

Ontogenetic habitat partitioning among four shark species within a nursery ground

Daniel P. Crear^{A,E,*} , Cassidy D. Peterson^B , Jeremy M. Higgs^C , Jill M. Hendon^C  and Eric R. Hoffmayer^D 

For full list of author affiliations and declarations see end of paper

***Correspondence to:**

Daniel P. Crear
Inter-American Tropical Tuna Commission,
La Jolla, CA, USA
Email: dcrear8@gmail.com

Handling Editor:

Colin Simpfendorfer

ABSTRACT

Context. Nursery areas provide refuge from predators, rich foraging grounds, and physical conditions conducive to growth and development of juvenile inhabitants. Specifically, the Mississippi Sound in the northern Gulf of Mexico is likely a nursery ground for multiple large and small coastal sharks. **Aims and methods.** Using over a decade of shark survey catch data, we employed habitat modelling approaches to identify preferred environmental conditions and spatial distribution, and quantify core habitat overlap within the Mississippi Sound for young-of-year (YOY), juvenile and adult life stages of four coastal shark species. **Results.** YOY Atlantic sharpnose (*Rhizoprionodon terraenovae*), blacktip (*Carcharhinus limbatus*) and finetooth (*Carcharhinus isodon*) sharks showed a preference for a combination of shallow, warm, low salinity, low dissolved oxygen and turbid waters. Corresponding to shared environmental preferences, spatial distributions of YOY sharks showed a high degree of overlap, particularly in the northern portion of the Mississippi Sound where few adult sharks were observed, suggesting that these life stages partition themselves to avoid predation. **Conclusion and implications.** With a continued rise in US coastal shark populations, we hope this study can help further refine essential fish habitat for these coastal species and provide a framework analysis that can be used to understand habitat partitioning in other regions.

Keywords: coastal shark, delta-lognormal model, essential fish habitat, generalised additive mixed effects model, habitat model, life stages, nursery ground, predator avoidance, resource partitioning, species distribution model.

Introduction

Many sharks exhibit a k-selected life history strategy characterised by low intrinsic population growth rates, late age at maturity and limited lifetime reproductive output (Stevens *et al.* 2000). As demonstrated by their history of overexploitation, this group is uniquely vulnerable and is often of conservation concern (Dulvy *et al.* 2021; Pacoureau *et al.* 2021). Much of their evolutionary success has been ensured by investing substantial energy in the production of large, precocious offspring at parturition (Parsons *et al.* 2008). This reproductive strategy implies that neonate and juvenile survival is a mechanism of density dependence (Cortés 2008; Peterson *et al.* 2017a; Sibly *et al.* 2018). Therefore, the use of a protected coastal area is essential for the population persistence of immature individuals for many species of sharks (Beck *et al.* 2001; Heupel *et al.* 2007, 2019).

Nursery areas can provide refuge from predators (Duncan and Holland 2006; Froeschke *et al.* 2010; Heupel and Simpfendorfer 2011), rich foraging grounds (Kneebone *et al.* 2012) and physical conditions conducive to growth and development (Parsons and Hoffmayer 2007) for juvenile inhabitants, and accordingly are particularly important for species that exhibit small size at birth and slow juvenile growth rates (Heupel *et al.* 2007). Because coastal shark nurseries are typically located nearshore in relatively sheltered waters, they are often communal or shared by many species (McCandless *et al.* 2007; Kinney *et al.* 2011; Oh *et al.* 2017). The presence of multiple species of similar trophic level within an area is ecologically beneficial, because the induced redundancy serves to buffer the ecosystem

Received: 7 July 2023

Accepted: 5 October 2023

Published: 31 October 2023

Cite this:

Crear DP *et al.* (2023)
Marine and Freshwater Research
doi:10.1071/MF23130

© 2023 The Author(s) (or their employer(s)). Published by CSIRO Publishing.

against catastrophic perturbations or collapse of a single stock (Heithaus *et al.* 2013).

Although species diversity is beneficial at the ecosystem level, it also subjects individuals to heightened competition for limited resources (Heithaus 2007). Movement and habitat use patterns are accordingly influenced by anti-predatory behaviours (Preisser *et al.* 2005; Heithaus 2007; Guttridge *et al.* 2012; Dhellemmes *et al.* 2021), intraspecific competition (Ward-Paige *et al.* 2015), foraging dynamics (Heithaus 2007) and environmental preferences or limitations (Crear *et al.* 2019). To limit competition, shark species often exhibit some form of interspecific habitat partitioning in shared ecosystems (Heithaus *et al.* 2013; Tickler *et al.* 2017; Latour *et al.* 2022), particularly nursery areas, either through unique spatiotemporal usage (DeAngelis *et al.* 2008; Oh *et al.* 2017), environmental preferences (Platell *et al.* 1998; Ward-Paige *et al.* 2015; Yates *et al.* 2015) or by prey partitioning (Bethea *et al.* 2004; Papastamatiou *et al.* 2006; Kinney *et al.* 2011). Habitat use and prey preferences are also known to shift across ontogeny (Papastamatiou *et al.* 2009; Grubbs 2010; Matich and Heithaus 2015).

Considering the importance of nurseries for many coastal shark species, these areas are deemed essential fish habitat (Heithaus 2007; Heupel *et al.* 2007); however, the same features that make nursery areas relatively safe and protected from predators (e.g. shallow, inshore) also subject inhabitants to significant anthropogenic impacts and environmental change (Chin *et al.* 2010; Knip *et al.* 2010). As such, it is necessary to fully understand and protect these regions (Norton *et al.* 2012; Heupel *et al.* 2019). Understanding habitat use patterns and partitioning, drivers of habitat preference and species movement, species interactions and ontogenetic changes of these factors will assist in our ability to effectively protect these areas, while serving as baseline data to monitor and predict how these dynamic ecosystems are changing (Crear *et al.* 2019, 2020). This type of information can advise fishery management on ways to best adapt in the future.

Habitat suitability modelling represents a method that has been used to better understand the relationship between species and their environment, other species, fisheries practices and management boundaries. Habitat modelling can help identify what environmental variables may be driving their distribution (Froeschke *et al.* 2010) as well as their preferred conditions (Ward-Paige *et al.* 2015; Crear *et al.* 2020). Predictions from habitat models have been used to project species occurrence probability and habitat distribution across various spatial domains (Hazen *et al.* 2018; Bangley *et al.* 2020). Habitat projections in combination with other spatial analyses have been used to investigate how habitat overlaps among multiple species (Hartog *et al.* 2011), how likely a species is to interact with a fishery (White *et al.* 2019) and how well a spatial management area may be protecting a species (Oh *et al.* 2017; Crear *et al.* 2021).

The Mississippi Sound is a dynamic and biologically productive area due to riverine inputs (Gunter 1963; Hendon *et al.* 2013). This causes an increasing salinity gradient from west to east. Although it has not been formally tested as a nursery area (Heupel *et al.* 2007), many young-of-year (YOY) and juvenile coastal shark species are known to occur within the Mississippi Sound (Parsons and Hoffmayer 2005, 2007). Accordingly, our use of the term 'nursery' is colloquial, representing areas in which neonate and juvenile individuals are repeatedly and commonly encountered. Specifically, the Mississippi Sound appears to be a nursery ground for the Atlantic sharpnose (*Rhizoprionodon terraenovae*), blacktip (*Carcharhinus limbatus*) and finetooth (*Carcharhinus isodon*) sharks based on their high abundance of juveniles in the area (Parsons and Hoffmayer 2007). Although YOY bonnetheads (*Sphyrna tiburo*) are not common in the Mississippi Sound, juvenile and adult bonnetheads use the area regularly (Parsons and Hoffmayer 2005; Bethea *et al.* 2015). In this study, we employed habitat modelling approaches to identify preferred environmental conditions and spatial distribution within the Mississippi Sound for YOY, juvenile and adult life stages for the Atlantic sharpnose, blacktip, finetooth and bonnethead sharks. Lastly, we quantified core habitat overlap among species' life stages to better understand the dynamics of this nursery area.

Materials and methods

Data collection

The University of Southern Mississippi's (USM) Center for Fisheries Research and Development (CFRD) routinely conducts fisheries-independent surveys using multiple gear types within Mississippi coastal waters. Bottom longline sampling was used monthly (March–October) from 2007 to 2020 using a random stratified design. Gear consisted of a 1.9-km mainline (4.0-mm monofilament) with 100 gangions (3.0-mm monofilament). Longline gangions were 3.7 m long and outfitted with 15/0 circle hooks (Mustad, Gjøvik, Norway) and baited with Atlantic mackerel (*Scomber scombrus*). The longline fished for 1 h prior to retrieval. Soak time was defined at the time of last high-flier deployment to the time of first high-flier retrieval.

Handline gear was used monthly (March–October) from 2004 to 2020 at various sites within the Mississippi Sound using a random stratified design. Gear consisted of a 152-m braided nylon rope mainline (6.4-mm diameter) with 50 gangions (2.0-mm monofilament) that were 0.9 m long and outfitted with 12/0 circle hooks (Mustad, Gjøvik, Norway) and baited with Gulf menhaden (*Brevoortia patronus*). The handline was fished for 1 h prior to retrieval, and soak time was defined by the time between the setting of the last hook and the retrieval of the last hook.

Gill-net gear was used monthly (March–October) from 2003 to 2020 at various sites within the Mississippi Sound

using a multi-panel gill-net. Following Parsons and Hoffmayer (2005) and Bethea *et al.* (2015), gill-net sampling was conducted with a 183-m monofilament net comprised six panels (30.5 × 3.0 m each) of differing mesh size (8.9-, 10.2-, 11.4-, 12.7-, 14.0- and 20.3-cm stretch mesh). The gill-net fished for 2 h, with a 1-h check, prior to retrieval. Soak time was defined as the time the gill-net was deployed to the time when the entire net was checked or retrieved from the water.

For all gear types, sampling occurred during daylight hours in water depths less than 10 m. Regardless of gear type, encountered sharks were identified to the lowest taxonomic level, and had sex, weight (kg) and length (mm) recorded. Traditional length measurements included pre-caudal (PCL; the length from the tip of the snout to the anterior margin of the precaudal pit), fork (FL; the length from the tip of the snout to the posterior notch of the caudal fin), and stretched total (STL; the length from the tip of the snout to the posterior tip of the fully extended terminal lobe of the caudal fin). Life stage was assigned based upon FL measurements for each target species following previous studies in the Gulf of Mexico (Table 1). At each station, surface and bottom water temperature (°C), salinity (ppt; grams of salts per kilogram of seawater) and dissolved oxygen (mg L⁻¹) were recorded. Average depth (m) was calculated using gear start and end points recorded from the vessel's depth finder, and water clarity (depth of the photic zone, mm) was measured using a Secchi disc. At times, not all environmental parameters were recorded due to logistics. Latitude and longitude were recorded at each sampling station. Sampling protocols were approved by the University of Southern Mississippi Institutional Animal Care and Use Committee: 9031202, 11092217, 13101704, 15101509, 18121301 and 18010502.

Table 1. Sex-specific life stage classifications for Atlantic sharpnose (*Rhizoprionodon terraenovae*), blacktip (*Carcharhinus limbatus*), bonnethead (*Sphyrna tiburo*) and finetooth (*C. isodon*) sharks in the Gulf of Mexico.

Species	Sex	Young-of-year (mm FL)	Juvenile (mm FL)	Adult (mm FL)	Reference
Atlantic sharpnose	F	255–489	490–632	>632	Hoffmayer <i>et al.</i> (2013)
Atlantic sharpnose	M	255–489	490–629	>629	Hoffmayer <i>et al.</i> (2013)
Blacktip	F	400–650	651–1192	>1192	Baremore and Passerotti (2013)
Blacktip	M	400–650	651–1058	>1058	Baremore and Passerotti (2013)
Bonnethead	F	250–462	463–700	>700	Lombardi-Carlson <i>et al.</i> (2003)
Bonnethead	M	250–462	463–635	>635	Lombardi-Carlson <i>et al.</i> (2003)
Finetooth	F	349–595	596–995	>995	Higgs <i>et al.</i> (2020)
Finetooth	M	349–595	596–961	>961	Higgs <i>et al.</i> (2020)

FL, fork length.

Data manipulation

Only longline, handline and gill-net sets that occurred inside the Mississippi Sound, within Mississippi waters, south of 30.33°N, and that had all environmental parameters measured were considered in the analysis to ensure data from all sources were uniform. A date cutoff was decided for each species around the known pupping season to determine if caught YOY would be included in the analysis. All sets prior to the cutoff were removed from the dataset for YOY species. This was done to prevent models confusing YOY absence attributed to environmental factors with YOY not being born yet. The cutoff for YOY blacktip sharks was 1 May, whereas the cutoff for YOY Atlantic sharpnose and finetooth sharks was 1 June. So, for example, any sets prior to 1 May of any year were removed for the YOY blacktip models. To improve sample size and model convergence, some life stages were grouped together within a species. This included combining finetooth shark YOY and juvenile individuals, as well as combining individuals of juvenile and adult bonnethead sharks (YOY bonnethead sharks are not common in the Mississippi Sound). Effort was calculated for each gear type, where bottom longline was 100 hooks multiplied by the soak time (h), handline was 50 hooks multiplied by the soak time and gill-net was simply the soak time. Catch per unit effort (CPUE) was then calculated by dividing the number of individuals caught for a given life stage in a set by the effort. To incorporate CPUE data across the three gear types in the model, CPUE were standardised to the grand mean CPUE of the gear type. First, CPUE for each set within a gear type was calculated as described above, but it was based on the total number of individuals caught across the four species. The mean was taken across all CPUE for a given gear type to represent the grand mean CPUE for that gear type. Each individual species' life stage CPUE were standardised by dividing them by the grand mean CPUE for the respective gear type (Gibson-Reinemer *et al.* 2017). Once the standardisation was complete, data were combined across all gear types for further analysis.

Habitat modelling

Separate habitat models were generated for each species' life stage. To account for the non-linear relationship between covariates and species abundance, a generalised additive mixed model (GAMM) was used (Hastie and Tibshirani 1990; Wood 2017). All models were constructed as delta-lognormal models, which consists of two components, a binomial and a lognormal component. Delta-lognormal models are often used with zero-inflated data. The first component modelled probability of occurrence using a binomial GAMM, whereas the second component only modelled log-transformed positive catch records using a GAMM with a normal distribution. Therefore, the response variable for the binomial GAMM was presence or absence of the given species' life stage, whereas

log-transformed non-zero CPUE was the response variable for the lognormal GAMM. Outputs from each component were then multiplied to generate estimated relative abundance (Aitchison 1955; Lynch *et al.* 2015; Brodie *et al.* 2020).

Two different sets of models were run for each species' life stage. The first only consisted of environmental variables (hereafter referred to as the 'environmental habitat model'). Those potential covariates consisted of variables collected during each set including bottom temperature, bottom salinity, bottom dissolved oxygen, Secchi depth (i.e. turbidity) and water depth. Other covariates considered were gear type and total monthly rainfall (see <https://www.srcc.tamu.edu/>). The second set of models considered set latitude and longitude, as well as gear type (here after referred to as the 'spatial habitat model'). Two sets of models were developed because often latitude and longitude explains variation actually attributed to environmental covariates. Therefore, the environmental habitat models were used to understand the relationship between species relative abundance and various important environmental variables, whereas the spatial habitat models were used to predict the distribution of each species' life stage within the Mississippi Sound. Both are explained in more detail below. All models were fit using the mgcv package (ver. 3.6.1, see <https://cran.r-project.org/package=mgcv/>; Wood 2011) in R (ver. 4.1.2, R Foundation for Statistical Computing, Vienna, Austria, see <https://www.r-project.org/>).

Environmental habitat model

Prior to generating the environmental habitat models, collinearity was examined among covariates for the presence-absence dataset (for the binomial GAMM) and separately for each individual species' life stage positive catch record dataset (for the lognormal GAMM) using correlation matrices. If collinearity was present, only one of the two collinear variables was included in the model. Temporal and spatial autocorrelation were assessed for preliminary model fits for both components using autocorrelation function plots and variograms respectively. When temporal autocorrelation was present, we reduced or removed it by adding year or year and month as random effects in the model. Spatial autocorrelation was not observed in these data. We then developed 20 models for each component that consisted of various combinations of environmental variables. Owing to the known importance of temperature on shark habitat distribution, bottom temperature was selected to be in the vast majority of the models. Model selection was performed using Akaike information criterion (AIC) to identify the best model for each component. If a variable was present in the best model for either the binomial or lognormal components, that variable was considered important. Relative abundance predictions for important variables were generated using marginal means (Searle *et al.* 1980). Environmental preferences were determined and defined as any conditions where the relative abundance was in the top 20th percentile. Uncertainty about marginal means was calculated by randomly resampling the data

1000 times, refitting the best model for each component to those resampled data and recalculating the marginal means (Efron and Tibshirani 1993). Of the 1000 bootstrapped samples attempted, all models that converged were used to calculate confidence intervals around the marginal means.

Spatial habitat model

Similar modelling steps described above were also conducted for the spatial habitat models. However, collinearity and model selection were not conducted because latitude, longitude and gear type were the only fixed effects in the model. Year and month were added as random effects when temporal autocorrelation was present. Relative abundance was then predicted spatially across the range of latitude and longitude observed in the surveys. Using the same 1000 bootstrapped samples from above, the spatial habitat models were refit for each component to those resampled data and spatial predictions were generated. The bootstrapped samples where the spatial habitat models converged were used to calculate uncertainty in the spatial overlap between two species' life stages as described in more detail below.

Core habitat overlap

Spatial relative abundance predictions were used to quantify core habitat and overlap among species' life stages. Core habitat was defined as the area that represented the top 25% of relative abundance predictions for a given species' life stage (Hazen *et al.* 2013; White *et al.* 2019). The percentage of core habitat overlap was calculated between each of the species' life stages. Species' life stages that shared 50% or more of their core habitat were considered to have shared similar habitat. The threshold of 50% was used because that was the percentage value where groupings of species' life stages started to emerge. To address the uncertainty in measured core habitat overlap, core habitat was also calculated for each species using bootstrap resampled datasets outlined above. The number of bootstraps where 50% of core habitat overlapped between each species' life stage was also examined.

Results

From 2003 to 2020, 1820 sets were made inside the Mississippi Sound, of which 206, 855 and 759 were bottom longline, handline and gill-net efforts respectively (Fig. 1). Adult Atlantic sharpnose sharks were caught most frequently (46.5%) and in the highest abundance (4825 individuals) over the time series (Table 2). Juvenile blacktip (20.9%) and juvenile Atlantic sharpnose (19.6%) sharks were caught at a relatively high frequency. All other species' life stages were caught in less than 10%, but greater than 3% (adult finetooth sharks) of all sets (Table 2).

For the environmental habitat models, the deviance explained varied across species' life stages and across the

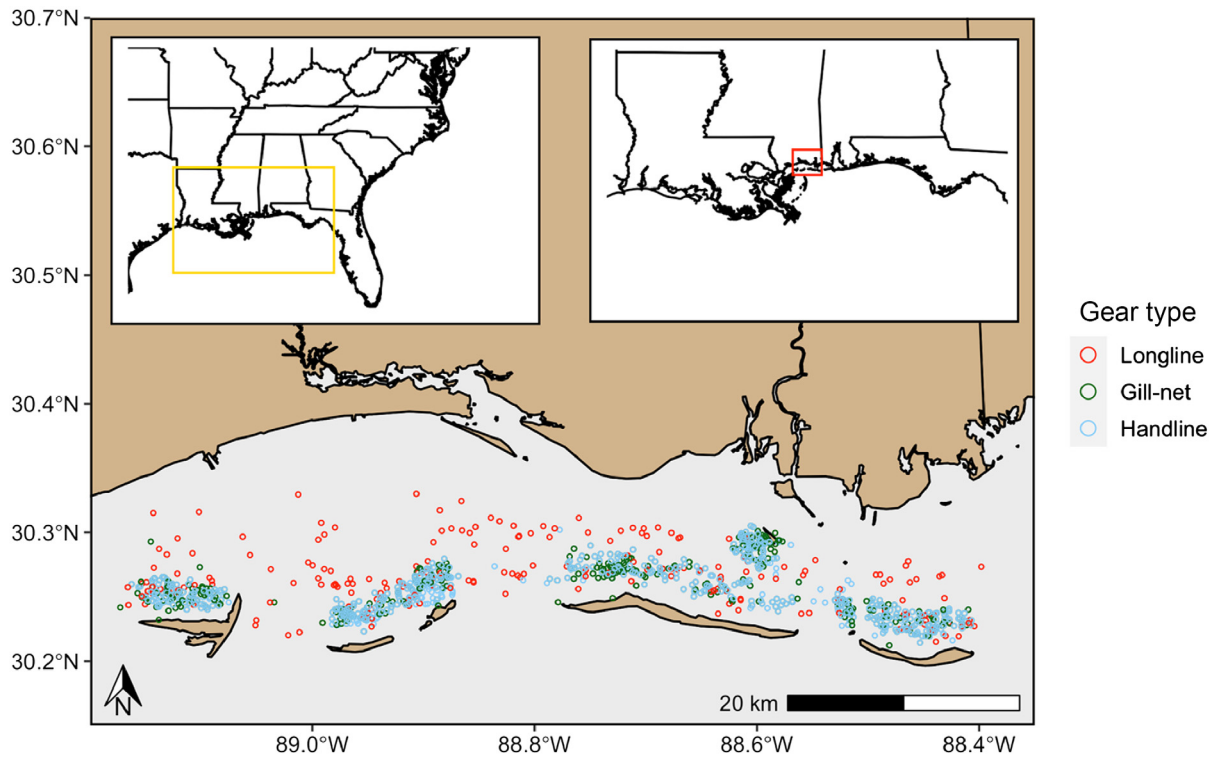


Fig. 1. Bottom longline (red), handline (blue) and gill-net (green) sets conducted from 2003 to 2020 in the Mississippi Sound. The two inset maps represent zoomed out views of the northern Gulf of Mexico (yellow box) and the location of the Mississippi Sound (red box).

Table 2. Occurrence rate (%) and number of individuals caught for each species’ life stage within the Mississippi Sound from bottom longline, handline or gill-net gear from 2003 to 2020.

Species and life stage	Occurrence rate (%)	Catch	Binomial DE	Lognormal DE
SN ADU	46.5	4825	27	26.3
SN JUV	19.6	1101	25.2	29.7
SN YOY	8.2	196	15.9	24.3
BT ADU	8	197	24.7	38.6
BT JUV	20.9	1046	19.2	15.3
BT YOY	7.2	255	25.7	18.4
FT ADU	3.1	94	24.6	14.7
FT YOY+JUV	8.8	793	23.7	12.5
BH JUV+ADU	8.7	310	24.3	12.2

The deviance explained (DE) for the binomial and lognormal components for each species’ life stage is provided. Abbreviations for species are: SN, Atlantic sharpnose; BT, blacktip; FT, finetooth; BH, bonnethead. Abbreviations for life stages are: ADU, adult; JUV, juvenile; YOY, young-of-year; YOY+JUV, young-of-year and juvenile combined; JUV+ADU, juvenile and adult combined.

two model components (binomial and lognormal). The highest deviance explained values for the binomial component (>25%) occurred for adult and juvenile Atlantic sharpnose and YOY blacktip shark models (Table 2). Similarly, the highest

deviance explained values for the lognormal component (>25%) occurred in adult and juvenile Atlantic sharpnose and adult blacktip sharks. All deviance explained values across species’ life stages were greater than 15 and 12% for the binomial and lognormal components respectively (Table 2).

When examining important covariates (present in either component) in the environmental habitat models, bottom temperature, bottom salinity and Secchi depth (i.e. turbidity) occurred the most frequently across species’ life stages (Fig. 2). Temperature was important for the binomial component for all species’ life stages and for the lognormal component for adult and juvenile Atlantic sharpnose and blacktip sharks, as well as for adult finetooth sharks. Salinity was important for the binomial component for all species except YOY Atlantic sharpnose sharks and was important for the lognormal component for adult Atlantic sharpnose sharks. Turbidity was important for the binomial component for all species except adult and juvenile Atlantic sharpnose and adult blacktip sharks. The covariate that was important for the least amount of species’ life stages was monthly rainfall (Fig. 2).

The range of conditions preferred for the important covariates varied by species’ life stages (Table 3). The smaller life stages (e.g. YOY and juvenile) followed specific trends when certain covariates were important. For example, juvenile Atlantic sharpnose sharks preferred depths less than 3.3 m (Fig. 3a, Table 3), whereas YOY and juvenile finetooth

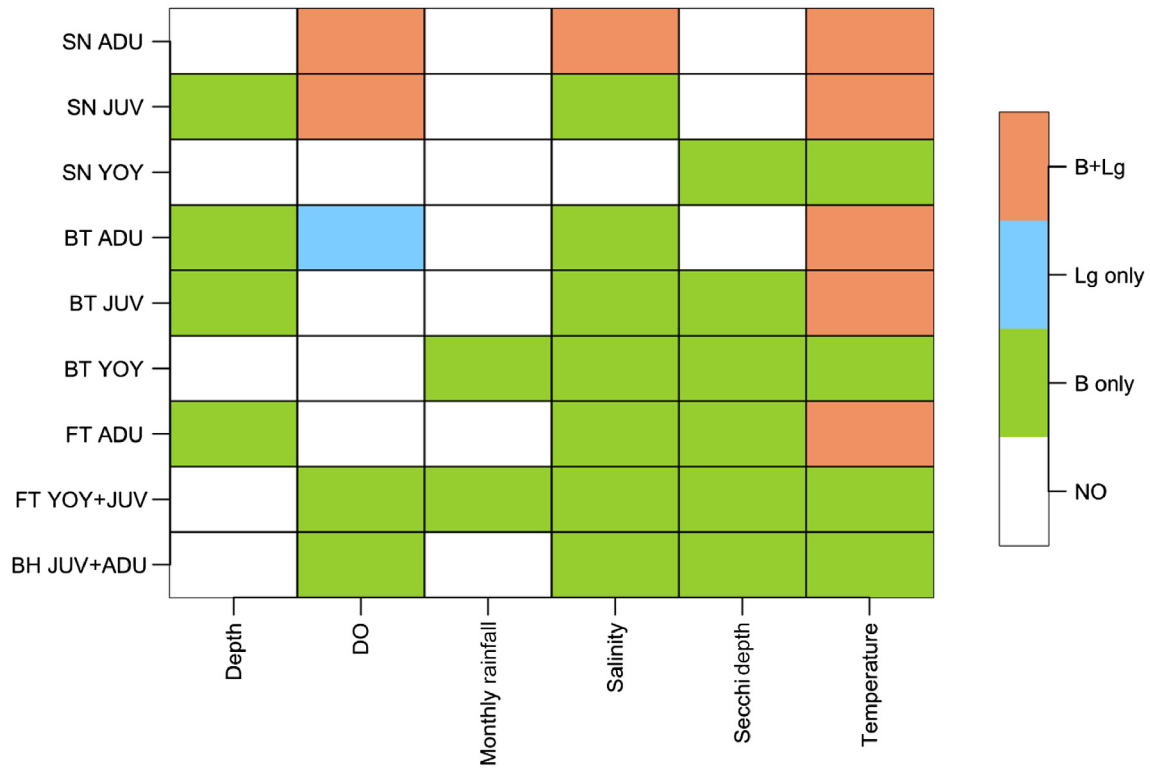


Fig. 2. Environmental covariates considered important in driving each species' life stage habitat suitability based on the best model for the binomial (B) and lognormal (Lg) components. If the grid colour is white (NO), it means that covariate was not in the best model for the given species and life stage for either component. Light green and light blue grids indicate that the covariate was in the best model for only the binomial (B only) or lognormal (Lg only) components respectively. If the grid is light orange it means that covariate was in the best model for both components (B+Lg). Abbreviations for species are: SN, Atlantic sharpnose; BT, blacktip; FT, finetooth; BH, bonnethead. Abbreviations for life stages are: ADU, adult; JUV, juvenile; YOY, young-of-year; YOY+JUV, young-of-year and juvenile combined; JUV+ADU, juvenile and adult combined.

Table 3. Preferred conditions for the important environmental covariates species' life stage, where preferred is defined as any conditions where the relative abundance was in the top 20th percentile within a given covariate.

Species and life stages	Depth (m)	DO (mg L ⁻¹)	Monthly rainfall (cm)	Salinity (ppt)	Secchi depth (mm)	Temperature (°C)
SN ADU	–	>6.3	–	26.0–35.2	–	25.1–31.5
SN JUV	<3.3	3.6–7.9	–	23.8–31.7	–	23.6–29.6
SN YOY	–	–	–	–	<38	>31.0
BT ADU	>10.0	<3.3	–	25.3–31.6	–	>30.8
BT JUV	>9.1	–	–	23.6–31.0	<147	>30.2
BT YOY	–	–	>18.0	15.8–24.4	<43	26.2–31.0
FT ADU	5.5–6.7	–	–	22.3–29.9	<68	24.3–27.5
FT YOY+JUV	–	3.0–6.5	>18.3	–	<47	>27.6
BH JUV+ADU	–	>7.8	–	20.4–28.2	<104	23.1–28.4

Any covariates with a dash (–) are those that the environmental covariate was not important for the given species' life stage. Abbreviations for species are: SN, Atlantic sharpnose; BT, blacktip; FT, finetooth; BH, bonnethead. Abbreviations for life stages are: ADU, adult; JUV, juvenile; YOY, young-of-year; YOY+JUV, young-of-year and juvenile combined; JUV+ADU, juvenile and adult combined.

sharks preferred dissolved oxygen values between 3.0 and 6.5 mg L⁻¹ and juvenile Atlantic sharpnose sharks preferred dissolved oxygen values between 3.6 and 7.9 mg L⁻¹ (Fig. 3b, Table 3). A higher relative abundance occurred for both YOY

blacktip and YOY and juvenile finetooth sharks when monthly rainfall was highest (Fig. 3c, Table 3). YOY blacktip sharks preferred the lowest bottom salinity (15.8–24.4 ppt) of species' life stages (Fig. 3d, Table 3). The relative abundance of YOY

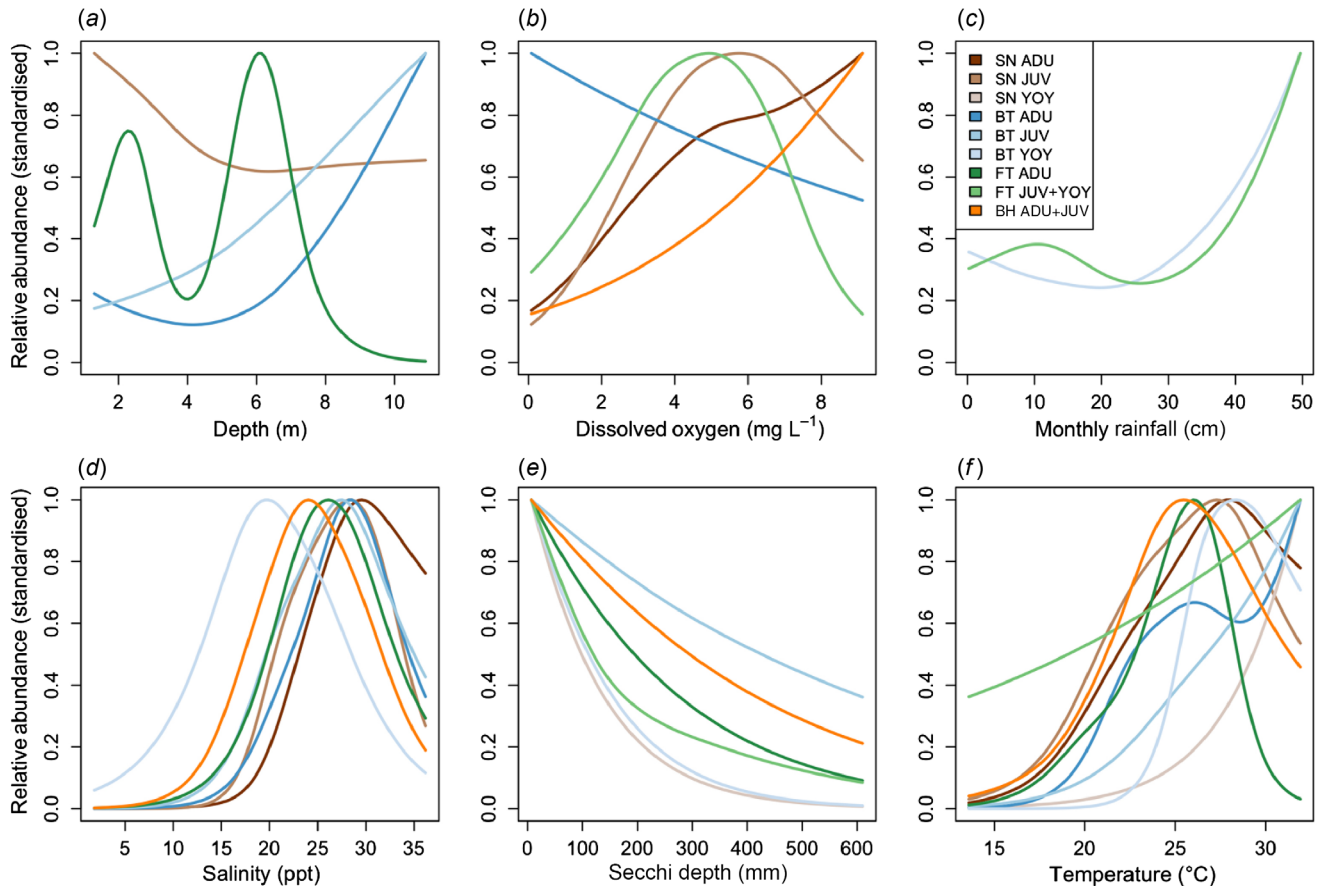


Fig. 3. Standardised marginal mean estimates of relative abundance of species' life stages across the covariates that were in the best binomial or lognormal models. Predicted estimates were standardised by dividing each value by the maximum estimate. Covariates are depth (a), dissolved oxygen (b), monthly rainfall (c), salinity (d), Secchi depth (e) and temperature (f). Different shades for a colour represent different life stages for a species: Atlantic sharpnose (SN, brown), blacktip (BT, blue), finetooth (FT, green) and bonnethead (BH, orange). Abbreviations for life stages are: ADU, adult; JUV, juvenile; YOY, young-of-year; YOY+JUV, young-of-year and juvenile combined; JUV+ADU, juvenile and adult combined.

blacktip, Atlantic sharpnose and finetooth (including juveniles too) were all estimated to increase in more turbid waters (<50 mm; lower Secchi depth; Fig. 3e, Table 3).

By contrast, the larger species' life stages like adult and juvenile blacktip and adult finetooth sharks did not often share similar preferences but did differ from many of the preferences of the smaller life stages. For example, both adult and juvenile blacktip sharks preferred deeper waters and temperatures greater than 30°C, whereas adult finetooth sharks preferred water depths between 5.5 and 6.7 m and bottom temperatures between 24.3 and 27.5°C (Fig. 3a, f, Table 3). Despite this, it is important to note that the sharp increase in relative abundance in deeper depths for juvenile and adult blacktip is likely driven by the small number of deeper sets (see Fig. S4 and S5 of the Supplementary material). Juvenile blacktip and adult finetooth sharks, similar to the smaller life stages, preferred more turbid waters (Fig. 3e, Table 3). The remaining two species' life stages, adult Atlantic sharpnose sharks and bonnetheads (juveniles and adults

combined), shared preferences among both the smaller and larger life stages. For example, bonnetheads preferred lower salinity conditions (20.5–28.2 ppt) and turbid waters, but also preferred the most oxygenated waters (>7.8 mg L⁻¹) and the coolest bottom temperatures of any species ranging from 23.1 to 28.4°C (Fig. 3, Table 3). Lastly, adult Atlantic sharpnose sharks preferred higher salinity (26.0–35.2 ppt) and higher dissolved oxygen waters (>6.3 mg L⁻¹). Marginal means plots with uncertainty for the important covariates for each of the species' life stages can be found in Fig. S1–S9 of the the Supplementary material.

The spatial habitat models were used to generate spatial relative abundance predictions. The areas within the Mississippi Sound where relative abundance was highest (core habitat) varied across species' life stages. Although the predicted relative abundance values were masked once core habitat was calculated for each species' life stage, it is important to note that species' life stages that were caught in higher abundance in the survey often had higher predictions

of relative abundance. The relative abundance of adult and juvenile Atlantic sharpnose sharks was highest towards the eastern part of the Mississippi Sound, whereas YOY Atlantic sharpnose preferred the more northern areas of the survey areas (Fig. 4). The relative abundance of adult blacktip sharks was highest towards the southern areas of the Mississippi Sound along the north side of the barrier islands. Juvenile blacktip sharks preferred three different areas in the sound, including more eastern waters, along the southern central areas and waters along the northern side of the two most western islands. The highest relative abundance of YOY blacktip sharks occurred in two locations, both along the more northern areas of the survey area (Fig. 5). Core habitat for adult finetooth sharks occurred along the eastern and central portions of the sound extending to the northern and southern boundaries. YOY and juvenile finetooth sharks preferred more northern areas of the survey area (Fig. 6). Bonnethead relative abundance (juveniles and adults combined)

was highest along the southeastern portions of the sound (Fig. 7).

Overlap of 50% of core habitat was often related to the size of the life stage of a given species. For example, at least 50% of the core habitat of three of the four smallest species' life stages (i.e. YOY Atlantic sharpnose, YOY blacktip and YOY and juvenile finetooth sharks) overlapped with each other (Fig. 8, Table 4). The 50% core habitat overlap trend occurred for the original best model and for at least 200 bootstrapped models for those three species' life stages (of the ~800 bootstrapped models that converged). The core habitat of the largest species' life stage, adult blacktips, overlapped with $58 \pm 13\%$ of the bonnetheads' (juveniles and adults combined) core habitat based on the original best model, whereas both bonnethead and juvenile blacktip sharks core habitat overlapped with adult blacktip sharks' core habitat for at least 300 bootstrapped models. The highest percentage overlap occurred between juvenile and adult Atlantic sharpnose sharks ($86 \pm 16\%$;

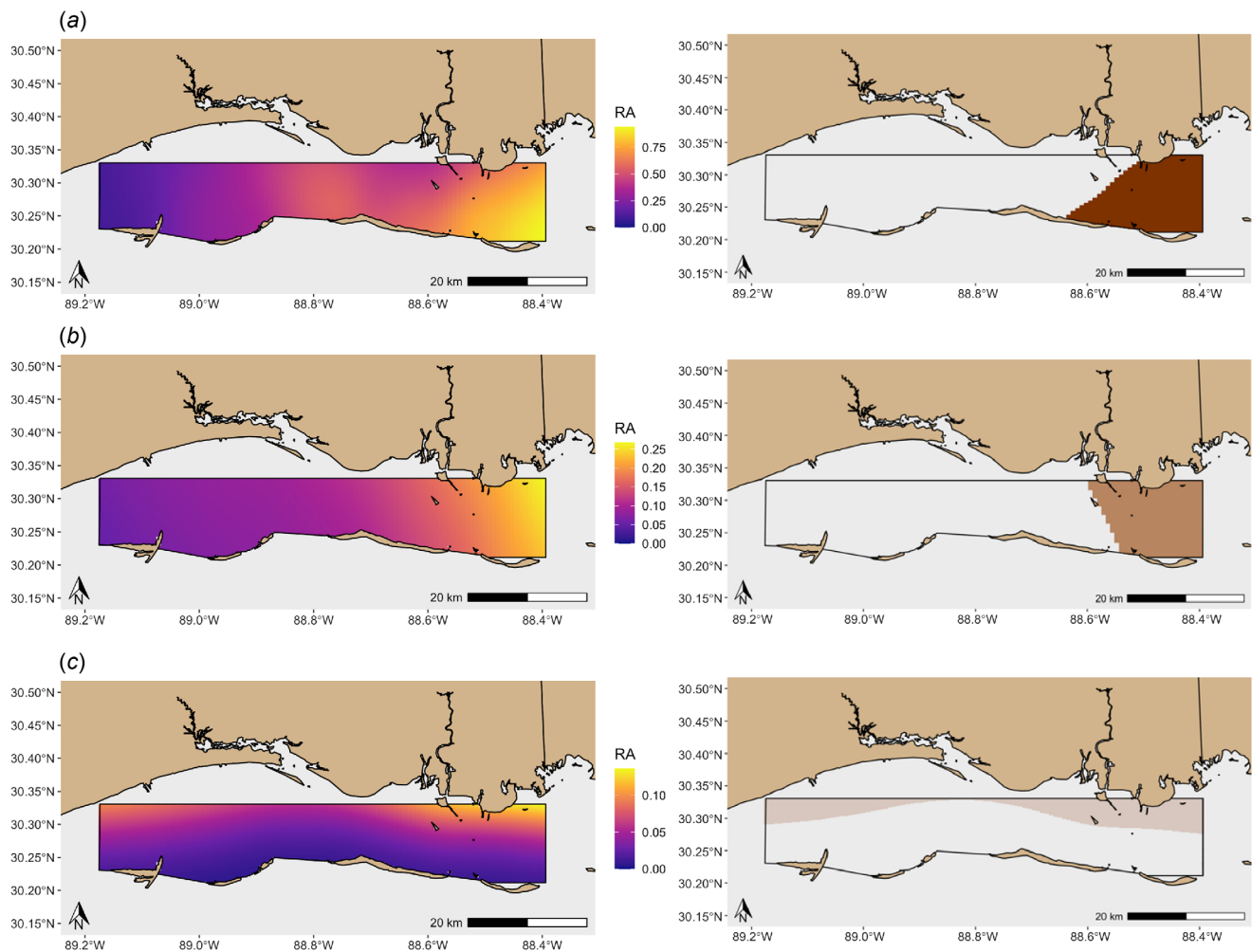


Fig. 4. Relative abundance (RA) estimates for adult (a), juvenile (b) and young-of-year (c) Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) in the Mississippi Sound (left column). Corresponding core habitat is based on the top 25% relative abundance estimates indicated in different shades of brown (right column).

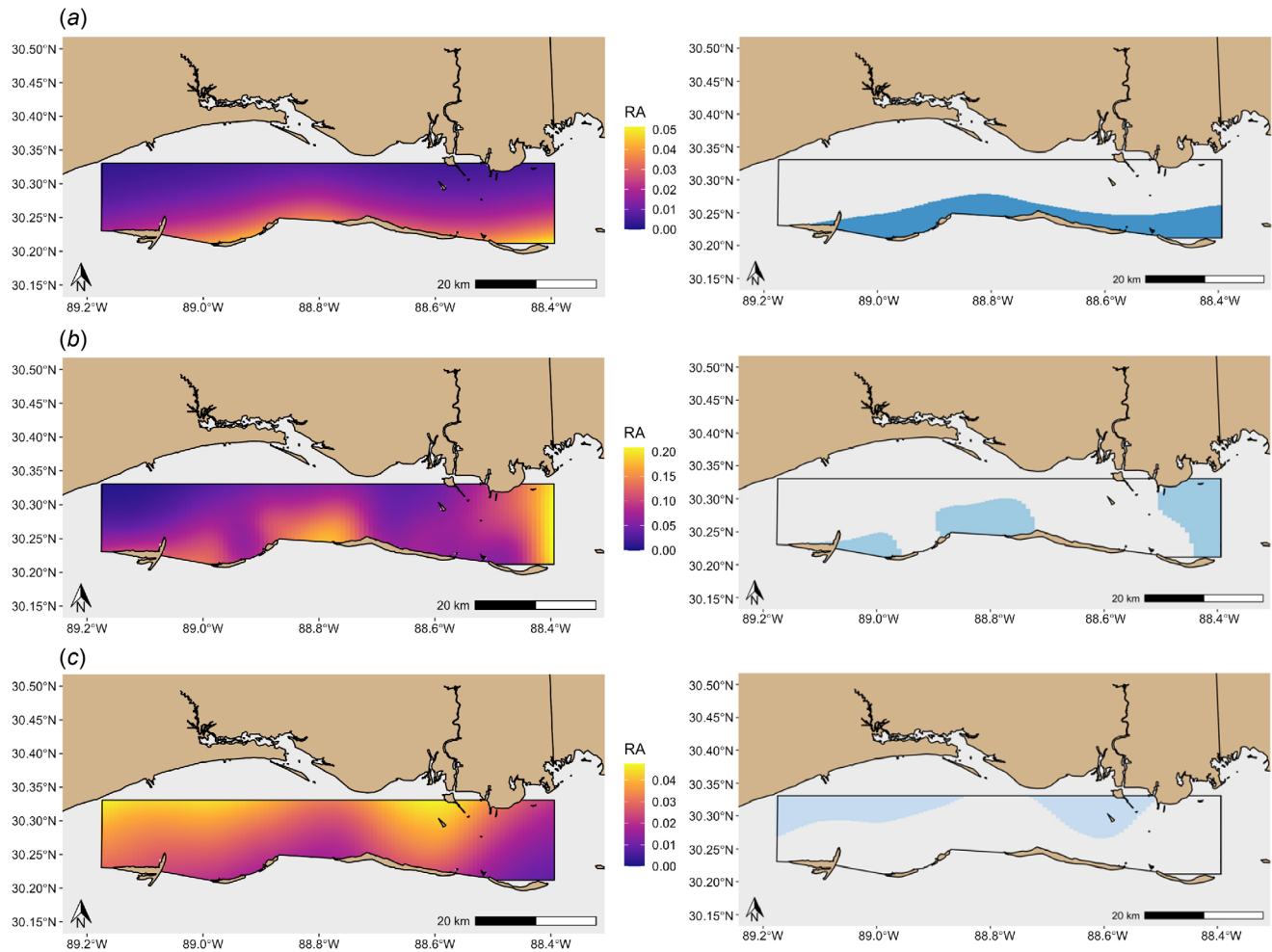


Fig. 5. Relative abundance (RA) estimates for adult (a), juvenile (b) and young-of-year (c) blacktip sharks (*Carcharhinus limbatus*) in Mississippi Sound (left column). Corresponding core habitat based on the top 25% relative abundance estimates indicated in different shades of blue (right column).

>500 bootstraps), YOY Atlantic sharpnose and YOY and juvenile finetooth ($77 \pm 16\%$; >500 bootstraps), and juvenile blacktip and adult finetooth sharks ($70 \pm 14\%$; >500 bootstraps) (Fig. 8, Table 4).

Discussion

In this study, YOY Atlantic sharpnose, blacktip and finetooth sharks showed a preference for some combination of shallow, warm, low salinity, low dissolved oxygen and turbid waters while they inhabited the waters of the Mississippi Sound (Fig. 3). Owing to these environmental preferences, these YOY sharks showed a high degree of overlap in their distribution (Table 4) and were restricted to the northern regions of the Mississippi Sound (Fig. 4–6). Parsons and Hoffmayer (2007) reported a similar distribution for YOY Atlantic sharpnose, blacktip and finetooth sharks, occurring in the northern region of the Mississippi Sound with a high degree of overlap among all three species using an older gill-net dataset (1998–2000) than the present study. Other studies in the northern Gulf of

Mexico have also shown similar environmental preferences for juvenile sharks. For example, Hueter and Tyminski (2007) revealed similar environmental preferences of warm, shallow and low salinity waters for neonate and YOY blacktip and Atlantic sharpnose sharks along the Gulf coast of Florida. Additionally, Ward-Paige *et al.* (2015) revealed that salinity, temperature and depth were significant factors for juvenile Atlantic sharpnose, blacktip and finetooth sharks in the northeastern Gulf of Mexico.

These juvenile sharks may be benefitting from the use of these shallow coastal areas, which potentially provide protection from predators or an abundance of prey resources (Simpfendorfer and Milward 1993; Heupel and Hueter 2002; Parsons and Hoffmayer 2007). Environmental and spatial partitioning of juveniles may be reflective of anti-predatory behaviours, wherein individuals forego essential habitat in favour of refuge, reflecting the risk trade-off between ensuring survival and optimising growth (Heithaus 2007; Heithaus *et al.* 2010). Notably, anti-predatory behaviours are often the result of indirect interactions that are not easily observed

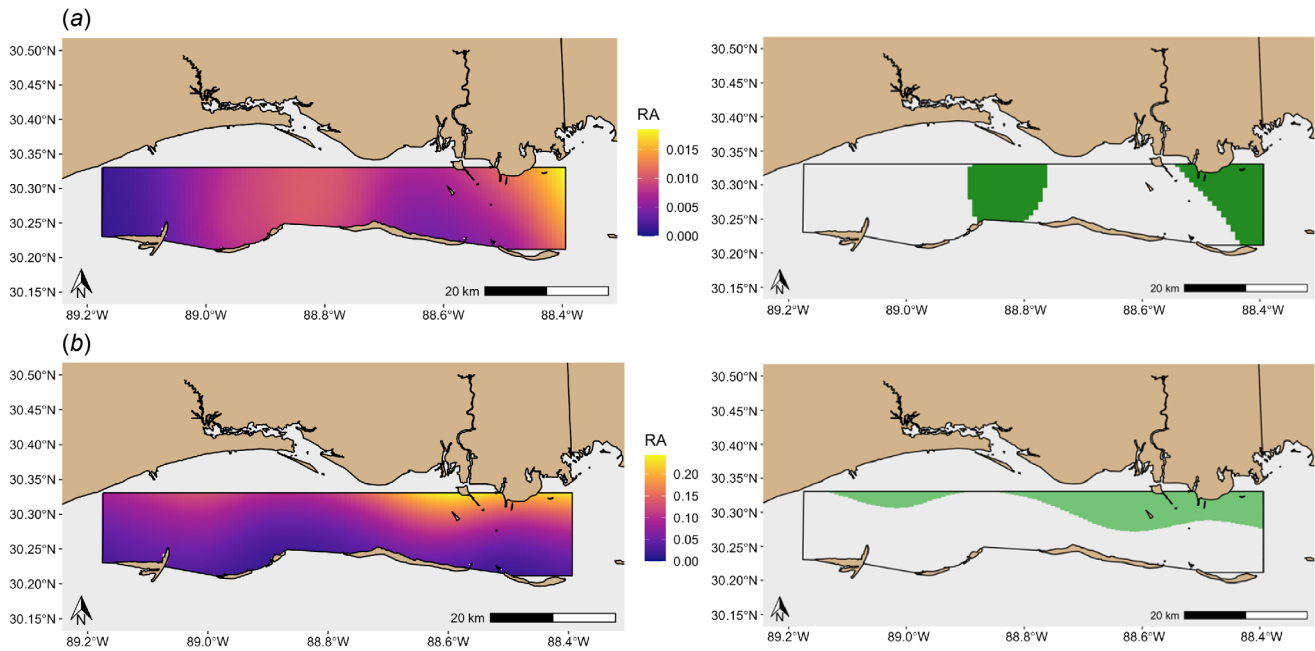


Fig. 6. Relative abundance (RA) estimates for adult (a) and juvenile and young-of-year (b) finetooth sharks (*Carcharhinus isodon*) in Mississippi Sound (left column). Corresponding core habitat based on the top 25% relative abundance estimates indicated in different shades of green (right column).

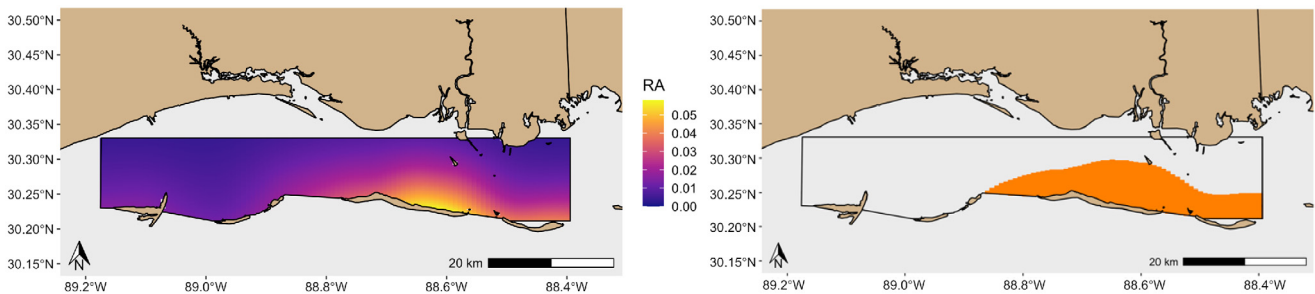


Fig. 7. Relative abundance (RA) estimates for juvenile and adult bonnetheads (*Sphyrna tiburo*) in Mississippi Sound (left column). Corresponding core habitat based on the top 25% relative abundance estimates indicated in orange (right column).

(as compared to direct consumptive predatory interactions) and serve to functionally reduce the carrying capacity of the affected species (Heithaus *et al.* 2010). This type of habitat partitioning has been shown to indirectly lead to starvation-induced mortality in YOY and juvenile scalloped hammerheads in Hawaiian waters, due to the lack of appropriate trophic resources (Lowe 2002; Duncan and Holland 2006). Similarly, Heupel and Hueter (2002) revealed that YOY blacktip sharks in Terra Ceia Bay, Florida, avoided areas of increased prey abundance due to the presence of larger predators, and speculated this behaviour could have contributed to high mortality rates for the YOY sharks.

In the current study, very few adult sharks were observed in the northern portion of the Mississippi Sound where most of the YOY sharks were caught, supporting the notion that the YOY sharks were partitioning themselves in areas away

from the larger predators. Though there is a direct benefit to this partitioning due to reduced predation, by doing this, these YOY sharks could potentially be placing themselves in suboptimal conditions (e.g. low salinity, shallow, high turbidity) that could result in poor habitat quality, low prey abundance and physiologically stressful environmental conditions (Hamilton *et al.* 2022). Other studies have reported similar partitioning with young sharks where they sought refuge in low salinity (Simpfendorfer *et al.* 2005; Heupel and Simpfendorfer 2011; Hamilton *et al.* 2022) and shallow, sheltered waters (Wetherbee *et al.* 2007; Papastamatiou *et al.* 2009; Guttridge *et al.* 2012) due to predator avoidance. For example, in the Chesapeake Bay sandbar shark nursery area, neonate sandbar sharks (*Carcharhinus plumbeus*) inhabited 'upstream' waters of the estuary relative to juvenile sandbar sharks, while also preferring different environmental

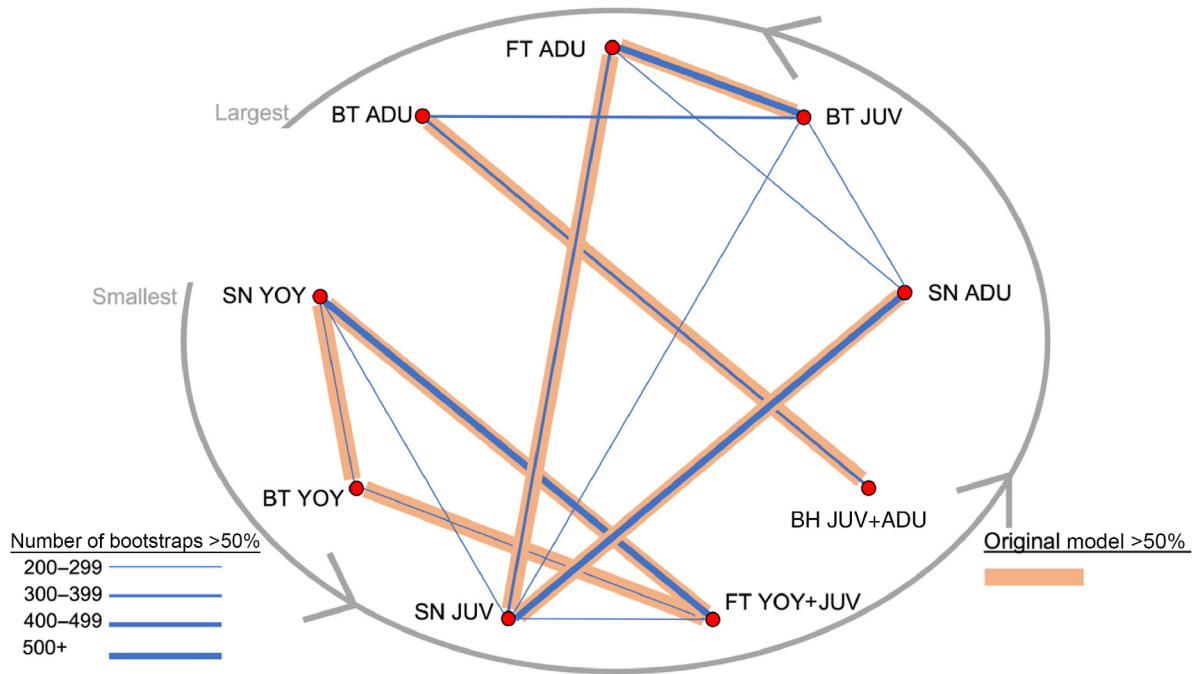


Fig. 8. Core habitat overlap among species' life stages. Blue lines indicate a connection between two species' life stages where 50% of their core habitats overlapped in at least 200 bootstraps. The thickness of the blue line represents the number of bootstrapped core habitats where 50% of the core habitat overlapped with another species' life stage core habitat. The orange highlighted lines represent species' life stages where 50% of their core habitat overlapped based on the original best model. The location of the species' life stage in the circle is based on the average size of that species' life stage caught in the survey going from smallest to largest in a counterclockwise direction as indicated by the grey circle and arrows. Abbreviations for species are: SN, Atlantic sharpnose; BT, blacktip; FT, finetooth; BH, bonnethead. Abbreviations for life stages are: ADU, adult; JUV, juvenile; YOY, young-of-year; YOY+JUV, young-of-year and juvenile combined; JUV+ADU, juvenile and adult combined.

Table 4. Percentage core habitat overlap between each species' life stage.

	SN ADU	SN JUV	SN YOY	BT ADU	BT JUV	BT YOY	FT ADU	FT YOY+JUV	BH JUV+ADU
SN ADU	100								
SN JUV	86 ± 16	100							
SN YOY	30 ± 15	44 ± 17	100						
BT ADU	39 ± 11	30 ± 10	0 ± 6	100					
BT JUV	47 ± 12	47 ± 14	25 ± 15	49 ± 11	100				
BT YOY	0 ± 11	13 ± 15	66 ± 19	0 ± 11	0 ± 11	100			
FT ADU	48 ± 15	50 ± 18	30 ± 18	26 ± 17	70 ± 14	4 ± 15	100		
FT YOY+JUV	29 ± 13	43 ± 15	77 ± 16	0 ± 6	23 ± 13	57 ± 19	29 ± 16	100	
BH JUV+ADU	46 ± 15	33 ± 14	0 ± 12	58 ± 13	28 ± 10	11 ± 16	17 ± 13	11 ± 12	100

Uncertainty around each overlap is the standard deviation calculated from the bootstrapped core habitats. Abbreviations for species are: SN, Atlantic sharpnose; BT, blacktip; FT, finetooth; BH, bonnethead. Abbreviations for life stages are: ADU, adult; JUV, juvenile; YOY, young-of-year; YOY+JUV, young-of-year and juvenile combined; JUV+ADU, juvenile and adult combined.

conditions (Latour *et al.* 2022). In the Mississippi Sound, YOY sharks were caught from May to October and continued to show consistent growth; therefore, it is assumed that there were enough prey resources to sustain their rapid growth rate during this critical life stage. However, since these biotic interactions (e.g. predator avoidance and prey abundance)

were not specifically addressed in this study, a more comprehensive study is needed to better understand how these YOY sharks are selecting their nursery habitat.

Risk of predation, and accordingly the need to exhibit anti-predatory behaviours, is reduced as shark size increases (Grubbs 2010). This, in addition to increased energetic

requirements and forage capacity, may explain the ontogenetic shift in observed habitat use for sharks within nurseries (Grubbs 2010; Matich and Heithaus 2015; Oh *et al.* 2017). We similarly noted ontogenetic shifts in spatial habitat utilisation for Atlantic sharpnose, blacktip and finetooth sharks in the Mississippi Sound. In all cases, younger individuals inhabited more inshore areas, and habitat utilisation shifted offshore with size. This spatial shift was supported by a shift in environmental preferences, primarily changes in salinity and temperature inhabited by subsequent life stages (Fig. 3).

Many shark nurseries are communal (McCandless *et al.* 2007; Kinney *et al.* 2011; Oh *et al.* 2017), and because they are typically limited to sheltered nearshore environments, these habitats subject their inhabitants to heightened competition (Heithaus 2007). Intraspecific habitat partitioning may serve to functionally reduce competition for resources by reducing space (DeAngelis *et al.* 2008; Oh *et al.* 2017), environmental (Platell *et al.* 1998; Ward-Paige *et al.* 2015; Yates *et al.* 2015) and diet overlap (Bethea *et al.* 2004; Papastamatiou *et al.* 2006; Kinney *et al.* 2011). Within the Mississippi Sound, we found a high degree of overlap in habitat use. Notable co-occurring species-life stages included: (a) YOY Atlantic sharpnose, YOY blacktip and YOY and juvenile finetooth sharks; (b) juvenile and adult Atlantic sharpnose, adult finetooth and juvenile blacktip sharks; and (c) adult blacktip and adult and juvenile bonnetheads (Fig. 8). Despite the observed spatial overlap, these species' life stages did exhibit some differences in environmental preferences. For example, despite co-occurring in space (group a), YOY Atlantic sharpnose sharks appeared to prefer warmer temperatures relative to YOY blacktip sharks. Juvenile Atlantic sharpnose sharks inhabited lower dissolved oxygen waters compared to adult Atlantic sharpnose sharks, while adult finetooth sharks exhibited a distinct, relatively lower temperature preference (group b). Further, adult blacktip and adult and juvenile bonnetheads (group c) exhibited clearly distinct dissolved oxygen and temperature preferences, along with slightly different preferred salinity. Contrarily, species that preferred similar environmental conditions, like salinity (juvenile and adult blacktip and adult Atlantic sharpnose sharks) and temperature (adult Atlantic sharpnose shark and YOY blacktip sharks, or adult and juvenile bonnetheads and adult finetooth sharks), were separated in space. These slight environmental and spatial preference distinctions between co-occurring species may support the hypothesis that these coastal shark species partition themselves to not only reduce predation by conspecifics but also to reduce competition.

Since juvenile and adult Atlantic sharpnose, blacktip and finetooth sharks reside in the waters of the Mississippi Sound, it can be difficult to meet the underlying principles of the nursery area theory that states that juvenile and adults of the same species reside in and use different areas (Beck *et al.* 2001; Heupel *et al.* 2007). Further, designation of essential nursery habitat is complicated by shark behaviour wherein individuals may forgo essential habitat for growth in favour

of essential habitat for refuge (Heithaus 2007). Heupel *et al.* (2007) proposed additional criteria for nursery areas, including: (1) juveniles are more common in those areas than in other areas; (2) juveniles have a tendency to remain in or return to such areas for extended periods; and (3) the areas are repeatedly used across years. Our results suggest that the northern portion of the Mississippi Sound is an important region for Atlantic sharpnose, blacktip and finetooth YOY sharks and could be considered vital 'nursery grounds' for this critical life stage of these species. The northern portion of the study area had higher abundances of YOY sharks than surrounding waters, YOY sharks tended to stay within this region throughout most of the year, and it appears that they consistently use this region from one year to the next. Additional field-based tagging studies such as passive acoustic telemetry could be used to additionally test how long these smaller life stages remain in the nursery grounds and whether they return in subsequent years, ultimately verifying that these shallow waters of the Mississippi Sound represent important nursery grounds for these YOY sharks (Heupel *et al.* 2019).

Characterisation of uncertainty is often overlooked in habitat modelling studies, particularly when spatial projections are used. Observation uncertainty can be attributed to many factors and stems from only sampling a portion of the population. By bootstrap resampling observed data, we are explicitly estimating observation uncertainty and propagating that uncertainty through to our results. These uncertainty estimates were presented around our estimates of both environmental (see Fig. S1–S9) and spatial preferences and in the core habitat and overlap among species' life stages within the Mississippi Sound (Fig. 8). Fully characterising the uncertainty in these analyses can help us to understand how variable the core habitat area is and how confident we are in our estimates of spatial overlap. For example, although our original model identified core habitat overlap between YOY sharpnose and YOY blacktip sharks, this overlap was not regularly identified with our resampled datasets. Out of the ~800 bootstraps that converged, less than 300 of them resulted in at least 50% overlap of core habitat between YOY blacktip and YOY Atlantic sharpnose sharks, meaning we are less confident in our estimates of overlap between these two species' life stages. By contrast, at least 50% overlap of core habitat between YOY Atlantic sharpnose and YOY and juvenile finetooth sharks occurred in over 500 bootstraps, meaning we are more confident in our estimates of overlap between these two species' life stages, as estimated in the original model. With this study, we present an approach to calculate uncertainty in observed habitat, and use this uncertainty to inform inferences on habitat partitioning.

In addition to uncertainty, other limitations exist with respect to the habitat models developed in this study. For example, we unfortunately had to combine life stages for finetooth (YOY and juvenile) and bonnethead (juvenile and adult life stages) because of low sample sizes. By combining

species' life stages, our inferences about habitat preference and spatial distribution are confounded across ontogeny for these species. It is usually beneficial to generate habitat models using data collected over multiple years because it increases the chance the model captures the variability in the system, while bolstering sample size. Although this is outside the scope of this study, these models could also be used to examine trends over time as conditions change (e.g. as a result of climate change; Turner *et al.* 2017).

We also expect that as climate change continues to alter ocean conditions, the spatial distribution, habitat use and ecosystem dynamics are likely to change in the future. Water temperatures are expected to continue to increase throughout the Northwest Atlantic, including in the northern Gulf of Mexico. The potential increase in the severity and frequency of storms are expected to increase streamflow and nutrient input in coastal habitats like the Mississippi Sound (Rabalais and Turner 2019). The combination of warmer and fresh nutrient-rich waters leads to water column stratification, algal blooms and the increase in the severity and duration of hypoxia along the bottom of the ocean in those areas (Rabalais *et al.* 2009; Rabalais and Turner 2019). In fact, a regular stratified anoxic zone has started to occur in the Mississippi Sound annually in the summer (Jill Hendon pers. comm.). Currently, YOY and juvenile sharks in coastal habitats rely on these environmental gradients, as seen in this study, to avoid predators and find prey. With conditions predicted to change, younger sharks may be forced into less suitable habitat to find food. The ability to withstand more extreme conditions is driven by a species' physiological tolerance to those conditions. For example, the distribution of juvenile sandbar shark nursery habitat in Chesapeake Bay is shaped by the shark's temperature and hypoxia thresholds (Crear *et al.* 2019, 2020). Based on these relationships it was predicted that juvenile sandbar shark nursery habitat would decrease along the bottom of Chesapeake Bay in the future (Crear *et al.* 2020). Environmental change can also lead to species expanding into new areas. Juvenile bull sharks, for example, have expanded their nursery habitat into Pamlico Sound, a trend strongly related to early summer temperatures (Bangley *et al.* 2018). Developing the current habitat distribution for multiple species' life stages within Mississippi Sound can be used as a baseline and compared to actual or predicted future distributions.

Shark nursery habitats are essential for the survival and persistence of coastal shark species. Particularly as coastal shark species populations improve along the US (Peterson *et al.* 2017b), it is important to understand how the environment is affecting habitat use during a critical life stage. This study demonstrates clear habitat partitioning among multiple shark species across their life stages, from both an environmental preference and spatial perspective. We hope this study can help further refine essential fish habitat for these coastal shark species in the Mississippi Sound and provide a

framework other studies can use to understand habitat partitioning in other regions.

Supplementary material

Supplementary material is available [online](#).

References

- Aitchison J (1955) On the distribution of a positive random variable having a discrete probability mass at the origin. *Journal of the American Statistical Association* 50(271), 901–908. doi:10.2307/2281175
- Bangley CW, Paramore L, Shiffman DS, Rulifson RA (2018) Increased abundance and nursery habitat use of the bull shark (*Carcharhinus leucas*) in response to a changing environment in a warm-temperate estuary. *Scientific Reports* 8(1), 6018. doi:10.1038/s41598-018-24510-z
- Bangley CW, Curtis TH, Secor DH, Latour RJ, Ogburn MB (2020) Identifying important juvenile dusky shark habitat in the Northwest Atlantic ocean using acoustic telemetry and spatial modeling. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 12(5), 348–363. doi:10.1002/mcf2.10120
- Baremore IE, Passerotti MS (2013) Reproduction of the blacktip shark in the Gulf of Mexico. *Marine and Coastal Fisheries* 5(1), 127–138. doi:10.1080/19425120.2012.758204
- Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, *et al.* (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. *Bioscience* 51(8), 633–641. doi:10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2
- Bethea DM, Buckel JA, Carlson JK (2004) Foraging ecology of the early life stages of four sympatric shark species. *Marine Ecology Progress Series* 268, 245–264. doi:10.3354/meps268245
- Bethea DM, Ajemian MJ, Carlson JK, Hoffmayer ER, Imhoff JL, Grubbs RD, Peterson CT, Burgess GH (2015) Distribution and community structure of coastal sharks in the northeastern Gulf of Mexico. *Environmental Biology of Fishes* 98(5), 1233–1254. doi:10.1007/s10641-014-0355-3
- Brodie SJ, Thorson JT, Carroll G, Hazen EL, Bograd S, Haltuch MA, Holsman KK, Kotwicki S, Samhouri JF, Willis-Norton E, *et al.* (2020) Trade-offs in covariate selection for species distribution models: a methodological comparison. *Ecography* 43, 11–24. doi:10.1111/ecog.04707
- Chin A, Kyne PM, Walker TI, McAuley RB (2010) An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. *Global Change Biology* 16(7), 1936–1953. doi:10.1111/j.1365-2486.2009.02128.x
- Cortés E (2008) Comparative life history and demography of pelagic sharks. In 'Sharks of the open ocean: biology, fisheries and conservation'. (Eds MD Camhi, EK Pikitch, EA Babcock) pp. 309–322. (Blackwell Publishing Ltd)
- Crear DP, Brill RW, Bushnell PG, Latour RJ, Schwieterman GD, Steffen RM, Weng KC (2019) The impacts of warming and hypoxia on the performance of an obligate ram ventilator. *Conservation Physiology* 7(1), cozo26. doi:10.1093/conphys/cozo26
- Crear DP, Latour RJ, Friedrichs MAM, St-Laurent P, Weng KC (2020) Sensitivity of a shark nursery habitat to a changing climate. *Marine Ecology Progress Series* 652, 123–136. doi:10.3354/meps13483
- Crear DP, Curtis TH, Durkee SJ, Carlson JK (2021) Highly migratory species predictive spatial modeling (PRiSM): an analytical framework for assessing the performance of spatial fisheries management. *Marine Biology* 168(10), 148. doi:10.1007/s00227-021-03951-7
- DeAngelis BM, McCandless CT, Kohler NE, Recksiek CW, Skomal GB (2008) First characterization of shark nursery habitat in the United

- States Virgin Islands: evidence of habitat partitioning by two shark species. *Marine Ecology Progress Series* **358**, 257–271. doi:10.3354/meps07308
- Dhellemmes F, Smukall MJ, Guttridge TL, Krause J, Hussey NE (2021) Predator abundance drives the association between exploratory personality and foraging habitat risk in a wild marine meso-predator. *Functional Ecology* **35**(9), 1972–1984. doi:10.1111/1365-2435.13874
- Dulvy NK, Pacoureau N, Rigby CL, Pollom RA, Jabado RW, Ebert DA, Finucci B, Pollock CM, Cheok J, Derrick DH, et al. (2021) Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology* **31**(21), 4773–4787.e8. doi:10.1016/j.cub.2021.08.062
- Duncan KM, Holland KN (2006) Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. *Marine Ecology Progress Series* **312**, 211–221. doi:10.3354/meps312211
- Efron B, Tibshirani RJ (1993) 'An introduction to the bootstrap.' (CRC Press: New York, NY, USA)
- Froeschke J, Stunz GW, Wildhaber ML (2010) Environmental influences on the occurrence of coastal sharks in estuarine waters. *Marine Ecology Progress Series* **407**, 279–292. doi:10.3354/meps08546
- Gibson-Reinemer DK, Ickes BS, Chick JH (2017) Development and assessment of a new method for combining catch per unit effort data from different fish sampling gears: multigear mean standardization (MGMS). *Canadian Journal of Fisheries and Aquatic Sciences* **74**(1), 8–14. doi:10.1139/cjfas-2016-0003
- Grubbs RD (2010) Ontogenetic shifts in movements and habitat use. In 'Sharks and their relatives II: biodiversity, adaptive physiology, and conservation'. (Eds JC Carrier, JA Musick, MR Heithaus) pp. 319–350. (CRC Press: Boca Raton, FL, USA)
- Gunter G (1963) The fertile fisheries crescent. *Journal of the Mississippi Academy of Science* **9**, 286–290.
- Guttridge TL, Gruber SH, Franks BR, Kessel ST, Gledhill KS, Uphill J, Krause J, Sims DW (2012) Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Marine Ecology Progress Series* **445**, 279–291. doi:10.3354/meps09423
- Hamilton BR, Shipley ON, Grubbs RD (2022) Multi-channel feeding by migratory sharks in a fluvial-dominated estuary. *Estuarine, Coastal and Shelf Science* **275**, 107977. doi:10.1016/j.ecss.2022.107977
- Hartog JR, Hobday AJ, Matear R, Feng M (2011) Habitat overlap between southern bluefin tuna and yellowfin tuna in the east coast longline fishery – implications for present and future spatial management. *Deep-Sea Research – II. Topical Studies in Oceanography* **58**(5), 746–752. doi:10.1016/j.dsr2.2010.06.005
- Hastie TJ, Tibshirani RJ (1990) 'Generalized additive models.' (CRC Press)
- Hazen EL, Jorgensen S, Rykaczewski RR, Bograd SJ, Foley DG, Jonsen ID, Shaffer SA, Dunne JP, Costa DP, Crowder LB, et al. (2013) Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change* **3**(3), 234–238. doi:10.1038/nclimate1686
- Hazen EL, Scales KL, Maxwell SM, Briscoe DK, Welch H, Bograd SJ, Bailey H, Benson SR, Eguchi T, Dewar H, et al. (2018) A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. *Science Advances* **4**(5), eaar3001. doi:10.1126/sciadv.aar3001
- Heithaus MR (2007) Nursery areas as essential shark habitats: a theoretical perspective. In 'Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States, Proceedings of the 50th American Fisheries Society Symposium', 19 August 2002, Baltimore, MD, USA. (Eds CT McCandless, NE Kohler, HL Pratt Jr) pp. 3–13. (American Fisheries Society: Bethesda, MD, USA) doi:10.47886/9781888569810.ch1
- Heithaus MR, Frid A, Vaudo JJ, Worm B, Wirsing AJ (2010) Unraveling the ecological importance of elasmobranchs. In 'Sharks and their relatives II'. (Eds JC Carrier, JA Musick, MR Heithaus) pp. 611–637. (CRC Press)
- Heithaus MR, Vaudo JJ, Kreicker S, Layman CA, Krützen M, Burkholder DA, Gastrich K, Bessey C, Sarabia R, Cameron K, et al. (2013) Apparent resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem. *Marine Ecology Progress Series* **481**, 225–237. doi:10.3354/meps10235
- Hendon JM, Hoffmayer ER, Driggers WB III (2013) First record of a nurse shark, *Ginglymostoma cirratum*, within the Mississippi sound. *Gulf and Caribbean Research* **25**(1), 137–139. doi:10.18785/gcr.2501.13
- Heupel MR, Hueter RE (2002) Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. *Marine and Freshwater Research* **53**(2), 543–550. doi:10.1071/MF01132
- Heupel MR, Simpfendorfer CA (2011) Estuarine nursery areas provide a low-mortality environment for young bull sharks *Carcharhinus leucas*. *Marine Ecology Progress Series* **433**, 237–244. doi:10.3354/meps09191
- Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series* **337**, 287–297. doi:10.3354/meps337287
- Heupel MR, Kanno S, Martins APB, Simpfendorfer CA (2019) Advances in understanding the roles and benefits of nursery areas for elasmobranch populations. *Marine and Freshwater Research* **70**(7), 897–907. doi:10.1071/MF18081
- Higgs JM, Hoffmayer ER, Sulikowski JA, Driggers WB, Stiller DA, Hendon JM (2020) Reproductive biology of the finetooth shark (*Carcharhinus isodon*) in the northern Gulf of Mexico, with evidence of both annual and biennial reproduction. *Marine and Freshwater Research* **72**(5), 693–708. doi:10.1071/MF20120
- Hoffmayer ER, Driggers WB III, Jones LM, Hendon JM, Sulikowski JA (2013) Variability in the reproductive biology of the Atlantic sharpnose shark in the Gulf of Mexico. *Marine and Coastal Fisheries* **5**(1), 139–151. doi:10.1080/19425120.2013.783518
- Hueter R, Tyminski J (2007) Species-specific distribution and habitat characteristics of shark nurseries in Gulf of Mexico waters off peninsular Florida and Texas. In 'Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States, Proceedings of the 50th American Fisheries Society Symposium', 19 August 2002, Baltimore, MD, USA. (Eds CT McCandless, NE Kohler, HL Pratt Jr) pp. 193–223. (American Fisheries Society: Bethesda, MD, USA) doi:10.47886/9781888569810.ch13
- Kinney MJ, Hussey NE, Fisk AT, Tobin AJ, Simpfendorfer CA (2011) Communal or competitive? Stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. *Marine Ecology Progress Series* **439**, 263–276. doi:10.3354/meps09327
- Kneebone J, Chisholm J, Skomal GB (2012) Seasonal residency, habitat use, and site fidelity of juvenile sand tiger sharks *Carcharias taurus* in a Massachusetts estuary. *Marine Ecology Progress Series* **471**, 165–181. doi:10.3354/meps09989
- Knip DM, Heupel MR, Simpfendorfer CA (2010) Sharks in nearshore environments: models, importance, and consequences. *Marine Ecology Progress Series* **402**, 1–11. doi:10.3354/meps08498
- Latour RJ, Gartland J, Peterson CD (2022) Ontogenetic niche structure and partitioning of immature sandbar sharks within the Chesapeake Bay nursery. *Marine Biology* **169**(6), 76. doi:10.1007/s00227-022-04066-3
- Lombardi-Carlson LA, Cortés E, Parsons GR, Manire CA (2003) Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo* (Carcharhiniformes: Sphyrnidae) from the eastern Gulf of Mexico. *Marine and Freshwater Research* **54**(7), 875–883. doi:10.1071/MF03023
- Lowe CG (2002) Bioenergetics of free-ranging juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in Kane'ohe Bay, O'ahu, HI. *Journal of Experimental Marine Biology and Ecology* **278**(2), 141–156. doi:10.1016/S0022-0981(02)00331-3
- Lynch PD, Nye JA, Hare JA, Stock CA, Alexander MA, Scott JD, Curti KL, Drew K (2015) Projected ocean warming creates a conservation challenge for river herring populations. *ICES Journal of Marine Science* **72**(2), 374–387. doi:10.1093/icesjms/fsu134
- Match P, Heithaus MR (2015) Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). *Oecologia* **178**(2), 347–359. doi:10.1007/s00442-015-3253-2
- McCandless C, Pratt H, Kohler N, Merson, Recksiek C (2007) Distribution, localized abundance, movements, and migrations of juvenile sandbar sharks tagged in Delaware Bay. In 'Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States, Proceedings of the 50th American Fisheries Society Symposium', 19 August 2002, Baltimore, MD, USA. (Eds CT McCandless, NE Kohler, HL Pratt Jr)

- p. 45. (American Fisheries Society: Bethesda, MD, USA). doi:10.47886/9781888569810.ch4
- Norton SL, Wiley TR, Carlson JK, Frick AL, Poulakis GR, Simpfendorfer CA (2012) Designating critical habitat for juvenile endangered smalltooth sawfish in the United States. *Marine and Coastal Fisheries* 4(1), 473–480. doi:10.1080/19425120.2012.676606
- Oh BZL, Sequeira AMM, Meekan MG, Ruppert JLW, Meeuwig JJ (2017) Predicting occurrence of juvenile shark habitat to improve conservation planning. *Conservation Biology* 31(3), 635–645. doi:10.1111/cobi.12868
- Pacoureau N, Rigby CL, Kyne PM, Sherley RB, Winker H, Carlson JK, Fordham SV, Barreto R, Fernando D, Francis MP, et al. (2021) Half a century of global decline in oceanic sharks and rays. *Nature* 589(7843), 567–571. doi:10.1038/s41586-020-03173-9
- Papastamatiou YP, Wetherbee BM, Lowe CG, Crow GL (2006) Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. *Marine Ecology Progress Series* 320, 239–251. doi:10.3354/meps320239
- Papastamatiou YP, Caselle JE, Friedlander AM, Lowe CG (2009) Distribution, size frequency, and sex ratios of blacktip reef sharks *Carcharhinus melanopterus* at palmyra atoll: a predator-dominated ecosystem. *Journal of Fish Biology* 75(3), 647–654. doi:10.1111/j.1095-8649.2009.02329.x
- Parsons GR, Hoffmayer ER (2005) Seasonal changes in the distribution and relative abundance of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the North Central Gulf of Mexico. *Copeia* 2005(4), 914–920. doi:10.1643/0045-8511(2005)005[0914:SCITDA]2.0.CO;2
- Parsons GR, Hoffmayer ER (2007) Identification and characterization of shark nursery grounds along the Mississippi and Alabama Gulf Coasts. In 'Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States, Proceedings of the 50th American Fisheries Society Symposium', 19 August 2002, Baltimore, MD, USA. (Eds CT McCandless, NE Kohler, HL Pratt Jr) pp. 301–316. (American Fisheries Society: Bethesda, MD, USA) doi:10.47886/9781888569810.ch19
- Parsons GR, Hoffmayer ER, Hendon JM, Bet-Sayad WV (2008) A review of shark reproductive ecology: life history and evolutionary implications. In 'Fish reproduction'. (MJ Rocha, A Arukwe, BG Kapoor) pp. 435–469. (Taylor and Francis)
- Peterson CD, Parsons KT, Bethea DM, Driggers WB III, Latour RJ (2017a) Community interactions and density dependence in the southeast United States coastal shark complex. *Marine Ecology Progress Series* 579, 81–96. doi:10.3354/meps12288
- Peterson CD, Belcher CN, Bethea DM, Driggers WB III, Frazier BS, Latour RJ (2017b) Preliminary recovery of coastal sharks in the south-east United States. *Fish and Fisheries* 18, 845–859. doi:10.1111/faf.12210
- Platell ME, Potter IC, Clarke KR (1998) Resource partitioning by four species of elasmobranchs (Batoidea: Urolophidae) in coastal waters of temperate Australia. *Marine Biology* 131(4), 719–734. doi:10.1007/s002270050363
- Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86(2), 501–509. doi:10.1890/04-0719
- Rabalais NN, Turner RE (2019) Gulf of Mexico hypoxia: past, present, and future. *Limnology and Oceanography Bulletin* 28(4), 117–124. doi:10.1002/lob.10351
- Rabalais NN, Turner RE, Díaz RJ, Justić D (2009) Global change and eutrophication of coastal waters. *ICES Journal of Marine Science* 66(7), 1528–1537. doi:10.1093/icesjms/bsp047
- Searle SR, Speed FM, Milliken GA (1980) Population marginal means in the linear model: an alternative to least squares means. *The American Statistician* 34(4), 216–221. doi:10.2307/2684063
- Sibly RM, Kodric-Brown A, Luna SM, Brown JH (2018) The shark–tuna dichotomy: why tuna lay tiny eggs but sharks produce large offspring. *Royal Society Open Science* 5(8), 180453. doi:10.1098/rsos.180453
- Simpfendorfer CA, Milward NE (1993) Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. *Environmental Biology of Fishes* 37(4), 337–345. doi:10.1007/BF00005200
- Simpfendorfer CA, Freitas GG, Wiley TR, Heupel MR (2005) Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a Southwest Florida estuary. *Estuaries* 28(1), 78–85. doi:10.1007/BF02732755
- Stevens J, Bonfil R, Dulvy NK, Walker P (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57(3), 476–494. doi:10.1006/jmsc.2000.0724
- Tickler DM, Letessier TB, Koldewey HJ, Meeuwig JJ (2017) Drivers of abundance and spatial distribution of reef-associated sharks in an isolated atoll reef system. *PLoS ONE* 12(5), e0177374. doi:10.1371/journal.pone.0177374
- Turner RE, Rabalais NN, Justić D (2017) Trends in summer bottom-water temperatures on the northern Gulf of Mexico continental shelf from 1985 to 2015. *PLoS ONE* 12(9), e0184350. doi:10.1371/journal.pone.0184350
- Ward-Paige CA, Britten GL, Bethea DM, Carlson JK (2015) Characterizing and predicting essential habitat features for juvenile coastal sharks. *Marine Ecology* 36(3), 419–431. doi:10.1111/maec.12151
- Wetherbee BM, Gruber SH, Rosa RS (2007) Movement patterns of juvenile lemon sharks *Negaprion brevirostris* within Atol das Rocas, Brazil: a nursery characterized by tidal extremes. *Marine Ecology Progress Series* 343, 283–293. doi:10.3354/meps06920
- White TD, Ferretti F, Kroodsmas DA, Hazen EL, Carlisle AB, Scales KL, Bograd SJ, Block BA (2019) Predicted hotspots of overlap between highly migratory fishes and industrial fishing fleets in the northeast Pacific. *Science Advances* 5(3), eaau3761. doi:10.1126/sciadv.aau3761
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society Series B: Statistical Methodology* 73(1), 3–36. doi:10.1111/j.1467-9868.2010.00749.x
- Wood SN (2017) 'Generalized additive models: an introduction with R', 2nd edn. (CRC Press: Boca Raton, FL, USA)
- Yates PM, Heupel MR, Tobin AJ, Simpfendorfer CA (2015) Spatio-temporal occurrence patterns of young sharks in tropical coastal waters. *Estuaries and Coasts* 38(6), 2019–2030. doi:10.1007/s12237-015-9952-4

Data availability. Data are available upon request by Gulf States Marine Fisheries Commission for Southeast Area Monitoring and Assessment Program data and Centers for Fisheries Research and Development for other data collection programs.

Conflicts of interest. The authors declare that they have no conflicts of interest.

Declaration of funding. Funding by this project was provided by the National Marine Fisheries Service-Gulf of Mexico Shark Pupping and Nursery Study, US Fish and Wildlife Service, and the Sport Fish Restoration with Mississippi Department of Marine Resources as a pass through, Southeast Area Monitoring and Assessment Program.

Acknowledgements. We thank the staff and students from the Gulf Coast Research Lab (GCRL) at the University of Southern Mississippi for all their help in collecting shark data from the longline, handline and gill-net surveys over the years, including William Dempster, Gary Gray, Jason Tilley, Christopher Butler, Matthew Donaldson, Monty Simmons, Justin Lewis, Sarah Ashworth, Patrick Graham, Anna Millender and Angie Hoover. We appreciate the preliminary review by John Carlson. We also thank two anonymous reviewers for helping to improve the manuscript.

Author affiliations

^AECS Federal, in Support of National Marine Fisheries Service, Atlantic Highly Migratory Species Management Division, Silver Spring, MD, USA.

^BNational Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort, NC, USA.

^CThe University of Southern Mississippi, Center for Fisheries Research and Development, Gulf Coast Research Laboratory, Ocean Springs, MS, USA.

^DNational Marine Fisheries Service, Southeast Fisheries Science Center, Pascagoula, MS, USA.

^EPresent address: Inter-American Tropical Tuna Commission, La Jolla, CA, USA.