Long-Term Movements, Migration, and Temporal Delineation of a Summer Nursery for Juvenile Sandbar Sharks in the Chesapeake Bay Region

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Abstract.-Delineation of essential fish habitat for exploited populations is critical to proper management. Spatial delineation of summer nurseries for elasmobranchs has received increased attention in recent years; however, temporal patterns of nursery use and the delineation of wintering areas are as critical. The lower Chesapeake Bay is the largest summer nursery for sandbar sharks Carcharhinus *plumbeus* in the western Atlantic. The goals of this study were to delineate temporally the use of the nursery and the migratory movements of juvenile sandbar sharks in this estuary, to determine the location of wintering areas, and to determine if philopatry or homing to natal summer nurseries occurs in subsequent years. Longline sampling conducted between 1990 and 1999 indicated that immigration to the bay occurred from late May to early July and was highly correlated with increasing water temperature. Emigration from the estuary occurred in late September and early October and was highly correlated with decreasing day length. We hypothesize that photoperiod is the environmental trigger to begin fall and spring migrations, whereas temperature may elicit the response to move into the estuaries that serve as summer nurseries. Between 1995 and 2003, we tagged 2,288 juvenile sandbar sharks. Seventy-three sharks were recaptured following 4–3,124 d at liberty and the distance from tagging locations ranged from 0 to 2,800 km. Recapture data suggest that most sandbar sharks return to their natal estuaries during summer for at least the first 3 years and return to adjacent coastal waters for up to 9 years. These data also indicate that wintering areas are concentrated off the coast of North Carolina between 33°30'N and 34°30'N latitude, primarily in nearshore waters less than 20 m deep, though sharks older than 7 years were recaptured as far as 60 km from shore. Temporal use of this area by juvenile sandbar sharks occurs from late October until late May for at least the first 7 years and up to 10 years.

Introduction

Most species of marine fishes are migratory to some degree (Meek 1916). Migration enables animals to utilize resources or habitats that are only temporarily, usually seasonally, suitable or tolerable (Aidley 1981). Migratory movements may be broadly divided, based on primary purpose, into alimentary, climatic, and gametic migrations (Heape 1931). The majority of studies of fish migration have been concerned with the timing of the gametic migrations and philopatry (natal homing) of diadromous species, primarily salmonids (Hallock et al. 1970; Smith 1973; Mundy 1984; Tarbox 1988), clupeids (Talbot and Sykes 1958; Melvin et al. 1986; Friedland and Haas 1988), and a few perciforms (Chapoton and Sykes 1961; Boreman and Lewis 1987). A large body of research also has been dedicated to the oceanic migrations of scombrids and other large pelagic teleosts (Mather 1962; Seckel 1972). Published studies of the migratory movements of sharks have primarily been restricted to large oceanic species (Stillwell and Kohler 1982; Casey 1985) or commercially valuable species such as tope Galeorhinus galeus (Holden and Horrod 1979) and spiny dogfish Squalus acanthias (Templeman 1954; Holden 1965; Templeman 1984). Research on the migratory movements of large coastal species, especially juveniles, has been sparse.

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Most temperate estuaries are seasonally dynamic; therefore, estuarine fauna tend to be highly seasonal as well. The diversity and abundance of fishes in estuaries tend to be highest in summer and early fall and lowest in winter (McErlean 1973; Merriner et al. 1976; Cowan and Birdsong 1985; Murdy et al. 1997). Most species migrate to highly productive estuaries for the abundant food sources (alimentary migration) or to bear young (gametic migration) that in turn benefit from increased food availability and potentially higher growth rates (Harden Jones 1968). Physiological limitations later force migrants to leave the estuary to avoid intolerable conditions (climatic migration). These forced migrations have been most often attributed to temperature tolerance (Merriner et al. 1976; Snelson and Williams 1981; Musick and Colvocoresses 1986; Francis 1988); however, it has also been suggested that salinity, turbidity, and dissolved oxygen influence movements and distribution in estuaries (Blaber and Blaber 1980; Cyrus and Blaber 1992). The Chesapeake Bay is one of the most seasonally dynamic marine environments in the world, with temperatures ranging as much as 28°C between summer and winter (Coutant 1985; Murdy et al. 1997). The demersal fish fauna of the region is dominated by a few boreal species in winter and many highly migratory subtropical and temperate species in summer (Musick et al. 1985). Many species rely on the estuary as crucial, seasonal nursery and spawning habitat.

The sandbar shark *Carcharhinus plumbeus* is the most common shark in Chesapeake Bay and is the dominant species in the directed commercial fishery for sharks along the East Coast of the United States (Branstetter and Burgess 1997). It is a large species, reaching at least 239 cm in total length (Compagno 1984), that inhabits insular regions to at least 250 m depth (Garrick 1982). Age at maturity is probably around 15 years (Sminkey and Musick 1995), though estimates have ranged from 12 and 29 years (Casey et al. 1985; Casey and Natanson 1992)

The distribution of sandbar sharks in the western Atlantic ranges from Massachusetts, USA, to the Yucatan Peninsula with another population along the coast of Brazil. They are highly migratory with several hundred kilometers separating summer and winter habitats (Bigelow and Schroeder 1948; Springer 1960). The historical nursery grounds for sandbar sharks along the East Coast of the United States included shallow, principally estuarine habitats from Long Island, New York (possibly north to Cape Cod, Massachusetts) to Cape Canaveral, Florida (Springer 1960). Merson (1998) suggested this range has contracted and now only extends from New Jersey south to South Carolina. A minor nursery area also exists in the northwestern Gulf of Mexico (Carlson 1999).

Chesapeake Bay is the largest nursery area for sandbar sharks in the western Atlantic. Mature females enter the lower reaches of the estuary in May and June to pup (Musick and Colvocoresses 1986). They then migrate offshore while the neonates remain in the highly productive estuarine waters until fall (Musick and Colvocoresses 1986), feeding on abundant blue crabs Callinectes sapidus, mantis shrimp Squilla empusa, Atlantic menhaden Brevoortia tyrannus, summer flounder Paralichthys dentatus, and miscellaneous sciaenid fishes (Medved and Marshall 1981; Cowan and Birdsong 1985; Ellis 2003). Young sandbar sharks continue to use Chesapeake Bay as a nursery during the warmer months for the first 4-10 years of life (Sminkey 1994). They then remain coastal, with the exception of mature females, which only enter temperate estuaries to bear young.

Young sandbar sharks are particularly susceptible to localized depletion when aggregated in the estuaries. A fishery developed in 1996 that may have harvested as much as 75% of the juvenile population in Chesapeake Bay (Grubbs and Musick, unpublished data). It has been hypothesized that many carcharhinid sharks are philopatric to their natal nurseries. Populations that show natal philopatry may be slower to recover from local overharvesting (Robichaud and Rose 2001) and may be more susceptible to habitat degradation. Therefore, defining nursery essential fish habitat (EFH) is of even greater importance for these species (Hueter et al. 2002). In addition, juvenile sharks are easily targeted when concentrated in wintering areas to the south (Camhi 1998; Jensen and Hopkins 2001). The spatial and temporal delineation of summer and winter nurseries is an important part of defining EFH for this species and is critical for effective management of the stock.

Grubbs and Musick (2005) reported that the principal nursery in Chesapeake Bay is limited to the southeastern portion of the estuary, where salinity is greater than 20.5 and depth is greater than 5.5 m. The temporal pattern of use and timing of migratory movements have not been formally investigated. The primary objectives of this study were to delineate the temporal use of summer nurseries in Chesapeake Bay by sandbar sharks and to determine what factors act as catalysts to begin migrations. Secondary objectives were to use mark-recapture data to delineate winter nurseries spatially and temporally and to determine if juvenile sandbar sharks return to their natal summer nurseries in subsequent years.

Methods

Sampling gear

Data were obtained during longline cruises conducted by the Virginia Institute of Marine Science (VIMS) to monitor coastal shark populations. We used commercial-style longlines consisting of 4.8-mm tarred, nylon mainline that was anchored at each end and marked by buoys equipped with radar reflectors. Three-meter gangions were spaced approximately 18 m apart along the mainline and a large inflatable buoy was attached to the mainline following every 20th gangion. Each gangion was composed of a stainless-steel tuna clip attached to a 2-m section of 3.2-mm tarred nylon trawl line, the end of which was attached to a large barrel swivel. We crimped one end of a 1-m section of 1.6-mm galvanized aircraft cable to the swivel and the other end to a Mustad-9/0, J-hook. A standard set consisted of 80-100 hooks and was approximately 2 km in length. Bait consisted mostly of Atlantic menhaden and Atlantic mackerel Scomber scombrus. Soak time for each set was between 3 and 4 h. Beginning in 1996, we expanded the survey to include sets using 12/0 circle hooks in addition to the sets using standard J-hooks. The circle hooks are smaller and more efficient at capturing juvenile sandbar sharks. Capture mortality is also lower with the circle hooks as they tend to hook the shark in the corner of the mouth. This increases the proportion of captured sharks that are healthy enough to be tagged and released.

Sampling design

Since its inception in 1974, the VIMS longline survey has routinely included stations in Chesapeake Bay. Two locations in the southeastern portion of the estuary, Kiptopeke $(37^{\circ}10'N, 76^{\circ}00'W)$ and Middleground $(37^{\circ}06'N, 76^{\circ}03'W)$, have been standard stations since 1980 (Figure 1). We used monthly data collected at these two sites over the 10-year period from 1990 to 1999 to delineate temporal migration patterns and use of Chesapeake Bay as a nursery.

The statistical unit was catch per unit of effort (CPUE) defined as the number of juvenile sandbar sharks per 100 hooks calculated for each set. For each shark caught, we recorded sex, hook type, precaudal length (PCL), defined as the distance from the tip of the snout to the caudal peduncle, and stretched total length, defined as the distance from the tip of the snout to the tip of the caudal fin when stretched in line with the body axis. We assigned a survival factor, consisting of five subjective levels, to all sharks captured (1 =excellent, 2 = good, 3 = fair, 4 = poor, and 5 =dead). Sharks that struggled vigorously while being measured and swam away rapidly following release were assigned survival factor 1. Those that struggled moderately but swam strongly upon release were assigned survival factor 2. Sharks that struggled very little while being measured and swam slowly upon release were assigned survival factor 3. Those that did not struggle at all but showed nictitating membrane and jaw response and attempted to swim when released, usually with apparent equilibrium disruption, were assigned survival factor 4. Sharks that showed no nictitating membrane or jaw responses were assumed dead and assigned survival factor 5.

We tagged all sharks that were in excellent, good, or fair condition using Hallprint nylontipped dart tags using a stainless-steel applicator. The tags were inserted into the musculature just below the first dorsal fin with an angle of attack of $40-50^{\circ}$ relative to the sagittal plane of the shark's body. The tag was pushed through the basal cartilages of the first dorsal fin with the barb facing the posterior direction, thereby locking the tag behind the cartilage.

Surface and bottom temperature (°C), minimum and maximum depth (m), and time of day were recorded for each longline set. We used a Hydrolab Multiprobe to measure temperature, salinity (practical salinity scale), and dissolved oxygen (ppm) at 2-m intervals from surface to bottom for stations sampled from 1996 to 1999. In addition, day length (hours), tidal phase



FIGURE 1. Study area and locations of stations K (Kiptopeke) and M (Middleground) sampled by the VIMS longline survey from 1973 to 1999.

(\pm meters per second), and lunar phase (1–8) were calculated for all stations. We defined day length as the time between sunrise and sunset, calculated for each set using data supplied by the U.S. Naval Observatory Astronomical Applications Department. Mean velocity of tidal current 1 h after setting the longline was estimated as a proxy for tidal phase. These data were from two current stations from the software program Tides and Currents 2.0 (Nautical Software Inc.). These stations were approximately 2 km from our Kiptopeke and Middleground stations. Velocities were given a positive sign during flooding tides and a negative sign during ebbing tides. Lunar phase was recorded for each set as one of eight phases (1 = new moon, 2 = waxing crescent, 3 =first quarter, 4 =waxing gibbous, 5 =full moon, 6= waning gibbous, 7 = third quarter, and 8 = waning crescent).

Analysis of CPUE data

Temporal nursery delineation.—The sampling period was 1 May to 15 October of each year. We divided this period into 11 semimonthly intervals and calculated the mean CPUE for each interval using the 10-year, J-hook data set and the 4-year, circle-hook data set. We plotted these results to determine the timing of the summer immigration to Chesapeake Bay and the fall emigration from the estuary. To account for interannual variability in CPUE, we multiplied individual CPUE values by a scaling factor so that yearly means at full recruitment were equal. The scaled CPUE data were not normally distributed; therefore, we used the square-root transformation where

CPUE' = $\sqrt{\text{CPUE} + 0.5}$

This transformation is appropriate for CPUE data due to the frequent occurrence of zero values and is preferred to the more common logarithmic transformation when the variances are proportional to the means (Bartlett 1936; Zar 1996). The transformed data were normally distributed according to Shapiro-Wilk and Anderson-Darling tests.

Correlation with environmental variables.— Linear regressions of the CPUE data were performed using bottom temperature, bottom salinity, bottom dissolved oxygen, day length, tidal phase, and lunar phase as independent variables to investigate potential stimuli for migration. The dependent variable for these regression analyses was the transformed CPUE for each individual set. We also performed regressions using the semimonthly CPUE means as the dependent variable and using the same independent variables as above. Regressions using aggregated data, such as averages, are commonly referred to as ecological correlations. Ecological correlations can be misleading because they typically overstate the strength of the associations since the individual variability is eliminated, and it is important to realize that the results apply to groups and not individuals (Robinson 1950). However, the results can be useful in comparing the relative strength of the correlations obtained from the regression analyses. Significance was evaluated at alpha = 0.05 in all cases. The coefficient of determination (r^2) was examined for all significant tests to predict which independent variable might influence migratory movements.

We only used the 10-year data set employing J-hooks for this analysis due to lower variance and larger sample sizes. Only samples where the independent variable under consideration was measured in situ were included in these analyses; therefore, the number of observations varied depending on the independent variable. For instance, salinity and dissolved oxygen were only measured for stations sampled from 1996 to 1999; therefore, the CPUE data from 1990 to 1995 were excluded for the analyses using these two variables. The fewest observations were available for dissolved oxygen due to occasional failure of the sensor.

Analysis of mark-recapture data

Recapture data were examined in several ways. Rates of tag recaptures were compared as a function of condition factor, gear type, and user group (e.g., recreational fishers, commercial fishers). Days at liberty were calculated for each recapture. We mapped all recaptures using ArcView 3.2 GIS software and calculated the distance between tagging and recapture locations as the shortest distance between the two points using land as a bounding graphic. In other words, sharks were not allowed to cross over land to reach the recapture location giving a conservative but realistic point-to-point distance estimate. Mean recapture distance and time at liberty were calculated. We used data from tag returns to investigate long-

term movements and migration patterns and to

validate the temporal nursery-delineation patterns determined using the CPUE data. The temporal distribution of sharks recaptured in Chesapeake Bay was used to estimate timing of arrival and departure from the summer nursery. These data provided an independent assessment temporal trend obtained using CPUE data. We used recaptures made in winter and spring to determine the general location of the principal wintering grounds for the juvenile sharks and to estimate the temporal use of these areas. Recaptures made in subsequent summers, those having completed at least one winter migration prior to recapture, were used to determine if these sharks return to their natal estuary as a summer nursery (i.e., evidence of philopatry) or move to new areas in subsequent years.

Finally, we compared growth data from sharks that were reliably measured at the time of recapture to three published growth models for this population. Based on aging using vertebral rings Casey et al. (1985) and Sminkey and Musick (1995) estimated the age at maturity at around 12 and 15 years, respectively. However, using growth data from tag recaptures, Casey and Natanson (1992) suggested that maturity may not be reached until 29 years. These differences substantially impact demographic analyses used in managing the stock (Sminkey and Musick 1996). We estimated the ages at tagging based on length frequencies and month. Based on the time at liberty, the ages at recapture and growth rates were calculated. These data gave an indication of the effect tagging had on growth and provided an independent assessment of the published growth curves for the first years of life.

Results and Discussion

Analysis of CPUE data

Sampling summary.—We made 100 standard longline sets (J-hooks) at the Kiptopeke (59 sets) and Middleground (41 sets) stations between 1990 and 1999 (8,619 total hooks) and 59 sets between 1996 and 1999 using the alternative gear with the smaller circle hooks (2,588 total hooks). The CPUE was generally higher for the circle hooks. Mean CPUE from 1996 to 1999 was 12.4 sharks per 100 hooks for the circle hook, compared to 4.9 sharks per 100 hooks for the J-hooks. The interannual variability in the J-hook data were very high (Figure 2). Populations of large coastal sharks along the East Coast declined precipitously throughout the 1980s, yet CPUE in Chesapeake Bay increased during this period and peaked in 1992. We hypothesize that this was a function of increased survivorship of juveniles due to lower predation pressure from large sharks. CPUE declined and then stabilized in the few years following the implementation of a federal management plan in 1993. In 1996 and 1997, a directed fishery developed for juvenile sandbar sharks in Chesapeake Bay, resulting in extremely



C. plumbeus CPUE (Stations K & M / June-September)

FIGURE 2. Mean summer CPUE (sandbar sharks per 100 hooks) using standard J-hooks at stations K and M during 1980, 1981, and 1990–1999. (Error bars = standard error).

depressed CPUE. These data were scaled to account for this variability prior to use in the regression and correlation analyses.

Temporal nursery delineation.—Using a second order polynomial, we fit a curve to the raw data (prior to scaling and transformation) of each gear type (Figure 3A). We also plotted the semimonthly means of these data (Figure 3B). The same temporal trend in CPUE was apparent for both hook types. No sharks were caught during the 1–15 May time period and very few were caught from 16 to 31 May. Most immigration (including neonates and juveniles) occurred from early June to early July and emigration occurred from early September to early October. Interestingly, circle-hook CPUE was depressed during the late July and early August time periods. This may be a function of the higher variance associated with this data set, or it may represent the dispersal of smaller juveniles to more suitable regions of the nursery farther from the mouth of the estuary. Similar dispersal trends have been



Sandbar shark: raw CPUE

FIGURE 3. Catch per unit of effort (sandbar sharks per 100 hooks) for Middleground and Kiptopeke stations using standard J-hooks hooks (1990–1999) and smaller circle hooks (1996–1999). (A) Raw CPUE versus day of year, (B) Semimonthly mean CPUE (error bars = SE).

observed in the movement patterns of other fishes in Chesapeake Bay, such as striped bass *Morone saxatilis* (Moore and Burton 1975). Perhaps this is an adaptation to avoid predators such as larger juvenile sandbar sharks and adult sand tigers *Carcharias taurus* that are found in the lower bay and are known to feed on neonate and small juvenile sandbar sharks.

Correlation with environmental variables.— Highest CPUE in the J-hook data were observed during the interval from 16 to 31 July; therefore, it was included in the immigration and emigration periods as an end point for the regression and ecological correlation analyses. We thereby defined the immigration period as the six sampling intervals from 1 May to 31 July and the emigration phase as the six sampling units from 16 July to 15 October for the ecological correlation analysis.

During the immigration period, bottom temperature was the only variable significantly correlated with CPUE (Table 1). Mean surface and bottom temperature mirrored the temporal trend in scaled CPUE very closely during this period (Figure 4A). We caught no sharks when surface and bottom temperatures were below 17.6°C and 15.9°C, respectively. Catch per unit of effort was greater than 2.0 only when surface and bottom temperatures were greater than 21°C and 20°C, respectively. Shark CPUE peaked when the bottom temperature was approximately 24°C. Linear regression of the transformed CPUE was highly significant (p < 0.001, $r^2 = 0.61$), using bottom temperature as independent variable (Table 1; Figure 5A). The ecological correlation using semimonthly mean temperature and CPUE values was also highly significant (p < 0.001, $r^2 = 0.95$) during immigration. Day length was nearly significant (p = 0.055) during immigration, however; the coefficient of determination (r^2) was only 0.07, suggesting little correlation between day length and CPUE during this period (Figure 5B). Indeed, day length changed little during the immigration period, varying by only 42 min between 1 May and 31 July (Figure 4B), and the ecological correlation was not significant (p = 0.257).

TABLE 1. Summary statistics for linear regression (Raw) and ecological correlation (Means) analyses for immigration and emigration periods. Dependent variables for regression analyses were all transformed CPUE values with corresponding values of the independent variable under consideration. Dependent variables for the ecological correlations were the semi-monthly means of the transformed CPUE values used in the regressions. df = degrees of freedom; F = calculated F-statistic; p = probability level (significant when ≤ 0.05).

Independent variable	Data	df	F	р
Immigration period (1 May–31 July)				
Bottom temperature	Raw	43	66.80	< 0.001
*	Means	5	78.43	< 0.001
Bottom salinity	Raw	28	0.54	0.469
	Means	5	2.16	0.216
Bottom dissolved oxygen	Raw	18	0.61	0.444
	Means	5	0.03	0.877
Day length	Raw	52	3.86	0.055
	Means	5	1.75	0.257
Tidal phase	Raw	52	2.63	0.111
	Means	5	4.14	0.112
Lunar phase	Raw	52	0.72	0.401
	Means	5	0.99	0.375
Emigration period (15 July-15 October)				
Bottom temperature	Raw	49	6.68	0.013
	Means	5	4.22	0.109
Bottom salinity	Raw	33	0.39	0.536
	Means	5	1.99	0.231
Bottom dissolved oxygen	Raw	25	0.66	0.424
	Means	5	0.54	0.514
Day length	Raw	59	29.23	< 0.001
	Means	5	51.16	0.002
Tidal phase	Raw	59	0.17	0.679
-	Means	5	1.78	0.253
Lunar phase	Raw	59	0.27	0.602
	Means	5	2.49	0.190



FIGURE 4. Mean semimonthly CPUE (sandbar sharks per 100 hooks) with (A) mean sea-surface temperature in degrees Celsius and(B) day length in hours at Middleground and Kiptopeke stations combined for the years 1990–1999 (standard 9/0 hooks only). All error bars = standard error.

The linear regression results for the emigration period were only significant for bottom temperature and day length (Table 1). Mean CPUE began to decline more than 1 month prior to significant declines in mean surface temperature, which never cooled below 21°C during the emigration period (Figure 4A). While the regression for bottom temperature was significant during emigration (p = 0.013, $r^2 = 0.12$), the coefficient of determination suggests that the association was not very strong, accounting for only 12% of the variation in CPUE (Table 1; Figure 5C). The ecological correlation for bottom temperature was not significant during emigration (p = 0.11). Day length declined continuously during the emigration period, decreasing by approximately 2.6 h (Figure 4B). Linear regression between transformed CPUE and day length was highly significant (p < 0.001, $r^2 = 0.34$) during this period, and mean day length was highly correlated (p = 0.002, $r^2 = 0.93$) with mean CPUE as well (Figure 5D). These data suggest that day length (photoperiod)



FIGURE 5. Scatter plots with fitted lines for transformed CPUE and semi-monthly mean CPUE (sandbar sharks per 100 hooks) versus (A) sea-surface temperature during immigration (1 May–31 July), (B) day length during immigration, (C) sea-surface temperature during emigration (15 July–15 October), and (D) day length during emigration. All error bars = standard error.

may be the environmental stimulant to initiate fall migrations. Photoperiod has been shown to initiate migration in birds (Berthold 1975), and Aidley (1981) suggested that it might be a possible trigger for fishes. Day length may also serve as the stimulus to begin spring migrations from wintering grounds. In other words, day length may signal juvenile sharks to begin migrating north, yet they remain in coastal waters until increasing temperatures stimulate movement into the estuarine nursery. Additional data from the wintering grounds are needed to test this hypothesis.

Salinity, measured on the practical salinity scale (Lewis and Perkin 1978; Joint Panel on Oceanographic Tables and Standards 1980) at the two standard stations ranged from a minimum of 17.0–30.2 on the surface and from 19.3 to 30.4 on the bottom. Bottom salinity was typically lowest in May and highest from late July to early September. Due to the complex circulation patterns in Chesapeake Bay, however, the temporal variability in salinity is highest on the scale of tidal cycles rather than seasons. Bottom salinity was not significantly correlated with CPUE during immigration or emigration periods (Table 1). Bottom dissolved oxygen ranged from 4.0 to 8.4 ppm; however, no relationship was found between dissolved oxygen and CPUE. Likewise, lunar phase and tidal cycle were not significantly correlated with CPUE (Table 1).

Analysis of mark-recapture data

Tagging summary.—We tagged 2,288 juvenile sandbar sharks from 1995 through 2003 (Figure

6A). We tagged 59.2% (n = 1,355) of the sharks inside Chesapeake Bay and 23.7% (n = 542) in seaside lagoons, tidal creeks, or inlets along Virginia's Eastern Shore. The remaining 17.1% (n = 390) were tagged in waters along the Virginia and North Carolina coasts. The mean precaudal length of tagged sharks was 61.3 cm (range: 37.0–118.0 cm), and 80% were less than 75 cm PCL. Exactly 50% of the sharks tagged were males and 50% were females. Length frequencies were comparable, though above 75 cm PCL, the majority of sharks tagged were females (Figure 6B). We tagged more sharks in 1998 (n = 416, 18.2% of total) and 1999 (n = 439, 19.1% of total) than any other years (Table 2). Sampling and tagging only occurred from May to October of each year. The fewest sharks were tagged in May (n = 67, 2.9%) and the most in July (n = 666, 29.1%).

Recapture rates.—To date, 73 shark recaptures have been reported giving an overall recapture rate of 3.2%. Recapture rates ranged,



FIGURE 6. (A) Geographic distribution of tagging effort for juvenile sandbar shark by VIMS during summers of 1995–2003. (B) Length frequencies of tagged sandbar sharks.

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Year	Total # (%)	May #	June #	July #	August #	September #	October #
1995	169 (7.4%)	0	0	36	34	99	0
1996	219 (9.6%)	10	37	54	61	30	27
1997	357 (15.6%)	2	31	132	55	96	41
1998	416 (18.2%)	9	44	149	137	62	15
1999	439 (23.8%)	30	107	138	121	21	22
2000	246 (10.8%)	0	52	41	49	64	40
2001	163 (7.1%)	0	63	30	49	20	1
2002	118 (5.2%)	1	49	44	6	18	0
2003	161 (7.0%)	15	55	42	1	28	20
Total #	2,288	67	438	666	513	438	166
(%)		(2.9%)	(19.1%)	(29.1%)	(22.4%)	(19.1%)	(7.3%)

TABLE 2. Tagging summary for juvenile C. plumbeus tagged by VIMS (1995–2003).

according to the year of tagging, from 1.84% for sharks tagged in 2001 to 4.48% for those tagged in 1997. Recreational fishers returned more tags than any other group in our study (n = 38). Commercial fishers accounted for 27 of the reported recaptures. Fourteen of these were reported from the longline fishery, seven from the North Carolina sinknet fishery, and six from the Virginia gillnet fishery. However, independent fishery observers were responsible for 80% of the commercial recaptures in spite of very low observer coverage in these fisheries. Coverage by observers in the longline fishery was between 1.7% (Branstetter and Burgess 1997) and 4.2% (Branstetter and Burgess 1998), and that of the sinknet fishery was much less than 1%1 (Jensen and Hopkins 2001), suggesting that underreporting in the commercial sector was extreme. Six tagged sharks were recaptured by our longline survey, and researchers from the North Carolina Aquarium and the National Marine Fisheries Service returned one tag each. Information from seven of the reported recaptures was discarded due to incomplete data, leaving 66 that were used in the analyses.

Recapture rate was not affected by shark condition. Those tagged in "excellent" condition were recaptured at a rate of 2.4%, while the return rates for those tagged in "good" and "fair" condition were 4.0% and 3.6% respectively. No sharks in "poor" condition were tagged. Recapture rates were affected by gear and hook type. The return rate was much higher for circle hooks (4.0%) than for the larger J-hooks (2.1%). Length frequencies were similar for sharks caught with each hook type; therefore, this may reflect a difference in hook-related survivorship. In addition, 76 sharks were tagged after being caught incidentally using rod and reel gear. The return rate for these (6.5%) was much higher than either of the longline gears.

Our overall recapture rate (3.2%) was onehalf of the rate (6.4%) reported for juvenile sandbar sharks in Delaware Bay (Merson and Pratt 2001). The difference may be attributed to experimental factors such as differences in gear type, tag types, or tagging methodology, or it may reflect heavier pressure from recreational fishers in Delaware Bay resulting in many short-term recaptures. Recreational fishers accounted for 92% of recaptures in the Delaware Bay study, and only 16% of the recaptured sharks were at liberty more than 100 d (rate = 1.0%). By comparison, recreational fishers only accounted for 52% of recaptures in our study in Chesapeake Bay, yet 59% of our recaptures were at liberty more than 100 d (rate = 1.9%). In addition, Merson and Pratt (2001) primarily tagged neonate sandbar sharks, and our recapture rate for neonates was more comparable at 5.5%.

Movements and nursery use.-Tagged sharks were recaptured after a mean of 457 d at liberty (range: 4-3,124 d). The mean distance between tagging location and recapture location was 190 km and ranged from 0 to 2,800 km. Fortysix of 66 (69.7%) recaptures were made in Virginia waters. Twenty-three of these were recaptured during the same summer they were tagged, following a mean of 30 d at liberty (range = 4-82d). The mean distance between tag and recapture locations for these sharks was 23.8 km (range = 0-89 km). All except one of these individuals were recaptured in Chesapeake Bay or tidal creeks on Virginia's Eastern Shore (Figure 7). The one exception was a larger juvenile estimated to be approximately 5 years old. All others were approximately 3 years old or younger. Our data suggest that the sharks show some degree of site

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FIGURE 7. Short-term tag recaptures. All sharks recaptured the same summer in which they were tagged.

fidelity but also actively move throughout the estuary during summer. For instance, one shark was recaptured approximately 32 km from its tagging location only 4 d after being tagged, whereas another was recaptured within 1 km of the tagging location after 44 d. Of the 23 short-term recaptures, three were recaptured within 1 km and seven were recaptured within 5 km of their tagging locations.

The remaining 23 Virginia recaptures occurred in subsequent summers following a mean of 587 d at liberty (range = 225-2,173 d). The mean distance between tag and recapture locations was 43.5 km (range = 0-135 km). One shark was recaptured in the same location after nearly 2 years at liberty, and seven were recaptured within 10 km of their tagging locations. Eleven of these long-term recaptures were made in Chesapeake Bay (Figure 8A), three were recaptured in tidal creeks on Virginia's Eastern Shore, and eight were recaptured in nearshore coastal waters (Figure 8B). All of the sharks recaptured in Chesapeake Bay were estimated to be 1 or 2 years old, while those recaptured in the tidal creeks or coastal waters were between 2 and 5 years old. One recapture was made offshore (~100 km from the Virginia coast) after 6 years at liberty and was estimated to be 9 years old at recapture.

The CPUE data suggested the summer nursery area is used from late May to mid-October. During the longline survey, the earliest sandbar sharks were caught in Chesapeake Bay was on 27 May and the latest they were caught was 11 October. Comparably, the earliest recapture of a tagged sandbar shark in Chesapeake Bay was on 28 May and the latest was on 15 October (Figure 9A). These results are similar to those found for sandbar sharks in Delaware Bay, where Merson and Pratt (2001) captured sandbar sharks as early as 3 June and as late as 2 October. These data indicate that the duration of seasonal use of Delaware Bay may be slightly shorter than for Chesapeake Bay. This would be reasonable due to the higher latitude of Delaware Bay; however, this apparent contraction may only reflect differences in sample size. Merson and Pratt (2001) included 31 sets (gill net and longline combined) over a 3-year period, compared to 159 sets (longline only) over10 years in our study.

Wintering areas.—Springer (1960) suggested that the wintering grounds for juvenile



FIGURE 8. Evidence of natal homing. Tag recaptures made in Virginia waters in subsequent years (A) < 32 km and (B) > 32 km from tagging location. All were recaptured in summer months following at least one winter migration.



FIGURE 9. (A) Temporal delineation of summer nursery of sandbar sharks using tag recapture data. Distance between tag and recapture location versus day of year of recapture. (B) Location and temporal delineation of winter nursery of *C. plumbeus* using tag recapture data. Latitude of recapture location versus day of year of recapture. (C) Evidence of natal homing from tag recaptures. Distance from tagging location versus recapture day of year for all sharks recaptured less than 140 km from the tagging location.

sandbar sharks are concentrated south of the summer nurseries in nearshore waters off the coast of North Carolina. Twelve tagged sharks in our study were recaptured between mid-October and mid-May. All of these were in North Carolina waters, generally between Avon and Cape Lookout (Figure 10A). Sharks were recaptured in this region from their first to their 10th winters of life. Most were caught within 20 km of shore, though older juveniles (7-10 years) were caught up to 60 km offshore. The mean distance from the tagging locations was 294 km (range = 200-390 km), and the mean time at liberty was 579 d (range = 70-3,124 d). The earliest of these recaptures was on the 25 October and the latest was on the 16 May, supporting the timing of the migratory movements based on the CPUE data. These data suggest that the nearshore waters between 34°30'N and 35°30'N latitude serve as principal winter nurseries for juvenile sandbar sharks (Figure 9B). These findings are in agreement with those of Jensen and Hopkins (2001), who reported, based on bycatch data from a sinknet fishery, that nearshore waters off Cape Hatteras serve as principal wintering areas from late October through May.

Philopatry.—Gerking (1959) defined homing or philopatry as "going to a place formerly occupied instead of equally probable places." Fiftyfour of the 66 recaptured sharks were caught during the period Chesapeake Bay is used as a summer nursery, late-May to mid-October. Thirty-one of these were recaptured after at least one winter at liberty, and 23 of these were recaptured in Virginia waters. Fourteen were recaptured after approximately 1 year at liberty, six after 2 years at liberty, and one each after 3, 4, and 6 years at liberty (Figure 9C). The age at recapture, based on estimated age at tagging from length-at-age data from Sminkey (1994), ranged from 1 to 9 years. In all, 14 sharks were2 years old or less when recaptured in subsequent summers. Twelve of these (86%) were recaptured in the estuary where they were tagged providing evidence for philopatry in this species (Figure 8). Additionally, 12 sharks were between 3 and 5 years old when recaptured in subsequent years and 10 of these (83%) were recaptured in the same region they were tagged, though most were caught in nearshore waters rather than in the estuaries or tidal creeks. Five sharks were 6 years or older when recaptured, and only one of these (20%) was recaptured in Virginia waters.

Eight sharks recaptured between late-May and mid-October were not caught in Virginia waters (Figure 10B). Three were recaptured north of Virginia and five were recaptured to the south. Two of the northern individuals were approximately 6 years old when recaptured near Brigantine Inlet, New Jersey and off Long Island, New York. Juvenile sandbar sharks are more coastal at this age and perhaps they show less regional fidelity in their migratory patterns. The third was tagged in Virginia coastal waters along Virginia Beach in October 1999. These nearshore waters are part of the migration route for sharks from nurseries north of Chesapeake Bay, and this shark was recaptured the following August in Little Egg Harbor, New Jersey. It is probable that this shark was tagged during its fall migration to southern wintering grounds and then returned the following summer to its natal summer nursery in New Jersey.

The five southern recaptures (Figure 10B) were made in the coastal waters off Florida (2), South Carolina (1), and North Carolina (2). Both of the sharks recaptured in Florida were approximately 3 years old when tagged. One was recaptured off of Jupiter Inlet, approximately 1,450 km from its tagging location, after nearly 7 years (2,525 d) at liberty, and the other was recaptured in the northern Gulf of Mexico near Destin, approximately 2,800 km from its tagging location, after nearly 6 years (2,180 d) at liberty. These recaptures are consistent with the hypothesis that, by age eight, most juvenile sandbar sharks no longer return to the summer nursery areas to the north. The three remaining recaptures represent one probable and two certain departures from philopatry. All three were tagged as neonates in Chesapeake Bay or nearby tidal creeks. One was recaptured in Calibogue Sound near Hilton Head, South Carolina on 23 May. While this is 5 d prior to the earliest recapture in Chesapeake Bay, the recapture location was 830 km from the tagging location; therefore, it is unlikely this animal would have returned to Chesapeake Bay during that summer. The remaining two were recaptured in subsequent summers in the Cape Fear River in North Carolina on 31 July and 22 September after 1 and 3 years at liberty.

These data indicate that most juvenile sandbar sharks return to their natal summer nurseries for the first 2 years and return to the region for at least 5 and up to 9 years. We consider this strong evidence of juvenile philopatry. Given the rela-

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FIGURE 10. Long-distance tag returns. (A) Recaptures made on wintering grounds between the 25th of October and the 16th of May. (B) Recaptures made between late May and early October that were not in Virginia waters.

tively small sample size, additional data are needed to corroborate these results and examine the duration of philopatry to determine if females maintain this bond to adulthood, returning when mature to deliver their own pups. In addition, future research directions should focus on determining what environmental cues the juvenile sharks use to discern their natal nursery. Olfaction has been well documented as the principal stimulus for homing in diadromous fishes (Hasler and Scholz 1980). Harden Jones (1968) suggested that marine fishes also might use olfactory cues from groundwater seepage to locate natal habitats.

Growth rates.—We obtained reliable length measurements for 22 recaptured sharks that were at liberty more than 120 d. Estimated age at recapture, based on size and month at tagging, ranged from 0.86 to 9.28 years. Mean precaudal growth was 9.9 cm/year and ranged from 1.2 to 24.2 cm/year. Growth vectors are shown in Figure 11A. These data are compared with the three published age and growth studies in Figure 11B. Growth rates of recaptured sharks in our study were slightly faster than predicted by Casey et al. (1985) and much faster than predicted by Casey and Natanson (1992). However, our growth data corresponded very closely to the growth curve published by Sminkey and Musick (1995), providing support for the validity of this model until 10 years of age.

The mean growth rate for recaptured sandbar sharks published by Casey and Natanson (1992) was 4.66 cm/year. This is less than one-half of the rate from recaptured sharks in our study (9.9 cm/ year). Some of this difference may be a function of the size of the tagged animals. Casey and Natanson (1992) included larger animals and much longer times at liberty in some instances. If this were true, however, it would suggest a very poor fit between the growth model published by Casey and Natanson (1992) and actual growth rates at younger ages. Much of the difference may be a function of tag type. The growth rate reported by Casey and Natanson (1992) for sharks tagged with rototags was 5.2 cm/year and that of steel dart tags was only 3.1 cm/year, compared to 9.9 cm/year for the nylon dart tags in our study. This suggests that nylon dart tags have less impact on growth rates in these sharks. This example also illustrates one problem associated with constructing growth curves from recapture data and the importance of considering tag effects when choosing tag types.

Conclusions

Temporally and spatially defining EFH for the various life stages of exploited species is critical for proper management. Defining EFH should be based on the importance of that particular habitat to the species, the susceptibility of the habitat to exploitation and degradation, and the availability of the habitat to the population. Estuarine habitats are critical to early life stages of many species and serve as important nurseries for sharks. Unfortunately, these areas are highly susceptible to anthropogenic degradation, and juvenile sharks are easily exploited while concentrated in these areas. In this study, we defined temporally summer EFH for sandbar sharks in Chesapeake Bay. We also provided supporting data for the temporal and spatial delineation of winter habitats for this population.

Sandbar sharks occurred in Chesapeake Bay from late-May until mid-October. The majority of immigration occurred after 15 June, and CPUE peaked in late July, indicating full recruitment to the estuary by this time. Immigration to the estuary was highly correlated with increasing water temperature. Sharks were absent from longline catches when bottom temperature was below 15.9°C, and most recruitment occurred when bottom temperature was above 20.0°C. Our data suggested sandbar sharks emigrated from Chesapeake Bay in late September and early October to begin the fall migration to wintering grounds. Catch per unit of effort was highly correlated with day length during the emigration period, suggesting that photoperiod may act as the stimulus to initiate the fall migration. Catch per unit of effort during immigration and emigration were not significantly correlated with salinity, dissolved oxygen, day length, tidal phase, or lunar phase.

Tagged sharks were recaptured as far north as New York and New Jersey and as far south as the Atlantic and Gulf coasts of Florida; however, most were recaptured in Virginia waters. Sharks were recaptured in Chesapeake Bay as early as 28 May and as late as 15 October, supporting the temporal pattern of use from the CPUE data remarkably well. In addition, our tag–recapture data indicate that the migrations of juvenile sandbar sharks are spatially extensive and that the principal wintering

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FIGURE 11. Growth data from recaptured sharks. (A) Growth trajectories connecting length (PCL) at tagging and recapture versus estimated age based on size and month of tagging. (B) Growth of recaptured sharks compared to von Bertalanffy growth curves from Casey et al. (1985), Casey and Natanson (1992), and Sminkey and Musick (1995). Error bars for data from Sminkey and Musick (1995) represent standard deviation.

areas are located off the coast of North Carolina. The earliest fall recapture in this region was on 25 October and the latest spring recapture in this area was on 23 May. Our tag–recapture data also provided preliminary evidence of philopatry, as most sharks recaptured in summer months in later years were caught very close to the area where they were tagged. Three published models have estimated that Atlantic sandbar sharks mature at approximately 12, 15, and 29 years of age. Growth data from recaptured sharks in this study, applicable to 10 years of age, agreed closely with the model that estimated age at maturity to be 15 years.

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