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Population structure and biology of shortfin mako *Isurus oxyrinchus* in the Southwest Indian Ocean

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Abstract

The population structure, reproductive biology, age and growth, and diet of shortfin makos caught by pelagic longliners (2005-2010) and bather protection nets (1978-2010) in the Southwest Indian Ocean were investigated. The mean fork length (FL) of makos measured by observers on longliners targeting tuna, swordfish and sharks was similar, and decreased from east to west, with the smallest individuals occurring near the Agulhas Bank edge, in June to November. Nearly all makos caught by longliners were immature, with equal sex ratio. Makos caught by bather protection nets were significantly larger, males were more frequent, and 93% of males and 55% of females were mature. Age was assessed from band counts of sectioned vertebrae, and a von Bertalanffy growth model fitted to sex-pooled length-at-age data predicted a birth size (L_0) of 90 cm, maximum FL (L_∞) of 285 cm and growth coefficient (k) of 0.113 y^{-1}. Males matured at 190 cm FL, aged 7 y, and females at 250 cm, aged 15 y. Litter sizes ranged from nine to 14 pups, and the presence of gravid females in bather protection nets suggested that some pupping occurred in shelf waters. Teleosts (mainly *Trachurus capensis*) occurred in 84% of stomachs collected on longliners, whereas elasmobranchs (63.5%) were most common in samples collected from bather protection nets, followed by teleosts (43.1%) and cephalopods (36.5%). Larger prey size may be a factor that attracts large makos to coastal waters.

Additional keywords: demography, GLM, pelagic longline fisheries, shark bycatch, stomach contents

Introduction

The shortfin mako (*Isurus oxyrinchus* Rafinesque, 1810, family Lamnidae), hereafter called mako, is a fast-swimming and active shark with a wide distribution in tropical and temperate waters above 16°C (Compagno 2001). It is a highly migratory species that inhabits the epipelagic zone down to about 500 m depth and also enters littoral waters (Casey and Kohler 1992; Loefer et al. 2005). Makos can reach 3.7 m fork length (FL) and a weight of 600 kg, and they are sexually dimorphic, with females becoming longer and heavier than males (Compagno 2001).

Ontogenetic and seasonal movements of makos give rise to demographically structured populations with high spatio-temporal variability. Makos exhibit sexual segregation (Mucientes et al. 2009) and also segregate by developmental stages (Nakano and Nagasawa 1996). Juvenile makos spend 90% of their time in the mixed layer near the surface, whereas adults dive much deeper (Holts and Bedford 1993; Sepulveda et al. 2004). Small immature makos observed near the coast of Chile suggest the existence of a nearshore pupping and nursery area in spring and summer (Bustamante and Bennett 2013). In the North West (NW) Atlantic, juveniles migrate seasonally between offshore wintering grounds and summer feeding grounds over the shelf (Casey and Kohler 1992). Mean lengths of makos caught by longliners in the North Atlantic and Mediterranean differed by area and latitude (Buencuerpo et al. 1998). Cliff et al. (1990) found more large males than females in coastal bather protection nets in eastern South Africa, and catches increased in winter and spring. The diffusive and highly dispersive nature of mako populations is supported by the absence of clear genetic population structure (Heist et al. 1996; Schrey and Heist 2003).

The reproductive mode of makos is aplacental viviparity, and the embryos develop by ingesting unfertilized ova supplied by their mother, a practice known as oophagy (Gilmore 1993). Information on mature and pregnant females is sparse (Semba et al.

2011), but litter and birth size, size at sexual maturity and parturition season have nevertheless been reported for populations in several regions. Litter size mostly ranges from 4 to 26 embryos (Stevens 1983; Mollett et al. 2000) with a possible maximum of 30 (Mollett et al. 2002), and larger females produce more offspring. Parturition appears to occur year-round, with a peak in late winter and spring (Stevens 1983; Cliff et al. 1990; Duffy and Francis 2001; Semba et al. 2011). Size at birth is around 60 cm fork length (FL), based on the size of near-term embryos (58 to 67 cm FL; Duffy and Francis 2001; Semba et al. 2011) and the smallest observed free-swimming specimens (57 to 61 cm; Cliff et al. 1990; Mollett et al. 2000; Bustamante and Bennett 2013).

Sexual maturity is reached at 2.5 to 2.9 m FL in female makos, based on measurements of reproductive organs, the presence of fertilized ova and indications of past pregnancy or mating (Stevens 1983; Cliff et al. 1990; Mollet et al. 2000; Francis and Duffy 2005; Joung and Hsu 2005; Bishop et al. 2006). Males mature at a smaller FL of 1.7 to 2.0 m, based on the calcification and development of claspers, which indicates the capacity to copulate (Maia et al. 2007; Semba et al. 2011; Bustamante and Bennett 2013). Estimates may vary according to sample size and the length range sampled, as well as the choice of maturity criteria and models (Francis and Duffy 2005; Semba et al. 2011). Real geographical or between-hemisphere differences in length-at-maturity have been suggested (Mollett et al. 2000), but estimates may have been affected by different length estimation methods used by individual researchers (Francis and Duffy 2005; Francis 2006).

Previous studies on makos have mainly used counts of alternately deposited calcified (opaque) and less-calcified (translucent) bands in vertebral centra to estimate age (Pratt and Casey 1983; Bishop et al. 2006; Natanson et al. 2006; Semba et al. 2009; Wells et al. 2013). Annual deposition of bands has been validated for many shark species, and is now widely regarded as the norm (Francis et al. 2007). Nevertheless, some uncertainty remains over band deposition rates in makos. Most studies on makos have demonstrated the deposition of a single annual band pair (Cailliet et al. 1983; Campana et al. 2002; Ribot-Carballal et al. 2005; Natanson et al. 2006; Semba et al. 2009), but some have shown biannual deposition (Pratt and Casey 1983), at least in young age classes where growth is rapid (Wells et al. 2013). Uncertainty over band deposition rates can affect estimates of growth rates, longevity and age-at-maturity. Apart from the deposition rate, band widths in large makos become narrower and more compacted towards the periphery of the corpus calcareum, and this leads to under-estimation of ages when they become too narrow to distinguish (Francis et al. 2007). Various mechanical, chemical and digital methods have been developed to enhance vertebral bands, including the use of whole vertebrae or sections thereof, stains, X-rays, and digital manipulation (Cailliet et al. 2006).

Makos are apex predators in the open-ocean pelagic environment, and can influence the abundance of other species across a range of trophic levels (Cortes 1999; Kitchell et al. 2002; Rogers et al. 2012). They feed mainly on teleosts, other elasmobranchs, pelagic cephalopods and marine mammals (Stevens 1984; Cliff et al. 1990; Maia et al. 2006; Preti et al. 2012), but are opportunistic in that they may switch between prey groups depending on availability (MacNeil et al. 2005). Makos in the California Current had a diverse diet of mainly teleosts and cephalopods, which was affected by season, size class and subregion (Preti et al. 2012). Makos caught in the NW Atlantic fed mainly on teleosts, with bluefish *Pomatomus saltatrix* making up >75% of the diet by volume (Stillwell and Kohler 1982; Wood et al. 2009). Cliff et al. (1990) found a large proportion of elasmobranchs in the stomachs of makos caught close to the shore in eastern South Africa. Large pelagic fish and cephalopods were dominant in the stomachs of juvenile and subadult makos sampled off southern Australia (Rogers et al. 2012).

Makos are taken as bycatch in commercial longline and gillnet fisheries that target tuna and swordfish, as well as in directed shark fisheries and artisanal and recreational fisheries in tropical and temperate oceans (Francis et al. 2001; Campana et al. 2005; Petersen et al. 2009; Bustamante and Bennett 2013). In the South West (SW) Indian Ocean, they are also taken as an incidental catch in bather protection nets, set in parallel and close to the shore (Dudley and Cliff 2010; Cliff and Dudley 2011). Statistics of mako catches made by international fishing fleets in the SW Indian Ocean are collected by the Indian Ocean Tuna Commission (IOTC), but records probably under-represent actual catches because of inaccurate or incomplete reporting (IOTC 2012). The total reported mako catch from South Africa was 581 tonnes dressed weight in 2011 (DAFF 2012). Makos are characterized by low rates of population increase and high fishing mortality throughout their range, and hence are considered to be vulnerable to overfishing (Dulvy et al. 2008; IUCN 2013).

Data collected by fisheries observers stationed on pelagic longliners and from makos caught in bather protection nets were used to assess spatio-temporal size and sex distribution in the SW Indian Ocean. Biological information was used to estimate age and growth, size at sexual maturity, and the number and size of pups carried by pregnant females. Stomach contents were used to compare the diets of makos caught near the shore in bather protection nets with those caught in oceanic waters by longliners. This study provides new information on makos from the SW Indian Ocean, a part of the world where they have been little studied, and as such it complements studies from other oceans.

Materials and methods

Study area

The study area off South Africa extended from Cape Point (18°E) to the Mozambique border, and 200 nautical miles (nm) offshore to the boundary of the exclusive economic zone (EEZ) (Fig. 1). This part of the SW Indian Ocean is characterized by a narrow and steep continental shelf, which gradually broadens to form the shallow (~200 m deep) Agulhas Bank in the west. The marine environment is dominated by the western boundary Agulhas Current which flows in a south-westerly direction, roughly steered by the shelf edge (see Lutjeharms 2006 for a review). The current is highly dynamic, forming eddies, rings, inshore counter currents and filaments of warm Indian Ocean waters. Sea surface temperatures in the current are typically 23 to 26°C, but coastal waters can range from 12 to 27°C (Beckley 1983).

Sampling gear and data collection

Pelagic longline fleets generally use 12–120 km of longline, 500–3800 hooks and an American or Asian longline configuration, depending on the fleet (South African or Asian flagged vessels) and target species (tuna, swordfish or sharks) (Petersen et al. 2009). The American system comprises of a monofilament mainline and droppers, and a rope upper section and 50 cm of steel trace is also used when targeting sharks.

The Asian tuna system uses a combination of braided monofilament, rope and a lead core to improve sinking rates. Circle and J-hooks with a size of 8/0 to 14/0 are commonly used. Bait comprises combinations of squid, mackerel and sardine. Longliners concentrate their fishing effort along the shelf break, near the 500 m isobath (Fig. 1), and vessels targeting swordfish and sharks set their hooks at 30-50 m depth, compared to 40-400 m depth for tuna. Of all reported hooks set between 1998 and 2010, 4% were directed at sharks, 68% at tuna, and 28% at swordfish.

Makos are also captured in bather protection nets (anchored gillnets set 300-500 m from the shore; 51 cm stretched mesh) at swimming beaches in KwaZulu-Natal (KZN) (Fig. 1). Some 44 km of nets in fixed positions along 325 km of coastline during the 1990s was reduced to 27.3 km by 2004, and in 2007 a further 4 km of nets were replaced with baited lines (Cliff and Dudley 2011). Nets are inspected each weekday at first light, when trapped animals are removed. Some nets are temporarily removed during winter, to avoid elevated shark catches associated with the sardine run (Dudley and Cliff 2010).

Fisheries observers stationed on pelagic longliners between 2005 and 2010 recorded the fork length (FL, cm), geographic coordinates and date of capture of 5819 makos (Fig. 1), and determined the sex of 525 individuals. The data were treated as the 'offshore' dataset. The sex, whole weight (WW, kg) and precaudal length (PCL, cm) or FL of 292 makos caught in bather protection nets between 1978 and 2010 were measured, and treated as the 'coastal' dataset. FL and PCL were measured as straight lines from the tip of the snout to the fork of the tail and the precaudal notch, respectively. PCL was converted to FL using the equation FL = 1.112 × (PCL - 2.053) (Cliff et al. 1990). Possible bias inherent in length measurements of makos have been described by Francis (2006). Potential bias inherent in size selectivity of the various longline configurations was tested by comparing the length frequency distribution of makos caught by tuna and swordfish directed longliners with that of shark directed longliners. The offshore and coastal datasets were not combined because they differed greatly in terms of gear-types used, data-collection methods, and spatial and temporal coverage.

Length frequency and sex ratio analyses

Variability in mako FL relative to sex, year, latitude, longitude, season, and flag state (Table 1) was explored using generalised linear models (GLM) in the statistical software package R, version 2.14.0 (R Development Core Team, 2011). Final models were selected based on a stepwise approach, in which combinations of error structures, link functions and explanatory variables were trialed. The most parsimonious models were selected based on Akaike's Information Criterion (AIC) (Akaike, 1974) and visual assessment of residual plots and quantile-quantile (QQ) probability plots (Table 2). For the offshore FL data, a gamma error structure and identity link function was selected as most appropriate after running trials on R software. Two-way (latitude × longitude; latitude × season; longitude × season) and three-way (latitude × longitude × season) interactions were tried, but they were not significant and were therefore omitted from the final model. A model was constructed in a similar way for the coastal FL data, but because of fewer records, year-groups were used instead of years (Table 2). A binomial error distribution with a logit link function was used to model sex distribution relative to year and season (Table 2).

Size at maturity

The inner clasper length of males was measured from the point of insertion at the cloaca to the tip of the clasper. Claspers with rigid calcification, a rhipidion (distal opening of the tube formed by the clasper) able to open freely to expose the spur, and anterior rotation capability were considered to be mature (Castro 1996). Fully grown but uncalcified claspers indicated adolescence. Bleeding claspers and swollen testes were interpreted as indicating recent mating activity.

Females were considered mature if distinct oocytes were present in the ovary and the uteri appeared distended. An uterus width (UW) > 50 mm was used as indicator of maturity; Mollett et al. (2000) found little overlap between mature and immature females at this measurement, although no evidence of knife-edge separation was found by Francis and Duffy (2005). Thin tube-like uteri were considered to be immature. The presence of a hymen indicated that a female was adolescent, although its absence is considered an unreliable indicator of maturity (Pratt 1979; Cliff et al. 1988; Francis and Duffy 2005). Mating scars on females were an indication of mating activity.

The coefficients (α and β) of a logistic equation to estimate size at maturity of male and female makos, respectively, were estimated using a GLM with a binomial error structure and logit link function (Table 2). In the model, sex was a categorical variable, and size was a continuous variable. The proportion of mature makos at each size was calculated as the inverse logit. The sizes at 25%, 50% and 75% probability of maturation, defining the mean size (L_{50}) and maturation range (L_{25}–L_{75}), were calculated upon simulation with the inverse logit and the estimated parameters.

Processing of vertebrae

A total of 177 vertebral samples consisting of 5–8 vertebrae each (post-cranial or anterior to the dorsal fin) was collected on a shark-directed pelagic longliner in 2010, and 30 additional samples were excised from makos caught in bather protection nets. Muscle tissue was removed from vertebrae and they were then soaked in 4.5% sodium hypochlorite for 45 minutes to 12 hours to remove further connective tissue (Yudin and Cailliet 1990). Cleaned vertebrae were embedded in polyester clear casting resin, and sectioned along the sagittal plane using an IsoMet® low speed diamond saw (Beuhler-Whitby, Ontario, Canada). Sections of 0.8 mm width were attached to glass slides with DPX slide adhesive. A Canon PowerShot S50 camera attached to a stereomicroscope was used to photograph sections in transmitted light on a dark field, and digital images were enhanced using the open source program, Paint.NET™.

Band pairs, defined as one calcified (opaque) and one less calcified (translucent) band, were counted by two independent readers. The first opaque band distal to the focus was assumed to be a pre-birth band, and the second a birth-band associated with an angle change in the corpus calcareum (Wintner et al. 2002; Goldman et al. 2006; Natanson et al. 2006). The angle change is generally associated with the transition from fast intra-uterine growth to slower post-natal growth (Walter and Ebert 1991), and was considered to represent age zero. Each opaque and translucent band thereafter was counted from digital images without prior knowledge of the length or sex of the specimen. Samples were counted three times by each reader, and the average percentage error (APE) was calculated to estimate the intra-reader average error (Beamish and Fournier 1981):

$$APE = \frac{100}{N}\sum_{i=1}^{N}\left[\frac{1}{R}\sum_{j=1}^{R}\frac{(x_{ij}-x_i)}{x_i}\right]$$

where N = number of makos aged, R = number of readings, x_{ij} = j^{th} count of the i^{th} shark, and x_i = final agreed count. Counts that differed by ≥3 band pairs or had an APE of > 20% were discarded. When the original counts differed by two band pairs, they were recounted. A paired t-test and an age-bias plot were used to assess inter-reader bias at the 5% level of significance (Neer et al. 2005; Natanson et al. 2006).

Growth models

Band pair deposition was assumed to occur annually, based on a mako injected with oxytetracycline (OTC) off eastern South Africa (Natanson et al. 2006) and radiocarbon methods (Campana et al. 2002). The von Bertalanffy (VBM; von Bertalanffy 1938) and Gompertz growth models (GM; Ricker 1979) were used to fit growth curves to estimate the theoretical maximum length (L_∞), growth coefficient (k) and a theoretical age at zero length (t_0) of makos. Natanson et al. (2006) found that the three-parameter VBM and GM produced biologically acceptable values for makos in the North Atlantic, and based on that study the original VBM,

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

was adapted as follows:

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

where L_t = predicted length at time t; L_∞ = theoretical maximum length; k = growth rate constant (y^{-1}); and L_0 = length at birth. The GM was specified as:

$$L_t = L_0\{e^{G[1-e^{(-kt)}]}\}$$

where G = ln(L_∞/L_0) is the initial exponential growth. The models were fit to individual length and age observations (averaged across readers and readings) by means of generalized nonlinear regression (in R-library *nmle*, Pinheiro *et al.* 2014), which allows for the comparison of different error structures. Makos grow fast during the first six months after birth (Bishop et al. 2006), but no neonates were represented in our aged material. The usual procedures of either fixing the size at birth (L_0) or totally relaxing it, resulted in fits that lacked biological realism. We therefore added four neonates with FL < 70 cm and an allocated age of 0.1 y to the growth data; this falls within the FL range reported for neonates (Semba et al. 2011). This increased the variance (uncertainty) of L_0 in the right direction, without unduly constraining the model. Comparison of error structures and growth models in both sex-dependent and sex-pooled formulations was performed, and quality of fit tested by means of likelihood ratio tests. In situations when no significant differences (χ^2-test) were found among models or formulations, the least complex model (lower AIC) was selected. Confidence bands of growth equations were generated after non-parametric bootstrapping of the best fitting model..

Analyses of stomach contents

The prey items in stomachs of makos sampled on longliners at sea were identified to the lowest possible taxonomic level and counted. Prey items of makos collected from bather protection nets were counted and weighed in the laboratory. The percentage contribution of a prey species in terms of number (%N), weight (%W) and frequency of occurrence (%F) in the stomachs examined were used to determine an index of relative importance (IRI) following Hyslop (1980):

$$\mathrm{IRI} = \%F\,(\%N + \%W)$$

Results

Length weight regressions

The regressions between FL (cm) and WW (kg) of makos caught in bather protection nets were significant ($p < 0.001$) and the high r^2 values indicated that the models fitted the data well (Fig. 2). Female FL ranged from 91.5–311.3 cm compared to 102.4–252.4 cm in males. FL and weight differed significantly between males and females (t-tests, $p < 0.0001$ in both cases), with females tending to be longer and heavier. Twenty females, but no males, exceeded 200 kg in weight.

Length frequencies and sex ratios

There was no significant difference in the mean FL (±SD) of makos caught by shark longliners, compared to those caught by longliners targeting tuna and swordfish (t-test, df = 1, p = 0.121; Fig. 3). Both gear types selected small to medium sized makos, despite the presence of a steel trace on hooks used by shark longliners, or the differences in depth targeted by tuna and shark directed vessels. The mean FL of makos caught in bather protection nets (228.6 ± 26.5 cm, n = 290; Fig. 4) was larger than that of makos caught by pelagic longliners (combined data; 146.5 ± 34.5 cm, n = 5738) (t-test, df = 1, p < 0.001).

Longitude, season and year of capture were significant explanatory variables of variation in mako FL in the gamma model of offshore data (Table 2). Vessel flag state did not affect offshore FL significantly, despite some differences in target species (generally tuna for Asian vessels; swordfish and sharks for local vessels), gear configurations and hook size preferences. The model showed an increase in mean FL from west to east over the study area, with the smallest individuals occurring at the edge of the Agulhas Bank and the largest ones near the Mozambique border (Fig. 4). On average, smaller makos were caught during winter (June to August) and spring (September to November) (Table 2). The mean FL was smallest in 2008, and largest in 2010, although the difference was only 10.5 cm. Equal numbers of male and female makos were observed during an observer trip on a shark-directed longliner in 2010 (1.1M : 1F, n = 525, p = 0.556).

In the gamma regression model of coastal data, sex and yeargroup were significant explanatory variables. The model predicted a mean FL of 246 cm and 218 cm for females and males, respectively, for 2005–2010 as reference period. By yeargroup, FL increased up to the early 1990s, and thereafter remained fairly constant, declining noticeably in 2005–2010 (Fig. 5). Males dominated mako catches in bather protection nets from 1990, comprising 77–87% of the catch. Although the decline in mean size of makos in the latest yeargroup is minor, it might be explained by the proportionate reduction of the catch of females, which are normally larger, at that time.

Size at maturity and reproduction

Some 90% of males and nearly 99% of females caught offshore were immature, compared to only 45% of females and 7% of males in coastal catches. Clasper length and calcification increased steeply in males >140 cm FL. Clasper articulation was not present in males <180 cm and became prevalent after 200 cm. Full clasper calcification and articulation was observed in all males with a FL >215 cm. Male size at maturity (L_{50}) was calculated as 190.2 cm, with a maturation range (L_{25}–L_{75}) of 182.4–198.0 cm, which indicates a steep transition to maturity (Fig. 6a).

A total of 44 females were considered to be mature, and had a mean FL of 271.1 ± 17.3 cm. Females < 250 cm were often considered to be immature, because their UW did not exceed 50 mm. L_{50} was estimated at 249.8 cm with a maturation range of 241.3–256.8 cm (Fig. 6b).

Five gravid females captured in the bather protection nets ranged from 252–263 cm FL. Three of these carried pups; the litters sizes were 14 (mean FL ± sd of 43.5 ± 1.8 cm), 12 (47.0 ± 1.1 cm) and nine (FL not measured). The other two possessed fertilized eggs in their uteri and bore mating scars on the pectoral fins and abdomen. A female which stranded in the centre of the netted region had a litter of 9 (51.8 ± 1.6 cm). No gravid females were observed on the longliners.

Vertebral analyses

Linear regressions of radius of post-cranial vertebrae (VR, mm) against FL were significant ($p < 0.001$) and fitted the data well for males ($VR = 0.0799 \times FL - 2.6775$, $n = 46$, $r^2 = 0.92$) and females ($VR = 0.0776 \times FL - 2.4212$, $n = 43$, $r^2 = 0.95$), respectively. No significant difference was found in the intercepts ($p = 0.925$) or slopes ($p = 0.929$) of the regressions, indicating that the VR increases linearly with FL, irrespective of growth rate differences between sexes. Therefore a sex-pooled regression was fitted as follows: $VR = 0.0799 \times FL - 2.7166$ ($n = 89$, $r^2 = 0.94$).

Sections of 18 mako vertebrae were unreadable, and a further 15 were rejected because replicate counts differed by >3 bands, or the APE was >20%. The remaining vertebral sections were from 43 females (91–297 cm FL) and 46 males (90–299 cm), and samples of at least two makos of each sex were available per 10 cm length class between 130 and 230 cm. A pre-birth band-pair was observed in most vertebral sections, but an angle change in the corpus calcareum coinciding with the birth band was not always evident (see Natanson et al. 2006).

The APE was 10.4% and 19.4% for primary and secondary readers respectively, falling within the stipulated 20% error margin (see Campana 2001), and the accuracy of counts did not differ between readers (paired t-test; $p>0.05$). The counts made by the two readers were strongly correlated ($r^2= 0.97$; $p<0.05$) and were identical in 25% of all counts; there was 87% agreement between counts for animals up to 1 year old, and 54% agreement between those aged 2 years.

Growth models

The smallest and largest makos in the aged material were both males, measuring 90 cm (1 y old) and 299 cm FL (17 y old), respectively (Fig. 7). Exploratory trials revealed no consistent differences in the growth of males and females, irrespective of model formulation (von Bertalanffy or Gompertz) and sex-pooled models were therefore preferred. Models in which L_0 was constrained to 65 cm resulted in a bad fit of length data to ages 1-4 (the bulk of the data), and a low L_∞ compared to the larger individuals observed in coastal samples. In these formulations, the VBM fitted the data significantly better than the GM (LRT; $p < 0.001$). Allowing the models to fit an unconstrained L_0 resulted in unrealistically high estimates of L_0 (109.0 cm) and L_∞ (367 cm). The introduction of four neonates with assumed age of 0.1 y to the data resulted in the best fit to the sex-pooled VBM, even though the model was unable to provide an L_0 estimate <79 cm (lower bound). In these formulations the VBM fitted marginally better (lower AIC), than the GM and it also fitted better than more complex VBM formulations with sex-dependent k and L_∞ parameters. The sex-pooled VBM was therefore selected as the most realistic model of mako growth, and growth parameters (with 95% confidence intervals) were estimated to be 90.4 cm (79.6 – 101.0 cm) for L_0, 285.4 cm (237.1 – 333.7 cm) for L_∞, and 0.113 y^{-1} (0.058 – 0.168 y^{-1}) for k. The global uncertainty in the model, as denoted by its 95% confidence bands, is greater for older mako (right side of Fig. 7). However, it increases as well for the length at birth (L_0), a consequence of the inclusion of neonates in the material.

Stomach contents

The stomach contents of 840 makos were analyzed; 292 of these were from the coastal dataset (Table 4) and 548 from the offshore dataset (Table 5). Of coastal samples, 107 stomachs (36.6%) were empty, and the remainder revealed 45 different types of prey item, of which 21 could be identified to species level, 21 to order or family, and three items (plastics, twine and terrestrial refuse) were of an anthropogenic origin. Elasmobranchs were the most common prey item in coastal samples (63.5%F and 72.8%W). Unidentified sharks of varying sizes contributed 36.5%F, followed by milk sharks *Rhizoprionodon acutus* (7.2%F), and dusky sharks *Carcharhinus obscurus* (5.0%F). Dusky sharks contributed 19.9%W, followed by spotted eaglerays *Aetobatus narinari* (6.7%W). Spotted eaglerays comprised two large individuals, and therefore contributed only 1.1%F. Prey items that only occurred once (IRI < 2) were dogfish *Squalus* sp., blacktip *Carcharhinus limbatus*, smooth hammerhead *Sphyrna zygaena* and spotted ragged-tooth *Carcharias taurus* sharks.

Teleosts contributed 43.1%F and 27.2%W in coastal samples, and based on IRI they were less important (1036) than elasmobranchs (1184). Most teleosts could not be identified (29.8%F), and of 13 species that could be identified, spotted grunter *Pomadasys commersonni* was most common (2.8%F). Although cephalopods were common (25.5%N; 36.5%F), only the digestion-resistant beaks were usually present, and this may lead to an overestimate of their true importance in mako diet. Squid (Teuthida) were the most common cephalopod prey (16.0%F) and the third most frequent prey item.

Of 548 mako stomachs from the offshore dataset, 379 (69.2%) were empty. Cape horse mackerel *Trachurus capensis* was the most common prey (35.5%F), followed by unidentified teleosts (14.8%F), sardine *Sardinops sagax* (14.2%F), and squid *Loligo spp* (13.6%F). Elasmobranchs were conspicuously absent from the offshore samples, with the exception of a single small mako (0.6%F) that was swallowed by a larger mako, presumably after being hooked on the long-line.

Discussion

Clear spatial trends in mako size composition emerged from the GLM models used to analyse offshore and coastal data (see Fig. 4). The offshore model showed an increase in mean FL from west to east, with the smallest individuals occurring at the Agulhas Bank edge and larger ones upstream in the Agulhas Current, near the Mozambique border. Nearly all makos caught in offshore samples were juveniles with a FL of 90 cm and greater. Much larger makos were captured in coastal bather protection nets, and unlike those from the offshore samples, a large percentage of these were mature and reproductively active. It is therefore hypothesized that mature makos move closer to the coast in eastern South Africa, where some females give birth. Boat anglers have reported catches of neonates (<75 cm) several kilometres offshore of the central KZN coast, suggesting that pupping takes place in these shelf waters (Cliff et al. 1990).

The above hypothesis assumes that the length distributions of catches made by longliners and bather protection nets were not biased by gear selectivity. No difference in length distributions of makos caught in shark directed, compared to tuna and swordfish directed vessels, could be found, despite the differences in longline configurations and depth intervals targeted. The sparsity of large makos in longline catches suggests that they are not abundant in offshore waters, or that the gear used do not retain large individuals long enough for them to be brought on board. A low abundance of large individuals in offshore waters appears to be the more likely explanation, because hooks directed at sharks and fitted with a 50 cm steel trace also failed to catch larger makos. Adult makos dive much deeper than juveniles (Sepulveda et al. 2004; Loeffer et al. 2005), but hooks set in deeper strata (40–400 m) for tuna did not catch more large specimens, suggesting that they are not abundant at greater depth.

Length frequency distributions of 14 shark species caught in the KZN bather protection nets showed little evidence of size selectivity (Dudley and Simpfendorfer 2006). These multifilament nets caught a broad size range, from neonate *Carcharhinus obscurus* to adult *Carcharodon carcharias*, through entangling. The capture method differs from commercial monofilament gill nets, which hook on the gills and select narrower size ranges (Kirkwood and Walker 1986; Simpfendorfer and Unsworth 1998). Makos caught in bather protection nets therefore probably represent the size and sex distribution of the nearshore populations accurately, rather than biasing the data by selecting only larger specimens.

The capture of mature females in bather protection nets, including five gravid females, confirms that some pupping occurs in coastal waters. However, these nets off eastern South Africa are restricted to a small area between Richards Bay (28°48’S) and Mzamba (31°05’S), and therefore no firm conclusions can be drawn on the extent of coastal pupping grounds. Bustamante and Bennett (2013) similarly suggested the existence of a coastal pupping and nursery area along the coast of northern Chile. The preponderance of juveniles at the Agulhas Bank edge suggests that it may be a juvenile feeding ground, and this is supported by high catch rates, compared to fishing grounds further east (Foulis 2013). Separate feeding grounds for juvenile makos were previously proposed for the NW Atlantic (Casey and Kohler 1992).

A key assumption when using band pair counts in vertebrae to age makos was that band pairs are deposited annually. Although some uncertainty remains over band deposition rates, especially in young makos (Wells et al. 2013), the bulk of the evidence supports annual depositions. Radiocarbon methods (Campana et al. 2002; Natanson et al. 2006), marginal increment analysis (Ribot-Carballal et al. 2005), and a mako injected with OTC off eastern South Africa (Natanson et al. 2006) have all suggested the deposition of a single band-pair per year. A second assumption was that the number of bands in vertebrae was independent of their exact place of excision along the vertebral column. Bishop et al. (2006) and Natanson et al. (2006) found no difference in mako band counts along the vertebral column. This finding is important in the present study, because post-cranial vertebrae as well as those from immediately anterior to the first dorsal fin were used for counts. The pre-birth band visible in most vertebrae has been attributed to a change in embryonic diet, from internal yolk to eggs (Branstetter and Musick 1994).

Vertebral band widths were broader in smaller (younger) makos than in larger (older) specimens, where bands became narrower and compacted towards the periphery of the corpus calcareum. Band counts for larger makos were therefore presumably less accurate than for smaller ones, causing under-estimation of ages when the peripheral bands become too narrow to distinguish (Francis et al. 2007). Cerna and Licandeo (2009) also attributed the larger variation observed in the band counts of older makos to the difficulty of reading the bands, and to the smaller number of available samples.

No consistent difference could be observed between male and female growth rates, and therefore a sex-pooled VBM was selected to describe mako length-at-age. In contrast, several other studies have found that males grow faster than females (larger k), but do not become as large (smaller L_∞) (Pratt and Casey 1983; Bishop et al. 2006; Natanson et al. 2006; Cerna and Licandeo 2009; Semba et al. 2009). With the exception of Bishop et al. (2006) (Schnute growth model), the above studies were also based on von Bertalanffy and Gompertz growth models. The failure of our model to distinguish between male and female growth rates can probably be attributed to a relatively small samples size, few large adults in samples, and high variability of band counts, particularly in large individuals where bands became difficult to distinguish. The growth coefficient in the present study ($k = 0.113\ y^{-1}$) compared well with previous estimates of 0.087–0.125 y^{-1} in the NW Atlantic (Natanson et al. 2006), 0.076-0.087 y^{-1} in the SE Pacific (Cerna and Licandeo 2009), and 0.09-0.156 in the North Pacific (Semba et al. 2009). The L_∞ estimate of 285 m (sexes pooled) was close to the FL of the largest observed mako in this study (311 cm), and comparable to estimates from the NW Atlantic and Pacific (255–366 cm; Pratt and Casey 1983; Natanson et al. 2006; Cerna and Licandeo 2009; Semba et al. 2009). The overall uncertainty in our growth model is largest for the oldest makos, a poorly represented group in most studies of makos.

Based on band counts, the oldest observed male mako was aged 19.5 y (267 cm FL) and the oldest female 18.5 y (249 cm). These counts most likely underestimate the real age of the specimens, because peripheral bands become too narrow to distinguish and count in older animals (Francis et al. 2007). Longevity in other regions have been estimated as 21-38 y in the NW Atlantic (Natanson et al. 2006) and 28-29 y in the Pacific (Bishop et al. 2006). Semba et al. (2009) counted a maximum of 14 annuli in a male mako of 264 cm FL and 20 in a female of 331 cm in the North Pacific. Pratt and Casey (1983) assumed biannual band pair deposition, and consequently reported younger longevity (10-17 y) relative to studies that assumed annual deposition. Age validation of juvenile makos tagged and marked with OTC off southern California suggested rapid growth, with biannual deposition of growth bands in vertebrae for the first 5 y (Wells et al. 2013).

Male makos reached maturity after 6.5–7 y and females after 13–13.5 y, and these estimates compared well with published values of 6–8 y and 15–20 y, respectively (Ribot-Carballal et al. 2005; Bishop et al. 2006; Natanson et al. 2006; Semba et al. 2009). Males reached maturity (L_{50}) at 190 cm FL, slightly larger than estimates of

180–185 cm off New Zealand (Francis and Duffy 2005), 180 cm in the eastern North Atlantic (Maia et al. 2007), 179 cm off New South Wales (Stevens 1983) and 171 cm in the west and central Pacific (Semba et al. 2011). Females reached maturity at 250 cm FL, compared to 275-285 cm off New Zealand (Francis and Duffy 2005), 282 cm in the west and central Pacific (Semba et al. 2011) and 258 cm of New South Wales (Stevens 1983). Mollet et al. (2000) found that southern hemisphere females matured at 249 cm, compared to 272 cm in the western North Atlantic, but in combination, the above studies do not support a larger maturation size in northern, than in southern waters, for either sex.

The observed litter sizes (9–14) fall within the general range of 4–18 (Stevens 1983, Gilmore 1993). Mollet et al. (2000; 2002) reported a mean litter size of 12.5 pups, and a possible maximum of 25 to 30 pups. The mean FL of pups removed from the uteri of three gravid females in the current study (43.5, 47.0 and 51.8 cm) was well below the birth length of around 60 cm (Mollet et al. 2000) suggesting that they were in mid-term.

Some 36.6% of makos caught in bather protection nets had empty stomachs, and this was similar to 40.9% reported for the same capture method and area for the period 1978–1989 (Cliff et al. 1990). The percentage of empty mako stomachs was 31.6% in the NW Atlantic (Stillwell and Kohler 1982), and 32.9% off New South Wales (Stevens 1984). Makos caught with longlines had empty stomachs in 69.8% of samples. A high percentage of empty stomachs is common among studies of sharks caught by longlines, and may be explained by ingestion of water and regurgitation of stomach contents while the shark attempts to free itself from the hook (Vaske and Rincón 1998; Wetherbee et al. 1990). Alternatively, sharks with full stomachs may not take bait as frequently as those with empty stomachs, or prey may have been scarce in the sampled area.

Makos in the present study preyed on teleosts (mainly *T. capensis* and *S. sagax*), elasmobranchs (*R. acutus* and *C. obscurus*) and cephalopods (*Loligo* sp.) Stevens (1984) found mainly teleosts in mako stomachs from Australia, and Maia et al. (2006) found mostly teleosts and cephalopods off Portugal. Jumbo squid *Dosidicus gigas* and Pacific saury *Cololabis saira* were important prey in the California Current (Preti et al. 2012) and in the NW Atlantic, 92%W comprised bluefish *Pomatomus saltatrix* (Wood et al. 2009). Rogers et al. (2012) showed preliminary evidence of diet specialization in makos, commensurate with other highly migratory species, despite relatively high prey diversity (Preti et al. 2012).

In agreement with Cliff et al. (1990), elasmobranchs were the most common prey of makos caught in bather protection nets in coastal waters (63.5%F; 72.8%W). We suggest that larger makos move closer to the coast because of increased food availability over the shelf compared to offshore waters. Presumably larger makos are able to manage larger prey items (Stillwell and Kohler 1982), and the most common prey in coastal waters in the present study was the milk shark *R. acutus,* which attains 1 m in length. Other relatively large and frequent prey items were the dusky shark *C. obscurus*, a common coastal species with its nursery grounds in KZN waters (Dudley et al. 2005), spinner *C. brevipinna* and blackspot sharks *C. sealei*. Makos caught offshore preyed mainly on much smaller pelagic teleosts, such as *T. capensis* and *S. sagax.*

To conclude, mako populations in the SW Indian Ocean were demographically structured, with juveniles occurring mainly in offshore waters and larger, reproductively active adults appearing in coastal waters. The Agulhas Bank edge appears to be a feeding ground for juveniles during winter and spring. Growth rates and age-at-maturity appear to be lower than in the NW Atlantic and Pacific, but this result may have been influenced by the small number of large individuals available for ageing. Makos captured near the coast preyed mainly on elasmobranchs, whereas smaller makos fed on teleosts and cephalopods in offshore waters. These differences in diet may reflect the relative abundance of prey in the two environments, but prey size may also be a factor that attracts larger makos to coastal waters. The occurrence of gravid females in coastal samples suggests that some females pup in shelf waters in the SW Indian Ocean.

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Figure captions:

Figure 1: GPS capture positions of *Isurus oxyrinchus* sampled by fisheries observers stationed on longliners between 2005 and 2010, and location of bather protection nets between Richards Bay (28°48'S) and Port Edward (31°04'S). Nets further south (Mzamba, 31°05'S) were removed in 2000. Nets are set parallel to beaches, 300-500 m offshore, and are ~214 m long by 6.3 m deep (Cliff and Dudley 2011).

Figure 2: Relationship between fork length and whole weight of a) female and b) male *Isurus oxyrinchus*, respectively, caught in bather protection nets.

Figure 3: Length frequency distributions of makos caught in offshore waters of the South West Indian Ocean by longliners targeting sharks, compared to those targeting tuna and swordfish.

Figure 4: Modelled versus observed fork length of *Isurus oxyrinchus* in offshore and coastal waters of the SW Indian Ocean. Observed fork length (± SD) is shown for three areas to illustrate increasing mako size: Agulhas Bank (20–22°E), South Coast (22–29°E), and East Coast (29–35°E). Makos captured outside of the three offshore areas were excluded.

Figure 5: Proportion of male *Isurus oxyrinchus* caught in bather protection nets (binomial model), and trends in male and female fork length, respectively, by year-group (gamma model) between 1978 and 2010.

Figure 6: Fitted logistic regression showing the predicted probability of maturity in (a) female and (b) male *Isurus oxyrinchus* relative to fork length. The histograms represent the observed data as frequency of immature individuals (bottom axis) and mature individuals (top axis).

Figure 7: Von Bertalanffy growth model fitted to sex-pooled fork length-at-age data of shortfin mako *Isurus oxyrinchus*. Non-integers are the average of counts between readers where final counts differed by one band. Female fish are indicated by circles

and males by crosses; the shaded area is the 95% confidence band of the growth model fitted.

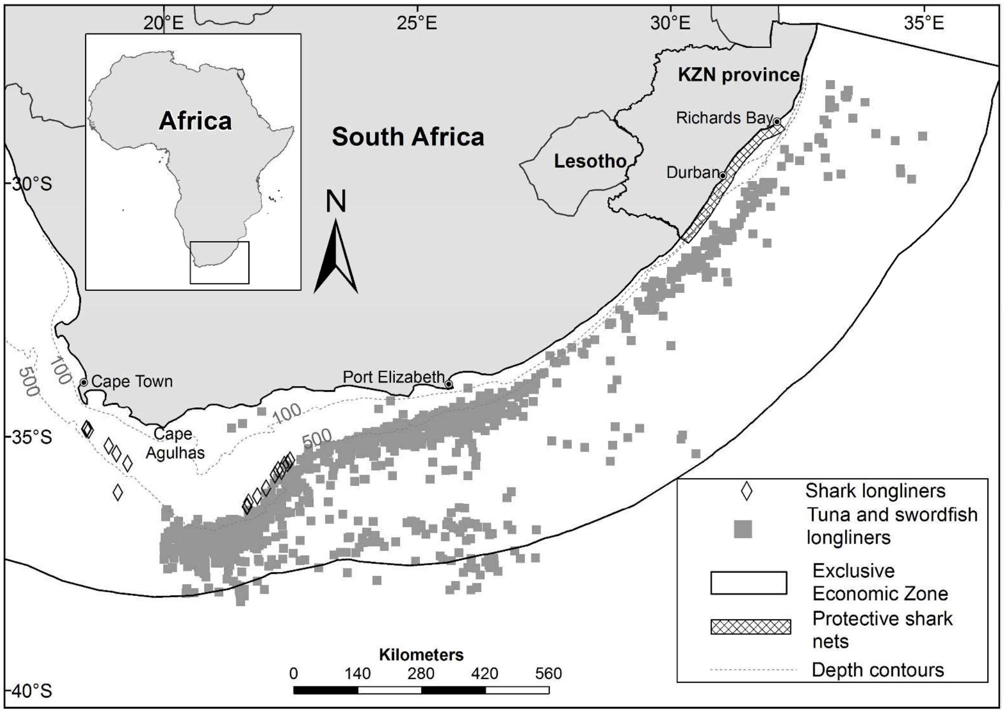


Figure 1: GPS capture positions of Isurus oxyrinchus sampled by fisheries observers stationed on longliners between 2005 and 2010, and location of bather protection nets between Richards Bay (28°48′S) and Port Edward (31°04′S). Nets further south (Mzamba, 31°05′S) were removed in 2000. Nets are set parallel to beaches, 300-500 m offshore, and are ~214 m long by 6.3 m deep (Cliff and Dudley 2011).
297x209mm (300 x 300 DPI)

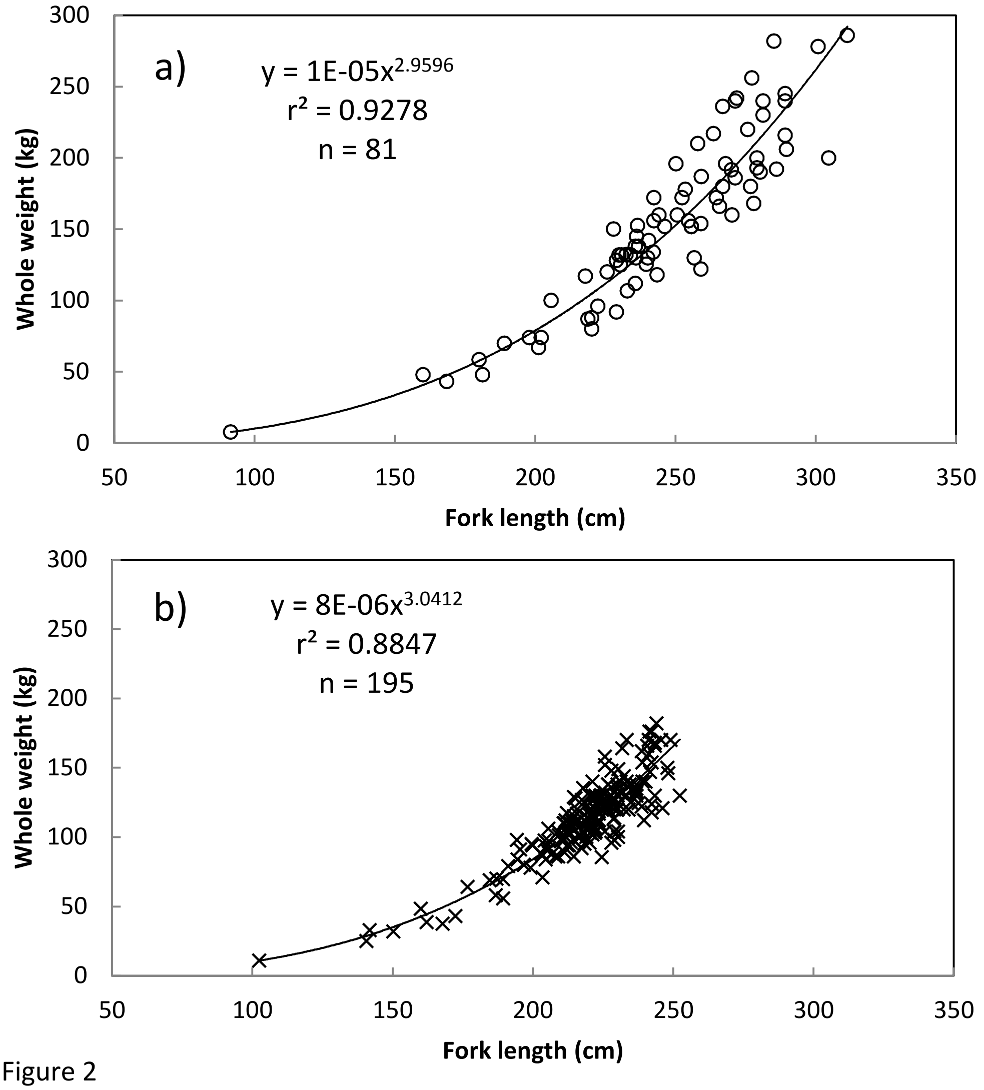
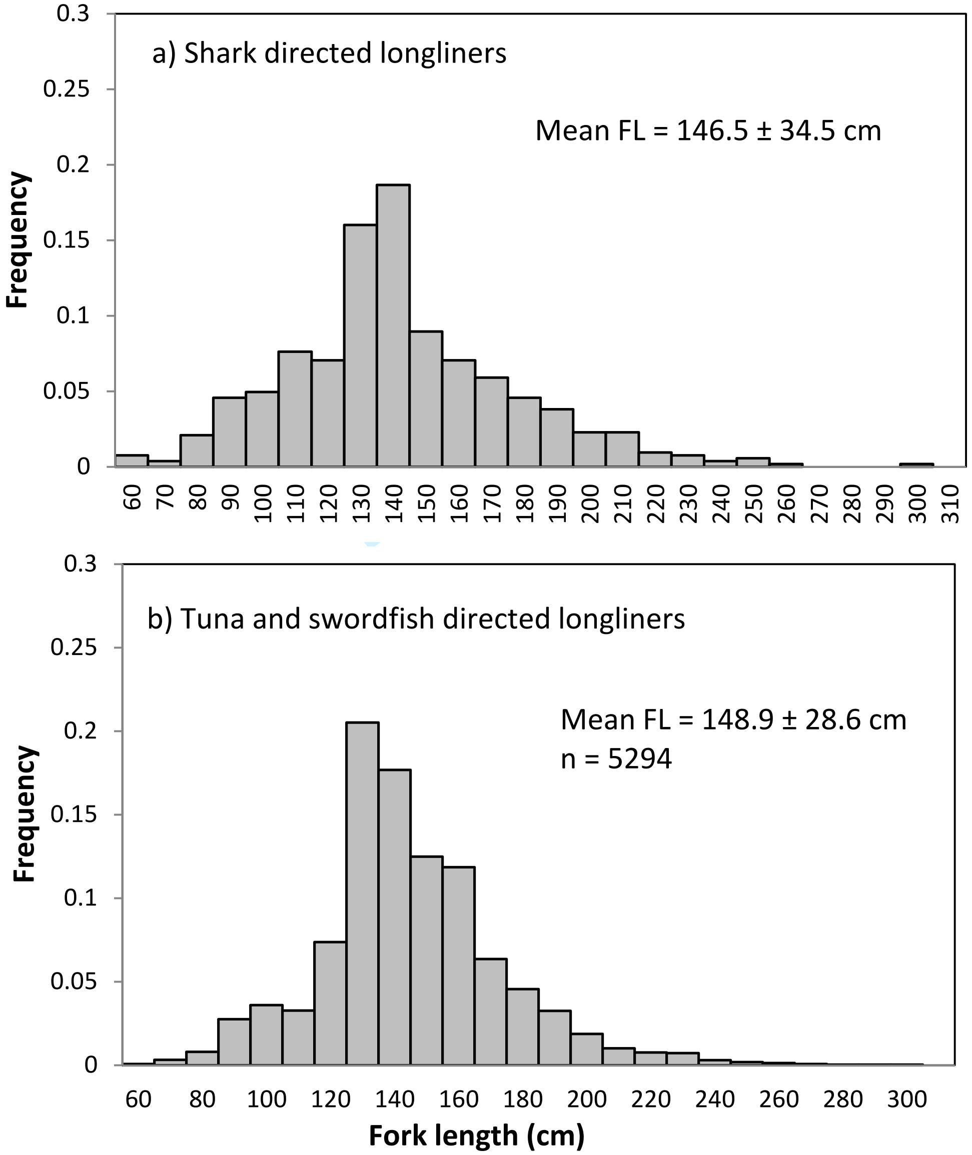

a)
$y = 1E\text{-}05x^{2.9596}$
$r^2 = 0.9278$
n = 81
Whole weight (kg)
0
50
100
150
200
250
300
Fork length (cm)
50
100
150
200
250
300
350
b)
$y = 8E\text{-}06x^{3.0412}$
$r^2 = 0.8847$
n = 195
Whole weight (kg)
0
50
100
150
200
250
300
Fork length (cm)
50
100
150
200
250
300
350

Figure 2


a) Shark directed longliners
Mean FL = 146.5 ± 34.5 cm
Frequency
0.3
0.25
0.2
0.15
0.1
0.05
0
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
240
250
260
270
280
290
300
310
b) Tuna and swordfish directed longliners
Mean FL = 148.9 ± 28.6 cm
n = 5294
Frequency
0.3
0.25
0.2
0.15
0.1
0.05
0
60
80
100
120
140
160
180
200
220
240
260
280
300
Fork length (cm)

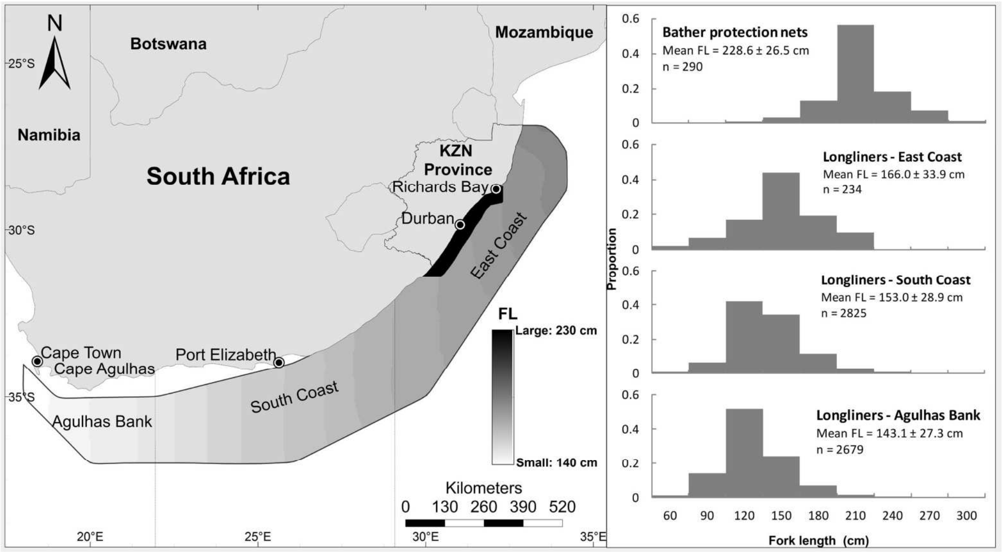


Figure 4: Modelled versus observed fork length of Isurus oxyrinchus in offshore and coastal waters of the SW Indian Ocean. Observed fork length (± SD) is shown for three areas to illustrate increasing mako size: Agulhas Bank (20–22°E), South Coast (22–29°E), and East Coast (29–35°E). Makos captured outside of the three offshore areas were excluded.
264x145mm (300 x 300 DPI)

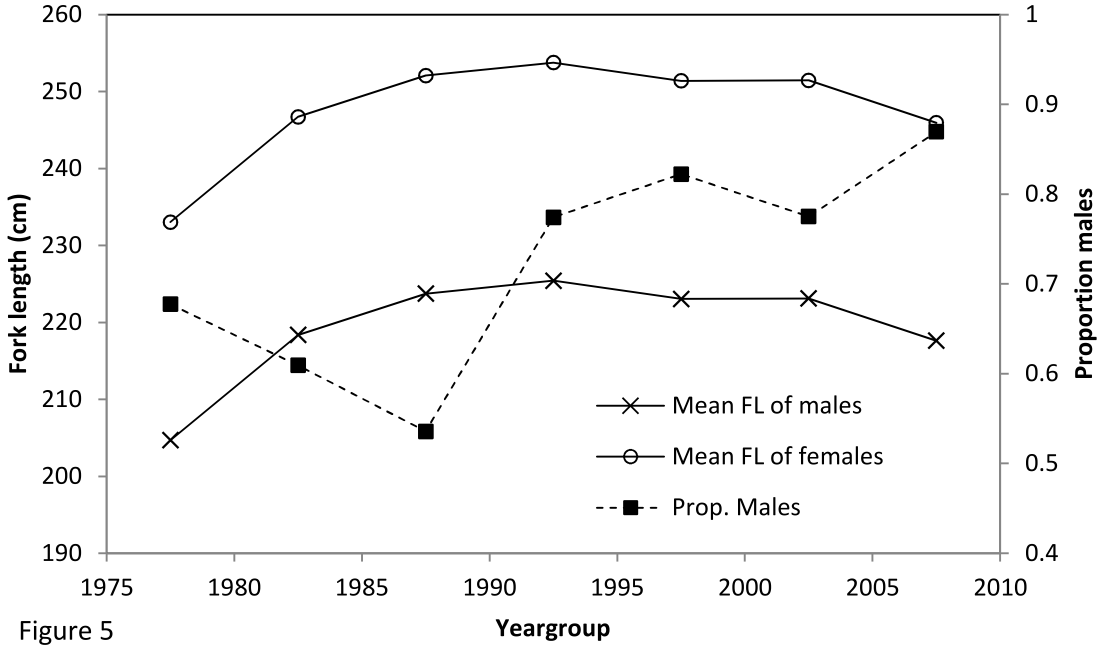

260
250
240
230
220
210
200
190
Fork length (cm)
1
0.9
0.8
0.7
0.6
0.5
0.4
Proportion males
1975
1980
1985
1990
1995
2000
2005
2010
Yeargroup
Mean FL of males
Mean FL of females
Prop. Males

Figure 5

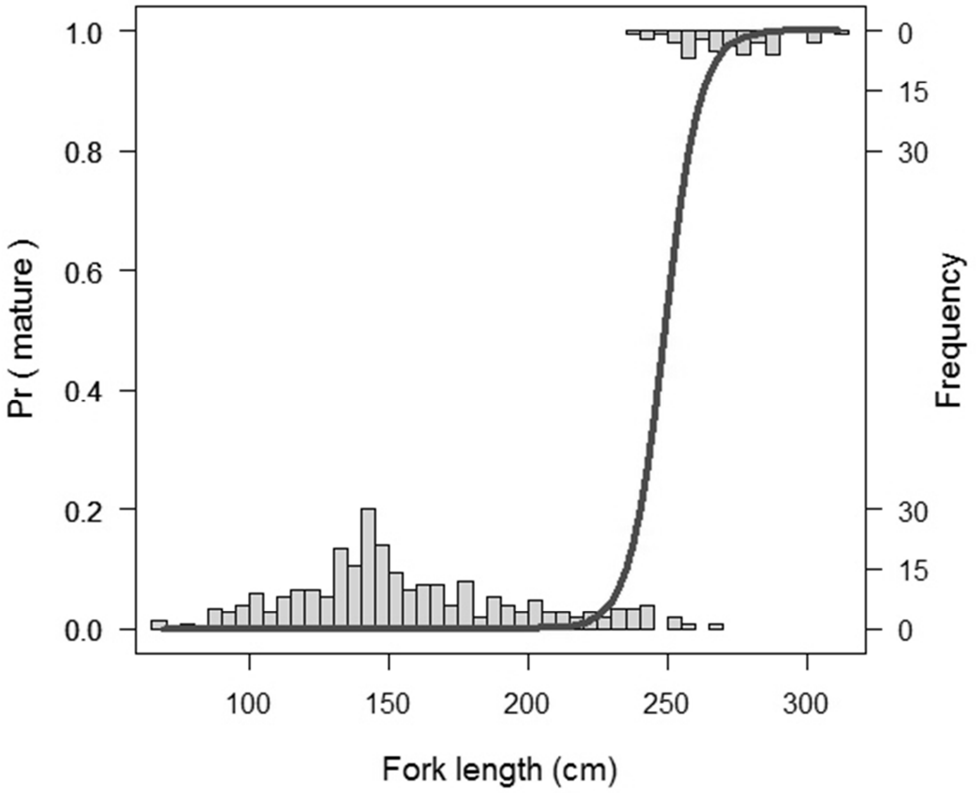


Figure 6a: Fitted logistic regression showing the predicted probability of maturity in (a) female and (b) male Isurus oxyrinchus relative to fork length. The histograms represent the observed data as frequency of immature individuals (bottom axis) and mature individuals (top axis).

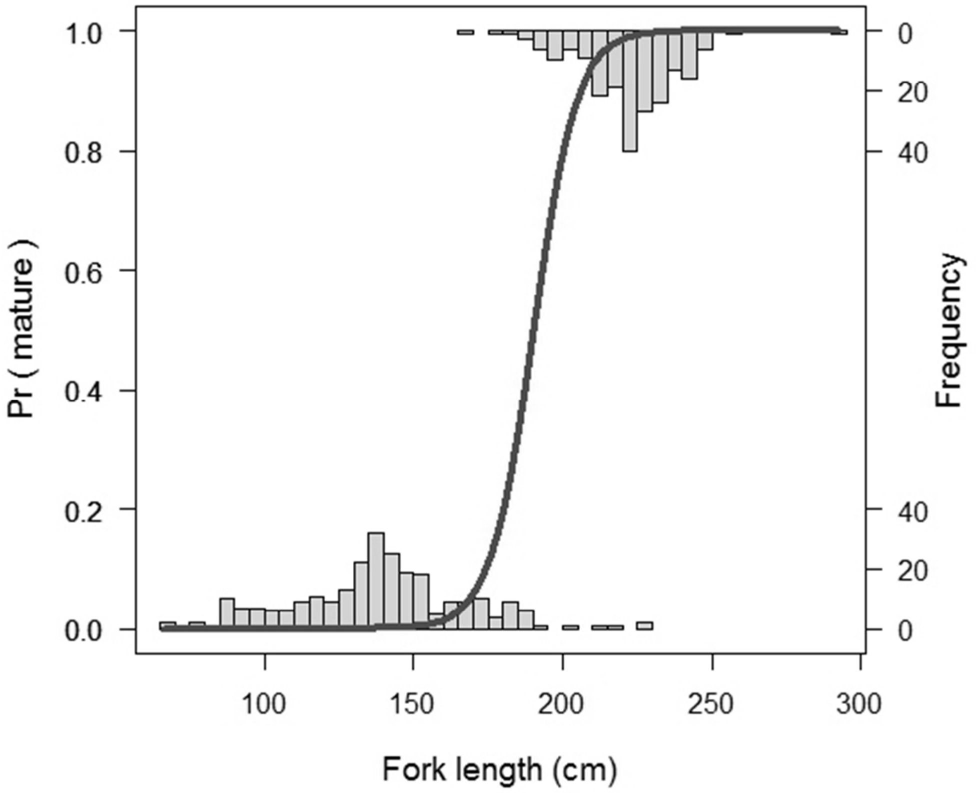
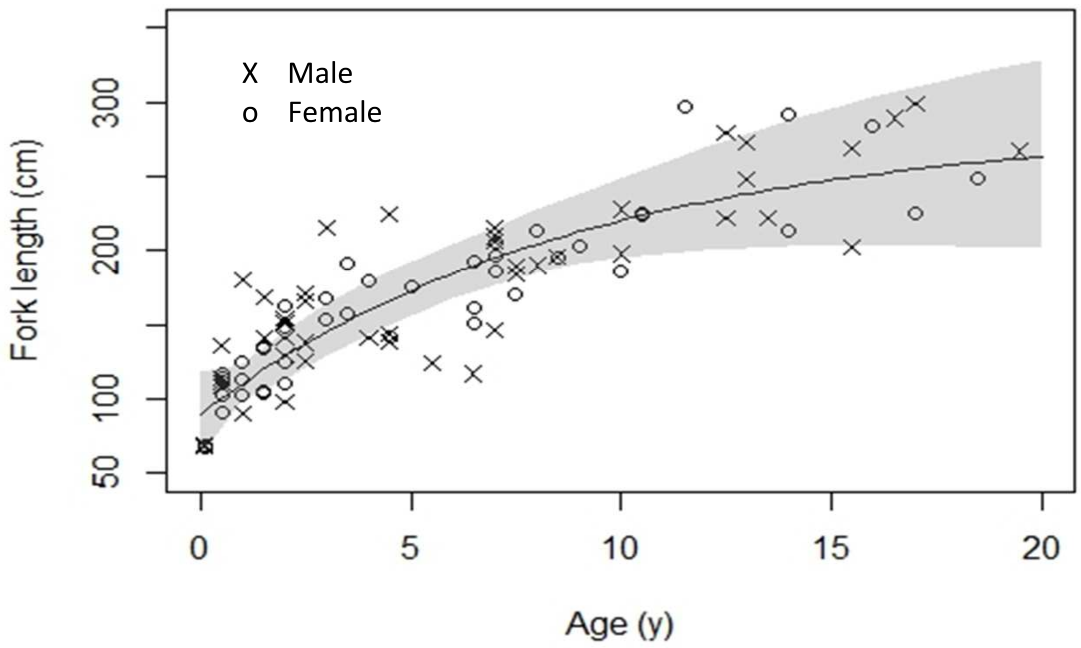


Figure 6b: Fitted logistic regression showing the predicted probability of maturity in (a) female and (b) male Isurus oxyrinchus relative to fork length. The histograms represent the observed data as frequency of immature individuals (bottom axis) and mature individuals (top axis).



X Male
o Female
Fork length (cm)
50
100
200
300
0
5
10
15
20
Age (y)

Table 1: Candidate factors hypothesized to affect fork length, sex ratio and size at maturity of shortfin mako, *Isurus oxyrinchus* , caught in pelagic longlines (offshore data) and bather protection nets (coastal data) off south-eastern South Africa

Variable	Type	Dataset	Description
Year	Categorical	Offshore	2005, 2007 - 2010 (5 levels)
Yeargroup	Categorical	Coastal	1978 - 2010; 5-year groups (7 levels)
Latitude	Continuous*	Offshore	28.1 to 39.7°S
	Categorical	Coastal	Beaches North and South of 30°S (2 levels)
Longitude	Continuous	Offshore	18.5 to 35.0°E
Season	Categorical	Coastal and Offshore	Summer = December to February
			Autumn = March to May
			Winter = June to August
			Spring = September to November
Flag state	Categorical*	Offshore	Japan, Korea, South Africa, Unknown (4 levels)
Sex	Categorical	Coastal	Male and Female
Size	Continuous	Coastal and Offshore	Fork length (cm)

* = Not used in final models

Table 2: Coefficients (± s.e.) of parameters retained in the final generalized linear models (GLM) that describe fork length (FL), maturity and sex distribution of shortfin mako *Isurus oxyrinchus.* Estimates marked with * were significantly different ($p < 0.05$) from the intercept. The offshore FL and maturity models were fit without a constant (intercept). The sex distribution model was based on coastal data only, and predicts the proportion of either sex.

	Offshore FL	Coastal FL	Sex distribution	Maturity
Factors	Longitude + Season + Year	Sex + Latitude + Yeargroup	Yeargroup	Sex + Size
Error	Gamma	Gamma	Binomial	Binomial
Link	Identity	Identity	Logit	Logit
AIC	54351	2649.9	351.67	142.78
n	5738	290	290	792
	Estimate (s.e.)	Estimate (s.e.)	Estimate (s.e.)	Estimate (s.e.)
Intercept	-	230.892 (4.469)*	0.742 (0.384)	-
Latitude		5.074 (2.727)		
Longitude	2.242 (0.146)*			
Summer	105.452 (4.256)*			
Autumn	104.903 (3.573)*			
Winter	98.723 (3.472)*			
Spring	99.828 (3.416)*			
2005	0			
2007	-4.216 (1.091)*			
2008	-9.314 (1.207)*			
2009	-2.933 (1.246)*			
2010	1.193 (1.552)			
1978-1979		0	0	
1980-1984		13.600 (4.623)*	-0.297 (0.462)	
1985-1989		17.994 (4.847)*	-0.599 (0.468)	
1990-1994		20.405 (5.470)*	0.490 (0.576)	
1995-1999		18.760 (4.964)*	0.790 (0.547)	
2000-2004		17.976 (5.106)*	0.495 (0.539)	
2005-2010		13.665 (5.826)*	1.155 (0.729)	
Sex		-27.960 (3.060)*		
Male				-35.872 (3.961)*
Female				-27.392 (3.063)*
FL (cm)				0.1440 (0.159) *

Table 3: Stomach contents of *Isurus oxyrinchus* caught in coastal waters by bather protection nets. Totals represent the number of prey items (N), the numbers of stomachs (F) with food and the weight of the prey (W, kg). IRI is the index of relative importance. UID is unidentified.

	Common name	Scientific name	%N	%F	%W	IRI
Elasmobranch	UID small shark		19.31	27.62	11.62	854.2
	Milk shark	*Rhizoprionodon acutus*	5.02	7.18	4.77	70.3
	UID shark		4.63	6.63	7.42	79.9
	Dusky shark	*Carcharhinus obscurus*	3.47	4.97	19.88	116.1
	UID elasmobranch		3.47	4.97	0.40	19.2
	UID large shark		1.54	2.21	0.51	4.5
	Requiem sharks	Carcharhinidae	1.16	1.66	3.65	8.0
	Stingray	Dasyatidae	1.16	1.66	3.38	7.5
	Blackspot shark	*Carcharhinus sealei*	0.77	1.1	5.32	6.7
	Spinner shark	*Carcharhinus brevipinna*	0.77	1.1	3.95	5.2
	Catsharks	Scyliorhinidae	0.77	1.1	0.01	0.8
	Spotted eagleray	*Aetobatus narinari*	0.77	1.1	6.73	8.2
	Dogfish	*Squalus sp.*	0.39	0.55	0.01	0.2
	Blacktip shark	*Carcharhinus limbatus*	0.39	0.55	0.85	0.7
	Smooth hammerhead shark	*Sphyrna zygaena*	0.39	0.55	2.77	1.7
	Spoted ragged-tooth shark	*Carcharias taurus*	0.39	0.55	1.49	1.0
	ALL ELASMOBRANCHS		**44.4**	**63.5**	**72.77**	**1184.4**
Teleost	UID teleost		19.35	29.83	13.38	1008.1
	Spotted grunter	*Pomadasys commersonnii*	1.79	2.76	1.33	8.9
	Tunas	*Scombridae*	1.43	2.21	2.13	8.3
	Spadefish	*Tripteron orbis*	0.72	1.1	0.86	1.8
	Dusky kob	*Argyrosomus japonicus*	0.72	1.1	1.95	3.1
	Needlefishes	Belonidae	0.39	0.55	0.38	0.4
	Sailfin rubberlip	*Diagramma pictum*	0.39	0.55	2.94	2.0
	Blacktail	*Diplodus sargus*	0.39	0.55	0.13	0.3
	Bronze bream	*Pachymetopon grande*	0.39	0.55	0.59	0.5
	German	*Polyamblyodon germanum*	0.39	0.55	0.52	0.5
	Geelbek	*Atractoscion aequidens*	0.39	0.55	0.08	0.2
	Cape knifejaw	*Oplegnathus conwayi*	0.39	0.55	0.03	0.2
	Blacktip kingfish	*Caranx sem*	0.39	0.55	0.78	0.7
	Giant yellowtail	*Seriola lalandi*	0.39	0.55	0.79	0.2
	Chub mackerel	*Scomber japonicus*	0.39	0.55	0.21	0.3
	Sailfish	*Istiophorus platypterus*	0.39	0.55	1.05	0.2
	ALL TELEOSTS		**28.3**	**43.05**	**27.15**	**1035.8**
Cephalopod	Squid	Teuthida	11.2	16.02	0.00	179.4
	Cuttlefish	Sepiida	8.88	12.71	0.00	112.9
	Loligo squids	*Loligo spp.*	3.09	4.42	0.00	13.7
	Octopus	Octopoda	2.32	3.31	0.00	7.7
	ALL CEPHALOPODS		**25.49**	**36.46**	**0.00**	**313.6**

Table 4: Stomach contents of *Isurus oxyrinchus* caught in coastal waters by bather protection nets. Totals represent the number of prey items (N), the numbers of stomachs (F) with food and the weight of the prey (W, kg). UID = Unidentified

	Common name	Scientific name	%N	%F	%W	IRI
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	UID shark		4.63	6.63	7.42	79.9
	Dusky shark	*Carcharhinus obscurus*	3.47	4.97	19.88	116.1
	UID elasmobranch		3.47	4.97	0.40	19.2
	UID large shark		1.54	2.21	0.51	4.5
	Requiem sharks	Carcharhinidae	1.16	1.66	3.65	8.0
	Stingray	Dasyatidae	1.16	1.66	3.38	7.5
	Blackspot shark	*Carcharhinus sealei*	0.77	1.1	5.32	6.7
	Spinner shark	*Carcharhinus brevipinna*	0.77	1.1	3.95	5.2
	Catsharks	Scyliorhinidae	0.77	1.1	0.01	0.8
	Spotted eagleray	*Aetobatus narinari*	0.77	1.1	6.73	8.2
	Dogfish	*Squalus sp.*	0.39	0.55	0.01	0.2
	Blacktip shark	*Carcharhinus limbatus*	0.39	0.55	0.85	0.7
	Smooth hammerhead shark	*Sphyrna zygaena*	0.39	0.55	2.77	1.7
	Spoted ragged-tooth shark	*Carcharias taurus*	0.39	0.55	1.49	1.0
	ALL ELASMOBRANCHS		**44.4**	**63.5**	**72.77**	**1184.4**
Teleost	UID teleost		19.35	29.83	13.38	1008.1
	Spotted grunter	*Pomadasys commersonnii*	1.79	2.76	1.33	8.9
	Tunas	*Scombridae*	1.43	2.21	2.13	8.3
	Spadefish	*Tripteron orbis*	0.72	1.1	0.86	1.8
	Dusky kob	*Argyrosomus japonicus*	0.72	1.1	1.95	3.1
	Needlefishes	Belonidae	0.39	0.55	0.38	0.4
	Sailfin rubberlip	*Diagramma pictum*	0.39	0.55	2.94	2.0
	Blacktail	*Diplodus sargus*	0.39	0.55	0.13	0.3
	Bronze bream	*Pachymetopon grande*	0.39	0.55	0.59	0.5
	German	*Polyamblyodon germanum*	0.39	0.55	0.52	0.5
	Geelbek	*Atractoscion aequidens*	0.39	0.55	0.08	0.2
	Cape knifejaw	*Oplegnathus conwayi*	0.39	0.55	0.03	0.2
	Blacktip kingfish	*Caranx sem*	0.39	0.55	0.78	0.7
	Giant yellowtail	*Seriola lalandi*	0.39	0.55	0.79	0.2
	Chub mackerel	*Scomber japonicus*	0.39	0.55	0.21	0.3
	Sailfish	*Istiophorus platypterus*	0.39	0.55	1.05	0.2
	ALL TELEOSTS		**28.3**	**43.05**	**27.15**	**1035.8**
Cephalopod	Squid	Teuthida	11.2	16.02	0.00	179.4
	Cuttlefish	Sepiida	8.88	12.71	0.00	112.9
	Loligo squids	*Loligo spp.*	3.09	4.42	0.00	13.7
	Octopus	Octopoda	2.32	3.31	0.00	7.7
	ALL CEPHALOPODS		**25.49**	**36.46**	**0.00**	**313.6**
	Totals		**259**	**185**	**118.95**	

Table 4: Stomach contents of *Isurus oxyrinchus* caught in offshore waters by longliners. Totals represent the number of prey items (N) and the numbers of stomachs (F) with food. UID = Unidentified.

Common name	Scientific name	%N	%F
Maasbanker	*Trachurus capensis*	46.38	35.5
Sardine	*Sardinops sagax*	21.74	14.21
UID teleost		9.06	14.79
Loligo squid	*Loligo spp.*	7.97	13.61
John Dory	*Zeus faber*	3.62	1.78
Snoek	*Thyrsites atun*	2.54	4.14
Mackerel	Scombridae	2.17	2.96
Kingklip	*Genypterus capensis*	2.17	0.59
Butterfish	*Lepidocybium flavobrunneum*	1.81	2.96
Miscellaneous		1.45	2.37
Panga	*Pterogymnus laniarius*	0.36	0.59
Shortfin mako	*Isurus oxyrinchus*	0.36	0.59
Hake	*Merluccius spp.*	0.36	5.91
Totals		276	169