

# How can the feeding habits of the sand tiger shark influence the success of conservation programs?

L. O. Lucifora<sup>1</sup>, V. B. García<sup>1</sup> & A. H. Escalante<sup>2,3</sup>

<sup>1</sup> Dalhousie University, Department of Biology, Halifax, NS, Canada

<sup>2</sup> Departamento de Biología, Universidad Nacional de Mar del Plata, Segundo Piso, Mar del Plata, Argentina

<sup>3</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

## Keywords

shark fisheries; Patagonia; hook damage; competition with fisheries; *Carcharias taurus*.

## Correspondence

Luis O. Lucifora, Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS, Canada B3H 4J1.

E-mail: luis.lucifora@dal.ca

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## Abstract

The feeding habits of the sand tiger shark *Carcharias taurus*, one of the most threatened sharks of the world, are poorly known. Sand tiger sharks are critically endangered in the South-west Atlantic. Since 2007, the law requires that all individuals caught in recreational fisheries off Argentina must be released. Using data from a north Patagonian recreational fishery ( $n = 164$  stomachs with contents), we analyzed the diet of sand tiger sharks in relation with size, sex, maturity stage and season; assessed prey consumption patterns and hooking location; and estimated diet overlap with fishery landings. Sand tiger sharks consumed mainly teleosts (55.4% of the total prey number,  $N$ ) and elasmobranchs (41.84%  $N$ ), and ate more benthic elasmobranchs (batoids and angel sharks) as they become larger. Sharks swallowed prey mostly in one piece (93.7%) and were hooked mainly in internal organs (87.4%,  $n = 175$ ), causing occlusion and perforation of the esophagus and stomach, and lacerations to the pericardium, heart and liver. Sand tiger sharks fed on the most heavily landed species, overlapping almost completely (>90%) with fishery landings. Conservation plans should take into account that releasing hooked sharks could be insufficient to minimize fishing mortality and that competition for food with fisheries is likely to occur.

## Introduction

The sand tiger shark *Carcharias taurus* is one of the most threatened sharks in the world and the first shark that received legal protection (Pollard, Smith & Smith, 1996; Smith & Pollard, 1999; Compagno, 2001; Otway, Bradshaw & Harcourt, 2004). Currently categorized as vulnerable at the global scale by the International Union for the Conservation of Nature (IUCN) (Pollard & Smith, 2000), this widespread, large and coastal lamnoid matures at 6–7 (males) and 10–12 (females) years old (Goldman, Branstetter & Musick, 2006), produces a litter of two newborns annually (Gilmore, Putz & Dodrill, 2005), biennially (Branstetter & Musick, 1994; Lucifora, Menni & Escalante, 2002; Dicken, Smale & Booth, 2006; Bansemer & Bennett, 2009) or even triennially (Bansemer & Bennett, 2009), migrates long distances along continental shorelines (Gilmore, 1993; Kohler, Casey & Turner, 1998; Lucifora *et al.*, 2002; Dicken *et al.*, 2006), and has low inter-population mixing (Lucifora *et al.*, 2003; Stow *et al.*, 2006). Quantitative studies about the feeding habits of this species are scarce and limited to descriptions of dietary composition. In the North-west Atlantic, the sand tiger shark feeds predominantly on teleosts and elasmobranchs, with skates (Rajidae) being the dominant individual prey (Gelsleichter, Musick & Nichols,

1999;  $n = 42$  stomachs with contents). Off South Africa, it feeds on teleosts, elasmobranchs and squids, taking larger and more active prey as it grows (Smale, 2005;  $n = 100$  stomachs with contents). Its trophic level has been estimated at 4.4 (Cortés, 1999).

In the South-west Atlantic, the sand tiger shark migrates seasonally in coastal waters off Brazil, Uruguay and Argentina, where it is caught in several fisheries. The South-west Atlantic population is categorized as critically endangered by the IUCN (Chiaramonte, Domingo & Soto, 2007). In Brazilian waters the species is considered overexploited, but fisheries targeting sand tigers are allowed (Vooren & Klippel, 2005). In Uruguay, it is caught mostly in artisanal fisheries and landings of the species have decreased between 1977 and 1997 (Nion, 1999). Off Argentina, the species has been caught mostly by recreational fishermen for decades. But since 2007, all medium-to-large coastal sharks (*Notorynchus cepedianus*, *Carcharias taurus*, *Galeorhinus galeus*, *Carcharhinus brachyurus* and *Sphyrna* spp.) caught in recreational fisheries off northern Argentina must be released in order to minimize fishing mortality (Ministerio de Asuntos Agrarios de la Provincia de Buenos Aires, 2007).

However, the success of catch-and-release measures in minimizing fishing mortality will depend on the shark's health after being released. The anatomical location were

the shark is hooked is the main factor determining post-release mortality relative to other factors, such as physiological stress (Bartholomew & Bohnsack, 2005; Skomal, 2007). Blue sharks *Prionace glauca* hooked in internal organs have been reported to suffer from severe pathologies such as perforation and partial obstruction of the esophagus, gastric perforation, gastritis and proliferative necrotizing peritonitis, hepatic lacerations with hepatitis and secondary bacterial infection (Borucinska *et al.*, 2002), that could eventually lead to different types of cancer (Borucinska, Harshbarger & Bogicevic, 2003). Also, large marine predators, such as striped marlins *Tetrapturus audax* hooked in internal organs suffer higher post-release mortality than if hooked in the mouth (Domeier, Dewar & Nasby-Lucas, 2003). Moreover, the hooking location would be related to the extent of prey handling by the predator. For example, the broadnose sevengill shark *N. cepedianus* cuts their prey in pieces before swallowing them and, consequently, the probability of being hooked in the mouth is high (Lucifora, Menni & Escalante, 2005). Sand tiger sharks have a dentition well suited for impaling and swallowing their prey whole with little handling (Lucifora, Menni & Escalante, 2001; Smale, 2005). We hypothesize that, because of this particular prey capture behavior, sand tiger sharks will tend to swallow the bait, leading to the hooking of internal organs.

Potential competition for food between predators and fisheries is a subject of growing concern. By reducing the abundance of prey populations, fisheries act as a superior competitor affecting both the food supply and, indirectly, the recovery of marine top predators (Okey & Wright, 2004; Karpouzi, Watson & Pauly, 2007; Atkinson, Demaster & Calkins, 2008). While substantial attention has been given to seabirds and marine mammals, only one study considered the effect of overexploitation on shark feeding habits. Koen Alonso *et al.* (2002) showed that the spiny dogfish *Squalus acanthias* shifted from a diet mainly composed of Argentine hake *Merluccius hubbsi* to a squid-based diet as a consequence of the overexploitation of *M. hubbsi*. Recognizing the potential threat of competition for food with fisheries, the recovery plan of the eastern Australian sand tiger shark population calls to ensure an adequate food supply (Environment Australia, 2002). As most coastal fish stocks are overexploited in the South-west Atlantic (Carozza *et al.*, 2005; Jaureguizar & Milessi, 2008), an evaluation of the overlap between the species caught by fisheries and those preyed upon by the sand tiger shark is necessary.

The present study analyzes the feeding habits of the sand tiger shark from the South-west Atlantic, particularly those characteristics that may further or hamper the efforts to conserve the species. First, we describe the feeding habits, considering the size, sex and maturity stage of the predator, and season; second, we quantify the prevalence of hooking in different anatomical locations and relate it with the prey consumption pattern resulting from feeding behavior; and finally, we measure the overlap between diet composition and fishery catches in the critically endangered population of the South-west Atlantic.

## Materials and methods

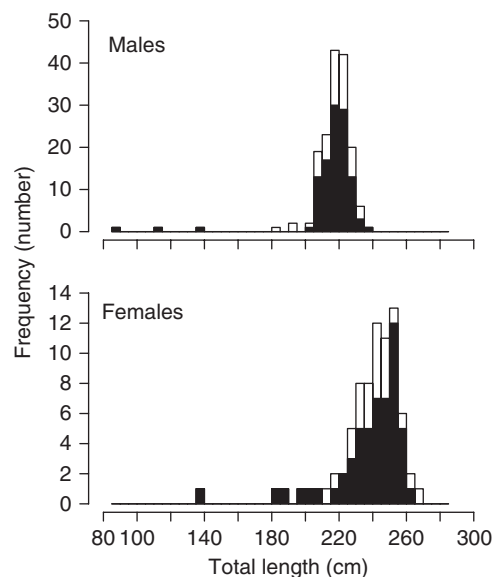
### Sampling

During the summer, sand tiger sharks arrive in Anegada Bay, northern Patagonia (Argentina), to mate; giving birth in the following summer off Uruguay and south Brazil, where most neonates remain until sexual maturity (Lucifora *et al.*, 2002). Samples (239 sharks, 164 with stomach contents, Fig. 1) were obtained during the mating season from a recreational shark fishery that occurs off Anegada Bay (Fig. 2). Sampling was performed each year from 1998 to 2001, from October to April. Three juvenile males of 89, 111 and 137 cm in total length (TL) from coastal Uruguay were also included in the analysis.

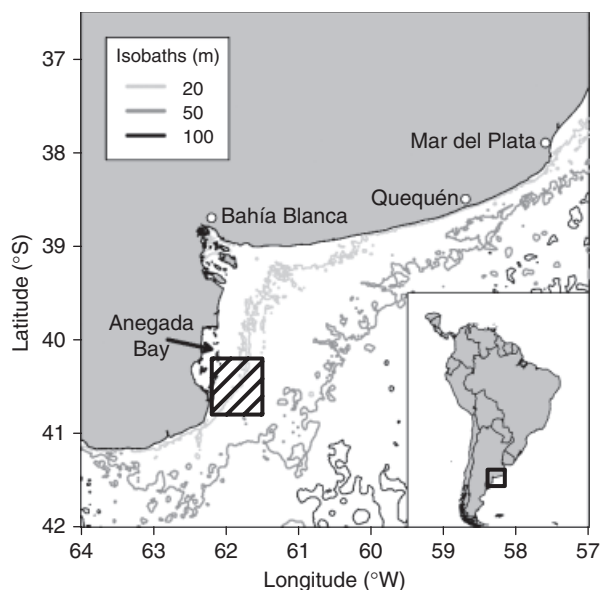
TL was measured as a straight line from the tip of the nose to the tip of the tail, with the tail in its natural position. Maturity stage (juvenile, adult) was determined according to the condition of reproductive organs (Lucifora *et al.*, 2002). Prey were identified to the lowest possible taxonomic level (using otoliths, pharyngeal teeth and other hard parts when necessary), weighed and counted.

To assess sample sufficiency, the order of stomachs sampled was randomized 1000 times and the mean cumulative exponential of Shannon diversity index was plotted as a function of sample size. Sample size was considered sufficient to describe diet if the cumulative diversity reached an asymptote (Magurran, 2004).

To make our results comparable with previous studies (e.g. Gelsleichter *et al.*, 1999; Smale, 2005), the composition of diet was presented as percentage in number of all prey sampled ( $N_i$ : 100 × number of individuals of prey  $i$  recorded



**Figure 1** Length frequency distribution of male ( $n=162$ ) and female ( $n=77$ ) sand tiger sharks *Carcharias taurus* from off Anegada Bay, Argentina. Black bars represent individuals with stomach contents ( $n=110$  males and 54 females).



**Figure 2** Map of the study area showing the area of operation of the shark recreational fishery where samples of sand tiger sharks *Carcharias taurus* were taken from (cross-hatched area), and the three main fishing ports whose landings were used in the analyses. The inset shows the location of the study area in South America (squared area).

in the stomachs divided by the sum of all prey individuals), percentage occurrence in stomachs sampled ( $O_i$ : percentage of stomachs which contained a particular prey  $i$ ), and percentage by mass ( $M_i$ : mass contribution of prey  $i$  expressed as percentage of total stomach content mass).

## Feeding habits

We evaluated if the consumption of the main prey varies with the size, sex, maturity stage and season using a multiple-hypothesis modeling approach. We grouped prey into invertebrates, teleosts and elasmobranchs, with the latter split into benthic (batoids and angel sharks) and demersal (small fusiform sharks). All teleost prey were grouped into a single category because most of them were demersal (221 demersal teleost vs. 21 pelagic teleosts). Unidentified elasmobranchs and teleosts were not included in the statistical analyses. Unidentified elasmobranchs represented a small proportion of the diet (eight prey individuals) and were found in large sharks (>215 cm TL). Unidentified teleosts (40 prey individuals) were uniformly distributed among sharks of different sizes (111–255 cm TL) and sexes (0.18 and 0.21 unidentified teleosts per female and male, respectively), and found in similar proportion in summer and in fall (0.23 and 0.17 unidentified teleosts per shark in summer and fall, respectively).

For each prey category, we built generalized linear models (GLM) (Venables & Ripley, 2002) where the response variable was the number of individuals consumed of that prey category and the independent variables were predator size (TL), sex, maturity stage and season (sum-

mer = December–January–February; fall = March–April). By using GLMs, we were able to consider each shark as a sample and to incorporate predator size as a continuous variable. Also, by using information theory we could weigh the importance of competing hypotheses, something not possible under the null-hypothesis-testing paradigm (Anderson, Burnham & Thompson, 2000; Franklin *et al.*, 2001; Johnson & Omland, 2004). Models with all possible combinations of the four independent variables were fitted. We also fitted a model without any of the independent variables (i.e. the model had only an intercept) in order to test the hypothesis that none of the variables tested had an effect on the consumption of a particular prey. All models had a negative binomial error distribution in order to account for the high number of zero-values, and a log link (Venables & Ripley, 2002).

The significance of size, sex, maturity stage and season as explanatory variables of consumption of each prey category was tested using information theory (Anderson *et al.*, 2000; Franklin *et al.*, 2001; Johnson & Omland, 2004). Within a prey category, each model was considered as a hypothesis explaining the consumption of that prey. For each hypothesis, we calculated the Akaike information criterion (AIC) and the Akaike weight ( $w$ ). AIC measures the amount of information lost when fitting a model, so the model with the lowest AIC is the best one explaining the observed data within the given set of models. The best hypothesis was weighed against the others using  $w$ , which gives an estimation of the likelihood of the hypothesis given the data (Anderson *et al.*, 2000; Franklin *et al.*, 2001; Johnson & Omland, 2004). If  $w$  did not provide strong support for any particular hypothesis, we used model averaging to estimate the parameters of the variables included in the best model (Anderson *et al.*, 2000; Johnson & Omland, 2004).

## Prey consumption patterns and hooking location

Whenever the state of digestion permitted it, we determined the pattern of prey consumption by classifying fish prey as whole or sectioned (Lucifora *et al.*, 2006, 2009); data on prey consumption pattern were obtained from 122 sharks.

To test the hypothesis that sand tiger sharks consume their prey whole or sectioned depending on prey type (teleost or elasmobranch), we built GLMs with prey consumption pattern (whole or sectioned) as the response variable, and prey type as the independent variable. The models had a binomial error distribution and a logit link, as the response variable can take only two states. The hypotheses were assessed with AIC and  $w$ , as before.

Finally, we recorded the location of the hook and the damage that it inflicted to the hooked organs in 175 sharks.

## Overlap of diet with fisheries

We analyzed the overlap between fisheries and the diet of sand tiger sharks by comparing the probability of preyed-upon and not preyed-upon fish species to be landed.

Fish species present in the study area were determined with data from a research cruise aimed to estimate fish abundance for stock assessments, conducted in March 2002. Twenty-three trawls were performed with a bottom trawl net (footrope = 40.3 m, headrope = 35.3 m, codend mesh size = 103 mm, in-trawl mesh size = 22 mm, trawl speed = 7.4 km hr<sup>-1</sup>, trawl duration = 15 min) in the same area in which the shark fishery occurs. These samples consisted of 34 687 individuals belonging to 48 species of teleosts and elasmobranchs.

Data on fish species consumed by sand tiger sharks were obtained from sharks sampled during fall, to control for seasonal effects that may affect the analysis; sharks from off Uruguay were excluded.

Data on landings (at the species and family level) during 1998, 1999 and 2000 for the three main ports whose fleets operate in the study area, Mar del Plata, Quequén and Bahía Blanca (Fig. 2), were obtained from the official Argentinean fishery statistics shown at the Secretaría de Agricultura, Ganadería, Pesca y Alimentos website (<http://www.sagpya.mecon.gov.ar>, last accessed on 25 February 2008). Fish species present in the study area were assigned to one of five annual landing categories: not landed, <1000, 1000–5000, 5000–10 000 and >10 000 metric tonnes. We had to use landing categories, rather than the actual landing figure for each species, because landing data were not species-specific for skates and flatfishes.

The five landing groups were treated as an ordinal response variable in a multinomial proportional log-odds model (Venables & Ripley, 2002; Faraway, 2006) with each species' presence or absence in the diet of sand tiger sharks as the independent variable; a logit link was specified. The estimated parameters of this model can be interpreted as the cutpoints to estimate the probability (from a logistic distribution) of a fish species to fall in a given landing category (Faraway, 2006). As for previous analyses, AIC and  $w$  were used to select the best model. All statistical analyses were performed using the R statistical software, version 2.6.1 (R Development Core Team, 2006).

## Results

### Feeding habits

Cumulative diversity curves reached an asymptote, indicating that sample size was large enough to adequately describe the diet of adults, males, females and sharks caught in summer and fall; only the curve of juveniles did not reach an asymptote (Fig. 3). Sand tiger sharks fed mainly on teleosts (55.41%  $N$ ) and elasmobranchs (41.84%  $N$ ); invertebrates represented only 2.75% of the total number of prey. Teleost prey included mostly demersal species, like the striped weakfish *Cynoscion guatucupa* (21.81%  $N$ ), and the whitemouth croaker *Micropogonias furnieri* (7.86%  $N$ ) (Table 1). The consumption of teleosts was independent of body size, sex and maturity stage; it only decreased slightly from summer (mean number per shark = 1.74, standard error = 0.29,  $n$  = 111 sharks) to fall (mean number

per shark = 0.94, standard error = 0.15,  $n$  = 53 sharks) (Table 2).

Demersal elasmobranch prey were almost exclusively the narrownose smooth-hound shark *Mustelus schmitti* (18.07%  $N$ , Table 1). The consumption of demersal elasmobranchs was independent of season, predator size, sex and maturity stage (Table 2).

Benthic elasmobranch prey included fanskates *Sympterygia* spp. (9.43%  $N$ ), eagle rays *Myliobatis* spp. (3.34%  $N$ ) and the angular angel shark *Squatina guggenheim* (2.16%  $N$ ). The consumption of benthic elasmobranchs increased with the size of the predator: larger sharks consumed a higher number of benthic elasmobranchs than smaller sharks (Table 2, Fig. 4). Because the hypothesis including predator size as an explanatory variable had a low  $w$ , we used model averaging to estimate the effect of predator size on consumption of benthic elasmobranchs. The estimated model-averaged slope of predator size was 0.0054 (standard error = 0.0047). The combined  $w$  for this averaged slope was 0.557, much higher than the model that included TL as the sole predictor (see Table 2). Sex, maturity stage and season were not important predictors of the consumption of benthic elasmobranchs.

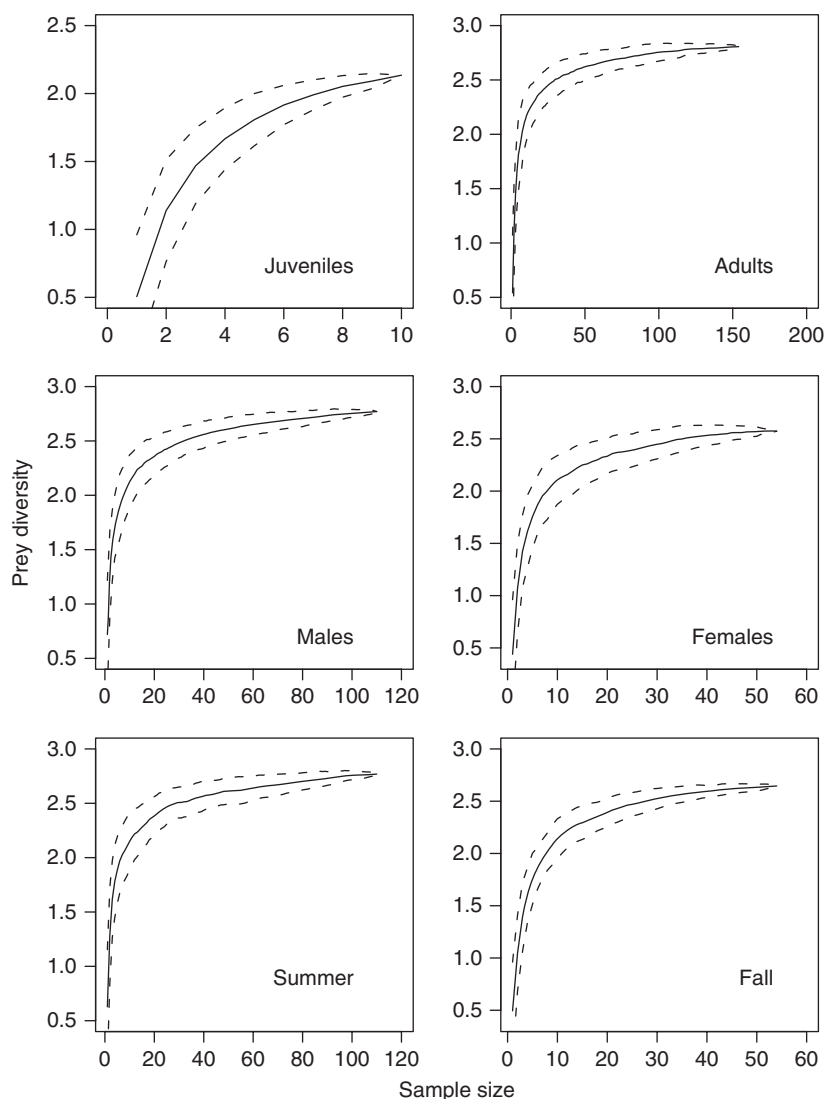
### Prey consumption patterns and hooking location

Patterns of prey consumption indicated that sand tiger sharks swallowed prey with minimal handling. Of 354 prey examined (198 teleosts and 156 elasmobranchs), 93.66% were consumed whole. Prey consumed in pieces (6.34%) consisted of anterior and posterior thirds or halves of teleosts and pieces of fins of large eagle rays or skates. The best model included only a constant (intercept = -2.69, standard error = 0.22, AIC = 158.46,  $w$  = 0.74), indicating that the prey consumption pattern was independent of prey type – elasmobranchs or teleosts.

Most sand tiger sharks examined (153 individuals, 87.4%) had swallowed the hook (Fig. 5a) and consequently were hooked in internal organs. This caused severe damage, such as occlusion and perforation of the esophagus and stomach, and lacerations to the pericardium, heart and liver. One individual (0.6%) was hooked in the gills causing the partial destruction of several branchial arcs and pharyngeal occlusion. Twenty individuals (11.4%) were hooked in the mouth (Fig. 5b) without causing any damage to internal organs and 1 individual (0.6%) was hooked on the external side of the belly, without perforating the body wall.

### Overlap of diet with fisheries

The 10 most landed species or species groups [in average metric tonnes (mt) for 1999, 2000 and 2001] from the trawl fishery operating in the study area were *Cy. guatucupa* (12661.7 mt), Argentine anchovy *Engraulis anchoita* (11519.3 mt), skates (Rajidae) (10486.3 mt), *Mu. schmitti* (9130.7 mt), Brazilian flathead *Percophis brasiliensis* (8207.1 mt), chub mackerel *Scomber japonicus* (7826.6 mt),



**Figure 3** Curves of cumulative mean diversity (exponential of Shannon index) within stomachs of sand tiger sharks *Carcharias taurus* from off Anegada Bay, Argentina, as a function of sample size (number of sharks). Dashed lines indicate standard deviation.

*Mi. furnieri* (7050.5 mt), flatfishes (Paralichthyidae) (6845.2 mt), Argentine seabass *Acanthistius brasiliensis* (4369.2 mt) and *Sq. guggenheim* (3671.3 mt).

Sand tiger sharks fed on the most heavily landed species, with the exception of the pelagic species *E. anchoita* and *Sc. japonicus*. The diet significantly overlapped with fisheries and species that were part of the diet had a higher probability to be landed (0.903) than species not eaten by sand tiger sharks (0.563) (Fig. 6). For species preyed upon by sand tiger sharks, the probability to be landed increased with landing categories; the probabilities to be landed by <1000, 1000–5000 and 5000–10 000 mt were 0.127, 0.114 and 0.231, respectively. On the contrary, for species not preyed upon, the probability to be landed decreased with landing categories; the probabilities to be landed by <1000, 1000–5000 and 5000–10 000 mt were 0.239, 0.118, and 0.117 respectively (Fig. 6). Moreover, the probability to be landed by more than 10 000 mt annually for a species preyed upon by sand tiger sharks was much higher than the same

probability for a species not preyed upon by sand tigers (0.426 vs. 0.093, respectively, Fig. 6).

## Discussion

### Feeding habits

Similar to the populations from South Africa and the northwest Atlantic (Gelsleichter *et al.*, 1999; Smale, 2005), sand tiger sharks from the South-west Atlantic feed mainly on teleosts and elasmobranchs. The consumption of teleosts was homogeneous among sharks of different sizes, sex and maturity stage but differed between seasons. Teleost consumption increased slightly in summer, coinciding with the peak in abundance of *Mi. furnieri* and *Cy. guatucupa* – the main teleost prey. Both prey species migrate seasonally to shallow waters during summer, where they form large spawning aggregations (Cousseau & Perrotta, 2000; López Cazorla, 2000). In Anegada Bay, *Mi. furnieri* peaks in

**Table 1** Diet composition of the sand tiger shark *Carcharias taurus* off Anegada Bay, Argentina expressed as percentage in number (%N), mass (%M), and percentage occurrence (%O)

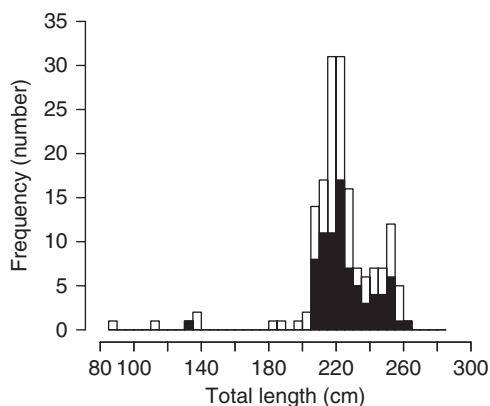
Group/Taxa	Prey	All samples			Summer			Fall		
		%N	%M	%O	%Ni	%M	%O	%Ni	%M	%O
<b>Benthic Elasmobranchs</b>		<b>21.61</b>	<b>36.01</b>	<b>48.17</b>	<b>18.18</b>	<b>33.76</b>	<b>45.45</b>	<b>31.11</b>	<b>41.63</b>	<b>53.7</b>
Myliobatidae	<i>Myliobatis</i> spp.	3.34	12.49	9.15	3.74	15.52	1.91	2.22	4.88	5.56
Rajidae	<i>Atlantoraja castelnaui</i>	0.59	5.27	1.83	0.53	3.36	1.82	0.74	1.7	1.85
	<i>A. cyclophora</i>	0.39	0.22	1.22	0.27	0.7	0.91	0.74	0.59	1.85
	<i>Psammobatis bergi</i>	0.20	0.24	0.61				0.74	0.85	1.85
	<i>P. extenta</i> (egg)	0.39	<0.01	0.61	0.53	<0.01	0.91			
	<i>Psammobatis</i> sp.	0.39	0.05	1.22	0.53	0.7	1.82			
	<i>Sympterygia acuta</i>	3.54	3.30	9.15	2.14	1.77	7.27	7.41	7.14	12.96
	<i>S. bonapartii</i>	3.34	4.42	9.15	1.87	2.26	6.36	7.41	9.81	14.81
	<i>Sympterygia</i> sp.	2.55	1.68	7.32	2.14	1.47	7.27	3.7	2.21	7.41
	Unidentified Rajidae		3.93	2.03	7.32	4.1	2.26	8.18	3.7	1.47
Unidentified batoids		0.79	0.17	2.44	0.53	0.11	1.82	1.48	0.33	3.7
Squatinidae	<i>Squatina guggenheim</i>	2.16	6.14	6.10	1.87	6.88	5.45	2.96	4.27	7.41
<b>Demersal</b>		<b>18.66</b>	<b>12.06</b>	<b>34.15</b>	<b>18.98</b>	<b>11.46</b>	<b>36.36</b>	<b>17.78</b>	<b>13.54</b>	<b>29.63</b>
<b>Elasmobranchs</b>										
Hexanchidae	<i>Notorynchus cepedianus</i>	0.20	0.08	0.61	0.27	0.12	0.91			
Triakidae	<i>Mustelus schmittii</i>	18.07	11.76	33.54	18.18	11.4	35.45	17.78	13.54	29.63
Unidentified shark		0.39	0.22	0.61	0.53	0.3	0.91			
<b>Unidentified</b>		<b>1.57</b>	<b>0.40</b>	<b>4.88</b>	<b>1.7</b>	<b>0.37</b>	<b>3.64</b>	<b>2.96</b>	<b>0.48</b>	<b>7.41</b>
<b>Elasmobranchs</b>										
<b>Teleosts</b>		<b>47.55</b>	<b>48.08</b>	<b>68.29</b>	<b>51.7</b>	<b>5.54</b>	<b>74.55</b>	<b>37.78</b>	<b>41.92</b>	<b>55.56</b>
Atherinopsidae	<i>Odonthestes argentinensis</i>	1.96	0.46	4.88	2.67	0.65	7.27			
Batrachoididae	<i>Porichthys porossissimus</i>	1.77	0.37	3.66	1.34	0.38	4.55	2.96	0.33	1.85
Carangidae	<i>Parona signata</i>	0.20	0.15	0.61	0.27	0.21	0.91			
Cheilodactylidae	<i>Cheilodactylus bergi</i>	5.11	1.15	0.61	6.95	1.61	0.91			
Clupeidae	<i>Brevoortia aurea</i>	0.59	0.33	0.61	0.8	0.46	0.91			
Congridae	<i>Conger orbignyanus</i>	0.59	0.50	1.83	0.53	0.46	1.82	0.74	0.61	1.85
Paralichthyidae	<i>Paralichthys patagonicus</i>	0.20	0.18	0.61	0.27	0.26	0.91			
	<i>Paralichthys</i> sp.	1.57	3.80	3.05	0.53	0.16	0.91	4.44	12.92	7.41
Percophidae	<i>Percophis brasiliensis</i>	1.38	1.79	4.27	1.34	1.54	4.55	1.48	2.42	3.7
Phycidae	<i>Urophycis brasiliensis</i>	0.39	0.49	1.22	0.53	0.68	1.82			
Pinguipedidae	<i>Pseudoperca semifasciata</i>	0.98	3.38	3.05	1.7	3.51	3.64	0.74	3.3	1.85
Pomatomidae	<i>Pomatomus saltatrix</i>	0.20	0.12	0.61	0.27	0.17	0.91			
Sciaenidae	<i>Cynoscion guatucupa</i>	21.81	22.22	39.63	22.46	25.18	42.73	2	14.81	33.33
	<i>Micropogonias furnieri</i>	7.86	11.43	20.12	8.29	12.92	23.64	6.67	7.72	12.96
	Unidentified Sciaenidae	0.20	0.02	0.61	0.27	0.3	0.91			
Serranidae	<i>Acanthistius brasiliensis</i>	0.98	0.70	2.44	1.34	0.98	3.64			
Stromateidae	<i>Stromateus brasiliensis</i>	1.18	0.29	3.05	1.6	0.4	4.55			
Triglidae	<i>Prionotus nudigula</i>	0.20	0.03	0.61	0.27	0.5	0.91			
	<i>Prionotus punctatus</i>	0.20	0.02	0.61				0.74	0.7	1.85
Uranoscopidae	<i>Astroscopus sexspinosus</i>	0.20	0.64	0.61	0.27	0.89	0.91			
<b>Unidentified teleosts</b>		<b>7.86</b>	<b>3.36</b>	<b>20.12</b>	<b>8.2</b>	<b>3.8</b>	<b>21.82</b>	<b>7.41</b>	<b>2.26</b>	<b>16.67</b>
<b>Invertebrates</b>		<b>2.75</b>	<b>0.09</b>	<b>6.71</b>	<b>2.67</b>	<b>0.6</b>	<b>7.27</b>	<b>2.96</b>	<b>0.16</b>	<b>5.56</b>
Crustacea	<i>Platyanthus</i> sp.	0.39	<0.01	1.22	0.27	<0.01	0.91	0.74		1.85
	Unidentified Paguridae	0.39	0.02	0.61				1.48	0.7	1.85
Echinodermata	<i>Ctenodiscus australis</i>	0.39	<0.01	0.61	0.53	<0.01	0.91			
Mollusca	<i>Buccinanops duartei</i>	0.20	<0.01	0.61	0.27	<0.01	0.91			
	<i>Adelomelon</i> sp. (egg)	0.39	0.03	1.22	0.27	<0.01	0.91	0.74	0.9	1.85
Polychaeta	<i>Aphrodita longicornis</i>	0.20	0.02	0.61	0.27	0.2	0.91			
Urochordata	Unidentified ascidian	0.79	0.01	1.83	1.7	0.2	2.73			
Total number of prey		509			374			135		
Total biomass (g)		212 431			151 805			60 626.5		
Number of stomachs		164			111			53		

Values in bold refer to calculations with individual prey grouped.

**Table 2** Best hypotheses explaining the consumption in number (*N*) of the three main prey groups by sand tiger shark *Carcharias taurus* off Anegada Bay, Argentina

Prey group	Intercept	Coefficient	<i>w</i>	AIC
Benthic elasmobranchs	-2.064 (1.140)	0.007 (0.005) TL	0.224	361.28
Demersal elasmobranchs	-0.546 (0.136)		0.293	341.35
Teleosts	-0.057 (0.250)	0.609 (0.292) Summer	0.481	542.31

The intercept and coefficient for the variables included in the best models are given, with standard errors in parentheses. The coefficient for season in the teleosts' model is relative to fall. Akaike's weights (*w*) and Akaike information criterion (AIC) for each model are shown. TL, total length (cm).

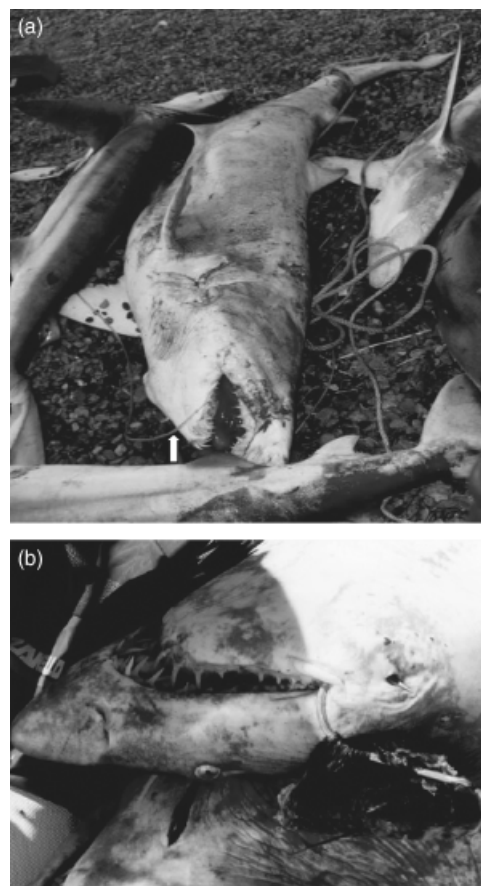


**Figure 4** Number of benthic elasmobranchs consumed by sand tiger sharks *Carcharias taurus* from off Anegada Bay, Argentina. Black bars represent the length frequency distribution of sharks that consumed benthic elasmobranchs; empty bars represent the distribution of sharks that did not consume benthic elasmobranchs.

abundance during late December and January (summer), when most individuals have hypertrophied gonads and are ready to spawn (L. O. Lucifora, pers. obs.). After that, the abundance of *Mi. furnieri* decreases, but *Cy. guatucupa* remains common throughout the year (L. O. Lucifora, pers. obs.).

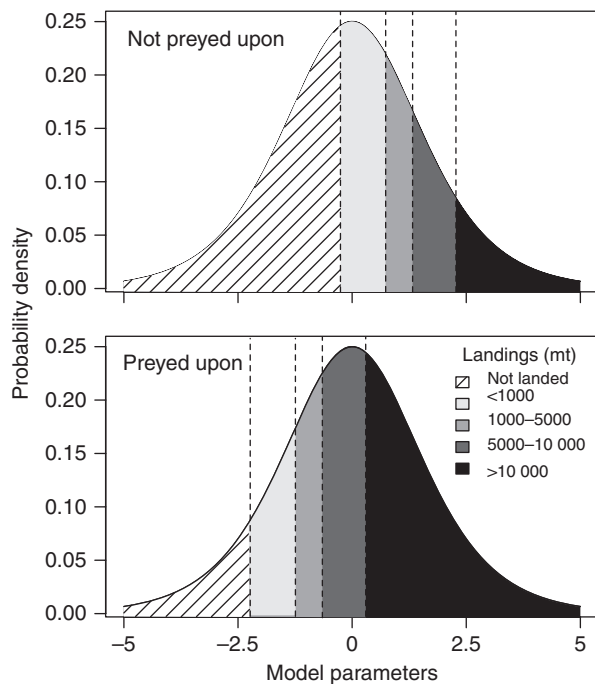
The vast majority of demersal elasmobranchs consumed were *Mu. schmitti* – a small species (maximum TL = 94 cm, Menni, 1985) that congregates in the study area during late spring and summer to give birth (Cousseau, 1986). By coinciding temporally with the months of highest abundance of sand tiger sharks (Lucifora *et al.*, 2002), *Mu. schmitti* offers a constant food supply during the stay of these predators off northern Patagonia. Also, the small size and slender shape of *Mu. schmitti* may make it easy to be handled and killed by sand tigers of most sizes examined.

The effect of body size on benthic elasmobranch consumption in sand tiger sharks is consistent with the pattern found in copper sharks, *Ca. brachyurus* (Lucifora *et al.*, 2009), and suggests that the pattern could be widespread among different shark species. This effect was detected even though our samples include mainly individuals larger than 180 cm TL, because our main sampling area is a mating ground harboring mostly adult individuals (Lucifora *et al.*, 2002). Benthic elasmobranch prey included large and dorso-



**Figure 5** Sand tiger sharks *Carcharias taurus* caught off Anegada Bay, Argentina, with different hooking locations. The individual in (a) had swallowed the hook (as can be seen from the line going into its mouth, marked with an arrow) and the hook damaged internal organs. The individual in (b) was hooked in the mouth and hook damage was restricted to the jaw musculature. The other four sharks depicted in (a) are copper sharks *Carcharhinus brachyurus*. The bait still in the hook in (b) is the head of a mullet *Mugil platanus*.

ventrally flattened species, such as eagle rays (*Myliobatis goodei* and an undescribed species of *Myliobatis*, both of which can weigh more than 10 kg, L. O. Lucifora pers. obs.), the spotback skate (up to 12 kg, L. O. Lucifora pers. obs.), the angular angel shark (up to 8 kg, Colonello, Lucifora & Massa, 2007) and a medium-sized skate (*Sympterygia*



**Figure 6** Probability (area below the solid line) of fish species not preyed-upon and preyed-upon by sand tiger sharks *Carcharias taurus* to fall in a given annual landing category (in metric tonnes). The solid line is the logistic probability density distribution. Broken lines represent the cutpoints between the different categories as estimated from a multinomial proportional log-odds model with a logit link.

*bonapartii*, which can weigh up to 3.5 kg, Mabragna, Lucifora & Massa, 2002). Given the positive correlation between size and physical strength (Huber, Weggelaar & Motta, 2006), we propose that only large sharks are able to capture and kill these prey. In addition, the handling and swallowing of these large- and wide-bodied prey may be more difficult for small sharks with a small gape.

The importance of body size as the main predictor of the consumption of benthic elasmobranchs suggests that fisheries, through their well-known effect of reducing mean body size (Ward & Myers, 2005), are affecting an important role of large sharks in marine ecosystems: the control of large mesoconsumers (Myers *et al.*, 2007; Heithaus *et al.*, 2008).

### Prey consumption patterns and potential success of catch and release

The dentition of sand tiger sharks may enable them to capture medium-sized prey and, at the same time, limit the sand tigers' ability to feed on very large prey. The broadnose sevengill shark, *N. cepedianus*, is another top predator inhabiting simultaneously Anegada Bay. *Notorynchus cepedianus* is able to prey on marine mammals, such as South American sea lions *Otaria flavescens* and franciscana dolphins *Pontoporia blainvillei* by cutting these prey in pieces

with serrated teeth (Lucifora *et al.*, 2005). This indicates that very large prey are available in the study area, but are not consumed by sand tiger sharks. The inability of sand tiger sharks to render its prey may impose an upper limit to the size of prey that can be consumed, and may therefore shape its role as a predator.

The dentition that enables sand tiger sharks to catch medium-sized teleosts and elasmobranchs so efficiently may be responsible for the potential failure of the catch-and-release strategy to minimize sand tiger shark mortality in recreational fisheries. Minimal handling and rapid swallowing of prey exposes sand tiger sharks to high levels of damage from hooks to internal organs, as hooks are easily swallowed with the bait. Hook damage to internal organs is more life-threatening than damage to the jaw musculature (Domeier *et al.*, 2003; Bartholomew & Bohnsack, 2005). In this way, it is likely that the release of hooked sand tiger sharks will not result in a substantial decrease of fishing mortality.

There are several possible measures to be evaluated in order to minimize hooking in internal organs. Circle hooks reduce hooking in internal organs in sharks (Kerstetter & Graves, 2006), however mortality does not differ between individuals caught with J or circle hooks (Yokota, Kiyota & Minami, 2006). A buoy set at a short distance from the hook is already in use by some recreational fishermen to avoid internal hooking in sand tiger sharks in Argentina (D. Dau, pers. comm.). The effectiveness of these measures in reducing post-release mortality must be assessed before accepting catch and release of sand tiger sharks as a successful conservation tool (Bartholomew & Bohnsack, 2005). Until then, we suggest that a complete ban of fishing on sand tiger sharks in the South-west Atlantic, like those already in place in Australia (Environment Australia, 2002) and the United States (Compagno, 2001), should be in place, given the critically endangered status of this population (Chiaromonte *et al.*, 2007).

### Overlap of diet with fishery landings

The diet of sand tiger sharks overlaps almost completely with fishery landings. The main prey of sand tiger sharks – skates (Rajidae), *Mu. schmitti*, *Cy. guatucupa* and *Mi. furnieri* – are of high commercial value and, at the time of sampling, populations of these species were already over-exploited and severely reduced (Carozza *et al.*, 2005). We believe that our estimations of overlap with fisheries are conservative because we used only landing data, the only estimations of fishery catches available. Many species consumed by sand tiger sharks are caught and discarded at sea by fishing vessels (Tamini *et al.*, 2006) and the potential effects of these practices could not be included in our analysis.

High overlap of the sand tiger shark's diet with fishery landings indicates that, even after tackling the problem of direct mortality, indirect effects, such as food shortages, could continue to affect this endangered species. Food shortages from overfishing have been suspected to affect



other endangered predators from the South-west Atlantic, like *P. blainvillei*, which feeds heavily on exploited species, such as *Cy. guatucupa* and *Mi. furnieri* (Rodríguez, Rivero & Bastida, 2002). Therefore, the unsustainable exploitation of prey species could not only affect sand tiger sharks but other Patagonian marine predators (Crespo *et al.*, 1997; Skewgar *et al.*, 2007), the marine ecosystem and the tourism industry that they support (Skewgar *et al.*, 2007). The cascading consequences of overfishing can be dealt with by shifting from the population-level management currently in practice on the Argentine shelf towards ecosystem-level management and conservation programs (Pauly *et al.*, 2002; Pikitch *et al.*, 2004; Myers & Ottensmeyer, 2005; Campagna *et al.*, 2008). Sand tiger sharks, currently critically endangered and in need of strong protection, will benefit from such an approach that takes into account the many connections of exploited species with the rest of the community.

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