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Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications

Abstract Ontogenetic diet shifts are a widespread phenomenon among vertebrates, although their relationships with life history traits are poorly known. We analyzed the relative importance of body size, age and maturity stage as determinants of the diet of a marine top predator, the copper shark, *Carcharhinus brachyurus*, by examining stomach contents using a multiple-hypothesis modeling approach. Copper sharks shifted their diet as size and age increased and as they became sexually mature, incorporated larger prey as they grew, and had a discrete shift in diet with body size, with only individuals larger than ≈200 cm total length able to prey on chondrichthyans. Body size was the most important trait explaining the consumption of chondrichthyans, while age determined the consumption of pelagic teleosts. Pelagic teleosts were consumed mostly by medium-aged sharks, a result, probably, of a risk-reducing feeding strategy at young ages coupled with either a senescence-related decline in performance or a change in sensory capabilities as sharks age. Copper sharks of all sizes were able to cut prey in pieces, implying that gape limitation (i.e., the impossibility of eating prey larger than a predator's mouth) did not play a role in producing the diet shift. Our results suggest that, contrary to the current practice of setting minimum but not maximum size limits in catches, any plan to conserve or restore the ecological function of sharks, through their predatory control of large prey, should aim to maintain the largest individuals.

Keywords Predation · Ontogenetic niche shift · Life history · Shark fisheries · Patagonia

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Introduction

Ontogenetic diet shifts are a widespread phenomenon among vertebrates. Juveniles of many fish (Fishelson et al. 1987; McCormick 1998), reptiles (Lind and Welsh 1994; Herrel and O'Reilly 2006), mammals (Page et al. 2005), and birds (Price and Grant 1984; Kitowski 2003) usually consume different types and size of prey than adults, which is explained by ecological theory as a result mainly of differences in body size among individuals (Werner and Gilliam 1984; Herrel and Gibb 2006).

Body size is one of the most fundamental life history traits that affects individual characteristics determining food acquisition. In gape-limited predators, the effect of body size on the foraging capacity is especially important (Forsman 1991). Gape limitation precludes a predator from eating prey larger than its mouth, setting the upper limit to its trophic position (Hairston and Hairston 1993; Arim et al. 2007). This limitation increases the likelihood for the occurrence of an ontogenetic dietary shift since the upper limit of prey size increases with predator's size (Arnold 1993).

Individual traits others than body size have received less attention as determinants of resource use. The age of the individuals, as well as their maturity stage, is related in a complex way with resource use capability (Werner and

Gilliam 1984). As a predator ages, theoretical models predict that it will feed on larger and potentially more dangerous prey since natural selection favors this behaviour as the reproductive value of an individual decreases with age (Engen and Stenseth 1989). In addition, as a predator ages it may learn how to hunt profitable, but difficult-to-catch prey, thereby increasing its consumption (Rutz et al. 2006). As animals become sexually mature, the demand for energy or specific nutrients for reproductive processes such as gonad development, egg formation, and gestation increases (Robbins 1983; King and Murphy 1985). To match these increased energy requirements, a quantitative or qualitative change in diet is expected (Fishelson et al. 1987; Cooper et al. 2007).

Discrete and continuous ontogenetic diet shifts have different ecological implications intra- and interspecifically (Werner and Gilliam 1984). At the population level, discrete shifts involve little or no overlap in resource use between different size, age, or maturity-stage classes resulting in little interaction among these classes. Continuous ontogenetic shifts, on the other hand, result in the inclusion of the niche of the smaller, younger, or juvenile individuals in the niche of the larger, older, or adult individuals, so that a complete overlap and strong interactions exist. At the community level, if a species shifts its diet in a discrete fashion incorporating former competitors as it grows, it will benefit from a species that previously affected it negatively; on the other hand, if the change is continuous the largest species will simultaneously compete with and prey on the smaller species (Werner and Gilliam 1984). To our knowledge, no study has evaluated the type of ontogenetic shift arising from the relationship between a large top marine predator and different types of prey.

Unveiling the relative importance of body size, maturity stage, and age in determining the diet shift of a predator is difficult in animals having small absolute size ranges, as is the case with many fish, animals showing little variation in age or size at maturity, or animals that stop growing after reaching sexual maturity, as is the case with mammals, birds, and lizards. Large predatory sharks (i.e., >200 cm maximum total length) offer a good model system to evaluate the relative effects of these traits because the sharks usually experience ontogenetic dietary shifts (e.g., Cliff and Dudley 1991; Lowe et al. 1996; Simpfendorfer et al. 2001; Ebert 2002; Lucifora et al. 2005a), have a large absolute range of body size, mature over a range of sizes and ages, and continue growing after reaching sexual maturity (e.g., Lucifora et al. 2005b; Bishop et al. 2006; Whitney and Crow 2007).

From an applied point of view, the lack of knowledge on the relative effects of body size, age, and maturity stage on a predator's diet is not trivial, as these traits may be affected differently by human activities. With particular regard to sharks, human exploitation usually targets the largest and oldest individuals of a population, resulting in truncated size and age distributions (Ward and Myers 2005). It is expected that maturity-stage composition will be less affected by exploitation, since density-dependent compensatory mechanisms leading to earlier maturity may operate to cope with increased mortality (Sminkey and Musick 1995; Carlson and Baremore 2003). Evaluating the relative effects of these traits on the diet of large sharks is crucial in order to predict the potential effect of harvesting on the role of sharks as predators in marine communities.

In this paper we evaluate the relative effects of body size, age, and maturity stage on the diet of the copper shark, *Carcharhinus brachyurus*, a large, widely distributed (Compagno et al. 2005) and exploited (Muñoz-Chápuli 1984; Taniuchi 1990; Chiaramonte 1998; Hemida et al. 2002; Lucifora et al. 2005b) top predator. The copper shark is a good model species for this purpose because of its characteristics common to other large predatory sharks: a broad ontogenetic size range [birth size: 59–70 cm total length (TL), maximum size: 294 cm TL, Compagno et al. 2005], a long lifespan (up to 40 years), and a smaller maturity size (male maturity: 200–220 cm TL, female maturity: 215–223 cm TL; Lucifora et al. 2005b) than its maximum size. Studies on the diet of copper sharks are restricted to South African waters (Smale 1991; Cliff and Dudley 1992), where differences between the diets of individuals smaller or larger than 200 cm TL were detected (Smale 1991).

Materials and methods

Sampling

Copper sharks arrive in Anegada Bay (Argentina, Fig. 1) in December, using the area as a feeding ground throughout the summer until leaving for more northern waters by the end of March (Lucifora et al. 2005b). No sharks were killed specifically for this work, since all copper sharks sampled ($n = 303$) were part of a recreational fishery catch taken during the 1998–2001 fishing seasons (October–April) in Anegada Bay. Food remains were found in 149 copper sharks [89 juveniles (100–222 cm TL) and 60 adults (212–256 cm TL)]. During the study period, fishermen consistently used the same fishing grounds during all their trips.

For each individual, total length with the tail in its natural position was recorded, and maturity stage (i.e., juvenile or adult) was determined according to the condition of reproductive organs (Lucifora et al. 2005b). Age was determined from growth rings of 10–12 vertebrae taken from the area immediately anterior to the first dorsal fin from 116 individuals (67 with stomach contents). Vertebrae were cleaned and cut to obtain sections 0.2–0.4 mm wide, which were read by two independent readers (each without knowledge of the other reader's results) with the digital image analyzer Otoli32 version 3.10 (Ratoc Engineering System, Japan). The birth mark was assumed to be the angle change in the vertebrae's corpus calcareum, the ring following the angle change was the first winter mark, which corresponds to an age of
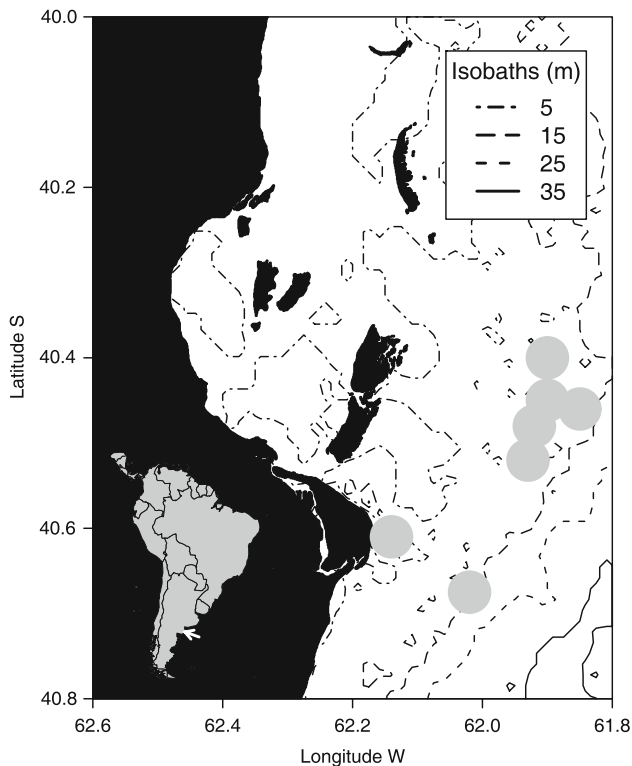
Fig. 1 Map of Anegada Bay, Argentina, showing the location of fishing grounds of the recreational fishery from which samples of copper sharks, *Carcharhinus brachyurus*, were taken (*gray circles*). The *inset* shows the location of Anegada Bay in South America (*white arrow*)

6 months and the following rings were considered to be annual (Walter and Ebert 1991).

Diet composition

Stomach contents were identified to the lowest possible taxon, counted and weighed. The order of stomachs sampled was randomized 100 times and the mean cumulative Shannon–Wiener diversity index was plotted as a function of sample size to assess sample sufficiency (Magurran 2004). Sample size was considered sufficient to describe diet if the cumulative Shannon–Wiener diversity index reached an asymptote. To allow for comparisons with other studies, we present diet composition as frequency of occurrence (*F*, proportion of stomachs that contained a given prey), frequency in number (*N*, number of individuals of a particular prey divided by the total number of consumed prey), and frequency in mass (*M*, mass of individuals of a particular prey divided by the total mass of consumed prey).

For statistical purposes, prey were grouped into five categories: pelagic teleosts, demersal teleosts, unidentified teleosts, chondrichthyans, and invertebrates. Pelagic and demersal teleosts were sorted according to Menni (1983) and Cousseau and Perrotta (2000). We conducted all analyses with both sexes pooled since a nonparametric multivariate analysis of variance (NPMANOVA)

with 5,000 permutations (Anderson 2001; McArdle and Anderson 2001) did not detect any significant difference in diet composition between the sexes ($F_{1,147} = 0.852$, $P = 0.390$).

Prey-predator size relationship

We first evaluated the relationship between prey mass and predator total length. The mass of undigested fish prey (i.e., those that did not show any sign of advanced digestion such as scale and skin loss and had no exposed bones) was used as a measure of body size, rather than length, width, or height, because of the large morphological differences among prey (e.g., fusiform pelagic teleosts vs. flattened, rhomboid-shaped eagle rays). We tested for an increase in minimum, median, and maximum size of consumed prey with increasing predator's size by testing the significance of the slopes of 10, 50, and 90% quantile regressions (Scharf et al. 1998), respectively.

Ontogenetic diet shifts

To explore if copper sharks experienced an ontogenetic diet shift, we evaluated differences in dietary composition between juveniles and adults. We used NPMANOVA on number and mass of prey groups as proportions of the total number or mass of prey consumed by each individual. These analyses were performed after 5,000 permutations of the data matrix.

Given the inherent logistic difficulties of performing field experiments with large marine top predators, we adopted a multiple-hypothesis modeling approach (Franklin et al. 2001) to identify the main traits related to diet shift in copper sharks. We tested the hypotheses that the consumption of each prey group is determined by (1) body size, (2) maturity stage, or (3) age using generalized linear models (GLM; Venables and Ripley 2002). For each prey group, three models were constructed where the number or presence/absence of each prey group was used as the response variable, and either shark body size, maturity stage, or age as explanatory variable. Since GLMs assume a linear relationship between the response and the explanatory variables, possible curvilinear relationships were assessed by fitting generalized additive models (GAM; Wood 2006). If GAMs detected a significant nonlinear relationship, then appropriate terms were included in the GLMs (e.g., quadratic functions) to account for this relationship (Crawley 2005). Models with number of prey as the response variable were specified to have a negative binomial error distribution to account for the large variance due to the large number of zero values in the samples, and a log link. Models with presence/absence of prey as the response variable had a binomial error distribution, due to the binary nature of the response variable, and a logit link. To obtain the likelihood of each hypothesis

given the data, Akaike's weights were computed for each model (Franklin et al. 2001).

If a significant relationship between prey consumption and shark size or age was detected, we tested whether this relationship was continuous or discrete (i.e., it had a threshold size or age at which sharks started to consume that prey). To do this, we fitted GLMs varying the threshold at intervals of 1 cm TL and selected the model with the threshold that produced the lowest deviance (Crawley 2005). Thresholds were modeled specifying that the consumption of the modeled prey was dependent on TL starting at the threshold value; below that threshold, prey consumption was independent of TL (Crawley 2005).

Finally, we tested if the potential for overcoming gape limitation by cutting prey (e.g., Helfman and Clark 1986; Scharf et al. 1997) varied with size, maturity stage, or prey mass, playing a role in producing ontogenetic diet differences in copper sharks. We classified prey in the stomachs as whole, sectioned (i.e., several parts of the same individual), or headless (only the rear 3/4 of the body found in the stomach) whenever the digestion stage allowed it. We determined the mass of sectioned prey by weighing together all the parts of the same individual. Differences in foraging mode (i.e., consuming prey whole or sectioned) between juveniles and adults were assessed by comparing the number of prey consumed whole, sectioned and headless between juveniles and adults with the log-likelihood test. To determine if the foraging mode varied with prey size we performed an ANCOVA to test for differences between whole and sectioned log-transformed prey mass for a given predator length. We expected differences between whole and sectioned prey mass if prey sectioning is related to differential prey handling and/or foraging mode due to prey size. Furthermore, we expected sectioned prey to be larger than nonsectioned prey if prey sectioning is related to overcoming gape limitation.

Results

Diet composition

The sample size was large enough to describe adequately the diet of this species in Anegada Bay, as cumulative diversity curves reached an asymptote (Fig. 2). Overall, the dominant prey groups consumed were pelagic teleosts (F = 40.3%, N = 88.0%, M = 21.4%) and chondrichthyans (F = 37.6%, N = 5.0%, M = 50.5%) (Table 1). Demersal teleosts (F = 24.2%, N = 3.0%, M = 23.0 %) and invertebrates (F = 4.0%, N = 0.5%, M = 0.1%) were less important components of the diet.

Prey-predator size relationship

Prey mass range increased with predator total length. Large sharks were able to feed on a wide range of prey
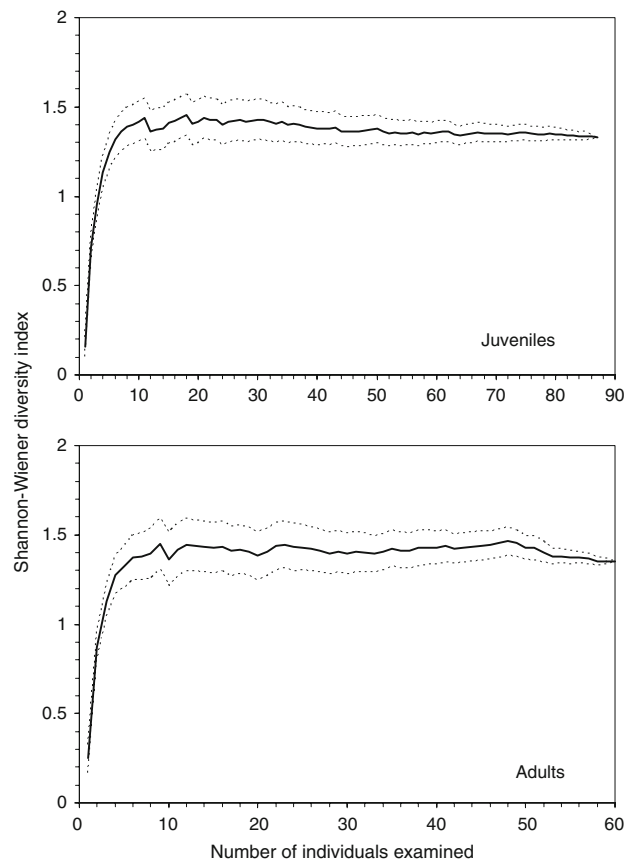

Fig. 2 Curves of cumulative mean diversity (Shannon–Wiener index) within stomachs of juvenile and adult copper sharks, *Carcharhinus brachyurus*, as a function of sample size

sizes, while small sharks fed only on small prey (Fig. 3). Minimum and median prey mass did not change significantly with predator's size (10% quantile regression slope = 0.267, t = 0.815, P = 0.417; 50% quantile regression slope = 0.310, t = 0.396, P = 0.693; Fig. 3), while maximum prey mass increased significantly with shark TL (90% quantile regression slope = 8.303, t = 3.952, P = 0.0001; Fig. 3).

Ontogenetic diet shifts

Copper sharks experienced an ontogenetic dietary shift, as evidenced by significant dietary differences between juveniles and adults both in number ($F_{1,147}$ = 5.886, P < 0.001) and mass ($F_{1,147}$ = 4.918, P = 0.002) of prey consumed.

As sharks' size and age increased, the consumption of chondrichthyans increased in number and presence/absence. A significant threshold was found for body size; copper sharks started to consume chondrichthyans when they were around 200 cm TL (208 and 198 cm TL for number and presence/absence of chondrichthyans consumed, respectively). The number of pelagic teleosts consumed had a curvilinear, humped relationship with total length and age (Fig. 4). All other prey did not have

Table 1 Diet composition of juvenile ($n = 89$) and adult ($n = 60$) *Carcharhinus brachyurus*

Prey		Juveniles			Adults		
		F (%)	N (%)	M (%)	F (%)	N (%)	M (%)
Pelagic teleosts							
Clupeidae	*Brevoortia aurea*	2.25	0.19	2.05	1.67	0.23	1.14
Engraulidae	*Engraulis anchoita*	7.87	87.96	14.13	6.67	71.95	8.82
Atherinopsidae	*Odonthestes argentinensis*	26.97	2.89	8.53	11.67	3.91	1.30
Stromateidae	*Stromateus brasiliensis*	11.24	0.96	5.66	15.00	2.30	3.92
Total pelagic teleosts		44.94	92.00	30.36	33.33	78.39	15.18
Demersal teleosts							
Congridae	*Conger orbignyanus*	2.25	0.19	4.20			
Batrachoididae	*Porichthys porosissimus*	1.12	0.10	0.05			
Serranidae	*Acanthistius brasilianus*	2.25	0.19	0.35			
Sparidae	*Pagrus pagrus*	1.12	0.10	2.40			
Sciaenidae	*Cynoscion guatucupa*	12.36	1.06	9.96	5.00	1.15	5.23
	Micropogonias furnieri	3.37	0.29	5.35	5.00	0.69	4.77
Percophididae	*Percophis brasiliensis*	3.37	0.29	3.77	3.33	0.46	1.39
Pinguipedidae	*Pinguipes brasiliensis*	1.12	0.10	1.46			
	Pseudopercis semifasciata	1.12	0.10	5.48	5.00	0.69	3.25
Paralichthyidae					3.33	1.38	1.25
Total demersal teleosts		25.84	2.41	33.02	21.67	4.37	15.88
Unidentified teleosts		28.09	2.89	7.54	23.33	4.83	3.12
Chondrichthyans							
Squatinidae	*Squatina guggenheim*	1.12	0.10	1.23	6.67	1.15	19.34
Triakidae	*Mustelus schmitti*	5.62	0.48	2.85	5.00	0.69	2.59
Rajidae	*Atlantoraja castelnaui*	2.25	0.19	5.23	1.67	0.23	8.33
	Psammobatis spp.				1.67	1.15	1.13
	Sympterygia bonapartii				1.67	0.23	0.10
	Unidentified rajidae	3.37	0.29	2.86	6.67	2.07	5.91
Myliobatidae	*Myliobatis* spp.	5.62	0.58	10.96	18.33	2.76	25.96
Unidentified batoids		4.49	0.39	4.59	10.00	1.38	1.51
Callorhynchidae	*Callorhinchus callorhynchus*	1.12	0.10	1.03	1.67	0.46	0.13
Unid. chondrichthyans		1.12	0.10	0.12	11.67	1.61	0.68
Total chondrichthyans		23.60	2.22	28.87	58.33	11.72	65.68
Invertebrates							
Porifera	Unidentified sponge	1.12	0.10	0.01			
Cnidaria	*Alcyonium* sp.				1.67	0.23	0.02
Mollusca	*Buccinanops duartei*	2.25	0.29	0.05	1.67	0.23	0.01
	Unidentified squid	1.12	0.10	<0.01			
Urochordata	Unidentified ascidian				1.67	0.23	0.11
Total invertebrates		4.49	0.48	0.06	3.33	0.69	0.14
Total		89	1,038	21,884.75	60	435	31,262.76

Frequency of occurrence (*F*), frequency in number (*N*), and frequency in mass (*M*) are presented as percentages. Total number and mass (in g) of all prey are shown at the bottom

a significant relationship with any of the three traits analyzed.

Gape limitation did not play a role in determining ontogenetic dietary differences since sharks of all sizes were able to cut prey in pieces (Fig. 3), and both juveniles and adults consumed their prey whole, sectioned and headless in similar proportions ($G = 2.3$, d.f. = 2, $P = 0.31$). Prey groups differed in how they were consumed: pelagic teleosts were found predominantly whole (97%, $n = 609$), whereas demersal teleosts and chondrichthyans were consumed whole or cut in pieces (i.e., sectioned or headless) in more similar proportions (39%, $n = 46$; and 56%, $n = 27$; respectively). The mean mass of the different prey was significantly different (Kruskal–Wallis $\chi^2 = 16.442$, d.f. = 2, $P < 0.001$): chondrichthyans (mean mass = 599.72 g, s.d. = 709.04 g) and demersal teleosts (mean mass = 347.48 g, s.d. =

250.87 g) were larger than pelagic teleosts (mean mass = 125.04 g, s.d. = 103.38 g) (pairwise Wilcoxon test with false discovery rate correction, $P < 0.05$). This affected the way in which prey were consumed by copper sharks (ANCOVA, $F_{3,96}$, $P < 0.001$): prey consumed sectioned had a significantly higher mass than prey consumed whole ($t = 6.106$, $P < 0.001$, Fig. 5).

The consumption of chondrichthyans (both in number and presence/absence) and pelagic teleosts (in number) changed significantly with body size and age, respectively. The best model explaining the consumption of chondrichthyans, both in number and frequency of occurrence, only included body size with a threshold (Tables 2 and 3). The effect of the threshold in body size on the number of consumed chondrichthyans was 2.68, 4.03, 17.81, and 18.63 times higher than body size without a threshold, maturity stage, age, or age with a
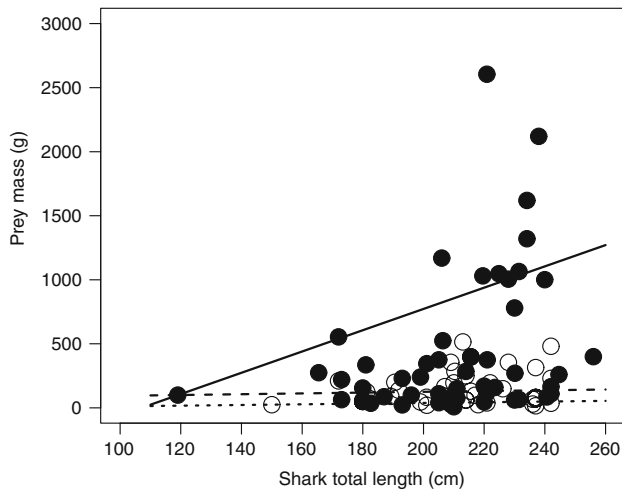
Fig. 3 Quantile regressions of prey weight and copper shark, *Carcharhinus brachyurus*, total length. The *dotted*, *dashed* and *solid lines* are 10, 50 and 90% quantile regressions used to estimate changes with shark length in minimum, median and maximum prey mass, respectively. Only the regression for maximum prey mass is significant ($P = 0.005$). *Dots*: prey consumed sectioned, *open circles*: prey consumed whole
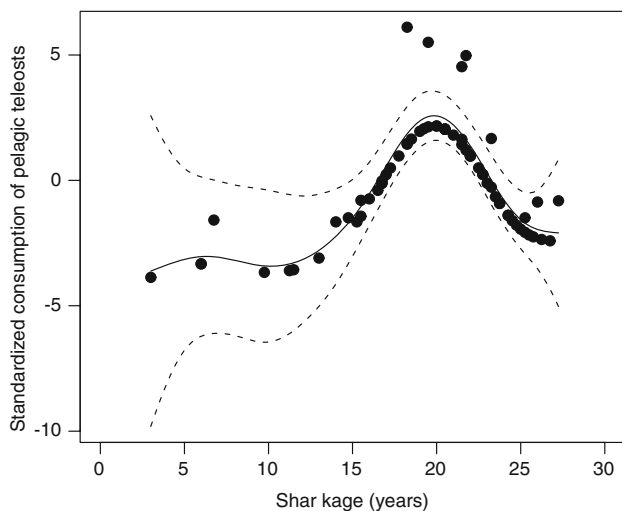

Fig. 4 Relationship between number of pelagic teleosts consumed and predator age for copper sharks, *Carcharhinus brachyurus*. The *dots* represent the residuals of number of pelagic teleosts while holding constant the effects of maturity stage, as estimated by a generalized additive model (GAM) with a log link and a negative binomial error distribution. The *solid line* is the function estimated by the GAM and *dashed lines* are 95% confidence intervals

threshold, respectively (Table 2). A body size threshold was also the best hypothesis explaining chondrichthyan consumption in frequency of occurrence, being 2.03, 7.13, 10.07, and 12.18 times more likely than the models containing body size without a threshold, maturity stage, age, or age with a threshold, respectively (Table 3). The consumption of pelagic teleosts in number was dependent on age, an explanation over four orders of magnitude more likely than the hypotheses including body size or maturity stage (Table 4).
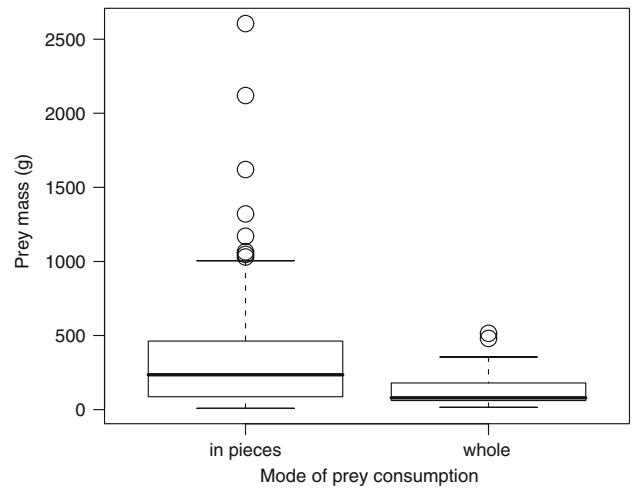

Fig. 5 Mass of fish prey consumed whole or in pieces by copper sharks, *Carcharhinus brachyurus*. *Bold line*: median, *boxes*: inter-quartile range, whiskers: range (excluding outliers), *open circles*: outliers

Discussion

Our results show that (1) copper sharks shift their diet as size and age increase, (2) copper sharks incorporate larger prey in their diet as they grow, (3) there is a discrete shift in diet with body size, with only large individuals (i.e., larger than ≈200 cm TL) able to prey on chondrichthyans, (4) body size is a stronger determinant of chondrichthyan consumption than age or maturity stage, and (5) pelagic teleosts were consumed mostly by medium-aged sharks.

Like in other sharks, individuals of all sizes preyed on small prey, but only large sharks were able to consume large prey (Chiaramonte and Pettovello 2000; Scharf et al. 2000; Bethea et al. 2004; Lucifora et al. 2006). The continued inclusion of small prey in the diet of large predators is likely a result of their low cost of capture (Pyke et al. 1977) and a high encounter probability (Scharf et al. 2000). Direct observations of copper sharks feeding on small fish showed that they attack the schools taking mouthfuls of prey without further handling (Smale 1991), which may reduce their acquisition cost.

The effect of body size in producing a discrete shift in chondrichthyan consumption cannot be explained by a differential ability to overcome gape limitation in large sharks. Copper sharks of all sizes were able to cut prey in pieces indicating that all individuals have the capacity to ingest prey larger than their mouth; however, small copper sharks do not include large prey, such as chondrichthyans in their diet. Chondrichthyans are not usually subdued in the initial attack and require additional handling by predatory sharks (Strong et al. 1990; Chapman and Gruber 2002). Small sharks may not be physically capable of performing the complete sequence of attack and handling successfully due to lack of strength, as suggested for example, by the allometric

Table 2 Summary of models used to explain chondrichthyan consumption in number in the copper shark, *Carcharhinus brachyurus*

Rank	Model	w	AIC
1	$-1.431\ (0.344)\ +\ 0.062\ (0.017)\ \mathrm{TL}_{>208}$	0.578	134.26
2	$-8.186\ (3.148)\ +\ 0.035\ (0.014)\ \mathrm{TL}$	0.216	136.23
3	$0.105\ (0.309)\ -\ 1.396\ (0.482)\ \mathrm{Juvenile}$	0.143	137.05
4	$-3.145\ (1.381)\ +\ 0.127\ (0.064)\ \mathrm{Age}$	0.032	140.02
5	$-1.229\ (0.425)\ +\ 0.196\ (0.088)\ \mathrm{Age}_{>18}$	0.031	140.11

For each model parameters and standard errors (in *brackets*) are given. The parameter for maturity stage is given as relative to adults. Models are ordered according to the rank from the highest (most likely explanation) to the lowest (least likely explanation) Akaike weight. Thresholds in body size and age were determined to be 208 cm total length and 18 years, respectively

TL total length in cm, *w* Akaike's weight, *AIC* Akaike's information criterion

Table 3 Summary of models used to explain chondrichthyan consumption as presence/absence in the copper shark, *Carcharhinus brachyurus*

Rank	Model	w	AIC
1	$-1.781\ (0.487)\ +\ 0.067\ (0.020)\ \mathrm{TL}_{>198}$	0.551	79.22
2	$-10.499\ (3.568)\ +\ 0.047\ (0.016)\ \mathrm{TL}$	0.271	80.64
3	$0.375\ (0.392)\ -\ 1.611\ (0.545)\ \mathrm{Juvenile}$	0.078	83.15
4	$-4.004\ (1.441)\ +\ 0.173\ (0.068)\ \mathrm{Age}$	0.055	83.84
5	$-1.360\ (0.421)\ +\ 0.264\ (0.096)\ \mathrm{Age}_{>18}$	0.045	84.22

For each model parameters and standard errors (in *brackets*) are given. The parameter for maturity stage is given as relative to adults. Models are ordered according to the rank from the highest (most likely explanation) to the lowest (least likely explanation) Akaike weight. Thresholds in body size and age were determined to be 198 cm total length and 18 years, respectively

TL total length in cm, *w* Akaike's weight, *AIC* Akaike's information criterion

Table 4 Summary of models used to explain pelagic teleost consumption in number in the copper shark, *Carcharhinus brachyurus*

Rank	Model	w	AIC
1	$-17.444\ (1.779)\ +\ 3.096\ (0.202)\ \mathrm{Age}\ -\ 0.092\ (0.005)\ \mathrm{Age}^2$	0.999	289.80
2	$-212.4\ (12.5)\ +\ 2.253\ (0.122)\ \mathrm{TL}\ -0.006\ (0.0003)\ \mathrm{TL}^2$	8×10^{-4}	303.93
3	$1.930\ (0.580)\ +\ 11.532\ (0.748)\ \mathrm{Juvenile}$	9×10^{-10}	331.39

For each model parameters and standard errors (in *brackets*) are given. The parameter for maturity stage is given as relative to adults. Models are ordered according to the rank from the highest (most likely explanation) to the lowest (least likely explanation) Akaike weight

TL total length in cm, *w* Akaike's weight, *AIC* Akaike's information criterion

scaling of bite force with shark size (Huber et al. 2006) and variation in prey capture kinematics with shark size (Motta and Wilga 2001). Alternatively, small sharks may be physically capable of killing and consuming chondrichthyan prey, but only after longer handling times than a large shark. Longer handling times may make large prey more costly for small sharks, resulting in the dropping of chondrichthyans as potential prey for small sharks.

For a predator feeding on multiple prey species, its capabilities to use each prey along its life may be determined by different traits, depending on the prey's characteristics, like size or grouping behaviour. The consumption of chondrichthyans and pelagic teleosts by copper sharks is dependent on different traits, which may reflect the different challenges posed to a predator by prey with radically different ecologies. While physical strength may be very important to hunt large prey like chondrichthyans, it is certainly less so when hunting for very small prey, such as pelagic teleosts. The limiting step in the prey-predator interaction for a copper shark feeding on pelagic teleosts could be finding and not being detected by them, rather than attacking and killing them, since these small prey form schools that protect them from predators (Pitcher and Parrish 1993).

We propose that the humped relationship of the consumption of pelagic teleosts with age could be the result of a risk-reducing feeding strategy at young ages coupled with either a senescence-related decline in performance or a change in sensory capabilities as sharks age. Very young sharks may avoid preying on pelagic teleosts because that will imply venturing into open, riskier waters (Heithaus 2004). As sharks grow older, natural selection favors riskier behaviour as their reproductive value decreases (Engen and Stenseth 1989), so they include pelagic teleosts in their diet. We hypothesize that the decrease in the importance of pelagic teleosts as prey later in copper sharks' life may be due to two possible causes. As they become even older, sharks may lose the agility necessary to catch fast and rapidly-turning pelagic teleosts producing the humped relationship due to a senescence-related decline in physical performance (Kardong 1996; Punzo and Chávez 2003). Alternatively, vision, a very important sense for catching fast pelagic teleosts, becomes less dominant relative to other senses in older sharks since the optic tectum decreases in size as sharks age (Lisney et al. 2007).

Large sharks have substantial impacts on marine communities through the control they exert on mesoconsumers such as smaller sharks, rays, marine mammals, seabirds and turtles (Lucas and Stobo 2000; Acevedo-Gutiérrez 2002; Heithaus and Dill 2002, 2006; Heithaus 2005; Heithaus et al. 2007; Wirsing et al. 2007). These mesoconsumers often have important roles in structuring marine communities (vanBlaricom 1982; Thrush et al. 1991; Bjorndal 1997; Hines et al. 1997) and they are preyed on mostly or solely by large sharks (Heithaus 2004). As a result, both theoretical (Stevens et al. 2000; Okey et al. 2004; Frid et al. 2008) and empirical (Ward and Myers 2005; Shepherd and Myers 2005; Myers et al. 2007) evidence indicates that when populations of large sharks are depleted or extirpated,

mesoconsumers are free of control and their influence cascades down the food web, affecting the whole community. As body size is very important in determining mesoconsumer consumption by sharks, human exploitation will have a major impact on the functional role of sharks in marine communities, since fisheries target the largest and oldest individuals, selecting against large size and long lifespan (Reznick and Ghalambor 2005; de Roos et al. 2006).

Furthermore, large shark individuals, by having a wider scope of prey size, have a wider trophic niche, which may help to maintain the stability of the ecosystem. Sharks are often key players in marine trophic webs because they are involved in strong predator-prey interactions that act as a buffer against trophic cascades and that, if weakened or disrupted, may destabilize food web structure (Bascompte et al. 2005). Our results suggest that body size determines the number of predator-prey interactions in which a shark is involved, with large individuals linked to more prey and then expanding their influence over more trophic links. This further implies that the loss of only the largest shark individuals is sufficient to affect ecosystem functioning.

The ecological importance of large shark individuals contrasts with their being the most common target of fisheries, indicating that a major shift in marine management and conservation planning is needed. At the population level, limiting fishery catches to the oldest and largest individuals may reduce the extinction risk of the population (Cortés 1998; Myers and Worm 2005), but this practice will remove the individuals with the highest value for the functioning of the ecosystem. Most current fishery management plans, which set minimum but not maximum size limits in catches, allow for the extirpation of the largest individuals, not considering the ecosystemic importance of large sharks. Any plan to conserve or restore ecosystem functioning—the goal of the ecosystemic approach to fisheries management (Pauly et al. 2002; Myers and Ottensmeyer 2005)—should aim to maintain the largest shark individuals.

References

Acevedo-Gutiérrez A (2002) Interactions between marine predators: dolphin food intake is related to the number of sharks. Mar Ecol Prog Ser 240:267–271

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Aust Ecol 26:32–46

Arim M, Bozinovic F, Marquet PA (2007) On the relationship between trophic position, body mass and temperature: reformulating the energy limitation hypothesis. Oikos 116:1524–1530

Arnold SJ (1993) Foraging theory and prey-size relations in snakes. In: Seigel RA, Collins JT (eds) Snakes: ecology and behaviour. McGraw-Hill, New York, pp 87–116

Bascompte J, Melián CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. Proc Nat Acad Sci USA 102:5443–5447

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

Bishop SDH, Francis MP, Duffy C, Montgomery JC (2006) Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus oxyrinchus*) in New Zealand waters. Mar Freshw Res 57:143–154

Bjorndal KA (1997) Foraging ecology and nutrition of sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, pp 199–231

Carlson JK, Baremore IE (2003) Changes in biological parameters of Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the Gulf of Mexico: evidence for density-dependent growth and maturity? Mar Freshw Res 54:227–234

Chapman DD, Gruber SH (2002) A further observation of the prey-handling behavior of the great hammerhead shark, *Sphyrna mokarran*: predation upon the spotted eagle ray, *Aetobatus narinari*. Bull Mar Sci 70:947–952

Chiaramonte GE (1998) Shark fisheries in Argentina. Mar Freshw Res 49:601–609

Chiaramonte GE, Pettovello AD (2000) The biology of *Mustelus schmitti* in southern Patagonia, Argentina. J Fish Biol 57:930–942

Cliff G, Dudley SFJ (1991) Sharks caught in the protective gill nets off Natal, South Africa. 4. The bull shark *Carcharhinus leucas* Valenciennes. S Afr J Mar Sci 10:253–270

Cliff G, Dudley SFJ (1992) Sharks caught in the protective gill nets off Natal, South Africa. 6. The copper shark *Carcharhinus brachyurus* (Günther). S Afr J Mar Sci 12:663–674

Cooper AB, Pettorelli N, Durant SM (2007) Large carnivore menus: factors affecting hunting decisions by cheetahs in the Serengeti. Anim Behav 73:651–659

Cortés E (1998) Demographic analysis as an aid in shark stock assessment and management. Fish Res 39:199–208

Cousseau MB, Perrotta RG (2000) Peces marinos de Argentina. Biología, distribución, pesca. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata

Compagno L, Dando M, Fowler S (2005) A field guide to the sharks of the world. Harper Collins, London

Crawley MJ (2005) Statistics: an introduction using R. Wiley, Chichester

de Roos AM, Boukal DS, Persson L (2006) Evolutionary regime shifts in age and size at maturation of exploited fish stocks. Proc R Soc B 273:1876–1880

Ebert DA (2002) Ontogenetic changes in the diet of the sevengill shark (*Notorynchus cepedianus*). Mar Freshw Res 53:517–523

Engen S, Stenseth NC (1989) Age-specific optimal diets and optimal foraging tactics: a life-history approach. Theor Pop Biol 36:281–295

Fishelson L, Montgomery LW, Myrberg AH Jr (1987) Biology of surgeonfish *Acanthurus nigrofuscus* with emphasis on changeover in diet and annual gonadal cycles. Mar Ecol Prog Ser 39:37–47

Forsman A (1991) Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. J Anim Ecol 60:253–267

Franklin AB, Shenk TM, Anderson DR, Burnham KP (2001) Statistical model selection: an alternative to null hypothesis testing. In: Shenk TM, Franklin AB (eds) Modeling in natural resource management: development, interpretation, and application. Island Press, Washington, pp 75–90

Frid A, Baker GG, Dill LM (2008) Do shark declines create fear-related systems? Oikos 117:191–201

Hairston NG Jr, Hairston NG Sr, (1993) Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. Am Nat 142:379–411

Heithaus MR (2004) Predator-prey interactions. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, pp 487–521

Heithaus MR (2005) Habitat use and group size of pied cormorants (Phalacrocorax varius) in a seagrass ecosystem: possible effects of food abundance and predation risk. Mar Biol 147:27–35

Heithaus MR, Dill LM (2002) Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480–491

Heithaus MR, Dill LM (2006) Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? Oikos 114:257–264

Heithaus MR, Frid A, Wirsing AJ, Dill LM, Fourqurean JW, Burkholder D, Thomson J, Berjder L (2007) State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. J Anim Ecol 76:837–844

Helfman GS, Clark JB (1986) Rotational feeding: overcoming gape-limited foraging in anguillid eels. Copeia 1986:679–685

Hemida F, Seridji R, Labidi N, Bensaci J, Capapé C (2002) Records of Carcharhinus spp. (Chondrichthyes: Carcharhinidae) from off the Algerian coast (southern Mediterranean). Acta Adriat 43:83–92

Herrel A, Gibb AC (2006) Ontogeny of performance in vertebrates. Physiol Biochem Zool 79:1–6

Herrel A, O'Reilly JC (2006) Ontogenetic scaling of bite force in lizards and turtles. Physiol Biochem Zool 79:31–42

Hines AH, Whitlach RB, Thrush SF, Hewitt JE, Cummings VJ, Dayton PK, Legendre P (1997) Nonlinear foraging response of a large marine predator to benthic prey: eagle ray pits and bivalves in a New Zealand sandflat. J Exp Mar Biol Ecol 216:191–210

Huber DR, Weggelaar CL, Motta PJ (2006) Scaling of bite force in the blacktip shark Carcharhinus limbatus. Zoology 109:109–119

Kardong KV (1996) Evolution of aging: theoretical and practical implications from rattlesnakes. Zoo Biol 15:267–277

King JR, Murphy ME (1985) Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? Am Zool 25:955–964

Kitowski I (2003) Age-related differences in foraging behavior of Montagu's harrier Circus pygargus males in south-east Poland. Acta Ethol 6:35–38

Lind AJ, Welsh HH Jr, (1994) Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, Thamnophis atratus hydrophilus. Anim Behav 48:1261–1273

Lisney TJ, Bennett MB, Collin SP (2007) Volumetric analysis of sensory brain areas indicates ontogenetic shifts in the relative importance of sensory systems in elasmobranchs. Raffles Bull Zool 14(Suppl):7–15

Lowe CG, Wetherbee BM, Crow GL, Tester AL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, Galeocerdo cuvier, in Hawaiian waters. Environ Biol Fish 47:203–211

Lucas Z, Stobo WT (2000) Shark-inflicted mortality on a population of harbour seals (Phoca vitulina) at Sable Island, Nova Scotia. J Zool 252:405–414

Lucifora LO, Menni RC, Escalante AH (2005a) Reproduction, abundance and feeding habits of the broadnose sevengill shark Notorynchus cepedianus in north Patagonia, Argentina. Mar Ecol Prog Ser 289:237–244

Lucifora LO, Menni RC, Escalante AH (2005b) Reproduction and seasonal occurrence of the copper shark, Carcharhinus brachyurus, from north Patagonia, Argentina. ICES J Mar Sci 62:107–115

Lucifora LO, García VB, Menni RC, Escalante AH (2006) Food habits, selectivity, and foraging modes of the school shark, Galeorhinus galeus. Mar Ecol Prog Ser 315:259–270

Magurran AE (2004) Measuring biological diversity. Blackwell, Malden

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82:290–297

McCormick MI (1998) Ontogeny of diet shift by a microcarnivorous fish, Cheilodactylus spectabilis: relationship between feeding mechanics, microhabitat selection and growth. Mar Biol 132:9–20

Menni RC (1983) Los peces en el medio marino. Editorial Hemisferio Sur, Buenos Aires

Motta PJ, Wilga CD (2001) Advances in the study of feeding behaviors, mechanisms and mechanics of sharks. Environ Biol Fish 60:131–156

Muñoz-Chápuli R (1984) Ethologie de la reproduction chez quelques requins de l'Atlantique Nord-Est. Cybium 8:1–14

Myers RA, Ottensmeyer CA (2005) Extinction risk in marine species. In: Norse EA, Crowder LB (eds) Marine conservation biology: the science of maintaining the sea's biodiversity. Island Press, Washington, pp 58–79

Myers RA, Worm B (2005) Extinction, survival or recovery of large predatory fishes. Phil Trans R Soc B 360:13–20

Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315:1846–1850

Okey TA, Banks S, Born AF, Bustamante RH, Calvopiña M, Edgar GJ, Espinoza E, Fariña JM, Garske LE, Reck GK, Salazar S, Shepherd S, Toral-Granda V, Wallem P (2004) A trophic model of a Galápagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecol Model 172:383–401

Page B, McKenzie J, Goldsworthy SD (2005) Dietary resource partitioning among sympatric New Zealand and Australian fur seals. Mar Ecol Prog Ser 293:283–302

Pauly DA, Christensen V, Guénette S, Pitcher TJ, Sumaila UR, Walters CJ, Watson R, Zeller D (2002) Towards sustainability in world fisheries. Nature 418:689–695

Pitcher TJ, Parrish JK (1993) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed) Behaviour of teleosts fishes. Chapman & Hall, London, pp 363–439

Price TD, Grant PR (1984) Life history traits and natural selection for small body size in a population of Darwin's finches. Evolution 38:483–494

Punzo F, Chávez S (2003) Effects of aging on spatial learning and running speed in the shrew (Cryptotis parva). J Mammal 84:1112–1120

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. Q Rev Biol 52:137–154

Reznick DN, Ghalambor CK (2005) Can commercial fishing cause evolution? Answers from guppies (Poecilia reticulata). Can J Fish Aquat Sci 62:791–801

Robbins CT (1983) Wildlife feeding and nutrition. Academic Press, New York

Rutz C, Whittingham MJ, Newton I (2006) Age-dependent diet choice in an avian top predator. Proc R Soc B 273:579–586

Scharf FS, Buckel JA, Juanes F, Conover DO (1997) Estimating piscine prey size from partial remains: testing for shifts in foraging mode by juvenile bluefish. Environ Biol Fish 49:377–388

Scharf FS, Juanes F, Sutherland MS (1998) Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. Ecology 79:448–460

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

Shepherd TD, Myers RA (2005) Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. Ecol Lett 8:1095–1104

Simpfendorfer CA, Goodreid A, McAuley RB (2001) Size, sex and geographic variation in the diet of the tiger shark, Galeocerdo cuvier, from Western Australian waters. Environ Biol Fish 61:37–46

Smale MJ (1991) Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the Eastern Cape coast of South Africa. S Afr J Mar Sci 11:31–42

Sminkey TR, Musick JA (1995) Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. Copeia 1995:871–883

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57:476–494

Strong WR Jr, Snelson FF Jr, Gruber SH (1990) Hammerhead shark predation on stingrays: an observation of prey handling by *Sphyrna mokarran*. Copeia 1990:836–840

Taniuchi T (1990) The role of elasmobranchs in Japanese fisheries. 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 Tech Rep NMFS 90:415–426

Thrush SF, Pridmore RD, Hewitt JE, Cummings VJ (1991) Impact of ray feeding disturbances on sandflat macrobenthos: do communities dominated by polychaetes or shellfish respond differently? Mar Ecol Prog Ser 69:245–252

VanBlaricom GR (1982) Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. Ecol Monogr 52:283–305

Venables WN, Ripley BD (2002) Modern applied statistics with S-Plus, 4th edn. Springer, New York

Walter JP, Ebert DA (1991) Preliminary estimates of age of the bronze whaler *Carcharhinus brachyurus* (Chondrichthyes: Carcharhinidae) from southern Africa, with a review of some life history parameters. S Afr J Mar Sci 10:37–44

Ward P, Myers RA (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology 86:835–847

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–425

Whitney NM, Crow GL (2007) Reproductive biology of the tiger shark (*Galeocerdo cuvier*) in Hawaii. Mar Biol 151:63–70

Wirsing AJ, Heithaus MR, Dill LM (2007) Fear factor: do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)? Oecologia 153:1031–1040

Wood S (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton