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Habitat Utilization, Relative Abundance, and Seasonality of Sharks in the Estuarine and Nearshore Waters of South Carolina

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Abstract.—Sharks were collected from the estuarine and nearshore waters of South Carolina in an effort to delineate nursery grounds for coastal sharks within state waters. From March 1998 through December 2003, 4,098 sharks, representing 12 species, were collected using gill-net and hand-deployed longline fishing gears provided by the Cooperative Atlantic States Shark Pupping and Nursery Survey. To supplement these data, records of 6,648 shark captures, representing 16 species, from a long-term longline survey in South Carolina coastal waters were incorporated into the analyses. The results of this study indicate that the estuarine and nearshore waters of South Carolina represent an important primary nursery area for finetooth sharks *Carcharhinus isodon*, blacktip sharks *C. limbatus*, sandbar sharks *C. plumbeus*, Atlantic sharpnose sharks *Rhizoprionodon terraenovae*, and scalloped hammerheads *Sphyrna lewini*.

Introduction

One of the most critical data needs for creating and implementing a rational management strategy to conserve and enhance coastal shark stocks is to identify habitats that facilitate the proliferation of exploited species (NMFS 1993). During the life cycle of most coastal sharks there are three geographic locales that are considered to be essential habitat: adult feeding areas, mating areas, and nursery areas (Castro 1993a). Springer (1967) noted that gravid female coastal sharks use shallow waters for parturition or oviposition, and neonates make use of these same waters as a nursery. Springer (1967) added that nursery areas are selected due to the absence or relatively low abundance of adult sharks, thus minimizing neonate mortality rates due to predation. Castro (1987) suggested that nursery areas are often associated with productive ecosystems, such as estuaries, which presumably facilitate rapid early growth of neonates. By attaining a large size relatively quickly the number of predators and competitors are reduced and predatory efficiency is increased due to greater swimming efficiency (Wourms 1977).

In an effort to examine the use of South Carolina's estuarine waters as nursery areas for coastal shark species the South Carolina Department of Natural Resources Marine Resources Division, in collaboration with the National Marine Fisheries Service's (NMFS) Cooperative Atlantic States Shark Pupping and Nursery (COASTSPAN) Survey, began sampling for sharks in several estuaries within South Carolina. This report covers the period from March 1998 to December 2003. In addition to the estuarine areas sampled specifically for sharks, this report includes shark catch data from a long-term longline survey designed to monitor adult red drum *Sciaenops ocellatus* in the coastal waters of South Carolina. The objective of this report was to combine the two data sets in an effort to understand the extent to which coastal sharks utilize the estuarine and nearshore waters of South Carolina as nursery areas both spatially and temporally. Ad-

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ditionally, the relative abundance, seasonality and habitat utilization of juvenile and adult sharks captured during the study are discussed.

Methods

Estuarine sampling locations were selected in the lower reaches of estuaries in areas that would facilitate the deployment and retrieval of gill nets and hand-deployed longlines (i.e., limited current velocity, tidal range, and vessel traffic). All estuarine sampling occurred inside of inlets and sampling locations varied with regard to distance from nearshore waters. Estuarine sampling was conducted from April through October with the majority of the effort occurring between May and September (Table 1). Nearshore sampling stations were those previously selected for adult red drum sampling. Nearshore sampling occurred from immediately outside of the surf zone to 8 km offshore with depths ranging from 3 to 15 m. These sites were primarily live-bottom areas with low relief consisting of rock or marl outcrops that were encrusted with sessile invertebrates such as sponges, gorgonians, and bryozoans. Nearshore sampling occurred throughout the year with the exception of February; however, nearshore sampling was most intense from September through December (Table 1). The locations of the fixed estuarine and nearshore sampling areas are shown in Figure 1.

The gill net used in this study was 231 m long, 3 m deep, and was constructed of #177 monofilament with a stretched mesh of 10.3 cm. The net was set and inspected for catch at approximately 20-min intervals to minimize mortality. The hand-deployed longline (here forth referred to as handline) consisted of 305 m of 0.64-cm braided nylon mainline, with 50 gangions. Each gangion consisted of a 0.5-m, 91-kg test monofilament leader, size 120 stainless steel longline snap with a 4/0 swivel, and a 12/0 circle hook. Prior to the 2000 sampling year, the handline was allowed to soak for 45–60 min and then retrieved. After retrieval, the gear was either reset or moved to a new location, depending on catch. High bait loss was noted on most sets; therefore, the sampling strategy was modified in 2000 and the handline was under run at 20–30-min intervals. Longline gear consisted of a 272-kg test monofilament mainline that was 1,829 m in length and had 30.5-m buoy lines attached at each end. The mainline was equipped with stop sleeves at 30.5-m intervals to prevent gangions from sliding together when a large fish was captured. The gangions were the same as those used on the handline with the exception that 14/0 and 15/0 circle hooks were employed. A full set consisted of 120 hooks although conditions in certain sampling areas dictated that 914 m of mainline and 60 gangions be used. Soak times for longline sets were limited to 45 min unless conditions or events dictated otherwise.

Latitude and longitude for the beginning and end of each set for all gear types were recorded along with start and end times of deployment and retrieval. Water temperature (°C) and salinity (parts per thousand [ppt]) were also recorded. Fork length (FL) and stretch total length (STL) were recorded for captured sharks that could be safely handled. Fork length was measured from the tip of the rostrum to the fork in the caudal fin. Stretch total length was measured from the tip of the rostrum to the terminal edge of the upper lobe of the caudal fin while fully extended. Both length measurements were made in a straight line along the axis of the body. For those sharks that could not be safely brought on the deck of the vessel, FL was estimated to the nearest 0.25 m FL. To classify small individuals as neonates or juveniles the ventral surface of all sharks within the known size range of neonates for each species was examined for the presence of an umbilicus. If present, the condition of the umbilicus (i.e., open, partially healed, healed, not present) was recorded. Sharks were

TABLE 1. Number of sets by gear type and month completed during the study from 1998 to 2003. LL = longline, HL = handline, GN = gill net.

Gear	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
LL	6	0	12	37	46	36	37	38	81	226	218	63
HL	0	0	0	0	33	45	60	60	44	0	0	0
GN	0	0	0	7	62	85	83	98	10	5	0	0

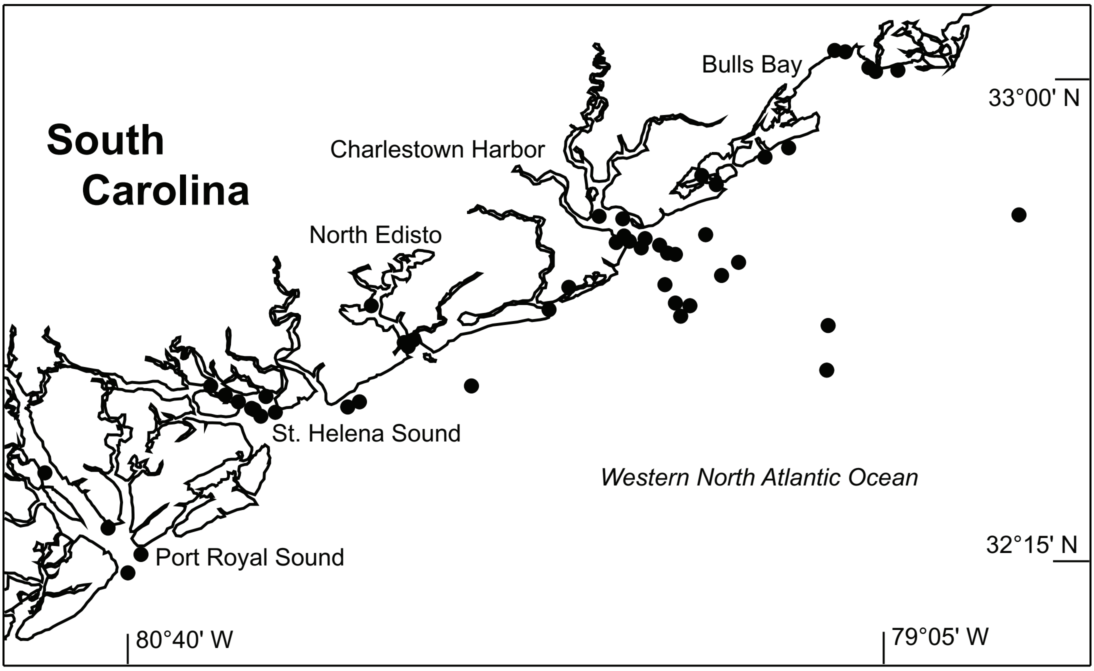

FIGURE 1. Map showing fixed sampling locations. Closed circles indicate the position of each sampling location. Estuarine sampling locations were restricted to areas inside of inlets. Nearshore sampling locations ranged from approximately 0.2–8.0 km offshore

considered neonates from the time of birth until the umbilical scar was no longer visible. Individuals classified as young of the year had no visible umbilical scar but were within the size range indicating that they had been born earlier that year.

Longline sampling occurred throughout the year, with the exception of February, and was used to analyze the seasonality of each species in South Carolina's coastal waters. As gill-net sampling only occurred from April through October and handline gear sampling only occurred from May through September data from these gear types were not useful in determining seasonality. To examine the relationship between sex and habitat specific occurrence a *t*-test was used (Zar 1999). Analysis of variance (ANOVA) and multiple range tests were used to examine the effects of gear selectivity on the mean size at capture for several of the dominant species (Zar 1999). To test for differences between observed and expected (1:1) sex ratios a chi-square test with Yates' correction for continuity was used (Zar 1999). A chi-square statistic greater than 3.84 was considered to be statistically significant at an α level of 0.05.

Results and Discussion

A total of 10,746 sharks were caught during sampling conducted with all gear types from March 1998 through December 2003 (Table 2). Over the course of the study, 800 longline, 350 gillnet, and 242 handline sets were completed. Although not directly comparable due to the selectivity of each gear type, the majority of sharks were captured by longline (6,648 individuals), followed by gill net (2,899 individuals), and handline (1,199 individuals). The relative abundance of each species is summarized by area in Table 3. The four small coastal shark species, as defined by NMFS (1993), made up 80.01% of the total catch. Atlantic sharpnose sharks constituted 57.56% of the total catch, with finetooth shark, bonnethead, and blacknose shark making up 9.01%, 8.57%, and 4.88% of the total catch, respectively. Large coastal shark species, as defined by NMFS (1993), made up 10.79% of the total catch. The dominant large coastal shark species collected were sandbar shark (4.55%), blacktip shark (2.64%), and scalloped hammerhead (2.39%). Smooth dogfish and

TABLE 2. Total number caught and relative abundance by species for each gear type. NA = not applicable. * indicates an estimated fork length; ** indicates an estimated total length (estimated lengths only apply to upper range).

Species	Total (%)	Longline	Handline	Gill net
		Total number caught (size range in mm FL)		
Atlantic sharpnose shark *Rhizoprionodon terraenovae*	6,185 (57.56)	4,359 (219–1,026)	811 (225–921)	1,015 (204–888)
Finetooth shark *Carcharhinus isodon*	968 (9.01)	51 (506–1,372)	192 (420–987)	725 (361–1496)
Bonnethead *Sphyrna tiburo*	921 (8.57)	26 (695–998)	25 (504–1001)	870 (371–1,074)
Smooth dogfish *Mustelus canis*	852 (7.93)	850 (495–1,186)	2 (579–738)	0 (NA)
Blacknose shark *C. acronotus*	524 (4.88)	520 (542–1,172)	2 (1,018–1,084)	2 (965–1,132)
Sandbar shark *C. plumbeus*	489 (4.55)	361 (477–1,829)*	88 (437–1,083)	40 (433–822)
Blacktip shark *C. limbatus*	284 (2.64)	159 (495–1,829)*	41 (479–1,524)	84 (447–1,075)
Scalloped hammerhead *S. lewini*	257 (2.39)	67 (373–1,829)*	32 (338–540)	158 (274–1,014)
Spiny dogfish *Squalus acanthias*	136 (1.27)	136 (490–891)	0 (NA)	0 (NA)
Tiger shark *Galeocerdo cuvier*	40 (0.37)	40 (568–2,286)*	0 (NA)	0 (NA)
Spinner shark *C. brevipinna*	36 (0.33)	31 (592–1,156)	3 (613–687)	2 (747–762)
Nurse shark *Ginglymostoma cirratum*	29 (0.27)	29 (1,105–3,048)**	0 (NA)	0 (NA)
Dusky shark *C. obscurus*	10 (0.09)	10 (718–975)	0 (NA)	0 (NA)
Lemon shark *Negaprion brevirostris*	7 (0.06)	2 (1,791–2,047)	2 (695–703)	3 (550–789)
Sand tiger *Carcharias taurus*	3 (0.03)	3 (2,286–2,438)**	0 (NA)	0 (NA)
Bull shark *Carcharhinus leucus*	3 (0.03)	2 (747–1,524)	1 (845)	0 (NA)
Silky shark *C. falciformis*	1 (0.01)	1 (864)	0 (NA)	0 (NA)
Thresher shark *Alopias vulpinus*	1 (0.01)	1 (1,828)	0 (NA)	0 (NA)

spiny dogfish, both late fall and winter transient species, made up 7.93% and 1.27% of the total catch, respectively. The months of occurrence and time of parturition, if applicable, for the dominant species encountered during this study are shown in Figure 2.

The occurrence and relative abundance of shark species varied between the nearshore and estuarine sampling areas (Table 3). Species diversity was higher in nearshore waters (16 species) than in estuarine waters (12 species). The total nearshore catch was 6,483 individuals, and the total estuarine catch was 4,263 individuals. There were obvious differences in the species composition, intraspecific size range, and relative abundance of each species among gear types, which was likely attributable to gear selectivity (Table 2). For example, there was a significant difference in the mean size at capture for finetooth, sandbar, and Atlantic sharpnose sharks among the three gear types, with the smallest individuals being captured with the gill net and the largest individuals being collected with the longline gear (ANOVA, $p < 0.01$, Scheffé's multiple range test). For blacktip sharks, there was no significant difference in mean size at capture between gill-net and handline gear; however, the longline gear caught significantly larger individuals than did the other two gear types (ANOVA, $p < 0.01$, Scheffé's multiple range test). In addition to gear type, size selection can also be influenced by area sampled, with smaller sharks generally predominating in estuarine areas. Another factor influencing differences in relative abundance among gear types was the

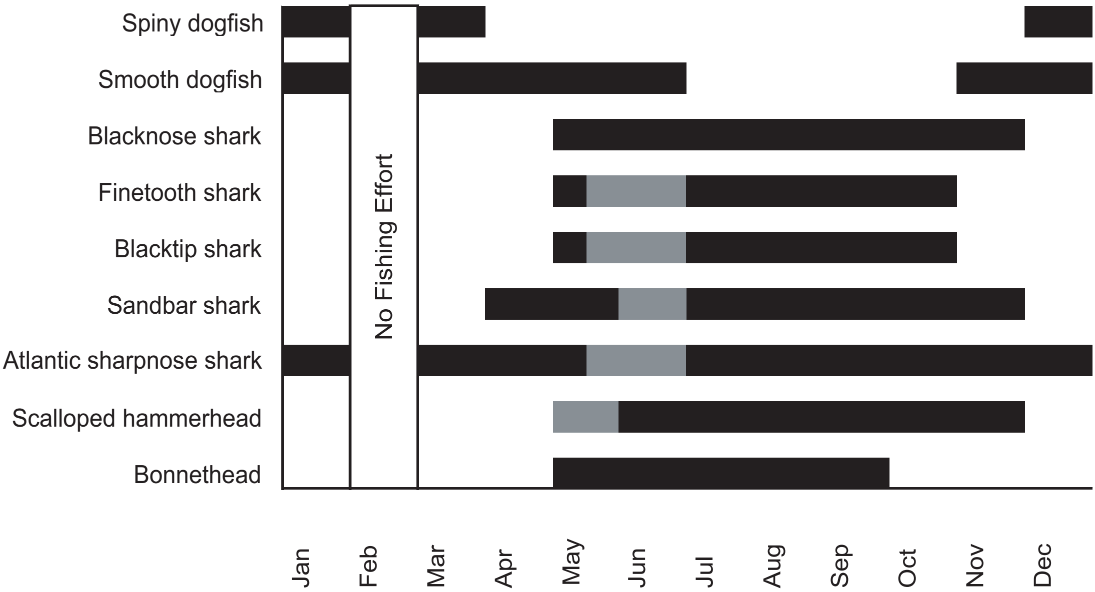

FIGURE 2. Seasonality of selected species. Dark bars indicate months in which a given species was observed. Gray areas indicate the time frame in which parturition occurred.

ineffectiveness of gear in capturing at least one species. In estuarine waters, 97.21% of bonnetheads were caught with gill nets. In South Carolina estuaries, bonnetheads feed almost exclusively on blue crabs *Callinectes sapidus* (W. B. Driggers, personal observation) and as the handline was baited solely with teleosts this gear did not capture bonnetheads effectively. Therefore, our data suggest that when attempting to characterize shark assemblages and habitat utilization the best information will be obtained when multiple gear types are utilized.

Several factors, primarily water temperature and salinity, affected the presence and abundance of sharks in nearshore and estuarine habitats. The mean temperature and salinity at time of capture

TABLE 3. Total number caught and relative abundance by species in nearshore and estuarine waters. NA = not applicable. * indicates an estimated fork length; ** indicates an estimated total length.

Species	Total (%)	Estuarine	Nearshore
		Total number caught (size range in mm FL)	
Atlantic sharkpnose shark	6,185 (57.56)	1,873 (204–888)	4,312 (219–1,026)
Finetooth shark	968 (9.01)	838 (361–1,496)	130 (435–1,372)
Bonnethead	921 (8.57)	903 (371–1,074)	18 (722–1,001)
Smooth dogfish	852 (7.93)	2 (579–738)	850 (495–1,186)
Blacknose shark	524 (4.88)	11 (855–1,132)	513 (542–1,172)
Sandbar shark	489 (4.55)	214 (433–1,280)	275 (475–1,829)*
Blacktip shark	284 (2.64)	188 (447–1,524)	96 (495–1,829)*
Scalloped hammerhead	257 (2.39)	217 (274–1,829)*	40 (373–825)
Spiny dogfish	136 (1.27)	0 (NA)	136 (490–891)
Tiger shark	40 (0.37)	1 (1,936)	39 (568–2,286)*
Spinner shark	36 (0.33)	6 (613–762)	30 (592–1,156)
Nurse shark	29 (0.27)	0 (NA)	29 (1,105–3,048)**
Dusky shark	10 (0.09)	0 (NA)	10 (718–975)
Lemon shark	7 (0.06)	7 (550–2,047)	0 (NA)
Sand tiger	3 (0.03)	0 (NA)	3 (2,286–2,438)**
Bull shark	3 (0.03)	3 (747–1,524)	0 (NA)
Silky shark	1 (0.01)	0 (NA)	1 (864)
Thresher shark	1 (0.01)	0 (NA)	1 (1,828)

for the predominant species, as well as the ranges for both variables, are presented in Table 4. The mean water temperatures for each month sampled are presented in Figure 3. Water temperature appeared to be the major factor determining the seasonal occurrence of sharks in South Carolina waters. Large and small coastal shark species were first observed in South Carolina's estuarine systems when water temperatures rose to approximately 19–20°C, with juvenile sandbar, adult male Atlantic sharpnose, and adult female bonnethead sharks being encountered in mid-April. Most shark species began to leave estuaries and move into nearshore waters when estuarine water temperatures decreased to approximately 26–28°C in the late fall. During the spring large and small coastal species migrated into South Carolina coastal waters at temperatures as low as 17°C. In the fall large and small coastal sharks were encountered in water temperatures between 19°C and 20°C and occasionally at temperatures as low as 14°C. A similar pattern of temperature-based occurrence in South Carolina waters was apparent for spiny dogfish and smooth dogfish. During the late fall, smooth dogfish were captured when water temperatures decreased to 18°C and spiny dogfish were first observed in water temperatures of 13°C. During late winter and the approach of early spring when water temperatures rose above 19°C both species migrated out of South Carolina waters.

Salinities in estuarine sampling areas ranged from 11 to 38 ppt but catches were highest when salinities were greater than 25 ppt. Salinity was more stable in nearshore sampling sites with values ranging between 31 and 35 ppt. When large influxes of freshwater occurred on normally high-salinity nearshore sampling sites both catches and species diversity declined precipitously. Tidal effects also appeared to influence catch rates in discrete areas. Estuarine sampling sites were characterized by tidal amplitudes of approximately 2 m, with strong currents in the proximity of channels where there were high amounts of suspended sediments, particularly during ebb tides. Bottom type at most estuarine sampling sites was primarily mud, although sand predominated at sampling areas near the mouths of inlets. Although not quantified, heavy tidal and wave action that increased turbidity appeared to negatively impact the catchability/abundance of sharks.

Castro (1993a) reported on the use of Bulls Bay, South Carolina as a nursery area by several species of sharks and reviewed the existing literature on southeastern United States shark nursery areas. Castro (1993a) determined that Bulls Bay is a nursery for blacknose, spinner, finetooth, blacktip, dusky, sandbar, Atlantic sharpnose, scalloped hammerhead, and smooth dogfish sharks. The results of this study indicate that the finetooth, blacktip, sandbar, Atlantic sharpnose, and scalloped hammerhead sharks utilize high salinity estuarine areas from Bulls Bay to Port Royal Sound as primary nursery habitat. Results also indicate that South Carolina's estuarine areas also serve as secondary nursery habitat, as indicated by the presence of juveniles, for the same species, with the exception of Atlantic sharpnose sharks. Furthermore, data collected during this study suggest the possibility that lemon and spinner sharks make limited use of South Carolina's nearshore waters as a nursery area.

The results of this study corroborate many of Castro's (1993a) observations concerning Bulls Bay and extend known nursery areas in South Carolina waters as far south as Port Royal Sound; however, results do not support Castro's (1993a) assertion that Bulls Bay is a primary nursery area for blacknose or dusky sharks. The blacknose shark was reported by Schwartz (1984) and Castro

TABLE 4. Ranges and mean values of temperature and salinity in which species collected during this study occurred.

Species	Temp range	Mean temp (S.D.)	Salinity range	Mean salinity (S.D.)
Spiny dogfish	10.5–29.1	15.45 (5.05)	NA	NA
Smooth dogfish	12.2–24.5	17.72 (1.76)	NA	NA
Blacknose shark	17.2–30.0	24.97 (2.99)	31–35	33.12 (1.05)
Spinner shark	16.9–30.3	24.47 (3.77)	26–36	32.50 (3.62)
Finetooth shark	19.6–31.0	27.77 (2.77)	13–38	33.60 (3.57)
Blacktip shark	19.0–31.0	26.25 (2.54)	13–38	31.78 (3.72)
Sandbar shark	15.0–30.0	24.81 (3.44)	13–37	28.43 (5.95)
Atlantic sharpnose shark	13.5–31.0	23.73 (3.43)	11–38	32.16 (3.78)
Scalloped hammerhead	17.6–31.0	25.94 (2.47)	20–37	33.69 (2.76)
Bonnethead	19.2–31.0	27.72 (2.10)	16–38	31.34 (5.03)

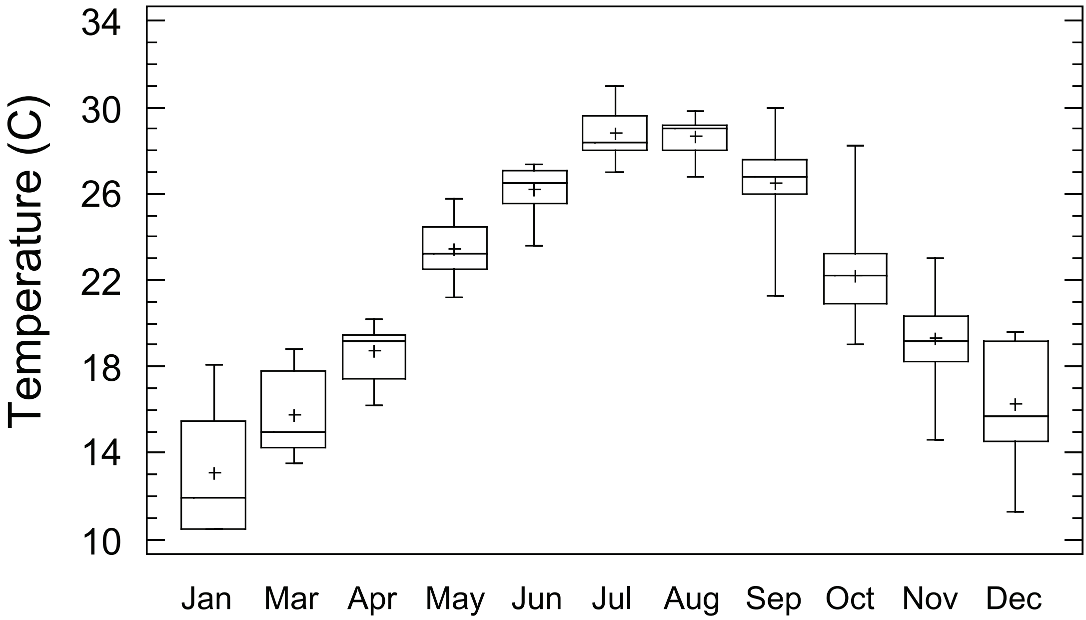

FIGURE 3. Box and whisker plot of temperature by month. Boxes indicate the lower and upper quartile. Horizontal line in each box represents the median temperature. The mean temperature for each month is indicated by a +. Vertical lines extending from each box represent the minimum and maximum temperature recorded for that month.

(1993a) to utilize nearshore waters in the Carolinas as pupping and nursery ground habitat. Our data do not support the findings of Castro (1993a) and Schwartz (1984), as no neonate blacknose sharks were captured over the course of the study despite the use of multiple gear types, two of which were effective at catching neonates of other species that are smaller than neonate blacknose sharks. We also could not confirm the presence of neonate dusky sharks in estuarine areas but have limited evidence that suggests nearshore waters are utilized by this species as nursery habitat. During November of 1998, 2000, and 2003 a total of 10 neonate dusky sharks were captured. All neonate dusky sharks were caught at nearshore sampling stations approximately 8 km offshore.

The discrepancies between this study and Castro's (1993a) could result from us classifying the estuarine environment somewhat differently than Castro in that estuarine stations in this study were restricted to areas inside barrier islands, while Castro included nearshore waters out to approximately 4.5 km from the beach as part of the Bulls Bay estuarine system. That our data do not support the findings of Castro (1993a) regarding the use of Bulls Bay as a nursery area by blacknose and dusky sharks could also be a function of the spatial and temporal distribution of our estuarine sampling. Additional stations near beaches using gill-net and handline gear in May and June may resolve these discrepancies.

Species profiles

The following species profiles are presented in the order of each species overall relative abundance in South Carolina waters. The profiles are general descriptions of the seasonality, sex ratio, habitat utilization, and, when applicable, time of parturition for each species. A quantitative analysis of the interannual variability in catch per unit effort for each species will be addressed in the future. Length frequencies and sizes at maturity for each of the nine species covered in this section are presented in Tables 5 and 6 respectively. Several species captured during this study, including nurse, spinner, dusky, and lemon sharks, were infrequently captured and are thus omitted from the species profiles. That we did not capture any of these species in significant numbers is probably due to the inability of the gear types we used to retain large sharks. Our limited data for each of these species indicate

TABLE 5. Length frequency distribution of selected species. M = male, F = female. Numbers correspond to the number of individuals collected for which fork length was measured.

Length-class mm FL	Atlantic sharpnose shark M	Atlantic sharpnose shark F	Finetooth shark M	Finetooth shark F	Bonnethead M	Bonnethead F	Smooth dogfish M	Smooth dogfish F	Blacknose shark M	Blacknose shark F	Sandbar shark M	Sandbar shark F	Blacktip shark M	Blacktip shark F	Scalloped hammerhead M	Scalloped hammerhead F	Spiny dogfish M	Spiny dogfish F
201–300	378	378													5	2		
301–400	338	321	1	3	1	2									63	61		
401–500	124	99	251	262	9	7	1				9	12	13	8	40	30		1
501–600	50	22	117	139	6	19	4	1		1	55	50	67	53	9	17		
601–700	139	34	12	22	42	105	1	5	8	12	17	13	21	25	5	9	5	32
701–800	2,425	433	12	21	65	148	2	3	52	57	27	24	3	6	4	5	6	73
801–900	770	589	15	22	10	194	4	15	69	76	21	30	12	11	3	1		19
901–1,000	8	6	18	13	19	267	8	184	78	68	34	39	8	14				
1,001–1,100		1	4	14		22		448	35	44	25	42	7	7		1		
1,101–1,200			15	8				42		13	7	10	5	2				
1,201–1,300				12							3	7	2	1				
1,301–1,400				1							3	8	3	2				
1,401–1,500				1														
1,501–1,600											7	6	2	3				
1,601–1,700											5	6						
1,701–1,800																		
1,801–1,900												1				1		

that three of these species make limited use of South Carolina's nearshore waters as a nursery. Neonate spinner (n = 2), dusky (n = 10) and lemon (n = 3) sharks were collected over the course of the study. Before we can determine the importance of South Carolina nearshore waters as a nursery area for these species it will be necessary to sample nearshore waters more vigorously with gill-net and handline gear. There was no indication that South Carolina waters are a primary nursery for nurse or tiger sharks. All of the nurse sharks caught during the study were adults and juveniles. Of the 40 tiger sharks collected all were juveniles and of the individuals who were considered young of the year, all were caught in nearshore waters from late July through December. Sand tiger, thresher, silky, and bull sharks were represented by three or less individuals and thus are also not covered in this section.

Atlantic sharpnose shark

A total of 6,185 Atlantic sharpnose sharks were caught over the 6 years covered by this study,

TABLE 6. Sizes at maturity and references for selected species. M = male, F = female. Some values were converted to fork length from total length or precaudal length for comparison.

Species	Sex	Size at maturity (mm FL)	Source
Spiny dogfish	M	509	Nammack et al. 1985
	F	689	
Smooth dogfish	M	739	Conrath and Musick 2002
	F	892	
Blacknose shark	M	896	Driggers et al. 2004
	F	964	
Finetooth shark	M	1,015	Drymon 2003
	F	1,021	
Blacktip shark	M	1,175	Castro 1996
	F	1,266	
Sandbar shark	M	1,467	Castro 1983
	F		
Atlantic sharpnose shark	M	672	Loefer and Sedberry 2002
	F	668	
Scalloped hammerhead	M	1,055–1,242	Compagno 1984
	F	1,614	
Bonnethead	M	661	Lombardi-Carlson et al. 2004
	F	815	C. M. Jones, unpublished data

ranging in size from 204 to 1,026 mm FL. Atlantic sharpnose sharks were captured over a temperature range of 13.5–31.0°C and in salinities ranging from 11 to 38 ppt. Adult males dominated catches until late May and early June when juveniles and neonates began to appear in the catch at water temperatures of 24–25°C. Throughout the summer, nearshore catches consisted of neonates, juveniles, and adults of both sexes. As water temperatures decreased in October the catch became heavily dominated by adult males. The catches in November and December, when temperatures had dropped to between 14°C and 20°C, had a relatively equal representation of adults of both sexes. In most years, by mid-November neonates and juveniles had migrated out of nearshore waters when temperatures had decreased to 18–19°C. A limited number of adult males and females remained in nearshore waters until mid-December occurring in water temperatures as low as 14°C. The ratio of adult females to adult males captured in estuarine and nearshore waters was 1:19.90 ($\chi^2 = 528.13$, $p < 0.01$) and 1:2.62 ($\chi^2 = 737.80$, $p < 0.01$), respectively.

Adult males were captured in nearshore waters during all months sampled and were most abundant during the early summer from May to June and least abundant in January and March. Adult males were observed in waters ranging from 11 to 38 ppt and utilized estuarine waters only during April, May, and June, with the exception of 31 males caught near the entrances of St. Helena Sound and North Edisto estuary during August, September and October. Adult males entered estuarine waters in mid-April when water temperatures were approaching 20°C and migrated out of estuarine areas into nearshore waters in mid-June, at approximately the same time that adult females gave birth.

Adult female Atlantic sharpnose sharks were also captured in nearshore waters during all months in which sampling occurred. They were most abundant during the fall and early winter and least abundant during the late winter and early spring. Adult females were captured in a more narrow salinity range, 32–37 ppt, than were adult males. There was a significant difference in the mean salinity adult males and females were collected in ($t = -4.76$, $p < 0.01$). Adult females did not appear to utilize estuarine waters as extensive sampling in estuarine areas, with all gear types, resulted in the capture of only 26 adult females over the course of the study. All of the 26 individuals were caught during late May and early June in waters with salinities ranging from 34 to 37 ppt in close proximity to inlets. Parturition occurred in shallow nearshore waters during late May and June as indicated by the presence of neonates with umbilical remains during this time. Neonates were initially observed in shallow nearshore waters and entered estuarine waters shortly after birth, a trend also noted by Castro (1993a). That neonates migrated into areas occupied by adult males and that adult females are absent from these areas indicates that a physiological mechanism could exist that prevents adult females and neonates from competing for food resources.

Neonates ranging in size from 204 to 312 mm FL (mean = 279.30 mm FL, SD = 15.80) were first observed during May and June of each year in estuarine and nearshore waters. Castro (1993a) found that parturition in Bulls Bay occurred in shallow nearshore waters at depths of 9 m or less in late May to early June. Our observations indicate that parturition occurred as early as the first week of May and continued through June. Water temperature and salinity during this period ranged from 21–29°C and 24–37 ppt, respectively. Of the 1,611 neonate and young-of-the-year individuals collected the ratio of female to male was 1:1.05, which was not different from the expected ratio of 1:1 ($\chi^2 = 0.89$, $p > 0.05$). The umbilicus was closed on most neonates approximately 2 weeks after birth and neonates with a fully healed umbilicus were observed from mid-June through early September. Given that neonates and young of the year constituted 26.04% of the total catch of Atlantic sharpnose sharks indicates that South Carolina's coastal waters represent an important primary nursery for this species.

Two-hundred and eleven juvenile Atlantic sharpnose sharks, ranging in size from 458 to 688 mm FL, were observed in the coastal waters of South Carolina between April and November, representing 3.41% of all Atlantic sharpnose sharks captured during this study. The ratio of female to male juvenile Atlantic sharpnose sharks was 1:2.35, which was significantly different from the expected ratio of 1:1 ($\chi^2 = 2.35$, $p < 0.01$), a sex ratio not as skewed as was observed for adults but showing the same trend of males outnumbering females. All juveniles, with the exception of one, were captured in nearshore waters indicating that South Carolina estuarine waters do not represent a secondary nursery for Atlantic sharpnose sharks. Furthermore, as juveniles represented only a small fraction of the total Atlantic sharpnose shark catch it appears that South Carolina nearshore waters are not an important secondary nursery for this species. Before the use of South Carolina waters as a secondary nursery for Atlantic sharpnose sharks can be discounted, additional sampling will need to be done in nearshore waters with gear types that target smaller individuals.

Finetooth shark

A total of 965 finetooth sharks were collected, ranging in size from 383 to approximately 1,370 mm FL. Finetooth sharks were first seen in South Carolina nearshore waters in mid-May, at water temperatures of approximately 22°C. Finetooth sharks were last observed in late October when water temperatures decreased to approximately 20°C. The ratio of adult males to females in nearshore waters was not significantly different than the expected ratio of 1:1 ($\chi^2 = 0.96$, $p > 0.05$). In estuarine waters, the ratio of adult males to females was 1:2.5, which was significantly different than the expected ratio of 1:1 ($\chi^2 = 5.45$, $p < 0.05$). Adults were captured in waters with salinity ranging from 30 to 37 ppt, while juveniles were caught over a salinity range of 25–37 ppt. Juveniles were present in both nearshore and estuarine sampling areas from May through August. During late August, juveniles left estuarine waters and were caught only in nearshore waters where they were present until the end of October. The ratio of juvenile males to females was 1:1.5, which was significantly different than the expected ratio of 1:1 ($\chi^2 = 4.17$, $p < 0.05$). As juveniles were caught in both estuarine and nearshore waters the results of this study suggest that both of these areas represent a secondary nursery for this species.

Neonate finetooth sharks with umbilical remains were collected from late May until mid-June and captured exclusively in estuarine waters in salinities ranging from 18 to 37 ppt, a range greater than that found for juveniles and adults. Observational data suggest umbilical remains stayed attached for a few days after parturition; therefore, free swimming neonates with umbilical remains were taken as good indicators of size at parturition. The size range of pups with umbilical remains was 409–463 mm FL, with the mean size at birth being 443 mm FL (SD = 14.68), which agrees with Castro's (1993b) findings for the size at parturition for this species. Of the finetooth shark neonates captured in July, most had healed umbilical scars and the remaining had mostly healed umbilical scars. By August, nearly all neonates sampled had completely healed umbilical scars. This suggests that the umbilicus persists for approximately 4 weeks after parturition, in agreement with Castro (1993b), who noted the umbilicus heals within 3–4 weeks of parturition. The ratio of neonate males to females was not significantly different than the expected 1:1 ($\chi^2 = 1.63$, $p > 0.10$). The abundance of neonate finetooth sharks in South Carolina's estuarine waters indicated that this area is a primary nursery for this species.

Bonnethead

During the study, 921 bonnetheads, ranging in size from 371 to 1,074 mm FL, were captured in waters with salinities between 16 and 38 ppt. Bonnetheads were first observed in South Carolina waters in mid- to late April when the water temperature was approximately 22°C. From April through August 99.34% of all bonnetheads collected were captured in estuarine waters. The six individuals that were caught in nearshore waters were caught in close proximity to inlets. During late August and early September bonnetheads began to migrate out of estuaries when water temperatures had decreased to 25°C and were caught in nearshore waters until mid-October. The ratio of males to females was 1:5.03, which was significantly different from the expected ratio of 1:1 ($\chi^2 = 406.67$, $p < 0.01$). Juveniles and adults of both sexes co-occured throughout the time that the species was present in South Carolina waters indicating that no habitat partitioning occurred.

All adult females whose reproductive tracts were examined, with the exception of one individual, were pregnant. Pregnant females caught in April and early May carried embryos in very early stages of development. By June the mean size of embryos was 34.03 mm FL (SD = 11.78). When pregnant females began to migrate out of estuarine waters in late August and September, the mean size of pups had increased to 240.14

mm FL (SD = 23.28) (C. M. Jones, unpublished data). During September of 2003, four free-swimming neonate bonnetheads, with a mean size of 230.50 mm FL (SD = 9.0), were collected in Georgia estuarine waters by biologists from the University of Georgia Marine Extension Service (C. Belcher, personal communication). That adult females migrated out of South Carolina estuarine waters during September, neonates were observed south of our sampling areas at approximately the same time, and the smallest bonnethead captured during this study measured 371 mm FL indicated that South Carolina is not a primary nursery area for bonnetheads. It is possible that the mesh size of the gill nets used was too large to collect neonate bonnetheads; however, since 694 neonate Atlantic sharpnose sharks ranging in size from 274 to 371 mm FL were collected with the same gear, it is probable that if neonate bonnetheads were present in South Carolina's estuarine waters, they would have appeared in our catch at sometime over the 6-year span of the study.

Smooth dogfish

A total of 852 smooth dogfish, ranging in size from 495 to 1,186 mm FL, were caught during the sampling period and, with the exception of two individuals, were all collected in nearshore waters. The catch was strongly dominated by females of which 96.56% were considered to be mature. The ratio of males to females was 1:39.57, which was significantly different from the expected ratio of 1:1 ($\chi^2 = 765.18$, $p < 0.01$). This indicates that the nearshore waters of South Carolina are used as an overwintering ground for mature, presumably pregnant (Conrath and Musick 2002) females.

Smooth dogfish migrated into South Carolina waters when the water temperature decreased to approximately 18°C in the mid- to late fall and became less abundant in the spring, when the water temperature rose to 18–19°C. Rarely were any smooth dogfish caught after mid-April. This was in contrast to the findings of Castro (1993a), who indicated that gravid female and neonate smooth dogfish were commonly found off South Carolina in late April and early May and reported that juveniles were occasionally caught in these waters throughout the summer. Despite sampling during this period, no neonates were caught in the nearshore or estuarine waters of South Carolina during this study. Since the movements of smooth dogfish seem to be greatly influenced by water temperature it is possible that during springs and summers when cooler temperatures persist migration may be delayed. If parturition begins in May (Compagno 1984; Rountree and Able 1996; Conrath and Musick 2002) and migration is delayed it is possible that parturition occurs in the nearshore waters of South Carolina. Additional sampling will be needed in nearshore waters during the spring to further examine if smooth dogfish use South Carolina nearshore waters as a primary nursery area.

In their study of smooth dogfish utilization of a New Jersey estuary, Rountree and Able (1996) indicated that adult smooth dogfish might exhibit gill-net avoidance. Smooth dogfish were frequently observed in the areas they sampled but were rarely caught in gill nets. Furthermore, they witnessed several adults come into contact with gill nets and fail to become entangled. If adult smooth dogfish are utilizing South Carolina estuarine and nearshore waters during April and May, as indicated by Castro (1993a), this may explain why they did not show up in our catch.

Blacknose shark

Adult and juvenile blacknose sharks were abundant in the coastal waters of South Carolina from May through October and were occasionally collected during late April and early December. The first occurrence of blacknose sharks during the spring coincided with a water temperature of approximately 24°C. During the late spring and early summer blacknose sharks utilize the coastal waters of South Carolina as a mating area (Driggers et al. 2004). In the late fall and early winter the abundance of blacknose sharks rapidly declined after water temperatures decreased to approximately 19°C. Blacknose sharks were captured in temperatures ranging between 17.2°C and 30.0°C and salinities ranging from 31 to 35 ppt. Of the 524 blacknose sharks, ranging in size from 542 to 1,172 mm FL, collected during the study, 97.90% were captured in nearshore waters. On the 11 occasions when blacknose sharks were captured in estuarine waters they were in close proximity to inlets and the salinity ranged from 34.0 to 35.0 ppt.

There was no indication of habitat partitioning, both spatially and temporally, between adult males and females or between adults and juveniles. Blacknose sharks were often caught in large schools that consisted of juveniles and adults of both sexes, which indicates that this species does not segregate by sex or state of maturity. The ratio of adult males to females was 1:2.34 (χ^2 = 61.28, p < 0.01) and juvenile males to females was 1:1.45 (χ^2 = 10.35, p < 0.01), which were both significantly different from the expected ratio of 1:1.

Castro (1993a) suggested that the estuaries of South Carolina, specifically Bulls Bay, serve as a primary nursery area for this species. Sampling efforts in estuarine waters were not able to confirm the occurrence of neonate blacknose sharks in Bulls Bay nor any other estuarine system sampled within the state. Driggers et al. (2004) examined the reproductive biology of blacknose sharks in the region and despite using multiple gear types, including gill nets, handlines, longlines, and trawls, did not capture neonate blacknose in estuarine waters. While it is possible that blacknose utilize shallow nearshore waters as a nursery, Driggers (unpublished data) extensively sampled this area with handline gear over a 3-year period and did not observe any neonate blacknose sharks. However, 15 young-of-the-year blacknose sharks were collected in nearshore waters, suggesting the possibility that blacknose sharks make limited use of South Carolina's nearshore waters as a nursery.

Sandbar shark

During the study, 421 sandbar sharks were collected, ranging in size from 433 to 1,350 mm FL, in salinities ranging from 13 to 37 ppt. Additionally, 68 individuals too large to be landed and measured were estimated to be up to approximately 1,850 mm FL. Sandbar sharks were abundant in South Carolina waters in mid-April once water temperatures reached approximately 20°C and migrated out of state waters at the end of November when water temperatures were approximately 16°C. The ratio of males to females in the catch was not significantly different than the expected ratio of 1:1 (χ^2 = 3.51, p > 0.05). Sandbar sharks were caught in both nearshore and estuarine waters; however, 93.92% of individuals caught in estuarine waters were under 900 mm FL while only 20.73% of the nearshore catch were less than 900 mm FL. This indicates that sandbar sharks utilize estuarine waters primarily as neonates and juveniles.

Of the 489 sandbar sharks collected only 31 were adults. This may indicate that the three gear types employed were not effective at capturing larger individuals. Juveniles inhabit both nearshore and estuarine waters, indicating that both these areas may serve as secondary nursery areas for this species. Nearly all neonates captured in this study were captured in estuarine waters. The ratio of male to female neonate sharks was not significantly different than the expected ratio of 1:1 (χ^2 = 1.60, p > 0.10). Mean size of neonate sandbar sharks was 524 mm FL (606 mm STL) (SD = 56.75), in agreement with Castro (1983), who described size at birth for neonates as approximately 600 mm STL. Neonates with umbilical remains or an open umbilicus were collected from late May through mid-July indicating that parturition for sandbar sharks may take place over a longer time period than observed for some other species of coastal sharks.

Blacktip shark

Blacktip sharks were captured in South Carolina waters from May until early November and ranged in size from 447 to approximately 1,850 mm FL. Blacktip sharks occurred at temperatures between 19°C and 31°C and over a salinity range of 13–37 ppt, although 98% were captured at salinities between 25 and 37 ppt. Of the 284 blacktip sharks collected during the study only 22 adults were caught, indicating that the three gear types employed were not effective at capturing larger individuals. Both adult female and male blacktip sharks were observed between June and November in nearshore waters and from May to early October in estuarine waters. The ratio of adult females to males was 1:1.38, which was not different than the expected ratio of 1:1 (χ^2 = 0.21, p > 0.50).

A total of 190 neonate and young-of-the-year blacktip sharks were collected during the study. With the exception of one individual, neonates and young of the year were captured exclusively in estuarine waters between May and early September, indicating the importance of the estuaries as primary nurseries for this species. Neonate blacktip sharks with umbilical remains ranged in size from 447 to 593 mm FL (mean = 511.46 mm FL, SD = 34.02), which was slightly larger than the size range at parturition reported by Castro (1996). Parturition occurred over an approximately 1-month period during May and June. The umbilicus healed within a month after parturition, and the umbilical scar was visible as much as 3 months later. By mid-September young of the year had migrated into nearshore waters and were no longer present in our study area by the beginning of November. The ratio of female to male neonate and young of the year blacktip sharks was 1:1.20, which was not different from the expected ratio of 1:1 ($\chi^2 = 1.19$, $p > 0.25$).

Juvenile blacktip sharks, ranging in size from 725 to 1,113 mm FL, were caught in both estuarine and nearshore waters, indicating that this species utilizes both of these areas as secondary nurseries. Juveniles were first seen in nearshore waters in mid-May. By the end of May juveniles were collected in both nearshore and estuarine waters. Juvenile blacktip sharks were not captured in estuaries after the beginning of September and presumably migrated out of South Carolina nearshore waters by the beginning of October.

Scalloped hammerhead

Two-hundred and fifty seven scalloped hammerhead sharks were collected in both estuarine and nearshore waters during this study, only one of which was mature. Not including the mature individual, which was estimated to be approximately 1,850 mm FL, sizes ranged from 274 to 1,014 mm FL. Scalloped hammerheads occurred over a temperature range of 18–31°C and a salinity range of 20–37 ppt. Scalloped hammerheads were present in South Carolina coastal waters from mid-April, when water temperatures had increased to approximately 18°C, through mid-November, when water temperatures decreased to 18°C. They were observed in estuarine waters from mid-May through early Sep- tember in a narrow temperature range from 25°C to 26°C. Scalloped hammerheads were collected in nearshore waters in November as they were presumably migrating out of South Carolina waters.

Neonates dominate the catch 67.31%, occurring from mid-May through the beginning of November. Of the 173 neonates caught only three were captured in nearshore waters, two of these being in October and November when these sharks were likely migrating out of South Carolina waters. The mean size of neonates with an open or partially healed umbilicus was 331.13 mm FL (SD = 25.68), which is in agreement with Castro's (1993a) estimates of size at parturition. The ratio of male to female neonate scalloped hammerheads was not different than 1:1 ($\chi^2 = 0.47$, $p > 0.50$). The data from this study suggests that estuarine waters of South Carolina are important primary nursery areas for this species.

With the exception of the single adult, the rest of the catch consisted of young of the year and juveniles. Of these the ratio of individuals caught in nearshore waters to those caught in estuarine waters was not different from 1:1 ($\chi^2 = 0.98$, $p > 0.25$), indicating that both of these areas are used as secondary nurseries by this species. Large juveniles and adults are frequently caught in South Carolina waters by commercial and recreational fishermen (Driggers, personal observation); however, 80.54% of our catch was com- posed of individuals below 500 mm FL, indicating that the gear used in this study may not be effective at capturing larger individuals of this species.

Spiny dogfish

A total of 136 spiny dogfish *Squalus acanthias* were collected, all from nearshore waters. The size distribution ranged from 490 to 891 mm FL with 91.91% being female, the majority of which (80.00%) were mature. This, and the lack of neonates in our samples, is consistent with the findings of Bigelow and Schroeder (1953) who indicated that mature females occur in nearshore waters and that parturition occurs offshore.

Jensen (1966) reported water temperature preferences for this species to be between 7°C and 13°C. We conducted very limited sampling during winter months but did collect spiny dogfish in late January at a water temperature of 13°C. Large catches of this species were also made in late March when water temperatures were 14°C. They were not encountered after March, a time that coincides with the northward migration of this species (Jensen 1966).

Conclusions

The coastal and estuarine waters of South Carolina represent important pupping and nursery habitats for two of the four species of small coastal sharks commonly encountered in state waters. Parturition of Atlantic sharpnose sharks was observed to occur exclusively in shallow nearshore waters, with neonates subsequently entering estuarine waters within days of birth (Ulrich, personal observation). Neonate Atlantic sharpnose sharks were found in all estuaries sampled, demonstrating that they are capable of utilizing brackish to high salinity waters. Finetooth shark neonates were usually associated with higher salinity estuarine systems such as Bulls Bay. As the majority of adult female finetooth sharks were captured in nearshore waters coinciding with the time of occurrence of neonates in estuarine waters, parturition likely occurs in shallow nearshore waters. However, this trend was not as well defined for finetooth sharks as it was for Atlantic sharpnose sharks since several adult females were captured within estuaries around the time of parturition.

Blacknose and bonnethead sharks apparently do not utilize South Carolina waters as a pupping or nursery ground as extensive sampling over 6 years in both estuarine and nearshore coastal waters did not yield any neonates of either species. Blacknose sharks were exclusively associated with high salinity nearshore waters or inlets. Adult and juvenile blacknose sharks of both sexes were abundant seasonally. The coastal waters of South Carolina are, however, utilized as a mating area for blacknose sharks (Driggers et al. 2004). The majority of bonnetheads collected over the course of the study were adult females. Female bonnetheads were infrequently captured outside of estuarine waters except during times that coincided with migrations into or out of the area during the spring and fall.

South Carolina estuaries are pupping and nursery grounds for three species of large coastal sharks. Neonate blacktip, sandbar, and scalloped hammerhead sharks were caught in all estuaries sampled. While neonate blacktip and sandbar sharks were almost exclusively captured in estuarine waters, neonate scalloped hammerhead sharks were on occasion collected in nearshore waters. South Carolina's importance as pupping and nursery habitats for several small and large coastal shark species emphasizes the need to protect the environmental health of the estuaries and to maintain conservative management strategies adhered to by the South Carolina Department of Natural Resources within state waters. These measures are vital to maintaining healthy stocks and to the recovery of currently overexploited species.

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