Food habits of the sandbar shark *Carcharhinus plumbeus* off the U.S. northeast coast, with estimates of daily ration*

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Abstract.–Food habits data from 415 sandbar sharks collected in the area between Cape Hatteras and Georges Bank (Great South Channel) were examined. Mean fork length (FL) and body weight (BW) were 55.0 cm and 1.72 kg for pups, 123.0 cm and 23.0 kg for juveniles, and 166.0 cm and 52.3 kg for adults. Of all juvenile and adult stomachs, 49% contained prey, primarily fish (teleosts and skates). Of stomachs from pups, 80% held food remains consisting almost exclusively of soft blue crabs. The mean percentage of stomach content volume to BW is 1.16 for pups, and 0.42 for juveniles and adults. Daily ration estimates as percentage of mean BW are 1.43 for pups, and 0.86 for juveniles and adults. Annual food consumption is estimated to be 5.1 times the mean BW for pups, and 3.1 times for juveniles and adults.

Manuscript accepted 19 August 1992.
Fishery Bulletin, U.S. 91:138-150 (1993).

The sandbar shark *Carcharhinus plumbeus* is a medium-sized species found in temperate and subtropical waters of the world's oceans and the Mediterranean Sea. It occurs from nearshore out to a depth of at least 250 m (Springer 1960, Garrick 1982). Evidence of its occurrence over deep water is provided by Springer (1960) who reports the capture of three specimens taken in midwater over depths of 1000–1800 m. Distribution of the sandbar shark along the U.S. east coast extends from Massachusetts to the Florida Keys in the summer and from the offings of the Carolinas to Cape Canaveral during the winter months (Bigelow & Schroeder 1948, Springer 1960). From May through September, newborn pups and small juveniles (<100 cm fork length, FL) are common to abundant in shallow bays and estuarine systems along the coast from Long Island, New York to Cape Canaveral, Florida. With the approach of autumn, young sharks migrate offshore and south to winter at depths approaching 137 m (Springer 1960, Medved & Marshall 1983). Casey (1976) and Casey et al. (1985) showed that when the juvenile sandbar sharks attain a size of about 110 cmFL, they no longer frequent the shallow nursery areas but remain off the coast, demonstrating more extensive seasonal migrations with increasing size.

The most detailed publications to date on food and feeding in the sandbar shark come from Springer (1960), Medved & Marshall (1983), Medved (1985), and Medved et al. (1985, 1988). These papers are important contributions to our knowledge of the diet, feeding behavior, and daily ration of young sandbar sharks and what impact they have on prey resources in the estuaries and nearshore areas. The first study to estimate digestion rate in the sandbar shark was conducted by Wass (1973) in a seawater enclosure at the Kewalo Basin facility in Hawaii.

The purpose of this paper is to present data on the food and feeding habits of sandbar sharks occurring from Georges Bank (Great South Channel) to Cape Hatteras, to define dietary differences and energy needs of pups, juveniles, and adults, and to estimate their daily ration.

Methods

Stomachs were sampled from 1972 through 1984 during (1) shark fishing tournaments held at several coastal ports from Rhode Island to southern New Jersey, (2) on cruises using

*MARMAP Contribution FED/NEFC 86-05.

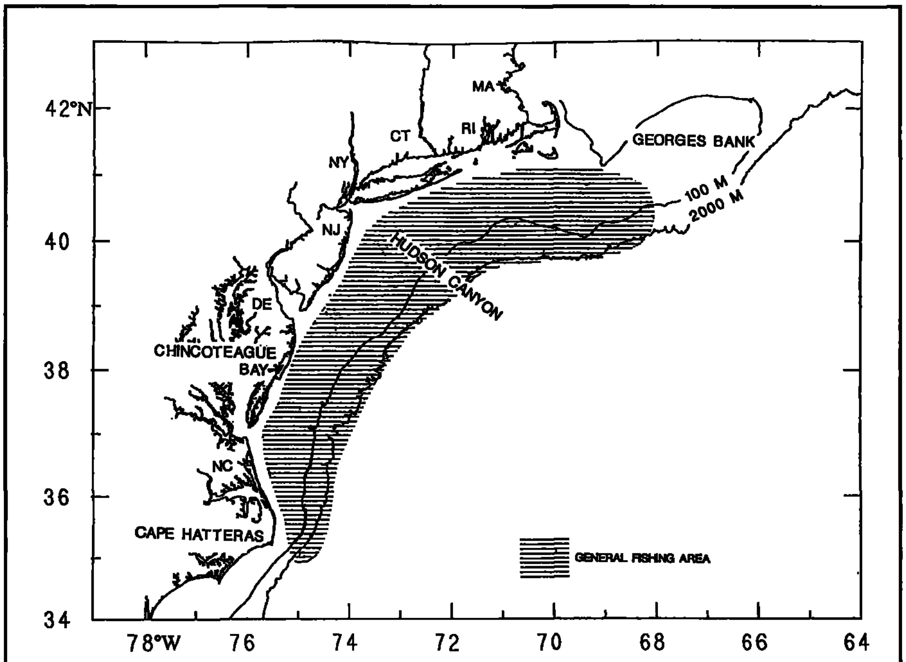

Figure 1

Fishing area off the U.S. northeast coast where 415 sandbar shark *Carcharhinus plumbeus* pups, juveniles, and adults were caught and examined for food habits studies, 1972–84. The 100 m depth contour separates the nearshore and offshore sampling areas.

longline gear aboard research and commercial fishing vessels from Cape Hatteras to Georges Bank, and (3) during a 6 d period of fishing at the end of June 1983 with rod-and-reel in Chincoteague Bay, Virginia (Fig. 1). Collections and examinations of all stomachs were made during March to September, with the majority being taken in June and July. Stomachs were excised and the volume of the contents (liquid and solids) measured as soon after capture as possible. Solid remains were drained, sorted, and identified to the lowest taxon possible, then enumerated and measured volumetrically by water displacement in a graduated beaker. A conversion of 1 mL=1 g was used to convert volume to weight for comparisons with shark body weights. Major forage categories were expressed as percentages by number of particular prey items, as total volume of the prey items, and as frequency of their occurrence (number of stomachs). Maximum capacity was estimated by filling the stomachs with water under low pressure, then measuring the volume of water in a graduated container. The maximum capacities of stomachs from Chincoteague Bay sharks were not determined because a pressurized water system was not available. Analysis of the data for differences in prey, food volumes by area, and daily ration was accomplished by separating the samples into three groups: Chincoteague Bay, nearshore (<100 m), and offshore (>100 m) (Fig. 1). The Chincoteague sample was further separated into two distinct age classes: newborn pups (estimated <3 d-old) and small juveniles (>3 d–3+ yr). Newborn pups were distinguished by pale, unpigmented edges on the fins, unhealed or partially-healed umbilical openings, and the presence of large cream-colored livers that floated slightly above the surface when placed in seawater. "Older" pups and small juveniles had livers that were reduced in size, varied in color from tan to gray-green, and sank slowly or floated just beneath the water surface. In addition, their umbilical openings were completely healed, visible only as white streaks 5–6 mm long. Juveniles and adults of both sexes were separated, based on a minimum reproductive size of 150 cmFL (Casey et al. 1985).

Results and discussion

Stomachs from 415 sandbar sharks were examined, including 321 from nearshore (268) and offshore (53) waters between Cape Hatteras, North Carolina and Georges Bank, and 94 from Chincoteague Bay, Virginia.

Analysis of nearshore and offshore samples

In the nearshore area, juvenile males and females and adult females were represented by almost equal numbers, i.e., 81, 84, and 89, respectively, whereas only 12 adult males were sampled. Offshore, juvenile males were most abundant (37), with adult males represented by four individuals. Females were limited to four adults and eight juveniles. Mean fork length (FL) and body weight (BW) of sandbar sharks for the whole sample were 138 cm (range 69.0–212.0) and 34.0 kg (3.0–145.0) (Table 1). Offshore, only juvenile males were numerous enough in the sample to derive reliable mean values.

Prey analysis Prey consumed by sandbar sharks in the study area consists primarily of benthic and demersal species, both vertebrate and invertebrate (Table 2). Of the 40 different prey types observed in

Table 1

Average fork lengths and body weights for 321 juvenile and adult sandbar sharks *Carcharhinus plumbeus* examined from nearshore (<100 m) and offshore (>100 m) waters of the U.S. northeast coast between Cape Hatteras and Georges Bank, 1972–84.

			Overall mean by sex		Adults			Juveniles		
	Overall mean		Male	Female	All	Male	Female	All	Male	Female
Total sample	*N*[a]	321	134	185	110	16	94	211	118	91
	FL[b]	138.0	125.0	147.5	166.0	156.3	167.6	123.0	120.8	126.0
	N	288	107	180	108	15	93	180	92	87
	BW[c]	34.0	23.8	40.3	52.0	40.0	54.3	23.0	21.0	25.0
Nearshore	*N*	268	93	173	102	12	90	166	81	83
	FL	142.3	130.5	149.0	165.0	157.0	166.0	128.3	126.5	130.4
	N	252	83	168	101	12	89	151	71	79
	BW	35.6	26.5	40.2	50.0	40.0	52.0	25.7	24.2	27.2
Offshore	*N*	53	41	12	8	4	4	45	37	8
	FL	114.5	112.6	120.5	178.3	153.5	203.2	103.0	108.0	79.0
	N	36	20	12	7	3	4	29	21	8
	BW	22.8	14.0	40.3	79.8	39.0	110.5	9.0	10.6	5.2

[a] *N* = number of sharks.
[b] FL = mean fork length in cm.
[c] BW = mean body weight in kg.

the stomachs, only six occurred in both the near- and offshore areas (Tables 3, 4), including squids, skates, skate egg cases, goosefish *Lophius americanus*, bluefish *Pomatomus saltatrix*, and Bothidae (flatfish). Summarizing the prey into major food groups (Fig. 2) shows that 43.0% (by frequency of occurrence) of the food was composed of teleosts, followed by elasmobranchs (16%), cephalopods (3.0%), and miscellaneous organisms and trash (pebbles, seagrass, paper scraps; 5.0%). The size of prey ingested appears to be an important factor in its selection, since the majority of prey items observed in the stomachs were small enough to be swallowed whole. Those that were consumed as bite-sized portions included larger skates, goosefish, bluefish, and smooth dogfish *Mustelus canis* and spiny dogfish *Squalus acanthias*. These food items were eaten by the larger juveniles and adults only. Earlier reports by Bigelow & Schroeder (1948), Springer (1960), Bass et al. (1973), and Lawler (1976) also indicate that small fish and invertebrates are most common in the diet. Springer (1960) adds that fresh fish is preferred over stale or decomposed fish and mammal flesh.

Teleosts The food group 'All Teleosts' (Fig. 2) was composed of species ranging from sedentary (goosefish) to actively-swimming forms (bluefish, mackerel *Scomber scombrus*). Flatfish (flounders) from the families Bothidae and Pleuronectidae occurred with the highest (10.0%) frequency overall (Fig. 2). Predation on these two families was most evident in sharks collected nearshore (Table 3). Goosefish comprised the second most-important fish in the diet by frequency of occurrence (6.0%) and was consumed by juvenile and adult sharks (Fig. 2). Goosefish remains varied from small (4 cmTL) to medium-sized (45 cmTL) individuals that were eaten in chunks. Remains of this prey item occurred most often in sandbar shark stomachs collected off the Long Island (NY) and New Jersey coasts. Bluefish occurred in nine stomachs (3.0%), seven of which were from females captured nearshore. Gadids consisted principally of hakes digested beyond species recognition, except for one silver hake *Merluccius bilinearis* that was relatively fresh. Scombrids occurred in seven stomachs (Fig. 2) and consisted almost exclusively of identifiable remains of common mackerel. The occurrence of fast-swimming scombrid species in stomachs agrees with the reported occurrence of bonito *Sarda sarda* [and weakfish *Cynoscion regalis*] by Bigelow & Schroeder (1948). "Other Teleosts" (Fig. 2), comprising 20.0% of the food by frequency of occurrence, is a group composed of at least 12 species from Table 1, each occurring infrequently in the diet but representative of local availability. Of this food category, 14% (by frequency of occurrence) also included fish remnants that could not be identified to family or species.

Table 2

Stomach contents from 321 sandbar sharks *Carcharhinus plumbeus* captured in nearshore (<100 m) and offshore (>100 m) waters between Cape Hatteras and Georges Bank.

	Food		Items		Stomachs	
	Vol. (mL)	%	*N*	%	*N*	%
Arthropoda						
Cancridae						
Cancer sp.	93	0.20	3	1.03	3	0.93
Unident. crab	1	0.00	1	0.34	1	0.31
Isopoda	8	0.02	10	3.46	1	0.31
Cephalopoda						
Gonatidae	120	0.26	1	0.34	1	0.31
Ommastrephidae	6	0.01	1	0.34	1	0.31
Illex illecebrosus	70	0.15	2	0.69	2	0.62
Unident. squids	141	0.30	9	3.11	7	2.18
Echinoderma						
Scutellidae (sand dollars)	13	0.02	4	1.38	3	0.93
Elasmobranchs						
Squalus acanthias	246	0.53	6	2.07	4	1.24
Mustelus canis	2365	5.12	1	0.34	1	0.31
Raja erinacea	6785	14.71	17	5.88	13	4.05
Raja sp.	5190	11.25	26	9.00	25	7.78
Dasyatidae	175	0.37	1	0.34	1	0.31
Skate eggs	192	0.41	11	3.80	7	2.18
Teleosts						
Congridae	925	2.00	1	0.34	1	0.31
Ophichthus cruentifer	55	0.11	13	4.49	2	0.62
Clupeidae	80	0.17	1	0.34	1	0.31
Chauliodontidae	75	0.16	1	0.34	1	0.31
Lophius americanus	7445	16.14	23	7.95	20	6.23
Synodontidae	75	0.16	3	1.03	3	0.93
Gadidae	1975	4.28	9	3.11	6	1.86
Merluccius bilinearis	100	0.21	1	0.34	1	0.31
Carangidae	50	0.10	1	0.34	1	0.31
Cottidae	965	2.09	6	2.07	3	0.93
Labridae	25	0.05	1	0.34	1	0.31
Ophidiidae	30	0.06	1	0.34	1	0.31
Pomatomus saltatrix	2792	6.05	9	3.11	9	2.88
Scombridae	50	0.97	1	0.34	1	0.31
Scomber scombrus	1410	3.05	6	2.07	6	1.86
Peprilus triacanthus	100	0.21	2	0.69	1	0.31
Triglidae	14	0.03	1	0.34	1	0.31
Zoarcidae	410	0.88	1	0.34	1	0.31
Macrozoarces americanus	350	0.75	1	0.34	1	0.31
Bothidae	1330	2.88	5	1.73	5	1.55
Limanda ferruginea	4627	10.03	21	7.26	8	2.49
Pleuronectidae	2780	6.02	20	6.92	18	5.60
Teleost unident.	4163	9.02	60	20.76	47	14.60
Miscellaneous						
Clam Shells	55	0.12	2	0.69	2	0.62
Marine mammal flesh	50	0.10	1	0.34	1	0.31
Animal remains	390	0.80	4	1.38	4	1.24
Trash	1	0.00	1	0.34	1	0.31
Totals	46,127		289			

Table 3

Stomach contents from 268 sandbar sharks *Carcharhinus plumbeus* captured in nearshore (<100 m) waters between Cape Hatteras and Georges Bank.

	Food		Items		Stomachs	
	Vol. (mL)	%	*N*	%	*N*	%
Arthropoda						
Cancridae						
Cancer sp.	93	0.22	3	1.37	3	1.10
Unident. crab	1	0.00	1	0.45	1	0.37
Cephalopoda						
Gonatidae	120	0.28	1	0.45	1	0.37
*Unident. squid	40	0.09	5	2.28	3	1.11
Echinoderma						
Scutellidae (sand dollars)	13	0.03	4	1.82	3	1.11
Elasmobranchs						
Squalus acanthias	180	0.42	2	0.91	2	0.75
Mustelus canis	2365	5.64	1	0.45	1	0.37
Raja erinacea	6785	16.20	17	7.76	13	4.80
**Raja* sp.	5140	12.27	25	11.41	24	8.95
*Skate eggs	186	0.44	9	4.10	6	2.20
Teleosts						
Congridae	925	2.20	1	0.45	1	0.37
Clupeidae	80	0.19	1	0.45	1	0.37
Chauliodontidae	75	0.17	1	0.45	1	0.37
**Lophius americanus*	5870	14.02	20	9.13	17	6.30
Synodontidae	75	0.17	3	1.36	3	1.10
Gadidae	1450	3.46	4	1.82	4	1.50
Merluccius bilinearis	100	0.23	1	0.45	1	0.37
Carangidae	50	0.11	1	0.45	1	0.37
Cottidae	965	2.30	6	2.73	3	1.10
Labridae	25	0.05	1	0.45	1	0.37
Ophidiidae	30	0.07	1	0.45	1	0.37
**Pomatomus saltatrix*	2765	6.60	8	3.65	8	3.00
Scomber scombrus	1410	3.36	6	2.73	6	2.20
Peprilus triacanthis	100	0.23	2	0.91	1	0.37
Zoarcidae	410	0.97	1	0.45	1	0.37
Macrozoarces americanus	350	0.83	1	0.45	1	0.37
*Bothidae	730	1.73	4	1.82	4	1.50
Limanda ferruginea	4627	11.05	21	9.58	8	3.00
Pleuronectidae	2780	6.64	20	9.13	18	6.71
Teleost unident.	3676	8.78	41	18.72	37	13.80
Miscellaneous						
Clam shells	55	0.13	2	0.91	2	0.75
Marine mammal flesh	50	0.11	1	0.45	1	0.37
Animal remains	340	0.81	3	1.36	3	1.10
Trash	1	0.00	1	0.45	1	0.37
Totals	41,862		219			

Note: Asterisk indicates prey items duplicated offshore.

Table 4

Stomach contents from 53 sandbar sharks *Carcharhinus plumbeus* captured offshore (>100m) between Cape Hatteras, North Carolina, and Georges Bank.

	Food		Items		Stomachs	
	Vol. (mL)	%	*N*	%	*N*	%
Arthropoda						
Isopoda	8	0.18	10	14.28	1	1.90
Cephalopoda						
Ommastrephidae	6	0.14	1	1.42	1	1.90
Illex illecebrosus	70	1.64	2	2.85	2	3.77
*Unident. squid	101	2.36	4	5.71	4	7.54
Elasmobranchs						
Squalus acanthias	66	1.54	4	5.71	2	3.77
**Raja* sp.	50	1.17	1	1.42	1	1.90
Dasyatidae	175	4.10	1	1.42	1	1.90
*Skate eggs	6	0.14	2	2.85	1	1.90
Teleosts						
Ophichthus cruentifer	55	1.28	13	18.57	2	3.77
Gadidae	525	12.50	5	7.14	2	3.77
**Lophius americanus*	1575	36.92	3	4.28	3	5.66
**Pomatomus saltatrix*	27	0.63	1	1.42	1	1.90
Scombridae	450	10.55	1	1.42	1	1.90
Triglidae	14	0.32	1	1.42	1	1.90
*Bothidae	600	14.06	1	1.42	1	1.90
Teleost unident.	487	11.41	19	27.14	10	18.86
Miscellaneous						
Animal remains	50	1.17	1	1.42	1	1.90
Totals	4265		70			

Note: Asterisk indicates prey items duplicated nearshore.

Elasmobranchs Elasmobranchs ranked second to teleosts as a major food group, accounting for 16.0% of the food by frequency of occurrence (Fig. 2). Skates of the family Rajidae were the principal representatives in this food group, with *Raja erinacea* occurring most frequently. Unspecified skate remains described as *Raja* spp. in Table 2 most likely included *R. erinacea* and possibly *R. eglanteria*, both which commonly occur in the sampling area. Eleven skate egg cases were also found in seven stomachs. These were generally torn and old looking. However, a few contained yolk material suggesting they were ingested as a food source rather than by accident. Based on frequency of occurrence, spiny and smooth dogfish sharks are relatively unimportant in the sandbar shark's diet when compared with the importance of skates in the diet (Table 2). Bigelow & Schroeder (1948), Bass et al. (1973), and Lawler (1976) also report the occurrence of shark remains in sandbar shark stomachs. Springer (1960), however, after examining several hundred sandbar sharks from the Florida coast, reported finding very few stomachs with shark remains. The high frequency of occurrence of skates in the sandbar shark's diet can be attributed to their general abundance over the continental shelf (Waring 1986).

Cephalopods From this study, cephalopods (squids and octopus) appear to be generally unimportant in the sandbar shark's diet by evidence of their low number, volume, and frequency of occurrence (Fig. 2). Earlier studies by Springer (1960), Clark & von Schmidt (1965), Lawler (1976), and Branstetter (1981) also showed low occurrences of squid in the sandbar shark's diet, but all were based on specimens obtained from inshore areas of low squid abundance. Our findings, however, suggest that predation on this food source is

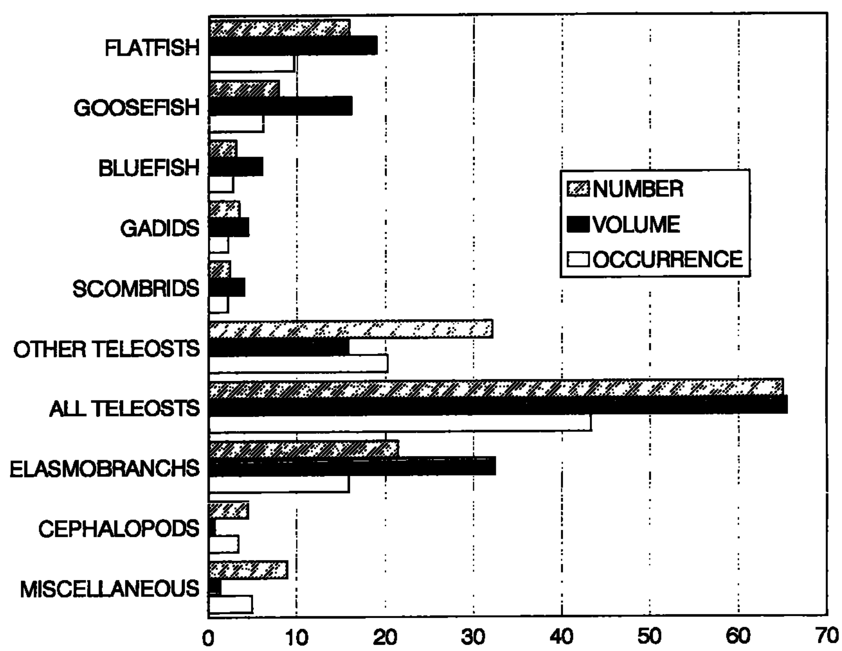

Figure 2

Major food categories consumed by 321 juvenile and adult sandbar sharks *Carcharhinus plumbeus* from the U.S. northeast coast, 1972–84.

probably linked to prey density, since 7 of the 11 stomachs containing squid were from sharks captured offshore where squid are most abundant. It is also possible that the four sharks captured nearshore with squid in their stomachs had moved inshore after eating the squid.

Areal comparisons Flatfish and cephalopods were the only food groups to show significant differences ($P<0.05$, χ^2 test) in importance between the areas. Flatfish occurred most often in nearshore stomach samples, probably as a result of their high summer abundance in shoaler waters along the coast (Bigelow & Schroeder 1953). Cephalopods occurred more often in stomachs offshore because of their high abundance off the U.S. northeast coast (Lange & Sissenwine 1980, Lange 1982), and hence their availability probably accounts for their appearance in the stomachs examined in this study.

Nearshore there was significantly ($P<0.05$, χ^2 test) more predation on elasmobranchs and goosefish by female sharks than by males. Offshore, juvenile males consumed significantly ($P<0.05$, χ^2 test) more 'Other Teleosts' than females. 'Other Teleosts' was the only food group in this area for which there was a difference between sexes. Overall, there was no difference in predation rates on the major food groups with respect to shark size (juveniles or adults).

Food volumes Overall, 49% of examined stomachs contained food. Wass (1973) found that 45% of stomachs from sandbar sharks captured by hook-and-line off Hawaii contained food remains. In other studies, averages have been lower, but up to 29% have been observed for the sandbar shark (Springer 1960, Bass et al. 1973, Lawler 1976).

Our findings show that stomach content volumes ranged from trace amounts to a maximum of 3102 mL, with a mean of 144 mL. The mean for adults was 175.4 mL and 125.2 mL for juveniles. Stomachs from adult and juvenile females contained more food (184.0 and 165.0 mL) on the average than their male counterparts (125.0 and 97.0 mL); however, differences were not significant at the α=0.05 level (t-test).

The ratio of stomach content volume to mean body weight ($\bar{x}$BW) varied between different groups of the population, from a low of 0.30% for adult males to a high of 0.83% for juvenile males offshore. The mean for adults and juveniles was 0.33% and 0.55%, respectively, with an overall sample mean of 0.42%. Means for adults of both sexes were similar for the whole sample and nearshore, ranging from 0.30 to 0.36%. Juvenile males and females from nearshore differed the most, with percentages of 0.42 and 0.66, respectively. The highest stomach content values were from an adult and a juvenile female. Stomach contents in these sharks amounted to 5.35 and 5.34% of their body weight, respectively. The adult's stomach contained a whole smooth dogfish and gadid remains. The stomach from the juvenile contained 10 yellowtail flounder *Limanda ferruginea* and a small goosefish. The flounders ($\bar{x}$ size=13.4 cm) may have been consumed as natural prey or obtained as culls from a trawl catch. However, other sandbar sharks caught in the area on the same day contained only 1 or 2 flounder, suggesting that this juvenile female was more successful in obtaining natural prey.

Overall mean stomach volume in terms of liquid capacity for the sharks in this study was 2.62 L which was 7.7% of the $\bar{x}$BW (34.0 kg). For adults, the mean was 5.15 L, amounting to 10.0% of their $\bar{x}$BW (52.3 kg).

A measure of stomach fullness was determined by calculating the ratios of food volume to maximum liquid capacity. The mean food volume (144 mL) was 5.5% of the mean maximum capacity. Dividing the sample by size-class showed that the percent stomach fullness was 5.2 and 13.5 for adults and juveniles, respectively. One stomach from a juvenile female was filled to 50.0% capacity, while two others approximated 40.0%. Just over half (53.0%) of the stomachs contained less than 10.0%. All adults had less than 10.0%, except for two that ranged from 15.0 to 19.0%.

Chincoteague Bay sample

The Chincoteague sample was composed of pups and young juvenile sandbar sharks captured at six fishing stations located in the lower bay estuaries. The overall mean fork length and body weight for these sharks was 55 cm and 1.72 kg, respectively. The mean for 65 newborn pups (39 males, 26 females) was 50.7 cm and 1.38 kg, while the mean for 29 (16 males, 13 females) "older" pups and small juveniles was 63.7 cm and 2.48 kg. There was no difference in mean fork length or body weight between the sexes within each size-class.

Food analysis Food items consisted of crustaceans and fish. By frequency of occurrence, these contributed 82.0 and 13.8%, respectively. Crustaceans were represented primarily by soft blue crabs (75.5%), with the remainder (6.3%) consisting of lady crabs and mantis shrimp. Fish prey consisted of small flounder, anchovy, Atlantic silver sides, mullet, and one smooth dogfish (48 cmTL) eaten in three pieces. A more complete prey list for young sandbar sharks captured in Chincoteague Bay during the summer of 1983 is given in Medved et al. (1985). Previous studies of young sandbar sharks along the Virginia coast also showed that their diets consisted of small fish and crustaceans but was dominated by soft blue crabs (Hoese 1962, Medved & Marshall 1981; V.J. Lascara, Jonathan Corp., Norfolk VA, pers. commun. 1987).

Food volumes Stomachs from 75 (79.8%) sharks contained food varying from trace amounts to a maximum of 125 mL. Nineteen stomachs (20.2%) were empty. Stomachs from 236 sharks caught by gillnets in Chincoteague Bay during the same time-period (Medved et al. 1985) showed that 85.6% (202) held food remains, while 14.4% (34) were empty.

The mean food volume for sharks considered to be newborn pups was 16.6 mL (1.2% of $\bar{x}$BW); for "older" pups and small juveniles, it was 27.0 mL (1.1% of $\bar{x}$BW). The whole sample mean was 20.0 mL or 1.2% of the $\bar{x}$BW.

Estimates of daily ration and annual food consumption

Daily ration Reviews are available of studies and techniques for determining stomach evacuation rates (Windell 1978, Fange & Grove 1979) and daily ration (Davis & Warren 1971, Conover 1978, Mann 1978) for several species of teleosts. Comparable types of studies for sharks are lacking in the literature, primarily because the technology for maintaining sharks in a healthy "normal" condition in the laboratory has not been perfected (Gruber & Keyes 1981). A few excep-

Table 5

A comparison of feeding-related variables for sandbar shark pups *Carcharhinus plumbeus*, and juveniles and adults caught by different gear types in Chincoteague Bay and in the nearshore (<100 m) and offshore (>100 m) waters of the U.S. northeast coast, 1972–84.

				$\bar{x}$ Stomach contents		$\bar{x}$ Meal size		Est. daily ration		
	N	Capture method	$\bar{x}$ BW[a] (kg)	(g)	% of $\bar{x}$ BW	(g)	% of $\bar{x}$ BW	(g)	% of $\bar{x}$ BW	Source
Pups	236	GN[b]	1.88	18.9	0.96	79.5	4.23	20.1	1.07	Medved 1985, Medved et al. (1988)
Pups	94	ST	1.72	20.0	1.16			24.4	1.43	This study
Juveniles and adults	321	ST&LL	34.0	144.0	0.42			293.0	0.86	This study

[a]BW = body weight.
[b]GN = gill net, ST = sport tackle, LL = longline.

tions do exist, however. These include food consumption studies for the lemon shark *Negaprion brevirostris* by Graeber (1974), Gruber (1982), and Longval et al. (1982); digestion rates in the blue shark *Prionace glauca* by Tricas (1977); stomach evacuation and food consumption experiments by Jones & Geen (1977) on the spiny dogfish and Cortés & Gruber (1990) on the lemon shark; stomach evacuation rates in captive sandbar sharks by Wass (1973); and stomach evacuation, food consumption, and daily ration estimates in the sandbar shark by Medved (1985) and Medved et al. (1985, 1988). The data for the last three papers came from experiments conducted on pups and small juvenile sandbar sharks maintained in a natural enclosure in Chincoteague Bay, Virginia. Knowing the rate of gastric evacuation is necessary for determining the daily ration of a species. A number of factors, both biological and physical, influence the evacuation rate in fish (Langton 1977), but temperature, food type, and predator size appear to have the greatest impact (Windell 1966 and 1968, Pandian 1967, Edwards 1971, Jones & Geen 1977, MacDonald et al. 1982, Medved et al. 1985). Jones & Geen (1977) maintained spiny dogfish in aquaria at about 10°C and found that 5 d were required to evacuate a meal of herring. At the same temperature, mature males required 10 d to evacuate a full stomach of herring, and the time required was probably influenced by the size of the dogfish. Wass (1973) found that sandbar sharks (95–101 cm caudal length) maintained in large experimental ponds (temperature unknown) required at least 2–3 d to evacuate their stomachs. In the natural environment around the Hawaiian Islands where surface-water temperatures average about 26°C, he suggested that 3–4+ d might be needed, depending on whether the prey was soft or hard and resistant to digestive enzymes.

Prior to the feeding study, the sharks were starved for 4 d. What effect this had on their gastric evacuation rate is unknown, but studies conducted on various species of teleosts starved before feeding resulted in slower evacuation rates (Windell 1967, Elliott 1972, Jones 1974). Medved et al. (1985) were able to demonstrate the variability in gastric evacuation rates that can occur between food types. Soft blue crabs and Atlantic menhaden *Brevoortia tyrannus* required 70.7 and 92.7 h, respectively, (81.5 h avg.) to be depleted to 98% of their original weight. The difference in depletion time was probably the result of a combination of factors, including a natural lag phase in initial enzyme action on the food items (Jennings 1972) and the resistance of the skin and scales of the fish prey to digestion (Windell 1967, Western 1971). Jobling (1987) also reported that the different surface-to-volume ratio of the two food types and their differing friability will affect gastric evacuation. In addition, a concentration of fat in some fish flesh, such as found in menhaden (Thayer et al. 1973), has been shown to delay gastric evacuation (Quigley & Meschan 1941, Windell 1967, Windell et al. 1969).

In the present study, two approaches were used to estimate daily ration. The first was by use of a calculated routine metabolic rate, and the second was the basic energy equation of Winberg (1956),

$$C = 1.37\,(R+G),$$

where C = energy of food consumed, R = total energy of metabolism, G = metabolic energy in terms of growth, and the coefficient 1.37 represents the 27% of food energy lost through excretion (Brett & Groves 1979). This is a more recent and accurate value than the 20% originally proposed by Winberg (1956).

A metabolic rate for the sandbar shark has not been determined. For our purposes, therefore, we assumed that a routine metabolic rate of 49.2 mgO_2/kg × h at 10°C for the spiny dogfish (Brett & Blackburn 1978) was appropriate for the sandbar shark. Adjusting for an increase in temperature to 18.5°C (J.C. Casey, Narragansett Lab., NMFS Northeast Fish. Sci. Cent., unpubl. longline data) and using a Q_{10} of 2.2, we derived a metabolic rate of 95.9 mgO_2/kg × h. Using an oxycalorific equivalent of 3.25 cal/mgO_2 cited for fishes (Elliott & Davison 1975), the routine metabolic expenditure is 311.7 cal/kg × h or 7.48 kcal/kg × d. The average sandbar shark at 34.0 kg BW would thus require 254.3 kcal/d. To compensate for the food energy lost through excretion, the sharks would have to consume 10.2 (7.48×1.37) kcal/kg × d. This would raise the total daily average intake to 346.8 kcal/d (10.2 × 34.0). If we consider the average caloric value of the foods eaten to be 1.195 kcal/g (Steimle & Terranova 1985), the energy intake in terms of food mass amounts to 290.2 g/d (346.8/1.195) or 0.85% of average body weight (BW). Yearly, this amounts to 105.9 kg (3.1 × $\bar{x}$BW).

To employ the Winberg (1956) energy equation, we calculated a value for G based on an average growth in weight estimate of 3.72 g/d for juveniles and adults (Casey & Natanson 1992). Using an average calorific value of shark flesh of 1.01 kcal/g (Sidwell et al. 1974), the daily increase in caloric content due to growth is 3.75 kcal/d (3.72×1.01). Substituting the energy values for metabolism and growth in the equation gives an energy value for food consumed of 353.5 kcal/d (1.37[254.3+3.75]) or 295.8 g/d (food energy = 1.195 kcal/g). Daily ration then is equal to 0.87% of BW/d and 3.2 × BW/yr.

To estimate daily ration for the sandbar pups from Chincoteague Bay, we assumed the metabolic rate above for the spiny dogfish was appropriate. Correcting for temperature (25.0°C) and using a Q_{10} of 2.2 resulted in a metabolic rate of 160.4 mgO_2/kg × h. When converted to calories, the routine metabolic expenditure is 521.3 cal/kg × h (160.4×3.25), or 12.5 kcal/kg × d. At this rate, the average sandbar pup (1.7 kg) in this study would require 21.2 kcal/d (12.5×1.7) for metabolic needs. When we consider the 27% of food energy lost through excretion, the daily ration would have to provide 17.1 kcal/kg × d (12.5×1.37) or 29.0 kcal/d (17.1×1.7) for the average pup.

Using a caloric value of 1.235 kcal/g for the foods consumed by sandbar pups (Medved et al. 1988), the daily ration required for routine metabolic needs would be 23.4 g/d (29.0/1.235). This is equivalent to 1.38% of the average BW and amounts to 5.0 times the average BW per year.

Daily growth in weight for sandbar pups was determined to be 1.74 g/d. This was based on the reexamination of existing age data and newly collected information by Casey & Natanson (1992). This amount of daily growth in weight is equivalent to 1.75 kcal/d assuming an average caloric value of 1.01 kcal/g for shark flesh (Sidwell et al. 1974). Substituting for metabolism and growth in the Winberg equation gives an energy value for food consumed of 31.4 kcal/d (1.37[21.2×1.75]). Taking the average caloric value of the food eaten to be 1.235 kcal/g, the daily ration would be 25.4 g/d (31.4/1.235) to meet the energy needs for routine metabolic expenditure. This is equivalent to 1.49% of the average BW and 5.4 times the average BW per year. Our average estimate of daily ration (1.43% BW) for sandbar pups above is in very close agreement to the 1.1% determined by Medved et al. (1988).

The validity of using the metabolic rate of one species for another is questionable and is especially so if the original rate is determined by laboratory studies and then extrapolated to studies in the wild. Not only could significant differences exist between species, but routine metabolic energy expended in the wild may be considerably less than that expended under experimental conditions. For instance, Medved et al. (1988) have shown that a large proportion of sandbar shark movement in Chincoteague Bay is accomplished by passively drifting with the currents. This behavior is most likely a way to increase energy efficiency, since locomotion is metabolically costly for fish (Brett & Groves 1979). No doubt there are other ways by which sharks conserve energy in the wild. With the limitations imposed by available data and literature values, we feel our daily ration estimates are reasonable and comparable with estimates for large sharks in other studies (Table 6). When reliable information specific to the metabolic rate of juvenile and adult sandbar sharks is available, better estimates may be possible.

Annual food consumption Estimates of annual food consumption indicated that the pups can ingest 5.2 times their average body weight in a year. The combined juveniles and adults, by comparison, will consume 3 times their average BW annually (Table 6). The gradual reduction in annual food consumption per kilogram of body weight is a normal result of increasing size. Brett & Groves (1979) show that at a young stage, the rate at which fish generally accumulate body mass exceeds the metabolic energy needs for maintenance. Both rates are relatively high initially, but with

Table 6

Comparison of daily ration and annual food consumption estimates for sandbar sharks *Carcharhinus plumbeus* in this study and for six other species of large sharks. BW = body weight.

Species	$\bar{x}$ length (cm)	$\bar{x}$ weight (kg)	kg/d	kg/yr	%BW/d	$\bar{x}$ BW/yr	Source
Mako *Isurus oxyrinchus*	175	63.0	2.000	730.0	3.2	11.6	Stillwell & Kohler (1982)
Lemon *Negaprion brevirostris*	70				3.0		Gruber (1982)
Lemon		2.4	0.020		2.0		Cortés & Gruber (1990)
Lemon	IMMATURE				1.4		Clark (1963)
Lemon	274				0.5		Clark (1963)
Scalloped hammerhead *Sphyrna lewini*		49.9	0.680	248.2	1.4	5.0	Clark (1963)
Blue *Prionace glauca*	187	48.6	0.276	100.7	0.6	2.1	Kohler (1987)
Nurse *Ginglymostoma cirratum*		152.4	0.450	164.3	0.3	1.1	Clark (1963)
Sand tiger *Odontaspis taurus*	137		0.680	248.2			Clark (1963)
Sandbar (juv.)		32.8	0.143	52.2	0.3–0.5	1.6	G. Early*
Sandbar (pups)	56	1.8	0.020	7.3	1.1	3.8	Medved et al. (1988)
Sandbar (pups)	55	1.7	0.024	8.7	1.4	5.1	This study
Sandbar (juv. & adults)	144	34.0	0.293	107.0	0.86	3.1	This study

*New England Aquarium, Central Wharf, Boston MA 02110 (1979).

increasing size and age they decrease at different declining slopes, until, eventually, large mature fish are eating for maintenance and gonad development only. In addition, a reduced capacity to grow may inhibit larger daily intakes of food among older, larger fish (Brett 1971).

Acknowledgments

Special thanks are extended to the many tournament officials and anglers who allowed us the privilege of examining and dissecting shark catches as they came to the docks, and to Dr. Robert "Bosco" Medved for providing space and opportunity for the senior author to collect samples and data from the Chincoteague sandbar sharks. We also acknowledge the support and assistance given by all the staff of the Apex Predators Investigation, especially Jack Casey for his infectious enthusiasm to continually probe into the unknown aspects of shark's lives.

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