Environ Biol Fish (2006) 76:81–92
DOI 10.1007/s10641-006-9010-y

ORIGINAL PAPER

Food habits and ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in Hawaii

W. David McElroy · Bradley M. Wetherbee · Carolyn S. Mostello · Christopher G. Lowe · Gerald L. Crow · Richard C. Wass

Received: 9 June 2005 / Accepted: 16 February 2006 / Published online: 5 June 2006
© Springer Science+Business Media B.V. 2006

Abstract The sandbar shark, *Carcharhinus plumbeus*, is a wide-ranging coastal species in tropical and temperate regions, and it is the most common species of shark in Hawaii, as in many locations where it occurs. Information on the diet and feeding habits of this species in the Pacific Ocean are extremely limited. For this study we quantified the diet of sandbar sharks in Hawaii based on records collected during the Hawaii Cooperative Shark Research and Control Program from 1967 to 1969. During this program a total of 565 stomachs were examined, of which 265 contained food. Sharks ranged in size from 59 to 190 cm total length. Teleosts were the most common prey group, but both cephalopods and crustaceans also occurred frequently. Ontogenetic changes in diet of sandbar sharks were apparent, with crustaceans forming a greater proportion of the diet of smaller sharks. Both cephalopods and elasmobranchs increased in importance with increasing shark size. Prey diversity also increased with size, with large, mobile, and reef prey species found more commonly in the diet of larger sharks. Mature male and female sharks appeared to segregate by depth, though major differences in the diet between the sexes were not apparent. However, there was some evidence of dietary differences between sharks caught in different depths and seasons. The results of this study suggest that sandbar sharks in Hawaii and throughout the world, are primarily piscivores, but also consume a variety of invertebrate prey, and that their diet varies with geographical location and stage of development.

Keywords Diet · Feeding · Sex segregation · Depth · Geographic variation

W. D. McElroy (✉)
Fisheries, Animal & Veterinary Sciences, University of Rhode Island, Kingston, RI 02881, USA
e-mail: wmce3776@postoffice.uri.edu

B. M. Wetherbee
Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA

C. S. Mostello
Natural Heritage & Endangered Species Program, Massachusetts Division of Fisheries & Wildlife, North Drive, Westborough, MA 01581, USA

C. G. Lowe
Department of Biological Sciences, California State University, Long Beach, 1250 Bellflower Blvd, Long Beach, CA 90840, USA

G. L. Crow
Waikiki Aquarium, 2777 Kalakaua Blvd., Honolulu, HI 96815, USA

R. C. Wass
Hakalau Forest National Wildlife Refuge, 32 Kino'ole Street, Suite 101, Hilo, HI 96720, USA

Introduction

The sandbar shark, *Carcharhinus plumbeus*, is a widespread coastal species found in warm and temperate seas on both sides of the Atlantic Ocean including the Mediterranean Sea, the Western Indian Ocean, the Western Pacific Ocean, and the Hawaiian Islands (Taniuchi 1971; Wass 1973; Compagno 1984; Cliff et al. 1988). This species is most often found in coastal waters, and uses bays, estuaries and shallow near-shore habitats as nursery areas during the first few years of their lives (Springer 1960; Compagno 1984; Carlson 1999; Merson and Pratt 2001), however, in Hawaii the young sharks are not found in estuaries but occur in deeper waters. Sandbar sharks are one of the most common species caught in directed commercial shark fisheries off the U.S. east coast and Gulf of Mexico and account for the second highest landings of any shark species in the United States (NMFS 1993).[1] As a result of a combination of the life history characteristics (slow growth, late maturity, and few offspring) of sandbar sharks and elevated fishing pressure, sandbar shark populations off the U.S. east coast declined dramatically over the past several decades, and sandbar sharks were included in a federal management plan to enhance recovery of stocks (Sminkey and Musick 1995; NMFS 2003).[2]

A number of aspects of the biology of sandbar sharks have been well studied in the Western Atlantic and several other locations. Movement patterns, distribution, and demographics have been investigated primarily in the Western Atlantic (Baughman and Springer 1950; Springer 1960; Cortés 1999; Rechisky and Wetherbee 2003). Several studies have examined age and growth in sandbar sharks in the Atlantic and have suggested that this species reaches maturity at between 15 and 30 years of age (Casey et al. 1985; Casey and Natanson 1992; Sminkey and Musick 1995). Reproductive characteristics have been examined at a number of locations where this species occurs, including the Western Atlantic Ocean (Springer 1960; Clark and von Schmidt 1965; Branstetter 1981), the Indian Ocean (Wheeler 1962; Bass et al. 1975; Baranes and Wendling 1981; Capapé 1984; Cliff et al. 1988) and the Pacific Ocean (Taniuchi 1971; Wass 1973; Stevens and McLoughlin 1991; Joung and Chen 1995). Size at maturity, size at birth, litter size, and parturition time were found to vary among these locations.

Sandbar sharks have been the subject of a suite of studies on rate of food passage, quantification of rate of consumption, and the role of these sharks in nursery areas along the U.S. east coast (Medved and Marshall 1981; Medved et al. 1988; Stillwell and Kohler 1993). Feeding habits of sandbar sharks have been described through qualitative listing of prey items found in stomachs (Springer 1946; Baughman and Springer 1950; Springer 1960; Clark and von Schmidt 1965; Bass et al. 1975) and more extensive quantitative studies of stomach contents (Medved et al. 1985; Stevens and McLoughlin 1991; Stillwell and Kohler 1993). These studies indicate that the general diet of adult sharks includes a wide variety of mostly benthic teleosts, elasmobranchs (predominately *Raja* sp.) and in some regions cephalopods. The diet of juveniles is characterized by consumption of a large proportion of crustaceans, especially crabs, and much smaller quantities of fish and elasmobranchs.

Although there have been reports on the diet of sandbar sharks from the Atlantic and Indian oceans, there have been few records on feeding habits of sandbar sharks in the Pacific. In Hawaii, sandbar sharks are the most common species of coastal shark (Wetherbee et al. 1994), yet reports on the food habits of sandbar sharks in Hawaiian waters have not been published. During the 1960s and 1970s several large-scale shark control programs were conducted in Hawaii, during which several thousand sharks were caught and dissected (Tester 1969;[3] Wetherbee et al. 1994). For the majority of sharks captured and killed during these control programs, information on stomach contents and reproduction was collected. This extensive database has been the source of several studies on the biology of sharks common in Hawaiian waters (Crow et al. 1996; Lowe et al. 1996; Wetherbee et al. 1996, 1997). Although sandbar sharks were the most common species captured in these control programs, accounting for nearly 50% of sharks landed, the only publication resulting from these data to date has been that of Wass (1973) on growth and reproduction. The purpose of the present

[1] NMFS (1993) Fishery Management Plan for Sharks of the Atlantic Ocean. 167 pp.

[2] NMFS (2003) Final Amendment 1 to the Fishery Management Plan for Atlantic Tunas, Swordfish, and Sharks. 512 pp.

[3] Tester AL (1969) Cooperative shark research and control program final report 1967–1969. University of Hawaii, Honolulu.

study was to analyze historical data on diet of sandbar sharks collected during large-scale shark control programs in Hawaii and to compare the feeding habits of sandbar sharks in Hawaii with other locations.

Methods

Data examined was collected during the Hawaii Cooperative Shark Research and Control Program. Stomachs of 565 out of 788 sandbar sharks captured between 1 June 1967 and 30 June 1969 were examined for prey (Tester 1969). Sharks were caught using standard longlines, light tackle longlines (consisting of 12 hooks) and handlines. Fishing was conducted at 77 designated stations around the eight main Hawaiian Islands, with the greatest effort concentrated around the island of Oahu. The majority of sharks were caught on standard longlines, which consisted of three 800 m sections with 24 hooks per section, set parallel to shore at an average depth of 45 m. Sets were made late in the afternoon and hauled back the next morning. The primary bait used was skipjack tuna, *Katsuwonus pelamis* (see Wetherbee et al. 1994).

Depth of capture, precaudal length (PCL), total length (TL), gender, and weight (occasionally) were recorded for each shark. Because PCL was not reported for all individuals all lengths referred to in this study are TL. Sharks were divided into three size classes for analysis of ontogenetic trends, small (< 125 cm), medium (125–150 cm), and large (>150 cm). The 150 cm division was based on the approximate size at maturity (144 cm for males and 155 cm for females) for this population (Wass 1973). The 125 cm division was based on dietary shifts that appeared to occur when sharks approached this size.

Prey found in stomachs were identified to the lowest possible taxon and were quantified as percent occurrence (%O), the number of stomachs that contained a prey item as a percentage of all stomachs that contained prey. Because many prey items were only identified to family, all analyses were conducted at this level. Cumulative diversity curves were fit to the data to evaluate the adequacy of the sample size for precisely describing the diet. A diversity curve (or a cumulative prey curve) reaches an asymptote as the sample size becomes sufficient to describe the entire breadth of the diet (Cailliet et al. 1986; Cortés 1997). The Shannon–Weiner diversity index was used (Cailliet et al. 1986; Krebs 1999), with the order of the cumulative stomachs randomized 10 times to eliminate bias (Ferry and Cailliet 1996, Cortés 1997).

Prey diversity was calculated for all three size classes using diversity indices of Shannon–Weiner (H') and Levin's (B_A) (Krebs 1999). Dietary overlap between groups of sandbar sharks was calculated using the Simplified Morisita Index (C_H) and the percentage overlap (P_{jk}), or Schoener Index (Krebs 1999). The standardized form of both indices was used, resulting in values ranging from 0 to 1, with 1.0 indicating identical diets, and 0 representing no common dietary items. Overlap values of C_H were considered low (0–0.29), medium (0.3–0.59), or high (>0.60) according to Langton (1982). The simplified Morisita index was found to produce homogeneous results when the number of prey categories was varied (Cortés 1997). Therefore, this is an appropriate measure even with identification only to the family level. The category 'unidentified teleosts' was excluded from overlap calculations, as it was extremely common in the diets of all sharks, and would have obscured differences in the diets. The community similarity between groups of sharks was also calculated, using all prey categories (Smith et al. 1990). This analysis of similarity (ANOSIM) test was done using PRIMER software (v 6.0). Jacard's coefficient was used to obtain the similarity matrix, which was then tested for differences in similarity between and within groups, and if overall significant differences were found, follow up tests were performed.

Results

Stomach content data from 565 sandbar sharks caught in the control program were analyzed in this study. Sharks ranged in size from 59 to 190 cm with a length–weight relationship given by the equation: Weight = $2e^{-06}\ TL^{3.2806}$ (with weight in kg and total length (TL) in cm; $r^2 = 0.967$, $n = 327$). Because PCL is less variable than TL and for comparison with the many studies that express length as PCL, a regression equation was calculated for PCL and TL (PCL = 0.7812*TL−2.5121; $r^2 = 0.988$, $n = 583$).

Females composed 63% (355) and males 37% (209) of sharks for which sex was recorded. Of the 565 stomachs examined, 265 (53%) contained food. The proportion of males (54%) with food in stomachs was significantly higher than for females (43%) ($\chi^2 = 6.68$, df = 1, $P < 0.05$). The proportion of sharks with empty stomachs was similar among size classes ($\chi^2 = 0.343$, df = 2, $P > 0.05$). Comparison of the cumulative trophic diversity and number of stomachs sampled did not result in a strongly asymptotic curve (Fig. 1). The slope of the curve did begin to increase less rapidly as if approaching an asymptote, but the lack of a distinct asymptote suggests that the sample size for this study may have been inadequate to fully describe the array of prey items in the diet of sandbar sharks in Hawaii.

In general, the diet of sandbar sharks was dominated by teleosts, which occurred in 70.6% of stomachs containing food (Table 1). A wide variety of teleost species, including 28 families, were recorded from stomachs. Cephalopods occurred in 26.8% of stomachs, with octopus representing the largest proportion (18.1%). Crustaceans occurred in 18.9% of stomachs and included a diversity of taxa, most commonly stomatopods and crabs. Elasmobranchs, undigestible items, and a few miscellaneous prey also occurred in the diet, but were not major contributors.

Although teleosts were the predominant prey found in all shark size groups, several ontogenetic changes in the diet of sandbar sharks were observed (Fig. 2). Sharks in the small size class consumed a larger proportion of crustaceans than sharks in the larger two size classes. Stomatopods were the dominant crustacean consumed by small sharks, but were uncommon in stomachs of the two larger size classes. Cephalopods occurred more frequently in stomachs of the two larger size classes, with octopus most common. Elasmobranchs did not occur in the small size class, but were present in small numbers for both larger size classes. Teleosts occurred least frequently in the medium size class, but these sharks also consumed a greater proportion of cephalopods. Though many teleost remains in stomachs were not identifiable, several families of reef associated fishes (Sygnathidae, Diodontidae, Holocentridae) and benthic fishes (Labridae, Mullidae) occurred only in the largest or two largest size classes of sandbar sharks (Table 1). Faster swimming families, e.g. Carangidae, and families with larger species, e.g. Scaridae, also occurred only in the two larger size classes.

Dietary overlap values calculated with the Simplified Morisita Index, C_H, for comparison of small and medium and small and large size groups fell just above the high range according to Langton's scale (1982), and were very high between large and medium sharks (Table 2). The percentage overlap index (P_{jk}) indicated the same pattern, that overlap was greatest between medium and large sized sharks, and least between large and small size classes. The results of the ANOSIM test indicated that the diets of the three size classes were not significantly different (Global R=−0.003, P=0.554). Dietary diversity increased with increasing size according to the Shannon–Weiner index of diversity (H′), with values of 2.42 for small sharks, 2.81 for the middle size class, and 3.19 for large sharks. The standardized Levin's index also suggested that small sharks had the lowest diet diversity (2.67), and that diversity of the medium (4.50) and large size classes (4.10) were considerably higher.

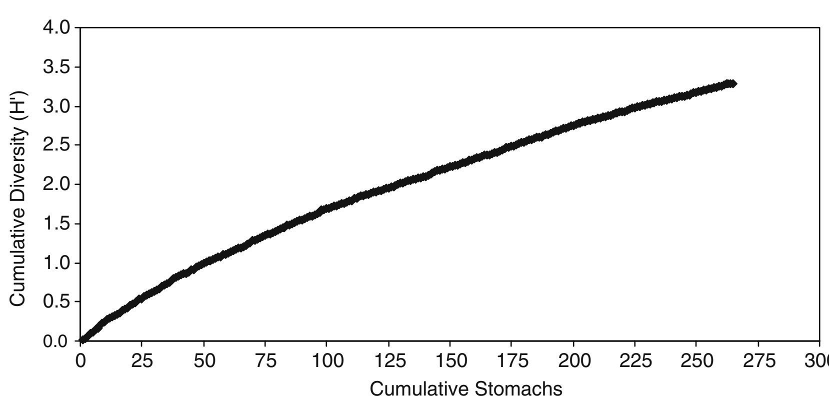


Fig. 1 Cumulative prey diversity curves for sandbar sharks, *Carcharhinus plumbeus*, caught during the Hawaii Cooperative Shark Research and Control Program, 1967–1969. The Shannon–Weiner Index (H′) was used. Stomach order was randomized 10 times, and the mean values are presented

Table 1 The number and percentage of occurrence (%O) of each prey taxa in the stomachs of sandbar sharks, *Carcharhinus plumbeus*, caught during the Hawaii Cooperative Shark Research and Control Program, 1967–1969

Dietary Item	<125 cm TL		125–150 cm TL		>150 cm TL		All sharks	
	N	%O	*n*	%O	*N*	%O	*n*	%O
Cephalopod	13	22.03	22	31.43	36	26.87	73	26.79
Unid. cephalopod	3	5.08	5	7.14	6	4.48	14	5.28
Octopus	7	11.86	15	21.43	26	19.40	48	18.11
Squid	3	5.08	2	2.86	6	4.48	11	4.15
Teleost	45	76.27	42	60.00	98	73.13	204	70.57
Unid. teleost	33	55.93	27	38.57	58	43.28	120	45.28
Unid. eel	0	0.00	2	2.86	2	1.49	4	1.51
Unid. Sygnathid	0	0.00	0	0.00	5	3.73	5	1.89
Acanthuridae	1	1.69	0	0.00	4	2.99	5	1.89
Aulostomidae	0	0.00	1	1.43	1	0.75	2	0.75
Balistidae	0	0.00	0	0.00	1	0.75	1	0.38
Belonidae	1	1.69	0	0.00	0	0.00	1	0.38
Bothidae	2	3.39	0	0.00	0	0.00	2	0.75
Carangidae	0	0.00	3	4.29	2	1.49	5	1.89
Chaetondontidae	1	1.69	0	0.00	1	0.75	2	0.75
Callionymidae	0	0.00	0	0.00	1	0.75	1	0.38
Congridae	0	0.00	0	0.00	2	1.49	2	0.75
Diodontidae	0	0.00	0	0.00	5	3.73	5	1.89
Exocoetidae	0	0.00	1	1.43	1	0.75	2	0.75
Fistularidae	0	0.00	0	0.00	2	1.49	2	0.75
Holocentridae	0	0.00	2	2.86	1	0.75	3	1.13
Labridae	0	0.00	3	4.29	6	4.48	9	3.40
Lutjanidae	1	1.69	0	0.00	1	0.75	2	0.75
Monacanthidae	2	3.39	0	0.00	1	0.75	3	1.13
Mullidae	0	0.00	2	2.86	2	1.49	4	1.51
Muraenidae	2	3.39	2	2.86	3	2.24	7	2.64
Ostraciontidae	0	0.00	1	1.43	0	0.00	1	0.38
Priacanthidae	0	0.00	1	1.43	1	0.75	2	0.75
Scaridae	0	0.00	2	2.86	4	2.99	6	2.26
Scombroidae	1	1.69	0	0.00	0	0.00	1	0.38
Scorpaenidae	1	1.69	0	0.00	1	0.75	2	0.75
Sphyraenidae	0	0.00	0	0.00	1	0.75	1	0.38
Synodontidae	1	1.69	0	0.00	0	0.00	1	0.38
Tetraodontidae	0	0.00	0	0.00	1	0.75	1	0.38
Triglidae	1	1.69	0	0.00	0	0.00	1	0.38
Zanclidae	0	0.00	0	0.00	1	0.75	1	0.38
Elasmobranch	0	0.00	3	4.29	3	2.24	6	2.264
Unid. Elasmobranch	0	0.00	1	1.43	0	0.00	1	0.38
Shark	0	0.00	2	2.86	1	0.75	3	1.13
Ray	0	0.00	0	0.00	2	1.49	2	0.75
Crustacean	16	27.12	11	15.71	23	17.16	51	18.87
Unid. Crustacean	5	8.47	7	10.00	5	3.73	17	6.42
Crab	1	1.69	2	2.86	6	4.48	9	3.40
Lobster	0	0.00	0	0.00	5	3.73	5	1.89
Shrimp	1	1.69	1	1.43	3	2.24	5	1.89
Stomatopod	10	16.95	1	1.43	3	2.24	14	5.28
Isopoda	0	0.00	0	0.00	1	0.75	1	0.38
Undigestable	1	1.69	2	2.86	5	3.73	8	3.02
Coral	0	0.00	2	2.86	1	0.75	3	1.13
Rock	1	1.69	0	0.00	0	0.00	1	0.38
Plant	0	0.00	0	0.00	3	2.24	3	1.13
Cellophane	0	0.00	0	0.00	1	0.75	1	0.38
Gastropod	0	0.00	1	1.43	1	0.75	2	0.75

Table 1 continued

Dietary Item	< 125 cm TL		125–150 cm TL		>150 cm TL		All sharks	
	N	%O	*n*	%O	*N*	%O	*n*	%O
Porpoise	0	0.00	1	1.43	0	0.00	1	0.38
Land mammal	0	0.00	0	0.00	1	0.75	1	0.38
Ophiurids	0	0.00	1	1.43	0	0.00	1	0.38

There appeared to be changes in the frequency of occurrence of several major prey categories on a seasonal basis. The occurrence of teleost prey was lower in summer and fall than during winter, whereas crustaceans and cephalopods tended to occur more frequently in summer and fall (Fig. 3). Apparent seasonal differences in the diet of sandbar sharks raised the question of distributional differences among sharks on the basis of season, gender, and size. Depth of capture data suggests that mature

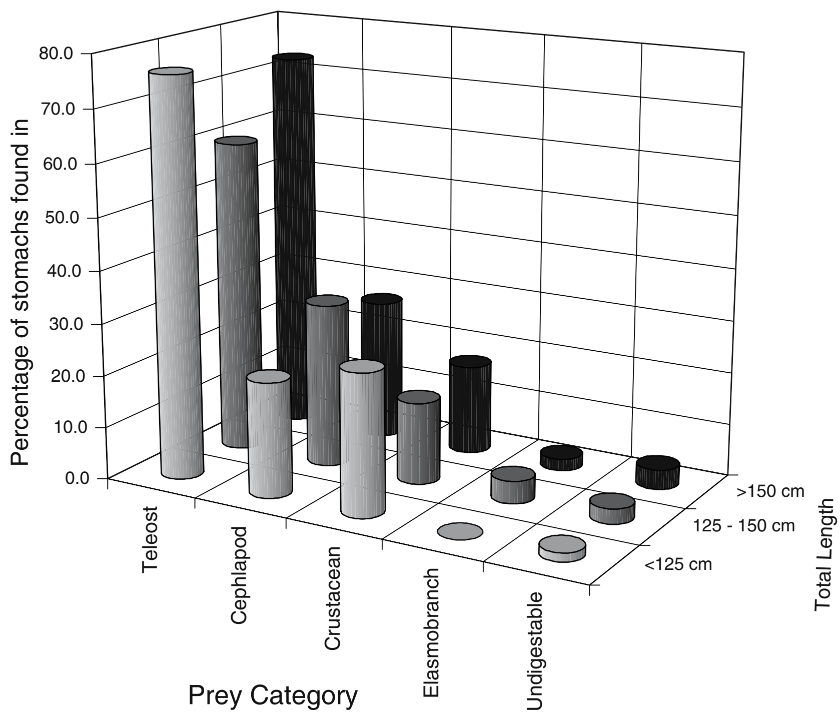


Fig. 2 The percent occurrence of the major prey categories found in the stomachs of three size classes of sandbar sharks, *Carcharhinus plumbeus*, caught during the Hawaii Cooperative Shark Research and Control Program, 1967–1969

Table 2 The dietary overlap values, excluding unidentified teleosts, for three size classes of sandbar sharks in the Hawaiian Islands. Values were calculated with the standardized forms of the Simplified Morisita Index (A) and Percentage Overlap Index (B)

Size class	Small	Medium	Large	N
A				
Small	–	–	–	59
Medium	0.642	–	–	70
Large	0.625	0.880	–	134
B				
Small	–	–	–	59
Medium	0.465	–	–	70
Large	0.460	0.635	–	134

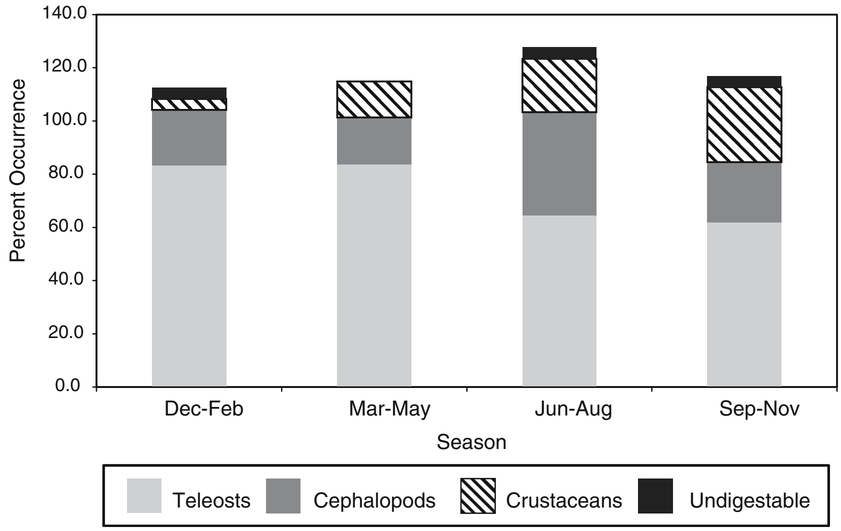


Fig. 3 The dietary composition for sandbar sharks in the Hawaiian Islands caught during different seasons. Data are in percentage of total stomachs sampled in each season in which each prey category occurred

sandbar sharks were segregated by depth. The overall ratio of mature females to mature males was 1.7:1, but for sharks caught at depths of less than 36 m, more than five times as many mature females were captured (Fig. 4). At depths greater than 110 m, the number of males was more than three times the number of females captured. Although there appeared to be an increase in the proportion of males captured at shallower depths in early summer, when these sharks are thought to mate, small sample sizes precluded statistical analyses of this apparent trend. Immature sharks were captured at all depth intervals, but tended to occur at greater depths than mature females and were captured most often at depths between 73 and 109 m (Fig. 4).

The occurrence of several prey items in stomachs of sharks appeared to be influenced by the depth at which sharks were captured. For example, cephalopods (both squid and octopus) occurred in 40% of stomachs of sharks captured between 18 and 35 m and in 30% of stomachs of sharks captured at depths of 36–53 m, but in only 10% of stomachs of sharks captured at depths greater than 73 m (Fig. 5). Stomachs of sharks captured at greater depths contained a greater proportion of teleosts and crustaceans.

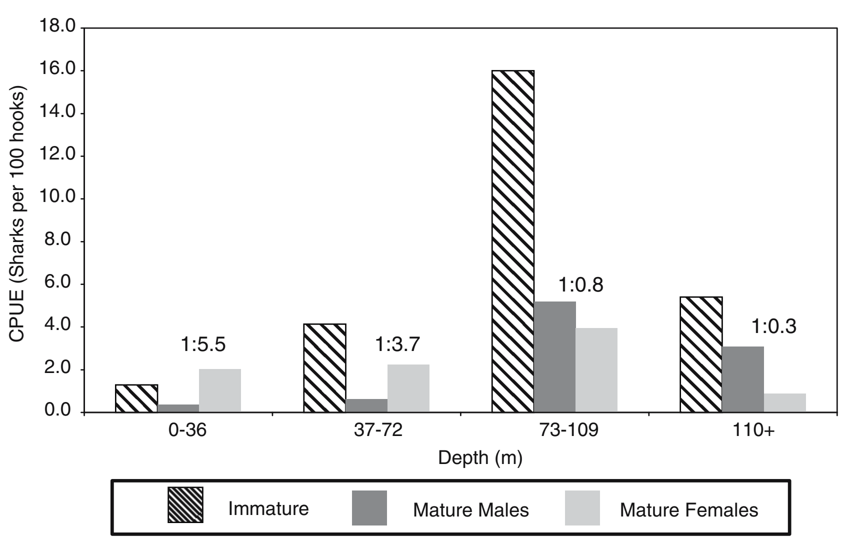
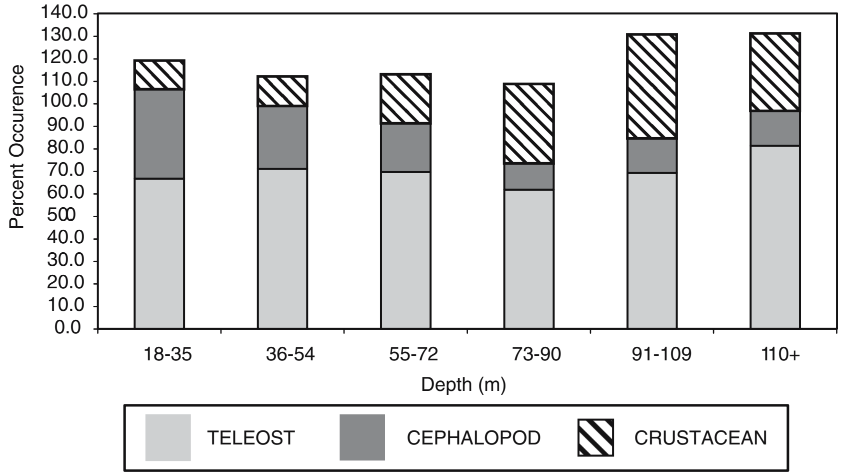


Fig. 4 The distribution of male and female sandbar sharks over different depth zones in Hawaiian waters based upon catch per unit effort data. Ratios above bars represent the ratio of mature males to mature females. Depth zones are based on 20 fathom intervals

Fig. 5 The dietary composition for sandbar sharks in the Hawaiian Islands caught at different depths. Data are in percentage of total stomachs sampled at each depth in which each prey category occurred. Depth zones are based on 10 fathom intervals



Despite differences in depth distribution of males and females and the depth-related occurrence of prey, dietary overlap between the sexes (at the family level) was extremely high. In a comparison of mature males and females, the Simplified Morisita Index was 0.802 and the percentage overlap index was 0.733. This analysis excluded unidentified teleosts, which was frequent in both sexes. ANOSIM found no significant difference in diet between the sexes (Global $R = 0.003$, $P = 0.326$). The most notable difference between the diet of mature males and females was in the occurrence of crustaceans, found in stomachs of 28% of males and only 12% of the females.

Discussion

Nearly half (47%) of sandbar sharks captured in Hawaii had empty stomachs. This proportion is similar to the 51% empty stomachs reported for large juvenile and adult sandbar sharks in the western Atlantic (Stillwell and Kohler 1993), and slightly higher than for sandbar sharks from northern Australia (36%) (Stevens and McLoughlin 1991). Several studies have reported a low frequency (18–20%) of empty stomachs for neonate and juveniles sandbar sharks captured in nursery areas (Medved et al. 1985; Stillwell and Kohler 1993). A high percentage of empty stomachs is not uncommon in studies of coastal carcharhinid species captured by longline—61% empty in gray reef sharks, *Carcharhinus amblyrhynchos* (Wetherbee et al. 1997), 46% in Galapagos sharks, *C. galapagensis* (Wetherbee et al. 1996), and 61% in dusky sharks *C. obscurus* (Gelsleichter et al. 1999). Sampling with non-baited gear (such as gillnet) frequently results in relatively lower percentages of empty stomachs (Medved 1985; Wetherbee et al. 1990).

The cumulative diversity curve does not achieve a distinct asymptote, indicating that even a sample size as large as 265 individuals may be insufficient to adequately characterize the diet of sandbar sharks in Hawaii, i.e. the occurrence of all the rare items. However, the sample size is sufficient to reveal major prey consumed and to observe general trends in the diet. In other studies on the diets of sharks, asymptotes were also not achieved for some species or size classes (Simpfendorfer 1998; Gelsleichter et al. 1999; Bethea et al. 2004).

The diet of sandbar sharks in the main Hawaiian Islands was dominated by teleosts, the majority of which were benthic or reef-associated species. The occurrence of teleosts in 70% of sandbar shark stomachs is similar to reports for two other common coastal carcharhinid sharks in Hawaiian waters, the Galapagos shark and the gray reef shark (Wetherbee et al. 1996, 1997). The diet of sandbar sharks in other locations throughout the world is also dominated by teleosts, but small sandbar sharks in nursery areas may feed to a much greater extent on invertebrate prey (Table 3). Teleosts occurred in 43% of adult sandbar sharks in the western North Atlantic (Stillwell and Kohler 1993), in 88% of stomachs of sharks from Australia (Stevens and McLoughlin 1991) and in 70% of stomachs of sharks from South Africa (Cliff et al. 1988). In each location, a variety of

Table 3 Diet of sandbar sharks as percent occurrence (%O) from various locations throughout their distribution

	Hawaii[1]	W. N. Atlantic[2]	N. Australia[3]	S. Africa[4]	Virginia nursery[5]
Teleosts	70.6	43.0	88.0	69.7	36.8
Cephalopods	26.8	3.0	22.0	57.3	1.2
Crustaceans	18.9	~1.0	8.0	16.9	72.0
Elasmobranchs	2.3	16.0	–	17.4	1.7
Size range (TL)	59–190[a]	81–256[b]	66–208[a]	95–202[c]	46–95[b]
# Stomachs w/food	265 (53%)	157 (49%)	116 (64%)	178 (n/a)	340 (82.1%)
Total *n*	565	321	181	n/a	414

[1]Present study; [2]Stillwell and Kohler (1993); [3]Stevens and McLoughlin (1991); [4]Cliff et al. (1988); [5]Estimated from Medved et al. (1988)
[a]Total Length
[b]Converted from fork length using regression in Kohler et al. (1995)
[c]Converted from precaudal length using regression in this study

teleosts was consumed, but the species were predominantly demersal. Elasmobranchs were of minor importance in the diet of sandbar sharks in Hawaii (2.3%) in comparison to other locations where they (primarily skates, *Raja* sp.) occurred in a greater proportion of stomachs—16% in the western North Atlantic and 17% in South Africa (Cliff et al. 1988; Stillwell and Kohler 1993).

Benthic invertebrates were important components of the diet of sandbar sharks in Hawaii and in other locations. Cephalopods (primarily octopus) occurred in roughly one quarter of stomachs of sharks from Hawaii (27%) and Australia (22%) (Stevens and McLoughlin 1991), but were consumed by a much higher proportion of sharks (57%) in South Africa (Cliff et al. 1988) and rarely by sharks (3%) in the western North Atlantic (Stillwell and Kohler 1993). Crustaceans were also a common prey item in stomachs of sharks from Hawaii (19%) and South Africa (17%), but were less common (8%) in Australia and nearly absent (~1%) in larger sharks in the western North Atlantic (Cliff et al. 1988; Stevens and McLoughlin 1991; Stillwell and Kohler 1993). Juvenile sandbar sharks occupying nursery areas along the U.S. east coast may rely much more heavily on crustacean prey. Crustaceans, especially soft shelled blue crab, occurred in relatively high proportions of stomachs of juvenile sharks from the Chincoteague Bay nursery in Virginia in studies by both Medved et al. (1985) (72%) and by Stillwell and Kohler (1993) (82%). Overall diets of juveniles in both of these studies in the Virginia nursery were extremely similar. Juvenile sandbar sharks in Delaware Bay also consume large numbers of crustaceans (45% by occurrence), but teleosts occur even more often in the stomachs (51%) (McElroy unpublished data). Crustaceans were important in the diet of young sandbar sharks in waters around Chesapeake Bay, but their importance compared to teleost prey was found to vary between habitats (Ellis 2003).[4] Crustaceans may be more prevalent in the diet of juveniles than adults throughout their range, but the degree of importance varies among habitats. A major different between sandbar sharks in Hawaii and other locations is that in Hawaii juvenile sharks do not occupy shallow bays and estuaries, which would result in habitat and prey availability differences in Hawaii compared to other locations.

The values of C_H indicated high overlap among the three size classes, and the ANOSIM tests also found no significant differences in diet among the size classes. The results of these analyses may be attributable to several aspects of the dataset. The level of identification of stomach contents was coarse, and ''unidentified teleosts'' was the most common prey item in all shark groups analyzed. This tended to elevate similarity among size groups, and diminish differences that may be detected through such analyses. Optimally, analysis would be conducted on data with most prey identified to the species level, and with a large sample size representing each size class. Also variability in the size of the prey consumed, by different sized sharks, is

[4] Ellis JK (2003) Diet of the sandbar shark, *Carcharhinus plumbeus*, in Chesapeake Bay and adjacent waters. Mater's thesis. College of William and Mary, Gloucester Point, Virginia.

obscured by the use of broad prey identification at the family level. Additionally, the inclusion of multiple indices, i.e. by number, weight, or volume, would improve the ability of these analyses to discern differences in diets than exclusive use of %O. In general, the utilization of multiple indices or a combination of indices, i.e. Index of Relative Importance (IRI), allows for a stronger and more balanced analysis of the diet.

Even with these limitations, there did appear to be some ontogenetic dietary changes observed for sandbar sharks in Hawaii. The importance of major prey taxa varied among size classes and larger sharks tended to prey upon a wider range of species, especially for teleosts, than did smaller sharks. Teleost and crustacean prey in larger sharks included more species that inhabit reefs, and suggests that young sharks expand their use of new habitats or increase their ability to hunt new prey. There was also a shift from consumption of smaller crustaceans (stomatopods) to larger crustaceans (crabs and lobster) as sharks increased in size. Although few sandbar sharks in Hawaii preyed upon elasmobranchs, this prey type was found only in stomachs of sharks belonging to the larger size classes. In the western North Atlantic Ocean there appeared to be more pronounced changes in diet of sandbar sharks with increased size, where crustaceans dominate the diet of juvenile sharks occupying nursery areas, compared with the dominance of teleost and elasmobranch prey in larger size classes (Medved et al. 1988; Stillwell and Kohler 1993, Ellis 2003).[4] Predation on crustaceans appears to be a common characteristic of young sandbar sharks, and so this prey group may provide an abundant or easily caught food source while the sharks occupy nursery areas and are small and learning to hunt. Ontogenetic changes in diet have been reported for the vast majority of species of shark for which diet has been compared between size classes and such changes appear to be a common theme among populations of elasmobranchs (reviewed in Wetherbee and Cortés 2004). Increases in the diversity, sizes, and behavioral characteristics of teleost and other prey consumed as sandbar sharks grow likely reflect several factors, including behavior, habitat, physical capabilities, and energetic requirements of sandbar sharks. These factors have all been cited as potential contributors to ontogenetic change in other shark species (Wetherbee et al. 1990; Cortés and Gruber 1990; Lowe et al. 1996; Simpfendorfer et al. 2001; Alonso et al. 2002; Wetherbee and Cortés 2004).

Stomach content data from sandbar sharks in Hawaii suggests that their diet varied with season, with the most notable change being an increase in consumption of crustaceans from winter to fall. The occurrence of teleosts in stomachs of sandbar sharks also declined during summer and fall. Seasonal variation in diet has been reported for a number of other species of shark (Talent 1976; Jones and Geen 1977; Tricas 1979; Stillwell and Kohler 1982; Cortés et al. 1996). Seasonal changes in diet could reflect changes in prey availability, or seasonal movements of prey or predator.

Catch data indicated that male sandbar sharks generally occurred in deeper water than females in Hawaii. Wetherbee et al. (1994) also suggested that male sandbar sharks inhabited deeper water than females based on average depth of capture. There is some evidence that the sandbar shark population structure and depth distribution changes during the early summer when males frequent shallower water than they normally inhabit, presumably to mate with females, which have a shallower distribution. Wetherbee et al. (1994) found a higher CPUE for males during summer than in spring and fall. However, based on analyses of data collected there was little evidence that differences in depth distribution between mature male and female sharks in Hawaii resulted in major differences between their diets. The diet of male and female sandbar sharks showed a high degree of overlap, with the possible exception of males consuming a greater proportion of crustaceans. Sandbar sharks segregate by size and sex in the Western Atlantic (Springer 1960), South Africa (Cliff et al. 1988) and in waters off Tunisia (Capapé 1984). Segregation by sex and age class has been demonstrated in several other carcharhinid sharks in Hawaii (Wetherbee et al. 1996, 1997).

Conclusions

Overall, the diet of *C. plumbeus* shows similar patterns in different geographic locations. Teleost fish are the dominant prey, and sandbar sharks feed largely on demersal species. The most important prey categories other than teleosts vary between regions.

Cephalopods, crustaceans or elasmobranchs are major prey categories for sandbar sharks in different geographic regions, and this probably reflects prey availability and use of nursery areas. Crustaceans are particularly important dietary items for young sandbar sharks in nursery areas, and definite ontogenetic changes in diet occur in this species. Larger and faster swimming prey species, as well as elasmobranchs and cephalopods are consumed more frequently by larger sharks. Despite the fact that these data are over 30 years old, they still provide a useful contribution for improved understanding of the biology of this heavily exploited species, particularly in the Hawaiian Islands, where it is the most common coastal species of shark.

Acknowledgements Thanks go to the late Albert L. Tester, for his efforts in leading the Hawaii Cooperative Shark Research and Control Program and to J. Stimson and the Zoology Department of the University of Hawaii at Manoa for maintaining the data collected during this program. Original funding for the Hawaii Cooperative Shark Research and Control Program was provided by NSF GB-6139, the Oceanic Institute and the State of Hawaii. The statistical advice of Dr. James Heltshe (University of Rhode Island) also aided the final completion of this manuscript.

References

Alonso MK, Crespo EA, García NA, Pedraza SN, Mariotti PA, Mora NJ (2002) Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. Environ Biol Fish 63:193–202

Baranes A, Wendling J (1981) The early stages of development in *Carcharhinus plumbeus*. J Fish Biol 18:159–175

Bass AJ, D'Aubrey J, Kistnasamy N (1975) Sharks of the east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). Investigational report no. 38 Oceanographic Research Institute (Durban) 33:168 pp

Baughman JL, Springer S (1950) Biological and economic notes on the sharks of the Gulf of Mexico, with special reference to those of Texas, with a key for their identification. Am Midl Nat 44:96–152

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

Branstetter S (1981) Biological notes on the sharks of the north central Gulf of Mexico. Contrib Mar Sci 24:13–34

Capapé C (1984) Nouvelles donnés sur la morphologie et la biologie de la reproduction de *Carcharhinus plumbeus* (Nardo, 1827) (Pisces, Carcharhinidae) des côtes tunisiennes. Investig Pesq 48:115–137

Cailliet GM, Love MS, Ebeling AW (1986). Fishes: a field and laboratory manual on their structure, identification, and natural history. Waveland Press Inc., Prospect Heights Illinois, 194 pp

Carlson JK (1999) Occurrence of neonate and juvenile sandbar sharks, *Carcharhinus plumbeus*, in the northeastern Gulf of Mexico. Fish Bull 97:387–391

Casey JG, Pratt HL Jr, Stillwell CE (1985) Age and Growth of the sandbar shark (*Carcharhinus plumbeus*) from the western north Atlantic. Can J Fish Aquat Sci 42:963–975

Casey JG, Natanson LJ (1992) Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. Can J Fish Aquat Sci 49:1474–1477

Clark E, von Schmidt K (1965) Sharks of the central Gulf coast of Florida. Bull Mar Sci 15:13–83

Cliff G, Dudley SFJ, Davis B (1988) Sharks caught in the protective gill nets off Natal, South Africa. 1. The sandbar shark *Carcharhinus plumbeus* (Nardo). S Afr J Mar Sci 7:255–265

Compagno LJV (1984) Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2, Carcharhiniformes. FAO Fish Synop (125) 4:251–655

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) A stochastic stage-based population model of the sandbar shark in the western north Atlantic. Am Fish Soc Symp 23:115–136

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

Cortés E., Manire CA, Hueter RE (1996) Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo* in southwest Florida. Bull Mar Sci 58:353–367

Crow GL, Lowe CG, Wetherbee BM (1996) Shark records from longline fishing programs in Hawaii with comments on Pacific Ocean distributions. Pac Sci 50:382–392

Ferry LA, Cailliet GM (1996) Sample size and data analysis: Are we characterizing and comparing diet properly? In: MacKinley D, Shearer K (eds) Feeding ecology and nutrition in fish. International Congress of the Biology of Fishes, American Fisheries Society, San Francisco, CA, 14–18th July 1996, pp 71–80

Gelsleichter J., Musick JA, Nichols S (1999) Food habits of the smooth dogfish, *Mustelus canis*, dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, and the sand tiger, *Carcharias taurus*, from the northwest Atlantic Ocean. Environ Biol Fish 54:205–217

Jones BC, Geen GH (1977) Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. J Fish Res Board Can 34:2067–2078

Joung SJ, Chen CT (1995) Reproduction in the sandbar shark, *Carcharhinus plumbeus*, in the waters off Northeastern Taiwan. Copeia 1995:659–665

Kohler NE, Casey JG, Turner PA (1995) Length-weight relationships for 13 species of sharks from the western North Atlantic. Fish Bull 93:412–418

Krebs CJ (1999) Ecological methodology, 2nd edn. Addison Wesley, Longman, New York

Langton RS (1982) Diet overlap between the Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis* and fifteen other northwest Atlantic finfish. Fish Bull 80:745–759

Lowe CG, Wetherbee BM, Crow GL (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier* in Hawaii. Environ Biol Fish 45:203–211

Medved RJ, Marshall JA (1981) Feeding behavior and biology of young sandbar sharks, *Carcharhinus plumbeus* (Pisces, Carcharhinidae), in Chincoteague Bay, Virginia. Fish Bull 79:441–447

Medved RJ, Stillwell CE, Casey JJ (1985) Stomach contents of young sandbar sharks, *Carcharhinus plumbeus*, in Chincoteague Bay, Virginia. Fish Bull 83:395–401

Medved RJ, Stillwell CE, Casey JJ (1988) The rate of food consumption of young sandbar sharks (*Carcharhinus plumbeus*) in Chincoteague Bay, Virginia. Copeia 1988:956–963

Merson RR, Pratt HL Jr (2001) Distribution, movements and growth of young sandbar sharks, *Carcharhinus plumbeus*, in the nursery grounds of Delaware Bay. Environ Biol Fish 61:13–24

Rechisky EL, Wetherbee BM (2003) Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environ Biol Fish 68:113–128

Simpfendorfer CA (1998) Diet of the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Queensland. Mar Freshw Res 49:757–761

Simpfendorfer CA, Goodreid AB, 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

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

Smith EP, Pontasch KW, Cairns J. Jr (1990) Community similarity and the analysis of multispecies environmental data: a unified statistical approach. Water Res 24:507–514

Springer S (1946) A collection of fishes taken from the stomachs of sharks off Salerno, Florida. Copeia 1946:174–175

Springer S (1960) Natural history of the sandbar shark, *Eulamia milberti*. US Fish Wildl Serv Fish Bull 61:1–38

Stevens JD, McLoughlin KJ (1991) Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. Aust J Mar Freshw Res 42:151–199

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

Stillwell CE, Kohler NE (1993) Food habits of the sandbar shark *Carcharhinus plumbeus* off the US northeast coast, with estimates of daily ration. Fish Bull 91:138–150

Talent LG (1976) Food habits of the leopard shark, *Triakis semifasciata*, in Elkhorn Slough, Monterey Bay, California. Calif Fish Game 62:286–298

Taniuchi T (1971) Reproduction of the sandbar shark, *Carcharhinus milberti*, in the east China Sea. Jpn J Ichthyol 18:94–98

Tricas TC (1979) Relationships of the blue shark, *Prionace glauca*, and its prey species near Santa Catalina Island, California. Fish Bull 77:175–182

Wass RC (1973) Size, growth, and reproduction of the sandbar shark, *Carcharhinus milberti*, in Hawaii. Pac Sci 27:305–318

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, vol 90. NOAA Technical Report NMFS, pp 29–47

Wetherbee BM, Lowe CG, Crow GL (1994) A review of shark control in Hawaii with recommendations for future research. Pac Sci 48:95–115

Wetherbee BM, Crow GL, Lowe CG (1996) Biology of the Galapagos shark *Carcharhinus galapagensis* in Hawaii. Environ Biol Fish 45:299–310

Wetherbee BM, Lowe CG, Crow GL (1997) Distribution, reproduction and diet of the gray reef shark *Carcharhinus amblyrhynchos* in Hawaii. Mar Ecol Prog Ser 151:181–189

Wetherbee BM, Cortés E (2004) Food consumption and feeding habits. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, pp 225–246

Wheeler JFG (1962) Notes on the three common species of sharks in the Mauritius-Seychelles area. Proc R Soc Arts Sci Mauritius 2:146–160