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Identification of estuarine nursery habitat for young-of-year scalloped hammerhead sharks (*Sphyrna lewini*) in the Tolomato River, Florida, USA

Bryanna Wargat[a], Clark Morgan[a,1], Michael McCallister[a,1], Bryan S. Frazier[b], James Gelsleichter[a,*]

[a] University of North Florida, 1 UNF Dr, Jacksonville, FL 32224, USA
[b] South Carolina Department of Natural Resources, Marine Resources Research Institute, 217 Fort Johnson Road, Charleston, SC 29412, USA

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ABSTRACT

The scalloped hammerhead (*Sphyrna lewini*) is a globally threatened shark species that has experienced significant declines throughout its range due to overfishing, along with high rates of post-release mortality. Because of this, there is a need to obtain data useful for the management of *S. lewini* populations, including information on nursery areas. This study describes a unique, inshore nursery for northwest Atlantic young-of-year (YOY) *S. lewini*, in the Tolomato River in northeast Florida, USA. Relative abundance of YOY *S. lewini* in the Tolomato River was determined over 10 years using bottom longline fishing and compared to that in two nearby estuaries previously shown to serve as communal shark nurseries, the St. Marys River and the Nassau River. Average catch rates were shown to be 10 – 30 times greater in the Tolomato River compared to those in other sites, demonstrating that YOY *S. lewini* are found more commonly in this river system. YOY *S. lewini* consistently made up a significant proportion of overall shark catch over the duration of the 10-year survey, demonstrating repeated use across years. YOY *S. lewini* were caught in the Tolomato River from May to September annually, suggesting that they only use the Tolomato River as a nursery for the first 4 – 5 months of life. This, along with the recapture of 3 individuals ranging from 6 – 59 days post-release, suggests that YOY *S. lewini* remain in this site for extended periods of time; however, future work using acoustic telemetry is needed to confirm this finding. Overall, this study shows that the Tolomato River meets previously established criteria needed to confirm that it serves as nursery habitat for YOY *S. lewini*. Future work is needed to examine microhabitat selection by YOY *S. lewini* in this site, and interactions between this species and other sharks.

1. Introduction

The scalloped hammerhead *Sphyrna lewini* is a large, viviparous shark species that occurs globally from inshore coastal areas to the open ocean in both temperate and tropical waters (Compagno, 1984). There are six existing distinct population segments (DPS) of *S. lewini* throughout the world, including the Northwest Atlantic and Gulf of Mexico DPS, Central and Southwest Atlantic DPS, Eastern Atlantic DPS, Indo-West Pacific DPS, Central Pacific DPS, and Eastern Pacific DPS (Miller et al., 2014). Due to late female sexual maturity of 14–16 years of age and fecundity of 7–30 pups annually (Moncrief-Cox et al., 2021), populations of this species may exhibit a low rate of increase and limited resilience to fishing pressure (Branstetter, 1987; Duncan and Holland, 2006; Piercy et al., 2007). As a function of this, along with intense fishery exploitation, most DPS of *S. lewini* have experienced significant population declines to the extent that several have been listed as threatened or endangered under the U.S. Endangered Species Act (ESA), and the IUCN has recently categorized the species as critically endangered globally (Rigby et al., 2019). Thus, there is a critical need to improve management and conservation of this species on a worldwide basis.

The Northwest Atlantic and Gulf of Mexico (NWA/GOM) DPS of *S. lewini* is found from New Jersey to Brazil in the western Atlantic Ocean, and in the Gulf of Mexico and Caribbean Sea (Miller et al., 2014). Although this DPS is not listed as threatened or endangered under the U. S. ESA, it has experienced significant exploitation in the recent past (Hayes et al., 2009). In fact, Hayes et al. (2009) estimated that these populations experienced an estimated 83% reduction from 1981 to the

* Corresponding author.
E-mail address: jim.gelsleichter@unf.edu (J. Gelsleichter).
[1] Present address: Harbor Branch Oceanographic Institute, Florida Atlantic University, 5600 North U.S. Highway 1, Fort Pierce, Florida 34946, USA.

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early 1990s due to overharvest by commercial and recreational fishing. Following the enactment of a multispecies Shark Fishery Management Plan (FMP) in 1994 (National Marine Fisheries Service, 1993), the population stabilized and began to recover at a slow rate; it has a strong probability of rebuilding over the course of 20–30 years provided that reduced fishing mortality is maintained. However, as Miller et al. (2014) indicated, this DPS may still be threatened by increases in illegal, unreported, and unregulated fishing, as well as high at-vessel mortality rates. It is also noteworthy that individuals from the western Atlantic have been shown to make up a not-insignificant proportion of *S. lewini* fins in the international shark fin trade (Chapman et al., 2009). Given these points, it is important to obtain management-relevant information on these populations as they still face threats that could reverse positive trends in population abundance.

In 1996, the reauthorization of the Magnuson-Stevens Fishery Conservation and Protection Act emphasized the importance of essential fish habitat to the maintenance of healthy fish populations (U.S. Department of Commerce, 2007). Essential Fish Habitat (EFH) represents areas that are necessary to the spawning, feeding, breeding, or growth of a marine organism. As locations where newborn and juvenile individuals may congregate for extended periods of time and possibly re-occur over multiple years, shark nursery habitats are typically considered to be EFH because of their potential importance to the early life stages of many shark species (Heupel et al., 2007; 2018). These habitats are typically found in estuaries, bays, sounds, and littoral zones, and may benefit juvenile growth and survival by providing a surplus of food and/or protection from predators, ultimately contributing positively to overall population stability (Sadowsky, 1965; Springer, 1967; Clarke, 1971; Branstetter, 1987; Branstetter, 1990; Castro, 1993; McCallister et al., 2013). Because of this, many studies have examined nursery habitat use in various shark species in an effort to contribute to the management and recovery of exploited and/or imperiled populations (Heupel et al., 2007; 2018).

Like many sharks, *S. lewini* is known to use inshore and/or nearshore nurseries throughout its range of occurrence, often exhibiting high abundance and strong residency in shallow, turbid, and sheltered coastal embayments with freshwater input (Clarke, 1971; Snelson and Williams, 1981; Compagno, 1984; Branstetter, 1990; Castro, 1993; Simpfendorfer and Milward, 1993; Duncan and Holland, 2006; Brown et al., 2016; Rosende-Pereiro and Corgos, 2018; Zanella et al., 2019; Cuevas-Gómez et al., 2020; Corgos and Rosende-Pereiro, 2022). Still, only limited directed studies have examined nursery habitat use for *S. lewini* belonging to the NWA/GOM DPS. This is particularly true for areas on the U.S. east coast, although information from multiple sources suggests that nursery habitats for this species occur broadly in coastal areas ranging from southern portions of North Carolina to the Texas coastline (Sadowsky, 1965; Clarke, 1971; Dodrill, 1977; Snelson and Williams, 1981; Branstetter, 1987; Castro, 1993; Adams and Paperno, 2007; Ulrich et al., 2007; McCallister et al., 2013; Miller et al., 2014; Barker et al., 2021). As part of a now, > 10-year survey of shark nursery habitats in northeast Florida waters (McCallister et al., 2013), we obtained evidence of a unique inshore nursery for *S. lewini* in the Tolomato River, a small portion of the Atlantic Intracoastal Waterway situated between southern Jacksonville and St. Augustine, FL. However, to confirm these findings, it is necessary to evaluate whether this habitat meets criteria established by Heupel et al. (2007) for differentiating between juvenile shark "occurrence" and more direct selection of a proposed nursery habitat, presumably because it holds some evolutionary significance for the species in question. These criteria are that: 1) sharks are more commonly found in the proposed nursery habitat than other available habitats, 2) individual sharks exhibit strong residency in the proposed site for extended periods of time, and 3) the proposed habitat should be used repeatedly across years. It is noteworthy to point out that while these criteria have been widely adopted and cited in the scientific literature, few studies have been capable of successfully testing all three of them (Heupel et al., 2018). This is especially true for Criterion 1, which requires that sampling occurs in areas outside of the proposed nursery so that comparisons of shark density can be made between these habitats.

Therefore, the goal of this study was to assess whether the Tolomato River is a nursery habitat for *S. lewini* based on the criteria established by Heupel et al. (2007). In particular, this study focused largely on addressing the rarely studied Criterion 1 by comparing the abundance of juvenile *S. lewini* in this proposed nursery with that in two nearby habitats previously found to serve as communal shark nurseries, the Nassau River estuary and the St. Marys River estuary (McCallister et al., 2013). We also present data pertaining to shark residency in this system (Criterion 2) and its re-use over multiple years (Criterion 3) based on a 10-year series of survey data, along with preliminary results from a two-year pilot mark-recapture study. The purpose of this research was to improve knowledge regarding nursery habitat use by the NWA/GOM DPS of *S. lewini* for use in fishery management.

2. Materials and methods

2.1. Study area

The proposed scalloped hammerhead nursery examined in this study was in the Tolomato River, a component of the Atlantic Intracoastal Waterway located in northeast Florida between southern Jacksonville and St. Augustine. The river is a narrow and relatively shallow, tidally influenced barrier island lagoon with a single primary inlet to its south (St. Augustine Inlet) connecting it to the Atlantic Ocean (Valle-Levinson et al., 2009). The river is also a portion of the larger Guana-Tolomato-Matanzas (GTM) estuary, which is primarily a marine-dominated system that is only transiently influenced by precipitation because of a water management system located on the Guana River (Williams et al., 2014). The GTM estuary is home to the GTM National Estuarine Research Reserve (NERR), a 76,000-acre research reserve that is one of 30 coastal sites belonging to a network of NERRs established by the U.S. Coastal Zone Management Act of 1972 as locations for estuarine research, education, and stewardship.

Catch data of scalloped hammerheads in the Tolomato River were compared with those from the Nassau River and St. Marys River estuary systems, which have been the focus of an annually conducted, fishery-independent shark abundance survey since 2009 (McCallister et al., 2013). The St. Marys River estuary forms the easternmost natural border between southeastern Georgia and northeastern Florida, emptying into the Atlantic Ocean through the Cumberland Sound Inlet. The Nassau River estuary lies to the south of the St. Marys River, between Nassau County and Duval County, and discharges into the Atlantic Ocean through the Nassau Sound Inlet. When including the Tolomato River study area, these three sites encompass the majority of available inshore habitats, apart from the St. Johns River, north of St. Augustine to the Florida-Georgia border (Fig. 1).

2.2. Animal collections

Shark abundance and species composition were surveyed in the Tolomato River from 2010 to 2019 using bottom longline fishing, following the methods described in McCallister et al. (2013). Longlines were composed of a 250- to 300-meter #8 braided nylon mainline, which was anchored at both ends and marked with buoys. The line contained 50 branchlines, each composed of a size 120 stainless steel longline snap with a 4/0 swivel connected to a 12/0 barbless circle hook by a 1-meter, 90-kg test monofilament leader. All hooks were baited with Atlantic Mackerel, *Scomber scombrus*. Lines were soaked for 15 min, as opposed to the 30-minute soak time used by McCallister et al. (2013), to minimize mortality of *S. lewini*. Set locations were haphazardly selected based on varying weather conditions, tides, and maritime conditions present at the time of sampling. Environmental data were collected at each sampling site using a YSI Pro2030 (YSI, Inc., Yellow

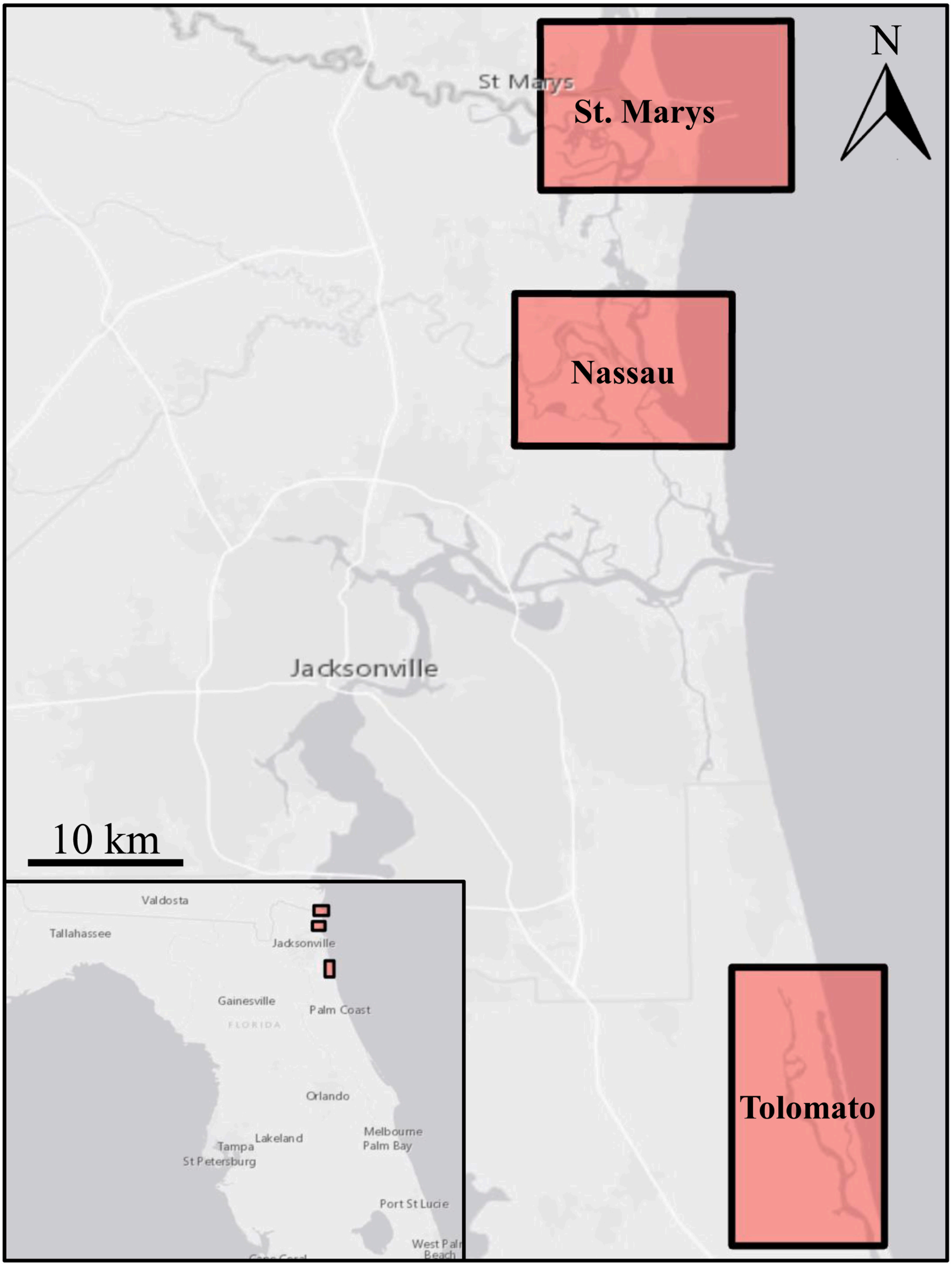

Fig. 1. Map of all three study sites used to assess scalloped hammerhead shark presence in northeast Florida.

Springs, Ohio), including bottom water temperature (°C), salinity (ppt), dissolved oxygen (mg/L), and conductivity (mS). Maximum and minimum water depth (m) were recorded for each set, and the mean depth was calculated.

Scalloped hammerhead abundance in the Tolomato River was compared with data from bottom longline surveys conducted in the St. Marys River and Nassau River estuaries during the same time period (i.e., 2010 to 2019). The sampling methodology used in the St. Mary River and Nassau River sites was identical to that conducted in the Tolomato River site with a single exception; that is, soak time was 30 min in duration as initially described in McCallister et al. (2013).

All sharks were identified to species, sexed, and measured (cm) in precaudal length (PCL; tip of rostrum to precaudal pit), fork length (FL; tip of the rostrum to fork in caudal fin) and stretched total length (STL; tip of the rostrum to the posterior end of the extended caudal fin) on a straight-line basis. Life stage was classified as young-of-year (YOY, Age

0), juvenile, or adult, based on length-at-birth and length-at-maturity estimates described in published literature. If the individual was categorized as YOY, the umbilical scar status was also recorded using five possible categories: 1 = umbilical remains present, 2 = open or fresh scar, 3 = partially open with some healing, 4 = well-healed with a visible scar, and 5 = no scar present (Aubrey and Snelson, 2007). Unless moribund or dead, most sharks were released live. Most sharks larger than 50 cm STL were tagged in the dorsal fin with a numbered rototag (provided by NOAA Fisheries Cooperative Shark Tagging Program) prior to release. Sharks less than 50 cm STL were generally released untagged because of concerns regarding tag biofouling and increased drag production, potentially leading to increased energy expenditures and decreased swimming efficiency (Lear et al., 2018). However, beginning in 2019, YOY scalloped hammerheads in good condition were tagged using 140-mm plastic-tipped dart tags (Hallprint Fish Tags, Hindmarsh Valley, South Australia, Australia), which have been used for small YOY sharks in comparable studies (Grubbs and Musick, 2007; Merson and Pratt, 2007).

Recent studies have demonstrated the occurrence of a sympatrically distributed cryptic congener to *S. lewini*, the Carolina hammerhead (*Sphyrna gilberti*), off the southeastern U.S. coast (Quattro et al., 2013). The two species are indistinguishable based on external features alone and can only be identified using precaudal vertebral counts or genetic analysis (Quattro et al., 2013), creating the potential for species misassignment in field studies. However, previous work conducted by Barker et al. (2021) have demonstrated that *S. gilberti* is seemingly absent from the Tolomato River, as all "scalloped hammerheads" sampled from this location (n = 148, all of which were obtained as part of this survey) were confirmed to be *S. lewini* using genetic analysis. Therefore, there is strong confidence that the current study represents nursery ground use by *S. lewini* alone rather than a species complex.

2.3. Data Analysis

Species composition, abundance, percentage of total catch, sex, and life stage was reported for all sharks caught in the Tolomato River survey. Catch rates of YOY *S. lewini* (the main life stage sampled during this study) were expressed as catch per unit effort (CPUE); i.e., the number of YOY scalloped hammerhead sharks caught per 50 hooks. Scalloped hammerhead CPUE was compared across months and years using Kruskal-Wallis nonparametric ANOVA because data did not meet assumptions of normality and homoscedasticity.

A binary logistic regression model was used to assess the effects of environmental conditions on the presence/absence of YOY *S. lewini*. Parameters included average depth, bottom temperature, salinity, dissolved oxygen, and conductivity. Only sets for which all environmental parameters were recorded (n = 350) were used for these analyses. Conditions were considered to significantly influence the probability of catching a scalloped hammerhead shark if $p < 0.05$. Catch rates were also mapped geographically using ArcGIS Pro to identify potential areas of importance within the Tolomato River.

Catch rates of YOY scalloped hammerheads in the Tolomato River were compared with those from the St. Marys River estuary and Nassau River estuary to test the first criterion of nursery habitat identification; that is, whether *S. lewini* is more abundant in the proposed nursery habitat than other available habitats (Heupel et al., 2007). Only sets for which all environmental parameters were recorded were used in these analyses. Catch per unit effort was expressed as the number of YOY scalloped hammerheads caught per 50 hook-hours to standardize for the difference in soak time between the Tolomato River (15 min) and other estuaries (30 min); however, differences in CPUE expressed as sharks per 50 hooks were also tested. Catch rates were compared between the three estuaries using Kruskal-Wallis nonparametric analysis because data did not meet assumptions of normality and homoscedasticity.

A general linear model was also used to determine factors that influenced *S. lewini* abundance. Depth, salinity, conductivity, dissolved oxygen, and bottom temperature were used as covariates in the model to account for varying environmental conditions across the three estuaries. All potential interactions between covariates were included in this analysis. Factors that were not significant were removed from the model until only significant variables remained. Variables were considered to be significant if $p < 0.05$. Once all factors that significantly affected YOY scalloped hammerhead abundance were identified, these variables were compared among the three estuaries. This was done to determine whether environmental conditions were responsible for any significant differences in YOY scalloped hammerhead abundance between the three estuaries.

Mark-recapture data were used to test the second and third criteria of nursery ground identification; that is, whether individuals exhibit strong residency in the proposed site for extended periods of time, and if the proposed habitat is used repeatedly over years (Heupel et al., 2007). For each shark recaptured, time at large was recorded, the location of release and recapture sites were mapped using ArcGIS Pro, and recapture distance was determined by calculating the distance between the two points following the midline of the river.

3. Results

3.1. Characterization of shark fauna in the Tolomato River

A total of 444 longline sets were completed in the Tolomato River between the months of April and November from 2010–2019. A total of 618 sharks were caught, representing 10 species (Table 1). Of the sharks caught, 248 (40.1%) were identified as scalloped hammerheads. Apart from three individuals for which life stage was not recorded, all *S. lewini* were categorized as YOY. For 224 *S. lewini* for which umbilical scar status was recorded, 0.9% were assigned to category 2, 11.2% were assigned to category 3, and 87.9% were assigned to category 4; no sharks were listed as having a category 1 or 5 status.

Morphometric data collected from 234 scalloped hammerhead sharks were used in length analyses. Fork lengths for these animals averaged 37.7 ± 0.2 cm (SE) and ranged from 29 to 45 cm. Fork length varied significantly among the months of May through August (one-way ANOVA, $F = 5.198$, $p = 0.002$, Fig. 2). Average FL was lowest in the month of May (36.8 ± 0.3 cm) and greatest in July (38.8 ± 0.4 cm).

The average CPUE of YOY scalloped hammerheads in the Tolomato River was 0.6 ± 0.1 (SE) sharks per 50 hooks from 2010 to 2019. YOY *S. lewini* were caught consistently throughout the ten-year survey, but average CPUE varied significantly among years (Kruskal-Wallis ANOVA, $H = 44.241$, $p < 0.001$, Fig. 3). Average annual CPUE was highest in 2010 (2.7 ± 0.5 sharks per 50 hooks) and lowest in 2012 (0.3 ± 0.1 sharks per 50 hooks). Average CPUE also varied significantly among months (Kruskal-Wallis ANOVA, $H = 42.750$, $p < 0.001$, Fig. 4). Average monthly CPUE increased from 0.7 ± 0.1 sharks per 50 hooks in May to a maximum of 0.8 ± 0.1 sharks per 50 hooks in June. Following this peak, monthly CPUE declined until no sharks were caught after September. No scalloped hammerheads were caught during the other surveyed months of April, October, or November.

The binary logistic regression model indicated good fit (Hosmer and Lemeshow test, $\chi 2 = 11.579$, $p = 0.171$) and correctly predicted whether a given set would catch at least one scalloped hammerhead YOY in 71.7% of the cases. Dissolved oxygen was the only significant habitat variable, with increases in dissolved oxygen associated with a reduction in the likelihood of catching a scalloped hammerhead shark ($p = 0.001$, Table 2).

Mapping scalloped hammerhead catch data indicated that sets with the highest scalloped hammerhead CPUE were concentrated around Pine Island, a small island within the Tolomato River situated approximately 16 km north of St. Augustine Inlet. High catch rates were also observed to the south of this site, just north of the confluence of the Tolomato and Guana Rivers (Fig. 5).

Table 1
Species composition, abundance, percentage of total catch, sex, and life stage for all sharks caught in the Tolomato River from 2010 to 2019. Species are listed in order of overall abundance from most to least abundant. NS = sex unknown, NR = not recorded.

			Sex			Life stage			
Shark Species	No. caught	% of catch	Male	Female	NS	YOY	Juvenile	Adult	NR
Scalloped Hammerhead, *Sphyrna lewini*	248	40.1	133	108	7	245	0	0	3
Atlantic Sharpnose, *Rhizoprionodon terrenovae*	152	24.6	70	75	7	144	1	5	2
Finetooth, *Carcharhinus isodon*	72	11.7	34	36	2	52	17	2	1
Blacktip, *Carcharhinus limbatus*	64	10.4	25	36	3	63	1	0	0
Sandbar, *Carcharhinus plumbeus*	60	9.7	34	26	0	57	3	0	0
Bonnethead, *Sphyrna tiburo*	12	1.9	4	8	0	3	9	0	0
Nurse, *Ginglymostoma cirratum*	4	0.6	2	1	1	0	3	0	1
Bull, *Carcharhinus leucas*	3	0.5	1	0	2	0	3	0	0
Lemon, *Negaprion brevirostris*	2	0.3	0	2	0	0	2	0	0
Dusky smooth-hound, *Mustelus canis*	1	0.2	1	0	0	0	1	0	0
Total	618	100.0							

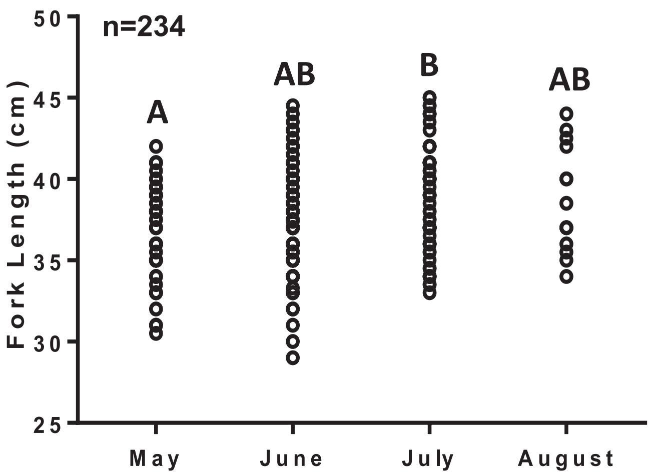

Fig. 2. Fork lengths of YOY *S. lewini* caught in the Tolomato River during the years of 2010–2019 divided by month of capture. Letters represent homogenous subsets as determined by a Tukey post-hoc test with multiple comparisons following one-way ANOVA analysis (p = 0.002). Sample size is presented.

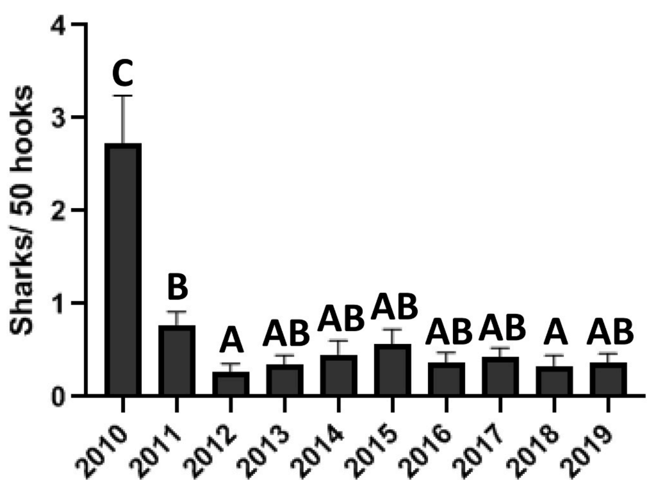

Fig. 3. The average CPUE for YOY scalloped hammerhead sharks in the Tolomato River per year from 2010–2019 with error bars representing SE. Letters represent homogenous subsets as determined by Dunn's post-hoc test following Kruskal-Wallis nonparametric analysis (p = 0.000).

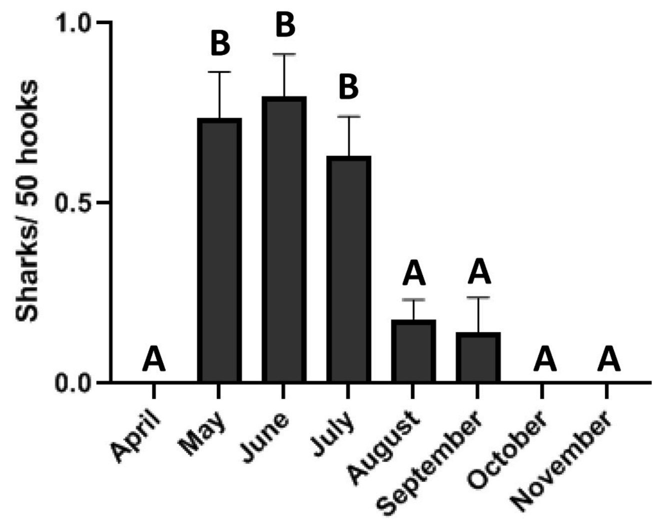

Fig. 4. The average CPUE for YOY scalloped hammerhead sharks in the Tolomato River per month from 2010–2019 with error bars representing SE. Letters represent homogenous subsets as determined by Dunn's post-hoc test following Kruskal-Wallis nonparametric analysis (p < 0.001).

Table 2
Results of binary logistic regression model analyzing the effects of environmental parameters on the presence/absence of young-of-the-year scalloped hammerhead sharks on bottom longlines conducted from the years 2010–2019 in the Tolomato River.

Environmental parameter	B	S.E.	Wald	Exp (B)	*P*
Average depth (m)	0.038	0.045	0.692	1.038	0.405
Bottom Temperature (℃)	0.060	0.071	0.709	1.062	0.400
Salinity (ppt)	0.053	0.053	1.004	1.054	0.316
Dissolved oxygen (mg/L)	-0.496	0.151	10.741	0.609	0.001
Conductivity (mS)	0.042	0.031	1.807	1.043	0.179
Constant	-4.031	2.412	2.793	0.018	0.095

3.2. Comparisons of S. lewini abundance in the Tolomato River and other northeast Florida estuaries

Catch rates of scalloped hammerheads were compared among sets completed in the St. Marys River estuary (n = 354), Nassau River estuary (n = 327), and Tolomato River (n = 350). Catch rates (sharks per 50 hook-hours) were significantly different among the three sites (Kruskal-Wallis ANOVA, H = 189.884, $p < 0.001$, Fig. 6a). The Tolomato River exhibited higher catch rates (2.3 ± 0.2 sharks per 50 hook-hours) as opposed to the other sites (St. Marys River estuary: 0.0 ± 0.0 sharks per 50 hook-hours; Nassau River estuary: 0.1 ± 0.0 sharks per 50

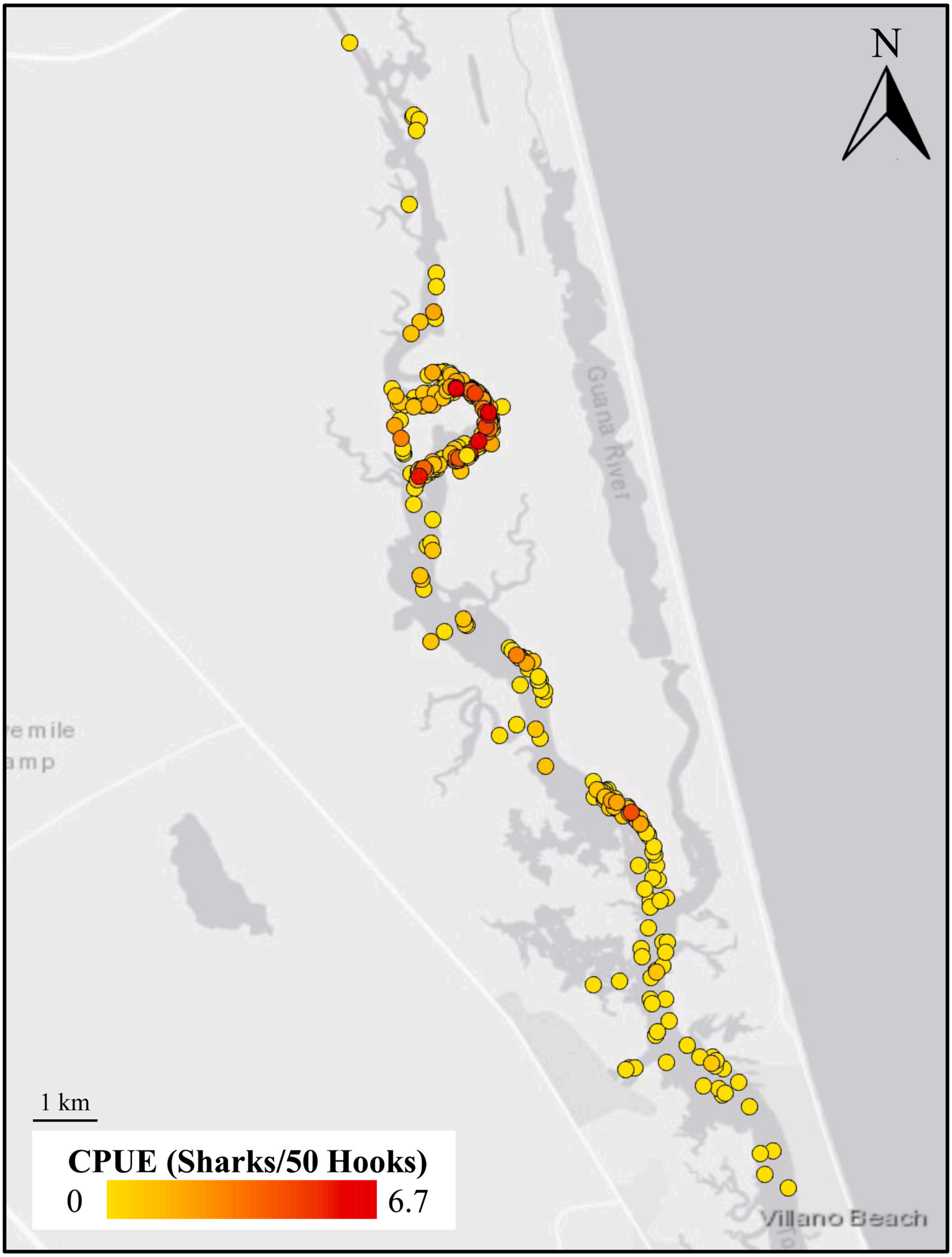

Fig. 5. CPUEs associated with geographic location of bottom longline sets completed in the Tolomato River from 2010–2019.

hook-hours), which did not significantly differ from each other. Statistical analysis resulted in the same outcome when the CPUE was expressed as sharks per 50 hooks (Kruskal-Wallis ANOVA, H = 183.678 $p < 0.001$, Fig. 6b). The average CPUE in the Tolomato River (0.6 ± 0.1 sharks per 50 hooks) was greater than that of the St. Marys River estuary (0.0 ± 0.0 sharks per 50 hooks) and the Nassau River estuary (0.1 ± 0.0 sharks per 50 hooks). Based on this, the latter unit of measurement was used for all subsequent analyses.

The general linear model (n = 1,031) revealed significant effects of site, salinity, and the interaction between salinity and conductivity on YOY scalloped hammerhead abundance in the northeast Florida region (F = 54.193, $p < 0.001$, $R^2 = 0.174$; Table 3). Overall, average salinity in northeast Florida estuaries was not significantly different (U = 62,726, p = 0.118) between sets that caught at least one scalloped hammerhead shark (31.23 ± 0.41 ppt) and those that caught none (30.29 ± 0.17 ppt, Fig. 7a). However, average salinity was significantly different (H =

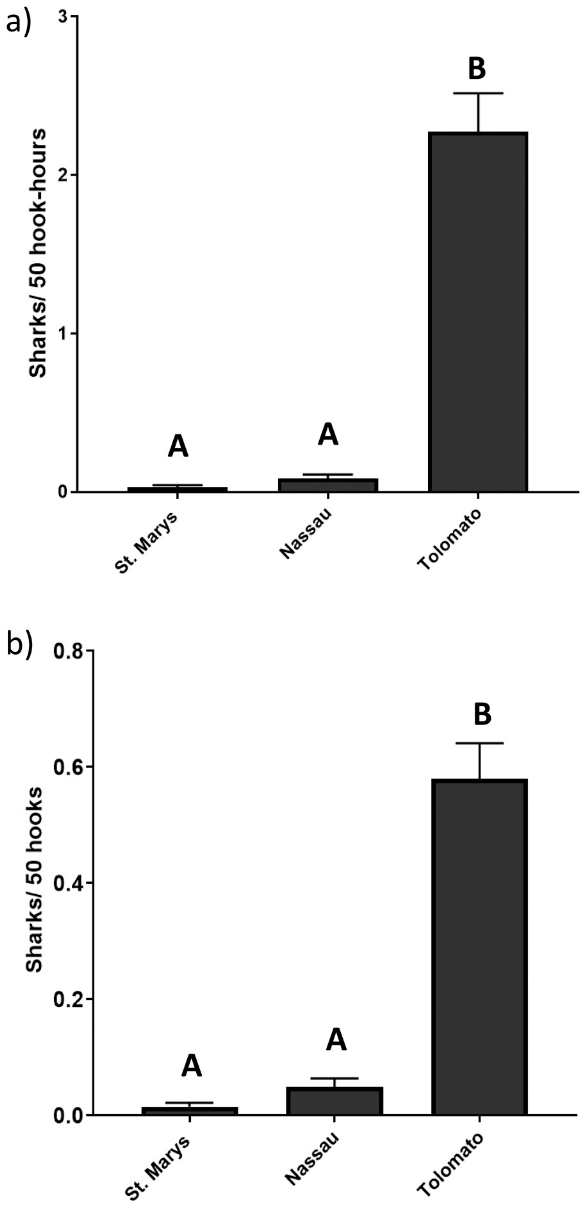

Fig. 6. Average CPUE in a) sharks per 50 hook-hours and b) sharks per 50 hooks of longline sets completed in the St. Marys River estuary (n = 354), Nassau River estuary (n = 327), and the Tolomato River (n = 350). Letter represent homogenous subsets as determined by Dunn's post-hoc test following Kruskal-Wallis nonparametric analysis (p < 0.0001). Bars represent means ± SE.

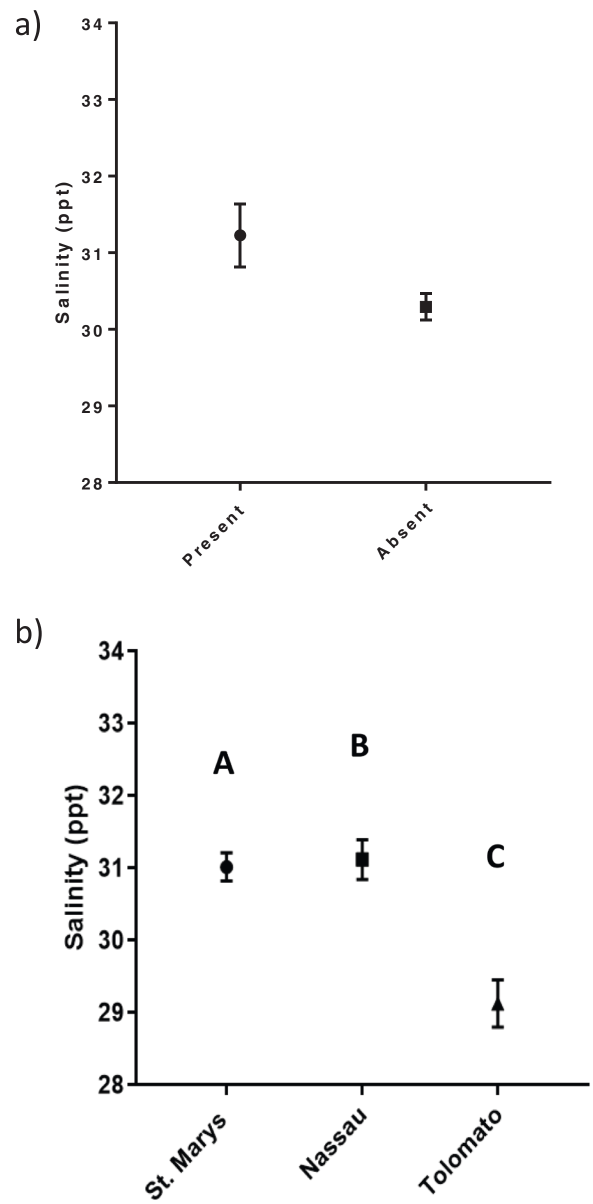

Fig. 7. Comparison of a) the average salinity conditions recorded for sets used in general linear model analysis when at least one scalloped hammerhead YOY was caught (Present) and for sets that caught no sharks (Absent), and b) the average salinity conditions recorded for sets completed in the St. Marys River estuary, Nassu River estuary, and Tolomato River. Bars represent SE. Letters represent homogenous subsets as determined by Dunn's post-hoc test following Kruskal-Wallis nonparametric analysis.

Table 3
Results of general linear model used to determine the effects of site and other environmental factors on the abundance (sharks/50 hooks) of young-of-the-year scalloped hammerheads in the northeast region of Florida ($F = 54.193$, $P = 0.000$, $R^2 = 0.174$). Covariates included depth, salinity, conductivity, dissolved oxygen, bottom temperature, and all potential interactions.

Variables	F-Value	*P*
Site	76.424	< 0.001
Salinity*Conductivity	24.252	< 0.001
Salinity	7.434	0.007

24.892, p = 0.000) among the three sites, with the lowest salinities in the Tolomato River (29.13 ± 0.33 ppt) compared to the St. Marys River estuary (31.02 ± 0.19 ppt) and Nassau River estuary (31.12 ± 0.28 ppt) (Fig. 7b). Conversely, conductivity was significantly different (U = 71,447.5, $p < 0.001$) between sets in which *S. lewini* were absent (48.48 ± 0.28 mS) and present (51.98 ± 0.77 mS, Fig. 8a), but there was no significant difference in average conductivity between the three sites (ANOVA Kruskal-Wallis, H= 4.000, $p = 0.135$. Fig. 8b). Average conductivity conditions were recorded as 47.93 ± 0.55 mS, 49.39 ± 0.45 mS, and 49.44 ± 0.36 mS for the Tolomato River, Nassau River estuary, and St. Marys River estuary, respectively.

3.3. Mark-recapture

During the years of 2019 and 2020, a total of 34 YOY scalloped hammerhead sharks were caught, tagged, and released in the Tolomato River; 24 sharks were tagged in 2019, while the remaining 10 were

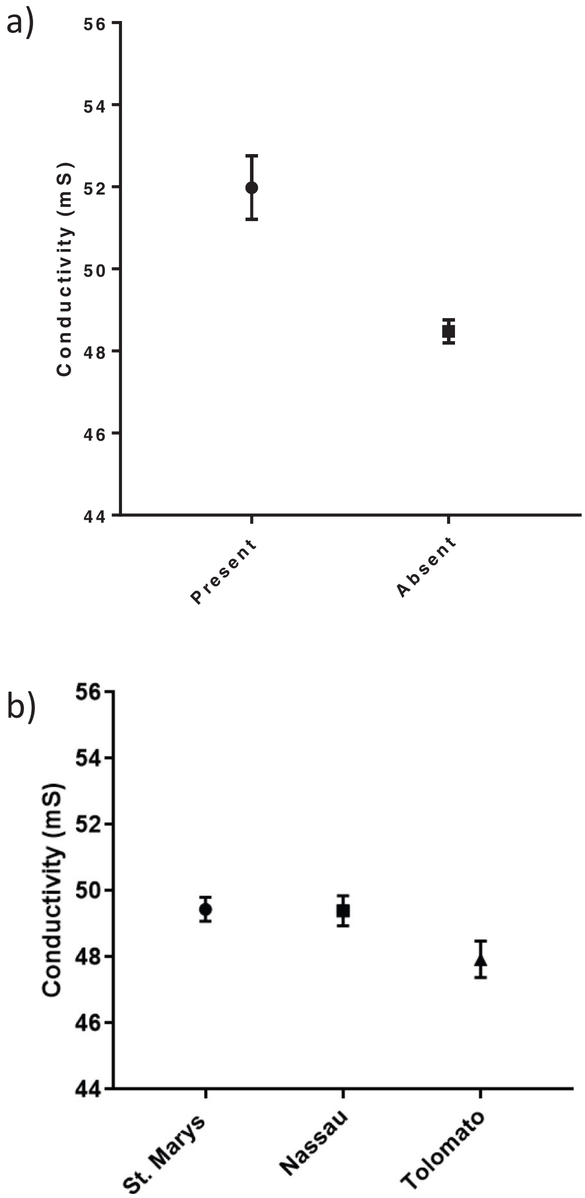

Fig. 8. Comparison of a) the average conductivity conditions recorded for sets used in general linear model analysis when at least one scalloped hammerhead YOY was caught (Present) and for sets that caught no sharks (Absent), and b) the average conductivity conditions recorded for sets completed in the St. Marys River estuary, Nassau River estuary, and Tolomato River. Bars represent SE. Conductivity differed significantly between sets in which sharks were present versus absent (Mann-Whitney U = 71,447.5, $p < 0.001$), but not by site.

tagged in 2020. Three males were recaptured, resulting in a total recapture rate of 8.8%. All sharks were recaptured during the same year in which they were released. Days at liberty ranged from 6 to 59 days, and distance between release and recapture locations ranged from 1.263 to 4.396 km (Table 4). Recaptures were mapped via ArcGIS Pro (Fig. 9).

4. Discussion

The results of this study support the hypothesis that the Tolomato River serves as a nursery habitat for YOY *S. lewini*. Of the 618 sharks caught in the Tolomato River from 2010–2019, 40.1% were identified as *S. lewini*, with approximately 98% of these individuals categorized as YOY based on size and umbilical scar status. Based on both monthly catch rates as well as preliminary results from our initial mark-and-recapture efforts, YOY *S. lewini* appeared to exhibit residency in the Tolomato River from May until late summer (August/September) annually, supporting a key criterion for defining shark nursery habitat (i.e., Criterion 2, Heupel et al., 2007). Furthermore, although only YOY *S. lewini* appear to make significant use of this nursery, they made up a significant proportion of the overall shark catch every year of our 10-year survey. Therefore, while individual sharks do not appear to return to this site as juveniles in subsequent years en masse, it is likely that offspring from the same population – perhaps even the same mothers (i.e., siblings) - occur in the Tolomato River over multiple years, suggesting repeated use of this nursery (i.e., Criterion 3, Heupel et al., 2007). Lastly, a direct comparison of *S. lewini* catch rates in the Tolomato River compared with those in two other nearby available habitats, the St. Marys River estuary and the Nassau River estuary, demonstrated that YOY *S. lewini* are more commonly encountered in the Tolomato River, addressing a rarely tested criterion of shark nursery habitat identification (i.e., Criterion 1, Heupel et al., 2007).

While the majority (i.e., 87.9%) of *S. lewini* sampled in the Tolomato River had well-healed (Category 4) umbilical scar, an appreciable number of individuals exhibited fresh (0.9%, Category 2) or partly healed (11.2%, Category 3) scar patterns. This suggests that YOY sharks may move into the Tolomato River as early as within one week following parturition, as previous studies have demonstrated that umbilical scar in *S. lewini* can change from open to partly healed in 4 ± 2.3 (SD) d and become fully closed after 10 ± 3.6 d (Duncan and Holland, 2006). These findings, as well as the first appearance of YOY *S. lewini* in the Tolomato River in mid-May, coincide well with the estimated time of parturition, which has been reported to occur in western North Atlantic waters between May and June by Ulrich et al. (2007). It is presumed that pupping occurs outside of estuarine waters along Florida's Atlantic coast since no gravid or recently pupped adult females have been sampled within the Tolomato River, even when fishing gear more appropriate for large shark capture has been used (e.g., drumline fishing, Gelsleichter, unpublished data). Nearshore as opposed to estuarine pupping in this species is also supported by anecdotal reports of near-term gravid adult females collected via netting in late May from shallow coastal waters adjacent to Bulls Bay, South Carolina (Castro, 1993), a high-salinity, mostly open water bar-built estuary that serves as nursery habitat for both *S. lewini* and *S. gilberti* (Barker et al., 2021). However, it is important to acknowledge that some authors have hypothesized that adult female *S. lewini* may not feed around the time of parturition (Clarke, 1971; Dodrill, 1977; Castro, 1993); therefore, our failure to sample adult females from the Tolomato River using hook-and-line fishing gear cannot be construed as conclusive evidence that pupping occurs outside of the nursery.

Although YOY *S. lewini* have been reported to occur at low to moderate abundance in estuaries throughout the South Atlantic Bight from southern portions of North Carolina to northeast Florida, the presence of a specific inshore nursery for this species in the Tolomato River was

Table 4
Recapture data for three male young-of-the-year scalloped hammerhead sharks tagged-and-recaptured between the years of 2019–2020 in the Tolomato River.

	Date		Tagging Location		Recapture Location			
Tag #	Tagged	Recaptured	Latitude	Longitude	Latitude	Longitude	Days at Liberty	Distance (km)
0028	05/14/2019	05/20/2019	30.0010	-81.3356	30.0261	-81.3614	6	4.4
0030	05/21/2019	05/31/2019	30.0578	-81.3552	30.0512	-81.3659	10	1.3
0044	08/12/2020	10/10/2020	30.0510	-81.3651	30.0258	-81.3614	59	3.2

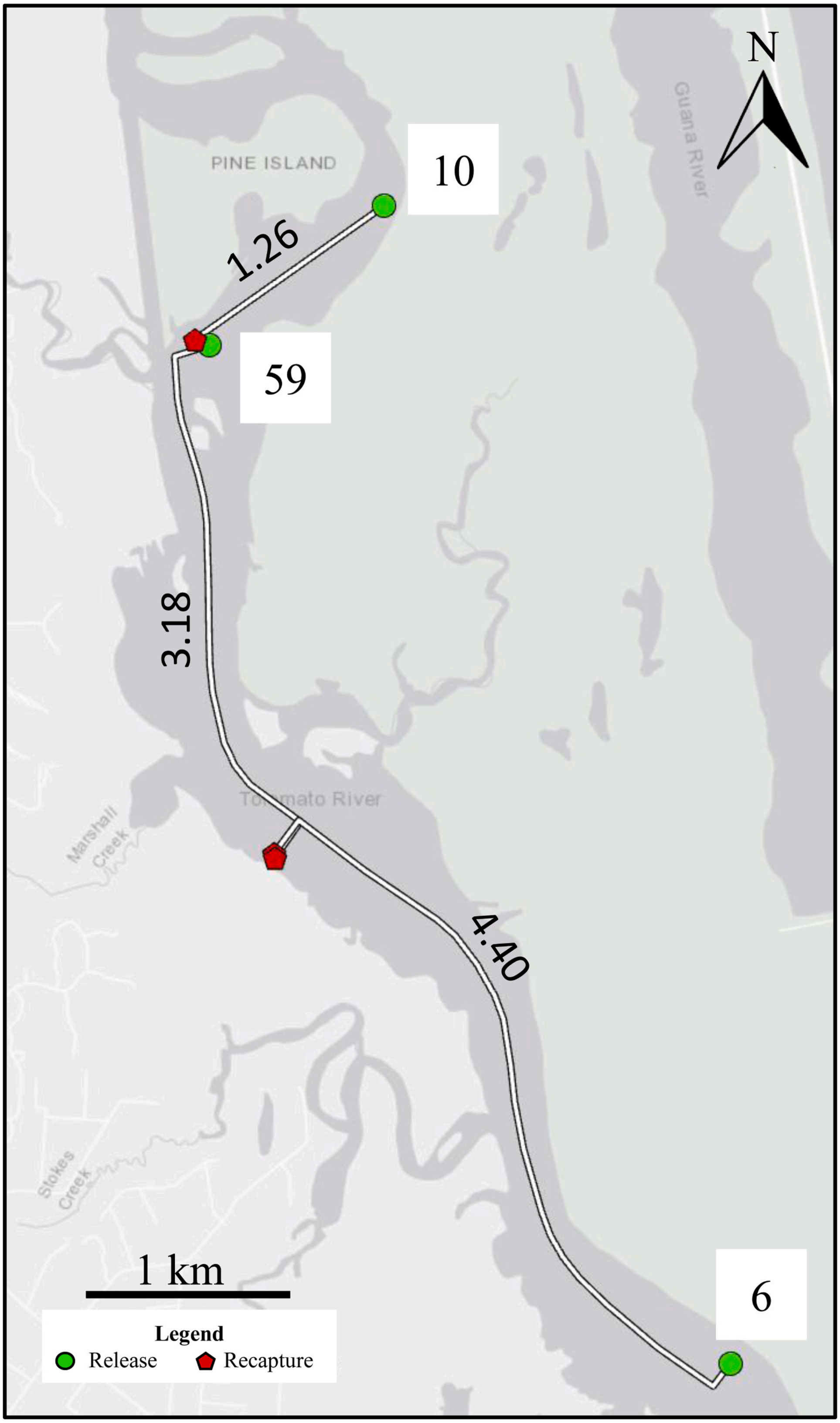

Fig. 9. Mark-recapture data collected for three scalloped hammerhead YOYs between 2019 and 2020. Numbers in white boxes near release location indicates days at liberty, whereas numbers along lines represent distance traveled in kilometers.

unexpected based on previous research conducted in Florida waters. In fact, in a study conducted on the east-central Florida coast, Adams and Paperno (2007) reported that shallow nearshore waters off of Cape Canaveral, FL appeared to serve as nursery habitat for YOY *S. lewini* rather than the adjacent estuarine waters of the Indian River Lagoon, where no neonates or juveniles of this species were captured despite extensive gillnet sampling over an 8-year period. It is probable that differences in nursery ground use between the northeast and east-central Florida coasts may in part reflect shelf conditions, as the Cape Canaveral coastline boasts a broader expanse of shallow (1–5 m) nearshore habitat (i.e., the Southeast Shoal) that extends close to 10 times further away from the shoreline than that in northeast Florida. Therefore, as Adams and Paperno (2007) suggested, the shallow waters and unique habitat of the Southeast Shoal along with other distinct features of the Cape Canaveral shoreline (e.g., the deeper turbid waters adjacent to the Shoal, where Reiyer et al., (2023) found YOY *S. lewini* to be more common in comparison with the shoal ridges) may provide suitable nursery habitat for YOY *S. lewini* such that movements to more inshore estuarine waters are not necessary. Still, it is interesting to consider additional abiotic and/or biotic factors that drive the preference for nearshore versus estuarine habitat in east-central Florida to better understand the selective pressures that have led to the use of this site and other areas such as the Tolomato River as nursery habitats.

One abiotic factor that may influence nursery ground use in YOY *S. lewini* is salinity as, aside from site and the not-surprising interaction between salinity and conductivity, it was the only environmental variable that was shown to explain deviance in longline catch rates in northeast Florida waters. As demonstrated by comparisons of salinity between the three study sites, mean salinity was lowest in the Tolomato River, suggesting that YOY *S. lewini* may prefer moderate as opposed to higher salinities. This was also proposed by Marie et al. (2017), based on research on a YOY and juvenile *S. lewini* nursery in Rewa Delta, Viti Kevu, Fiji; however, associations between salinity and catch rates were not determined in their study. Interestingly, Barker et al. (2021) also cited the lower salinities of the Tolomato River compared to other hammerhead nurseries on the southeast U.S. coast as a possible reason for why *S. gilberti* appears to be absent in this site, suggesting that differences in salinity preferences between the two congeners may drive dissimilar habitat use patterns. Nonetheless, while other studies have also found evidence for moderate salinity preferences in juvenile *S. lewini* (Yates et al., 2015), it is important to acknowledge that the present study found no significant difference in the average salinity of sets that caught YOY *S. lewini* compared with that of sets that did not. Furthermore, a preference for moderate salinities would not explain the preferential use of the high-salinity nearshore waters off Cape Canaveral to the moderate salinities found in portions of the Indian River Lagoon in east-central Florida. Therefore, it is likely that additional abiotic factors that were not addressed in the present study – perhaps turbidity, which was also found to be positively associated with YOY and juvenile *S. lewini* catch rates by Yates et al. (2015) and Reyier et al. (2023) – also influence habitat use patterns and should be examined in follow-up studies.

As first suggested by Duncan and Holland (2006), a key biotic factor that likely drives YOY *S. lewini* nursery habitat use is the avoidance of predators, including larger sharks. We hypothesize that this may at least partly explain differences between YOY *S. lewini* abundance in the Tolomato River compared to that in other northeast Florida estuaries, as both published and anecdotal data suggests that predation risk likely differs between these sites. For example, as observed by both McCallister et al. (2013) and Morgan (2018), adult sharks comprise a larger proportion of longline catch (~30 – 40%) and, presumably, overall shark populations in the St. Marys River estuary and Nassau River estuary compared to that reported in the Tolomato River in the present study (~1 – 2%). Even with the removal of adults from species unlikely to prey on YOY *S. lewini* (e.g., Atlantic Sharpnose shark *Rhizoprionodon terraenovae*, bonnethead *Sphyrna tiburo*, dusky smoothhound *Mustelus canis*), the abundance of possible adult predatory sharks is lower in the Tolomato River (~0.3% of catch) than in other northeast Florida sites (~3–5%). In addition, unpublished data from drumline fishing efforts conducted in all 3 locations suggests a greater abundance of large juvenile and adult predatory sharks from multiple species (e.g., sandbar shark *Carcharhinus plumbeus*, blacktip shark *Carcharhinus limbatus*, lemon shark *Negaprion brevirostris*) in the St. Marys River estuary and Nassau River estuary compared to the Tolomato River. However, we have occasionally sampled juvenile bull sharks *Carcharhinus leucas* (~90 – 115 cm FL) from the Tolomato River via drumline and have recently experienced depredation of YOY *S. lewini* by this species in our longline survey (Gelsleichter, unpublished data). Therefore, future research should conduct more direct comparisons of predator abundance between this site and other northeast Florida estuaries to properly address this hypothesis. Still, the possibility that predator avoidance may contribute to the use of the Tolomato River as a nursery for YOY *S. lewini* is a compelling premise as this may also explain the preference of these sharks for nearshore sites off Cape Canaveral rather than the Indian River Lagoon, which is well known to serve as an important nursery habitat for YOY and juvenile *C. leucas* (Snelson et al., 1984; Adams and Paperno, 2007; Curtis et al., 2011).

A key reason for why Duncan and Holland (2006) concluded that predator avoidance was likely to be the primary biotic factor influencing the use of Kāne'ohe Bay in Ō'ahu, Hawai'i as a nursery for YOY and juvenile *S. lewini* was the apparent loss of weight and reduced condition factor of individuals in the first few weeks after birth (i.e., using umbilical scar status as a proxy for "age"). These findings suggested that use of Kāne'ohe Bay is unlikely to provide enhanced foraging opportunities, another commonly hypothesized benefit of shark nursery ground use. However, this may be unique to Kāne'ohe Bay, which has been described as a sub-optimal foraging habitat in part because of significant declines in marine resources due to anthropogenic influences (Bush, 2003; Bahr et al., 2015). In contrast, Corgos and Rosende-Pereiro (2022) found no decline in the size and weight of YOY *S. lewini* sampled for up to 8 months following birth from nursery habitats off of the central Mexican Pacific coast, suggesting that high juvenile mortality due to starvation is not a hallmark trait of all populations of this species. Although we also found no evidence for growth impairment in Tolomato River *S. lewini* (e.g., mean FL of individuals captured in July was determined to be significantly greater than that of May individuals), more direct assessments of changes in body weight and animal condition are needed to fully understand resource availability in this nursery habitat. Direct investigations of potential prey abundance (e.g., squid, shrimp) from fisheries-independent monitoring surveys in this site may also highlight biotic variables driving abundance differences between the three study sites.

Although YOY *S. lewini* were sampled from a broad portion of the Tolomato River, catch rates were shown to be greatest in a small number of sites, including the Pine Island region and areas of the river just north of its confluence with the Guana River. Spatial differences in catch rates have also been observed in earlier studies on *S. lewini* nurseries (Marie et al., 2017), suggesting that these sharks likely exhibit preferences for certain microhabitats within their nursery systems. Additional evidence for this behavior has been provided by catch-and-release studies on YOY *S. lewini* in Kāne'ohe Bay, Ō'ahu, Hawai'i, which found that individual sharks may swim long distances within this nursery but tended to reuse certain core areas (Duncan and Holland, 2006). Similar findings have also been reported in other shark species, including *C. plumbeus* (Rechisky and Wetherbee, 2003). This behavior also appears likely to occur in Tolomato River YOY *S. lewini* based on preliminary results from our modest tagging efforts (e.g., recapture sites for the three sharks recaptured in this study ranged from 1.26 to 4.40 km from the initial point of capture in 6 – 59 days at large). However, more direct studies employing active and/or passive telemetry are needed to examine microhabitat selectivity within this nursery and the factors that drive these preferences. The possible attraction of YOY *S. lewini* to the Pine

Island site is interesting as this location lies near the natural headwaters of the Tolomato River. North of this site, the river is connected to a channel that was dredged by 1912 to link this waterbody to the Atlantic Intracoastal Waterway (Parkman, 1983). Given this, we hypothesize that there are certain features of Pine Island (e.g., chemical signatures, perhaps from adjacent terrestrial habitats, Gardiner et al., 2015) that may serve as the initial cues that attract YOY *S. lewini* to this nursery, as well as explain possible microhabitat preferences.

Data from the present study demonstrates that in addition to YOY *S. lewini*, the Tolomato River also appears to provide essential habitat to juveniles from several other shark species, suggesting that it serves as a communal shark nursery (Simpfendorfer and Milward, 1993). Because of this, it is possible that competition between species may limit food resources in this site, providing greater support for the argument that predator avoidance rather than high resource availability may drive use of this nursery. Given this, it is valuable to examine niche overlap and dietary resource partitioning in Tolomato River sharks to assess the degree of competition among species and its possible impacts on animal condition and survival. Information on food web interactions in communal shark nurseries may also be useful for developing strategies to best manage these sites, given the possibilities for the occurrence of a complex trophic structure and the importance of considering the needs for multiple co-occurring species (Kinney et al., 2011).

Given that the primary forms of commercial shark fishing (e.g., gillnetting, longline fishing) are prohibited in Florida state waters, the main human-related risks posed to shark nursery areas in the Tolomato River include recreational fishing and habitat degradation. However, since *S. lewini* and its congeners, the great hammerhead (*Sphyrna mokarran*) and the smooth hammerhead (*Sphyrna zygaena*), are prohibited from harvest in Florida waters, the risk from recreational fishing is likely to be limited. Still, because they have been shown to exhibit high rates of at-vessel and post-release mortality due to a pronounced capture stress response (Morgan and Burgess, 2007; Morgan and Carlson, 2010; Gulak et al., 2015; Gallagher et al., 2014), the possibility for unintended mortality related to catch-and-release fishing remains present. Therefore, information on the temporal and spatial patterns of YOY *S. lewini* habitat use in the Tolomato River may be useful for reducing negative fishery interactions with these species, e.g., by avoidance of high use areas during the period of occurrence. This information, along with guidance on how to quickly and safely release hooked YOY *S. lewini* in good condition can be shared by the GTM NERR, which also conducts long-term water quality monitoring in this region and can address concerns regarding habitat degradation (Kennish, 2019).

Information from this study has direct value for fishery management. As previously mentioned, while the NWA/GOM DPS for *S. lewini* is believed to be in a rebuilding phase with optimistic potential for recovery (Hayes et al., 2009; Miller et al., 2014), any factors that slow or reverse positive trends in population growth can hinder this process. This includes both fishery and non-fishery impacts to critical habitat, which requires that EFH for this species is properly delineated. Preliminary results from this long-running study have already contributed to U.S. federal designation of small portions of the Tolomato River as EFH for neonate *S. lewini* (NOAA Fisheries EFH mapper, https://www.habitat.noaa.gov/apps/efhmapper/, last accessed 17 January 2024), although updated mapping using our more recent datasets is needed. Establishment of the Tolomato River as YOY *S. lewini* EFH provides U.S. fishery managers and other resource managers with the tools needed to assess actions that can result in direct or indirect effects on the quality and/or quantity of this habitat, as well as approaches for mitigating possible effects (National Marine Fisheries Service, 2017). This can include the potential impacts of coastal development in regions to the west of the Tolomato River nursery, which lie outside of the protected areas of the GTM NERR and represent some of the most rapidly growing communities in the U.S. (Gardner, 2022).

5. Conclusions

In conclusion, this study has provided compelling evidence that the Tolomato River in northeast Florida, USA represents a unique inshore nursery for YOY *S. lewini* for the first 4 – 5 months of life. Still, while we have reached this conclusion by in part addressing all 3 criteria for the identification of shark nursery habitats established by Heupel et al. (2007), additional research is needed to fully understand spatial differences in habitat use within this nursery, as well as the abiotic and/or biotic factors that drive microhabitat selection and overall nursery use. This can be accomplished through a combination of active and passive acoustic telemetry, the latter of which – as Heupel et al. (2018) pointed out – can also provide a more specific evaluation of long-term use patterns (i.e., Criterion 2), as well as environmental factors driving the eventual emigration from this site. More data is also needed on relationships between *S. lewini* and other sharks occurring within this site, as it also appears to serve as a communal nursery for juveniles of several shark species, creating the potential for competition for food resources.

CRediT authorship contribution statement

Gelsleichter James: Conceptualization, Data curation, Funding acquisition, Investigation, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Frazier Bryan S.:** Funding acquisition, Writing – review & editing. **Wargat Bryanna:** Conceptualization, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. **McCallister Michael:** Conceptualization, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Morgan Clark:** Investigation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Adams, D.H., Paperno, R., 2007, Preliminary assessment of a nearshore nursery ground for the scalloped hammerhead off the Atlantic coast of Florida, in: McCandless, C.T., Kohler, N.E., Pratt, H.L. (Eds.), Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society Symposium 50. American Fisheries Society, Bethesda, MD. pp. 165–174. https://doi.org/10.47886/9781888569810.ch11.

Aubrey, C.W., Snelson, F.F., Jr, 2007, Early life history of the spinner shark in a Florida nursery, in: McCandless, C.T., Kohler, N.E., Pratt, H.L. (Eds.), Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society Symposium 50. American Fisheries Society, Bethesda, MD. pp. 175 – 189. https://doi.org/10.47886/9781888569810.ch12.

Bahr, K.D., Jokiel, P.L., Toonen, R.J., 2015. The unnatural history of Kāne'ohe Bay: coral reef resilience in the face of centuries of anthropogenic impacts. PeerJ 3, e950. https://doi.org/10.7717/peerj.950.

Barker, A.M., Frazier, B.S., Adams, D.H., Bedore, C.N., Belcher, C.N., Driggers, W.B., Galloway, A.S., Gelsleichter, J., Grubbs, R.D., Reyier, E.A., Portnoy, D.S., 2021. Distribution and relative abundance of scalloped (*Sphyrna lewini*) and Carolina

(*S. gilberti*) hammerheads in the western North Atlantic Ocean. Fish. Res. 242, 106039 https://doi.org/10.1016/j.fishres.2021.106039.

Branstetter, S., 1987. Age, growth, and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. Environ. Biol. Fishes 19, 161–173. https://doi.org/10.1007/BF00005346.

Branstetter, S., 1990, Early life history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic, in: Pratt. H.L., Jr., Gruber, S.H., Taniuchi, T. (Eds.), Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Technical Report NMFS 90. National Marine Fisheries Service, Washington, D.C. pp. 17–28.

Brown, K.T., Seeto, J., Lal, M.M., Miller, C.E., 2016. Discovery of an important aggregation area for endangered scalloped hammerhead sharks, *Sphyrna lewini*, in the Rewa River estuary, Fiji Islands. Pac. Conserv. Biol. 22, 242–248. https://doi.org/10.1071/PC14930.

Bush, A., 2003. Diet and diel feeding periodicity of juvenile scalloped hammerhead sharks *Sphyrna lewini*, in Kaneohe Bay, Oahu, Hawaii. Environ. Biol. Fish. 67, 1–11. https://doi.org/10.1023/A:1024438706814.

Castro, J.I., 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ. Biol. Fishes 38, 37–48. https://doi.org/10.1007/BF00842902.

Chapman, D.D., Pinhal, D., Shivji, M.S., 2009. Tracking the fin trade: genetic stock identification in western Atlantic scalloped hammerhead sharks *Sphyrna lewini*. Endanger. Species Res. 9, 221–228. https://doi.org/10.3354/esr00241.

Clarke, T.A., 1971. The ecology of the scalloped hammerhead shark, *Sphyrna lewini*, in Hawai'i. Pac. Sci. 25, 133–144.

Compagno, L.J.V., 1984, FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2 - Carcharhiniformes. FAO Fish. Synop. 125 (4/2):251–655. Rome: FAO.

Corgos, A., Rosende-Pereiro, A., 2022. Nursery habitat use patterns of the scalloped hammerhead shark, *Sphyrna lewini*, in coastal areas of the central Mexican Pacific. J. Fish. Biol. 100, 117–133. https://doi.org/10.1111/jfb.14925.

Cuevas-Gómez, G.A., Pérez-Jiménez, J.C., Méndez-Loeza, I., Carrera-Fernández, M., Castillo-Géniz, J.L., 2020. Identification of a nursery area for the critically endangered hammerhead shark (*Sphyrna lewini*) amid intense fisheries in the southern Gulf of Mexico. J. Fish. Biol. 97, 1087–1096. https://doi.org/10.1111/jfb.14471.

Curtis, T.H., Adams, D.H., Burgess, G.H., 2011. Seasonal distribution and habitat associations of bull sharks in the Indian River Lagoon, Florida: a 30-year synthesis. Trans. Am. Fish. 140, 1213–1226. https://doi.org/10.1080/00028487.2011.618352.

Dodrill, J., 1977. A hook and line survey of the sharks found within five hundred meters of shore along Melbourne Beach, Brevard County, Florida. M. S. Thesis, Fla. Inst. Technol., Melb. 304 pp..

Duncan, K.M., Holland, K.N., 2006. Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. Mar. Ecol. Prog. Ser. 312, 211–221. https://doi.org/10.3354/meps312211.

Gallagher, A.J., Serafy, J.E., Cooke, S.J., Hammerschlag, N., 2014. Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. Mar. Ecol. Prog. Ser. 496, 207–218. https://doi.org/10.3354/meps10490.

Gardiner, J.M., Whitney, N.M., Hueter, R.E., 2015. Smells like home: the role of olfactory cues in the homing behavior of blacktip sharks, *Carcharhinus limbatus*. Integr. Comp. Biol. 55, 495–506. https://doi.org/10.1093/icb/icv087.

Gardner, S. 2022, Nocatee named one of the top-selling master-planned communities in America. St. Augustine Record, 7 January 2022. https://www.staugustine.com/story/news/local/2022/01/07/report-nocatee-top-selling-master-planned-community-us/9102305002/, last accessed 17 January 2024.

Grubbs, R.D., Musick, J., 2007, Spatial delineation of summer nursery areas for juvenile sandbar sharks in Chesapeake Bay, in: McCandless, C.T., Kohler, N.E., Pratt, H.L. (Eds.), Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society Symposium 50. American Fisheries Society, Bethesda, MD. pp. 63−86. https://fisheries.org/doi/9781888569810.ch5.

Gulak, S.J.B., de Ron Santiago, A.J., Carlson, J.K., 2015. Hooking mortality of scalloped hammerhead *Sphyrna lewini* and great hammerhead *Sphyrna mokarran* sharks caught on bottom longlines. Afr. J. Mar. Sci. 37, 267–273. https://doi.org/10.2989/1814232X.2015.1026842.

Hayes, C.G., Jiao, Y., Cortes, E., 2009. Stock assessment of scalloped hammerheads in the western north Atlantic Ocean and Gulf of Mexico. N. Am. J. Fish. Manag. 29, 1406–1417. https://doi.org/10.1577/M08-026.1.

Heupel, M.R., Carlson, J.K., Simpfendorfer, C.A., 2007. Shark nursery areas: concepts, definition, characterization and assumptions. Mar. Ecol. Prog. Ser. 337, 287–297. https://doi.org/10.3354/meps337287.

Heupel, M.R., Kanno, S., Martins, A.P.B., Simpfendorfer, C.A., 2018. Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. Mar. Freshw. Res. 70, 897–907. https://doi.org/10.1071/MF18081.

Kennish, M., 2019. The National Estuarine Research Reserve System: A Review of Research and Monitoring Initiatives. Open J. Ecol. 9, 50–65. https://doi.org/10.4236/oje.2019.93006.

Kinney, M.J., Hussey, N.E., Fisk, A.T., Tobin, A.J., Simpfendorfer, C.A., 2011. Communal or competitive? Stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. Mar. Ecol. Prog. Ser. 439, 263–276. https://doi.org/10.3354/meps09327.

Lear, K.O., Gleiss, A.C., Whitney, N.M., 2018. Metabolic rates and the energetic cost of external tag attachment in juvenile blacktip sharks *Carcharhinus limbatus*. J. Fish. Biol. 93, 391–395. https://doi.org/10.1111/jfb.13663.

Marie, A.D., Miller, C., Cawich, C., Piovano, S., Rico, C., 2017. Fisheries-independent surveys identify critical habitats for young scalloped hammerhead sharks (*Sphyrna lewini*) in the Rewa Delta, Fiji. Sci. Rep. 7, 17273 https://doi.org/10.1038/s41598-017-17152-0.

McCallister, M., Ford, R., Gelsleichter, J., 2013. Abundance and distribution of sharks in northeast Florida waters and identification of potential nursery habitat. Mar. Coast. Fish. 5, 200–210. https://doi.org/10.1080/19425120.2013.786002.

Merson, R.R., Pratt, H.L., 2007, Sandbar shark nurseries in New Jersey and New York: evidence of northern pupping grounds along the United States east coast, in: McCandless, C.T., Kohler, N.E., Pratt, H.L. (Eds.), Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society Symposium 50. American Fisheries Society, Bethesda, MD. pp. 35 – 43. https://doi.org/10.47886/9781888569810.ch3.

Miller, M.H., Carlson, J., Cooper, P., Kobayashi, D., Nammack, M., Wilson, J., 2014, Status review report: scalloped hammerhead shark (*Sphyrna lewini*). Office of Protected Resources, NMFS, Silver Spring, MD. ⟨https://repository.library.noaa.gov/view/noaa/17835⟩ (accessed 5 June 2023).

Moncrief-Cox, H.E., Hannan, K.M., Passerotti, M.S., Driggers III, W.B., Frazier, B.S., 2021. Reproductive parameters of great hammerhead sharks (*Sphyrna mokarran*) and scalloped hammerhead sharks (*Sphyrna lewini*) from the western North Atlantic Ocean. SEDAR77-DW18. SEDAR, North Charleston SC, p. 19.

Morgan, A., Burgess, G.H., 2007. At-vessel fishing mortality for six species of sharks caught in the Northwest Atlantic and Gulf of Mexico. Gulf Caribb. Res. 19, 123–129. https://doi.org/10.18785/gcr.1902.15.

Morgan, A., Carlson, J.K., 2010. Capture time, size and hooking mortality of bottom longline-caught sharks. Fish. Res. 101, 32–37. https://doi.org/10.1016/j.fishres.2009.09.004.

Morgan, C.R., 2018, Distribution and community structure of first coast shark assemblages and their relative trophic niche dynamics. UNF Graduate Theses and Dissertations. ⟨https://digitalcommons.unf.edu/etd/838⟩.

National Marine Fisheries Service, 1993, Fishery Management Plan for Sharks of the Atlantic Ocean. ⟨http://www.nmfs.noaa.gov/sfa/hms/hmsdocument_files/FMPs.htm/⟩.

National Marine Fisheries Service, 2017. Final amendment 10 to the 2006 Consolidated HMS Fishery Management Plan. Essential Fish Habitat. https://www.fisheries.noaa.gov/action/amendment-10-2006-consolidated-hms-fishery-management-plan-essential-fish-habitat.

Parkman, A., 1983. History of the waterways of the Atlantic coast of the United States. U. S. Army Engineer Water Resources Support Center, Institute for Water Resources, Fort Belvoir, VA.

Piercy, A.N., Carlson, J.K., Sulikowski, J.A., Burgess, G.H., 2007. Age and growth of the scalloped hammerhead shark, Sphyrna lewini, in the north-west Atlantic Ocean and Gulf of Mexico. Mar. Freshw. Res. 58, 34–40. https://doi.org/10.1071/MF05195.

Quattro, J.M., Driggers, W.B., Grady, J.M., Ulrich, G.F., Roberts, M.A., 2013. Sphyrna gilberti sp. nov., a new hammerhead shark (Carchiniformes, Sphyrnidae) from the western Atlantic Ocean. Zootaxa 3702, 159–178. https://doi.org/10.11646/zootaxa.3702.2.5.

Rechisky, E.L., Wetherbee, B.M., 2003. Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environ. Biol. Fishes 68, 113–128. https://doi.org/10.1023/B:EBFI.0000003820.62411.cb.

Reyier, E., Ahr, B., Iafrate, J., Scheidt, D., Lowers, R., Watwood, S., Back, B., 2023. Sharks associated with a large sand shoal complex: Community insights from longline and acoustic telemetry surveys. PLoS ONE 18, e0286664. https://doi.org/10.1371/journal.pone.0286664.

Rigby, C.L., Dulvy, N.K., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., Herman, K., Jabado, R.W., Liu, K.M., Marshall, A., Pacoureau, N., Romanov, E., Sherley, R.B., Winker, H., 2019. Sphyrna lewini. The IUCN Red List of Threatened Species 2019: e.T39385A2918526. https://www.iucnredlist.org Accessed on 05 June 2023.

Rosende-Pereiro, A., Corgos, A., 2018. Pilot acoustic tracking study on young of year scalloped hammerhead sharks, *Sphyrna lewini*, within a coastal nursery area in Jalisco, Mexico. Lat. Am. J. Aquat. Res. 46, 645–659. https://doi.org/10.3856/vol46-issue4-fulltext-2.

Sadowsky, V., 1965. The hammerhead sharks of the littoral zone of Sao Paulo, Brazil, with the description of a new species. Bull. Mar. Sci. 15, 1–12. ⟨https://www.ingentaconnect.com/contentone/umrsmas/bullmar/1965/00000015/00000001/art00001#⟩.

Simpfendorfer, C.A., Milward, N.E., 1993. Utilization of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environ. Biol. Fishes 37, 337–345. https://doi.org/10.1007/BF00005200.

Snelson, F.F., Williams, S.E., 1981. Notes on the occurrence, distribution, and biology of elasmobranch fishes in the Indian River lagoon system, Florida. Estuaries 4, 110–120. https://doi.org/10.2307/1351673.

Snelson, F.F., Mulligan, T.J., Williams, S.E., 1984. Food habits, occurrence, and population structure of the bull shark, Carcharhinus leucas, in Florida coastal lagoons. Bull. Mar. Sci. 34, 71–80. ⟨https://www.ingentaconnect.com/content/umrsmas/bullmar/1984/00000034/00000001/art00004#⟩.

Springer, S., 1967. Social organization of shark populations, in: Gilbert, P.W., Mathewson, R.F., Rall, D.P. (Eds.), Sharks, skates, and rays. John Hopkins Press, Baltimore, MD, pp. 149–174.

U.S. Department of Commerce, 2007. Magnuson-Stevens Fish. Conserv. Manag. Act., Amend. Jan. 12, 2007. ⟨https://www.fisheries.noaa.gov/resource/document/magnuson-stevens-fishery-conservation-and-management-act⟩.

Ulrich, G.F., Jones, C.M., Driggers, W.B., I.I.I., Drymon, J.M., Oakley, D., Riley C., 2007. Habitat utilization, relative abundance, and seasonality of sharks in the estuarine

and nearshore waters of South Carolina, in: McCandless, C.T., Kohler, N.E., Pratt, H. L. (Eds.), Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. American Fisheries Society Symposium 50. American Fisheries Society, Bethesda, MD. pp.125–139. https://fisheries.org/doi/9781888569810-ch8.
Valle-Levinson, A., Gutierrez de Velasco, G., Trasvina, A., Souza, A., Durazo, R., Mehta, A., 2009. Residual exchange flows in subtropical estuaries. Estuar. Coast. 32, 54–67. https://doi.org/10.1007/s12237-008-9112-1.
Williams, A.A., Eastman, S.F., Eash-Loucks, W.E., Kimball, M.E., Lehmann, M.L., Parker, J.D., 2014. Record northernmost endemic mangroves on the United States Atlantic Coast with a note on latitudinal migration. Southeast. Nat. 13, 56–63. https://doi.org/10.1656/058.013.0104.
Yates, P.M., Heupel, M.R., Tobin, A.J., Simpfendorfer, C.A., 2015. Ecological drivers of shark distributions along a tropical coastline. PLOS ONE 10, e0121346. https://doi.org/10.1371/journal.pone.0121346.
Zanella, I., López-Garro, A., Cure, K., 2019. Golfo Dulce: Critical habitat and nursery area for juvenile scalloped hammerhead sharks *Sphyrna* lewini in the Eastern Tropical Pacific Seascape. Environ. Biol. Fish. 102, 1291–1300. https://doi.org/10.1007/s10641-019-00907-1.