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The Dynamic Nature of Nearshore Shark Nurseries in the Northern Gulf of Mexico

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ABSTRACT

Aim: Some habitats serve particularly important functions for wildlife. Identifying and appropriately managing these 'essential habitats' is critical, especially for wildlife that have faced severe population declines like sharks. Nursery habitats aid in the survival and development of juvenile sharks, which until recently were not formally identified or managed throughout most regions. Managing shark nurseries was in part challenging because there was no standardized quantitative method to delineate these essential habitats prior to the seminal paper written by Michelle Heupel and colleagues in 2007. Management in some regions now includes the protection of shark nurseries; however, changes in nursery dynamics in response to environmental change and human impacts are unclear. Here, we used long-term monitoring data to identify bull shark (*Carcharhinus leucas*) and blacktip shark (*C. limbatus*) nurseries and assess how they have changed over time.

Location: Alabama coast and Texas coast, USA.

Time Period: 1982–2023.

Taxa: Bull shark, blacktip shark.

Methods: Shark catch records (catch per unit effort) from long-term gillnet monitoring were assessed with general linear models and generalized linear models to determine (1) if shark nurseries exist in the Northern Gulf of Mexico, and (2) if and how they have changed over the study period using the shark nursery criteria established in 2007.

Results: Northern Gulf of Mexico nurseries first (re)emerged in the early 2000s on the Texas coast for bull sharks, followed by a relatively rapid expansion along the Texas and Alabama coast. Fewer nurseries were identified for blacktip sharks, which (re) emerged more recently starting in the 2010s.

Main Conclusions: Improved management has led to the re-establishment of shark nurseries. We expect that changes in these essential habitats will continue as environmental conditions and human impacts shape coastal ecosystems and the dynamics of nurseries within their waters. The delineation, management and reassessment of nurseries will therefore be imperative moving forward as shark populations continue to recover from historic and persistent overfishing and habitat degradation. Predicting where nurseries will (re)emerge in response to improved management and habitat suitability will also be essential to achieve conservation goals.

1 | Introduction

The value of resources varies within and across ecosystems. For example, prey are not equally selected by predators (Heithaus 2004), mate choice leads to intraspecific variation in fitness (Jennions and Petrie 1997), and habitats are not homogeneous in their functions as foraging grounds, migratory routes and refuges (MacArthur and Wilson 1967). Assessing these differences is a hallmark of ethology, and as climate change and human impacts continue to alter ecosystems (Blois et al. 2013; McCauley et al. 2015; Braun et al. 2023), understanding the value of resources for wildlife populations is paramount for making decisions tied to conservation and management. Among these priorities, predicting shifts in the geographic ranges of species provides a foundation for understanding how ecosystems will change in response to future conditions (Lenoir and Svenning 2015).

Endemic and physiologically sensitive species are at great risk because of their narrow niches, and have deservedly received considerable attention as it relates to environmental and ecological disturbance (e.g., Riddell et al. 2018; Chen et al. 2025). Comparatively, shifts among phenotypically flexible species, which can adjust to changing environments by altering their behaviour and inhabiting more suitable areas is also consequential, because of the changes their presence, absence and densities can have on ecological stability (Miner et al. 2005). For example, Hawaiian monk seals (*Neomonachus schauinslandi*) change their feeding tactics in response to changing environments (Kienle et al. 2019, 2020), while leopard seals (*Hydrurga leptonyx*) alter their dive behaviour based on prey-selection (Kienle et al. 2022). This is particularly relevant for predators, because of the roles they play in their respective ecosystems, and their historic declines across many areas (Dedman et al. 2024).

Human-induced changes in landscapes and seascapes in the 20th century were in part attributed to the systematic removal of predators by humans, which has had cascading effects on ecosystem resilience (Estes et al. 2011). The consequences of predator mismanagement are still apparent today (McCauley et al. 2015), but the recovery of predators has been a priority in some regions in recent years, with some success stories (Lotze et al. 2011). Sharks are among the predators that were systematically removed from many ecosystems at a global scale (Dulvy et al. 2021), and still are in many countries (Dulvy et al. 2024). But management has led to increased shark densities in some regions (Pacoureau et al. 2023). While the value of healthy predator populations and the consequences of their declines are unequivocal (Dedman et al. 2024), the ecological outcomes of the recovery and re-establishment of large-bodied predators are, however, less clear, including the effects this will have on human actions (Carlson et al. 2019).

The implications of shifting geographic ranges of predator populations attributed to changes in habitat suitability are similarly uncertain (e.g., Sequeira et al. 2014; Hammerschlag et al. 2022; Bowlby et al. 2023). As a group, sharks and other elasmobranchs are wide-ranging in part due to their geographically broad evolutionary history across ocean basins (Musick et al. 2004). However, the range of many species is limited because they are ectothermic and the temperatures of polar and some temperate waters are unsuitable (Angilletta Jr et al. 2002). As temperatures rise, temperate and subtropical shark populations are predicted to extend to higher latitudes as the waters they can thermally tolerate shift or expand (Braun et al. 2023). For example, blacktip sharks (*Carcharhinus limbatus*) and tiger sharks (*Galeocerdo cuvier*) in the Northwestern Atlantic Ocean have exhibited northward shifts in their distribution in recent decades, which have been attributed to warming waters (Hammerschlag et al. 2022; Bowers and Kajiura 2023).

The locations where sharks establish juvenile habitats have also recently expanded to higher latitudes for some species (e.g., Bangley et al. 2018; Tanaka et al. 2021; Mullins et al. 2024). Quality nursery habitat is essential for the successful recruitment of many sharks, as nursery habitat ideally provides refuge from predation and abundant food resulting in higher survival rates (McCandless, Pratt, et al. 2007). As such, assessing the trajectory of habitat quality and availability as it relates to nursery dynamics is of great value for understanding what shark populations will look like in the future, and how they fit into 'new' ecological communities (Crear et al. 2020; Mullins et al. 2024). Improved management and warming waters are expected to lead to the emergence or re-emergence of shark nurseries in many areas, because of higher parturition rates and densities of juvenile sharks, as well as more habitats that meet physiological requirements (e.g., Froeschke et al. 2013; Bangley et al. 2018; Udovičić et al. 2018; Mullins et al. 2024). However, there is uncertainty in the frequency and speed at which this will occur, and if species will respond similarly within and across ecosystems.

Shark nurseries have been of interest for generations of scientists, first identified based on the occurrence of juveniles within an area (Springer 1967; Bass 1978; Branstetter 1990; Castro 1993), then their contributions to adult populations (Beck et al. 2001; Dahlgren et al. 2006). There were, however, no true quantitative assessments of shark nurseries until Heupel et al. (2007) proposed criteria requiring the assessments of juvenile shark density, site fidelity and residency, which have since been cited extensively, but less frequently applied (Heupel et al. 2019). Our understanding of shark nurseries is thus limited, particularly how dynamic they are in response to environmental, ecological and anthropogenic change. Here, we assess spatiotemporal variability in the nursery status of two different regions in the Northern Gulf of Mexico—the coastal waters of Alabama (ca. 975 km of shoreline) and Texas, USA (ca. 5400 km of shoreline). Using the criteria established by Heupel et al. (2007), we identify shark nurseries based on long-term monitoring data (20–40 years), assess how these nurseries have functionally changed through time, and make predictions concerning nursery dynamism as climate change and human disturbance persist.

2 | Methods

2.1 | Study Systems & Species

2.1.1 | Alabama Coast

The nearshore waters of Alabama support a diverse assemblage of sharks, including bull sharks (*Carcharhinus leucas*; Drymon et al. 2010), which have increased in abundance in

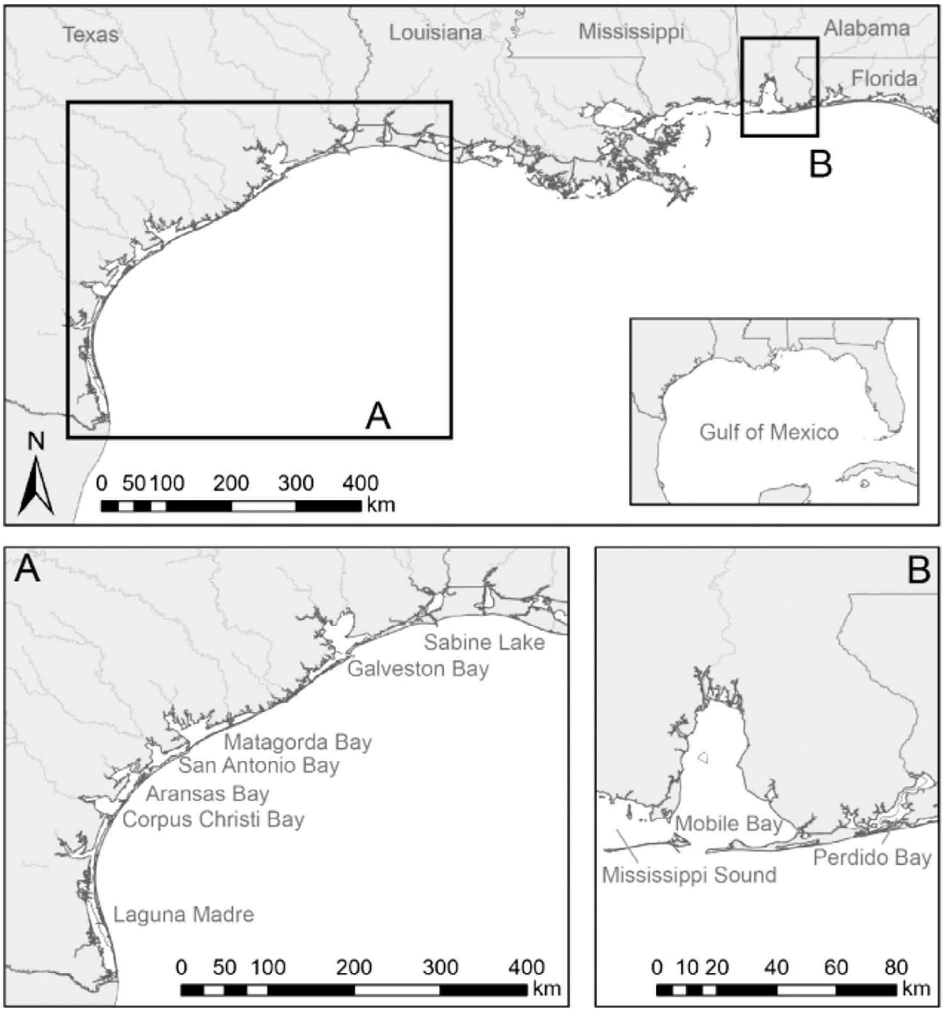

FIGURE 1 | Study regions for nursery assessment along the (A) Texas coast and (B) Alabama coast.

recent years (Mullins et al. 2024). To assess the Alabama coast as a bull shark nursery, the region was divided into four subregions based on differences in hydrology and environmental conditions: Upper Mobile Bay, Lower Mobile Bay, Perdido Bay and Mississippi Sound (Figure 1). Mobile Bay comprises much of the Alabama coastline, with freshwater inflow from the Mobile-Tensaw River creating a gradient of more thermally dynamic, freshwater habitats near the river mouth to more stable, saline habitats at the Main Pass (Orlando and Klein 1989). Mobile Bay was divided into two distinct units due to the highly stratified north–south gradient that occurs, especially in rainy seasons, where the northern portion of the bay essentially functions as an extension of the river mouth (Mullins et al. 2024). Sampling strata were designed by the Alabama Department of Conservation and Natural Resources Marine Resource Division (ADNR-MRD) to reflect the distinct hydrological zones of this highly riverine-influenced system. East of Mobile Bay, Perdido Bay extends from Southeastern Alabama to Northwestern Florida, with freshwater input from the Perdido River and tidal inflow at Perdido Pass (Croteau et al. 2023). West of Mobile Bay, the eastern Mississippi Sound is influenced by freshwater input from the Mobile-Tensaw Rivers; however, it is generally higher in salinity than Mobile Bay (Cambazoglu et al. 2017, 2024). For the scope of this study, references hereafter to Perdido Bay and Mississippi Sound will only consider habitat in Alabama waters.

2.1.2 | Texas Coast

Juvenile bull sharks and juvenile blacktip sharks inhabit estuaries along the Texas coast (Froeschke, Stunz, and Wildhaber 2010). These ecosystems are largely isolated from the Gulf of Mexico by seven barrier islands and vary in freshwater and tidal inflow that leads to hydrodynamic variability within and among estuaries (Longley 1994). In Texas, as in many other regions, bull sharks exhibit an ontogenetic shift from low to high salinity waters during their first few years (Matich, Nowicki, et al. 2020), with blacktip sharks predominantly found in more saline habitats (Plumlee et al. 2018). Two estuaries—Matagorda Bay and San Antonio Bay—have previously been classified as bull shark nurseries based on the criteria of Heupel et al. (2007), with others projected to serve this role after the most recent coastwide assessment based on trends in shark abundance (Froeschke, Stunz, Sterba-Boatwright, and Wildhaber 2010). Matagorda Bay is the only estuary that has been identified as a blacktip shark nursery based on the criteria of Heupel et al. (2007), however, areas within Galveston Bay, Matagorda Bay, San Antonio Bay, Corpus Christi Bay and Laguna Madre have been classified as blacktip shark nursery habitat (Matich et al. 2022). Seven estuaries along the Texas coast were included for consideration as potential shark nurseries for this study (Figure 1).

2.2 | Data Collection

2.2.1 | Alabama Coast

Data from the ADNR-MRD gillnet sampling program were analysed from 2004 to 2023. Large and small gillnets were deployed randomly within sampling areas perpendicular or parallel to the shore for *ca*. 1 h (see Mullins et al. 2024 for details). There was no significant difference in selectivity between different sized or oriented nets with respect to juvenile bull shark relative abundance, thus data were pooled (Mullins et al. 2024). Gillnet sampling was conducted year-round, and monthly effort ranged from 8 to 13 nets deployed for a total of 240 nets per year. Captured individuals were identified, counted and measured. Data included in analyses encompassed March–October when sharks were present in the study system (spring: Mar–May, summer: Jun–Aug, fall: Sep–Oct; Drymon et al. 2020). Data were filtered for young-of-the-year (YOY; age 0) bull sharks, identified as sharks with fork lengths (FL) < 84.4 cm according to Neer et al. (2005).

2.2.2 | Texas Coast

Data were obtained from standardized gillnet sampling conducted by Texas Parks and Wildlife Department Coastal Fisheries Division from 1982 to 2021. Annual sampling consisted of 45 gillnets set concurrently in each estuary in each 10-week spring (Apr–Jun) and fall (Sep–Nov) season (90 total gillnets per year per estuary), with the exception of Spring 2020 due to COVID-19. Monofilament gillnets were set overnight perpendicular to shore (see Froeschke, Stunz, and Wildhaber 2010 for details). All organisms captured were identified, counted and measured. Bull sharks and blacktip sharks were classified as YOY following the framework of Matich et al. (2022). YOY bull sharks were < 86.0 cm total length (TL) in spring and < 101.1 cm TL in fall, and YOY blacktip sharks were < 70.6 cm TL in spring and < 91.6 cm TL in fall, which conservatively fit age-growth studies for the region (Branstetter and Stiles 1987; Natanson et al. 2014; Deacy and Moncrief-Cox 2019).

2.3 | Data Analysis

Following the framework developed by Heupel et al. (2007), there are three criteria that define a 'shark nursery area'. (1) Sharks are more commonly encountered in the area than in other areas, i.e., density in the area is greater than the mean density over all areas. (2) Sharks have a tendency to remain or return for extended periods (weeks or months). (3) The area or habitat is repeatedly used across years. To test this framework, we calculated the relative abundance/density of YOY sharks quantified as catch per unit effort (CPUE) by calculating the number of YOY sharks caught per standardized sampling event for each region (i.e., Alabama, Texas). Data were compared among ecosystems within regions (not across regions), therefore differences in gear selectivity or effort did not impact interpretation of results. Monthly, seasonal, and annual CPUE was calculated for each ecosystem (Upper Mobile Bay, Lower Mobile Bay, Perdido Bay and Mississippi Sound for Alabama Coast; Sabine Lake, Galveston Bay, Matagorda Bay, San Antonio Bay, Aransas Bay, Corpus Christi Bay and Laguna Madre for Texas coast). Analysis of variance (ANOVA) or Kruskal-Wallis tests (if ANOVA assumptions were violated) were used to quantify differences in annual CPUE among ecosystems within each region. Post hoc Tukey's Test (ANOVA) or Dunn's Test (Kruskal-Wallis test) were then used to identify ecosystems with significantly more YOY sharks within each region, thereby meeting Criterion 1 ('sharks are more commonly encountered in the area than other areas'; Heupel et al. 2007). Criterion 1 was tested for the entire study duration for each region (Alabama, 2004–2023; Texas, 1982–2021), as well as 5-year periods representing reasonable minimum time-frames to measure population-level trends in bull sharks and blacktip sharks (2004–2008, 2009–2013, 2014–2018 and 2019–2023 for Alabama coast; 1982–1986, 1987–1991, 1992–1996, 1997–2001, 2002–2006, 2007–2011, 2012–2016, 2017–2021 for Texas coast).

Criterion 1 can be interpreted in a minimum of two ways based on Heupel et al. (2007): (1) 'density in the area is greater than the mean density over all the areas' requires sampling areas to have a significantly higher CPUE than the mean of the entire region, and/or (2) density in one area must be greater than the density in another area based on pairwise comparisons. Considering studies employing Heupel et al.'s (2007) criteria have used both interpretations, estuaries in Alabama and Texas were first tested using interpretation 1 ('density in the area is greater than the mean density over all the areas'). If no estuaries within a region met this criterion, they were tested using the more liberal interpretation 2 (density in one area must be greater than another area based on pairwise comparisons) to determine if they met Criterion 1.

For potential nurseries that met Criterion 1, general linear models were used to quantify the interaction of year and sampling month/season on YOY shark CPUE to assess if sharks exhibited repeated use (i.e., site fidelity) of potential nurseries to meet Criterion 2 ('sharks have a tendency to remain or return for extended periods'; Heupel et al. 2007). Non-normal data were analysed using generalized linear models with a gamma distribution, appropriate for continuous, positive and right-skewed data. Criterion 2 was tested for the study duration for each region, as well as the 5-year intervals. Potential nurseries that met Criterion 1, but exhibited a significant interaction between year and month that indicated limited residency (i.e., densities that satisfied Criterion 1 but were attributed to a narrow time period (e.g., single season)), were removed from consideration.

For systems that met Criteria 1 & 2, general linear models were used to quantify the effect of year on YOY shark CPUE to assess if YOY sharks exhibited repeated residency in potential nurseries (i.e., consistently across years) to meet Criterion 3 ('the area or habitat is repeatedly used across years'; Heupel et al. 2007). Non-normal data were analysed using generalized linear models with a gamma distribution. Criterion 3 was tested for the study duration for each region, as well as the 5-year intervals. Potential nurseries that met Criteria 1 & 2, but exhibited a significant negative trend in CPUE with year were identified as essential habitats in need of improved management/restoration.

3 | Results

3.1 | Alabama Coast

From March 2004 to October 2023, 586 YOY bull sharks were captured along the Alabama coast. Across the entire study period and for all 5-year intervals, no part of the Alabama coast qualified as a nursery using interpretation 1 for Criterion 1 ('density in the area is greater than the mean density over all the areas'), because no sampling area had significantly higher CPUE than the coastwide mean (Table 1). However, based on interpretation 2 for Criterion 1 (density in one area must be greater than another area based on pairwise comparisons), Upper Mobile Bay and Lower Mobile Bay were identified as bull shark nurseries when the entire study period was considered (Table 1, Figure 2, Supplemental Table S1, Supplemental Figure S1). Within 5-year intervals, Lower Mobile Bay was a bull shark nursery from 2009 to 2018 (two consecutive 5-year intervals), and Upper Mobile Bay was a bull shark nursery from 2014 to 2023 (two consecutive 5-year intervals; Table 1, Figure 2, Supplemental Table S1, Figure S1).

3.2 | Texas Coast

From April 1982 to November 2021, 3978 YOY bull sharks and 2832 YOY blacktip sharks were caught within the seven study estuaries along the Texas coast. When the entire study period was considered (40 years), Matagorda Bay and San Antonio Bay were identified as bull shark nurseries, and no estuaries were identified as blacktip shark nurseries (Table 2, Figure 3, Table S1, Supplemental Figure 2). However, nursery status varied temporally. No nurseries were identified in Texas estuaries for the first 20 years of the study from 1982 to 2001 measured in 5-year intervals. Matagorda Bay was identified as a bull shark nursery from 2002 to 2021 (four consecutive 5-year intervals), San Antonio Bay was a bull shark nursery from 2007 to 2021 (three consecutive 5-year intervals) and Galveston Bay was a bull shark nursery from 2012 to 2021 (two consecutive 5-year intervals; Table 2, Figure 3, Supplemental Table S1, Supplemental Figure 2). San Antonio Bay was a blacktip shark nursery from 2012 to 2021 (two consecutive 5-year intervals), and both Corpus Christi Bay and Matagorda Bay were blacktip shark nurseries for the last 5-year interval, 2017 to 2021 (Table 3, Figure 4, Supplemental Table S1, Supplemental Figure 3).

4 | Discussion

Within ecosystems, some areas are particularly important for reproduction, survival, or feeding (Hyde et al. 2022), leading to variability in the value of habitats and the distribution of wildlife (Van Horne 1983). Essential habitats that offer these ecological services have been described in scientific literature for > 100 years (e.g., Vestal 1913). Authors like Langlois (1941) have identified the need for fisheries management to restore essential habitat for more successful reproduction and recruitment, and those like Cahalan (1951) have described management failures tied to the lack of protection of essential habitat. In the late 20th century, the United States formally recognized essential habitats for management purposes (US Sustainable Fisheries Act, 1996, Public Law 104-297) as well as enacted the first federal fisheries management plan for sharks in its waters (Fisheries Management Plan for Sharks of the Atlantic Ocean, 1993). These policies have led to conservation benefits as our results show with the (re)establishment of bull shark and blacktip shark nurseries in the Northern Gulf of Mexico.

The (re)emergence of shark nurseries in the 21st century has not been restricted to the Gulf of Mexico. For example, bull shark nurseries in the Northwestern Atlantic have expanded to higher latitudes (Bangley et al. 2018), white shark (*Carcharodon carcharias*) nurseries have grown in Eastern Australia (Spaet, Manica, et al. 2020) and sand tiger shark (*Carcharias taurus*) nurseries have (re)emerged in New England, USA (Kneebone et al. 2012). Changes in water temperature, primary productivity, prey availability and fisheries/ecosystem management have all been described as factors leading to these changes. Yet, the (re)establishment of shark nurseries does not equate to their persistence nor lasting conservation success, because sharks are still overfished in many areas (Dulvy et al. 2024), which has negative consequences for nurseries (e.g., Williams and Schaap 1991; Carlisle et al. 2007; Skomal 2007; Bustamante and Bennett 2013; Bom et al. 2020; Corgos and Rosende-Pereiro 2022). The persistent loss of global biodiversity and the alteration of ecosystem function attributed to climate change, human disturbance and other factors necessitates the continued delineation, protection and restoration of essential habitats like nurseries (Heithaus 2007), particularly for vulnerable taxonomic groups like sharks. Understanding the spatiotemporally dynamic nature of nurseries as it relates to their recovery and expansion is crucial for achieving this goal (Yates et al. 2012).

Our results show that bull shark and blacktip shark nurseries in the Northern Gulf of Mexico were first (re)established in the 2000s. The first bull shark nurseries detected in our study areas were in 2002–2006 along the central Texas coast (Matagorda Bay) 20 years after monitoring began. This was followed by an expansion of nursery habitat into a connected estuary (San Antonio Bay, 2007–2011), then in disparate and more northern estuaries (Galveston Bay, TX and Mobile Bay, AL). Previous studies hypothesized that these more northern estuaries would become nurseries due to warming water temperatures that would extend residency and therefore survival (e.g., Froeschke, Stunz, and Wildhaber 2010; Froeschke, Stunz, Sterba-Boatwright, and Wildhaber 2010; Bethea et al. 2015), which was confirmed for these systems in 2024 (Matich et al. 2024; Mullins et al. 2024). Previous work in Texas also showed the importance of environmental factors like salinity for juvenile bull sharks (e.g., Froeschke, Stunz, and Wildhaber 2010; Plumlee et al. 2018; Lofthus et al. 2024). Habitat management, particularly freshwater flow into estuaries for ecological benefits, has therefore also likely contributed to nursery re-establishment for juvenile bull sharks, because of their reliance on low salinity habitats (Matich, Nowicki, et al. 2020). Blacktip sharks more recently

TABLE 1 | Test statistics and *p*-values assessing the nursery status of study areas in Alabama estuaries for YOY bull sharks.

		Criterion 1				Criterion 2			Criterion 3
		Post hoc Dunn's test				Generalized linear regression			
Location	Timeframe	vs. entire coast	vs. Lower Mobile	vs. MS Sound	vs. Perdido Bay	spring * Year	summer * Year	fall * Year	Linear regression
Upper Mobile Bay	2004–2023	−1.26, 0.63	−0.36, 0.74	***−3.96, < 0.01**	***−5.87, < 0.01**	***−1.73, 0.09**	***1.64, 0.11**	***0.61, 0.54**	***$y = 0.018x - 35.04$, 7.36, 0.01**
	2004–2008	−0.04, > 0.99	−0.40, > 0.99	−2.68, 0.07	−2.60, 0.08				
	2009–2013	0.11, > 0.99	1.38, 0.68	−1.70, 0.44	−2.07, 0.27				
	2014–2018	−1.85, 0.35	−0.91, > 0.99	***−2.80, 0.04**	***−3.93, < 0.01**	***−0.38, 0.72**	***1.35, 0.21**	***0.29, 0.78**	***$y = 0.022x - 44.40$, 0.41, 0.57**
	2019–2023	−1.03, > 0.99	−0.86, > 0.99	−1.72, 0.55	***−3.48, 0.01**	***−2.23, 0.06**	***2.05, 0.07**	***1.89 0.09**	***$y = 0.110x - 213.28$, 14.01, 0.03**
Lower Mobile Bay	2004–2023	−0.90, 0.74	—	***−3.60, < 0.01**	***−5.52, < 0.01**	***−0.43, 0.67**	***0.39, 0.70**	***0.16, 0.87**	***$y = 0.009x - 17.82$, 4.57, 0.05**
	2004–2008	0.26, > 0.99	—	−2.33, 0.12	−2.24, 0.12				
	2009–2013	−1.27, 0.68	—	***−3.08, 0.02**	***−3.45, < 0.01**	***1.67, 0.13**	***−1.59, 0.15**	***−1.87, 0.09**	***$y = -0.002x + 4.56$, < 0.01, 0.96**
	2014–2018	−0.95, > 0.99	—	−1.90, 0.35	***−3.02, 0.02**	***0.91, 0.39**	***−0.91, 0.39**	***−0.91, 0.39**	***$y = 0.013x - 26.65$, 0.24, 0.66**
	2019–2023	−0.17, > 0.99	—	−0.86, > 0.99	−2.62, 0.08				
Mississippi Sound	2004–2023	2.70, 0.03	—	—	−1.92, 0.22				
	2004–2008	2.64, 0.08	—	—	0.09, > 0.99				
	2009–2013	1.81, 0.42	—	—	−0.37, > 0.99				
	2014–2018	1.95, > 0.99	—	—	−1.12, > 0.99				
	2019–2023	0.69, > 0.99	—	—	−1.76, 0.55				
Perdido Bay	2004–2023	4.62, < 0.01	—	—	—				
	2004–2008	2.55, 0.08	—	—	—				
	2009–2013	2.18, 0.23	—	—	—				
	2014–2018	2.07, 0.27	—	—	—				
	2019–2023	2.45, 0.11	—	—	—				

Note: Bold values with asterisks denote when Heupel et al. (2007) criteria were met (significant for Criterion 1, positive slope or insignificant for Criterion 2, insignificant for Criterion 3). Greyed-out text indicates where a sampling area failed to meet previous criterion and thus was not assessed.

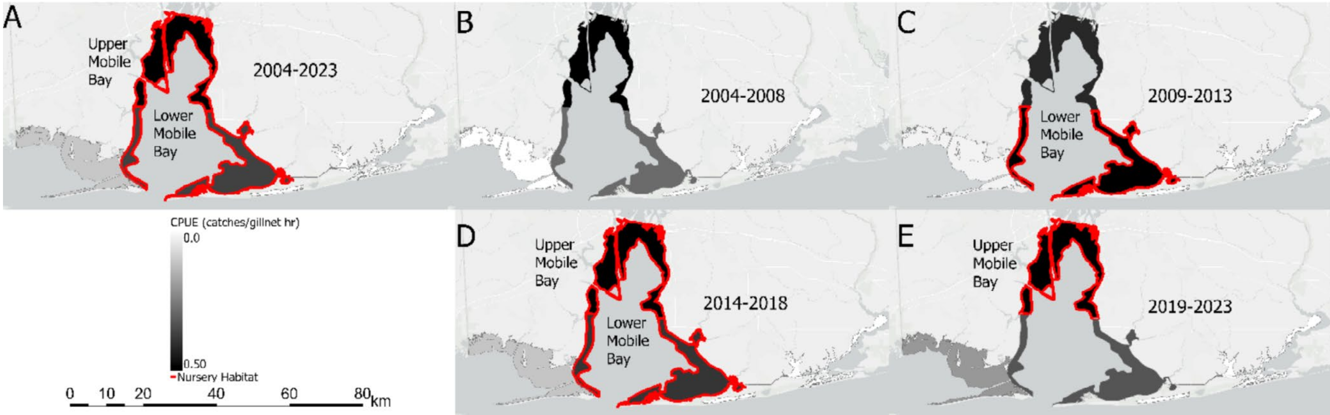

FIGURE 2 | Bull shark densities along the Alabama coast for (A) the entire study period (2004–2023) and (B–E) 5-year study periods. Regions with red outlines indicate locations identified as bull shark nurseries.

(re)established nurseries in the region based on our results (2012–2021), which could be tied to differences in their physiology, fisheries pressure and/or other factors, indicating that the establishment of a shark nursery for one species does not equate to its establishment for all species inhabiting an area.

Our study only included 42 years of monitoring data, and considering the consequences of the lack of shark fisheries management in the 20th century (Barker and Schluessel 2005; Pacoureau et al. 2021; Dulvy et al. 2024), combined with the propensity for at least some shark species, including bull sharks, to exhibit regional philopatry (Tillett et al. 2012; Chapman et al. 2015; Sandoval Laurrabaquio-Alvarado et al. 2019), we suspect that the estuaries identified as nurseries in our study were nurseries prior to the 1980s. These nurseries were, however, likely undetectable until the 2000s based on Heupel et al.'s (2007) criteria due to persistent overfishing of sharks, including pregnant females thereby limiting parturition, and may have only recently begun rebounding (Pacoureau et al. 2021, Dulvy et al. 2024). After complete nursery collapse resultant from an extreme environmental disturbance, juvenile bull sharks required *ca.* 5 years to recover in a South Florida estuary (Matich, Strickland, and Heithaus 2020). The duration of time for the nurseries of the Northern Gulf of Mexico to recover (20+ years) shows that mature females were severely impacted by overfishing in the 20th century, which was widespread as exhibited by the continued depletion of most shark species across the Northwestern Atlantic (Pacoureau et al. 2023).

The Gulf of Mexico is among the most well-studied regions in the world for sharks, and nurseries have been qualitatively identified based on the presence of young-of-the-year individuals of many shark species (e.g., McCandless, Kohler, and Pratt 2007). Yet only a limited number of studies in the region have applied Heupel et al.'s (2007) criteria (Froeschke, Stunz, Sterba-Boatwright, and Wildhaber 2010; Bethea et al. 2015; Cuevas-Gómez et al. 2020; Swift and Portnoy 2021; Matich et al. 2022). Data limitations are in part responsible, but so too are low shark densities resultant from overfishing that have led to a lack of geographic differences in CPUE and therefore inhibited differentiation between nursery and non-nursery habitats (Pacoureau et al. 2021, Dulvy et al. 2024). Fisheries management has therefore been an important factor contributing to increased juvenile shark densities in our study areas and the re-establishment of nurseries as previously suggested (Froeschke et al. 2013).

As waters continue to warm and shark management improves in some regions, we expect that the establishment, expansion and re-establishment of shark nurseries will occur in a variety of regions as it already has for some species (e.g., Bangley et al. 2018; Udovičić et al. 2018; Traylor-Holzer 2021). Shark nurseries are found across the world, including subtropical Latin America (e.g., Ruiz-Abierno et al. 2020), the Pacific coast of North America (e.g., Nosal et al. 2019), South Africa and adjacent waters (e.g., da Silva et al. 2021), the Northeastern Atlantic (e.g., Afonso et al. 2022), the Mediterranean (e.g., Leonetti et al. 2020) and the Southwestern Pacific (e.g., Harasti et al. 2017). The number of identified nurseries in these areas, however, is currently small compared to other regions (e.g., Western Atlantic, Tropical Eastern Pacific, Northern Australia; e.g., McCandless, Kohler, and Pratt 2007, Thornburn and Rowland 2008, Guzman et al. 2020, Rodriguez-Arana Favela et al. 2022). Several hypotheses could explain the reason for these geographic differences, including differences in management, data for delineating shark nurseries and habitat suitability tied to environmental conditions. Water temperatures are warming globally (McCulloch et al. 2024), which has led to changes in shark nurseries. While some habitats are becoming more suitable for juvenile sharks as they warm (e.g., Bangley et al. 2018; Mullins et al. 2024), increased temperatures have had negative consequences for sharks in other nurseries due to greater thermal stress imparted on juvenile sharks and their prey (Bernal et al. 2012; Tanaka et al. 2021). In our study area, Lower Mobile Bay was a bull shark nursery from 2009 to 2018, and the more northern Upper Mobile Bay was a bull shark nursery from 2014 to 2023. While subtle, this geographic shift may have resulted from warming waters and indicate that as some waters become more suitable and emerge as essential habitats (Mullins et al. 2024), others may decrease in suitability leading to decreases in shark densities (Braun et al. 2023), or shifts in the locations of shark nurseries (e.g., Tanaka et al. 2021).

However, the loss of nursery status in Lower Mobile Bay in 2019–2023 was not due to a decline in juvenile bull shark densities, rather an increase in their densities in the Mississippi Sound and the lack of statistical differentiation between these

TABLE 2 | Test statistics and *p*-values assessing the nursery status of study areas in Texas estuaries for YOY bull sharks.

		Criterion 1	Criterion 2	Criterion 3
		Post hoc Dunn's test		
Location	**Timeframe**	**vs. entire coast**	**General linear model**	**Linear regression**
Sabine Lake	1982–2021	−3.29, <0.01		
	1982–1986	NA, NA		
	1987–1991	−3.12, 0.01		
	1992–1996	−3.38, 0.01		
	1997–2001	−2.66, 0.03		
	2002–2006	−0.24, 0.87		
	2007–2011	−0.74, 0.51		
	2012–2016	0.02, 0.98		
	2017–2021	0.51, 0.66		
Galveston Bay	1982–2021	1.15, 0.28		
	1982–1986	−1.83, 0.16		
	1987–1991	−2.78, 0.02		
	1992–1996	−2.10, 0.11		
	1997–2001	−1.09, 0.35		
	2002–2006	1.19, 0.33		
	2007–2011	1.18, 0.29		
	2012–2016	***2.72, 0.02**	***−1.84, 0.12**	***$y=0.008x-15.015$, 0.02, 0.90**
	2017–2021	***2.72, 0.02**	***1.24, 0.27**	***$y=0.058x-56.209$, 0.22, 0.67**
Matagorda Bay	1982–2021	***3.42, <0.01**	***−0.61, 0.54**	***$y=0.006x-11.335$, 6.412, 0.016**
	1982–1986	1.38, 0.33		
	1987–1991	1.20, 0.41		
	1992–1996	0.27, 0.85		
	1997–2001	1.91, 0.11		
	2002–2006	***3.20, <0.01**	***2.30, 0.06**	***$y=-0.009x+18.858$, 0.06, 0.83**
	2007–2011	***3.30, <0.01**	***−0.95, 0.38**	***$y=-0.031x+62.072$, 3.08, 0.18**
	2012–2016	***3.35, <0.01**	***0.68, 0.52**	***$y=0.027x-53.567$, 0.13, 0.74**
	2017–2021	***3.20, <0.01**	***1.15, 0.30**	***$y=0.067x-134.789$, 5.30, 0.11**
San Antonio Bay	1982–2021	***2.13, 0.04**	***−1.39, 0.17**	***$y=0.067x-12.979$, 10.99, <0.01**
	1982–1986	0.27, 0.92		
	1987–1991	0.59, 0.68		
	1992–1996	1.20, 0.41		
	1997–2001	1.51, 0.20		
	2002–2006	−2.03, 0.09		
	2007–2011	***2.77, 0.01**	***0.17, 0.87**	***$y=-0.025x+51.264$, 0.75, 0.45**
	2012–2016	***2.82, 0.02**	***−0.93, 0.39**	***$y=0.066x-132.132$, 0.50, 0.53**
	2017–2021	***2.45, 0.03**	***−0.82, 0.45**	***$y=0.055x-110.659$, 1.67, 0.29**

(Continues)

Location	Timeframe	Criterion 1 Post hoc Dunn's test vs. entire coast	Criterion 2 General linear model	Criterion 3 Linear regression
Aransas Bay	1982–2021	−0.99, 0.34		
	1982–1986	−0.06, 0.95		
	1987–1991	−1.87, 0.12		
	1992–1996	−0.80, 0.50		
	1997–2001	−0.61, 0.61		
	2002–2006	−0.10, 0.92		
	2007–2011	0.98, 0.38		
	2012–2016	0.72, 0.63		
	2017–2021	1.27, 0.29		
Corpus Christi Bay	1982–2021	−4.50, < 0.01		
	1982–1986	−2.60, 0.04		
	1987–1991	−2.05, 0.08		
	1992–1996	−0.98, 0.46		
	1997–2001	−2.14, 0.08		
	2002–2006	−2.65, 0.03		
	2007–2011	−2.48, 0.03		
	2012–2016	−0.24, 0.90		
	2017–2021	−1.75, 0.15		
Laguna Madre	1982–2021	−7.47, < 0.01		
	1982–1986	−2.09, 0.10		
	1987–1991	−2.99, 0.01		
	1992–1996	−3.11, 0.13		
	1997–2001	−3.66, < 0.01		
	2002–2006	−3.07, < 0.01		
	2007–2011	−0.48, 0.68		
	2012–2016	−2.88, 0.02		
	2017–2021	−3.03, < 0.01		

Note: Bold values with asterisks denote when Heupel et al. (2007) criteria were met (positive and significant for Criterion 1, positive slope or insignificant for Criterion 2, insignificant for Criterion 3). Greyed-out text indicates where a sampling area failed to meet previous criterion and thus was not assessed.

areas. The absence of correlation between latitude and nursery establishment in Texas also suggests that while warming could reduce habitat suitability, and therefore nursery status in more equatorial subtropical ecosystems, reductions in habitat suitability is unlikely in the near future for species like bull sharks and blacktip sharks that use environmentally dynamic estuaries as nurseries. Indeed, juvenile bull shark densities in lower latitude estuaries in the Gulf of Mexico (e.g., South Florida) have remained stable or increased during the 21st century, suggesting bull sharks are currently well suited to handle the persistently warming environments in the region (e.g., Matich, Strickland, and Heithaus 2020; Zikmanis et al. 2025). Other studies similarly show the ability of juvenile sharks to tolerate warming temperatures (e.g., Bouyoucos et al. 2022; Trujillo et al. 2025). This is, however, not true for all species, especially those with a limited thermal tolerance/preference range, or in regions where warming may occur too rapidly as exhibited by white sharks in California (e.g., Tanaka et al. 2021; Spurgeon et al. 2024).

The emergence and re-establishment of shark nurseries provides hope for conservation initiatives that have sought to help shark populations recover from human impacts (e.g., Traylor-Holzer 2021). However, the consequences of these changes are

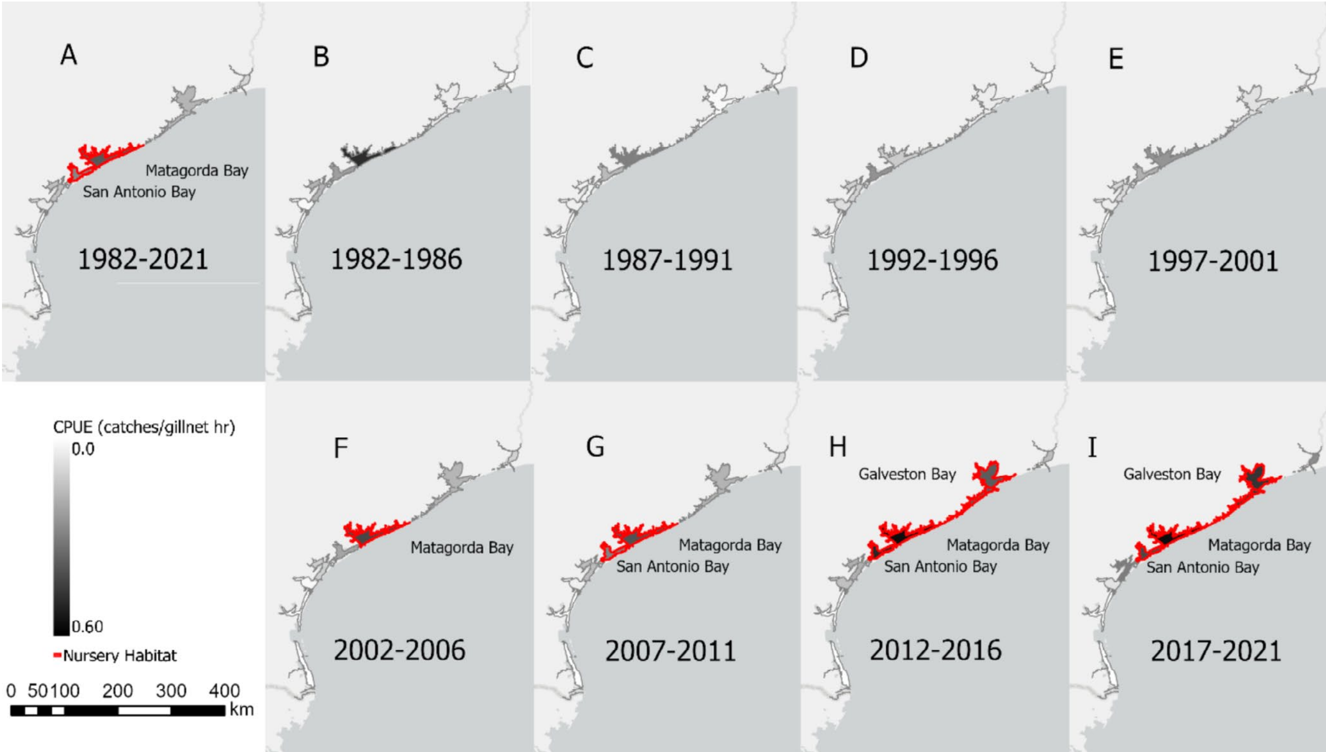

FIGURE 3 | Bull shark densities along the Texas coast for (A) the entire study period (1982–2021) and (B–I) 5-year study periods. Regions with red outlines indicate locations identified as bull shark nurseries.

unclear, because recovery has been very limited in most regions (Dulvy et al. 2024) and changes are occurring not just among populations, but at community and ecosystem levels (e.g., Storm et al. 2025). Beyond these uncertainties, the problem of scale is ever-present (Levin 1992). Some habitats are easily defined and designated as essential or non-essential habitats, while others are more ambiguous. For example, Texas estuaries are geographically and physically distinct from one another, and therefore shark nurseries at an estuary-scale can clearly be delineated. Comparatively, Mobile Bay was assessed as two regions to reflect the hydrologic latitudinal gradient of the system and sampling design of the ADNR-MRD, of which nursery status varied geographically despite the physical and biological connectivity between these areas. Further, while most estuaries in Texas are not blacktip shark nurseries based on our results, previous research shows that certain locations (2.6–12.9 km^2) within many estuaries ($n = 5$) are nursery habitats (Matich et al. 2022). Other nurseries, including those of white sharks in California (e.g., Anderson et al. 2021), great hammerheads (*Sphyrna mokarran*) in south Florida (e.g., Macdonald et al. 2021), sand tiger sharks (*Carcharias taurus*) across the Eastern Cape of South Africa (e.g., Dicken et al. 2007; Klein et al. 2019), and many others face this challenge because of the physically connected nature of marine systems. Thus, the spatial scale of how essential habitats are evaluated is an important consideration and should be aligned with how ecosystems are and can be managed.

The approach by which ecosystems are evaluated for essential habitat is also an important consideration. As we illustrate with the assessment of the Alabama coastline, the application of Heupel et al.'s (2007) framework can lead to different conclusions depending on its interpretation, which we expect to be true of other locations. If we only considered the first interpretation of criterion 1 ('density in the area is greater than the mean density over all the areas'), then we would have concluded bull sharks do not have nursery habitat in Alabama waters despite their high densities and reliance on Mobile Bay. Consequently, more clarity is needed on the interpretation and flexibility of shark nursery criteria (Heupel et al. 2019). While this is beyond the scope of our study, future work using sensitivity models to assess shark densities across different spatial and temporal scales would be helpful in determining how discrete 'habitats' and 'seasons' should be when delineating nurseries, the interpretation of each criterion and how data-limited regions should be handled; the latter of which is particularly important considering much of the world is understudied as it relates to shark nurseries.

Other considerations also make the delineation of essential habitats like shark nurseries challenging. Nurseries support sustained populations of juvenile sharks that are found in higher densities than surrounding areas. However, the underlying mechanism(s) leading to density differences should be considered. Nurseries can emerge if the number of sharks inhabiting an area increases, but also if their residency within that area increases. Matich et al. (2024) recently showed that warming waters and changes in prey populations led to juvenile bull sharks residing in Texas estuaries for weeks-months longer in the 2020s compared to the 1980s. As such, juvenile bull shark densities increased during months when they would previously have been absent (e.g., October–November), with similar results found in other regions of the world (e.g., Lubitz et al. 2025). The (re)establishment of nurseries could therefore be attributed to longer residency rather than greater numbers of sharks.

TABLE 3 | Test statistics and *p*-values assessing the nursery status of study areas in Texas estuaries for YOY blacktip sharks.

Location	Timeframe	Criterion 1: Post hoc Dunn's test vs. entire coast	Criterion 2: General linear model	Criterion 3: Linear regression
Sabine Lake	1982–2021	−7.92, < 0.01		
	1982–1986	NA, NA		
	1987–1991	−3.13, 0.03		
	1992–1996	−3.64, < 0.01		
	1997–2001	−3.34, < 0.01		
	2002–2006	−3.43, < 0.01		
	2007–2011	−3.96, < 0.01		
	2012–2016	−3.36, < 0.01		
	2017–2021	−2.99, 0.01		
Galveston Bay	1982–2021	−1.39, 0.21		
	1982–1986	−1.00, 0.53		
	1987–1991	−0.49, 0.79		
	1992–1996	−0.89, 0.75		
	1997–2001	0.68, 0.60		
	2002–2006	−1.77, 0.17		
	2007–2011	−0.46, > 0.99		
	2012–2016	−0.15, 0.88		
	2017–2021	0.54, 0.66		
Matagorda Bay	1982–2021	0.53, 0.67		
	1982–1986	−1.45, 0.34		
	1987–1991	0.73, 0.69		
	1992–1996	−0.20, 0.95		
	1997–2001	1.33, 0.32		
	2002–2006	0.02, > 0.99		
	2007–2011	−0.53, > 0.99		
	2012–2016	1.58, 0.18		
	2017–2021	***3.42, < 0.01**	***1.45, 0.21**	***$y = 0.050x - 99.316$, 4.48, 0.13**
San Antonio Bay	1982–2021	−1.45, 0.20		
	1982–1986	−2.25, 0.14		
	1987–1991	−1.01, 0.55		
	1992–1996	−0.92, 0.77		
	1997–2001	−1.01, 0.44		
	2002–2006	−0.99, 0.41		
	2007–2011	−0.65, 0.97		
	2012–2016	***2.59, 0.03**	***−1.36, 0.22**	***$y = 0.042x - 83.707$, 2.65, 0.20**
	2017–2021	***2.32, 0.04**	***0.74, 0.50**	***$y = 0.075x - 151.721$, 3.97, 0.14**

(Continues)

TABLE 3 | (Continued)

Location	Timeframe	Criterion 1: Post hoc Dunn's test vs. entire coast	Criterion 2: General linear model	Criterion 3: Linear regression
Aransas Bay	1982–2021	−2.57, < 0.01		
	1982–1986	−0.61, 0.66		
	1987–1991	−2.62, 0.05		
	1992–1996	−3.45, < 0.01		
	1997–2001	−2.96, 0.01		
	2002–2006	−3.43, < 0.01		
	2007–2011	−3.42, < 0.01		
	2012–2016	−2.33, 0.05		
	2017–2021	−1.88, 0.11		
Corpus Christi Bay	1982–2021	−0.07, 0.98		
	1982–1986	0.61, 0.69		
	1987–1991	−0.80, 0.66		
	1992–1996	−0.65, 0.96		
	1997–2001	−0.86, 0.52		
	2002–2006	1.53, 0.23		
	2007–2011	−0.90, 0.74		
	2012–2016	0.35, 0.76		
	2017–2021	***2.82, 0.01**	***1.17, 0.30**	***$y = 0.042x - 83.633$, 1.12, 0.37**
Laguna Madre	1982–2021	−2.21, 0.05		
	1982–1986	−0.95, 0.53		
	1987–1991	< 0.01, > 0.99		
	1992–1996	0.62, 0.93		
	1997–2001	0.43, 0.75		
	2002–2006	−1.98, 0.15		
	2007–2011	0.92, 0.77		
	2012–2016	−1.75, 0.16		
	2017–2021	−0.50, 0.67		

Note: Bold values with asterisks denote when Heupel et al. (2007) criteria were met (significant for Criterion 1, positive slope or insignificant for Criterion 2, and insignificant for Criterion 3). Greyed-out text indicates where a sampling area failed to meet previous criterion and thus was not assessed.

As conditions change and we seek to proactively manage coastal and marine systems, it will be important to assess if newly identified nurseries result from (1) more females giving birth and/or neonates migrating into an area, (2) changing conditions that extend periods of habitat suitability, (3) improved conditions, including fisheries management, that increase juvenile shark survival, or (4) a combination of these mechanisms. As shark nurseries (re)emerge, it is also unclear when juvenile sharks will reach their carrying capacities within these systems, and if they will do so gradually or disruptively, potentially creating unstable equilibriums or shifts in stable states (Beverton and Holt 1957; Myers et al. 2001). Considering increased reports of human conflicts with sharks in many fisheries (Mitchell et al. 2018), we may be approaching this situation or have reached it in some systems due to growing shark populations and/or greater harvesting of resources sharks rely on for prey (Carlson et al. 2019; Mitchell et al. 2023; Drymon et al. 2024). It is also uncertain how species in regions with range restrictions that limit shifts to higher latitudes (e.g., Gulf of Mexico and Caribbean Sea, Mediterranean Sea, Red Sea, Gulf of California) will respond to increasing densities of juvenile sharks, because there are few locations where healthy nurseries have been studied long enough to understand how these systems function when juvenile sharks are at their carrying capacities.

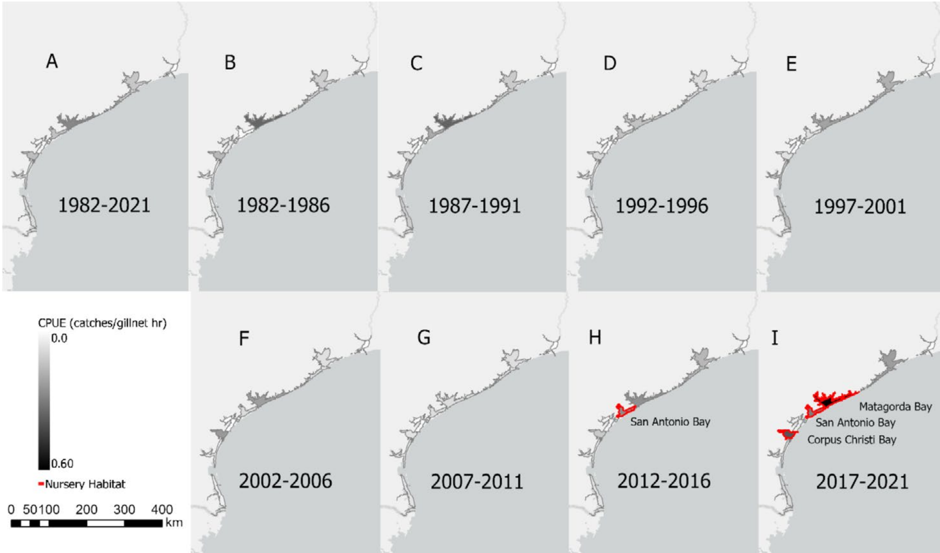

FIGURE 4 | Blacktip shark densities along the Texas coast for (A) the entire study period (1982–2021) and (B–I) 5-year study periods. Regions with red outlines indicate locations identified as blacktip shark nurseries.

Regardless of the mechanisms leading to their (re)establishment and their future status, it is clear that the dynamics and distributions of shark nurseries change in space and time. Geographic shifts are likely an inherent characteristic of nearshore nurseries due to the dynamic nature of the ecosystems in which they are found and the response sharks have to environmental and ecological variability (e.g., Hannan and Coan 1993; McCandless, Pratt, et al. 2007; Parsons and Hoffmayer 2007; Montealegre-Quijano and Vooren 2010; Spaet, Patterson, et al. 2020; Pillans et al. 2021). Ecological theory predicts that populations benefit from such variability—if juveniles inhabit diverse habitats that necessitate intraspecific variation in behaviours and epigenetics, then adult populations will be more resilient in light of natural and anthropogenic perturbations because of this variability (Yates et al. 2012). This portfolio effect (Schindler et al. 2015) was not evaluated in our study, however it is expected to occur considering annual fluctuations in parturition, survival, habitat suitability and the more regional nature of philopatry, at least among bull sharks in the Gulf of Mexico (Sandoval Laurrabaquio-Alvarado et al. 2019; TinHan et al. 2020), which contribute to spatiotemporal variability in juvenile shark densities within coastal estuaries (Froeschke et al. 2013).

The challenges this creates for management agencies cannot be understated because of the importance essential habitats play for many shark species (Hyde et al. 2022), which are still in decline across most of the world (Dulvy et al. 2024). Consequently, some essential habitats may not be labelled as such, because the densities of juvenile sharks are too low as a result of human impacts (overfishing, habitat deterioration; Dulvy et al. 2024, Gausmann et al. 2025) or natural variability via the portfolio effect (Yates et al. 2012), and therefore do not meet the criteria necessary to be labelled as nurseries despite their ecological and conservation value (e.g., Lower Mobile Bay and Mississippi Sound, AL; Sabine Lake, TX). Similarly, our interpretation of criterion 3 ('the area or habitat is repeatedly used across years'; Heupel et al. 2007) led to the conclusion that if shark densities declined within the study period, then they may no longer be nurseries despite their importance to juvenile sharks. While none of our potential nurseries met criteria 1 & 2 and failed criterion 3, other studies have detected declining juvenile shark densities in nurseries that could lead to a loss of nursery status and therefore management as essential habitat (e.g., Bustamante and Bennett 2013; Corgos and Rosende-Pereiro 2022).

Identifying the characteristics that promote juvenile shark residency, development and survival (e.g., Kanno et al. 2023), and improving the management of habitats that offer these benefits is therefore a necessary component to managing sharks moving forward to ensure suitable nursery habitats for recovering populations. Additionally, the need to reassess the status of these nurseries is clear based on our results—these habitats are not static, and essential habitat should not be a permanent designation. We cannot assume species will use these systems in the same way and in the same densities as environmental and ecological conditions change. The value of non-nursery habitats that support juvenile sharks is also important considering the value they offer via the portfolio effect (Yates et al. 2012) and the potential for these habitats to (re)emerge as nurseries. Long-term monitoring and predictive modelling are therefore critical to appropriately manage these systems (Crear et al. 2020). It is unclear how frequently reassessments should take place, but as our data show for bull sharks and blacktip sharks, the status of long-lived, late maturing species in essential habitats can change within 5-year periods. Thus, at a minimum, decadal evaluations should be strongly considered.

Author Contributions

Philip Matich: led the study conception, data analysis and writing. **Lindsay L. Mullins:** contributed to the study conception, data analysis and writing. **Jeffrey D. Plumlee:** contributed to the study conception, data analysis and writing. **Mark R. Fisher:** led the Texas data collection and management. **John Mareska:** led the Alabama data collection and management; **J. Marcus Drymon:** contributed to the study conception and writing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data are publicly available at: https://doi.org/10.7910/DVN/RVLJ6U.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Kruskal–Wallis test results assessing differences in CPUE of YOY sharks between sampling areas within regions (Criterion 1). **Figure S1:** Catch per unit effort (CPUE—sharks per standardized gillnet) of YOY bull sharks in Alabama estuaries for the entire study period (top left panel) and 5-year study periods starting from 2004 to 2008. **Figure S2:** Catch per unit effort (CPUE—sharks per standardized gillnet) of YOY bull sharks in Texas estuaries for the entire study period (top left panel) and 5-year study periods starting from 1982 to 1986. **Figure S3:** Catch per unit effort (CPUE—sharks per standardized gillnet) of YOY blacktip sharks in Texas estuaries for the entire study period (top left panel) and 5-year study periods starting from 1982 to 1986.