STOMACH CONTENTS OF YOUNG SANDBAR SHARKS, *CARCHARHINUS PLUMBEUS*, IN CHINCOTEAGUE BAY, VIRGINIA[1]

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ABSTRACT

During the summer of 1983 the stomach contents of 414 sandbar sharks captured by gill nets, and rod and reel fishing gear in Chincoteague Bay, Virginia, were examined. The blue crab, *Callinectes sapidus*, occurred in 67.4% of the stomachs and Atlantic menhaden, *Brevoortia tyrannus*, occurred in 13.3% of the stomachs. Other species of small crustaceans and fishes were found in < 6.0% of the stomachs, and 17.9% of the stomachs were empty. Data collected concerning the amount, stage of digestion, and number of food items in the stomachs indicated that feeding occurred during relatively short periods of time separated by long periods during which food was digested and no additional food was consumed. Sharks caught in gill nets were found to be in various stages of the feeding cycle and were more representative of the entire population than those caught by rod and reel. In the stomachs of these sharks, crustaceans accounted for nearly twice as much of the mean weight of food as did fish. The mean quantity of food in the stomachs was 0.96% of body weight (BW) and the maximum quantity was 5.28% of BW. The quantity of food in all stomachs was significantly less than the estimated maximum stomach capacity (13.0% BW). Sharks caught between 0130 and 0430 were found to contain considerably more food in their stomachs than sharks caught during other times of the day. The data collected from this study when combined with information concerning gastric evacuation will provide the basis for food consumption estimates in this species.

Traditionally the management of commercially valuable fisheries has been based on single-species production models and the concept of maximum sustainable yield (Hennemuth 1979). Although generally accepted as an objective of management, the estimation and application of maximum sustainable yield have not provided satisfactory results and have, in fact, led to significant declines of some traditional and highly valued fisheries (Edwards and Hennemuth 1975; Hennemuth 1977; Holt and Talbot 1978). The poor results of single-species models in allocating fishing quotas may be due in part to the fact that they assume no interactions of the target species with other components of the ecosystem. In recent years it has become clear that this assumption is unrealistic and that variables such as competition, predation, and abiotic factors should be considered in any assessment of fishery productivity and potential yields to man. It has been pointed out (Gulland 1978, 1983; Mercer 1982) that the future success of our attempts at managing fishery resources will depend, to a large extent, on our ability to develop multispecies production models that adequately account for interactions among species. An important component of these models is predator-prey interactions. In fact, collection of data on the diets of the major predators is considered absolutely necessary for the progress of multispecies assessment techniques (Hennemuth 1980[4]; Mercer 1982). Considering their position as one of the most abundant apex predators in the sea, predation by sharks undoubtedly plays a major role in the exchange of energy in the marine environment. In fact, a study by Jones and Geen (1977) has indicated that the spiny dogfish, *Squalus acanthias*, in British Columbia waters annually consumes over 5 times the commercial catch of herring and up to 44% of the total stock. The impact that sharks have on commercial fisheries can only be determined by knowing the diversity of prey items and the biomass of each consumed. While numerous publications on sharks incorporate lists of items found in their stomachs, very little is known about daily ration and the amounts of food consumed annually.

[1]MARMAP Contribution No. MED/NEFC 84-02.

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[4]Hennemuth, R. C. 1980. Research needs for multispecies fisheries. Office of Technology Assessment Workshop, Seattle, WA., 21-23 April.

Manuscript accepted October 1984.

In most investigations the food consumption of fishes has been studied by methods that involve laboratory techniques to estimate various parameters relating to growth, metabolism, digestion, and excretion (reviews by: Davis and Warren 1971; Mann 1978). These methods, however, are of limited value for fishes such as sharks that are difficult to maintain in captivity. An alternate method for determining food intake that can be applied to fishes in the wild has been successfully used in several studies (Bajkov 1935; Swenson and Smith 1973; Eggers 1977; Thorpe 1977; Elliott and Persson 1978; Jobling 1981; Stillwell and Kohler 1982; Durbin et al. 1983). This approach requires information concerning the quantity of food found in the stomachs of fishes sampled at regular intervals over 24-h periods and the rate at which food is evacuated from the stomach. The objective of the present study was to obtain the quantitative stomach content data needed to use this approach to estimate the daily food ration of the sandbar shark, *Carcharhinus plumbeus*. The sandbar shark was selected for this study because it is one of the few sharks for which gastric evacuation data are available (Medved in press). It is also an abundant, widely distributed shark (Springer 1960; Casey 1976) known to feed on commercially valuable species (Medved and Marshall 1981). In addition, it is a member of a large family of sharks (Carcharhinidae) and data collected for this species will provide the basis for making preliminary estimates of food consumption for the other members of the family.

METHODS

During the summer of 1983, young sandbar sharks were collected from Chincoteague Bay, VA, for stomach content analysis. The study area is located within the summer distribution of this species and supports a relatively large number of young sandbar sharks from early June through September. The bay is about 40 km long and 8 km wide at its widest point, and the average water depth is 2 m. A tidal inlet connects the bay with the Atlantic Ocean, and the tidal range varies from 0.75 to 1.50 m. The area is also characterized by strong tidal currents, vast salt marshes, and brackish to seawater salinities.

A 4.9 m outboard motor boat was used as a fishing platform, and sharks were caught using monofilament gill nets and rod and reel fishing gear. The gill nets were 91 m long, 1.8 m deep, and had a stretched mesh size of 10.8 cm. They were anchored at both ends and were buoyed so the foot rope touched the bottom. Net retrieval was made every 1 to 2 h. The fishing rods were equipped with Penn[5] reels of 3/0 size, and the terminal tackle consisted of two wire leaders, each with a 4/0 fishing hook baited with squid. The hooks were set 1 m off the bottom. Both types of gear were used during all hours of the day. Upon capture each shark was brought into the boat where it was sexed, measured, and weighed. The sharks were then cut open and the stomach contents were removed and stored on ice in plastic bags.

In the laboratory each food item was identified to species and a length measurement was made when possible. Each item in the stomach was also assigned a stage-of-digestion value ranging from 1 to 6 with a higher number indicating a greater extent of digestion. The stage-of-digestion scale was based on a gastric evacuation study (Medved in press) in which sandbar sharks were fed preweighed meals of either blue crab, *Callinectes sapidus*, or Atlantic menhaden, *Brevoortia tyrannus*, and were maintained in an enclosure constructed in the natural environment. The range of water temperatures in the enclosure (22.0°-30.0°C) was close to that recorded during the present study (20.0°-27.3°C). The sharks were sacrificed at various time intervals after feeding, and the food remains were weighed and described. The food item descriptions were used to arbitrarily establish six stages of digestion that were each one-sixth of the total evacuation time. Each stage of digestion was about 12 h long for crustacean prey and 15 h long for fish prey. After identification of food items and assignment of digestion values, the stomach contents of each shark were separated into fish and crustacean components that were weighed to 0.01 g after draining off excess water. Each sample was then dried at 80°C to constant weight (about 72 h) and again weighed to 0.01 g.

RESULTS

During the study 414 sharks were captured for stomach content analysis. The numbers of sharks caught by each fishing method and during various time periods of the day are summarized in Table 1. The number of male and female sharks collected was nearly equal (210 and 204 respectively), and they ranged in size from 40.0 to 80.0 cm fork length (FL) ($\bar{x}$ = 56.1, SD = 6.8). Body weights were obtained from 369 (89.1%) of these sharks, and ranged from 720.0 to 5,690.0 g ($\bar{x}$ = 1,885.5, SD = 738.8). The body weight of the sharks not weighed was estimated from a regression equation derived from the

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of sharks caught for stomach content analysis during different time intervals and by the two capture methods.

Time interval	Rod and reel	Gill net	Total
2230-0130	19	33	52
0130-0430	11	27	38
0430-0730	20	20	40
0730-1030	21	27	48
1030-1330	27	27	54
1330-1630	39	39	78
1630-1930	18	30	48
1930-2230	23	33	56
Total	178	236	414

animals that were measured and weighed: Wt = 0.0123 $(FL)^{2.9577}$ (n = 369, R^2 = 0.97). Water temperature during the fishing periods ranged from 20.0° to 27.3°C (n = 172, $\bar{x}$ = 25.1) but 90% of the temperatures were between 23.9° and 26.4°C.

Fifteen different food types were identified in the stomachs (Table 2). A relatively large number of stomachs (n = 74, 17.9%) were empty, and unidentifiable fish remains occurred in others (n = 21, 5.1%). The blue crab was the most frequently occurring food item and was found in 279 (67.4%) of the stomachs examined and in 82.1% of the stomachs containing food. Of the food remains that could be positively identified as individual blue crabs (n = 309), 88.0% of the crabs had recently molted and were soft. The crabs that could be measured ranged in size from 1.0 to 14.0 cm between the two points of the carapace (n = 136, $\bar{x}$ = 7.4). Although exact numbers were difficult to determine, it appeared that less than half of the blue crabs were consumed whole. The only other prey frequently found was the Atlantic menhaden, which occurred in 55 (13.3%) of the stomachs examined and in 16.2% of the stomachs with food. Of the 61 cases where it was possible to determine if the fish was consumed whole or in part, 28 (45.9%) of the menhaden were whole and ranged in size from 5 to 10 cm total length (TL) ($\bar{x}$ = 7.3). The estimated sizes of the partially eaten menhaden ranged from 5 to 17 cm TL ($\bar{x}$ = 8.6). All other prey items were found in < 6.0% of the stomachs examined.

The distributions of stage-of-digestion values assigned to the food items in the stomachs of sharks caught by the two different fishing methods are shown in Figure 1. The distribution for sharks caught by rod and reel indicated that 71.8% of the food items were in either the first or last stage of digestion. In contrast, food items in the stomachs of sharks caught by gill nets were divided more evenly among all the stages of digestion. The two capture methods also differed in the proportion of sharks

TABLE 2.—Stomach contents found in a sample of 414 sandbar sharks.

Stomach content	No. of stomachs found in	Percent of stomachs found in
Blue crab, *Calinecties sapidus*	279	67.4
Empty	74	17.9
Atlantic menhaden, *Brevoortia tyrannus*	55	13.3
Summer flounder, *Paralichthys dentatus*	24	5.8
Unidentified fish	21	5.1
Mantis shrimp, *Squilla emprisa*	18	4.4
American eel, *Anguilla rostrata*	15	3.6
Spot, *Leiostomus xanthurus*	14	3.4
Atlantic silverside, *Menidia menidia*	9	2.2
Smooth dogfish, *Mustelus canis*	7	1.7
Northern pipefish, *Syngnathus fuscus*	6	1.5
Anchovy, *Anchoviella mitchilli*	5	1.2
Squid, *Loligo pealei*	5	1.2
Bluefish, *Pomatomus saltatrix*	3	0.7
Calico crab, *Ovalipes ocellatus*	1	0.2
Mummichog, *Fundulus heteroclitus*	1	0.2
Northern seahorse, *Hippocampus hudemius*	1	0.2

caught with empty stomachs. The percentage of the 178 sharks caught by rod and reel with empty stomachs (22.5%) was significantly higher than that found for the 236 sharks caught by gill nets (14.4%; z-test, P = 0.015).

Of the 414 stomachs examined, 203 contained a single food item. A stage-of-digestion value of 5 or 6 was assigned to 89 (43.8%) of these items, indicating that many sharks went at least the time equivalent of 5 stage-of-digestion units between meals (48 to 60 h for crustacean prey or 60 to 75 h for fish prey).

Multiple food items were found in 137 stomachs. The difference between the stage-of-digestion values

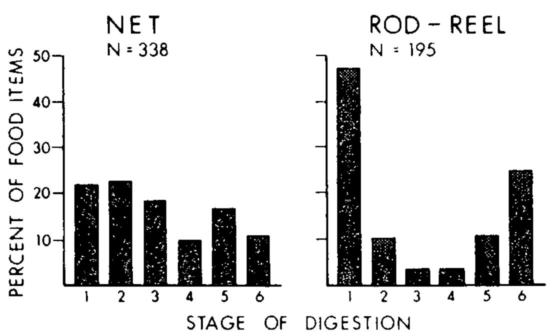

FIGURE 1.—Distributions of stage-of-digestion values assigned to food items present in the stomachs of sharks caught with gill net and rod and reel.

of the first and last eaten food items within each stomach was calculated to assess the amount of time that passed during consumption of multiple item meals. In 19 stomachs a food item in the sixth stage of digestion and one in the first stage of digestion were found. In these cases a time equivalent of 5 stage-of-digestion units had passed between consumption of the two food items, and since a stomach containing an item in stage 6 of digestion would be relatively empty, the two food items were considered to represent two different meals. Excluding the above 19 stomachs from analysis, the mean difference between the stage-of-digestion values of the first and last eaten food items was calculated for stomachs containing from 2 to 5 items (Table 3). The overall mean difference was 0.60 stage-of-digestion units indicating that multiple food items in the stomachs were in similar stages of digestion.

The quantity of food in each stomach examined was measured on a wet weight and dry weight basis. Excluding empty stomachs from analysis, the total dry weight of food (TDW) was found to be linearly related to the total wet weight of food (TWW) in the stomachs (TDW = −0.24 + (0.22) TWW; n = 318, R^2 = 0.96). Since the two measurements were highly correlated (r = 0.98) and wet weight measurements have frequently been used in similar food studies on other species, it seemed valid to express the food quantity results in this paper on a wet weight basis. Table 4 summarizes the descriptive statistics of the quantity of food in 414 stomachs examined. The mean total weight of food found in the stomachs of sharks caught by gill nets was significantly higher than that found for sharks caught by rod and reel (18.91 and 13.09 g respectively; z-test, P = 0.003). Similar results were obtained when food quantity was measured as a percentage of shark body weight (0.96 vs. 0.76%; z-test, P = 0.043). This result, in conjunction with the other differences between the two capture methods mentioned above, suggested that sharks caught by rod and reel may not have been representative of the entire population (see section on Discussion). Because the primary value of the stomach content data in this study will be in the estimation of food consumed by the population, the following results concerning the amount of food in the stomachs were based on sharks caught by gill nets since they were probably more representative of the entire population of young sandbar sharks in the study area. For sharks caught by gill nets, crustaceans accounted for nearly twice as much of the mean total wet weight of food in the stomachs than did fish. The mean wet weight of crustaceans in the 236 stomachs (12.37 g) was significantly higher than the mean of 6.53 g found for fish (z-test, $P < 0.001$). Similar results were obtained when food quantity was expressed as a percentage of shark body weight (0.65 vs. 0.31%; z-test, $P < 0.001$). The mean weights of the two food components in the stomachs

TABLE 3.—Number of stomachs for which the stage-of-digestion value of the first eaten food item minus the stage-of-digestion value of the last eaten food item was equal to the given difference. The data are broken down into groups based on the number of food items present in the stomachs. Stomachs that contained an item at stage 1 of digestion and an item at stage 6 of digestion are not included (see text).

No. of items in stomach	No. of stomachs with indicated difference between stage-of-digestion values of first and last food items eaten						Mean difference	SD
	Difference							
	0	1	2	3	4	N		
2	44	25	9	0	1	79	0.60	0.78
3	13	17	0	0	0	30	0.57	0.50
4	2	3	2	0	0	7	1.00	0.76
5	2	0	0	0	0	2	0	0
Overall	61	45	11	0	1	118	0.60	0.78

TABLE 4.—Summary statistics of the amount of food in the stomachs of a sample of 414 sandbar sharks. Sharks were captured with gill nets and rod and reel gear. The z-test statistic was used to test the equality of the indicated pairs of mean values.

Stomach contents	Capture method	Mean	N	SE mean	Max	Min	z-test stat.	P-value 2-tailed test
Fish (g)	Gill net	6.53	236	1.10	114.80	0	3.74	< 0.001
Crustacea (g)	Gill net	12.37	236	1.11	102.20	0		
Fish (% BW)	Gill net	0.31	236	0.04	3.93	0	4.84	< 0.001
Crustacea (% BW)	Gill net	0.65	236	0.06	5.28	0		
Total (g)	Gill net	18.91	236	1.53	135.68	0	2.95	0.003
Total (g)	Rod and reel	13.09	178	1.25	100.30	0		
Total (% BW)	Gill net	0.96	236	0.06	5.28	0	2.02	0.043
Total (% BW)	Rod and reel	0.76	178	0.07	6.92	0		

were also calculated for each of eight consecutive 3-h time intervals of the day (Fig. 2). The means ranged from 1.05 to 14.92 g for fish, from 7.51 to 19.72 g for crustaceans, and from 11.74 to 34.64 g for the total wet weight of food in the stomachs. When 95% confidence bounds were placed around the means, considerable overlap of the confidence intervals was observed (Fig. 2). However, the mean total wet weight in the stomachs of sharks captured between the time of 0130 and 0430 was considerably higher than the other means, and the confidence interval for the mean during this time period overlapped substantially with only two of the remaining seven intervals. Similar results were obtained when food quantity was expressed as a percentage of shark body weight.

During the study one stomach was examined that contained a total wet weight of 444.0 g of food (10.3% BW (body weight)). This shark was not included in the results presented above because the quantity of food in the stomach was substantially greater than for any other shark. It is mentioned here because it does indicate that the stomach capacity of this species is considerably greater than the amount of food typically found in the stomach. In an attempt to estimate maximum capacity, the stomachs of 23 sharks were removed, ligated, and filled with water to the point at which they were about to burst. This point was determined by filling several stomachs until they burst and noting the changes that occurred in the stomach wall just before the bursting point. The average maximum capacity of the stomachs was found to be 13.0% of BW (range: 8.04 to 19.8%). For sharks caught by gill nets the mean quantity of food in the stomachs (0.96% BW) was 7.4% of maximum capacity and the largest quantity of food in a stomach (5.28% BW) was 40.6% of maximum capacity.

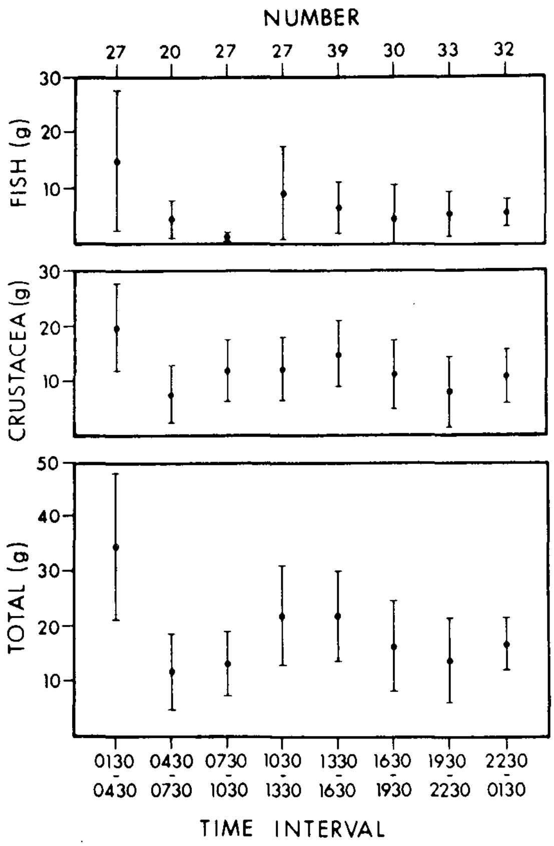

FIGURE 2.–Amount of food in the stomachs of sandbar sharks caught by gill nets during various time intervals of the day. Dots indicate mean wet weight in grams, and bars represent 2 standard errors on each side of the mean. The number of stomachs examined during each interval is given at the top of the figure.

DISCUSSION

Several investigations conducted in other areas have reported the sandbar sharks' diet to consist of small crustaceans and fish (Bigelow and Schroeder 1948; Springer 1960; Clark and von Schmidt 1965; Bass et al. 1973; Lawler 1977). With the exception of squid in several stomachs, the prey items of the sandbar sharks captured in Chincoteague Bay, VA, were also found to be small crustaceans and fish (Table 2) and agree with those reported by Medved and Marshall (1981) for this species in Chincoteague Bay. The studies above provided little specific information concerning the frequency of occurrence, size, relative amounts, or physical state of the food items. In the present study, small blue crabs that had recently molted were, by far, the predominant food item in terms of both weight and numbers. Small menhaden were also found to comprise a significant portion of the food consumed, but other species appeared to be of minor importance in the diet of the sandbar shark in the study area.

The results of this study strongly suggest that the feeding behavior of sandbar sharks in the study area was characterized by relatively short periods of feeding activity separated by substantially longer periods of time during which stomach contents were digested and no additional feeding occurred. An indication that this species may go relatively long periods of time without feeding was the high percentage (21.5%) of sharks that had a single food item in their stomach that was in a late stage of digestion (stage 5 or 6). Based on the approximate duration of each stage of digestion (12 or 15 h depending on prey type) these sharks apparently had gone at least 48 h without consuming additional food. Another 17.9% of the sharks captured had empty stomachs. None of these were found to have an everted stomach, indicating that regurgitation of food was not responsible for the high percentage of empty stomachs. Additionally, 98 sandbar sharks fed preweighed meals and released in an enclosure in the natural environment were not observed to regurgitate food when recaptured at a later time (Medved in press). Thus it appears that the sharks with empty stomachs had not consumed food for a period of time greater than the time required to evacuate the last meal (at least 72 h). Given the long duration of gastric evacuation, a shark feeding nearly continuously would have many food items at various stages of digestion in the stomach. Multiple food items were found in some stomachs, but 90.6% of the stomachs contained less than three food items. Multiple food items in a stomach were also generally in similar stages of digestion (Table 3). The sharks with a single food item in their stomach consumed that meal in a very short period of time. The mean difference between the stage-of-digestion values of the first and last prey item consumed by sharks with multiple items in their stomach was 0.60 units (Table 3). Considering that digestion was divided into six stages, the feeding duration of sharks that consumed a meal of multiple food items was also very short relative to the time required for complete gastric evacuation. Observations made during a study of gastric evacuation in the sandbar shark also suggested that feeding ceased after the consumption of a meal (Medved in press). In that study the stomachs of 98 sharks were lavaged to remove all food and a preweighed meal was then fed to each animal. The sharks were released in a large enclosure in the natural environment that contained an abundance of prey and were recaptured at various times after feeding. Of the 54 sharks sacrificed within 40 h of feeding, only 4 had consumed additional food. In contrast, of 11 sharks that had their stomachs lavaged but were not fed a meal before release all but 2 were found to have food in their stomachs when sacrificed 24 h later. The results discussed above indicate that the feeding activity of sandbar sharks in the study area was intermittent rather than continuous. Similar models have been proposed in several other feeding behavior studies on fishes. Diana (1979) proposed an intermittent feeding model for the northern pike, *Esox lucius*, and suggested that such a model was appropriate for many top carnivores. Longval et al. (1982) have shown that after captive lemon sharks, *Negaprion brevirostris*, have fed to satiation, it takes a few days for the appetite to become reestablished. Carey et al. (1982) suggested that the great white shark, *Carcharodon carcharias*, may maintain itself for more than a month on a single large meal. Holden (1966) and Jones and Geen (1977) indicated that the spiny dogfish, *Squalus acanthias*, consumes a meal and then ceases to feed until digestion is complete. Observations made by Sano (1959) suggest that this may be typical of other shark species as well.

The differences observed between the stomach contents of sharks caught by the two capture methods are consistent with the model of feeding postulated above. The majority of sharks caught by rod and reel had stomachs that were empty or that contained food items in the first or last stage of digestion (Fig. 1). The sharks with empty stomachs had apparently not consumed food for a long period of time. Those with a food item in the last stage of digestion had relatively empty stomachs and had also gone a considerable time without feeding. Finally, the sharks with a food item in the first stage of digestion had eaten within several hours of being caught. Assuming that these sharks were actively feeding since they were inclined to consume the squid used as bait, it appears that the sharks in a "feeding mode" were those with relatively empty stomachs that had not fed for some time and those that had just eaten but were inclined to consume additional food. The stomachs of sharks caught by gill nets were empty or contained a single food item or multiple food items in similar stages of digestion suggesting, as indicated above, that feeding was intermittent. However, the stage-of-digestion values of the food items in the stomachs were spread more evenly over the digestion scale than for sharks caught by rod and reel, indicating that these sharks were in various stages of the feeding cycle (Fig. 1). The higher percentage of empty stomachs and lower mean stomach content weight found for sharks caught by rod and reel than for those caught by gill nets also suggested that sharks caught by rod and reel were those in a "feeding mode" and that sharks caught by gill nets were probably more representative of the entire population.

For sharks caught by gill nets the mean quantity of food in the stomach was 0.96% of BW and the maximum quantity was 5.28% of BW (Table 4). Considering that the mean stomach content was based on sharks containing food in various stages of digestion, it probably is a significant underestimation of the average meal size of sharks in the area. In contrast, the maximum quantity of food found in a stomach is undoubtedly an overestimate and the average meal size should be considered to have been somewhere between the two values. It would then appear that the average meal size of the sharks captured was substantially less than the estimated stomach capacity (13.0% BW). The mean stomach content weights found for various time intervals of the day in this study suggested that sandbar sharks contained more food in their stomachs between 0130 and 0430 than during other times of the day (Fig. 2). The evidence was not overwhelming but these results do agree with a study by Medved and Marshall (1981), indicating that night hours may be a period of increased feeding activity for the sandbar shark.

Although this paper has provided a quantitative description of the stomach contents of the sandbar shark, data concerning stomach contents alone are not sufficient for estimating food consumption. As pointed out by numerous researchers, the amount of food in a fish's stomach is a function of both the rate of ingestion and the rate of gastric evacuation (Eggers 1977; Thorpe 1977; Elliott and Persson 1978; Jobling 1981). However, when combined with detailed information concerning gastric evacuation, the results of this study will provide the basis for the construction of an appropriate model of food consumption for the sandbar shark.

ACKNOWLEDGMENTS

We would like to acknowledge the management and staff of the Wallops Island Marine Science Center for their cooperation. This study was supported by the Narragansett Laboratory of the National Marine Fisheries Service, the Montauk (New York) Captains' Association, the National Wildlife Federation, and the Society of the Sigma Xi. It constitutes a portion of a thesis submitted by the first author in partial fulfillment of the requirements for the degree of Ph.D. in oceanography at the Graduate School of Oceanography of the University of Rhode Island. Special thanks go to Ann Durbin and Howard Winn for reviewing the manuscript and to Jim Donovan, Jeremy Donovan, Brad Thompson, Herb Morgan, and Todd Stephens for assisting with the field work.

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