

# Ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in lower Chesapeake Bay and Virginia (USA) coastal waters

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**Abstract** This study describes the diet of the sandbar shark, *Carcharhinus plumbeus*, highlighting differences in diet within various regions of the Virginia (USA) nursery area, as well as ontogenetic changes in diet. Stomach samples were obtained in 2001 and 2002 from 232 sharks caught by gillnets or longlines. Historical data from the Virginia Institute of Marine Science (VIMS) Shark Ecology Program were also analyzed. Ontogenetic changes in diet were evident, with crustacean prey decreasing in frequency with increasing shark size, and elasmobranch prey importance increasing with increasing shark size. Whereas previous research in Chincoteague Bay, VA showed the blue crab, *Callinectes sapidus*, was the dominant crustacean in sandbar shark diet, the mantis shrimp, *Squilla empusa*, dominated the crustacean portion of the diet in this study. Differences in diet of sharks were observed among locations within the study area. Small juveniles ( $\leq 80$  cm precaudal length) in the lower Chesapeake Bay ate more fishes, whereas Eastern Shore juveniles ate more crustaceans. Crustacean prey items varied among locations along the Eastern Shore, with more portunid crabs

consumed in waters near Wachapreague and more mantis shrimp consumed near Sand Shoal Inlet. Our study showed that *Carcharhinus plumbeus* is a generalist predator and is thus unlikely to strongly impact the population of any particular prey species, and in turn is not likely to be strongly affected by fluctuations in abundance of a single prey species.

**Keywords** Carcharhinidae · Feeding habits · Nursery grounds · Correspondence analysis

## Introduction

As the most abundant large coastal shark in the temperate and subtropical waters of the northwest Atlantic Ocean, *Carcharhinus plumbeus*, the sandbar shark, is a top predator linked with many species in the food web. In the northwest Atlantic, the sandbar shark reaches maximum total lengths (TLs) of 234 cm (females) and 226 cm (males) and inhabits a range from southern New England to southern Florida and the Gulf of Mexico (Bigelow and Schroeder 1948; Springer 1960; Compagno 1984).

Within this range, the sandbar shark undertakes seasonal migrations to and from summer feeding and nursery grounds (Springer 1960; Musick and Colvocoressess 1986). Chesapeake Bay is considered one of the primary nursery

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grounds for this population (Musick and Colvocoressess 1986). In late May to early June, adult females (greater than 180 cm TL) migrate north and enter Chesapeake Bay (hereafter referred to as the 'Bay') and inlets as well as bays along Virginia's Eastern Shore (among other bays and estuaries north to New Jersey) to pup (Springer 1960; Musick and Colvocoressess 1986). Between June and August, females give birth to 6–13 pups ranging between 54 and 68 cm TL (45 and 50 cm precaudal length or PCL) (Springer 1960; Compagno 1984). After pupping, postpartum females migrate offshore to depths of 21–40 m (Musick and Colvocoressess 1986). All ages of *C. plumbeus* leave the Bay in September and October as temperatures fall and photoperiod shortens (Musick et al. 1985; Musick and Colvocoressess 1986; Grubbs and Musick 2005). Juveniles of both sexes return annually to summer nursery grounds until at least 4 years of age (Grubbs et al. 2005).

While in Chesapeake Bay and adjacent waters, *C. plumbeus* fits into an extremely complex food web composed of many seasonal residents. During the course of a year, the Chesapeake Bay ecosystem supports approximately 3000 animal and plant species (Murdy et al. 1997). The Bay is an estuarine system with complex physical and chemical dynamics (Murdy et al. 1997) and its food web varies spatially as well as temporally. The large activity space (110.26 km<sup>2</sup>; SD = 77.60, Grubbs 2001) of juvenile sandbar sharks (< 62 cm PCL) suggests that sandbar shark predation may impact a number of species in various areas of the lower Bay. Previous diet studies and recent tracking studies suggest that sandbar sharks forage in the water column as well as on and near the benthos, preying on teleost fishes, mollusks, crustaceans, and other elasmobranchs (Bigelow and Schroeder 1948; Springer 1960; Clark and von Schmidt 1965; Grubbs 2001). Understanding linkages between predators and prey is an important component of ecosystem-based fishery management (NMFS 1999<sup>1</sup>), enabling researchers to model population trends of target species in Chesapeake Bay and elsewhere.

Trophic interactions may change with time and may be affected by fishing pressure (Alonso et al. 2002), making periodic diet studies necessary for accurate monitoring of food webs. Medved et al. (1985) found the blue crab, *Callinectes sapidus*, to be an important part of sandbar shark diet in Chincoteague Bay, Virginia. The blue crab population has declined since these data were collected in 1983, with spawning stock and recruitment declines, as well as a population reduction (~70%) occurring from 1991 to 2000 (Lipcius and Stockhausen 2002). These population changes may be reflected in the current diet of the sandbar shark.

Sandbar shark diet has been previously studied in varying detail in Virginia (Medved et al. 1985), the northwest Atlantic (Stillwell and Kohler 1993), Hawaii (McElroy et al. 2006), Australia (Stevens and McLoughlin 1991), and South Africa (Cliff et al. 1988). These studies taken collectively indicate regional differences in prey (McElroy et al. 2006). Teleosts are important prey items in all locations, appearing in 37–88% of stomachs examined. Occurrence of cephalopod prey varies between 3.0% in the northwest Atlantic (Stillwell and Kohler 1993) and 56.3% in South Africa (Cliff et al. 1988). Elasmobranchs appeared less frequently in Hawaiian sandbar shark stomachs (2.3%, McElroy et al. 2006) than in northwest Atlantic (16.0%, Stillwell and Kohler 1993) and South African (17.4%, Cliff et al. 1988) sharks. (Elasmobranchs were not a component of the diet of the 181 Northern Australian sharks examined by Stevens and McLoughlin (1991).)

Diet may also differ between age classes of *C. plumbeus* in Virginia waters, as it does in many sharks (Wetherbee and Cortés 2004). McElroy et al. (2006) noted increased cephalopod consumption with increasing shark size as well as more frequent consumption of reef-associated teleosts and larger crustaceans. The only quantitative data on stomach contents of *C. plumbeus* in the northwest Atlantic is based on work by Medved et al. (1985) and Stillwell and Kohler (1993), which, when examined together, suggest ontogenetic changes in the diet. However, the geographic range of sampling by Stillwell and Kohler (1993) was very broad (Georges Bank to

<sup>1</sup> NMFS (1999) Ecosystem-based fishery management, 54 pp.

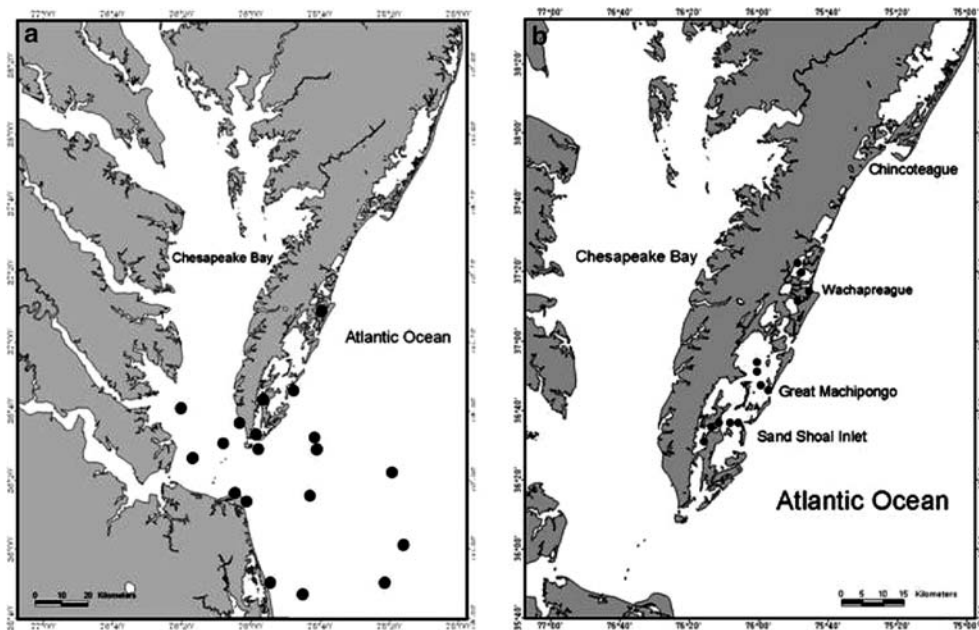
Cape Hatteras) while that of Medved et al. (1985) was very restricted (Chincoteague Bay, Virginia). Additionally, intermediate changes in diet, which cannot be revealed by comparing Medved et al.'s (1985) neonate and juvenile diet data to Stillwell and Kohler's (1993) juvenile and adult samples, may exist. To address these questions, this study proposed to revisit sandbar shark diet with the following objectives: (1) describe the current diet of the sandbar shark in Chesapeake Bay and adjacent waters and (2) describe differences in diet among age or size classes of sandbar sharks.

**Materials and methods**

Data for this study were obtained from two sources: (1) archival (1974–1998) diet data from the Virginia Institute of Marine Science Shark Ecology Program database; and (2) samples collected from sharks caught with gillnet and longline in 2001 and 2002. Archival data were based on records of stomach contents from sandbar sharks caught at fixed and ancillary stations (Fig. 1a) on longline cruises from 1974 through 1998. A listing of prey items found in stomachs, as well as shark length and sex data were obtained

from these records. (Standardized data on prey item weight were not available for this data set.)

Current samples were obtained from May through October using longline (2001 and 2002) and gillnet (2002) gears. Longline samples were obtained at fixed and ancillary stations in Chesapeake Bay and adjacent waters (Fig. 1a); gillnet samples were obtained from four stations in each of three regions of Virginia's Eastern Shore (Wachapreague, Great Machipongo Channel, and Sand Shoal Inlet) (Fig. 1b). Animals were sacrificed and the stomachs were preserved in 10% formalin for at least 24 h before analysis in the laboratory (Creaser and Perkins 1994). Gillnet samples were stored on ice before being put in 10% formalin. Only the stomach portion of the digestive tract was excised due to the difficulty in identifying items further advanced in the digestion process (Berg 1979). Empty stomachs were discarded. A portion of sharks from the longline catch were tagged and released, so the calculation of percentage of empty stomachs was not based on all sharks in the catch. Total and precaudal lengths were measured to the nearest centimeter and recorded for all sharks sampled. All lengths referred to hereafter are precaudal (PCL).



**Fig. 1** Map of stations sampled (a) using longline gear (2001–2002 and archival data) and (b) using gillnet gear (2002)

Items in each stomach were sorted, identified to the lowest taxonomic level possible, and counted. Bait or secondary baits—animals eaten while hooked on the longline—were not counted or weighed. If bait or secondary bait was the only item in the stomach, the stomach was considered empty. If prey items were not whole or nearly whole, numbers were based on countable parts, such as claws and legs for crustaceans, otoliths for fishes and beaks for cephalopods. After sorting and identification, prey items were rinsed with fresh water and blotted dry with a paper towel, and wet and dry weights were recorded ( $\pm 0.1$  g). Unidentifiable matter that could not be assigned to a prey taxon was labeled as unidentified and weighed separately.

To assess the adequacy of the number of samples gathered for each subgroup (size class), cumulative prey curves were constructed from the 2001–2002 data, as well as the combined data set (2001–2002 and archival). For each curve, the order of stomachs was randomized 10 times, and the mean number of unique prey items was plotted to minimize bias resulting from sampling order (Ferry and Caillet 1996; Gelsleichter et al. 1999). Cumulative prey curves were generated using the lowest taxa identified as well as prey families (Ferry et al. 1997).

Common indices were used to describe the diet of the sandbar shark for the data obtained from the 2001–2002 samples and for subsets of that data set. Following Hyslop (1980), percent frequency of occurrence (%*F*), percent number (%*N*), and percent wet weight (%*W*) indices were calculated for broad and specific prey categories. Index of relative importance (IRI) was also calculated (Pinkas et al. 1971):  $IRI = (\%N + \%W) \times \%F$ .

Percent IRI was also calculated for both for both broad (e.g., teleosts, crustaceans, and elasmobranchs) and specific taxonomic categories of prey groups following Cortés (1997):  $\%IRI_i = 100 IRI_i / \sum IRI_i$ .

Only one index, %*F*, was calculated for the historical data because of the paucity of weight and count information originally recorded. Additionally, prey items in the archival data set were examined onboard and did not undergo preservation in formalin. Because formalin tends to increase prey item weight (DiStefano et al.

1994) and because the weights in the data sheets were measured by different people using different equipment, the weights recorded in the data sheets were not compared to those obtained from the 2001–2002 samples.

The Simplified Morisita index of overlap ( $C_H$ ), which is commonly used in carcharhinid diet studies (Lowe et al. 1996; Wetherbee et al. 1996; Wetherbee et al. 1997; Simpfindorder et al. 2001; McElroy et al. 2006), was used to compare the similarity of diet between male and female sandbar sharks (combined data set) as well as three size classes of sandbar sharks in the 2001–2002 data set. For the size class comparison, sharks were grouped arbitrarily based on pre-caudal length (PCLs). These groups were designated classes I (<61 cm), II (61–90 cm), III (>90 cm). Prey items were grouped into their respective families.  $C_H$  was calculated following Krebs (1989),

$$C_H = 2 \left( \sum p_{ij} p_{ik} \right) / \left( \sum p^2_{ij} + \sum p^2_{ik} \right)$$

where  $p_{ij}$  is the proportion of prey category *i* used by size class (or sex) *j*, and  $p_{ik}$  is the proportion of prey category *i* used by size class (or sex) *k*. Langton's scale was used to determine degree of overlap: low (0.29), medium (0.30–0.60) and high (>0.60) (Langton 1982).

Prey diversity (*H*) was calculated using the Shannon–Wiener method. Percent frequency values from the entire data set were used in the following equation, where  $P_i$  is the contribution of prey category *i* to the diet (Zar 1996):  $H = -\sum (P_i \log[P_i])$ .

Simple correspondence analysis (CA) was used to detect general trends in the diet of small juvenile sandbar sharks ( $\leq 80$  cm PCL) caught at different locations (Davis 1986; Graham and Vrijenhoek 1988). Using Minitab software (Minitab, Inc. 1998), CA was performed to examine variation in %IRI data among Bay, Eastern Shore and Coastal locations. Prey items were grouped by families. Intra-regional variation in diet was also examined by comparing %*F* of crustaceans in stomachs of juvenile sandbar sharks ( $\leq 80$  cm) from three regions of the Eastern Shore (Wachapreague, Great Machipongo, and

Sand Shoal Inlet) using CA. Crustaceans were pooled into four categories—mantis shrimp, *Squilla empusa*, portunid crab (blue crabs, lady crabs, and unidentified portunids), other (e.g., penaeid shrimp, mud shrimp, and spider crabs), and unidentified—so that fewer than 20% of the cells had values less than five (Crow 1979; Cortés 1997). In all cases, integer values of percentages were used.

## Results

Stomach samples from 232 sandbar sharks measuring 40–150 cm PCL (mean =  $69.3 \pm 18.4$  cm PCL) were collected from 2001 to 2002. Eighty-three of these samples were obtained with gillnets during 2002; the remaining 139 stomachs were obtained from animals caught on longline gear. Of all stomachs examined from gillnet samples, 19.2% were empty, compared to 34.1% of longline-obtained samples. The archival data included prey records for 376 sandbar shark stomachs, ranging in size from 40 to 165 cm PCL (mean =  $82.8 \pm 27.3$  cm). In the entire data set, the female-to-male ratio increased drastically with increasing size. The smallest size class (<61 cm) consisted of 67 females and 65 males, but the largest size class (>90 cm) had 154 females and 13 males. The relationship between PCL and total length (TL) for sandbar sharks sampled in this study was:  $TL = 1.3351 * PCL + 0.8777$ , ( $R^2 = 0.993$ ,  $n = 598$ ).

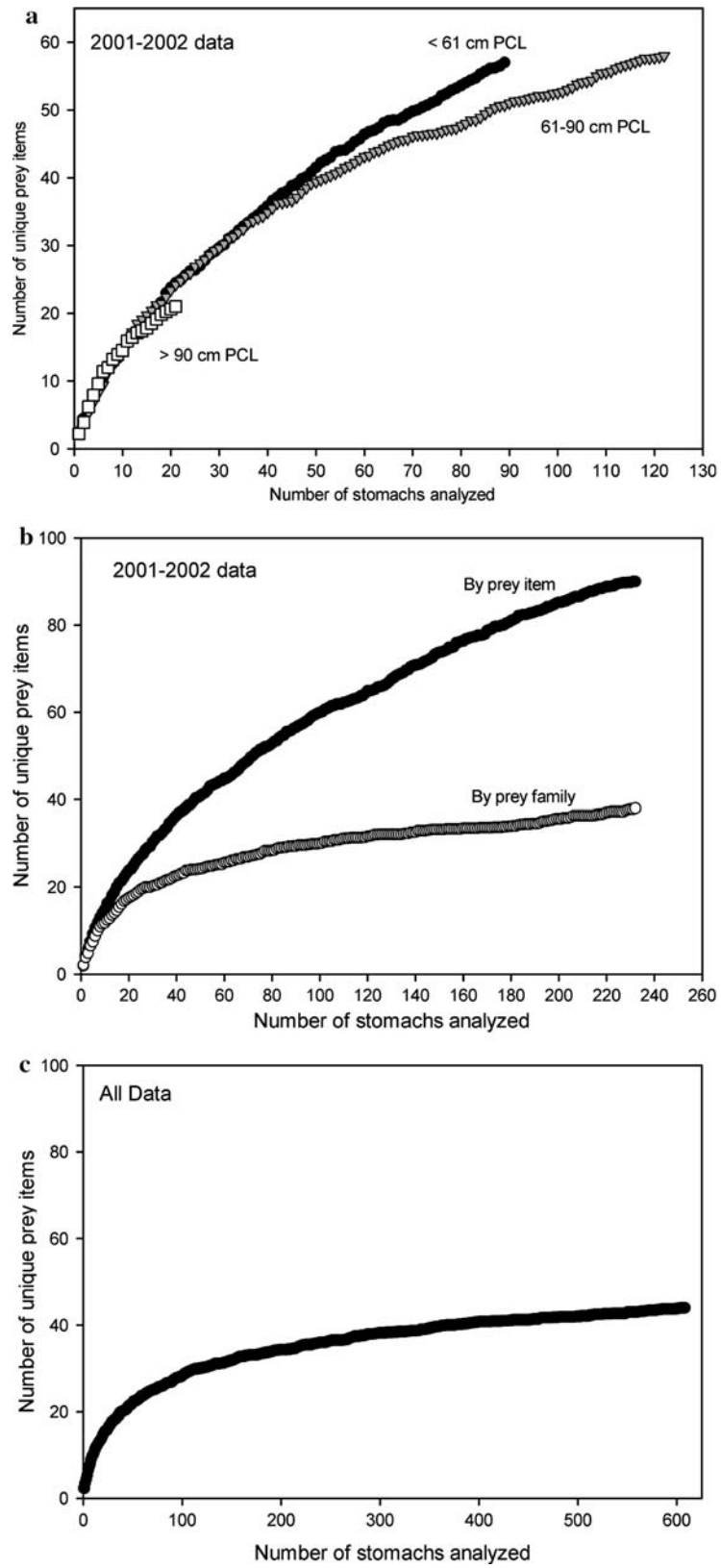
The 608 sandbar shark stomachs included in this study contained prey items from 28 families of teleosts, 12 families of crustaceans, 6 families of elasmobranchs, and 11 families of molluscs (Appendices 1–3). Teleosts consumed were primarily demersal or epibenthic species (sciaenids and flatfish), but more “pelagic” species were also present (e.g. clupeids, engraulids, bluefish). Cephalopods, gastropods, bivalves, bryozoans, hydrozoans, plants, trash, and unidentified biological matter were also found in stomach samples. In total, approximately 65 species were identified. (This number may be an underestimate if unidentified prey items represent previously uncounted species). Only two instances of cannibalism were recorded: a chunk of sandbar shark

was found in the stomach of a 59 cm PCL female, and a whole sandbar shark pup was found in the stomach of a pregnant female (145 cm PCL). These samples were caught on a longline, so it is possible that the sandbar sharks were consumed as secondary baits. Prey items were consumed in chunks and whole. A few prey items consumed whole retained bite marks halfway along the body. In general, the carapaces of crustaceans found in *C. plumbeus* stomachs, particularly those of crabs, were soft in texture.

The Simplified Morisita index of overlap for males and females was 0.99 indicating a high degree of diet overlap. Males and females appeared to have similar diets with %IRI values of 58.1 and 62.8, respectively, for teleosts. Relative importance of crustaceans was also similar at 37.8% for males and 32.6% for females.

Lack of a distinct asymptote for cumulative prey curves calculated on the basis of prey items (to species) for each size class (Fig. 2a) indicates that the diet for size class III has not been completely characterized. Size classes I and II decrease in slope but do not reach asymptotes. Cumulative prey curves for all 2001–2002 data by prey item do not approach asymptote; however, the curve analyzed by prey family has a decreasing slope and is closer to asymptotic (Fig. 2b). The curve for the combined data set calculated using prey family appears to reach asymptote (Fig. 2c).

Crustaceans were the most important prey items for the smallest size class of sandbar sharks (<61 cm) both as a category and as specific prey items (Tables 1 and 2). Crustaceans were found in 70.5% of all sharks examined in the combined 2001–2002 and archival data sets (Table 2). Mantis shrimp, *Squilla empusa*, (43.0%) and blue crab, *Callinectes sapidus*, (36.5%) had the greatest %IRI values (Table 1), followed by flat-browed mud shrimp, *Upogebia affinis* (4.6%) and lady crab, *Ovalipes ocellatus* (0.8%). Teleosts were of secondary importance in the diet (30.6% IRI, Table 2), particularly unidentified teleosts (5.5% IRI) and hogchoker, *Trinectes maculatus* (2.9% IRI) (Table 1). Unidentified teleosts (26.5% *F*) appeared more frequently in stomachs examined in the combined data set (2001–2002 and archival) than blue crabs (20.5% *F*) (Table 1). Unidentified teleosts were recorded more frequently in the



◀ **Fig. 2** Cumulative prey curves for: (a) 2001–2002 data by size class (b) 2001–2002 data calculated using lowest taxon identified and using prey family and (c) all data calculated using prey family. Mean values of 10 randomizations are presented

archival stomach data than the 2001–2002 data (Table 1).

The diet of sharks in size class II (61–90 cm) contained a greater proportion of teleosts. Unidentified teleosts were found in 33.7% of all stomachs examined and 11.5% of 2001–2002 stomachs examined (Table 1). Teleosts appeared in more than 60% of sharks in size class II from both 2001–2002 and the combined data sets, whereas crustaceans occurred more frequently in

the 2001–2002 data set (65.6% *F*) than the combined data set (39.5% *F*) (Table 2). Mantis shrimp and Atlantic croaker, *Micropogonias undulatus*, had the greatest %IRI values at 58.4 and 16.0, respectively (Table 1).

Sharks in size class III (>90 cm) in the 2001–2002 data subset contained predominantly teleosts (44.8% IRI, ~60% *F* and *F*<sub>all</sub>), as well as a substantial proportion of elasmobranchs (29.9% IRI, 29.3% *F*<sub>all</sub>) (Table 2). Teleost prey consisted primarily of Atlantic croaker and round herring, *Etrumeus teres*, and unidentified teleosts (Table 1). Unidentified teleosts, which were found in only 2 of the 21 2001–2002 samples, were the most frequently occurring prey item for size class III sharks in the combined data set (Table 1).

**Table 1** Selected (greatest %IRI) frequency of occurrence (*F*), number (*N*), wet weight in grams (*W*) and Index of Relative Importance (IRI) values and

percentages by size class for 2001–2002 data (*n* = 89, 122, and 21 for Classes I, II and III, respectively)

Size class	Prey item	All data		2001–2002 data							
		<i>F</i> <sub>all</sub>	% <i>F</i> <sub>all</sub>	<i>F</i>	% <i>F</i>	<i>N</i>	% <i>N</i>	<i>W</i> (g)	% <i>W</i>	IRI	%IRI
<61 cm PCL	<i>Squilla empusa</i>	39	29.5	33	37.1	41	20.8	222.4	18.6	1460.2	43.0
	<i>Callinectes sapidus</i>	26	20.5	24	27.0	29	14.7	375	31.3	1241.3	36.5
	Unidentified teleost	35	26.5	15	16.9	16	8.1	36.1	3.0	187.7	5.5
	<i>Upogebia affinis</i>	14	10.6	14	15.7	15	7.6	26.8	2.2	155.0	4.6
	<i>Trinectes maculatus</i>	7	5.3	7	7.9	8	4.1	103.4	8.6	99.8	2.9
	Unidentified biological	13	9.9	12	13.5	3	1.5	25.4	2.1	49.1	1.4
	<i>Ovalipes ocellatus</i>	7	5.3	5	5.6	5	2.5	28.7	2.4	27.7	0.8
61–90 cm PCL	<i>Squilla empusa</i>	60	19.4	50	41.0	77	23.7	705.6	18.0	1707.6	58.4
	<i>Micropogonias undulatus</i>	25	8.1	21	17.2	30	9.2	703.3	17.9	467.3	16.0
	Unidentified teleost	104	33.7	14	11.5	16	4.9	604.3	15.4	233.1	8.0
	Unidentified biological	26	8.4	20	16.4	20	6.2	20.6	0.5	109.5	3.7
	<i>Cynoscion regalis</i>	9	2.9	8	6.6	15	4.6	324.1	8.3	84.4	2.9
	<i>Raja eglanteria</i>	8	2.6	5	4.1	5	1.5	509.5	13.0	59.5	2.0
	<i>Trinectes maculatus</i>	27	8.7	9	7.4	11	3.4	103.5	2.6	44.4	1.5
	<i>Ovalipes ocellatus</i>	20	6.5	8	6.6	11	3.4	23.3	0.6	26.1	0.9
	<i>Callinectes sapidus</i>	16	5.2	8	6.6	8	2.5	23.6	0.6	20.1	0.7
>90 cm PCL	<i>Micropogonias undulatus</i>	7	4.2	6	28.6	8	14.0	664.8	36.2	1435.7	38.4
	Unidentified biological	10	6.0	9	42.9	9	15.8	24.2	1.3	733.2	19.6
	<i>Raja eglanteria</i>	9	5.4	3	14.3	3	5.3	294.3	16.0	304.2	8.1
	<i>Ovalipes ocellatus</i>	10	6.0	4	19.1	7	12.3	50.5	2.8	286.3	7.7
	Unidentified elasmobranch	3	1.8	2	9.5	2	3.5	473.8	25.8	279.2	7.5
	<i>Squilla empusa</i>	9	5.4	4	19.1	5	8.8	48.3	2.6	217.2	5.8
	<i>Raja</i> sp. egg case	5	3.0	3	14.3	4	7.0	21.9	1.2	117.3	3.1
	<i>Etrumeus teres</i>	2	1.2	2	9.5	2	3.5	94.8	5.2	82.6	2.2
	<i>Raja</i> sp.	19	11.4	2	9.5	2	3.5	68.4	3.7	68.9	1.8
	<i>Pagurus pollicaris</i>	2	1.2	2	9.5	2	3.5	39.5	2.2	53.9	1.4
	Unidentified teleost	52	31.1	2	9.5	2	3.5	0.4	0.0	33.6	0.9
	Unidentified cephalopod	10	6.0	–	–	–	–	–	–	–	–
	<i>Loligo pealei</i>	9	5.4	–	–	–	–	–	–	–	–

Frequency of occurrence (*F*<sub>all</sub>) values for all data (2001–2002 and archival) are also included (*n* = 132, 309, and 167 for Classes I, II and III, respectively). Dashes indicate prey items not found in 2001–2002 samples

**Table 2** Frequency of occurrence ( $F$ ), number ( $N$ ), weight ( $W$ ) and index of relative importance (IRI) values for prey categories by size class for 2001–2002 data ( $n = 89, 122,$  and  $21$  for Classes I, II and III, respectively)

	All data		2001–2002 data							
	$F_{\text{all}}$	$\%F_{\text{all}}$	$F$	$\%F$	$N$	$\%N$	$W$ (g)	$\%W$	IRI	$\%IRI$
<i>Size class I (&lt;61 cm PCL)</i>										
Teleost	78	59.1	52	58.4	71	35.5	428.0	35.6	4157.0	30.6
Crustacean	93	70.5	72	80.9	108	54.0	713.2	59.4	9174.2	67.6
Elasmobranch	3	2.3	0	0.0	0	0.0	0.0	0.0	0.0	0.0
Cephalopod	6	4.5	5	5.6	5	2.5	23.7	2.0	25.1	0.2
Unknown	13	9.8	12	13.5	12	6.0	25.4	2.1	109.4	0.8
Other	13	9.8	11	12.4	13	6.5	10.3	0.9	90.9	0.7
<i>Size class II (61–90 cm PCL)</i>										
Teleost	213	68.9	75	61.5	128	39.3	2231.3	56.8	5907.9	56.6
Crustacean	122	39.5	80	65.6	130	39.9	839.6	21.4	4017.3	38.5
Elasmobranch	36	11.7	15	12.3	16	4.9	760.4	19.4	298.5	2.9
Cephalopod	22	7.1	13	10.7	23	7.1	58.3	1.5	91.0	0.9
Unknown	26	8.4	20	16.4	20	6.1	20.6	0.5	109.2	1.0
Other	15	4.9	7	5.7	9	2.8	15.5	0.4	18.1	0.2
<i>Size class III (&gt;90 cm PCL)</i>										
Teleost	99	59.3	13	61.9	19	33.3	782.8	42.6	4703.2	44.8
Crustacean	35	21.0	11	52.4	16	28.1	143.6	7.8	1880.1	17.9
Elasmobranch	49	29.3	10	47.6	11	19.3	858.4	46.8	3145.6	29.9
Cephalopod	19	11.4	0	0.0	0	0.0	0.0	0.0	0.0	0.0
Unknown	10	6.0	9	42.9	9	15.8	24.2	1.3	733.2	7.0
Other	13	7.8	2	9.5	2	3.5	26.8	1.5	47.3	0.5

Frequency of occurrence ( $F_{\text{all}}$ ) values for all data (2001–2002 and archival) are also included ( $n = 132, 309,$  and  $167$  for Classes I, II and III, respectively)

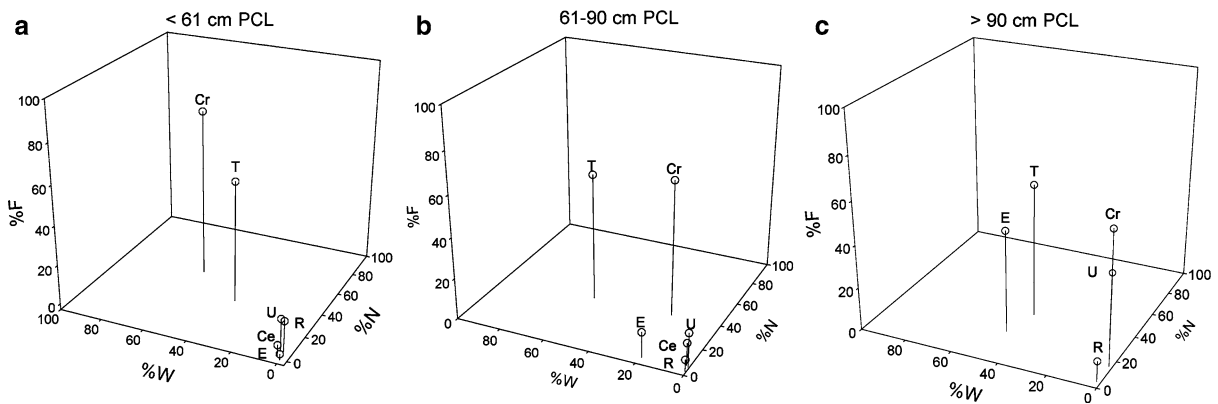
Elasmobranchs, specifically *Raja* spp. and their egg cases and unidentified elasmobranchs, were more important by weight than both teleosts and crustaceans (Table 2). Lady crab, mantis shrimp and flat-clawed hermit crabs, *Pagurus pollicaris*, were the most frequently occurring and most important (IRI) crustaceans (Table 1). Cephalopods were found in 11.4% of stomachs in this size class, but were only found in the archival samples.

Prey categories consumed changed with increasing shark size. Crustaceans decreased in importance and frequency, while elasmobranchs increased in importance and frequency. Teleosts were important to all size classes. These trends were noted in both 2001–2002 (Fig. 3) and combined (Table 2) data sets. An increased frequency in pelagic teleost prey as sharks increased in size was indicated by the overall data set (Table 3). Consistent trends in other families/groups of teleost prey were not seen as shark size increased (Table 3). Presence of cephalopods in the diet increased with increasing shark size though none occurred in class II sharks in the 2001–2002 data

set (Table 2). There was little overlap between size classes I and III ( $C_H = 0.19$ ) and moderate overlap between classes I and II (0.59) and II and III (0.48). Prey diversity was similar among size classes but appeared to decrease slightly with increasing shark size: class I (1.21), class II (1.10), and class III (1.09).

Correspondence analysis for juveniles of  $\leq 80$  cm PCL showed clear groupings of crustaceans with Eastern Shore sites, elasmobranchs with Coastal sites, and teleosts with Bay sites. Eastern Shore-caught sandbar sharks were closely associated with portunid crabs, as well flat-browed mud shrimp (Upogebiidae). Mantis shrimp (Squillaidae) fell between Bay and Eastern Shore designations, but was more closely associated with the Eastern Shore. Bay stomach samples were allied with fishes of the families Triglididae (sea robins) and Achiridae (hogchokers). Sciaenids and loligonids fell between Bay and Coastal stations. Clupeids and engraulids were found associated with coastal samples, as were crustaceans including hermit crabs (Paguridae), penaeid





**Fig. 3** Prey categories—Cephalopod (Ce), Crustacean (Cr), Elasmobranch (E), Other (R), Teleost (T) and Unknown (U)—and their index values of Number (%N), weight (%W) and frequency of occurrence (%F) for three

size classes of sandbar shark from 2001–2002 samples: **(a)** < 61 cm PCL ( $n = 89$ ); **(b)** 61–90 cm PCL ( $n = 122$ ); **(c)** > 90 cm PCL ( $n = 21$ )

**Table 3** Percent frequency of occurrence (%F), number (%N), weight (%W) and index of relative importance (%IRI) values for prey families/categories by size class for 2001–2002 data ( $n = 89, 122,$  and  $21$  for Classes I, II and III, respectively)

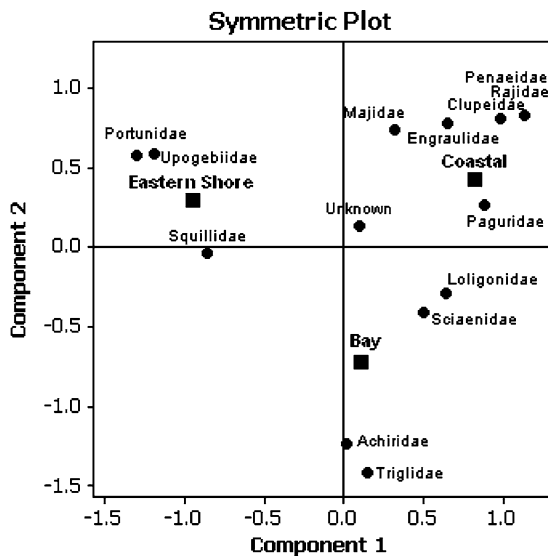
Prey group	Class I (<61 cm PCL)					Class II (61–90 cm PCL)					Class III (>90 cm PCL)				
	%F <sub>all</sub>	%F	%N	%W	%IRI	%F <sub>all</sub>	%F	%N	%W	%IRI	%F <sub>all</sub>	%F	%N	%W	%IRI
<i>Crustaceans</i>															
Portunidae	26.52	34.83	16.90	34.14	39.26	11.97	13.93	6.13	1.22	2.45	9.58	23.81	14.04	3.01	6.70
Other crabs	8.33	8.99	3.76	1.73	1.09	3.88	5.74	2.15	0.61	0.38	4.79	4.76	1.75	0.03	0.14
Shrimp/hermit crabs	17.42	21.35	10.33	3.47	6.50	8.09	14.75	6.44	1.42	2.77	1.80	9.52	3.51	2.15	0.89
Squillidae	30.30	37.08	19.25	18.52	30.93	19.42	40.98	23.62	17.97	40.76	5.39	19.05	8.77	2.63	3.59
Unid. Crustacean	8.33	5.62	2.35	1.54	0.48	3.24	4.10	1.53	0.16	0.17	1.20	0.00	0.00	0.00	0.00
<i>Teleosts</i>															
Clupeidae	3.79	3.37	1.88	1.36	0.24	5.18	4.10	1.84	6.31	0.80	4.79	19.05	7.02	5.57	3.96
Engraulidae	4.55	6.74	4.23	2.08	0.94	5.18	9.84	4.91	0.45	1.26	1.20	4.76	1.75	0.02	0.14
Pelagic	0.76	1.12	0.47	1.64	0.05	1.29	1.64	0.61	1.92	0.10	4.79	0.00	0.00	0.00	0.00
Sciaenidae	9.85	13.48	5.63	6.71	3.67	16.50	27.87	15.34	26.67	28.00	6.59	33.33	15.79	36.21	28.63
Flatfish	10.61	14.61	7.98	11.83	6.39	13.92	15.57	7.67	3.71	4.24	3.59	0.00	0.00	0.00	0.00
Other Epibenthic	6.06	7.87	3.76	4.16	1.37	8.09	8.20	3.07	2.21	1.03	14.97	9.52	5.26	0.82	0.96
Shallow/marsh	3.79	4.49	1.88	4.87	0.67	1.29	1.64	0.61	0.19	0.03	0.00	0.00	0.00	0.00	0.00
Unid. teleost	26.52	15.73	7.51	3.01	3.65	33.66	11.48	5.21	15.39	5.66	31.14	9.52	3.51	0.02	0.90
Elasmobranchs	2.27	0.00	0.00	0.00	0.00	11.65	12.30	4.91	19.37	7.14	29.34	38.10	19.30	46.76	41.56
<i>Other</i>															
Cephalopod	4.55	5.62	2.35	1.97	0.54	7.12	10.66	7.06	1.49	2.18	11.38	0.00	0.00	0.00	0.00
Incidental	6.06	12.36	6.10	0.86	1.90	3.56	5.74	2.76	0.39	0.43	2.40	9.52	3.51	1.46	0.78
Unid. Biological	9.85	13.48	5.63	2.12	2.31	8.41	16.39	6.13	0.52	2.61	5.99	42.86	15.79	1.32	12.11

Frequency of occurrence for all data (2001–2002 and archival, %F<sub>all</sub>) are also included ( $n = 132, 309,$  and  $167$  for Classes I, II and III, respectively)

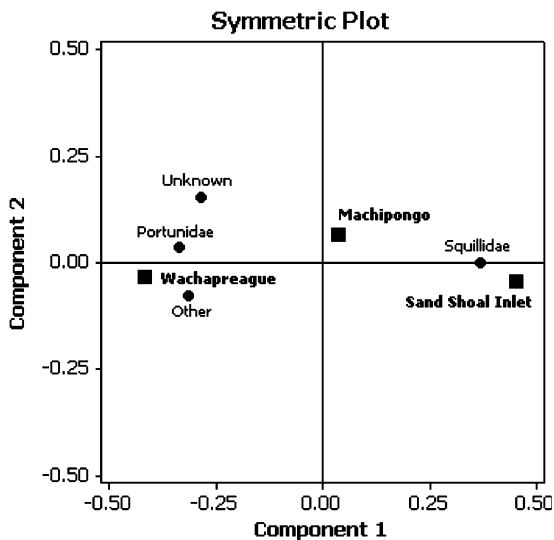
shrimps, and spider crabs (Majidae). Rajids in the diet were associated with coastal samples. Unidentified diet items were common to all three station types (Fig. 4). The first axis explained 67% of the variation in the diet and the second axis accounted for 32%.

Further examination of Eastern Shore juvenile diet through CA showed clear variation in

crustacean consumption by region (98% explained by axis 1). Portunid crabs occurred more frequently in the diet of Wachapreague small juveniles, and mantis shrimp occurred more frequently in the diet of Sand Shoal Inlet sharks. Machipongo, the central region, had sharks with intermediate frequencies of portunid crab and mantis shrimp (Fig. 5).



**Fig. 4** Biplot of station type (Coastal, Eastern Shore and Bay) and prey families using principal components (PCs) for component 1 and component 2 of a correspondence analysis using %IRI data (2001–2002 data) from sandbar sharks of PCL  $\leq 80$  cm



**Fig. 5** Biplot of Eastern Shore regions—Wachapreague, Machipongo and Sand Shoal Inlet—and crustacean type (Squillidae, Portunidae, unknown and other) principal components (PCs) for component 1 and component 2 of a correspondence analysis using %F data (archival and 2001–2002 data) from sandbar sharks of PCL  $\leq 80$  cm

## Discussion

Sandbar sharks in Virginia waters exhibited ontogenetic changes in diet, with elasmobranchs

and cephalopods increasing in importance with shark size and crustaceans decreasing in importance. Teleosts remained a staple throughout their development, although taxa and sizes of fishes consumed varied. The larger sharks fed more evenly among prey categories, while the smaller sharks foraged on a wider variety within those categories, as seen by the slight decrease in prey diversity with increasing shark size. These ontogenetic changes in diet mostly reflect habitat use, although physiological and morphological constraints certainly play some role. Chesapeake Bay and Virginia's Eastern Shore serve as nursery grounds for many seasonally abundant species; offshore regions inhabited by larger sharks may have fewer prey species in relation to square kilometers of activity space.

Larger sandbar sharks in the northwest Atlantic spend more time in deeper coastal waters and thus are likely to encounter more cephalopods and elasmobranchs. Salini et al. (1992) noted that Australian *Carcharhinus amblyrhynchos* and *Carcharhinus sorrah* both consumed more cephalopods at offshore sites than at estuarine sites. The trend toward increased use of larger prey items (e.g., elasmobranchs) with increased size is seen in many sharks, including the Galapagos shark, *Carcharhinus galapagensis* (Wetherbee et al. 1996) and the tiger shark, *Galeocerdo cuvier* (Lowe et al. 1996). Incorporation of larger, heavier prey items is an energetic benefit, giving the predator more return on its energetic investment (search and capture) (Labropoulou et al. 1999). Regional differences in diet for the larger sharks cannot be detected with any certainty due to small sample sizes in this study.

The frequent occurrence of crustaceans, particularly mantis shrimp, in juvenile sandbar shark diet is an indication of shared habitat preferences for predator and prey. *Squilla empusa* prefers deep (10–20 m) areas with high salinities (VIMS 2002<sup>2</sup>). Tracking studies indicate that juvenile sandbar sharks frequent the deep, saline (> 20.5 practical salinity scale)

<sup>2</sup> VIMS (2002) Status of stock assessment knowledge used to manage important Virginia fisheries species of ecological importance. Report of VIMS Trawl Survey to Virginia Environmental Endowment, Gloucester Point, VA.

pockets of the bay (Grubbs 2001). What is available for forage in areas of this preferred salinity may vary by region. The neonates and juveniles in Medved et al.'s (1985) study in Chincoteague frequently fed on blue crab, whereas overall numbers for the current study suggest that mantis shrimp are more frequently consumed. This difference in diet is likely due to regional habitat use and opportunism, with more portunid crabs consumed in the Wachapreague region and more mantis shrimp consumed in the Sand Shoal Inlet region and Machipongo as a transitional region, with values in between.

Although sampling was initially attempted in Chincoteague, efforts were discontinued due to extremely small catches (1 sandbar shark in 20 gillnet sets). Due to the lack of Chincoteague samples, direct comparisons between Medved et al.'s (1985) study of juvenile diet cannot be made, and it is uncertain whether blue crab abundance, mantis shrimp abundance and/or time played a role in the differing results of these two studies. The most likely scenario, however, is regional diet differences based on prey abundance. This conclusion is borne out by the importance of fish to the Bay juveniles and neonates and the importance of crustaceans to the sharks in the Eastern Shore nursery. Juvenile sharks do move between the Eastern Shore and the lower Bay during their summer residence in the nursery (Grubbs et al. 2005), so interregional differences in diet may be difficult to confirm. However, juvenile sharks tracked in lower Chesapeake Bay did not leave that region in 50 h (Grubbs 2001), so frequent Bay to Eastern Shore movements are unlikely. Current efforts to monitor movements of sharks in Eastern Shore waters should shed light on home ranges in that area.

In terms of diet overlap, neonate and juvenile males and females appear to use the nursery habitat in the same way, with no apparent difference in diet. Stillwell and Kohler (1993) noticed some differences in diet between nearshore males and females, which may have been due to segregation by sex or to sampling location. Overlap in diet of Hawaiian sandbar shark males and females was high, but diet analysis

was not completed to species level (McElroy et al. 2006). Comparison of diet by sex for larger juveniles and adults was not possible in this study due to the small number of males captured. This is not unusual. Sex segregation is evident in mature sandbar sharks (Springer 1960), and larger males are infrequently encountered at the stations fished by the VIMS Shark Ecology Program (Sminkey and Musick 1995). Of 631 sharks with precaudal lengths greater than 100 cm that were caught by the project, only 53 were male.

The large number of fish families (28) consumed by the sharks in this study is a reflection of the diversity of habitat and fauna present in Chesapeake Bay and Virginia coastal waters, as well as an indication of opportunistic feeding habits. Similar diversity of teleost prey exists in the diet of Hawaiian sandbar sharks (McElroy et al. 2006). Two of the fishes found most frequently in sandbar shark stomachs were hogchoker and croaker, which were the second and fourth most abundant finfish species captured by the VIMS Trawl Survey in lower Chesapeake Bay from May through October, 2002 (VIMS 2003<sup>3</sup>). The types of fishes found in sandbar shark stomachs also reflected the species' habitat use. Tracking studies have indicated that while in Chesapeake Bay *C. plumbeus* spends significant amounts of time at least three meters above the bottom (Grubbs 2001). The data presented here suggest, as do the data of Medved et al. (1985) and Stillwell and Kohler (1993), that sandbar sharks feed on mostly demersal species (e.g., croaker and hogchoker) but do make forays into the water column, as seen by the presence of mid-water or pelagic fishes in the diet (e.g., menhaden and bluefish). This increased utilization of the water column occurs mostly at night, and sandbar sharks have been observed at the mouths of tidal creeks near large aggregations of menhaden and croaker (Grubbs 2001); sandbar sharks may also be attracted to similar aggregations of crustaceans. (Surface swarming of mantis shrimp has been

<sup>3</sup> VIMS (Virginia Institute of Marine Science). 2003. Juvenile fish and blue crab trawl survey. VIMS, PO Box 1346, Gloucester Point, VA 23062.

reported in Narragansett Bay and in the Gulf of Aden (McCluskey 1977), although this behavior has not yet been explained and has not been reported in Chesapeake Bay.) Other types of prey—gastropods, bivalves, and other benthic organisms—appear infrequently in the diet and are likely incidentally consumed.

The abundance of unidentified teleosts in this diet study was due in part to the methods used for sorting and weighing prey items. Higher frequency of unidentified teleosts in the archival data may reflect a more cursory shipboard method of stomach content examination. Pieces of flesh that could not be assigned to an identified prey item in the stomach were labeled as ‘unidentified’ and weighed and counted separately. Many of these unidentified teleosts are probably represented by the species listed; however, given the diversity of fishes consumed, there are likely additional unlisted species in the ‘unidentified’ category. Taking stomach samples from sharks feeding with almost empty stomachs can render identification difficult due to the advanced digestion stage of the items present in the gut, and samples obtained with baited lines (i.e., longlines) are more likely to be from sharks with empty or almost empty stomachs (Medved et al. 1985). Digestive action made it difficult to tell if crabs found in the stomachs were molting or ‘soft crabs’. The low pH of sandbar shark stomachs, which has been measured at approximately 1.8, makes the stomach a very effective area for digestion (Papastamatiou 2003<sup>4</sup>). Enzyme activity may also play a role. It is possible that some elasmobranchs such as *Squalus acanthias* utilize chitinolytic enzymes to speed crustacean digestion (Fänge et al. 1979), but it is not yet known if sandbar sharks produce this enzyme.

Weights of prey items may also have been influenced by method of capture. Medved et al. (1985) found that the mean total weight of food items found in sandbar sharks captured using

longline gear was significantly less than the weight of food items from sandbar sharks caught in gillnets. Because over half of the samples from this study were obtained using longline gear, the weight and, consequently, the IRI values calculated in this study may be an underestimate. If possible, it is preferable to use gillnets to obtain sharks for use in diet studies. Percent of empty stomachs is usually greater with samples obtained using baited gear (Medved et al. 1985); the percent of empty stomachs in this study is likely an underestimate because not all sharks were sacrificed and sampled.

## Conclusions

Ontogenetic changes in sandbar shark diet in Virginia waters, with increasing incorporation of elasmobranchs and cephalopods in diet with size and decreasing predation on crustaceans, likely reflects habitat use as well as physiological development. The regional variation in the prey of juvenile sandbar sharks replicates on a smaller scale the more global differences in sandbar shark diet and underscores the opportunistic feeding habits of the species. Ongoing tracking studies on the Eastern Shore should reveal more about behavioral patterns of sandbar sharks in this ecosystem compared to the lower Bay. Other future studies might involve prey handling and selectivity experiments, which would indicate if any preference for higher-energy prey items exists. Because *Carcharhinus plumbeus* has a very diverse prey base, it is unlikely to strongly impact the population of any particular species, and in turn is less likely to be strongly affected by fluctuations in abundance of a single prey species than specialist feeders. The diversity of its diet at both broad and specific levels attests to the sandbar shark’s ability to sample new prey and confirms its versatility as a predator.

<sup>4</sup> Papastamatiou, Y. 2003. Personal commun. Hawaii Institute of Marine Biology, Department of Zoology, University of Hawaii at Manoa, PO Box 1346, Kaneohe, HI 96744.

**Appendix 1** Frequency and percent frequency of occurrence of fish prey items found in all sandbar shark stomachs, including archival and 2001–2002 samples ( $F_{\text{all}}$  and  $\%F_{\text{all}}$ ) and 2001–2002 samples only ( $F_{\text{new}}$  and  $\%F_{\text{new}}$ )

	Prey item	$F_{\text{all}}$	$\%F_{\text{all}}$	$F_{\text{new}}$	$\%F_{\text{new}}$
<i>Teleosts</i>					
Anguillidae	<i>Anguilla rostrata</i>	2	0.3	1	0.4
Congridae	<i>Conger oceanicus</i>	4	0.7	2	0.9
	Unidentified eel	1	0.2	1	0.4
Clupeidae	<i>Alosa</i> spp.	2	0.3	2	0.9
	<i>Brevoortia</i> spp.	16	2.6	–	–
	<i>Brevoortia tyrannus</i>	5	0.8	5	2.2
	<i>Etrumeus teres</i>	4	0.7	4	1.7
	<i>Opisthonema oglinum</i>	1	0.2	–	–
	Unidentified clupeid	2	0.3	1	0.4
Engraulidae	<i>Anchoa hepsetus</i>	6	1.0	5	2.2
	<i>Anchoa mitchilli</i>	5	0.8	5	2.2
	<i>Anchoa</i> spp.	13	2.1	9	3.9
Cyprinodontidae	<i>Fundulus heteroclitus</i>	2	0.3	2	0.9
	<i>Fundulus majalis</i>	1	0.2	1	0.4
Gadidae	<i>Urophycis regia</i>	2	0.3	2	0.9
	<i>Urophycis</i> spp.	2	0.3	–	–
	Unidentified gadiform	1	0.2	–	–
Lophiidae	<i>Lophius americanus</i>	2	0.3	2	0.9
Ophidiidae		1	0.2	–	–
Ammodytidae		3	0.5	–	–
Carangidae		1	0.2	–	–
Ephippidae	<i>Chaetodipterus faber</i>	1	0.2	1	0.4
Moronidae	<i>Morone saxatilis</i>	1	0.2	1	0.4
Mugilidae	<i>Mugil cephalus</i>	1	0.2	1	0.4
Pomatomidae	<i>Pomatomus saltatrix</i>	9	1.5	–	–
Rachycentridae	<i>Rachycentron canadum</i>	1	0.2	–	–
Sciaenidae	<i>Bairdiella chrysoura</i>	1	0.2	–	–
	<i>Cynoscion nebulosus</i>	2	0.3	2	0.9
	<i>Cynoscion regalis</i>	12	2.0	11	4.7
	<i>Cynoscion</i> spp.	5	0.8	3	1.3
	<i>Leiostomus xanthurus</i>	9	1.5	2	0.9
	<i>Micropogonias undulatus</i>	38	6.3	33	14.2
	Unidentified sciaenid	10	1.6	2	0.9
Serranidae	<i>Centropristis striata</i>	4	0.7	1	0.4
Sparidae	<i>Lagodon rhomboides</i>	1	0.2	1	0.4
	<i>Stenotomus chrysops</i>	3	0.5	1	0.4
Uranoscopidae	<i>Astroscopus guttatus</i>	7	1.2	–	–
Achiridae	<i>Trinectes maculatus</i>	37	6.1	16	6.9
Cynoglossidae	<i>Symphurus plagiusa</i>	3	0.5	3	1.3
Paralichthyidae	<i>Etropus microstomus</i>	3	0.5	3	1.3
	<i>Etropus</i> spp.	1	0.2	–	–
	<i>Paralichthys dentatus</i>	3	0.5	–	–
	<i>Paralichthys</i> spp.	1	0.2	1	0.4
	Unidentified paralichthyid	1	0.2	1	0.4
Pleuronectidae	<i>Pleuronectes americanus</i>	1	0.2	1	0.4
Scophthalmidae	<i>Scophthalmus aquosus</i>	4	0.7	3	1.3
	Unidentified flatfish	14	2.3	5	2.2
Triglidae	<i>Prionotus carolinus</i>	4	0.7	2	0.9
	<i>Prionotus</i> spp.	6	1.0	6	2.6
	Unidentified triglid	13	2.1	–	–

## Appendix 1 continued

	Prey item	$F_{\text{all}}$	$\%F_{\text{all}}$	$F_{\text{new}}$	$\%F_{\text{new}}$
Fistularidae	<i>Fistularia tabacaria</i>	1	0.2	1	0.4
	Syngnathidae	1	0.2	–	–
	Unidentified syngnathiform	1	0.2	1	0.4
Tetradontidae	<i>Spheroides maculatus</i>	1	0.2	1	0.4
	Unidentified puffer	2	0.3	–	–
Unidentified teleost		191	31.4	30	12.9
<i>Elasmobranchs</i>					
Carcharhinidae	<i>Carcharhinus plumbeus</i>	2	0.3	–	–
Dasyatidae	<i>Dasyatis</i> spp.	4	0.7	–	–
Myliobatidae		1	0.2	–	–
Rajidae	<i>Leucoraja erinacea</i>	2	0.3	–	–
	<i>Raja eglanteria</i>	17	2.8	8	3.4
	<i>Raja</i> spp. egg case	7	1.2	5	2.2
	Unidentified rajid	34	5.6	9	3.9
Rhinopterae	<i>Rhinoptera bonasus</i>	2	0.3	–	–
Triakidae	<i>Mustelus canis</i>	1	0.2	–	–
Unidentified batoid		13	2.1	–	–
Unidentified shark		1	0.2	–	–
Unidentified elasmobranch		7	1.2	4	1.7

**Appendix 2** Frequency and percent frequency of occurrence of crustacean prey items found in all sandbar shark stomachs, including archival and 2001–2002 samples ( $F_{\text{all}}$  and  $\%F_{\text{all}}$ ) and 2001–2002 samples only ( $F_{\text{new}}$  and  $\%F_{\text{new}}$ )

	Prey item	$F_{\text{all}}$	$\%F_{\text{all}}$	$F_{\text{new}}$	$\%F_{\text{new}}$
Squillidae	<i>Squilla empusa</i>	108	17.8	87	37.5
Portunidae	<i>Arenaeus cribrarius</i>	1	0.2	1	0.4
	<i>Callinectes sapidus</i>	45	7.4	32	13.8
	<i>Carcinus maenus</i>	1	0.2	–	–
	<i>Ovalipes ocellatus</i>	37	6.1	17	7.3
	Unidentified portunid	5	0.8	3	1.3
Majidae	<i>Libinia emarginata</i>	7	1.2	7	3.0
	<i>Libinia</i> spp.	4	0.7	4	1.7
	<i>Pelia mutica</i>	4	0.7	4	1.7
	Unidentified majid	12	2.0	–	–
Cancriidae	<i>Cancer irroratus</i>	2	0.3	–	–
Leucosiidae	<i>Persephona punctata</i>	1	0.2	1	0.4
Unidentified crab		12	2.0	1	0.4
Paguridae	<i>Pagurus longicarpus</i>	1	0.2	1	0.4
	<i>Pagurus pollicaris</i>	15	2.5	12	5.2
	<i>Pagurus</i> spp.	6	1.0	–	–
Hippolytidae	<i>Hippolysmata wurdemanni</i>	1	0.2	1	0.4
Penaeidae	<i>Penaeus aztecus</i>	1	0.2	1	0.4
	<i>Penaeus duorarum</i>	1	0.2	1	0.4
	<i>Penaeus</i> spp.	1	0.2	2	0.9
Callianassidae	<i>Callianassa atlantica</i>	1	0.2	1	0.4
Upogebiidae	<i>Upogebia affinis</i>	21	3.5	21	9.1
Crangonidae	<i>Crangon septemspinosa</i>	2	0.3	–	–
Unidentified shrimp		1	0.2	1	0.4
Isopoda		1	0.2	–	–
Unidentified crustacean		11	1.8	9	3.9

**Appendix 3** Frequency and percent frequency of occurrence of mollusc, plant, and other prey items found in all sandbar shark stomachs, including archival and 2001–2002 samples ( $F_{\text{all}}$  and  $\%F_{\text{all}}$ ) and 2001–2002 samples only ( $F_{\text{new}}$  and  $\%F_{\text{new}}$ )

	Prey item	$F_{\text{all}}$	$\%F_{\text{all}}$	$F_{\text{new}}$	$\%F_{\text{new}}$
<b>Molluscs</b>					
<i>Bivalves</i>					
Mactridae	<i>Spissula solidissima</i>	1	0.2	1	0.4
Mytilidae	<i>Mytilus</i> spp.	2	0.3	1	0.4
Nuculidae	<i>Nucula proxima</i>	1	0.2	1	0.4
Solenidae	<i>Ensis directus</i>	2	0.3	–	–
Unidentified bivalve		2	0.3	1	0.4
<i>Cephalopods</i>					
Loligonidae	<i>Lolliguncula brevis</i>	7	1.2	7	3.0
	<i>Loligo pealei</i>	13	2.1	2	0.9
	Unidentified loligonid	9	1.5	9	3.9
Ommastrephidae	<i>Illex</i> spp.	1	0.2	–	–
Unidentified cephalopod		17	2.8	–	–
<i>Gastropods</i>					
Buccinidae		1	0.2	–	–
Littorinidae	<i>Littorina</i> spp.	3	0.5	–	–
Nassariidae	<i>Nassarius obsoletus</i>	1	0.2	1	0.4
	<i>Nassarius trivittatus</i>	1	0.2	1	0.4
	<i>Nassarius</i> spp.	4	0.7	2	0.9
Natacidae		1	0.2	–	–
Nudibranchia		2	0.3	–	–
Unidentified mollusc		1	0.2	–	–
<b>Plants</b>					
	<i>Aghardiella tenera</i>	1	0.2	1	0.4
	<i>Gracilaria</i> sp.	2	0.3	2	0.9
	<i>Punctaria</i> sp.	1	0.2	1	0.4
	<i>Ulva</i> sp.	3	0.5	3	1.3
	<i>Zostera marina</i>	2	0.3	1	0.4
	Unidentified plant	3	0.5	2	0.9
<b>Other/Incidental</b>					
	Anemone	1	0.2	–	–
	Bryozoan	4	0.7	3	1.3
	Hydrozoa	1	0.2	1	0.4
	<i>Limulus polyphemus</i>	1	0.2	–	–
	Polychaete	1	0.2	–	–
	Trash	3	0.5	–	–
	Tunicate	1	0.2	1	0.4
	Unidentified invertebrate	1	0.2	–	–
	Unidentified biological	47	7.7	41	17.7

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