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Characterizing and predicting essential habitat features for juvenile coastal sharks

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Abstract

The successful management of shark populations requires juvenile recruitment success. Thus, conservation initiatives now strive to include the protection of areas used by pre-adult sharks in order to promote juvenile survivorship. Many shark species use inshore areas for early life stages; however, species often segregate within sites to reduce competition. Using a fisheries-independent gillnet survey from the Northern Gulf of Mexico (2000–2010) we describe distribution patterns and preferred habitat features of the juveniles of six shark species. Our results suggest that multiple shark species concurrently use the area for early life stages and although they overlap, they exhibit distinct habitat preferences characterized by physical variables. Habitat suitability models suggest that temperature, depth, and salinity are the important factors driving juvenile shark occurrence. Within each site, across the sampled range of physical characteristics, blacktip shark (*Carcharhinus limbatus*) preferred higher temperature (>30 °C) and mid-depth (~5.5 m); bonnethead shark (*Sphyrna tiburo*) preferred higher temperature (>30 °C) and mid-salinity (30–35 PSU), finetooth shark (*Carcharhinus isodon*) preferred low salinity (<20 PSU) with mid-depth (~4 m), scalloped hammerhead shark (*Sphyrna lewini*) preferred high temperature (>30 °C) and salinity (>35 PSU), Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) preferred high temperature (>30 °C) and deep water (>6 m), and spinner shark (*Carcharhinus brevipinna*) preferred deep water (>8 m) and high temperature (>30 °C). The other investigated factors, including year, month, latitude, longitude, bottom type, inlet distance, coastline and human coast were not influential for any species. Combining habitat preferences with the sampled environmental characteristics, we predicted habitat suitability throughout the four sites for which physical characteristics were sampled. Habitat suitability surfaces highlight the differences in habitat use between and within sites. This work provides important insight into the habitat ecology of juvenile shark populations, which can be used to better manage these species and protect critical habitat.

Introduction

Many coastal shark populations have significantly declined from their original abundance as a result of fishing (Heithaus *et al.* 2007; Hayes *et al.* 2009; Ward-Paige *et al.* 2010) and, due to their low rebound potential, management of catch alone may not be sufficient for the recovery of depleted populations (Ward-Paige *et al.* 2012). Evidence suggests that all life stages should be considered for proper management (Kinney & Simpfendorfer 2009) and that elasmobranch population growth and productivity are influenced by juvenile survivorship (Smith *et al.* 1998; Cortés 2002). Thus, successful management of sharks also depends on their survival to age at maturity (Heupel *et al.* 2007).

It is well documented that many coastal shark species use inshore bays and estuaries for early life stages (Heupel *et al.* 2007; McCandless *et al.* 2007). It is often presumed that the abundance of prey and protection from predators in these habitats are the essential features for juvenile sharks (Branstetter 1990; Simpfendorfer & Milward 1993; Heupel *et al.* 2007); however, these reasons are contentious as there are cases of starvation (Lowe 2002) and inadequate protection from predation (Heupel & Simpfendorfer 2002; Heupel *et al.* 2007). As well, there is evidence that, for example, juvenile Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) have high mobility and regularly leave and enter bays and inlets (Carlson *et al.* 2008). This level of mobility suggests that juveniles may actively select habitats to improve their chance for survival.

Recently, studies have begun to demonstrate the importance of physical factors in determining the presence and abundance of juvenile sharks in different habitats. Temperature, salinity, turbidity, dissolved oxygen and proximity to tidal inlets have been shown to be important factors for the distribution and relative abundance of a range of species in the Gulf of Mexico and the east coast of the United States (Simpfendorfer *et al.* 2005; Heithaus *et al.* 2009; Belcher & Jennings 2010; Froeschke *et al.* 2010). For example, benthic habitat type (e.g. seagrass beds) has been shown to be an important factor influencing the distribution of blacktip (*Carcharhinus limbatus*) and lemon sharks (*Negaprion brevirostris*; DeAngelis *et al.* 2008). Due to the inshore nature of many shark species and their dependence on a range of physical factors, populations are also susceptible to coastal anthropogenic stressors such as exploitation, pollution, habitat destruction, altered freshwater inputs and shifts in predator or prey abundance (Knip *et al.* 2010; Ward-Paige *et al.* 2010). With the exception of exploitation (Heupel & Simpfendorfer 2011), the effects of these anthropogenic stressors on shark nurseries have rarely been investigated.

Despite long-term anthropogenic pressures from overfishing, pollution, freshwater diversion and coastal development in the northern Gulf of Mexico, the area still supports the juveniles of at least 16 shark species (Carlson 2002; Parsons & Hoffmayer 2005; McCandless *et al.* 2007). However, there is still question as to which habitat features are preferred by juvenile sharks in the northern Gulf of Mexico. Indeed, identification of critical areas and essential features for shark populations is just beginning to be uncovered and in most cases potential nursery areas are identified simply by the presence of juvenile sharks (e.g. McCandless *et al.* 2007). Herein, we examine and characterize distribution patterns and identify essential habitat features for the juveniles of six shark species in the Northeastern Gulf of Mexico.

Methods

Study site

This study was conducted in four coastal sites along the Northeastern Gulf of Mexico, around Panama City, FL, USA (Fig. 1), starting in the mid-1990s, by the National Marine Fisheries Service (NMFS) (Carlson & Brusher 1999). From west to east, the four sites include Saint Andrew Bay (SAB), Saint Andrew Sound (SAS), Saint Joseph Bay (SJB) and Indian Pass at the mouth of the Apalachicola River delta (IP). Each site varies in area, coastline length, tidal inlet length and human population density in the nearby vicinity, and therefore has a range of fishing pressure, freshwater input, depth, coastline modification, and water quality parameters. The dataset contains shark-specific information such as species and abundance; sampling information including location, date, set-begin time, soak time; physical factors including temperature, salinity, dissolved oxygen, bottom type and depth (see Fig. 2 for the distribution of environmental variables). However, for the purposes of this study a subset of the data was used, as explained below.

Data collection

The four sites were regularly sampled, where sets were deployed between March and November, excluding the winter months when sharks are not present (J.K. Carlson personal observation). A 186-m-long gillnet consisting of six different mesh size panels was used for sampling. Stretched mesh sizes ranged from 7.6 to 14.0 cm in steps of 1.3 cm, with an additional multifilament panel of 20.3 cm. In 2005, the 20.3-cm panel was removed and a 7.6-cm panel inserted. However, the removal of this panel did not have a significant effect on the catchability of juvenile coastal sharks (Carlson & Bethea 2010). Panel depths were 3.1 m. Webbing for all panels were composed of clear monofilament, double-knotted and double-selvaged. Nets were positioned with the wind or perpendicular to shore. Deployment times were mostly during daylight hours with 96% starting between 6:00 and 17:00 h. Soak times ranged from 0.4 to 7.2 h with a mean of 1.25 h. Captured sharks were measured to the nearest centimeter for body lengths (precaudal, fork, total, and stretch total length, and disc width for rays). Here we limited the data analysis to juveniles (neonates, young-of-year and pre-mature individuals) of each species.

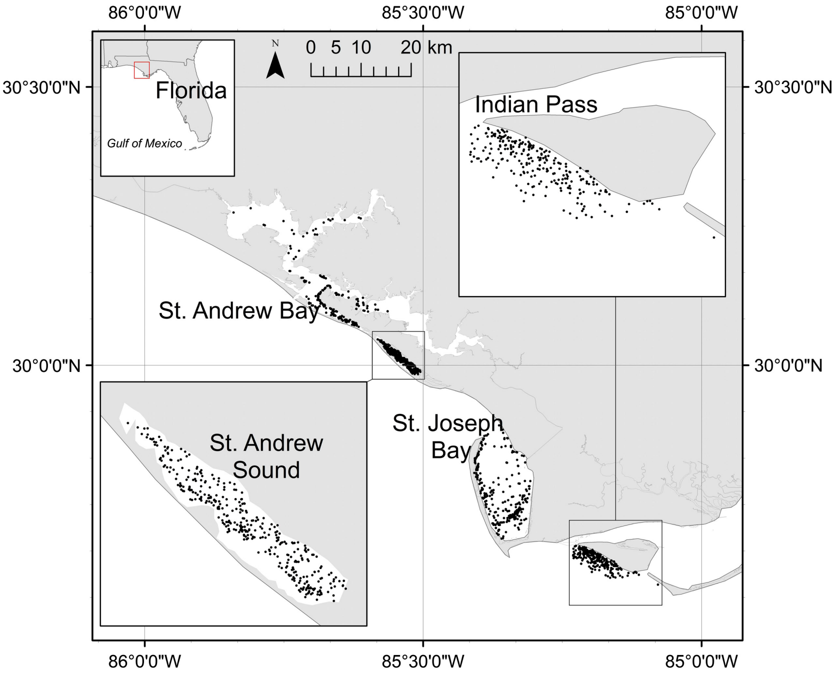

Fig. 1. Map of study site in the northeastern Gulf of Mexico, USA. Filled circles are gillnet sample locations.

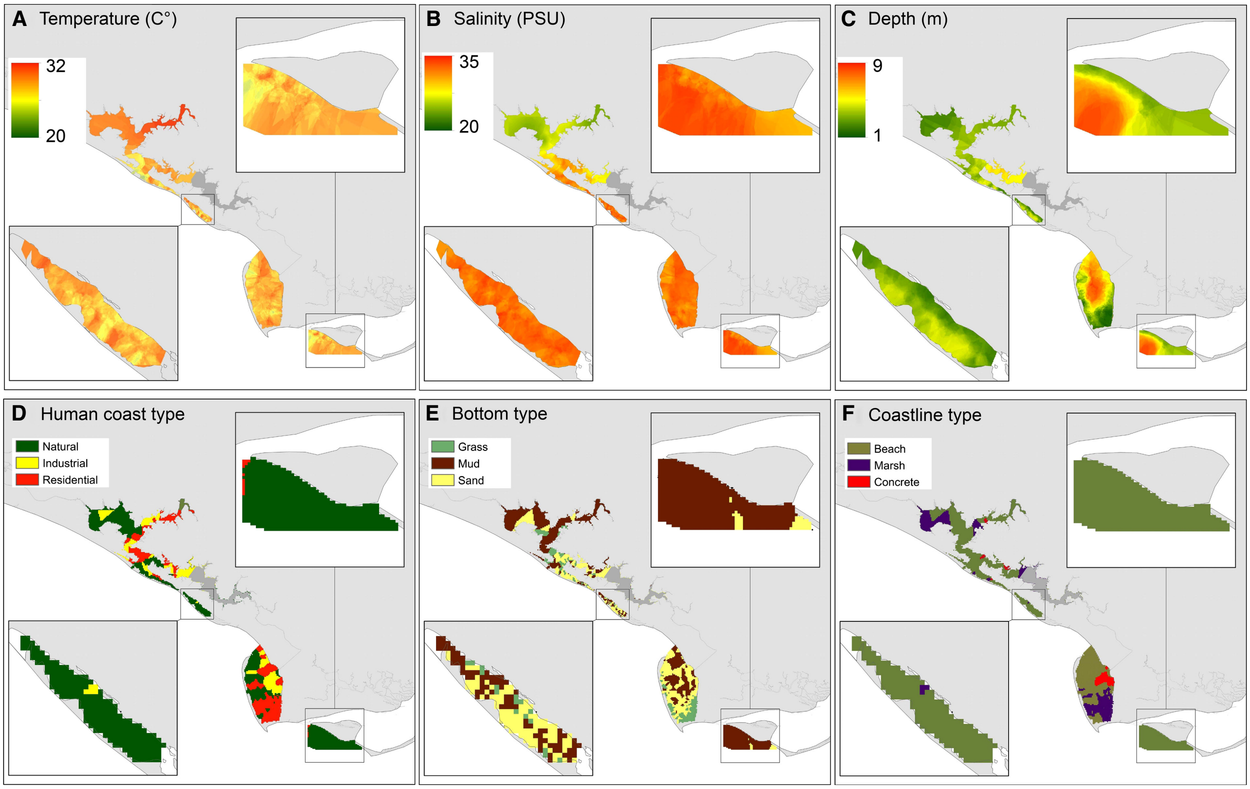

Fig. 2. Sampled habitat characteristics across four sampled sites.

We considered each of the collected variables as potential explanatory variables (Table 1). Variables for distance to tidal inlet, coastline type and human coastal development were also included as explanatory variables because they have been described as important variables for sharks in other systems (e.g. Froeschke *et al.* 2010).

Table 1. Predictors used in the analyses.

Variable	Description	Values
Year	Year of sample	2000–2010
Month	Month of sample	March-November
Latitude	Latitude of sample	29.61 to 30.28
Longitude	Longitude of sample	−85.05 to −85.50
Site	Location of sample	SAB, SAS, SJB, IP
Bottom	Predominant substrate type	Sand, mud, grass
Set-begin	Time of day the gillnet was deployed	00:17–23:50 h
Soak	Hours gillnet was deployed	00:42–07:17 h
Temperature (°C)	Temperature (midwater)	15.5–34.2
Salinity	Salinity (midwater)	14.3–40.0
Depth (m)	Depth (average over net length)	0–9.8
Inlet distance (km)	Distance to tidal inlet (Haversine length)	0.0–21.5
Coastline	Nearest coastline type	Beach, marsh, concrete
Human coast	Type of anthropogenic development behind nearest coast	Natural, residential, industrial

Distance to tidal inlet was calculated using the Haversine formula (i.e. as the crow flies) for each set to the midpoint for the respective tidal inlet. For Indian Pass, which has multiple inlets and is a relatively wide-open site, the perpendicular distance to the main tidal inlet was measured using the *Line Ruler* tool in Google EARTH PRO version 6.1.0.5001. Coastline type and human coastal development was determined in Google EARTH PRO using the *Circle Ruler* tool and describing the nearest coastline intersected by the circle. Coastline was described as beach (clearly defined boundary, often white coastline), marsh (undefined boundary, green coastline) or concrete (straight edged boundary, white with grass or buildings adjacent). Human coast, in the vicinity of the nearest coastline, was defined as natural (little or no evidence of anthropogenic disturbance), residential (houses, docks) or industrial (managed forest in rows, golf course or large clearings, big buildings, holding ponds, parking lots). We also included squared terms (for continuous variables only) to identify quadratic relationships that would indicate optimal values for the variables. Since the four sites are relatively close together, can be reached within a few hours' drive, and because human population density data is relatively course for the scale of this study, we did not include local human population density. The sampling gear does not reliably catch large individuals and, therefore, it was not possible to test the effect of larger sharks on the abundance of juvenile sharks. Similarly, it does not reliably catch small fish and therefore we were unable to test the effect of prey abundance.

Data treatment

Only capture records of neonate, young-of-the-year, and juvenile sharks were extracted from the database. Records with spurious values (i.e. one record with salinity of 2.3) and variables with more than 5% missing values (i.e. dissolved oxygen with 14% missing) were excluded. Bottom type was condensed into three categories (sand, mud, grass) based on the predominant type listed. Because the first and last sampled months had no observations for some species, they were combined with the adjoining months (i.e. March with April, October with November) to create a consistent variable across species. Records with missing values were excluded. The dataset was explored and summarized by individual species. We included the six most commonly caught shark species that were classified in the field as juvenile by examining claspers for males or published lengths of maturity for females, including Atlantic sharpnose shark (*Rhizoprionodon terraenovae*; <65 cm FL) (Carlson & Baremore 2003), blacktip shark (*Carcharhinus limbatus*; <120 cm FL) (Carlson *et al.* 2006), finetooth shark (*Carcharhinus isodon*; <100 cm FL) (Carlson *et al.* 2003), spinner shark (*Carcharhinus brevipinna*; <140 cm FL) (Branstetter 1987), bonnethead shark (*Sphyrna tiburo*; <90 cm FL) (Lombardi-Carlson *et al.* 2003) and scalloped hammerhead shark (*Sphyrna lewini*; <180 cm TL) (Piercy *et al.* 2007), thus excluding six species (blacknose shark *Carcharhinus acronotus*, bull shark *Carcharhinus leucas*, sandbar shark *Carcharhinus plumbeus*, Florida smoothhound shark *Mustelus norrisi*, lemon shark *Negaprion brevirostris*, and great hammerhead shark *Sphyrna mokarran*) because of low sample size.

Identifying habitat suitability

Using the treated dataset, two generalized linear mixed models (GLMM) of shark occurrence (presence/absence Bernoulli trials with logit link) were fit for each species; one to find the best overall model and a second bivariate model to isolate the best two predictors of shark occurrence. This modeling framework allowed us to screen the environmental variables for those that best predict the occurrence of individual shark species. To combine all sampling sites into one dataset, the site effect was modeled as a random intercept, which allows for different mean occurrence probabilities by bay. GLMMs were fit in R (www.r-project.org) using the *lme4* package (Bates *et al.* 2012). We minimized the Bayesian information criterion (BIC; Schwarz 1978) for variable selection under exhaustive screening of all possible variable combinations including two-way interactions. We applied the rule of marginality where interactions are only considered after the main effects are in the model. To identify the best bivariate model, the variable search was restricted to models containing two predictors (and their potential interaction). A summary of the candidate predictors used is presented in Table 1. Models were fit with soak time as an offset, which transforms the response variable from presence/absence to presence/absence *per unit soak time*, to standardize sampling effort across sets. The chosen fixed effects and their associated direction and magnitude were used to describe shark habitat preferences and predict habitat suitability, where habitat suitability is defined as predicted occurrence probability. Using the full models, predictions were mapped according to their longitude and latitude, and spatially interpolated across each bay to produce habitat suitability surfaces (note that for scalloped hammerhead shark, the *set-begin* variable was assumed constant for mapping purposes). The interpolation rasters were calculated using Bayesian Empirical Kriging within ARCGIS (version 10.0).

Results

In total, 1088 sets were used in the analyses (109 sets were excluded). Tables 2 and 3 provide set, site and occurrence characteristic summaries. A total of 6422 juvenile sharks were sampled on 695 sets (64%), with a mean of 8.5 (±0.41 SE) individuals and 2.0 (±0.04 S.E.) species caught when sharks were present (i.e. positive sets), or 5.9 (±0.31 S.E.) individuals and 1.3 (±0.04 S.E.) species overall. Average size of juvenile sharks was 48.0 (±9.4 SD) cm fork length (FL) for Atlantic sharpnose shark, 71.2 (±15.2 SD) cm FL for blacktip shark, 79.0 (±15.8 SD) cm FL for finetooth shark, 62.8 (±12.5 SD) cm FL for spinner shark, 50.3 (±10.5 SD) cm FL for bonnethead shark and 45.5 (±10.6 SD) cm FL for scalloped hammerhead shark. Occurrence was highest, by presence/absence and number, for the Atlantic sharpnose shark followed by the blacktip shark (Table 3). Overall, highest occurrence, in number of sets with sharks present, number of species, and number of sharks, occurred in IP and SAS.

Juvenile sharks occurred in all four sites, and multiple species were present across most months and throughout the survey duration of 10 years (Fig. 3). Among the surveyed sites, SAS had the highest occurrence rates of Atlantic sharpnose and bonnethead sharks followed by SJB and then IP (Fig. 3, Table 3). IP had the highest occurrence rate for blacktip, finetooth, spinner and scalloped hammerhead sharks, followed by SAS, then SJB. SAB had the lowest occurrence rates for all species.

According to the best-fit models, temperature, depth, salinity, and the squares of these terms (indicating optimal values) were the important factors driving juvenile shark occurrence across multiple species (Fig. 4, Table 4). Set-begin was only important for juvenile scalloped hammerhead sharks and was dropped in the bivariate model. These overall models were similar to the bivariate models, with a maximum of only one term being dropped from the overall model. The other investigated factors, including year, month, latitude, longitude, bottom type, inlet distance, coastline and human coast, were not influential for any species. Habitat suitability varied by site (Fig. 5), where Indian Pass and St. Andrew Sound had the highest predicted habitat suitability for four and two species, respectively, and St. Andrew Bay had the lowest predicted suitability for five of the six species. The predicted surfaces, which combine each shark's bivariate habitat preference model (Fig. 4, Table 4) and the sampled habitat characteristics (Fig. 2), highlight the differences between sites and within sites (Fig. 6).

Blacktip shark

Temperature and depth-squared were the two most influential factors affecting juvenile blacktip shark occurrence (Table 4). Within each site, across the sampled range of variables, this species preferred higher temperatures (>30 °C) and mid-range depths centered around 5.5 m (Fig. 4a). Mean occurrence probability was highest in Indian Pass (0.64; more than double the second highest site, St. Andrew Sound 0.26) and lowest in St. Andrew

Table 2. Number of samples and mean predictor values for each site and overall.

	No. of records	Set-begin	Soak (h)	Temperature (°C)	Salinity (PSU)	Depth (m)	Bottom (S:M:G)	Inlet distance (km)	Coastline (B:M:C)	Human coast (N:I:R)
SAB	198	10:25	1.17	27.7	29.96	4.0	97:57:44	8.5	179:15:4	95:59:44
SAS	364	10:55	1.19	27.7	32.49	3.5	183:154:27	2.4	361:3:0	359:5:0
SJB	275	9:50	1.20	27.3	31.99	4.2	192:45:38	12.5	149:116:10	107:32:136
IP	251	9:55	1.46	27.4	32.38	4.7	4:247:0	2.9	251:0:0	244:0:7
Total	1088	10:20	1.25	27.5	31.88	4.0	476:503:109	6.2	940:134:14	805:96:187

SAB, St. Andrew Bay; SAS, St. Andrew Sound; SJB, St. Joseph Bay; IP, Indian Pass. Bottom types are S:M:G, sand, mud; grass; coastline types are B:M:C, beach; marsh, concrete; human coast types are N:I:R, natural, industrial, residential.

Table 3. Catches and catch rates by site for each shark species. Under the occurrence categories, occurrence is the total number of sets with positive catches, occurrence rate is occurrence divided by the total number of sets, and total sharks is the number of sets, and rate of positive catches, where sharks occurred (i.e. not a sum of total sharks). Under the abundance categories, abundance is the total number of individuals caught, abundance rate is abundance divided by the number of sets, and total sharks is the total number, or rate, of sharks caught. Note: Number of sets used for rate calculations are shown in Table 2.

	Site	Blacktip shark	Bonnethead shark	Finetooth shark	Scalloped hammerhead shark	Atlantic sharpnose shark	Spinner shark	Total sharks
Occurrence	SAB	9	14	2	1	19	2	39
	SAS	94	167	21	68	227	33	289
	SJB	43	58	9	10	113	25	149
	IP	162	43	91	99	80	77	218
	Total catch	308	282	123	178	439	137	695
Occurrence rate	SAB	0.05	0.07	0.05	0.01	0.10	0.01	0.2
	SAS	0.26	0.46	0.06	0.19	0.62	0.09	0.79
	SJB	0.16	0.21	0.03	0.04	0.41	0.09	0.54
	IP	0.65	0.17	0.36	0.39	0.32	0.31	0.87
	Total	0.283	0.259	0.113	0.164	0.404	0.126	0.64
Abundance	SAB	10	43	2	1	38	2	96
	SAS	227	517	37	287	1712	107	2887
	SJB	113	181	14	67	598	95	1068
	IP	858	117	386	383	345	282	2371
	Total catch	1208	858	439	738	2693	486	6422
Abundance rate	SAB	0.05	0.22	0.01	0.01	0.19	0.01	0.48
	SAS	0.62	1.42	0.10	0.79	4.70	0.29	7.93
	SJB	0.41	0.66	0.05	0.24	2.18	0.35	3.88
	IP	3.41	0.47	1.54	1.53	1.38	1.12	9.44
	Total	1.11	0.78	0.40	0.68	2.48	0.45	5.90

SAS, St. Andrew Sound; SAB, St. Andrew Bay; SJB, St. Joseph Bay; IP, Indian Pass.

Bay (0.05; Fig. 5). The habitat suitability surfaces indicate that the highest predicted occurrence of juvenile blacktip sharks is throughout Indian Pass, with increased occurrence in the northwestern area close to the tidal inlet. Predicted occurrence was much lower in St. Andrew Sound, St. Joseph Bay and St. Andrew Bay (Fig. 6a).

Bonnethead shark

For juvenile bonnethead sharks, temperature and salinity-squared were the two most influential factors affecting occurrence (Table 4). Within each site, across the sampled range, bonnethead shark occurrence increased with temperature (>30 °C) and preferred a mid-range of salinity centered around 30–35 PSU (Fig. 4b). Habitat suitability was highest in St. Andrew Sound (0.21), followed by St. Andrew Bay (0.14), and was very low in both St. Joseph Bay (0.08) and Indian Pass (0.04; Fig. 5). These findings are similar to that shown in Fig. 6b, where juvenile bonnethead shark predicted occurrences were highest in St. Andrew Sound, with pockets of higher predicted occurrence throughout the bay. The same was found for St. Andrew Bay, where predicted occurrences were lower than St. Andrew Sound but also varied throughout the bay. Predicted habitat suitability for juvenile bonnethead in Indian Pass and St. Joseph Bay approached zero.

Finetooth shark

Salinity and depth-squared were the most important factors influencing juvenile finetooth shark occurrence (Table 4). Within each site, across the sampled range, this species preferred the lower salinity range (<20 PSU) and the mid-depth range centered on 4 m (Fig. 4c). Mean predicted occurrence probability for finetooth sharks was highest in Indian Pass (0.12) followed by St. Andrew Sound (0.02), and was very low for St. Andrew Bay and St. Joseph Bay (<0.01; Fig. 5). Prediction surfaces showed similar trends, with juvenile finetooth sharks being restricted to the inshore side of Indian Pass (Fig. 6c).

Scalloped hammerhead shark

Temperature and salinity were the two most influential factors determining juvenile scalloped hammerhead shark occurrence (Table 4), where occurrence increased with both temperature (>30 °C) and salinity (>35 PSU) within sites across the sampled range (Fig. 4d). Indian Pass had

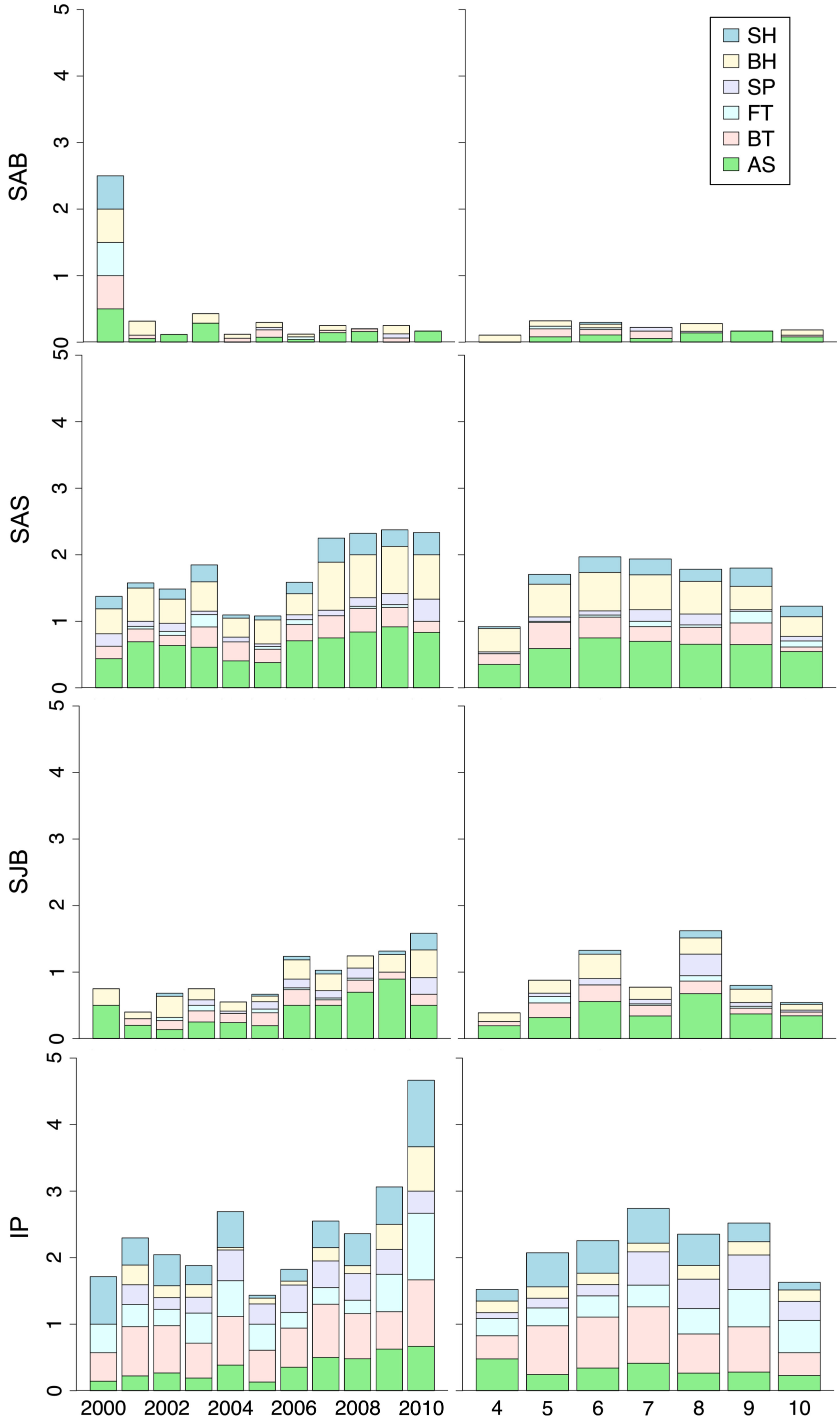

Fig. 3. Catch rates of juvenile sharks per year and month – demonstrating the use of each site by species across years and months. SAS, St. Andrew Sound; SAB, St. Andrew Bay; IP, Indian Pass; SJB, St. Joseph Bay. AS, Atlantic sharpnose shark; BT, blacktip shark; FT, finetooth shark; SP, spinner shark; BH, bonnethead shark; SH, scalloped hammerhead shark.

the highest mean occurrence (0.14), followed by St. Andrew Sound (0.06), St. Joseph Bay (0.01) and St. Andrew Bay (<0.01; Fig. 5). The predicted surfaces show that the highest occurrence rates are expected in the offshore areas of Indian Pass, between the two inlets (Fig. 6d). Predicted occurrences in the three other sites approached zero (Fig. 6d).

Atlantic sharpnose shark

Atlantic sharpnose shark was most influenced by temperature and depth (Table 4), occurrence increasing with both factors within each site across the sampled range (Fig. 4e). St. Andrew Sound had the highest mean occurrence of juvenile Atlantic sharpnose sharks (0.35),

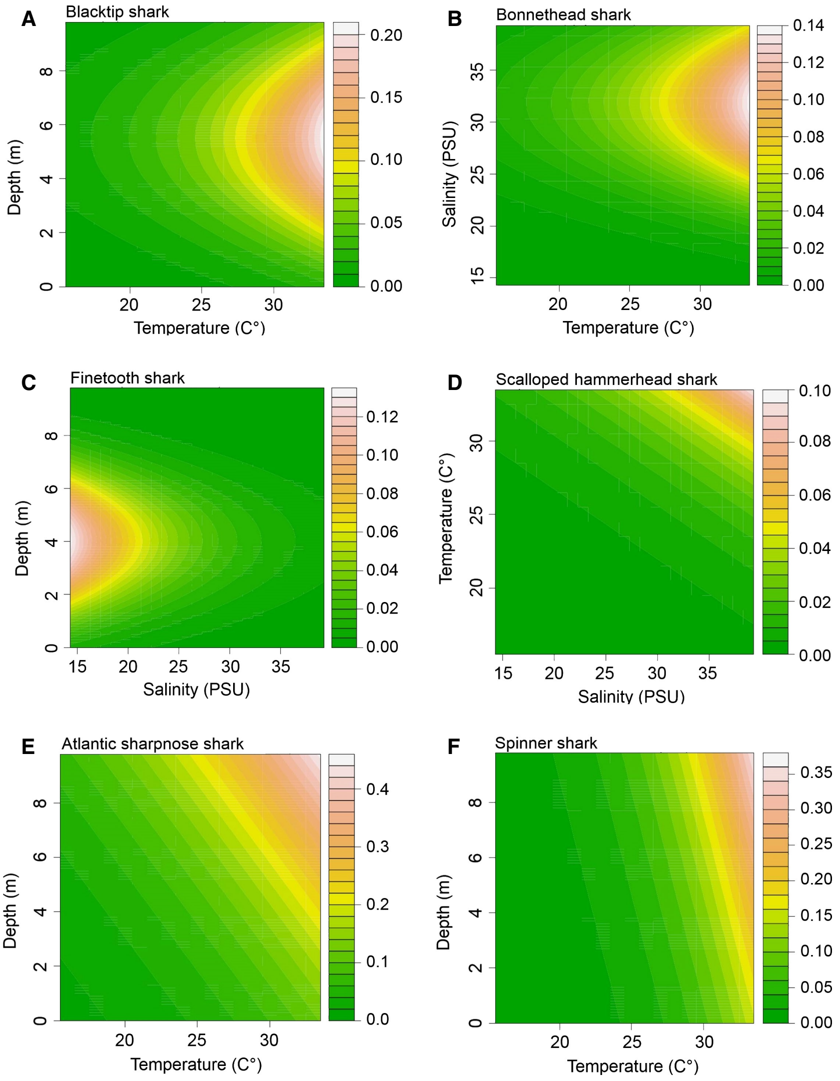

Fig. 4. Habitat preference of juvenile sharks. Shown are bivariate contour plots of the two most influential variables affecting occurrence for each of six shark species. Note that the occurrence probability scale differs for each plot.

followed by St. Joseph Bay (0.19) and Indian Pass (0.10), and St. Andrew Bay had low mean occurrence (0.03; Fig. 5). The predicted surfaces show the highest Atlantic sharpnose occurrences in the center of both St. Andrew Sound and St. Joseph Bay, increasing with distance from shore in Indian Pass (Fig. 6e).

Spinner shark

Temperature and depth were the most influential factors affecting juvenile spinner shark occurrence (Table 4), with occurrence increasing with both depth (>8 m) and temperature (>30 °C) within each site and across the sampled range (Fig. 4f). Indian Pass had the highest mean occurrence probability for this species (0.12), followed by St. Joseph Bay (0.03), St. Andrew Sound (0.03) and St. Andrew Sound (<0.01; Fig. 5). According to the prediction surfaces, the mid-offshore area of Indian Pass is expected to have the highest occurrences, with all other sites having very low predicted occurrences (Fig. 6f).

Discussion

This study improves our general understanding of juvenile shark distribution patterns in the northeastern Gulf of Mexico. The juveniles of at least six shark species co-occurred in the study region across months and years, suggesting that the region is valuable for the early life stages of multiple shark species. Occurrence and abundance rates varied between sites, with the highest rates in Indian Pass and St. Andrew Sound and the lowest in St. Andrew Bay, suggesting preferences among sites. Bivariate analyses indicate that occurrence patterns are primarily influenced by temperature, salinity and depth, whereas

Table 4. Coefficients (β) and level of significance (P-values) from GLMM best overall (shown first) and bivariate (shown second and denoted with *) models for juvenile shark occurrence by minimizing BIC, with soak time as an offset and area as a random effect. Year, month, latitude, longitude, set-begin, bottom type, coastline and human coast were tested but were not found to be influential for any of these species. Note that in three cases the best models were also the best bivariate models and therefore only one model is shown. Negative squared terms indicate that optimum values were found, positive squared terms indicate avoidance from the mean values.

	β	P-value
Blacktip shark		
$\sim X_{\text{temperature}} + X_{\text{depth}} + X^2_{\text{depth}}$		
$X_{\text{temperature}}$	(+) 0.136	4.01×10^{-7}
X_{depth}	(+) 0.218	0.00023
X^2_{depth}	(−) 0.085	0.00014
Bonnethead shark		
$\sim X_{\text{temperature}} + X^2_{\text{salinity}}$		
$X_{\text{temperature}}$	(+) 0.129775	0.025478
X^2_{salinity}	(−) 0.014626	0.006625
Finetooth shark		
$\sim X_{\text{salinity}} + X^2_{\text{depth}}$		
X_{salinity}	(−) 0.12236	0.000572
X^2_{depth}	(−) 0.15089	0.00074
Scalloped hammerhead shark		
$\sim X_{\textit{set-begin}} + X_{\text{temperature}} + X_{\text{salinity}}$		
$X_{\textit{set-begin}}$	(+) 0.09389	0.00201
$X_{\text{temperature}}$	(+) 0.18302	2.89×10^{-7}
X_{salinity}	(+) 0.08876	0.00999
$\sim X_{\text{temperature}} + X_{\text{salinity}}$*		
$X_{\text{temperature}}$	(+) 0.19167	7.59×10^{-08}
X_{salinity}	(+) 0.09125	0.00768
Atlantic sharpnose shark		
$\sim X_{\text{depth}} + X_{\text{temperature}} + X^2_{\text{salinity}}$		
X_{depth}	(+) 0.172071	2.78×10^{-05}
$X_{\text{temperature}}$	(+) 0.134501	2.29×10^{-09}
X^2_{salinity}	(−) 0.015799	0.006304
$\sim X_{\text{depth}} + X_{\text{temperature}}$*		
X_{depth}	(+) 0.18041	9.41×10^{-06}
$X_{\text{temperature}}$	(+) 0.12965	4.93×10^{-09}
Spinner shark		
$\sim X_{\text{temperature}} + X^2_{\text{temperature}}$		
$X_{\text{temperature}}$	(+) 0.319819	9.95×10^{-14}
$X^2_{\text{temperature}}$	(+) 0.029143	0.00047
$\sim X_{\text{temperature}} + X_{\text{depth}}$*		
$X_{\text{temperature}}$	(+) 0.27348	7.67×10^{-10}
X_{depth}	(+) 0.13708	0.0209

other factors, such as human development, set-begin time and bottom type, were not significant. Habitat suitability models, as determined by merging the important physical factors for each species with the site-specific characteristics of the selected factors, show the areas where high and low abundances of each species may be expected based on these variables alone.

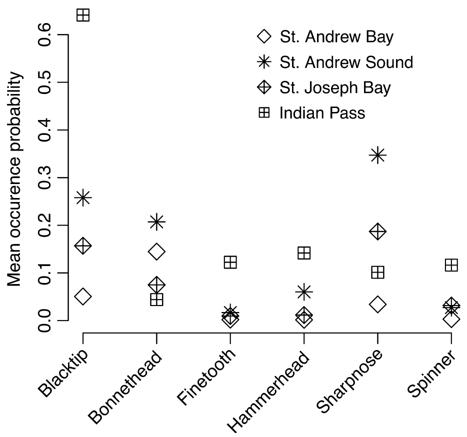

Fig. 5. Mean occurrence probability of juvenile blacktip shark, bonnethead shark, finetooth shark, scalloped hammerhead shark, Atlantic sharpnose shark and spinner shark for four samples sites in the Northern Gulf of Mexico.

The importance of temperature, salinity and depth in driving shark distribution patterns is not novel. Studies investigating juvenile shark habitat preference are limited, but those that exist, corroborate the importance of temperature (Morrissey & Gruber 1993; Matern *et al.* 2000; Ortega *et al.* 2009), salinity (Heupel & Simpfendorfer 2008) and depth (Morrissey & Gruber 1993; Heithaus *et al.* 2007) in a variety of species, including the species investigated in the current study (see Table 5). Across studies, blacktip sharks preferred warmer temperatures (or summer seasons) and mid-range depths in Texas (Froeschke *et al.* 2010), the US Virgin Islands (DeAngelis *et al.* 2008) and Florida (current study). For bonnethead sharks, salinity is an important factor driving distributions in Georgia (Belcher & Jennings 2010), Texas (Froeschke *et al.* 2010) and Florida (Ubeda *et al.* 2009; current study). Warm temperatures (or summer season) are important for Atlantic sharpnose sharks (Carlson *et al.* 2008, current study). There are no published studies describing the habitat preferences of juvenile scalloped hammerhead, spinner or finetooth sharks.

Despite similarities between studies, there are important differences. For example, bottom type and inlet distance have been identified as important features driving bonnethead and blacktip shark distributions (Heupel *et al.* 2006; DeAngelis *et al.* 2008; Froeschke *et al.* 2010), but this was not the case in the current study. As well, sharks are said to be more active at certain times of the day (e.g. dusk and dawn; Gruber *et al.* 1988; Bres 1993) – increased activity would increase the likelihood of sharks entering the gillnets. However, set-begin (the time of day when the survey was conducted) was not an important factor in the current study. Likewise, anthropogenic

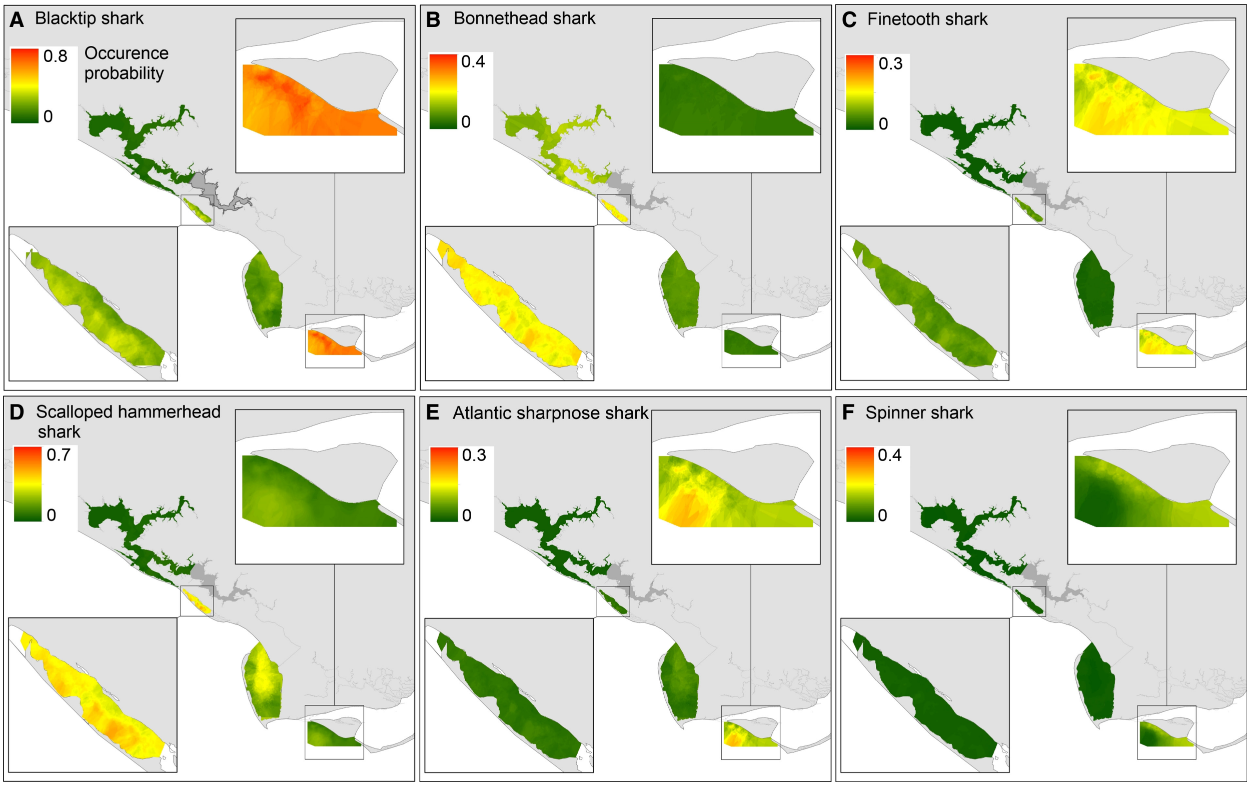

Fig. 6. Prediction surfaces of juvenile shark occurrence based on shark habitat preferences and the distribution of environmental variables. Note that the occurrence probability scale differs for each plot.

impacts (i.e. coastline type, human coast) were not found to be important drivers for the occurrence of any of these six species, but pollution, exploitation, and habitat degradation have been implicated in decreased resilience and abundances (Sandin *et al.* 2008; Carlisle & Starr 2009; Knip *et al.* 2010; Ward-Paige *et al.* 2010).

There are a number of potential explanations for results being different between studies. These discrepancies could be due to real variations in shark preference between sites or populations. For example, studies showing the effect of human population on shark abundance took place on coral reef areas (Sandin *et al.* 2008; Ward-Paige *et al.* 2010), rather than in bays or estuaries, and likely report on adult populations as opposed to juveniles that use inshore areas for refuge.

Differences could also be a function of the goals, scale, sampling methods or statistical analysis of the study. Sampling method and techniques depend on the study goals, location, scale and species. As such, a variety of sampling methods have been deployed to sample sharks, including longlines (DeAngelis *et al.* 2008), acoustic monitoring (Heupel *et al.* 2006; Ubeda *et al.* 2009), tag–recapture (Heupel *et al.* 2006) and underwater visual census (Sandin *et al.* 2008; Ward-Paige *et al.* 2010). Sampling methods can dramatically affect results. For example, Ubeda *et al.* (2009) found that salinity was unimportant or important for bonnethead shark distribution and movement, depending on whether acoustic monitoring (continuous data) or gillnet survey data (snapshots) were used. Scale of a study can also be important, where some studies include a single (Heupel *et al.* 2006; DeAngelis *et al.* 2008) and some multiple bays and estuaries (Froeschke *et al.* 2010), which can increase the variation of the parameters investigated.

As well, the intentions of the study and the factors that are investigated may impact the results of the important drivers. For example, Froeschke *et al.* (2010) investigated a suite of variables but this did not include any direct anthropogenic activities such as human population or coastal development.

As well, we could not test a few potentially important factors, which could revise the factors found to be important drivers of distribution. Increasing the range of the variables sampled (e.g. covering a wider range of temperatures, salinities, distance to tidal inlet, etc.) may have increased the number of important squared-terms as a result of including optimal ranges. It is widely assumed that coastal areas benefit young sharks by providing

Table 5. Summary of important features found to influence juvenile habitat use patterns in other areas of the Gulf of Mexico and adjacent regions. Heupel *et al.* (2006), Ubeda *et al.* (2009) and DeAngelis *et al.* (2008) combined data on adults. Froeschke *et al.* (2010) ranked factors and the top four are shown here. Note that not all the other factors tested in the current study were tested by these other studies.

Common	Location	Important variables	References
Bonnethead shark	GA, USA	Depth, salinity, turbidity	Belcher & Jennings (2010)
Bonnethead shark	TX, USA	Depth, salinity, inlet distance	Froeschke *et al.* (2010)
Blacktip shark	US Virgin Islands	Depth, season, bottom type	DeAngelis *et al.* (2008)
Blacktip shark	TX, USA	Salinity, depth, inlet distance, temperature	Froeschke *et al.* (2010)
Bonnethead shark	FL, USA	Depth, bottom type	Heupel *et al.* (2006)
Bonnethead shark	FL, USA	Salinity	Ubeda *et al.* (2009)
Bonnethead shark	TX, USA	Salinity, depth, inlet distance, temperature	Froeschke *et al.* (2010)
Atlantic sharpnose	FL, USA	Season	Carlson *et al.* (2008)

protection from predators and adequate food resources to support early growth rates (Simpfendorfer & Milward 1993; Heupel & Hueter 2002; Heithaus *et al.* 2007, 2009). However, we could not test whether predator avoidance or prey abundance is driving juvenile shark site selection because the sampling gear did not allow for reliable sampling of larger sharks or smaller prey species. It is possible that these factors may have been important if investigated. As well, we could not test for the importance of turbidity, dissolved oxygen or freshwater inflow because they were inadequate or not sampled, but they have been shown to be important for other species (Belcher & Jennings 2010; Froeschke *et al.* 2010).

Our results, showing the presence and abundance of these six shark species across months and years in three of the sampled sites, suggests the region is important for juvenile sharks and may be considered important 'nursery areas'. However, because encounter rates were not compared with those in other regions, it is not clear that they are 'nurseries' as defined by Heupel *et al.* (2007). However, there are lines of evidence that suggest at least two of the sites may be considered nurseries. For example, Indian Pass and St. Andrew Sound had the highest occurrence and abundance rates of juvenile sharks from spring to fall, and across all years. IP had the highest rates of four species, including blacktip, finetooth, spinner and scalloped hammerhead sharks, with a total shark occurrence rate of 0.87 (Table 3). Indian Pass is also the only site where sandbar sharks, a species whose commercial and recreational harvest is prohibited, were encountered (Carlson 1999). St. Andrew Sound, the smallest surveyed site, had the highest rates of juvenile Atlantic sharpnose and bonnethead sharks, with a total shark occurrence rate of 0.79 (Table 3). In contrast, St. Andrew Bay had the lowest occurrence and abundance for most shark species and occurrence was intermittent, with absences in many months and years, and a total occurrence rate of 0.2 (Table 3). Therefore, when compared with each other, it seems that at least two of the sites may be considered nursery areas, but this requires further investigation.

The site with the lowest shark occurrence and abundance rates, St. Andrew Bay, also has the largest human population; however, our results do not suggest the absence of sharks is related to humans. This may be the natural condition, or a result of lurking variables. Although higher human population density has been linked with the absence of sharks in some tropical reef communities (Sandin *et al.* 2008; Ward-Paige *et al.* 2010), our bivariate analysis and the prediction surfaces do not suggest that these are important features driving the absence of sharks in this bay. However, temperature, salinity and depth could be affected by lurking anthropogenic variables, such as freshwater discharge inputs, which can alter site conditions such as dissolved oxygen, turbidity and salinity, and contribute pollutants and nutrients that negatively influence water quality (e.g. nitrogen and phosphorus runoff from golf courses). Therefore, unless anthropogenic activity has altered these three important variables, it is likely that St. Andrew Bay naturally has a lower juvenile shark population abundance. This suggests that although humans heavily influence adult sharks, the juveniles are less affected.

Overall, our study informs on these six species in the Northeastern Gulf of Mexico. When used in context with other studies, the study suggests that temperature, depth and salinity are important factors, but that preferences are species- and site-specific. Historically, fisheries management focused on a single target species and was mostly concerned with regulating catch and bycatch through limiting fishing effort, catch quotas, and gear modifications. Today, however, there is an increasing movement towards an ecosystem-based approach to fisheries that requires the consideration of abiotic and biotic factors, such as water quality and habitat needs for spawning, foraging and nurseries (Pikitch *et al.* 2004; Marasco *et al.* 2007). To support these progressive conservation initiatives that strive to protect sites that contribute disproportionately to the population, it is essential to identify environmental factors influencing juvenile habitat use. The results of this study demonstrate that, although numerous sites may support juvenile shark populations, some sites are better suited than others, and these differences are likely a result of the availability of specific physical factors. Our results show that there is overlap between juveniles of multiple species through time and space, which should make multi-species management and conservation strategies practicable.

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