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[Article]

# Distributions of Sharks across a Continental Shelf in the Northern Gulf of Mexico

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*Abstract*.—Declines in shark populations have sparked researchers and fishery managers to investigate more prudent approaches to the conservation of these fish. As managers strive to improve data collection for stock assessment, fisheries-independent surveys have expanded to include data-deficient areas such as coastal regions. To that end, a catch series from a nearshore survey off Alabama was combined with data from a concurrent offshore survey with identical methodology to examine the depth use of sharks across the continental shelf (2–366 m). The combined data set contained 22 species of sharks collected from 1995 to 2008: 21 species in the offshore data set (1995–2008) and 12 species in the nearshore data set (2006–2008). Depth was a significant factor determining species' distributions, primarily for Atlantic sharpnose *Rhizoprionodon terraenovae*, blacknose *Carcharhinus acronotus*, and blacktip *C. limbatus* sharks. Blacknose sharks had the highest catch per unit effort (CPUE) in the middepth stratum (10–30 m), blacktip sharks had consistently higher CPUE in the shallow depth stratum (<10 m), and Atlantic sharpnose sharks showed high abundance throughout both the shallow and middepth strata. Length frequency and sex ratio analyses suggest that Atlantic sharpnose and blacknose sharks are using waters greater than 30 m deep for parturition, whereas adult blacktip sharks are probably using shallow waters for parturition. Our abundance patterns illustrate a continuum of depth use across the inner continental shelf. Surveys that do not encompass the entirety of this ecosystem fail to accurately characterize the distributions of these important predators.

Understanding the distribution of an organism is central to both fisheries and ecology. In the marine environment, distributions can be viewed in many dimensions. For sharks, studies of horizontal distribution abound while studies of vertical (i.e., depth) distribution have received less attention (Speed et al. 2010). This is particularly true of coastal systems, which sharks are traditionally thought to inhabit early in their life history (Springer 1967). For instance, neonate to 3-year-old sandbar sharks *Carcharhinus plumbeus* in the western north Atlantic Ocean frequent waters less than 10 m deep, while large animals inhabit waters greater than 20 m deep (Grubbs 2010). While many species appear to use coastal areas as outlined in Springer (1967), recent attention has focused on the importance of nearshore habitat throughout the ontogeny of smaller species of shark. A new theoretical population model suggests that species such as Atlantic sharpnose *Rhizoprionodon terraenovae* and blacknose *Carcharhinus acronotus* sharks inhabit nearshore areas throughout their lifespan, while not using these regions as discrete nursery areas (Knip et al. 2010). Conversely, larger species such as blacktip shark *Carcharhinus limbatus* likely follow the original population model outlined by Springer (1967). Given the current management emphasis on ecosystem approaches, it is critical to determine how species occurring in both nearshore and offshore environments partition the use of these areas.

Only in the past few decades has the management of sharks been considered in the United States. In 1993, the first fishery management plan (FMP) for sharks in

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U.S. Atlantic waters was drafted by the National Marine Fisheries Service (NMFS). In response to this FMP, a fisheries-independent longline survey was initiated to monitor the status of sharks in the U.S. Atlantic Ocean and Gulf of Mexico (hereafter referred to as the offshore survey), and the resulting data have been used to evaluate stocks for both large and small coastal sharks. To complement the data from that survey, a nearshore survey was recently initiated in the northern Gulf of Mexico to capture the seasonal variation in the distribution and abundance of sharks in coastal areas. Whereas generalized linear models are widely used to standardize catch series (i.e., to make indices comparable between surveys with varying fishing gear and location; Ward and Myers 2006), we combine data from these two fisheries-independent surveys, which use identical methodology and occur during the same time period in adjacent areas, to assess depth usage for sharks found along the continental shelf of the north-central Gulf of Mexico. The goals of this analysis were to (1) examine differences in the overall shark community between the nearshore and offshore surveys and (2) determine species-specific patterns of depth use for two shark species hypothesized to fit the model proposed by Knip et al. (2010) and one species thought to fit the model proposed by Springer (1967).

## Methods

Offshore surveys were conducted primarily on the U.S. National Oceanic and Atmospheric Administration (NOAA) RV *Oregon II*, beginning in 1995 and continuing annually through the present, usually during the months of August and September. From its inception, the offshore survey used a random stratified design within 110 kilometer (1 degree latitude) zones. During 1995–2000, the survey was modified several times with respect to depth and hook type. Since 2001, the survey has used a standard hook type (15/0 Mustad circle hook, Model 39960D) and sampling effort is proportionally allocated by area of the continental shelf representing three depth strata (50% from 9 to 55 m [~75 stations], 40% from 55 to 183 m [~60 stations], and 10% from 183 to 366 m [~15 stations]). Bottom longline gear consists of 1.85 km of 454-kg monofilament main line sampled with 100 gangions, each gangion being 3.66 m long. Gangions consist of a longline snap and a number 15 circle hook baited with Atlantic mackerel *Scomber scombrus*. The length of the main line, number of gangions, and bait type has been consistent from the inception of the survey (for a complete description, see Driggers et al. 2008). Abiotic variables collected at each station using a Seabird SBE911-plus or an SBE25 conductivity–temperature–depth (CTD) probe include depth as well as surface and bottom values for temperature, salinity, and dissolved oxygen.

Nearshore surveys began in May 2006 and have been conducted by both NOAA and Dauphin Island Sea Laboratory (DISL) research vessels (RVs *HST*, *Gandy*, *Caretta*, and *E. O. Wilson*). The nearshore survey employed a random stratified block design. Four blocks were established along the Mississippi–Alabama coast. Each block was 37 kilometers longitudinally and extended from the shoreline to approximately the 20-m isobath. Sampling was evenly allocated and replicated within each block, and 12 stations were randomly selected each month. To facilitate data comparisons, all gear was identical to that in the NMFS offshore survey. All sharks that could be safely boated were removed from the main line, unhooked, and identified to species. Biotic variables collected included sex, length (precaudal, fork, natural, and stretch total), weight, and maturity (when possible). Maturity in males was assessed following Clark and von Schmidt (1965). Abiotic variables collected using a Seabird SBE911-plus or an SBE25 CTD included depth as well as surface and bottom values for temperature, salinity, and dissolved oxygen. To expand, both temporally and spatially, the resolution of the physical–chemical environment, abiotic data from an additional nearshore time series encompassing our study area were included in our analysis (Park and Dzwonkowski unpublished data).

A series of comparisons using (1) all available data from the coastal study area, (2) a subset of the offshore data and all the nearshore data collected from 2006 to 2008, and (3) a subset of both surveys collected during just the August–September time frame, which provides the greatest temporal overlap between the offshore and nearshore data, were performed (Figure 1). Catch data were combined and standardized to catch per unit effort (CPUE, i.e., the number of sharks/100 hooks/h) before comparisons were made. To examine overall differences in species composition (the dependent variables) among three levels of the independent variable depth stratum (0–9.9 m, 10–29.9 m, and >30 m), multivariate analysis of similarity (ANOSIM) tests were conducted on a Bray–Curtis zero-adjusted similarity matrix (Clarke et al. 2006) constructed using the entire data set ($n$ = 633 sets, 42% offshore and 58% nearshore). These depth bins were chosen based on the physical–chemical gradient present on the continental shelf. Specifically, the 0–9.9-m depth bin normally encompasses the highly variable estuarine waters of the nearshore environment, the 10–29.9-m depth zone represents the range through which thermal and salinity fronts propagate, and the >30-m depth bin

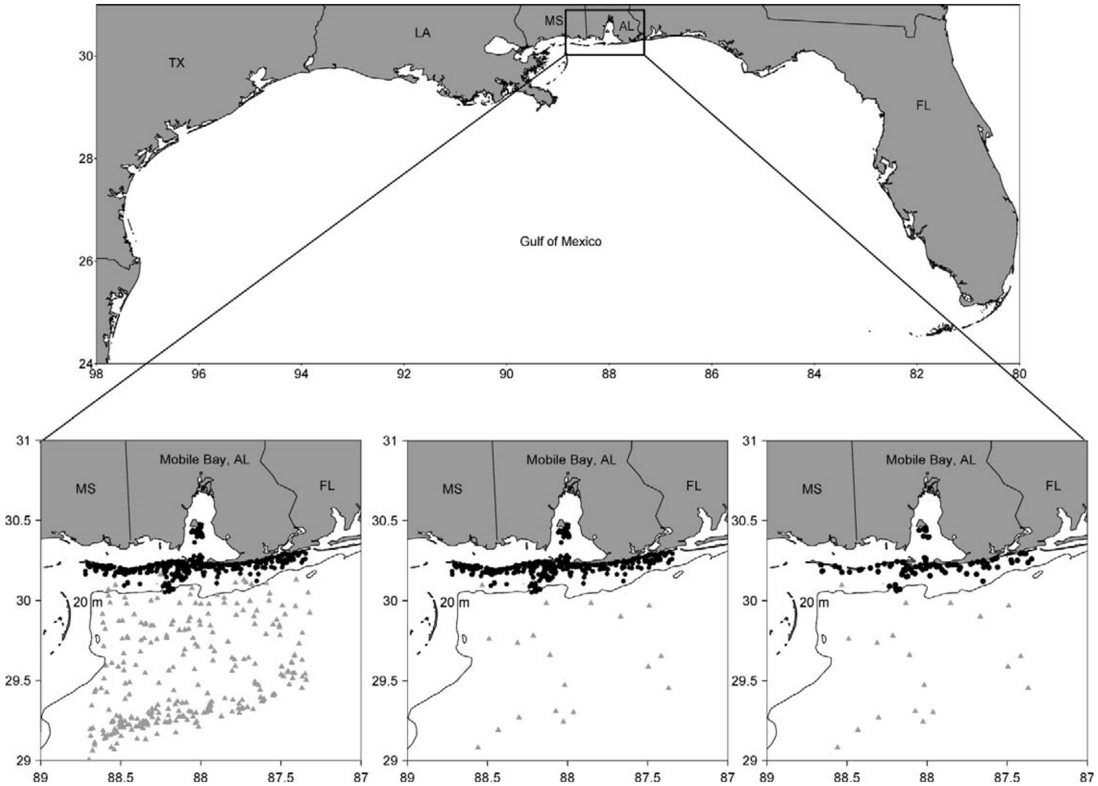


FIGURE 1.—Locations of stations sampled during (left to right) 1995–2008, 2006–2008 (year-round), and 2006–2008 (August and September). Stations sampled during the nearshore survey are indicated by black circles, stations sampled during the offshore survey by gray triangles.

represents a relatively stenohaline and thermally stable bottom environment (Figure 2). Prior to multivariate analysis, the data were pretreated with a square root transformation to reduce the influence of dominant species. Similarity percentage tests were used to identify the sharks most responsible for differences among depths. To remove the temporal bias of the longer-duration offshore survey, we performed the second set of analyses on data collected from 2006 to 2008, a time period during which both surveys were conducted ($n = 380$ sets, 6% offshore and 94% nearshore). Our last analysis was performed using those longline sets that met the strictest temporal consistency (i.e., collected only in the months of August and September; $n = 112$ sets, 18% offshore and 82% nearshore). Because of departures from normality and homoscedasticity, nonparametric Kruskal–Wallis and Dunn's post hoc tests with depth as a factor were performed on square-root-transformed data for the species identified as most responsible for patterning shark assemblage. Chi-square analysis was used to test for deviations from an expected sex ratio of 1:1. Visual inspection of length frequency diagrams was done to qualitatively describe the differences in depth distribution by size.

## Results

Salinity and temperature varied both spatially and temporally as predicted by the climatology of the area. Temporally, CTD data from the shallow depth stratum provided complete annual resolution and showed bottom temperatures ranging from a low of 13.5°C in February to a high of 31.5°C in August. Salinity was highly variable on an annual basis. The lowest bottom salinities were recorded in the spring (6.4‰), which coincides with peak rainfall events and river discharge. The highest salinity (36.5‰) was recorded in late summer. Spatially, a typical cross-shelf pattern in temperature and salinity was observed during the August–September time frame (Figure 2), when samples were collected over all depth strata. Bottom temperature generally decreased with depth, with the highest temperatures (31.5°C) being recorded in the shallow depth stratum and the lowest temperatures

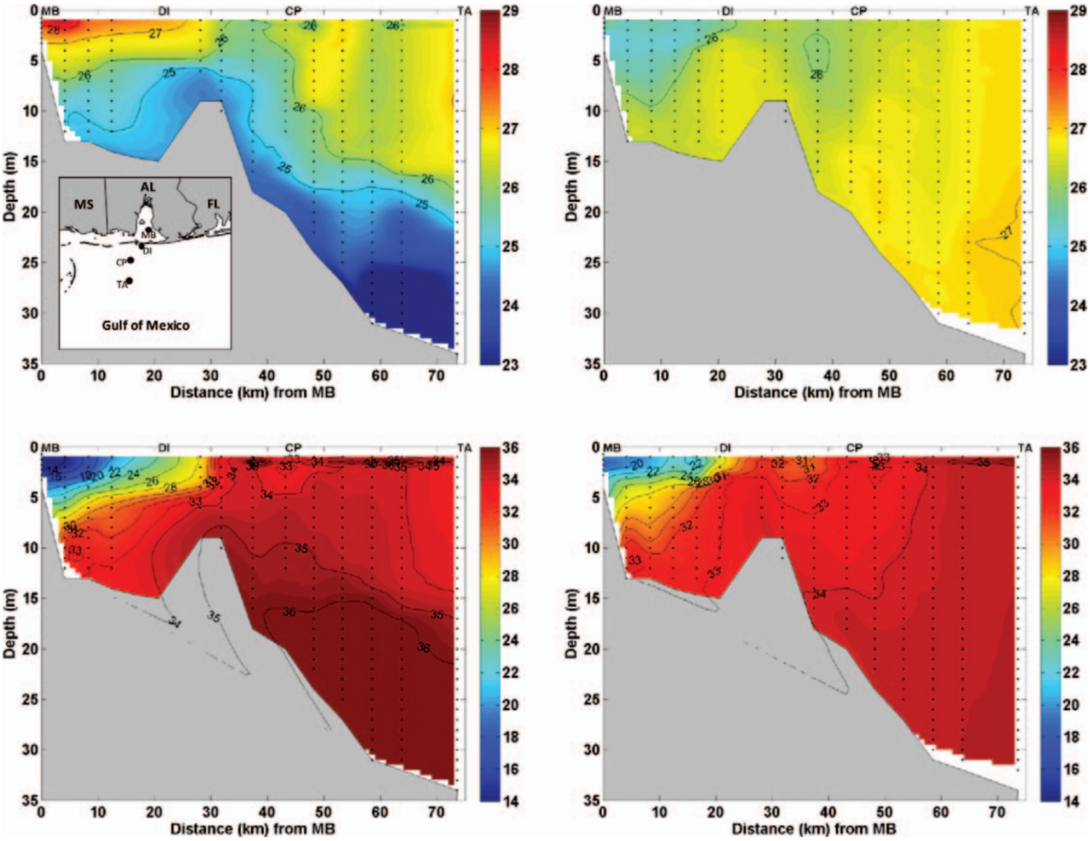


FIGURE 2.—Cross-shelf profiles based on CTD casts (dots) for temperature (top row) and salinity (bottom row) made in August (left column) and September (right column) 2008. The acronyms MB, DI, CP, and TA designate four fixed sampling stations. Data were collected by the Dauphin Island Sea Laboratory as part of its Fisheries Oceanography of Coastal Alabama (FOCAL) project (K. Park and B. Dzwonkowski, unpublished data).

(10.5°C) recorded in the mid and deep depth strata. Bottom salinities were generally lower and more variable in the shallow and middepth strata (range = 12.0–36.4‰) than in the deep stratum (range = 35.3–36.5‰).

Based on all available longline sets, which included all sets from the offshore survey (1995–2008) and all sets from the nearshore survey (2006–2008), 22 shark species were captured (Table 1). Eleven species were common to both surveys. Depth was a significant factor describing shark assemblages (ANOSIM $R = 0.04$, $P \leq 0.01$). There was a significant difference in abundance between shallow and midwater depths ($R = 0.058$, $P \leq 0.001$), with Atlantic sharpnose, blacknose, and blacktip sharks contributing over 70% to the overall dissimilarity.

Analysis of monthly catch data from the nearshore survey during the period 2006–2008 indicated seasons of peak occurrence for several species of shark (Table 2). Ten of the 12 species in the nearshore survey occurred during all seasons sampled. Bonnetheads and nurse sharks were absent during the spring. Peak periods of occurrence were noted for Atlantic sharpnose, finetooth, and spinner sharks during the fall; all other species showed relatively stable catch rates across seasons.

To better resolve the depth pattern identified by the multivariate analysis for the three dominant species (Atlantic sharpnose, blacknose, and blacktip sharks), we restricted our univariate analysis to data collected from 2006 to 2008. Kruskal–Wallis tests using depth as a factor revealed a significant effect for Atlantic sharpnose ($P \leq 0.006$), blacknose ($P \leq 0.001$), and blacktip sharks ($P \leq 0.044$). For all three species, Dunn's procedure indicated different depth associations. For Atlantic sharpnose sharks, CPUE was significantly higher at mid than at deep depths. For blacknose sharks, abundance was significantly higher

TABLE 1.—Catch per unit effort (CPUE [sharks/100 hooks/h]) across shallow (S; 0–9.9 m), mid (M; 10–29.9 m) and deep (D; >30 m) depths for sharks encountered in nearshore (N) and offshore (O) surveys from 1995 to 2008. A similarity percentage test revealed that the sharks in bold italics were most responsible for the differences observed among depths. Presence is indicated by an X.

| Species | N | O | S | M | D |
|---|---|---|---|---|---|
| Bignose shark *Carcharhinus altimus* |  | X | 0.00 | 0.00 | <0.01 |
| ***Blacknose shark Carcharhinus acronotus*** | ***X*** | ***X*** | ***0.77*** | ***2.11*** | ***0.51*** |
| ***Blacktip shark Carcharhinus limbatus*** | ***X*** | ***X*** | ***1.36*** | ***1.01*** | ***0.53*** |
| Bonnethead *Sphyrna tiburo* | X | X | <0.01 | 0.01 | <0.01 |
| Bull shark *Carcharhinus leucas* | X | X | 0.33 | 0.15 | 0.08 |
| Caribbean lanternshark *Etmopterus hillianus* |  | X | 0.00 | 0.00 | <0.01 |
| Cuban dogfish *Squalus cubensis* |  | X | 0.00 | 0.00 | 0.03 |
| Dusky shark *Carcharhinus obscurus* |  | X | 0.00 | 0.00 | <0.01 |
| Finetooth shark *Carcharhinus isodon* | X |  | 0.24 | 0.02 | 0.00 |
| Great hammerhead *Sphyrna mokarran* | X | X | 0.04 | 0.08 | 0.00 |
| Gulper shark *Centrophorus granulosus* |  | X | 0.00 | 0.00 | 0.29 |
| Mustelus *Mustelus* spp. |  | X | 0.00 | 0.00 | 3.07 |
| Night shark *Carcharhinus signatus* |  | X | 0.00 | 0.00 | <0.01 |
| Nurse shark *Ginglymostoma cirratum* | X | X | <0.01 | 0.07 | 0.02 |
| Sandbar shark *Carcharhinus plumbeus* | X | X | 0.01 | 0.04 | 0.22 |
| Scalloped hammerhead *Sphyrna lewini* | X | X | 0.02 | 0.06 | 0.22 |
| ***Atlantic sharpnose shark Rhizoprionodon terraenovae*** | ***X*** | ***X*** | ***2.01*** | ***2.82*** | ***5.22*** |
| Shortfin mako *Isurus oxyrinchus* |  | X | 0.00 | 0.00 | 0.01 |
| Shortspine dogfish *Squalus mitsukurii* |  | X | 0.00 | 0.00 | <0.01 |
| Silky shark *Carcharhinus falciformis* |  | X | 0.00 | 0.00 | 0.11 |
| Spinner shark *Carcharhinus brevipinna* | X | X | 0.31 | 0.36 | 0.23 |
| Tiger shark *Galeocerdo cuvier* | X | X | 0.02 | 0.10 | 0.06 |

at middepths than at both shallow and deep depths, and for blacktip sharks CPUE was significantly higher at shallow than at deep depths (Table 3).

Using the most restrictive criterion for analysis by including only those data collected in the August–September time frame from both surveys, univariate analysis showed a similar trend, although some of the contrasts were no longer significant at $P < 0.05$. Kruskal–Wallis tests using depth as a factor identified a significant effect for blacknose sharks ($P \leq 0.003$). Dunn's procedure showed that middepths were significantly different from both shallow and deep depths (Table 3) for blacknose sharks. Depth was no longer a significant factor for Atlantic sharpnose ($P \leq 0.220$) or blacktip sharks ($P \leq 0.107$), although a strong depth trend was still evident in the data set.

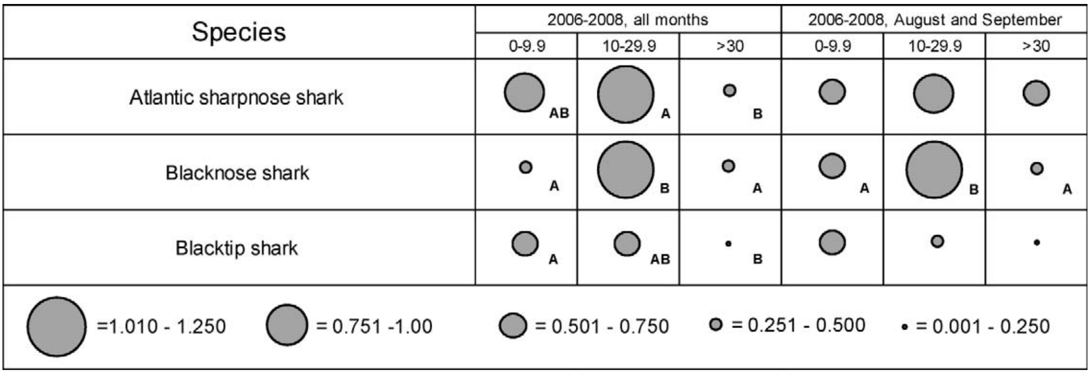
Examining the most restrictive subset of data, chi-square analysis of sex ratios, coupled with sex-specific length frequency analysis, revealed sexual segregation of life history phases across depth for several shark species. For Atlantic sharpnose sharks, a significant bias toward females was observed in deep waters (2.9:1, $P \leq 0.01$; Figure 3). Length frequency analysis by sex indicated that the dominant size-class offshore was mature females (NMFS 2007), whereas waters less than 10 m deep were dominated by mature and near-mature males (2:1, $P \leq 0.01$; Figure 4). A significant bias was observed toward male blacknose sharks at shallow (3.4:1, $P \leq 0.01$) and mid (4.6:1, $P \leq 0.01$) depths (Figure 3). Length frequency analysis for this species shows that mature males dominated the nearshore catch (Figure 4). Unlike Atlantic sharpnose and blacknose sharks, blacktip sharks showed a significant bias towards mature females at shallow (6.9:1, $P \leq 0.01$) and mid (2.2:1, $P \leq 0.05$) depths (Figure 3), the majority of which were between 115 and 120 cm fork length (FL; Figure 4).

Abundances for taxa besides blacktip, blacknose, and Atlantic sharpnose sharks were generally too low to produce statistically rigorous contrasts; however, two general trends are evident for these other species. *Mustelus*, gulper, sandbar, scalloped hammerhead, and silky sharks were rarely encountered in shallow and middepth strata and were generally encountered in the

TABLE 2.—Seasonal (X) and peak (*) occurrence for 12 species of sharks sampled during spring (March–May), summer (June–August), and fall (September–November) 2007 and 2008.

| Species | Spring | Summer | Fall |
|---|---|---|---|
| Atlantic sharpnose shark | X | X | * |
| Blacknose shark | X | X | X |
| Blacktip shark | X | X | X |
| Bonnethead |  | X | X |
| Bull shark | X | X | X |
| Finetooth shark | X | X | * |
| Great hammerhead | X | X | X |
| Nurse shark |  | X | X |
| Sandbar shark | X | X | X |
| Scalloped hammerhead | X | X | X |
| Spinner shark | X | X | * |
| Tiger shark | X | X | X |

TABLE 3.—Dunn's pairwise comparison across three levels of depth from a Kruskal–Wallis test. The circles indicate relative CPUE; depths with different letters are significantly different at $\alpha \leq 0.05$.



| Species | 2006-2008, all months | | | 2006-2008, August and September | | |
|---|---|---|---|---|---|---|
| | 0-9.9 | 10-29.9 | >30 | 0-9.9 | 10-29.9 | >30 |
| Atlantic sharpnose shark | ● AB | ⬤ A | ∘ B | • | ● | • |
| Blacknose shark | ∘ A | ⬤ B | ∘ A | • A | ⬤ B | ∘ A |
| Blacktip shark | • A | • AB | · B | • | ∘ | · |

⬤ =1.010 - 1.250 ● = 0.751 -1.00 • = 0.501 - 0.750 ∘ = 0.251 - 0.500 · = 0.001 - 0.250

deep stratum (Table 1). In contrast, bull and finetooth sharks showed their highest CPUE in the shallow stratum (Table 1). For all remaining taxa, CPUE was too low to infer any depth pattern.

## Discussion

The stepwise nature of the comparisons presented here balances the benefits of a large sample size by including all geographically relevant longline data while examining several levels of temporal bias associated with the two data sets. The offshore data set extends our observational period back to 1995; however, it provides no intra-annual information since all samples were collected during a short time period (usually August and September). In contrast, the nearshore survey provides monthly resolution, although it only extends back to 2006. Using all available data, our analyses suggest broad-scale differences in shark assemblages, whereas fine-scale analysis of temporally truncated data sets reveals

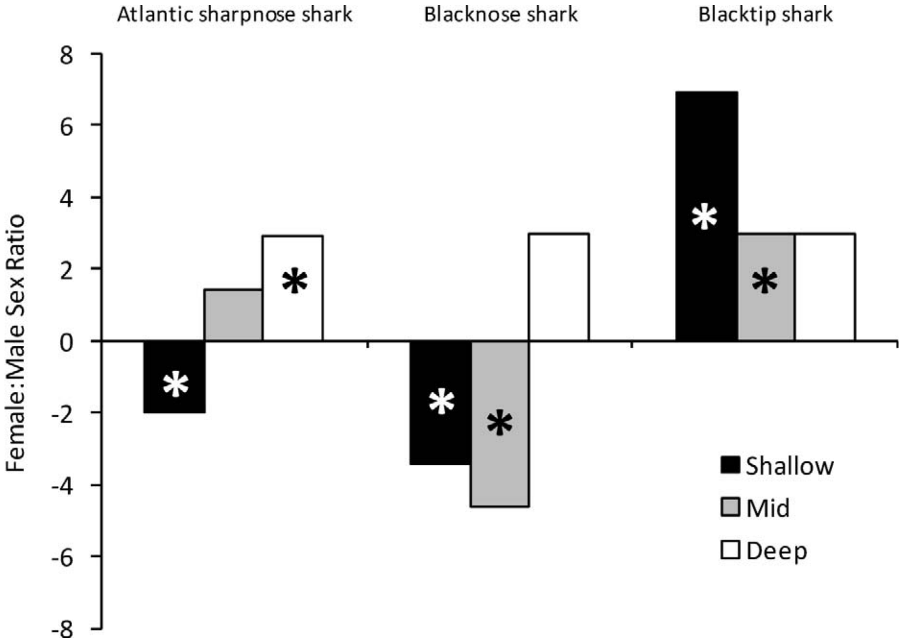


FIGURE 3.—Female : male sex ratios for Atlantic sharpnose, blacknose, and blacktip sharks across depths, August and September 2006–2008. Asterisks indicate significance differences ($P \leq 0.05$) from the expected 1:1 sex ratio.

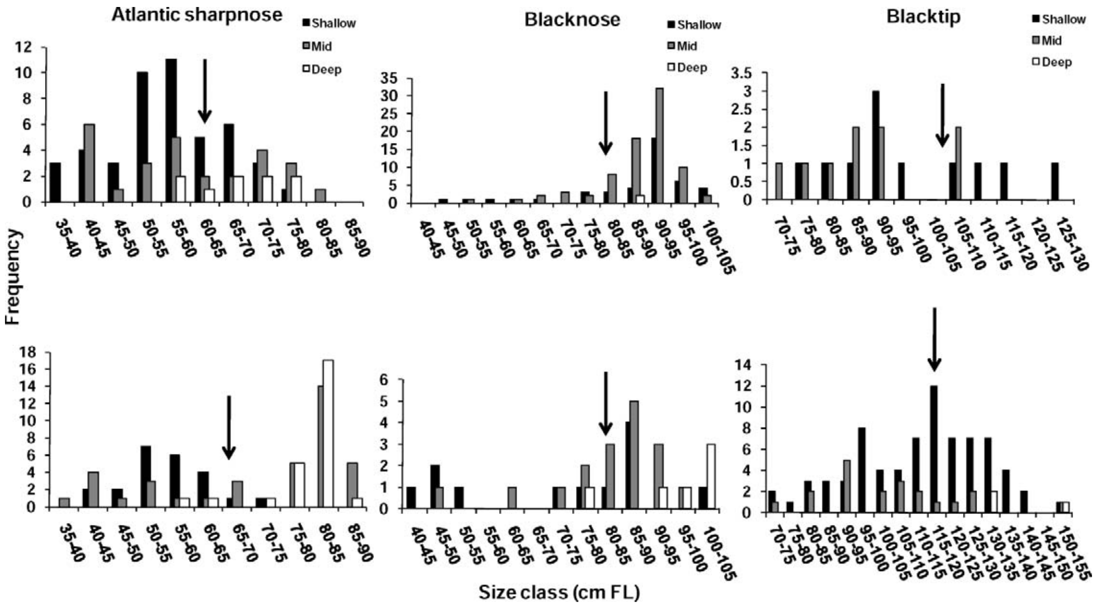


FIGURE 4.—Length frequency plots for Atlantic sharpnose, blacknose, and blacktip sharks caught in August and September 2006–2008, by depth stratum. Males are shown in the top row, females in the bottom row. Arrows indicate median size at maturity.

specific depth associations and segregation of life history phases for Atlantic sharpnose, blacknose, and blacktip sharks.

### *All Data: 1995–2008*

The coarsest examination of data from the two surveys reveals several community-level trends for sharks. Twenty species occurred in waters deeper than 30 m, nearly twice as many as the 12 species occurring in shallow waters. With the exception of finetooth and great hammerhead sharks, all species sampled in shallow waters also occurred in deep waters, leaving 10 species that occurred exclusively in waters deeper than 30 m. Even with rare species (CPUE $\leq$ 0.01 sharks/100 hooks/h) removed, four shark species were never captured in shallow water despite year-round monthly sampling. One of these, *Mustelus* spp., is the second most abundant component of the deep water catch, with an average CPUE of 3.07 (SE, 0.35) sharks/100 hooks/h. It has been sampled in shallow waters along the west coast of Florida (R. E. Hueter and J. P. Tyminski, unpublished shark nursery overview, National Oceanic and Atmospheric Administration, Highly Migratory Species Office, Narragansett, Rhode Island) and off the Florida panhandle (J. K. Carlson, unpublished report on shark nurseries in the northeastern Gulf of Mexico, National Oceanic Atmospheric Administration, Highly Migratory Species Office, Narragansett, Rhode Island), yet never in shallow waters in our study area. Shallow estuarine waters have been described as critical habitat for the smooth dogfish *Mustelus canis* in New Jersey, yet populations outside of the North Atlantic may only inhabit deeper waters (Rountree and Able 1996). Off the coast of Massachusetts, Nantucket Sound and adjacent bays are an important primary nursery for smooth dogfish, which occur in waters as warm as 27°C (Skomal 2007). Further south, smooth dogfish are seasonal migrants in the coastal waters of South Carolina, appearing only in waters cooler than 20°C (Ulrich et al. 2007). Despite the presence of this species in the shallow waters off Florida, the year-round, shallow water absence of *Mustelus* spp. off the coast of Mississippi and Alabama represents a departure from the distributional trends described above.

Similar to *Mustelus* spp., scalloped hammerhead and sandbar sharks were sampled at rates an order of magnitude higher in deeper waters than in shallow waters (CPUE = 0.22 and 0.22, compared with 0.02 and 0.01, respectively), indicating an affinity for deep waters in the northern Gulf of Mexico. In contrast to the distribution of *Mustelus* spp., finetooth sharks were absent from deep water. Shallow estuarine waters off South Carolina have been shown to be an important nursery area for finetooth sharks (Drymon et al. 2006). In the Gulf of Mexico, adult finetooth sharks are relatively abundant in shallow waters, and neonates with open umbilical scars occur frequently off coastal Alabama in nearshore gill nets (Bethea et al. 2009). Similarly, juvenile and young-of-the-year finetooth sharks are common in the Mississippi Sound (Parsons and Hoffmayer 2007). Unlike finetooth sharks, which were totally absent from deep waters, bull sharks were captured across the continental shelf. However, bull sharks were captured at a rate four times higher in shallow waters than in deep waters (CPUE = 0.33 in shallow waters, compared with 0.08 in deep waters; Table 1). The absence of finetooth sharks in deep waters and the low capture rate of bull sharks suggest that these species have a coastal life history in the northern Gulf of Mexico. The distribution of finetooth sharks in the area we sampled suggests a population that is highly reliant on nearshore areas throughout their lifespan, like those proposed by Knip et al. (2010).

The absence of finetooth sharks in deep water and the absence of *Mustelus* spp. in shallow water highlight broad-scale differences in depth usage that are not noticeable when one examines data from only one of the two surveys. The lack of spatial and methodological confounds allows for these simple CPUE comparisons between surveys to demonstrate the relative depth preferences for scalloped hammerhead, bull, and sandbar sharks. Vidal and Pauly (2004) described ecosystem feeding interactions across the Gulf of Mexico by integrating models across subsystems, noting that these subsystems span distinct depths (notably 0–20 m for coastal systems and 20–200 m for continental shelf systems). While the southern Gulf of Mexico is rife with examples of subsystem models describing fisheries impacts, the identification of functional groups to populate these subsystem models in the northern Gulf of Mexico requires knowledge of species' distributions.

### *Temporally Restricted Comparisons: 2006–2008*

The temporally restricted data allow for more rigorous comparisons of depth use for several sharks species, notably the Atlantic sharpnose shark, which is ubiquitous in the northern Gulf of Mexico across a range of depths. Previous studies in the region have shown the highest CPUE for Atlantic sharpnose sharks in the spring and fall and the lowest CPUE in the summer, when condition factor is lowest (Parsons and Hoffmayer 2005). The lack of Atlantic sharpnose sharks in the Mississippi Sound during the summer may result from a physiologically motivated migration of these sharks offshore that is driven by high temperature and/or low dissolved oxygen (Parsons and Hoffmayer 2005). In addition to a clear seasonal trend in abundance, extreme sexual segregation was seen for adult Atlantic sharpnose sharks, represented by 718 males and 9 females (Parsons and Hoffmayer 2005). By analyzing all depths used by Atlantic sharpnose sharks we can further examine the sexual segregation in this species. In this study, males outnumbered females 2:1 in shallow depth strata, and none of the females sampled in the shallow depth strata were of a size indicative of maturity (Carlson and Baremore 2003). While adult male Atlantic sharpnose sharks occupied nearshore waters, females outnumbered males nearly 3:1 in waters deeper than 30 m. Most of these sharks were mature, which suggests that females aggregate in offshore waters for parturition of their young, a notion also hypothesized by Parsons and Hoffmayer (2005). Specific nurseries may be of little benefit for small, fast-growing sharks such as Atlantic sharpnose sharks (Heupel et al. 2007). In Crooked Island Sound, Florida, Atlantic sharpnose sharks showed low residency times in areas characteristic of high-quality nursery habitat (shallow, nearly predator free; Carlson et al. 2008). Age-0 sharpnose sharks (defined in Carlson and Baremore 2003) were encountered in the shallow waters of our study area using both longlines (this study) and gill nets (Bethea et al. 2009). We suggest that Atlantic sharpnose sharks are using the offshore waters of Alabama for parturition, as suggested by Parsons (1983), after which neonate Atlantic sharpnose sharks migrate to shallow waters, as suggested by Parsons and Hoffmayer (2005). In the northern Gulf of Mexico, this species serves as an example of a small-bodied shark fitting the theoretical population model proposed by Knip et al. (2010).

Another small coastal shark, the blacknose shark, was encountered in relatively high abundance in both surveys and was sampled at a significantly higher CPUE in waters 10–30 m deep, where males outnumbered females nearly 5:1. Male blacknose sharks attain 50% maturity at 79.5 cm FL, indicating that the dominant group of blacknose sharks captured in the survey were mature. The nearshore surveys allow greater temporal resolution and provide evidence that this is not a seasonal effect, as the higher CPUE at middepths was observed for the most restrictive analysis (only August and September) as well as when all months were combined. Gear bias does not explain the absence of blacknose sharks in our nearshore study area; no blacknose sharks have been captured during a year-round, multiple-mesh gill-net sampling program from the same area (Bethea et al. 2009). Given the absence of neonate blacknose sharks and the low abundance of females in the current study, we speculate that the north-central Gulf of Mexico is not a large nursery area for this species, in agreement with Parsons and Hoffmayer (2007). Multiple-gear-type sampling in the estuarine and nearshore waters of South Carolina produced no neonate blacknose sharks, suggesting that if these sharks were using coastal nurseries the areas were poorly defined (Driggers et al. 2004). It would thus appear that blacknose sharks are another species following the theoretical population model proposed by Knip et al. (2010); however, the presence of neonate blacknose sharks is well documented around Tampa Bay, Florida, suggesting that this area serves a nursery function for this species (Hueter and Tyminski 2007), illustrating that habitat type or environmental characteristics may dictate the behavior of small-bodied shark populations (Knip et al. 2010).

In contrast to Atlantic sharpnose and blacknose sharks, blacktip sharks are known to use coastal waters and bays as nurseries (Castro 1993; DeAngelis et al. 2008). Blacktip sharks were shown to have a high residence time in coastal waters in Terra Ceia Bay, Florida, before migrating south during winter months (Heupel and Hueter 2001; Heupel et al. 2004). In this study, sex ratio analysis for blacktip sharks demonstrated that females outnumbered males nearly 7:1 in waters less than 10 m. The majority of females caught in shallow water are 115–120 cm FL or greater, indicating maturity (Carlson et al. 2006). Size at age 0 was reported to range from 53.6 (females) to 54.5 (males) cm FL for blacktip sharks in the Gulf of Mexico (Carlson et al. 2006). This size-class occurs in the shallow waters of our survey area, and neonates with umbilical scars are commonly encountered in waters less than 10 m (Bethea et al. 2009). These data suggest that female blacktip sharks are using the coastal waters of Alabama for parturition, which has also been suggested by Parsons and Hoffmayer (2007). Previous studies examining blacktip sharks in the Gulf of Mexico reported fewer males than females in sample collections (Branstetter 1987; Killam and Parsons 1989; Carlson et al. 2006), suggesting that the lower ratio of males collected in this study is not anomalous.

### *Conclusions*

Analysis of CPUE between these concurrent surveys provides unique insight into depth partitioning for several species of sharks in the northern Gulf of Mexico. Our data demonstrate that in the area surveyed, Atlantic sharpnose and blacknose sharks follow a population model proposed by Knip et al. (2010); based on our survey comparisons, we propose that finetooth shark populations conform to the same population model. In addition, our analysis shows that populations of the same species behave differently across their range, as exemplified by blacknose shark populations off Florida (Hueter and Tyminski 2007). This population-level departure underscores the need for increased sampling in nearshore areas across the entire Gulf of Mexico. The simple, direct nature of this comparison forgoes the need to standardize CPUE by gear type and fishing location. Furthermore, this comparison demonstrates how analyses using only offshore data sources would lead one to draw spurious conclusions about sharks such as finetooth sharks (whose preferred depth is not encompassed in the offshore survey) and blacktip sharks (which occur in both surveys but at a significantly higher CPUE nearshore). The examples above highlight the benefits of expanding catch series data both temporally and spatially to encapsulate a species' entire distribution and underscores the utility of comparing data from surveys using standardized methods.

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