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Food habits of the shortfin mako, *Isurus oxyrinchus*, off the southwest coast of Portugal

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Abstract The shortfin mako, *Isurus oxyrinchus*, is caught in the eastern North Atlantic as a regular bycatch of the surface-drift longline fishery, mainly directed towards swordfish, *Xiphias gladius*. Stomachs of 112 shortfin mako sharks, ranging in size from 64 cm to 290 cm fork length, showed teleosts to be the principal component of the diet, occurring in 87% of the stomachs and accounting for over 90% of the contents by weight. Crustaceans and cephalopods were also relatively important in this species' diet, whereas other elasmobranchs were only present in lower percentages. Meal overlap was observed in half of the sampled sharks. No clear trend of prey size selectivity was found, despite smaller individuals seeming incapable of pursuing larger and faster prey. The retention of small prey was also observed in the diet of all sizes of shark. Seasonality in food habits was in accordance with the current availability of food items. The observed vacuity index of 12% is comparable to foraging ecology studies using gillnetting and appears not to be influenced by baited longline gear. Morphological relationships of the digestive system might add important information to the foraging ecology studies and to ecosystem modelling.

Keywords Diet · Digestive morphology · Elasmobranches · Lamnidae · Prey selectivity

Introduction

The shortfin mako shark, *Isurus oxyrinchus* Rafinesque, 1810, belongs to the Lamnidae family, also known as mackerel sharks due to their speed and shape; this pelagic species has a distribution through all tropical and warm temperate oceans (Compagno 1984). The shortfin mako (from now on referred to as 'mako') is caught as a steady bycatch of commercial fisheries in the Atlantic Ocean that target tuna and swordfish, *Xiphias gladius* Linnaeus, 1758 (Casey and Kohler 1992). Traditionally, both Spanish and Portuguese swordfish fleets use surface-drift longline gear, up to a depth of 18 m (Mejuto et al. 1992) with hooks on monofilament, baited with Atlantic mackerel (*Scomber scombrus* Linnaeus, 1758) and Ommastrephidae squids. Genetic studies, by

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Schrey and Heist (2003), concluded that the North Atlantic receives a low number of migrants per generation from the Southern Atlantic, creating the conditions for at least two separate stocks in the Atlantic, hence requiring independent management. However, it remains to be determined if the gene flow between sharks from the eastern and western North Atlantic is sufficient to consider them as belonging to the same stock (Anonymous 2005).

The predominant predators of the mako are other sharks, mainly the white shark *Carcharodon carcharias* (Linnaeus, 1758) (Fergusson et al. 2000), and cannibalism has not yet been reported. The feeding habits of makos' are not well documented, and comprehensive studies are restricted to the western North Atlantic (Stillwell and Kohler 1982), South Africa (Cliff et al. 1990) and the South Pacific (Stevens 1984). Sporadic observations for other geographical areas can be found in studies by Strasburg 1958 (Central Pacific), Bass et al. 1975 (South Africa), Capapé 1975 (Mediterranean Sea) and Gubanov 1978 (Indian Ocean). Stillwell and Kohler (1982) reported a wide variety of teleosts and cephalopods in the diet, including the predation upon large and fast-swimming teleosts, such as swordfish.

The regulatory role of sharks in marine ecosystems should not be over simplified, depicting them solely in the role of the top predators (Cortés 1999). Accurate biological and ecological information should be gathered for posterior modelling. Furthermore, extensive biological data from single location fisheries are necessary towards a more comprehensive management (Mollet et al. 2000). To investigate the foraging ecology of the shortfin mako in eastern North Atlantic waters, this study (1) describes and quantifies the diet of different life stages, (2) assesses dietary overlap in different life stages and sexes, and (3) investigates prey size selectivity.

Methods

From January to July 2004, 112 mako sharks were sampled from the landings of the surface-drift swordfish longline fishery that operates off the southwest coast of Portugal, mainly off Cape São Vicente, in the eastern North Atlantic. The mako sharks were weighed using a floor scale (precision 0.1 kg); fork length (FL, distance between the tip of the snout and the caudal fork over the body curve) and stretched total length (STL, distance from the tip of the snout to the stretched upper caudal tip over the body curve) were measured to the nearest centimetre. Sex and life stage were assigned based on clasper calcification for males and gonad development for females, while youngs-of-the-year were identified based on cohort analysis for the same individuals (Maia et al. unpublished data). Stomach and spiral intestine were also collected and frozen until further analysis. In the laboratory, spiral intestine was weighed and discarded. The stomach (from oesophageal sphincter to pyloric sphincter) was weighed then everted into a 500 micrometers sieve and weighed again. When possible, the stomach was filled with water under a hose up to the oesophageal sphincter and the capacity determined by measuring the water volume to the nearest 10 ml. Contents were identified to the lowest taxa possible, counted and weighed. Diet was quantified using three simple indices (Hyslop 1980)—percentage by number (%N), percentage by weight (%W), and percentage by frequency of occurrence (%O); and one compound one—index of relative importance (%IRI) (Cortés 1997). The vacuity index was also calculated as the number of empty stomachs divided by the number of stomachs analyzed.

The digestion index for each prey item was recorded using the following scale (Cortés 1987): 1 – prey was recently ingested, easy to identify and is all in one piece or bitten in half; 2 – prey is intact or bitten in half and it is possible to take most of standard measurements; 3 – most of the prey is present, although in various pieces and only one or two measurements can be taken; 4 – measurements cannot be made, some meat pieces still together, loose scales and skeleton pieces united; 5 – random loose pieces (e.g. otoliths, vertebrae, eyes, telson, beaks); 6 – empty stomach or unidentifiable mush. Whenever possible, standard measurements (total length for fishes, carapace width for crabs, carapace length for other crustaceans, and mantle length for cephalopods) were taken in order to study size selectivity. In order to determine whether the number of analyzed stomachs was representative to describe the shortfin mako diet, cumulative prey curves were obtained for each life stage and life stages combined (Bethea et al. 2004).

The Schoener's overlap index was used to quantify the dietary overlap between age classes (Schoener 1970) (α),

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} \left|p_{ij} - p_{ik}\right|\right)$$

(where p_{ij} = proportion of the functional group j that consumes the i prey category; p_{ik} = proportion of the functional group k that uses the i prey category), was calculated using the four indices (%N, %O, %W, %IRI) to test for food resource partitioning between young-of-the-year and juvenile, juvenile and adult, young-of-the-year and adult and females and males. Values over 0.60 are considered biologically significant (Pianka 1976).

Correspondence analysis was conducted for combinations of life stage and season (nine samples) as well as the main prey items in the diet (six 'species') with CANOCO for Windows v4.5 (Biometrics Plant Research International 2002). Seasons were defined as winter (January–February), spring (March–May) and summer (June–July). The main prey items in the diet were: T, Teleosts; Cp, Cephalopods; Cr, Crustaceans; E, Elasmobranchs; OA, Other Animals; PA, Plant and Algae.

Bait preference for mako shark was tested using chi-square tests against 1:1 and 1:3 squid/mackerel bait ratio, to accommodate for possible deviations to the 1:1 rate in some fishing trips. Size selectivity of prey was tested using the larger items found in each stomach plotted against shark's fork length. This was based on the assumption that adults retain smaller prey in their diet (Schari et al. 2000). Regression analyses were computed for digestive tract morphological relationships and models were fitted and tested. Numerical data, unless stated otherwise, represent mean and standard deviation (mean ± SD).

Results

Food habits

From all 112 mako stomachs analyzed, only 13 were found to be empty (vacuity index = 11.6%). Cumulative prey curves are presented (Fig. 1). It can be observed that young-of-the-year, juveniles and life stages combined show a trend towards an asymptote, suggesting that the number of stomachs analyzed in this study is close to the optimal number needed to accurately describe the diet of this species and these two life stages.

Prey taxa and their respective indices can be found in Table 1. Unidentified teleosts remains, mainly composed of eyeballs, backbones and scales, accounted for a high percentage of prey. The average number of prey encountered per stomach was 11.7, with a median value of five prey per stomach. The maximum number of items in a single stomach was 117 and it consisted mainly of unidentifiable teleost eyeballs. Teleosts had the highest index of relative importance for main prey items (%IRI = 93.7), and occurred in 86 of the 99 stomachs with food. This was followed by cephalopods (%O = 40.4; %IRI = 1.6), however the occurrence of these were surpassed in terms of %IRI by crustaceans (%O = 36.4; %IRI = 4.2). Mean digestion state (1–6) was 4.3 ± 1.1, which was concordant with the high percentage of unidentified teleost remains and squid beaks.

Schoener's overlap index (Table 2) showed significant overlap between shortfin mako males and females for all of the diet indices. It also suggested trophic niche overlap between young-of-the-year and juvenile sharks for all indices. On the contrary, young-of-the-year versus adult (%N) and juvenile versus adult pairs (%N, %O) showed no significant overlap.

Correspondence analysis using the index of relative importance and the percentage of weight failed to reveal a good separation of season and life stage arrangements according to main prey dietary items. The most informative index regarding correspondence analysis is the percentage of occurrence (Fig. 2; Table 3) as it showed that juvenile mako sharks sampled in the winter ingested relatively less frequently of crustaceans

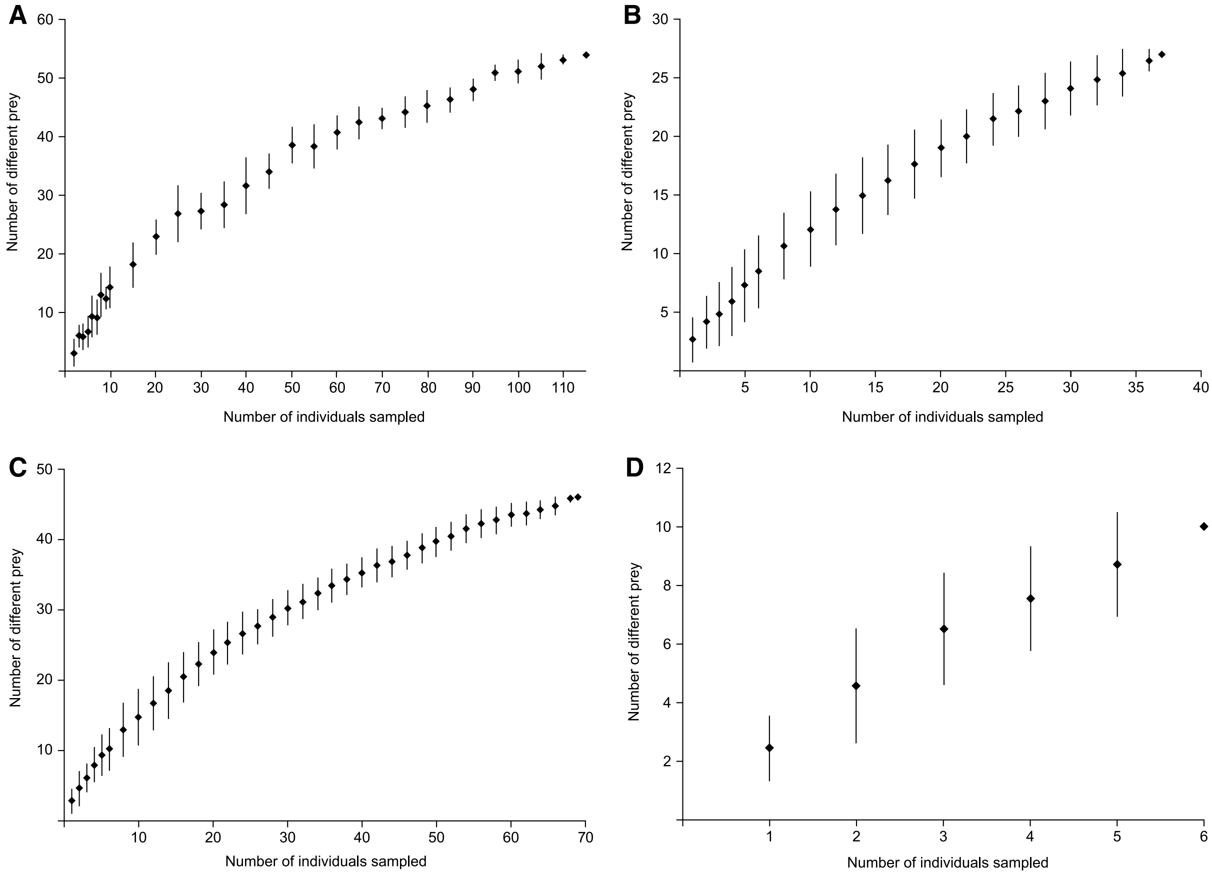

Fig. 1 Cumulative prey curve for the 112 shortfin mako shark stomachs analyzed (bars represent standard deviation), (**A**) all life stages combined, (**B**) young-of-the-year, (**C**) juvenile, (**D**) adult

in comparison to other preys. It also revealed that young-of-the-year sampled in winter and spring exhibit similar behaviour. In general, juveniles appeared to prefer to consume other elasmobranchs. Unfortunately, small adult sample sizes mean that conclusions cannot be drawn.

Prey and bait selectivity

Analysis of larger prey found in young-of-the-year and juvenile sharks' stomachs revealed no clear trend of prey size selectivity. This was mainly due to two lancetfish, *Alepisaurus* sp., found on sharks with 114 and 115 cm FL. Prey size, as a percentage of predator size, averaged 22.6% and had a maximum value of 87.0%. It was also observed that sharks of all sizes ingested smaller prey items. Seven sharks ranging between 120 cm (18.5 kg) and 290 cm (293 kg) fork length had swordfish in their stomach and gear effect was only apparent in two of them (155 and 158 cm FL). Unfortunately, the size of the swordfish present in stomachs could not be determined.

Bait preference for mako shark towards Atlantic mackerel in detriment of Ommastrephidae squid was statistically significant ($P < 0.05$). Both chi-square tests against 1:1 and 1:3 squid/mackerel bait ratio were significant.

Morphological relationships

Empty stomach weight describes a well-defined power regression whereas, as expected, stomachs with contents showed greater variability (Fig. 3; Table 4). Spiral intestine weight exhibited higher variability when plotted against FL (Fig. 4; Table 4). However, residual analysis failed to reveal any relation with digestion state.

Table 1 Preys found in the shortfin mako stomachs and the respective indices: percentage in number (%N); percentage of occurrence (%O); percentage in weight (%W); index of relative importance (%IRI) [(–) not found; (und) undetermined]

Preys	Young-of-the-year				Juvenile				Adult				Overall			
	%N	%O	%W	%IRI	%N	%O	%W	%IRI	%N	%O	%W	%IRI	%N	%O	%W	%IRI
Teleosts	73.3	93.5	97.5	95.0	81.7	92.7	94.8	96.1	17.6	100.0	97.6	68.2	73.2	86.9	91.4	93.7
Clupeiformes	28.1	12.9	25.2	12.9	1.4	4.8	9.1	0.9	–	–	–	–	8.9	7.1	9.4	2.6
Alepisaurus sp.	0.8	9.7	57.7	10.6	0.1	1.6	5.0	0.2	–	–	–	–	0.3	4.0	7.7	0.7
Belone belone	4.1	9.7	5.4	1.7	11.0	11.3	5.0	3.3	–	–	–	–	8.0	10.1	4.7	2.6
Scomberesox saurus	–	–	–	–	0.1	1.6	0.4	<0.1	–	–	–	–	0.1	1.0	0.4	<0.1
Carangidae	–	–	–	–	0.1	1.6	15.0	0.4	–	–	–	–	0.1	1.0	13.0	0.3
Sparidae	0.3	3.2	<0.1	<0.1	–	–	–	–	–	–	–	–	0.1	1.0	<0.1	<0.1
Scomber japonicus	–	–	–	–	0.3	3.2	0.2	<0.1	–	–	–	–	0.2	2.0	0.2	<0.1
Scomber sp.	0.3	3.2	0.5	<0.1	0.4	4.8	2.3	0.2	–	–	–	–	0.2	3.0	2.0	0.1
Scombridae unid.	–	–	–	–	0.1	1.6	<0.1	<0.1	–	–	–	–	0.1	1.0	<0.1	<0.1
Xiphias gladius	–	–	–	–	0.6	8.1	40.2	6.0	1.7	33.3	97.5	38.5	0.6	7.1	38.2	4.7
Phycis blennoides	–	–	–	–	0.1	1.6	<0.1	<0.1	–	–	–	–	0.1	1.0	<0.1	<0.1
Balistes carolinensis	–	–	–	–	0.1	1.6	2.7	0.1	–	–	–	–	0.1	1.0	2.3	<0.1
Tetrodontiformes unid.	0.3	3.2	7.2	0.5	0.5	3.2	12.6	0.8	–	–	–	–	0.4	3.0	11.3	0.7
Teleosts unid.	39.4	80.6	5.2	67.5	66.8	66.1	2.5	84.0	16.0	83.3	0.8	16.3	54.2	71.7	2.5	82.2
Chondrichthyes	–	–	–	–	0.5	6.5	4.0	0.5	–	–	–	–	0.3	4.0	7.0	0.2
Rajidae	–	–	–	–	0.3	3.2	<0.1	<0.1	–	–	–	–	0.2	2.0	<0.1	<0.1
Rajiformes unid.	–	–	–	–	0.1	1.6	4.0	0.1	–	–	–	–	0.1	1.0	7.0	0.1
Chondrichthyes unid.	–	–	–	–	0.1	1.6	<0.1	<0.1	–	–	–	–	0.1	1.0	<0.1	<0.1
Crustaceans	16.3	29.0	1.1	3.0	10.4	37.1	0.2	2.3	67.2	66.7	1.3	27.0	17.4	36.4	0.3	4.2
Atelecyclus sp.	–	–	–	–	0.1	1.6	<0.1	<0.1	–	–	–	–	0.1	1.0	<0.1	<0.1
Atelecyclidae unid.	–	–	–	–	–	–	–	–	2.5	16.7	0.3	0.6	0.2	1.0	<0.1	<0.1
Axiidae	–	–	–	–	0.1	1.6	<0.1	<0.1	–	–	–	–	0.1	1.0	<0.1	<0.1
Crabs unid.	0.6	6.5	0.2	0.1	2.2	14.5	<0.1	0.6	–	–	–	–	1.5	11.1	<0.1	0.3
Shrimps unid.	–	–	–	–	0.9	4.8	<0.1	0.1	–	–	–	–	0.6	3.0	<0.1	<0.1
Squillidae	–	–	–	–	0.1	1.6	<0.1	<0.1	–	–	–	–	0.1	1.0	<0.1	<0.1
Decapoda unid.	0.8	9.7	0.1	0.2	1.1	8.1	<0.1	0.2	2.5	16.7	<0.1	0.5	1.2	9.1	<0.1	0.2
Amphipoda	0.3	3.2	0.1	<0.1	1.9	4.8	<0.1	0.2	–	–	–	–	1.3	4.0	<0.1	0.1
Isopoda	1.9	9.7	<0.1	0.4	1.5	8.1	<0.1	0.2	–	–	–	–	1.5	8.1	<0.1	0.2
Crustaceans unid.	12.7	16.1	0.7	4.1	2.3	12.9	<0.1	0.5	62.2	50.0	0.9	36.8	10.9	16.2	0.1	3.6
Cephalopods	5.0	45.2	1.2	1.7	3.8	37.1	0.6	1.0	15.1	50.0	1.2	4.8	5.3	40.4	0.7	1.6
Alotheutis sp.	0.3	3.2	<0.1	<0.1	–	–	–	–	–	–	–	–	0.1	1.0	<0.1	<0.1
Histiotheutis boneli	0.3	3.2	<0.1	<0.1	0.1	1.6	<0.1	<0.1	1.7	16.7	0.1	0.3	0.5	4.0	<0.1	<0.1
Histiotheutis dolfeini	0.3	3.2	<0.1	<0.1	0.3	3.2	<0.1	<0.1	0.8	16.7	0.1	0.2	0.5	6.1	<0.1	0.1
Histhiotheutis sp.	0.3	3.2	<0.1	<0.1	0.4	4.8	<0.1	<0.1	1.7	16.7	0.2	0.4	0.5	5.1	<0.1	<0.1
Illex coindetti	0.3	3.2	0.1	<0.1	–	–	–	–	–	–	–	–	0.5	2.0	<0.1	<0.1
Spirula sp.	0.3	3.2	0.1	<0.1	–	–	–	–	–	–	–	–	0.1	1.0	<0.1	<0.1
Todarodes sagittatus	0.6	6.5	0.1	0.1	0.5	3.2	0.2	<0.1	0.8	16.7	0.1	0.2	1.2	10.1	0.3	0.3
Teuthoidea unid.	2.8	22.6	0.8	1.5	2.3	21.0	0.2	1.0	10.1	50.0	0.8	6.4	1.8	14.1	0.1	0.6
Octopoda	–	–	–	–	0.1	1.6	<0.1	<0.1	–	–	–	–	0.2	3.0	0.2	<0.1
Other animals	3.3	12.9	0.1	0.3	1.0	12.9	<0.1	0.1	–	–	–	–	1.6	13.1	<0.1	0.1
Bivalvia	2.2	3.2	<0.1	0.1	–	–	–	–	–	–	–	–	0.6	1.0	<0.1	<0.1
Gastropoda	–	–	–	–	0.1	1.6	<0.1	<0.1	–	–	–	–	0.1	1.0	<0.1	<0.1
Opistobranchia	0.3	3.2	<0.1	<0.1	–	–	–	–	–	–	–	–	0.1	1.0	<0.1	<0.1
Mollusca unid.	–	–	–	–	0.1	1.6	<0.1	<0.1	–	–	–	–	0.1	1.0	<0.1	<0.1
Polichaetae	0.3	3.2	<0.1	<0.1	0.1	1.6	<0.1	<0.1	–	–	–	–	0.2	2.0	<0.1	<0.1
Cnidaria	–	–	–	–	0.3	3.2	<0.1	<0.1	–	–	–	–	0.2	2.0	<0.1	<0.1
Nemertea	0.6	3.2	<0.1	<0.1	–	–	–	–	–	–	–	–	0.2	1.0	<0.1	<0.1
Eggs unid.	–	–	–	–	und	<0.1	<0.1	–	–	–	–	–	und	1.0	<0.1	–
Animal matter unid.	–	–	–	–	0.4	4.8	<0.1	<0.1	–	–	–	–	0.2	3.0	<0.1	<0.1
Plant/Algae	1.4	3.2	<0.1	<0.1	0.6	8.1	<0.1	<0.1	–	–	–	–	0.8	6.1	<0.1	<0.1
Cystoseira sp.	–	–	–	–	0.3	3.2	<0.1	<0.1	–	–	–	–	0.2	2.0	<0.1	<0.1
Plant or algae unid,	1.4	3.2	<0.1	0.1	0.4	4.8	<0.1	<0.1	–	–	–	–	0.6	4.0	<0.1	0.1

Table 1 continued

Preys	Young-of-the-year				Juvenile				Adult				Overall			
	%N	%O	%W	%IRI	%N	%O	%W	%IRI	%N	%O	%W	%IRI	%N	% O	%W	%IRI
Non living material	0.8	9.7	< 0.1	< 0.1	1.9	24.2	0.3	0.3	–	–	–	–	1.4	18.2	0.3	0.2
Plastic	–	–	–	–	0.4	4.8	< 0.1	< 0.1	–	–	–	–	0.2	3.0	< 0.1	< 0.1
Hairpin	–	–	–	–	0.1	1.6	< 0.1	< 0.1	–	–	–	–	0.1	1.0	< 0.1	< 0.1
Hook	0.3	3.2	< 0.1	< 0.1	0.9	11.3	0.3	0.2	–	–	–	–	0.6	8.1	0.3	0.1
Fishing monofilament	0.3	3.2	< 0.1	< 0.1	0.1	1.6	< 0.1	< 0.1	–	–	–	–	0.2	2.0	< 0.1	< 0.1
Non living material unid.	0.3	3.2	< 0.1	< 0.1	0.4	4.8	< 0.1	< 0.1	–	–	–	–	0.3	4.0	< 0.1	< 0.1
Stomachs with food	31				62				6				99			
Stomachs analyzed	37				71				6				112			

Table 2 Schoener's overlap index for the different indices: percentage in number (%N); percentage of occurrence (%O); percentage in weight (%W); index of relative importance (%IRI)

	%N	%O	%W	%IRI
YOY–JUV	0.899	0.786	0.957	0.984
YOY–ADULT	0.389	0.626	0.998	0.728
JUV–ADULT	0.318	0.493	0.956	0.714
F–M	0.937	0.791	0.962	0.976

The comparisons were made among life stages (YOY: young-of-the-year; JUV: juvenile; and adult) and sexes (F: female; M: male)

Stomach volume (Fig. 5; Table 4) is correlated with individual size. Stomach content in relation to body weight averaged 1.1% for all stomachs and 1.2% for stomachs with contents. Percentage of shark's weight, stomach fullness, and stomach contents in weight failed to show significant correlations with fork length (Table 4). The presence of food items with different digestion states in the same individual for 63 (56.25%) stomachs provided evidence of meal overlap.

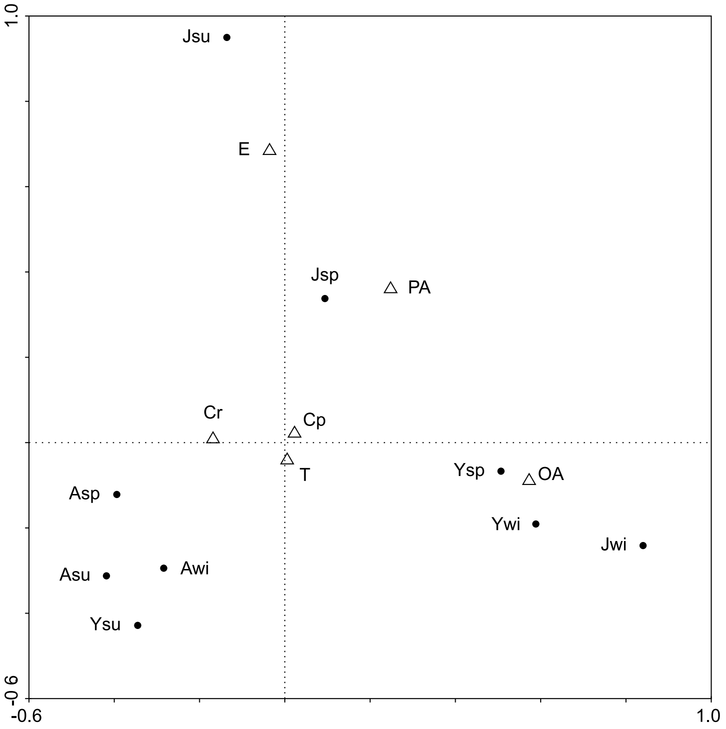

Fig. 2 Correspondence analysis of main prey items in the diet using %O index (triangles: T, Teleosts; Cp, Cephalopods; Cr, Crustaceans; E, Elasmobranchs; OA, Other Animals; PA, Plant and Algae) and life stages and seasons combined (circles: Ywi, Ysp, Ysu – young-of-the-year caught in winter, spring and summer respectively; Jwi, Jsp, Jsu – juveniles caught in winter, spring and summer; Awi, Asp, Asu – adults caught in winter, spring and summer)

Table 3 Sample size and average values of %O for correspondence analysis between life stages and seasons combined

Samples	*n*	T	E	Cp	Cr	OA	PA
Ywi	14	91.67	0	41.67	8.33	16.67	8.33
Ysp	10	100	0	77.78	22.22	22.22	11.11
Ysu	13	100	0	18.18	45.45	0	0
Jwi	19	56.25	0	31.25	18.75	25.00	6.25
Jsp	39	94.29	8.57	31.43	40.00	11.43	5.71
Jsu	11	88.89	11.11	66.67	66.67	0	22.22
Awi	2	100	0	50.00	50.00	0	0
Asp	1	100	0	100	100	0	0
Asu	3	100	0	33.33	66.67	0	0

Samples, Ywi, Ysp, Ysu: young-of-the-year caught in winter, spring and summer respectively; Jwi, Jsp, Jsu: juveniles caught in winter, spring and summer; Awi, Asp, Asu: adults caught in winter, spring and summer) and main prey items (T: Teleosts; E: Elasmobranchs; Cp: Cephalopods; Cr: Crustaceans; OA: Other Animals; PA: Plant and Algae

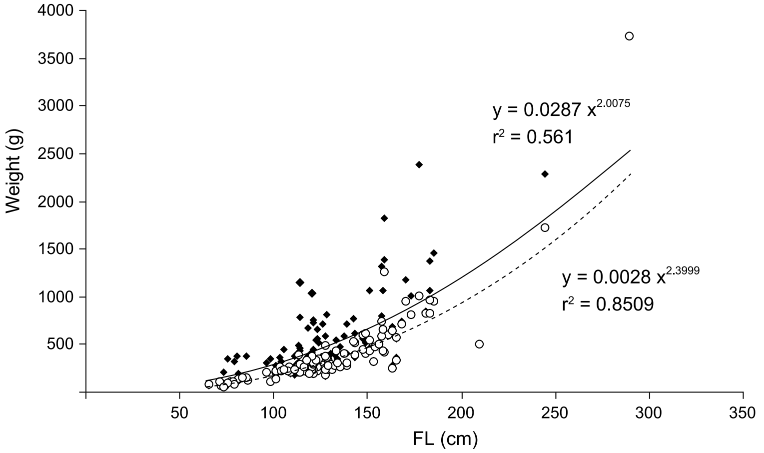

Fig. 3 Plotting of mako stomach weight with contents (■) and empty stomach weight (○) against fork length (FL); power regression was computed for stomach weight versus fork length (—), *n* = 108 and empty stomach weight versus fork length (- - -), *n* = 94

Table 4 Morphological relationships and regression coefficient (r^2) for the best fitting models (Wt: weight; FL: fork length)

Relationship	Best fit	r^2
Stomach Wt w/contents versus FL	Power regression	0.561
Stomach Wt versus FL	Power regression	0.851
Spiral intestine Wt versus FL	Power regression	0.884
Stomach capacity versus FL	Exponential regression	0.702
Stomach fulness versus FL	Negative log regression	0.107
Stomach contents as % body Wt versus FL	Negative log regression	0.212

Discussion

The high temperature differential between the water temperature and stomach, ranging from 1.7°C to 5.7°C reported for mako sharks (Sepulveda et al. 2004) might account for the high degree of digestion of prey items analyzed in this study. Gear effect—by baiting—could also be attracting a higher percentage of empty stomach individuals, although the fact that the low vacuity index is close (11.61%) to the reported values for sharks caught by non-baited methods (Wetherbee et al. 1990) suggests otherwise.

At first glance, given the high variability in terms of food items (especially teleosts), this species would be considered as an opportunistic feeder. Nevertheless, a more detailed analysis showed that some of these prey are fast swimmers, for example swordfish and lancetfish. Sepulveda et al. (2004) suggested that mako's behaviour is similar to that described for white sharks (Klimley 1994) i.e., the use of the

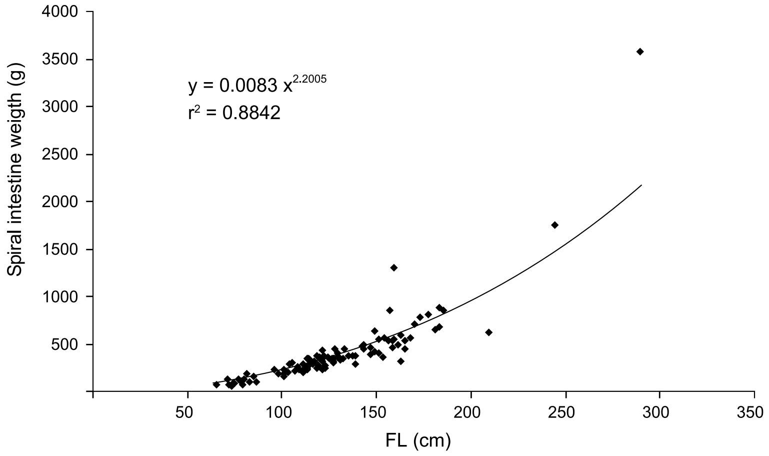

Fig. 4 Spiral intestine weight plotted against fork length (FL) in mako sharks; power regression computed, $n = 108$

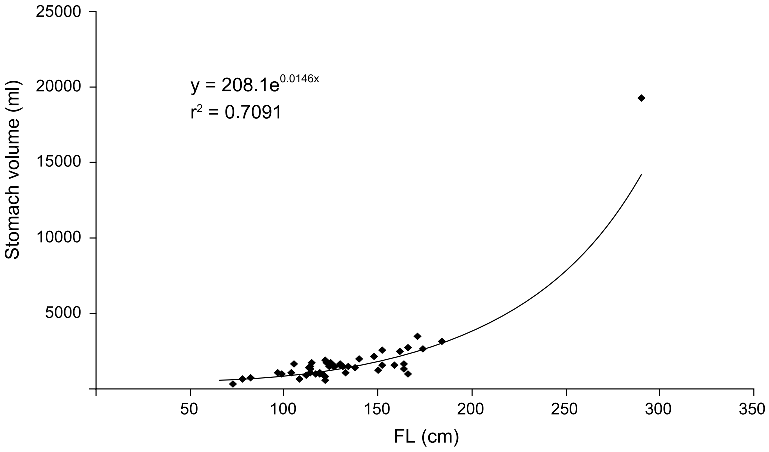

Fig. 5 Stomach volume after emptied of contents and refilled with water under pressure plotted against mako fork length (FL); power regression computed, $n = 54$

counter-shading and burst speed allied to vertical excursions to surprise prey from below.

Contrary to other feeding studies of mako sharks (Bass et al. 1975; Cliff et al. 1990), elasmobranchs appear not to be an important component of the makos' diet in eastern North Atlantic waters. This could be due to lower elasmobranch densities in oceanic environments when compared to more complex habitats (Pikitch et al. 2005). *X. gladius* was confirmed as prey since it was found in advanced stages of digestion. However, this study's data disagrees with Stillwell and Kohler (1982) who stated that only sharks over 150 kg are capable of preying on swordfish. Observed differences from previous studies include higher consumption of cephalopods and crustaceans than that reported for South Pacific mako sharks (Stevens 1984).

In regard to teleost prey—both Clupeiformes and garpike, *Belone belone* (Linnaeus, 1761), were common items in stomachs. Garpike occupies the upper water column (Muus and Nielsen 1999) and appears to have a seasonal abundance off the Portuguese coast, since it was mostly found in stomachs collected during spring. Feeding on a particularly seasonally abundant prey, such as the blue fish, *Pomatomus saltatrix* (Linnaeus, 1776), was also reported by Stillwell and Kohler (1982) for the western North Atlantic.

From the four indices used (%N, %O, %W and %IRI), percentage of occurrence (%O) was the most indicative for mako sharks, mainly because it reflected crustacean consumption. Although relatively low in weight, crustaceans cannot be regarded as incidental due to their high number in each stomach. In the past, there has been much debate about the utility of different indices (e.g. Cortés 1997; Pope et al. 2001). However, it is generally accepted that calorific content of prey and the energy dispended on capture should be evaluated. Nevertheless, these are difficult to measure in the wild, laboratory experiments are few, and extrapolations to the wild are complex. Pope et al. (2001) stated that percentage in weight showed the best correlation with calorific content of the diet. Considering the previous statement, teleosts are the principal contributors to the makos' diet in all life stages.

The preference of *S. scombrus* for baited hooks rather than the consumption of Ommastrephidae squid is in accordance with the overall preference of teleosts over cephalopods observed in the stomach analysis. This is also corroborated by previous studies on the mako's diet (Stillwell and Kohler 1982; Stevens 1984; Cliff et al. 1990).

Contrary to other species where there is an ontogenic shift in the diet as early as from young-of-the-year to juveniles (Wetherbee et al. 1990; Bethea et al. 2004), this species was observed to have a high niche overlap between young-of-the year and juveniles.

The diet of makos exhibited seasonal variation, especially in juveniles and young-of-the-year, which consumed a greater quantity of crustaceans during summer. This could be due to greater crustacean abundances in the study area during this season, similarly to the Mediterranean (Sbrana et al. 2003). During the winter, it was also observed that young-of-the-year and juvenile ingested more quantities of other animals, indicating a greater degree of opportunistic feeding. This was triggered by fewer available of conventional prey. Seasonal changes in prey categories have also been previously reported (see Wetherbee et al. 1990 for a review).

Increasing weight of stomach contents with FL and decreasing percentage of shark's weight is in accordance with results from Stillwell and Kohler (1982) for this species and with Joyce et al. (2002) for the related species *Lamna nasus* (Bonaterre, 1788). This is due to a decrease in energy requirements per unit of body weight with increasing size (Carlson et al. 2004).

Cortés and Gruber (1990) reported that the lemon shark, *Negaprion brevirostris*, (Poey 1868), similarly to other sharks such as *Squalus acanthias* Linnaeus, 1758 and *Carcharhinus plumbeus* (Nardo 1827), cease feeding until digestion of the prior meal is complete or near completion. This study indicates that this is not the case for makos, as items in different digestive states were present in over half the stomachs with contents. The high metabolic requisites of this endothermic species (Goldman 1997) as well as the great stomach capacity, allow mako sharks to feed on larger quantities of prey whenever available. Mako shark foraging behaviour may be more influenced by suitable prey encounters, rather than completion of digestion.

Prey selectivity analysis failed to display clear trends. This could be explained by the great biting capacity of these sharks (Shimada 2002) and the fact that they ingest most of the larger teleosts in bite size portions. The bite marks on some of the largest prey suggest that mako sharks use successive biting to progress along their prey. Also important is the retention of small prey by larger animals. According to Schari et al. (2000) the high relative abundance of small prey and the reduced handling time might explain this.

The quantification of shortfin mako foraging ecology, as well as other top predators of marine food webs, is urgently needed in order to model trophic relationships and ecosystem changes in the eastern North Atlantic area.

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References

Anonymous (2005) Report of the 2004 inter-sessional meeting of the ICCAT subcommittee on bycatches: shark stock assessment. SCRS/2004/014. Collective Volume of Scientific Papers 58:799–890

Bass AJ, D'Aubrey D, Kistnasamy N (1975) Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidar, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. Oceanographic Research Institute, Investigational Report No. 39, Durban, South Africa, 102 pp

Bethea DM, Buckel JA, Carlson JK (2004) Foraging ecology of the early life stages of four sympatric shark species. Mar Ecol Prog Ser 268:245–264

Capapé C (1975) Observations sur le régime alimentaire de 29 Selaciens pleurotêrmes des côtes tunisiennes. Arch Inst Pasteur Tunis 52:395–414

Carlson JK, Goldman KJ, Lowe CG (2004) Metabolism, energetic demand, and endothermy. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, USA, pp 203–224

Casey JG, Kohler NE (1992) Tagging studies on the shortfin mako shark (*Isurus oxyrinchus*) in the western north Atlantic. Aust J Mar Freshw Res 43:45–60

Cliff G, Dudley SFJ, Davis B (1990) Sharks caught in the protective gill nets of Natal, South Africa. 3. The shortfin mako shark (*Isurus oxyrinchus*) (Rafinesque). S Afr J Mar Sci 9:115–126

Compagno LJV (1984) FAO species catalogue: sharks of the World: an annoted and illustrated catalogue of shark species known to date. FAO Fish Synop 4:665 pp

Cortés E (1987) Diet, feeding habits, and daily ration of young lemon sharks, *Negaprion brevirostris,* and the effect of ration size on their growth and conversion efficiency. MS Thesis, University of Miami, Florida, 146 pp

Cortés E (1997) A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can J Fish Aquat Sci 54:726–738

Cortés E (1999) Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707–717

Cortés E, Gruber SH (1990) Diet, feeding habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). Copeia 1990:204–218

Fergusson IK, Compagno LJV, Marks MA (2000) Predation by white sharks *Carcharodon carcharias* (Chondrichthyes: Lamnidae) upon chelonians, with records from the Mediterranean Sea and a first record of the ocean sunfish *Mola mola* (Osteichthyes: Molidae) as a stomach contents. Environ Biol Fish 58:447–453

Goldman KJ (1997) Regulation of body temperature in the white shark, *Carcharodon carcharias.* J Compar Physiol Ser B 167:423–429

Gubanov YP (1978) The reproduction of some species of pelagic sharks from the equatorial zone of the Indian Ocean. J Ichthyol 18:781–792

Hyslop EJ (1980) Stomach contents analysis—a review of methods and their application. J Fish Biol 17:411–429

Joyce WN, Campagna SE, Natanson LJ, Kohler NE, Pratt HL Jr, Jensen CF (2002) Analysis of stomach contents of the porbeagle shark (*Lamna nasus* Bonaterre) in the northwest Atlantic. ICES J Mar Sci 59:1263–1269

Klimley AP (1994) The predatory behaviour of the White Shark. Am Sci 82:122–133

Mejuto J, Scanchez P, de la Serna JM (1992) Nominal catch per unit of effort by length groups and areas of the longline Spanish fleet targeting swordfish (Xiphias gladius) in the Atlantic, years 1988 to 1990, combine. International Commission for the Conservation of Atlantic Tunas SCRS 91/49

Mollet HF, Cliff G, Pratt HL Jr., Stevens JD (2000) Reproductive biology of the female shortfin mako, *Isurus oxyrhinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. Fish Bull 98:299–318

Muus BJ, Nielsen JG (1999) Sea fish Scandinavian Fishing Year Book. Hedehusene, Denmark, 340 pp

Pianka ER (1976) Competition and niche theory. In: May RM (eds) Theoretical ecology: principles and applications. WD Saunders, Philadelphia, PA, pp 114–141

Pikitch EK, Chapman DD, Babcock EA, Shivji MS (2005) Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). Mar Ecol Prog Ser 302:187–197

Pope KL, Brown ML, Duffy WG, Michaletz PH (2001) A caloric-based evaluation of diet indices for largemouth bass. Environ Biol Fish 61:329–339

Sbrana M, Sartor P, Belcari P (2003) Analysis of the factors affecting crustacean trawl fishery catch rates in the northern Tyrrhenian Sea (western Mediterranean). Fish Res 65(1–3): 271–284

Schari FS, Juanes F, Rountree RA (2000) Predator size – prey size relationship of marine fish predators: interspecific variation and effects of ontongeny and body size on trophic-niche breath. Mar Ecol Prog Ser 208:229–248

Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418

Schrey AW, Heist EJ (2003) Microsatellite analysis of population structure in the shortfin mako (*Isurus oxyrinchus*). Can J Fish Aquat Sci 60:670–675

Sepulveda CA, Kohin S, Chan C, Vetter R, Graham JB (2004) Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. Mar Biol 145:191–199

Shimada K (2002) Dental Homologies in Lamniform Sharks (Chondrichthyes: Elasmobranchii). J Morphol 251:38–72

Stevens JD (1984) Biological observations on sharks caught by sport fishermen off New South Wales. Aust J Mar Freshw Res 35:573–590

Stillwell CE, Kohler NE (1982) Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic. Can J Fish Aquat Sci 39:407–414

Strasburg DW (1958) Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. Fish Bull Fish Wildl Serv 138:335–361

Wetherbee BM, Gruber SH, Cortés E (1990) Diet, feeding habits, digestion, and consumption in sharks, with special reference to the lemon shark, *Negaprion brevirostris.* In: Pratt HL Jr, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Technical Report NMFS pp 29–47