1} year^{-1}). However, due to the short time-frame of deployment and low catches when compared with the nets, spatial and temporal trends in CPUE were not explicitly modelled using a GAMM. The ratio of the mean CPUE in the nets (in this case using the number of sharks per net) to the mean CPUE on the drumlines was used to provide an indication of the number of drumlines needed to catch the same number of *S. zygaena* as a net. The replacement ratio was calculated using CPUE data for nets and drumlines at locations only where drumlines had been deployed, for the period 2007–2014.

All GAMMs were fitted using the mgcv (Wood 2006) and nlme (Pinheiro et al. 2007) packages within the statistical computing environment R (Bolker and R Development Core Team 2014).

Length and reproductive data
Annual values of the mean size, for both male and female sharks, were calculated from field measurements. Field measurements rather than laboratory measurements of dissected animals were used to increase the sample size as only 69.4% of animals were returned to shore for dissection. Sex ratio was analysed using an exact binomial test.

The length data from nets and drumlines (1978–2014) for both sexes combined were used to investigate the temporal and spatial dynamics in the size distribution of *S. zygaena* and any size differences between sharks caught in the nets and on drumlines. Changes in mean length were modelled using the GAMM framework described for the CPUE standardisation. The full GAMM was:

$$Length = e^{\beta_0 + year + s(month) + s(latitude) + gear + \alpha_j}$$ (15)

where 'gear' is the categorical variable denoting whether the specimen was caught in a net or on a drumline. The length data were fitted by assuming a gamma distribution with a log-link function. This distribution type was chosen because of its flexibility in modelling positive and typically right-skewed continuous-response variables, such as length data (Thorson et al. 2015). As for the CPUE standardisation GAMMs, the significance of including beach as a random effects term was supported as judged by the AIC. F-tests were used to determine the covariates that contributed significantly ($p < 0.05$) to the deviance explained in the length data.

Reproductive structures for all dissected sharks (caught on both gear types) were measured as defined by Cliff et al. (1988), and visually assessed for maturity using the criteria of Bass et al. (1975). Maturity status (juvenile, adolescent or mature) was based on the size/condition of the uterus and the diameter of the largest ovarian follicle (females) or the size/condition of the claspers, epididymis, siphon sac and seminal vesicles (males).

Dietary indices
Stomach-contents data were analysed for the period 1983–2014, because prior to 1983 individual prey items were not counted or weighed. For each shark dissected, the complete stomach was removed and prey items were identified to the lowest possible taxon, counted and weighed (wet mass) to the nearest 1.0 g. Prey items were identified at various

levels of digestion, including whole animals, teleost otoliths (Smale et al. 1995) and cephalopod beaks (Clarke 1986; Smale et al. 1993). Diet composition was calculated as percentage number (%N), percentage mass (%M), percentage occurrence (%F) and percentage index of relative importance (%IRI) of prey, from non-empty stomachs, according to the definitions of Hyslop (1980). To avoid any bias in the analyses, stomachs containing only otoliths or beaks, which may remain undigested for long periods of time, were considered empty. This procedure has been followed in all previously published diet studies from the KZN bather protection programme. The exclusion of cephalopod beaks, however, would result in the loss of a wealth of information on the species of cephalopods that are consumed by *S. zygaena*. As a result, their contribution (as %N and %F) to the diet of *S. zygaena* was analysed separately.

Cumulative prey curves were constructed to determine whether a sufficient number of stomachs had been collected to accurately describe total diet. The order in which the stomachs were analysed was randomised 500 times and the mean cumulative number of new prey items plotted against the number of stomachs sampled.

Liver mass was recorded from all dissected sharks. Hepatosomatic index (HSI) was calculated as liver mass/shark mass × 100. Seasonal variations in HSI between summer (December–February), autumn (March–May), winter (June–August) and spring (September–November) were investigated using a Kruskal–Wallis *H*-test. This test was considered appropriate since a Shapiro–Wilk test of normality indicated that the HSI data were not normally distributed ($p < 0.001$).

Results

Catch and effort

Between 1978 and 2014, a total of 2 512 *Sphyrna zygaena* were caught in the bather-protection nets (annual mean 67.9 ind. [SD 50.9]; range 9–271). Of these, 52.6% were females, 42.6% males and 4.8% were unsexed. The average annual survival rate (sharks found alive in a net or on a drumline when serviced) ranged from zero to 16.8% (mean 2.4% [SD 0.03]), with no significant change over the study period ($p = 0.749$). The highest annual capture ($n = 271$) of *S. zygaena* was in 1980. Interestingly, 13 of the 17 incidents of mass captures (defined as between 5 and 15 *S. zygaena* caught in the same net installation on a single day) were also recorded in that year, between July and August. In addition, 39.0% of non-empty stomachs sampled in 1980 contained sardines as compared with <11.0% in any other year of the study period (see below). Thus, it is highly likely that the anomalously high capture rate of sharks in 1980, unlike all other years, was directly linked to the presence of sardines; hence, the CPUE value for that year was excluded as an outlier from any catch analysis.

Table 1: Summary statistics for covariates tested in the quasi-Poisson generalised additive mixed models (GAMMs) fitted to CPUE data (no. sharks km-net^{-1} month^{-1}) for *Sphyrna zygaena* caught in nets of the KwaZulu-Natal bather protection programme from 1981–2014, and the gamma-distribution GAMMs fitted to length data for 1978–2014. The *p*-values denote the significance levels of the deviance explained by each effect; P/A refers to presence/absence

| Covariate	CPUE		Length	
	F-test	*p*-value	*F*-test	*p*-value
s(Year)	26.71	<0.001	2.53	<0.001
s(Month)	87.8	<0.001	15.54	<0.001
s(Latitude)	18.8	<0.001	6.73	<0.001
s(ΔSST)	17.79	<0.001	–	–
Drumline(P/A)/Gear-type	61.14	<0.001	0.37	0.54
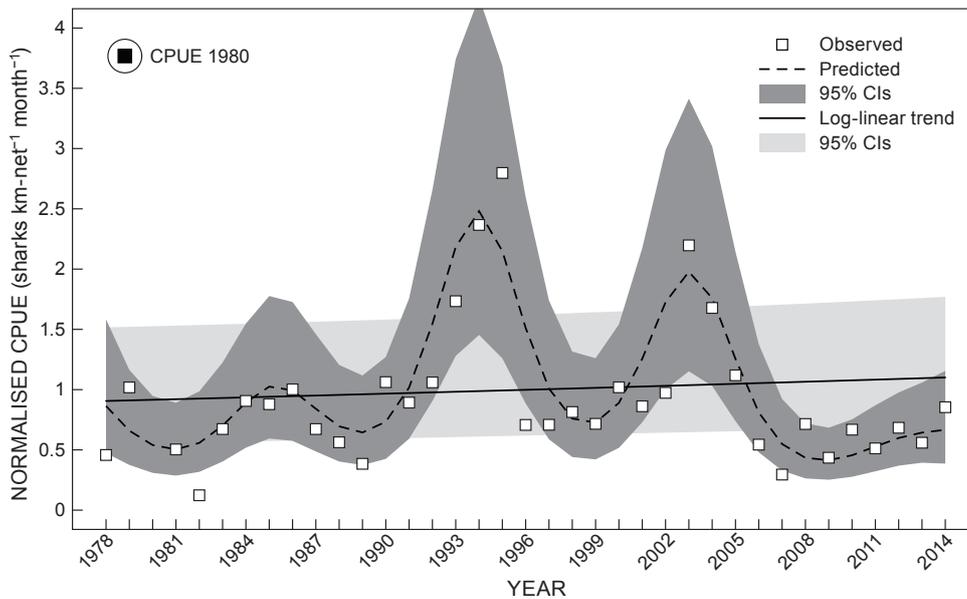
Figure 3: Observed (open squares) and predicted (dashed line) CPUE values for *Sphyrna zygaena* caught in the bather-protection nets, standardised for years. Solid line represents the log-linear trend in predicted CPUE. The CPUE value for 1980 (filled square) was excluded from the analysis

Although the catch rate of *S. zygaena* varied markedly between years, there was no significant log-linear year trend over the time period 1978–2014 (slope = 0.0054, *t* = 1.808, *p* = 0.071), which corresponds to an average rate of increase of 0.5% per year (Figure 3). All of the GAMM covariates fitted to the subset 1981–2014 explained highly significant proportions of variation in the CPUE of *S. zygaena* caught in the nets (Table 1). The sharks were recorded along the entire coastline; however, catch rates were highest along the south coast of KZN, from Port Edward to Durban, with few sharks caught north of Umhlanga Rocks (beach 11, Figure 1; latitude 29.7° S,

Figure 4). The sharks were caught throughout the year but were significantly more abundant from May to October when mean SSTs are cooler (Figure 5). Both monthly and annual catch rates were higher during periods of below-average SSTs (Figure 6a and 6b, respectively).

Between 2007 and 2014, drumlines caught a total of 72 *S. zygaena* (annual mean 9.0 [SD 4.9]; range 5–20). The majority were males (48.6%), and females and unsexed sharks accounted for 31.9% and 19.4%, respectively. Only a single shark (1.4%) was released alive. The mean annual net CPUE at beaches where drumlines had been deployed since 2007 was 0.94 sharks net^{-1} year^{-1} (SD 0.388), and for
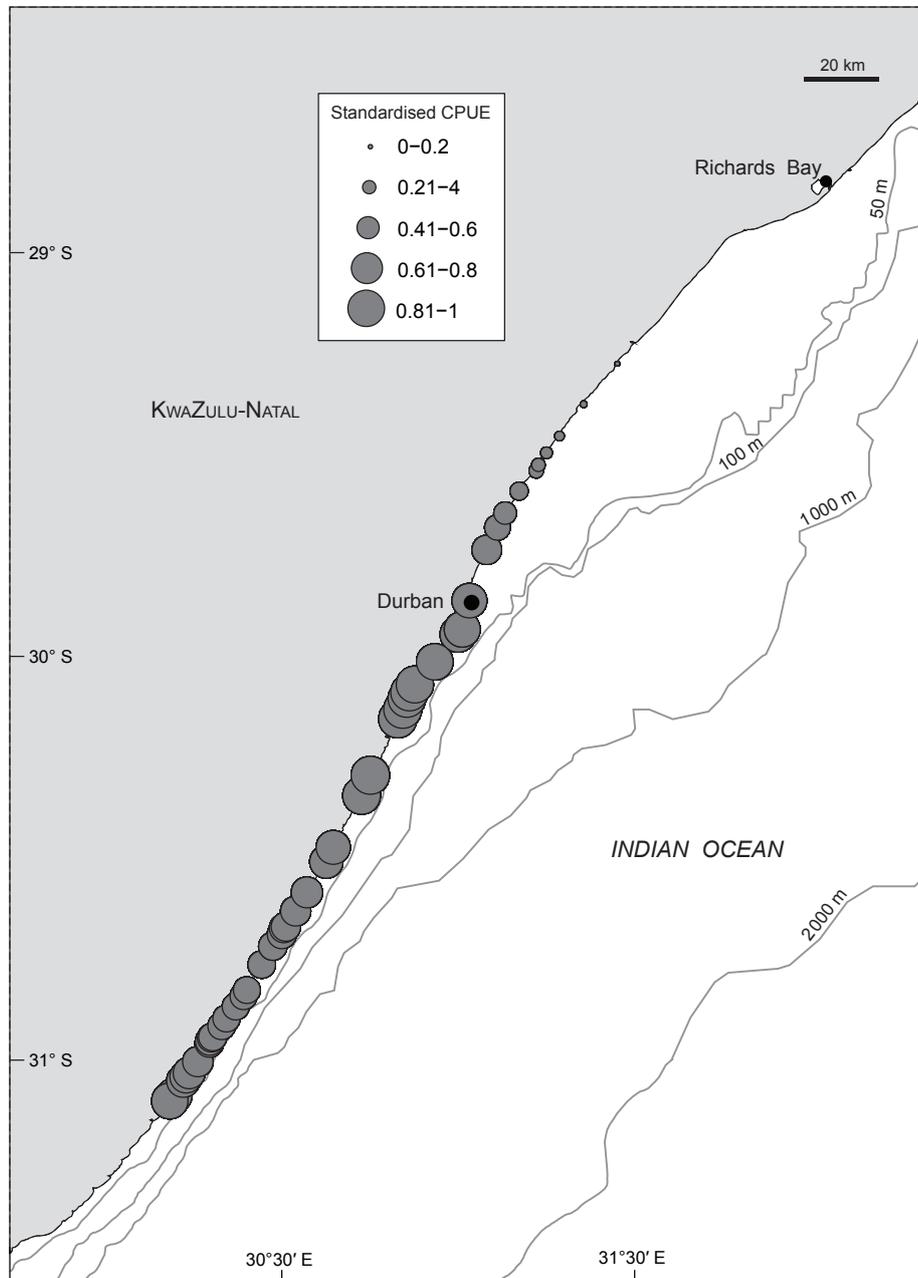
Figure 4: Spatial distribution of standardised CPUE (no. sharks km-net^{-1} month^{-1}) for *Sphyrna zygaena* caught in the nets of the KZN bather protection programme (standardised using 2014 data)

drumlines it was 0.12 sharks drumline^{-1} year^{-1} (SD 0.064). This equates to a drumline-to-net replacement ratio of 7.94 for the capture of *S. zygaena*. The final GAMM results predicted that catch rates decreased significantly, by about 23%, in installations with drumlines (slope = 0.260, *t* = −2.050, *p* < 0.05).
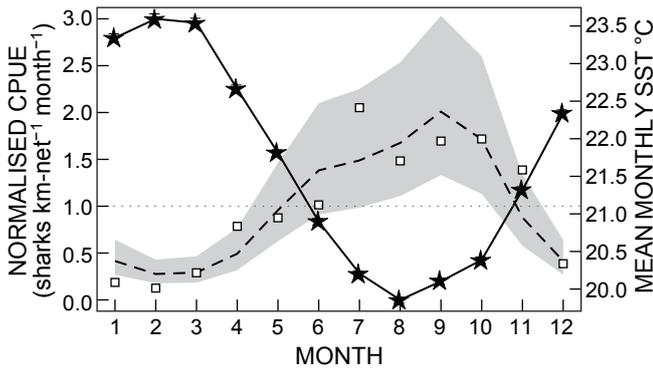
Length distributions and sex ratios

Field length was measured for 2 426 and 60 *S. zygaena* captured in the nets and on drumlines, respectively. The length frequency distributions of males and females were unimodal for both gear types (Figure 7). The size range of sharks was 40–220 cm (mean 95.0 cm, SD 150.6) in the nets, and 66–140 cm (mean 101.0 cm, SD 14.9) on the drumlines. Only one young-of-the-year (<45 cm) and four sharks larger than size at maturity (>160 cm) (although not examined) were caught by either gear type. The majority (93.1%) of all sharks caught were between 80 and 120 cm

Figure 5: Observed (open squares) and predicted (dashed line) CPUE values (±95% CI, grey area) for *Sphyrna zygaena*, standardised for months (period 1981–2014). Filled diamonds along the solid line represent mean monthly sea surface temperatures (SST, ±95% CI); dotted horizontal line indicates mean CPUE

in length. Using the growth curve of Coelho et al. (2011), this corresponds to an estimated age range of 2 to 4 years.

All of the GAMM covariates, with the exception of gear type, were significant in predicting the length of *S. zygaena* caught in the nets (Table 1). The log-linear year trend from the GAMM fitted to mean length indicated a highly significant log-linear increase over time (slope = 0.0012, *t* = 3.502, *p* < 0.001) (Figure 8a). Significantly larger-sized sharks were caught in the summer and with decreasing latitude. There was no significant difference in the mean size of sharks caught in the nets (mean 95.1 cm, SD 15.1) or on drumlines (mean 101.5 cm, SD 14.9) (Figure 8b–d).

The sex ratio of the overall catch of *S. zygaena* in the nets was biased significantly towards females, with a ratio of 1.23:1 (*p* < 0.001). In contrast, drumlines caught more males, with a sex ratio of 1.52:1. However, this difference was not significantly different from unity (*p* = 0.111).

A total of 1 073 males and 1 322 females were dissected. Based on the size and condition of the reproductive organs, all *S. zygaena* examined were juveniles or adolescents.

### Stomach contents

The stomachs of 1 413 *S. zygaena*, ranging in size from 57 to 170 cm (mean 96.4 cm, SD 13.0), were examined. Of these, 468 (33.1%) had empty stomachs and 12 (0.8%) had regurgitated the stomach contents during capture. A cumulative prey curve was constructed using data from the remaining 933 stomachs, which contained food items (including stomachs containing only fish otoliths or cephalopod beaks). The curve (Figure 9) did not reach an asymptote, indicating that a greater number of individuals would be required to more accurately describe the diet of *S. zygaena*.

The number of unique prey items identified from stomach contents was 111, representing 57 families. The mean mass of stomach contents containing food was 82.3 g (SD 154.4, range 1–1 535 g) and the mean number of unique prey items was 1.8 (SD 1.1, range 1–8). Details of the prey items are presented in Tables 2 and 3.
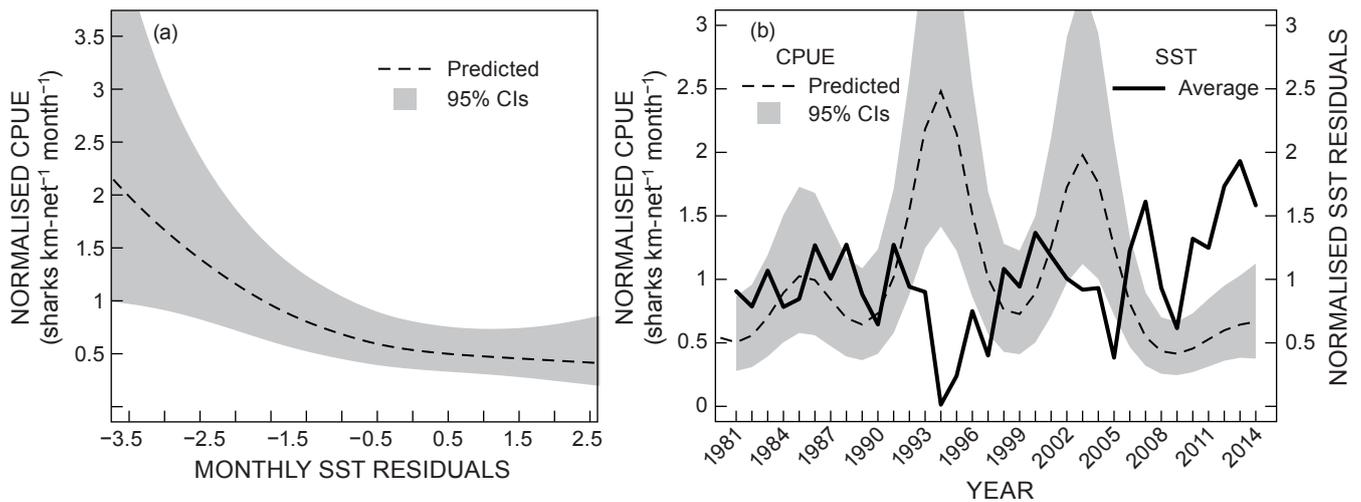
Figure 6: (a) Predicted effect of normalised sea surface temperature (SST) residuals on CPUE of *Sphyrna zygaena* (dashed line), with ±95% CIs, and (b) predicted year-effect (dashed line) plotted against annual average of monthly SST residuals (solid line) for the period 1981–2014
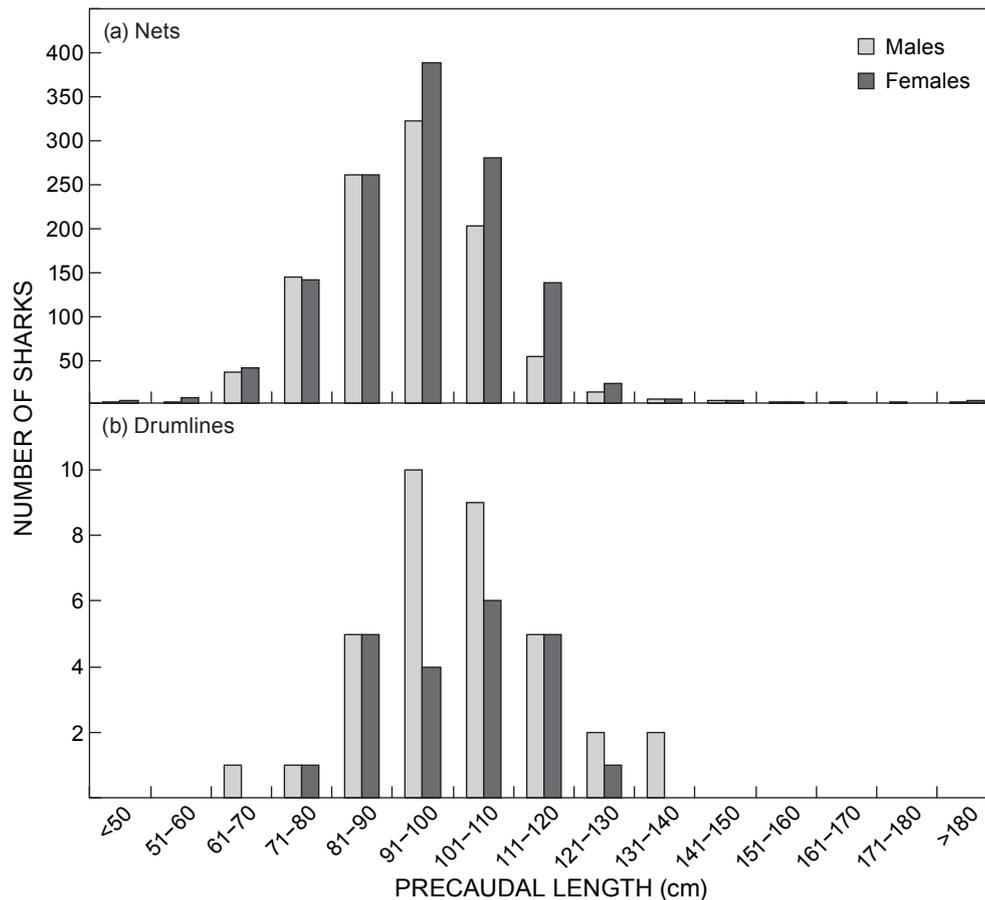
Figure 7: Length frequency distribution of *Sphyrna zygaena* caught in nets (1978–2014) and on drumlines (2007–2014) in the KZN bather protection programme

Teleosts were the most important functional prey group (%IRI) for *S. zygaena*, recorded from 93.7% of the stomachs with food (Table 2). A total of 61 teleost species were identified, representing 28 families. Although a wide variety of teleost prey was consumed, many of these taxa had a low incidence. The most common species in terms of %IRI were small-sized pelagic schooling fishes, including *Sardinops sagax* (sardine), *Pomatomus saltatrix* (elf) and *Scomber japonicus* (mackerel). Other common prey included inshore demersal fishes, such as mullets (family Mugilidae), *Pomadasys olivaceum* (piggy) and *Pagellus bellottii natalensis* (red tjor-tjor).

Although sardines formed an important prey source, it is interesting to note that even in the cyclically high-capture years these fish were recorded in <11.0% of the shark stomachs sampled during June and July. The exception was in 1980, when sardines were recorded in 39.0% (*n* = 89) of the stomachs. Fish otoliths without any associated soft tissue (excluded from Table 2) were collected from seven shark stomachs and identified as: *Johnius dussumieri* (small kob), *Thryssa vitrirostris* (orange-mouth glassnose), *Pomadasys striatus* (striped grunter), *Saurida undosquamis* (brushtooth lizardfish), *Sphyraena acutipinnis* (sharpfin barracuda) and the grenadier species *Coelorinchus denticulatus* and *C. karrerae*.

Cephalopods were the second most-important functional prey group in terms of %IRI, and were recorded in 23.1% of the stomachs (Table 2). Cuttlefishes (Sepiidae) as well as 19 species (11 families) of squids (Teuthoidea) and 5 species (2 families) of octopus (Octopoda) were identified from beaks (Table 3). The most commonly recorded squids were loliginids (52.1 %F) and *Ancistrocheirus lesueurii* (28.2 %F), which is an oceanic deepwater species. Other lower epipelagic to mesopelagic species identified included *Octopoteuthis rugosa*, *Ommastrephes bartramii* (red flying squid) and *Ornithoteuthis volatilis* (shiny bird squid). In comparison to cuttlefishes and squids, the dietary importance of octopus, in terms of both %F and %N, was low, with *Octopus* cf. *vulgaris* (common octopus) the most commonly recorded species (Table 3).

The dietary importance of other prey categories was extremely low, and comprised elasmobranchs (0.3 %IRI), crustaceans (0.3 %IRI) and miscellaneous items (0.3 %IRI). The latter category included plastic pieces (2 stomachs), a mollusc (1 stomach) and seaweeds (4 stomachs). No mammal, reptile or bird species were recorded in the stomachs.

There was no significant difference in the HSI values between the male and female sharks (Kruskal–Wallis *H*-test, $\chi^2(1) = 1.333$, *p* = 0.248). However, there was a significant variation in HSI values (both sexes combined)
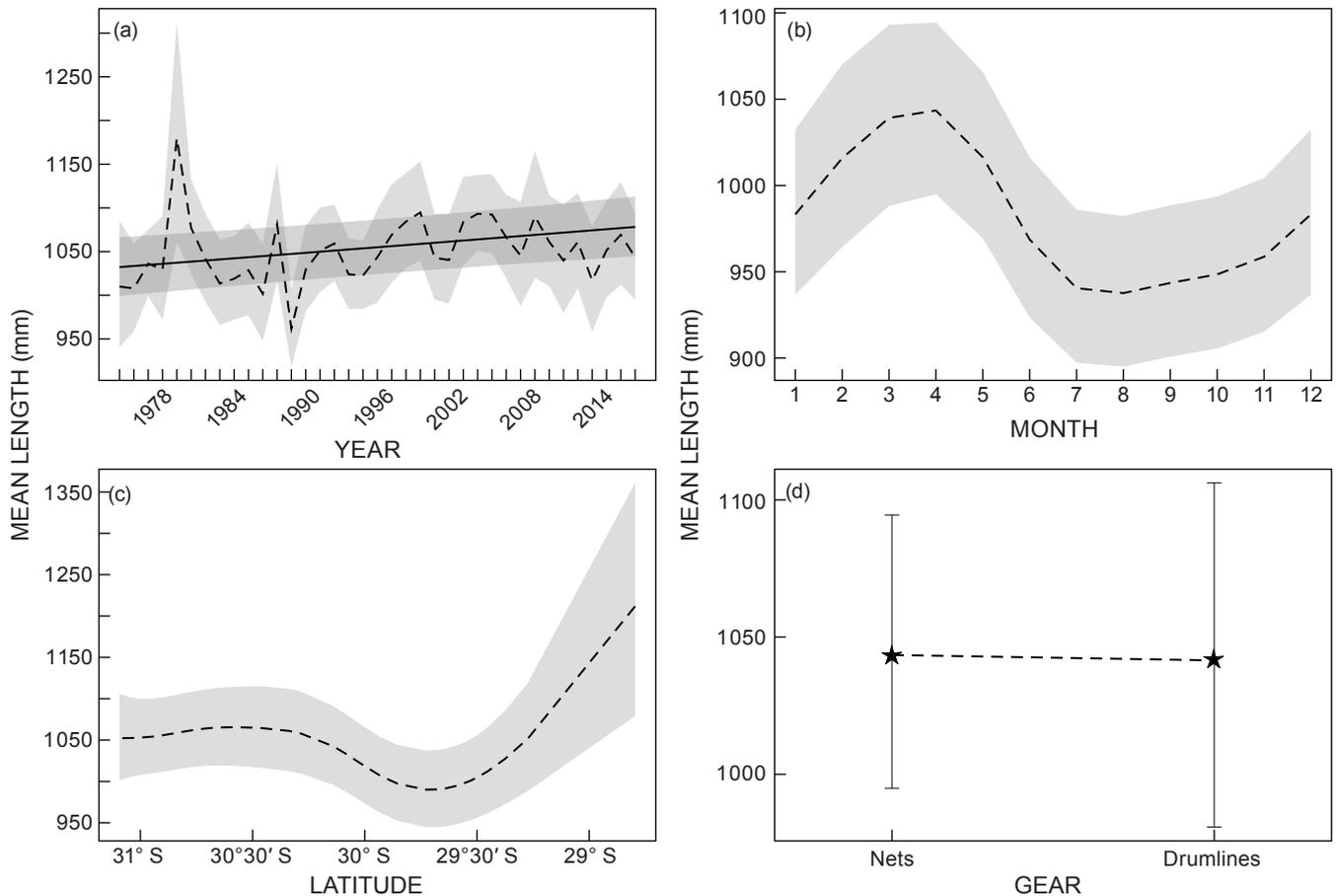
Figure 8: Predicted values (±95% CI, grey areas) for mean precaudal length of *Sphyrna zygaena* caught in nets of the KZN bather protection programme, 1978–2014, standardised for (a) year, (b) month, (c) latitude, and (d) gear type
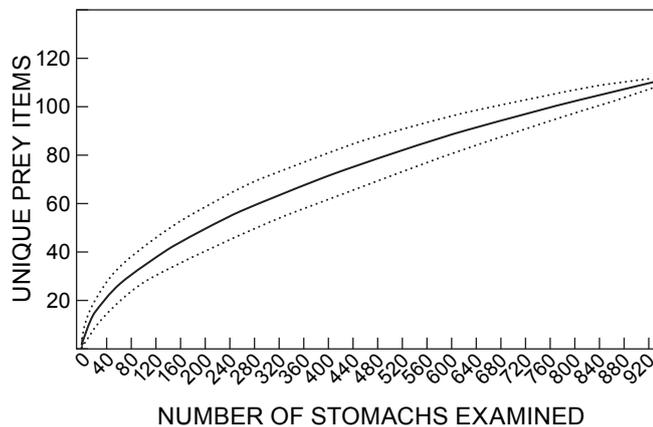
Figure 9: Randomised cumulative prey curve derived from the stomach-contents analysis of *Sphyrna zygaena* caught in nets and on drumlines of the KZN bather protection programme, 1983–2014. The order in which the stomachs were analysed was randomised 500 times before plotting the means (solid line) and 95% CIs (dashed lines)

between seasons ($\chi^2(3) = 137.682$, $p < 0.001$) (Figure 10), with the highest values in autumn and winter and the lowest in spring and summer.

Discussion

Catch rates and patterns

The population status of *Sphyrna zygaena* in South Africa is unknown. However, this shark is highly susceptible to over-fishing and capture stress (Casper et al. 2005), which has resulted in population declines in many parts of the world (Baum et al. 2003; Pérez-Jiménez 2014). In the shark-meshing programme of New South Wales, Australia, there was a significant and protracted decline in hammerhead sharks, predominantly *S. zygaena*, over two decades (Reid et al. 2011). In contrast to global trends, it is encouraging that the catch rates within the KZN bather protection programme revealed no evidence of a decline of this shark over the last four and a half decades, but an overall small yet significant increase in their mean length, suggesting a relatively healthy population of *S. zygaena* along the east coast of South Africa.

Like many species of sharks (Myers et al. 2007; Meyer et al. 2010), the catch rate of *S. zygaena* exhibited short-term fluctuations in CPUE, possibly in response to variability in SST and prey availability (Smale 1991). However, excluding the anomalously high capture rate in 1980, a longer-term trend was also evident, with catches of this species rising and falling over an approximate

Table 2: Stomach-contents analysis of *Sphyrna zygaena* caught in nets and drumlines of the KZN bather protection programme, 1983–2014. Details of the prey are presented as percentage of occurrence (%*F*), mass (%*M*), number (%*N*), and index of relative importance (%IRI). Totals represent the number of non-empty stomachs (*F*), the mass of prey items (*M*, kg) and the number of individual prey items recorded (*N*). Species are listed in phylogenetic order following Smith and Heemstra (1986)

Prey category	%*F*	%*M*	%*N*	%IRI
ELASMOBRANCHS	0.29	0.82	0.11	0.27
Sphyrnidae—				
Unidentified *Sphyrna* sp. (hammerhead)	0.15	0.81	0.05	0.13
Unidentified elasmobranchs	0.15	0.01	0.05	0.01
TELEOSTS	93.72	83.20	79.38	15 237.24
Anguilliformes—				
Unidentified anguilliforms (eels and morays)	0.15	0.01	0.05	0.01
Congridae—				
Gnathophis capensis (southern conger)	0.15	0.07	0.05	0.02
Clupeidae—				
Unidentified clupeids (herrings)	1.02	0.78	2.07	2.92
Etrumeus teres (redeye round herring)	0.58	0.56	1.91	1.44
Etrumeus whiteheadi (round herring)	0.29	0.20	0.38	0.17
Sardinops sagax (South African sardine)	8.03	7.21	11.02	146.34
Herklotsichthys quadrimaculatus (bluestripe herring)	0.15	0.03	0.11	0.02
Centriscidae—				
Aeoliscus strigatus (razorfish)	0.15	0.04	0.05	0.01
Ariidae—				
Unidentified ariids (sea catfish)	0.44	0.05	0.27	0.14
Myctophidae—				
Unidentified myctophids (lanternfishes)	0.15	0.09	0.22	0.04
Unidentified *Diaphus* sp. (lanternfish)	0.29	0.09	0.11	0.06
Gymnoscopelus piabilis (southern blacktip lanternfish)	0.15	0.01	0.65	0.10
Macrouridae—				
Unidentified *Coelorinchus* sp. (grenadier)	0.15	0.06	0.05	0.02
Belonidae—				
Unidentified belonids (needlefishes)	0.44	0.52	0.16	0.30
Ablennes hians (barred needlefish)	0.15	0.34	0.05	0.06
Exocoetidae—				
Unidentified exocoetids (flyingfishes)	1.17	2.45	0.44	3.37
Cheilopogon pinnatibarbatus (small-head flyingfish)	0.58	1.92	0.27	1.28
Parexocoetus brachypterus (sailfin flyingfish)	0.29	0.89	0.27	0.34
Serranidae—				
Unidentified serranids (rockcods)	0.15	0.48	0.05	0.08
Epinephelus andersoni (catface rockcod)	0.15	0.22	0.05	0.04
Pomatomidae—				
Pomatomus saltatrix (elf)	4.96	10.25	2.35	62.51
Haemulidae—				
Unidentified haemulids (rubberlips and grunters)	0.29	0.00	0.11	0.03
Pomadasys commersonnii (spotted grunter)	0.15	0.16	0.05	0.03
Pomadasys olivaceum (piggy)	2.63	1.36	1.69	8.01
Lutjanidae—				
Unidentified lutjanids (snappers)	0.15	1.12	0.22	0.19
Lutjanus russellii (Russell's snapper)	0.15	0.04	0.22	0.04
Sparidae—				
Unidentified sparids (seabreams)	0.29	0.08	0.11	0.06
Chrysoblephus puniceus (slinger)	0.29	0.19	0.11	0.09
Diplodus sargus (blacktail)	0.15	0.10	0.16	0.04
Pagellus bellottii natalensis (red tjor-tjor)	1.61	0.85	1.09	3.12
Porcostoma dentata (Dane seabream)	0.15	0.18	0.05	0.03
Rhabdosargus holubi (Cape stumpnose)	0.15	0.04	0.05	0.01
Rhabdosargus sarba (Natal stumpnose)	0.15	0.15	0.05	0.03
Rhabdosargus sp. (stumpnose)	0.15	0.10	0.05	0.02
Sarpa salpa (strepie)	0.44	0.26	0.16	0.18
Scorpididae—				
Neoscorpis lithophilus (stonebream)	0.15	0.00	0.05	0.01
Ephippidae—				
Unidentified ephippids (batfishes)	0.29	0.29	0.11	0.12

Table 2: (cont.)

Prey category	%F	%M	%N	%IRI
Sciaenidae—				
Unidentified sciaenids (kob)	0.15	0.02	0.11	0.02
Johnius amblycephalus (bellfish)	0.29	0.21	0.11	0.09
Otolithes ruber (baardman)	0.15	0.10	0.16	0.04
Umbrina ronchus (slender baardman)	0.15	0.01	0.05	0.01
Leiognathidae—				
Unidentified leiognathids (ponyfishes)	0.15	0.03	0.11	0.02
Oplegnathidae—				
Oplegnathus robinsoni (Natal knifejaw)	0.15	0.42	0.05	0.07
Carangidae—				
Unidentified carangids (kingfish)	0.29	0.18	0.27	0.13
Scomberoides tol (needlescaled queenfish)	0.29	0.48	0.11	0.17
Unidentified *Decapterus* sp. (scad)	0.15	0.07	0.05	0.02
Trachurus trachurus (horse mackerel)	1.31	0.74	0.87	2.11
Coryphaenidae—				
Coryphaena hippurus (common dolphinfish)	0.15	0.77	0.05	0.12
Cheilodactyleidae—				
Chirodactylus jessicalenorum (Natal fingerfin)	0.15	0.11	0.05	0.02
Cichlidae—				
Oreochromis mossambicus (Mozambique tilapia)	0.15	0.08	0.05	0.02
Mugilidae—				
Unidentified mugilids (mullets)	2.34	5.19	0.98	14.42
Valamugil robustus (robust mullet)	0.29	0.49	0.38	0.25
Valamugil seheli (bluespot mullet)	0.15	0.23	0.11	0.05
Liza dumerili (groovy mullet)	0.15	0.25	0.05	0.04
Sphyraenidae—				
Unidentified *Sphyraena* sp. (barracuda)	0.15	0.01	0.05	0.01
Sphyraena jello (pickhandle barracuda)	0.15	0.13	0.05	0.03
Trichiuridae—				
Trichiurus lepturus (cutlassfish)	0.29	0.30	0.16	0.14
Scombridae—				
Unidentified scombrids (tunas)	2.34	5.67	0.93	15.40
Scomber japonicus (mackerel)	3.65	8.00	1.53	34.77
Katsuwonus pelamis (skipjack tuna)	0.15	0.68	0.05	0.11
Unidentified pleuronectiforms (flatfishes)	0.15	0.06	0.05	0.02
Unidentified teleosts	53.72	27.80	48.01	4 072.80
CEPHALOPODS	23.07	15.94	19.75	823.25
Sepiidae—				
Unidentified sepiids (cuttlefishes)	8.18	3.43	4.47	64.60
Teuthoidae—				
Unidentified teuthoids (squids)	6.42	8.32	6.76	96.88
Loliginidae—				
Unidentified loliginids (loliginid squids)	6.28	3.07	7.20	64.46
Ancistrocheiridae—				
Ancistrocheirus lesueurii (sharpear enope squid)	0.88	0.46	0.82	1.12
Octopodidae—				
Unidentified *Octopus* sp. (octopus)	0.15	0.09	0.05	0.02
Unidentified cephalopods	1.17	0.58	0.44	1.19
CRUSTACEANS	0.58	0.04	0.44	0.28
Brachyura—				
Unidentified brachyurans (crabs)	0.15	0.00	0.33	0.05
Macrura—				
Unidentified crayfishes	0.15	0.02	0.05	0.01
Unidentified crustaceans	0.29	0.02	0.05	0.02
MISCELLANEOUS ITEMS	1.02	0.00	0.33	0.33
Unidentified molluscs	0.15	0.00	0.00	0.00
Unidentified seaweeds	0.58	0.00	0.22	0.13
Plastic pieces	0.29	0.00	0.11	0.03
Totals	685	76.63	1 833	

Table 3: Cephalopod species identified from beaks found in the stomachs of *Sphyrna zygaena* caught in nets and on drumlines of the KZN bather protection programme, 1983–2014. Details of the prey are presented by frequency of occurrence (%*F*) and by number (%*N*). Totals represent number of non-empty stomachs (*F*) and number of individual prey items recorded (*N*)

Prey category	%*F*	%*N*
SEPIOIDEA (cuttlefishes)		
Unidentified sepiids	40.93	12.73
TEUTHOIDEA (squids)		
Unidentified teuthoids	7.34	5.74
Loliginidae—		
Unidentified loliginids (loliginid squids)	52.12	43.34
Enoploteuthidae—		
Unidentified enoploteuthid	0.39	0.08
Unidentified *Abralia* sp.	0.39	0.08
Ancistrocheiridae—		
Ancistrocheirus lesueurii (sharpear enope squid)	28.19	9.82
Octopoteuthidae—		
Octopoteuthis rugosa	11.20	3.24
Onychoteuthidae—		
Unidentified *Onychoteuthis* sp.	1.16	0.33
Lycoteuthidae—		
Lycoteuthis lorigera	3.86	1.08
Histioteuthidae—		
Histioteuthis macrohista (jewel squid)	0.39	0.08
Histioteuthis miranda	3.47	0.75
Ommastrephidae—		
Unidentified ommastrephid	3.86	1.16
Unidentified *Todarodes* sp.	2.32	0.92
Ommastrephes bartramii (red flying squid)	15.83	7.40
Ornithoteuthis volatilis (shiny bird squid)	10.42	9.15
Sthenoteuthis oualaniensis (purpleback flying squid)	5.41	1.50
Chiroteuthidae—		
Chiroteuthis veranyi (long-armed squid)	0.39	0.08
Thysanoteuthidae—		
Thysanoteuthis rhombus (diamond squid)	2.32	0.50
Cranchidae—		
Unidentified cranchid	0.77	0.17
Unidentified *Liocranchia* sp.	0.39	0.08
OCTOPODA		
Octopodidae—		
Unidentified *Octopus* sp.	5.79	1.33
Octopus cyanea (big blue octopus)	0.39	0.08
Octopus cf. *vulgaris* (common octopus)	0.77	0.17
Argonautidae—		
Unidentified argonautid	0.39	0.08
Argonauta argo (greater argonaut)	0.39	0.08
Total number	259	1 202

Figure 10: Mean monthly hepatosomatic index for immature *Sphyrna zygaena* of both sexes combined. Bars represent standard errors of the means; data labels show the sample sizes

tagged and released by members of the Oceanographic Research Institute (ORI) cooperative fish tagging project (Diemer et al. 2011). Over the course of the study period, there were no major changes in gear selectivity within either the KZN bather protection programme or the ORI tagging programme. As a result, cyclically high captures may reflect inshore movement patterns of this shark in response to cooler SSTs. Alternatively, SST may be an indirect controlling factor, in that *S. zygaena* might be influenced by one or more other variables that are closely associated with sea temperature, such as the availability of prey. A third hypothesis is that cyclically high captures might be indicative of a multi-annual population cycle. Population cycles can originate from a variety of intrinsic (e.g. maternal effects) and extrinsic (i.e. resources or predators) interactions (Kendall et al. 1999; Ims et al. 2008). The identity of the decisive interactions generating the cycle are beyond the scope of this current study. Even so, the existence of the pattern is important: first, because it is likely to profoundly influence the functioning of ecosystems; and second, it provides a unique insight into the mechanisms of the species' population and community dynamics. Owing to the direct relationship between stock size and recruitment for sharks (Holden 1977; Hoenig and Gruber 1990), catch rates of juvenile and adolescent *S. zygaena* from the KZN bather protection programme might provide a useful indication of the current and future stock sizes. Apparent population cycles have not previously been documented for any of the other 13 shark species commonly caught in the KZN bather protection programme (Dudley and Simpfendorfer 2006). Long-term and accurate dataseries are critical to understand long-term environmental effects and to plan mitigation measures against the effects of climate change.

As a primarily temperate species, and given the maturity status of the sharks caught (juveniles and adolescents), sea temperature is likely to be not only a major factor influencing annual catch rates, but also the species' habitat use along the KZN coastline. Catch rates were highest along the KZN south coast, from Port Edward to Durban, whereas few

decadal cycle. This cycle coincides generally with periods of below-average SSTs. A comparison of catch trends within other South African fisheries is difficult because of failures to distinguish between *S. zygaena* and the scalloped hammerhead *S. lewini* (which often results in use of the term 'unspecified hammerhead') and to variable fishing effort (Pradervand and Govender 2003; Pradervand 2004; Pradervand et al. 2007; Diemer et al. 2011; da Silva et al. 2015). However, despite these limitations, it is noteworthy that a similar decadal pattern was also evident elsewhere along the South African coast in the annual numbers of unspecified *Sphyrna* spp.

sharks were caught north of Umhlanga Rocks (latitude 29.7° S). This spatial pattern coincides with an increase in mean summer and winter sea temperatures along the coast from south to north and a transition from warm-temperate to more tropical waters (Smit et al. 2013).

Seasonal patterns of abundance are also probably temperature-related, with the highest catches off KZN occurring during the winter and spring months when the mean August SST is ~20.5 °C, and the lowest catches were during the summer months when the mean February SST is ~25 °C (Smit et al. 2013). In contrast, juvenile and adolescent *S. zygaena* are more common in shallow waters of the Eastern Cape and southern Cape regions in summer than in winter (Smale 1991; Diemer et al. 2011), when mean SSTs are ~19–22 °C and ~15 °C, respectively (Smit et al. 2013). In the former Transkei region (i.e. eastern part of the Eastern Cape, immediately southwest of KZN), shore-angling catches of *S. zygaena* are higher than anywhere else along the South African coast (Pradervand 2004; Diemer et al. 2011). There is less variation between mean summer (~22 °C) and winter (~19 °C) SSTs (Smit et al. 2013) in those regions and no seasonality in catch rates. This suggests that the Transkei region constitutes the core area for juvenile and adolescent *S. zygaena* year-round. Decreasing sea temperatures in the northern part of the range in winter, and increasing temperatures in the southern part of the range in summer, are likely the primary factors resulting in the contrasting seasonality of catches evident between KZN and the Eastern and southern Cape regions.

In any given month catches of *S. zygaena* within the KZN bather protection programme were higher when temperatures in that month were lower than the 35-year mean. This suggests that temperature also plays a direct role in influencing the magnitude of seasonal range expansions, or movement inshore from cooler (Smit et al. 2013) shelf waters. As a result, oceanic climate change along the east coast of South Africa (Rouault et al. 2010) may exert a profound influence on the distribution and abundance of *S. zygaena*. Sea temperature, as a cue for the movement of and habitat use by juvenile sharks, has been inferred for several shark species on the east coast of South Africa, including *S. lewini* (de Bruyn et al. 2005), spotted raggedtooth *Carcharias taurus* (Dicken et al. 2007) and dusky shark *Carcharhinus obscurus* (Bass et al. 1973; Hussey et al. 2009; Dicken 2011).

Sphyrna zygaena is not as common (68 per annum) as the conspecific *S. lewini* (166 per annum) also caught in the nets of the KZN bather protection programme (de Bruyn et al. 2005). Catches of the latter were likewise strongly seasonal but highest in the summer months; this seasonality was also evident in catches by shore anglers along the east and south coasts (Diemer et al. 2011). *Sphyrna lewini* is a warmer-water species yet, similar to *S. zygaena*, it is highly mobile and able to move along the coast to take advantage of optimal water-temperature regimes.

Mass captures (simultaneous capture of multiple individuals in a single net installation) of *S. zygaena* were recorded on only 17 (>5 sharks) and 5 (>10 sharks) occasions. In contrast, between 1978 and 2005 mass captures of more than 10 *C. obscurus* and copper shark *Carcharhinus brachyurus* were recorded on 34 and 31 occasions, respectively (Dudley and Cliff 2010). These

mass captures, unlike those of *S. zygaena,* all occurred in June and July and were strongly associated with the sardine run. The rarity of mass-capture events for *S. zygaena* and the low occurrence of *Sardinops sagax* in its diet suggest a much weaker relationship between the spatial and temporal occurrence of *S. zygaena* and *S. sagax*. An exception to this statement relates to the unusually high catch in 1980, which coincided with the late arrival of sardines in August and their penetration farther north along the coast (Dudley and Cliff 2010). The relatively low number of mass-capture events is also evidence that *S. zygaena* does not appear to exhibit any aggregating behaviour once it begins to move along the KZN coastline. This is in direct contrast to its behaviour off the Eastern Cape, where large aggregations of thousands of juveniles have been observed (Bass et al. 1975; Smale 1991).

The survival rate of *S. zygaena* caught in both the nets (2.4%) and on drumlines (1.4%) was extremely low, but similar to that of *S. lewini.* These two species have the lowest release rates of all the shark species commonly caught in the KZN bather protection programme (Cliff and Dudley 2011), indicating that they are highly susceptible to capture stress. Indeed, studies focused on capture mortality have indicated that *S. zygaena* has one of the lowest post-release survival rates of any elasmobranch species (Braccini et al. 2012; Coelho et al. 2012).

The deployment of drumlines resulted in a significant increase in the number of *S. zygaena* caught in the nets. This is an unexpected result and one which is difficult to explain biologically as it is unlikely that the presence of 0.3–0.5 kg drumline baits (median of 4 per beach) attracted a greater number of sharks inshore. It is possible that the result is rather an artefact of the model structure linked to the following: (i) low number of drumline catches (*n* = 72); (ii) drumline deployment in 2007 coincided with the beginning of the cyclic decadal increase in *S. zygaena* abundance; and (iii) net saturation (i.e. the removal of nets has no impact on the number of sharks caught). The replacement ratio of 7.94 drumlines to catch the same number of *S. zygaena* as a net is almost double the current replacement ratio of 4. The drumlines are effectively catching half as many sharks of this species as the nets they have replaced. Given that this shark poses little threat to bathers, this is an encouraging result with regard to ongoing attempts to reduce the environmental impact of the KZN bather protection programme.

Length-distribution and reproductive data

The tiger shark *Galeocerdo cuvier* (Dicken et al. 2016) and *S. zygaena* are the only shark species to exhibit a significant increase in mean length among captures in the KZN bather protection programme (Dudley and Simpfendorfer 2006). Unlike *G. cuvier* (Dicken et al. 2016), there was no statistically significant difference in the size of *S. zygaena* caught in nets or on drumlines. This is perhaps not surprising, given that juvenile and adolescent *S. zygaena* have relatively small jaws and teeth and commonly feed on teleosts similar in size to the bait used on drumlines. In contrast, *G. cuvier* exhibits a preference for elasmobranchs, particularly after it reaches a size of 150 cm (Dicken et al. 2017).

Despite the widespread occurrence of *S. zygaena*, published biological data are limited. Compagno (1984)

described the size at birth as between 35 and 45 cm. The presence of neonates with open umbilical scars in waters off the Eastern Cape during summer (Smale 1991) and catches of sharks <40 cm off the southern Cape (Diemer et al. 2011) suggest that these are the primary pupping areas in South Africa. The sizes of juvenile and adolescent sharks caught in the KZN bather protection programme and along the Transkei coast (Diemer et al. 2011) suggest that movement out of the nursery area begins at about two years of age. The range expansion exhibited by juvenile sharks might be attributable to an increased availability of habitat owing to a reduced risk of predation (Heupel and Hueter 2002; Heupel and Simpfendorfer 2005), or might be a response to the presence of other factors, such as optimal temperatures or food, which lead to an increased growth rate (Heupel et al. 2007).

The size class of sharks caught in the KZN bather protection programme and in other fisheries along the South African coast suggests that *S. zygaena* utilises shallow inshore waters (<3 m deep) up to a length of 120 cm (approximately four years of age) before moving into deeper water offshore (Smale 1991). Similar size-related movement patterns have been reported for *S. zygaena* in New Zealand (Francis 2016) and Brazil (Vooren et al. 2005), and have been inferred from catches in the Atlantic pelagic longline fishery (Coelho et al. 2012). The narrow continental shelf along the Transkei region of the Eastern Cape might explain the higher abundance of sharks of 100–150 cm there than elsewhere along the South African coastline (Deimer et al. 2011).

Male and female *S. zygaena* reach maturity at between 160 and 190 cm (Compagno 1984). Although a pregnant shark (240 cm) with near-term embryos was recorded by Bass et al. (1975) from the Eastern Cape, and two mature non-pregnant females (205 and 210 cm) by Smale (1991), also from the Eastern Cape, catches of adult sharks anywhere along the South African coast are rare. Although assumed to come inshore to pup during the summer months along the Eastern and southern Cape coasts, the exact whereabouts of adults (especially males) for the rest of the year are unknown. Limited catch records and interviews with fishers, however, suggest that adults inhabit deeper waters along the continental shelf (Smale 1991); it is also possible that they are found in more tropical waters to the north of South Africa.

Significantly larger sharks were caught in the summer at lower latitudes (i.e. equatorward) and smaller sharks during the winter at higher latitudes (i.e. poleward). As a primarily temperate-water species that prefers cooler waters, these seasonal and spatial patterns may reflect the ability of larger sharks to tolerate higher sea temperatures. An increased thermal tolerance with size has been demonstrated in numerous shark species, including the white shark *Carcharodon carcharias* (Weng et al. 2007) and the sandbar shark *Carcharhinus plumbeus* (McAuley et al. 2007).

Based on seven pregnant females, the *in utero* sex ratio for *S. zygaena* is close to 1:1 (Stevens 1984). Similarly, the sex ratio of immature *S. zygaena* sampled from their nursery area in the Eastern Cape did not differ significantly from unity (Smale 1991). The female-biased sex ratio (1.23:1) in the nets of the KZN bather protection programme suggests some sexual segregation, with a greater number of females moving north from their nursery area in the Eastern Cape. Sexual segregation has been observed for numerous shark species, including juvenile *S. lewini* caught in the same nets, where males outnumbered females by 2.2:1 (de Bruyn et al. 2005). The modal size of *S. zygaena* (91–100 cm) caught in the KZN bather protection programme was slightly smaller than that of *S. lewini* (111–120 cm; de Bruyn et al. 2005). No neonates of either species were caught, but the catch of *S. lewini* did include some mature individuals, with 50% of the females pregnant.

Diet

The diet of immature *S. zygaena* was dominated by small pelagic schooling fishes and squids, as similarly documented by Smale (1991) and Smale and Cliff (1998). Demersal fishes and cephalopods were less common, and benthic species were rare. The most commonly consumed cephalopods were neritic species, including sepiids and loliginids, and probably *Loligo vulgaris reynaudii*. The latter species is rarely found off KZN and is more likely to have been consumed by the sharks while in Eastern Cape waters, where the squid spawns close inshore (Sauer and Smale 1991). Since cephalopod beaks may remain undigested for long periods, these squid could have been consumed in the Eastern Cape many months before the sharks migrated to KZN. Oceanic cephalopods were less prevalent and comprised primarily the deepwater species *Ancistrocheirus lesueurii* (sharpear enope squid) and *Ommastrephes bartramii* (red flying squid). These data provide strong evidence that immature *S. zygaena* are feeding primarily within the pelagic zone in shallow coastal habitats. It is notable that cephalopods in the stomachs of adult *S. zygaena* included deeper offshore species, such as *Lycoteuthis diadema* (Smale 1991), providing further support for occurrence of the adult sharks in shelf waters. In Brazil, large adults of *S. zygaena* have been observed feeding on dolphins (Sucunza et al. 2015). In this study, the rarity of elasmobranch prey and the absence of any marine mammals in the stomachs, however, is not surprising given the small jaw and teeth size of the sharks sampled.

Both *S. zygaena* and *S. lewini* caught in the KZN bather protection programme are of similar size and feed predominantly on a wide variety of small, shoaling teleost species. De Bruyn et al. (2005) recorded teleosts comprising 60 species from 42 families in 77% of *S. lewini* stomachs containing food, followed by cephalopods in 25% of the stomachs. Although competition between these two hammerhead species is greatly reduced by seasonal and geographic differences in their abundance close inshore on the KZN coast, Smale and Cliff (1998) found marked differences in the cephalopod prey consumed: there was a higher incidence of neritic cephalopods in *S. zygaena* (73% by number and 65% by mass of prey) than in *S. lewini* (53% by number, 24% by mass), indicating that these two predators have different feeding habits, and the dominant neritic cephalopods in *S. zygaena* were loligonids, whereas *S. lewini* fed more on octopodids.

Conclusions

To our knowledge, this study presents the longest time-series and most detailed analysis of catch-rate and

stomach-contents data among *Sphyrna zygaena* worldwide. The research is the first to present baseline information on the population status of *S. zygaena* in South Africa. As one of the least-studied species of large-sized sharks, and one considered particularly susceptible to over-exploitation, such information is vital for monitoring trends in its abundance. Information gained from this study can be used for the development of a species-specific management plan to ensure its sustainable long-term utilisation.

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