



# A critical evaluation of adult blacktip shark, *Carcharhinus limbatus*, distribution off the United States East Coast

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**Abstract** Global climate change affects a suite of oceanic characteristics including temperature, salinity, currents, and animal distribution. It is imperative that accurate baselines in distribution and range are used to measure changes in the behavior of marine animals that occur in response to climate change. Current knowledge on the migratory movement of the blacktip shark, *Carcharhinus limbatus*, off the United States East Coast is challenged by inconsistent reports. Published data on the migration and sexual segregation of the U.S. East Coast blacktip shark population can be interpreted a variety of ways and the scientific literature continues to perpetuate historical and uncertain observations on this population derived from the older literature, which carries low certainty. Here, we provide an overview of the biology and life history of the blacktip shark, consolidate the migratory pattern of the species off the U.S. East Coast, and then critically dissect the many inconsistencies perpetuated in the literature. We argue that (1) blacktip sharks that inhabit the Florida Keys may belong to the Gulf of Mexico stock, (2) the currently accepted northern extent of this species (Massachusetts) may be inaccurate, and (3) that environmental variability and/or sexual segregation of this population may play a role in the inconsistent reports. In addition,

we identify future topics of research that will help to close the gaps in the current knowledge of the movement ecology of the blacktip shark off the U.S. East Coast.

**Keywords** Migration · Range · Misidentification · Movement · Nursery · Behavior

## Introduction

Globally, ocean temperatures are expected to rise 1–4 °C by 2100 (Pachauri et al. 2014), which will affect a variety of marine dynamic processes, including ocean currents (Alexander et al. 2020), coastal salinity (Pachauri et al. 2014), phytoplankton concentrations (Boyce et al. 2010), and therefore consumer distribution (Cheung et al. 2009; Sorte et al. 2010). In addition, some regions, such as the northwestern Atlantic Ocean, are warming at a rate disproportionate to the global average (Saba et al. 2016), although within this region, warming rates are heterogeneous (Pershing et al. 2015). Climate change is likely to affect the distribution of shark species since the same environmental conditions affected by climate change (e.g., sea temperatures, salinity, and primary productivity) correlate with the occurrence of many sharks species (Weng et al. 2008; Kessel et al. 2014; Ward-Paige et al. 2015; Bangley et al. 2018a; Diaz-Carballido et al. 2022). Because climate change will continue to alter the marine environment and shark

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populations will respond in kind, it is imperative to establish accurate baselines so that these changes in species range, distribution, and behavior can be accurately measured.

Information on baseline movement ecology of the blacktip shark, *Carcharhinus limbatus* (Valenciennes in Müller and Henle, 1839), population off the United States East Coast is an amalgamation of historic and more recent information. While there is a natural progression of scientific discovery over time, historic information on the U.S. East Coast blacktip shark population is often presented on equal footing with newer information (e.g., Castro 1996, 2011; Compagno 1984; Ebert et al. 2013). Secondary resources that collate information from the primary literature are extremely valuable, but often perpetuate inaccurate or outdated information from earlier sources. These secondary resources are referenced in other literature, which results in these inaccuracies being further perpetuated. Therefore, there exists a need for a critical review of the current knowledge gaps in the distribution of the U.S. East Coast blacktip shark population that can be used as a basis for future studies. Here, we provide an overview of the biology of the species and life history of the population, and then synthesize the migratory pattern of blacktip sharks off the U.S. East Coast (Table 1) while critically dissecting inconsistencies perpetuated in the scientific literature. We offer our interpretation of the scientific literature given confounding factors such as inconsistent information, uncertainty, species misidentification, potential climate change effects, and sexual segregation. In doing so, we identify future topics of research that will help to close gaps in the current knowledge of the movement ecology of the blacktip shark off the U.S. East Coast.

Geographic terms used herein are defined as follows: the western North Atlantic Ocean is defined as northeastern South America north of the Equator, the Caribbean Sea, the U.S. Eastern Seaboard, and the Gulf of Mexico; the U.S. East Coast is defined as the U.S. Atlantic Seaboard from Miami, FL, northward through coastal Maine out to the continental shelf edge; and the Florida Keys are defined as southeastern Florida southward of Miami, FL, encompassing Biscayne Bay and Key Biscayne, and westward through Dry Tortugas National Park out to the edges of the insular shelves, encompassing Florida Bay. Even though Key Biscayne is not geographically part

**Table 1** Summary of blacktip shark distribution off the United States East Coast taken from the scientific literature. Occurrence is represented by an “X” and “X+” represents an increase in abundance in a region where blacktip sharks occur year-round

Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Reference
Buzzards Bay, MA													Bigelow and Schroeder (1948)
Long Island, NY							X	X					Helmuth (1916); Thorne (1916)
Delaware						X	X	X					Kohler and Turner (2019)
North Carolina					X	X	X	X					Castro (1996); Bigelow and Schroeder (1948)
South Carolina				X	X	X	X	X	X				Castro (1993a, b); Castro (1996)
Georgia					X	X	X	X	X				Castro (1996); Dahlberg and Heard (1969)
Daytona Beach, FL	X	X	X+	X+	X	X	X	X	X+	X+	X	X	Castro (1996)
Melbourne Beach, FL	X	X	X	X	X+	X+	X	X	X	X	X+	X+	Dodrill (1977)
SE FL	X	X	X	X	X	X	X	X	X	X	X	X	Tinari and Hammerschlag (2021); Kajjura and Tellman (2016); Bigelow and Schroeder (1948)
Miami/Key Biscayne, FL	X	X	X	X	X	X	X	X	X	X	X	X	Tinari and Hammerschlag (2021); Bigelow and Schroeder (1948)
Florida Keys	X	X	X	X	X	X	X	X	X	X	X	X	Castro (1996); Wright (1983); Tinari and Hammerschlag (2021); Bigelow and Schroeder (1948)

of the Florida Keys, the region around Key Biscayne (e.g., Biscayne Bay) is geologically more similar to the Florida Keys than to the Atlantic coast north of Miami and this definition enables us to describe the behavior of blacktip sharks off the U.S. East Coast more succinctly.

## Biology

The blacktip shark, *C. limbatus*, is circum-global in tropical to warm-temperate zones. It inhabits shallow coastal waters over insular and continental shelves and is rarely found below 30-m depth (Compagno 1984; Castro 2011). Genetically distinct populations of this species occur in western Africa, South Africa, the Indian Ocean, eastern Australia (Keeney and Heist 2006), the Pacific Ocean (Almojil et al. 2018), northeastern Brazil (Sodré et al. 2012), the Caribbean Sea (Gledhill et al. 2015), the Gulf of Mexico, and the U.S. East Coast (Keeney et al. 2003). The maximum documented size of a blacktip shark is 260 cm total length (TL), which was recorded in the Pacific Ocean (Tester 1969). The maximum length in the western North Atlantic, however, is 218 cm, measured from a specimen in the southern Caribbean Sea, off the coast of Venezuela (Tavares 2008). Off the U.S. East Coast, the maximum recorded size of the blacktip shark is 202 cm TL (Castro 1996).

Life history characteristics may differ among the western North Atlantic populations (Carlson et al. 2006). When only fork length (FL) was available in the literature (Baremore and Passerotti 2013), lengths at maturity were converted from FL to TL using the formula  $(TL = 1.12(FL) + 1.12)$  (Carlson et al. 2006) to facilitate comparison. Whereas the growth rates of blacktip sharks from the Gulf of Mexico and U.S. East Coast are similar, lengths and ages at maturity differ (Carlson et al. 2006). Off the U.S. East Coast, female blacktip sharks reach maturity at a size of 112 to 137 cm FL (127 to 155 cm TL), at about 6.7 years of age, whereas males mature at a size of 111 to 128 cm FL (125 to 145 cm TL), at about 5.0 years of age (Castro 1996; Carlson et al. 2006). In the Gulf of Mexico, female blacktip sharks mature between 109 and 122 cm FL (123 and 138 cm TL), at about 5.7 years, and males mature between 102 and 106 cm FL (115 and 120 cm TL), at about 4.5 years (Carlson et al. 2006; Baremore and Passerotti 2013).

Blacktip sharks exhibit a synchronous reproductive cycle, during which mating and parturition peak in May and June (Castro 1996; Baremore and Passerotti 2013). This cycle is biennial in females, in which 1 year of gestation is followed by a year of rest (Castro 1996, 2009; Baremore and Passerotti 2013). During the reproductive year, female blacktip sharks off the U.S. East Coast carry 1–9 embryos with an average of 4.6 (Bigelow and Schroeder 1948; Dodrill 1977; Castro 1996, 2011). This species is viviparous and placentotrophic, which means that embryos transition from yolk nutrient supplies (lecithotrophic) to placental connection (matrotrophic) during development (Castro 1996, 2009; Bester-van der Merwe et al. 2022). Nutrients are offloaded from the liver to the developing offspring (Castro 1996, 2009), which is evident by the emaciated livers that are observed in female blacktip sharks just after parturition (Castro 1996). This suggests that the gestation cycle is more energetically costly than the resting cycle.

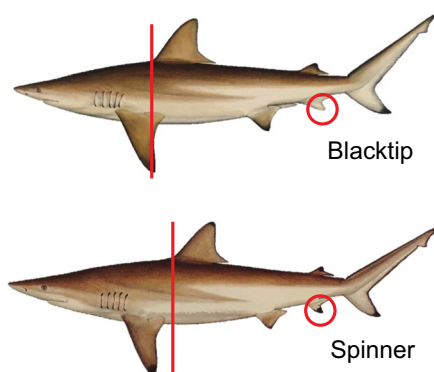
The diet of adult blacktip sharks is comprised primarily of teleosts, with some smaller elasmobranchs and crustaceans (Compagno 1984). Stomach contents of blacktip sharks off Melbourne Beach, FL, were comprised of 12 teleost species, Atlantic horseshoe crab (*Limulus polyphemus*), and unidentified crab and shrimp species (Dodrill 1977). The stomach contents of blacktip sharks taken off Daytona Beach, FL, and Folly Beach, SC, in a commercial shark fishery were comprised of at least 7 teleost species, 2 shark species, and shrimp trawl bycatch (Castro 1996). Their broad diet appears to lack specialization.

## Misidentification

The blacktip shark, *C. limbatus*, and spinner shark, *C. brevipinna*, have only subtle morphological distinctions and both species exhibit the same leaping and spinning behavior (McCormick et al. 1963; Dodrill 1977; Branstetter 1982; Castro 1996). One of the most common identification methods used by fishers to discern blacktip sharks from spinner sharks is the coloration of the anal fin. Counterintuitively, the anal fin is generally black-tipped in the adult spinner shark but lacks markings in the adult blacktip shark in the western North Atlantic (Bigelow and Schroeder 1948). However, the markings on these species are highly variable among individuals and change throughout ontogeny (Branstetter 1982; Garrick 1982). The

black markings of a spinner shark are absent in the neonate stage, but gradually develop in the juvenile stage (Garrick 1982). In younger specimens of Atlantic blacktip sharks, the black markings are generally more prominent and are always present on the tips of the second dorsal fin, the ventral lobe of the caudal fin, and the pectoral fins, particularly on the ventral side, but the markings on the pelvic fins are sometimes faint and anal fin markings are usually absent (Branstetter 1982; Garrick 1982; Castro 2011). However, Bigelow and Schroeder (1948) state that black markings on the anal fin are present in young blacktip sharks of the western North Atlantic. With the exception of the ventral pectoral fin tips, the markings on the blacktip shark fade over ontogeny becoming less prominent (Bigelow and Schroeder 1948; McCormick et al. 1963; Branstetter 1982; Garrick 1982). Thus, at an intermediate size range, the markings on both spinner and blacktip sharks look nearly identical, which makes it very difficult to identify juvenile specimens correctly using markings alone.

Another common characteristic used to discern spinner and blacktip sharks is the origin of the first dorsal fin. The first dorsal fin of a blacktip shark originates over the insertion of the pectoral fins, whereas the dorsal fin of a spinner shark originates posterior to the insertion of the pectoral fins (Fig. 1) (Bigelow and Schroeder 1948; Branstetter 1982; Castro 2011). The relationship between the dorsal fin origin and pectoral fin insertion also changes throughout ontogeny



**Fig. 1** The blacktip shark (above) and spinner shark (below) exhibit similar morphological characteristics, which could have caused misidentification in landings reports. Red lines and circles indicate morphological distinctions commonly used to distinguish these species. Illustrations adapted from *Sharks of North America* (Castro 2011 used with permission)

and so it can be used as a distinguishing characteristic only in adult specimens (Branstetter 1982), which increases the uncertainty in identification of immature individuals.

The most reliable methods to differentiate a blacktip from a spinner shark are to examine the posterior mandible of the jaw for a notch (F. Crooke from Branstetter 1982), to compare the interdorsal distance to the height of the first dorsal fin, or to compare the measurements of the prenarial length to the distance between the anterior nares and the anterior mouth (Bass 1973; Branstetter 1982). In *C. limbatus*, a posterior mandibular notch is present, the interdorsal distance is less than or equal to 2.2 times the height of the first dorsal fin, and the prenarial length is less than the nares:mouth length whereas in *C. brevipinna*, a mandibular notch is absent, the interdorsal distance is greater than 2.2 times the dorsal fin height, and the prenarial length is greater than the nares:mouth length (Branstetter 1982). Without a dead specimen or measuring tape, these methods are cumbersome (Branstetter 1982) and are unlikely to be used in situations that require rapid identification.

In addition to morphological similarity potentially causing confusion, *C. limbatus* and *C. brevipinna* were previously reported as the same species. Despite *C. brevipinna* having been recognized as a separate species by Poey in 1865, *C. brevipinna* was reported as the same species as *C. limbatus* prior to 1938 (Springer 1938; Bigelow and Schroeder 1948; McCormick et al. 1963). The dynamic, inconsistent, and counterintuitive nomenclature of these two species may also contribute to confusion. The common name “black-tip shark” was previously used to refer to the species that we now call the “spinner shark.” Springer (1938) referred to *C. brevipinna* as *Isogomphodon maculipinnis* (Poey, 1865), and used the common name black-tip shark, and *C. limbatus* as *Isogomphodon limbatus* (Müller and Henle) with the common name, spot fin shark. Bigelow and Schroeder (1948) also used confusing common nomenclature by referring to *C. limbatus* and *C. brevipinna* as the small and large black-tipped sharks, respectively.

## Distribution

Whereas the range of blacktip sharks in the western Atlantic Ocean reportedly spans from southern Brazil to Massachusetts in some literature (Bigelow and

Schroeder 1948; Compagno 1984), sampling data from a mark and recapture study show a range from French Guiana to Delaware Bay (Kohler and Turner 2019). These range descriptions include the Gulf of Mexico and at least the eastern portion of the Caribbean (Bigelow and Schroeder 1948; Compagno 1984; Kohler and Turner 2019). Descriptions of the distribution of blacktip sharks off the U.S. East Coast are highly variable throughout the scientific literature. Because this species is considered highly migratory, the distribution is dependent upon migratory movements. Regions that are in between northern and southern migratory termini will generally experience two increases in abundance per year; once during the northward migration and once during the southward migration.

Bigelow and Schroeder (1948) stated that the blacktip shark is common in “southern Florida” through spring, summer, and fall but is not reported there in December through February. This absence of blacktip sharks in Florida during the winter is perpetuated by Compagno (1984). It is unclear precisely what Bigelow and Schroeder (1948) classified as “southern Florida” or what Compagno (1984) meant by “Florida” since “southern Florida” and “Florida” can refer to either the east (Atlantic) or west (Gulf of Mexico) coast or both. It is possible that Bigelow and Schroeder (1948) and Compagno (1984) were referring to the west coast of Florida when they made their assertions. Blacktip sharks were caught off the central Gulf coast of Florida in all months except December, January, and February during a monthly sampling study conducted from Boca Grande Pass to Longboat Key, Sarasota, from 1955 through 1963 (Clark and Von Schmidt 1965), which is consistent with what Bigelow and Schroeder (1948) and Compagno (1984) described in “southern Florida.” Further, Springer (1938) described a similar lack of *C. limbatus* catch during December, January, and February off the coast of Englewood, which is also located on the southwestern coast of Florida. It is plausible that Bigelow and Schroeder (1948) and Compagno (1984) were referring to the Gulf Coast of Florida when stating that blacktip sharks were not reported in “southern Florida” from December through February.

It is also possible that “southern Florida” was meant literally as the southern tip of Florida (Florida Bay and the Florida Keys). Castro (2011) stated that blacktip sharks overwinter off southern

Florida including the Keys. Tabb and Manning (1961) reported that blacktip sharks were the most abundant shark in the “shallow waters of Florida Bay and associated brackish water” but were uncommon in December, January, and February, which is consistent with Bigelow and Schroeder (1948). However, Wright (1983) stated that blacktip sharks were one of the most abundant shark species in the Florida Keys and occurred there year-round, with no mention of the decrease in abundance in winter described by Tabb and Manning (1961). However, Wright (1983) also described increases in abundance in late October and early November, which he concluded is a result of seasonal migrations of blacktip sharks through the Florida Keys. The reported year-round occurrence of blacktip sharks in the Florida Keys is further supported by mark and recapture data (Kohler and Turner 2019) and a sampling study conducted in Everglades National Park (Wiley and Simpfendorfer 2007).

Blacktip sharks that inhabit the Florida Keys may be an extension of the Gulf of Mexico stock. Wright’s (1983) notion that blacktip sharks move across the Florida Keys in October and November is seasonally consistent with the migration pattern of juvenile blacktip sharks in the eastern Gulf of Mexico (Clark and Von Schmidt 1965; Castro 2011). Juvenile blacktip sharks move from nurseries in the eastern Gulf of Mexico to the Florida Keys when water temperatures decrease (Hueter et al. 2005; Heithaus et al. 2007), although Wright (1983) caught both mature and immature blacktip sharks in the Florida Keys. Blacktip sharks have been observed to move between the southwestern Florida Keys and the Gulf of Mexico (Kohler and Turner 2019). In contrast to the apparent movement of blacktip sharks between the Florida Keys and the Gulf of Mexico, no blacktip shark has ever been observed to travel between the U.S. East Coast and the Gulf of Mexico, which contain genetically distinct populations (Keeney et al. 2003). This lack of movement is based on 10,652 tags being deployed on blacktip sharks in the western North Atlantic Ocean and 294 recaptures over a 52-year mark and recapture study (Kohler and Turner 2019). However, no obvious physical or oceanographic barrier exists that would prevent this movement (Castro 2011; Kohler and Turner 2019). This lack of migratory connectivity suggests that the Florida Keys cohort of blacktip sharks is an extension of the Gulf of Mexico population rather than the U.S. East



Coast population, but further movement and genetics research on the Florida Keys population is needed to bolster this claim.

Whereas there is no evidence of blacktip shark migratory connectivity between the Gulf of Mexico and the U.S. East Coast, connectivity between Biscayne Bay, FL, and Florida Bay was recently documented (Tinari and Hammerschlag 2021). Blacktip sharks are found year-round in Biscayne Bay, which is immediately south of Miami, FL (Tinari and Hammerschlag 2021). Most individuals that left Biscayne Bay, FL, moved southward and westward into Florida Bay ( $N=3$ ) (Tinari and Hammerschlag 2021). Another individual relocated from Florida Bay to Biscayne Bay (Tinari and Hammerschlag 2021). This east and west movement within the Florida Keys aligns with Wright's notion (1983) of a migration through this region; however, the timing may be outside October and November, which was when Wright postulated that this migration occurred. One individual that moved from Biscayne Bay into the Florida Keys did so between May and mid-June (Tinari and Hammerschlag 2021). The time between observations that corresponded to the remainder of these movements between Biscayne Bay and Florida Bay encompassed October and November, as Wright (1983) suggested, but the average time between observations was 174 days, half a year (Tinari and Hammerschlag 2021), and so the potential timeframe of travel was about as likely to incorporate these months as it was likely to exclude them. These instances may serve as evidence of connectivity between the Florida Keys and the U.S. East Coast, even though our geological-based definitions do not support this claim. Our geological-based definitions were chosen in the interest of concise descriptions of movement and are not based on geographical definitions, and thus, further investigation of connectivity between the Florida Keys and U.S. East Coast may be warranted. In addition, one individual left Key Biscayne and traveled northward to Lake Worth, FL (Tinari and Hammerschlag 2021). This variation in the movement patterns among blacktip sharks in Biscayne Bay, FL, may suggest that there exists some overlap between the distributions of the U.S. East Coast blacktip shark cohort and the Florida Keys cohort of blacktip sharks. In contrast, Kajiura and Tellman (2016) reported a singular annual increase in abundance of blacktip sharks off the coast of southeastern Florida (Palm

Beach County, FL) in January, February, and March. Because only one seasonal increase in blacktip shark abundance occurs per year off Palm Beach County, FL, it is most likely the southern terminus of the U.S. East Coast blacktip shark migration (Kajiura and Tellman 2016). Thus, if overlap between the Florida Keys and U.S. East Coast blacktip shark distributions exists in Biscayne Bay, it may be sparse. In addition, this singular annual increase in abundance off Palm Beach County, FL, may further substantiate dissociation between the Florida Keys and U.S. East Coast blacktip shark populations.

Whereas Keeney et al. (2003) and Keeney et al. (2005) determined the blacktip shark population along the western coast of Florida to be genetically distinct from the blacktip shark population off the U.S. East Coast, blacktip sharks found in the Florida Keys were not included in the sampling from those studies. In addition, Keeney et al. (2005) found greater genetic differentiation in the mitochondrial control region of neonates in the U.S. East Coast and Gulf of Mexico populations, and microsatellite homogeneity of neonates among the northwestern Atlantic populations, which could indicate philopatric females and more highly dispersive males. Keeney et al. (2005) suggested that females may mate with males from other regions and return to their natal nurseries to give birth. Thus, it is possible that male and female blacktip sharks travel between the Gulf of Mexico and U.S. East Coast to mate but that females exhibit greater site fidelity towards their natal nurseries than males. Further investigation of the movement patterns and genetic structure of the Florida Keys blacktip shark inhabitants is warranted to ensure that the current stock boundaries between the Gulf of Mexico and U.S. East Coast are appropriate.

Although no blacktip shark migratory connectivity between the U.S. East Coast and Gulf of Mexico has ever been documented, there is some movement between the Caribbean and the U.S. East Coast populations, which was speculated by Castro (1996). The population of blacktip sharks in the Caribbean was demonstrated to be genetically distinct from other surrounding populations, but based on mark and recapture and/or telemetry data, at least four blacktip sharks traveled from the Caribbean to the east coast of the USA (Gledhill et al. 2015; Kohler and Turner 2019; Legare et al. 2020). One traveled from Bimini, Bahamas, to Melbourne Beach, FL (Gledhill

et al. 2015); one from the U.S. Virgin Islands to Cape Canaveral, FL (Kohler and Turner 2019); one from the U.S. Virgin Islands to the coast east of Port St. Lucie, FL (Legare et al. 2020); and another from the U.S. Virgin Islands to Jekyll Island, GA (Legare et al. 2020). Genetic distinction between two populations does not necessarily imply a lack of movement between two regions. In the case of synchronous reproducers, genetic distinction merely suggests differences in spatial distribution during the mating season. Thus, it is important to investigate the composition of the Florida Keys population of blacktip sharks using both genetic and behavioral tools.

Accounts in Bigelow and Schroeder (1948) may be subject to misidentification because the description of the *C. brevipinna* seasonal distribution is more similar to current observations of *C. limbatus* (Bigelow and Schroeder 1948). These authors state that *C. brevipinna* was “common in winter off southeastern Florida,” which could include anywhere between the Upper Florida Keys and Sebastian, FL (Bigelow and Schroeder 1948). The winter distribution of *C. brevipinna* described by Bigelow and Schroeder (1948) is consistent with recent observations of winter aggregations of *C. limbatus* off Palm Beach County in southeastern Florida (Kajiura and Tellman 2016) and inconsistent with the complete absence of *C. brevipinna* in that region from coastal fishing surveys performed between 2014 and 2022 (Kajiura, unpublished data). Bigelow and Schroeder note that even though *C. brevipinna* (formerly *maculipinnis*) was described over 75 years prior to their 1948 description, it was generally confused with and reported as *C. limbatus* (Springer 1938; Bigelow and Schroeder 1948). Springer (1963) claimed that spinner sharks passed Salerno, FL, during an early spring northward migration, during which they regularly leapt and spun out of the water. Whereas Springer (1963) states that he is confident that sharks spinning within 30 yards of himself were spinner sharks, he notes that substantial efforts to land these fish were unsuccessful and that many sharks were seen spinning out of the water considerable distances from shore and so there is no way to tell whether all the breaching sharks were spinner sharks. Dodrill (1977) caught only two adult spinner sharks, one each during February and April, off the coast of Melbourne Beach, FL, which is 100 km north of Port Salerno, FL. Dodrill (1977) reported that blacktip sharks were caught within

500 m of Melbourne Beach, FL, year-round between November 1974 and January 1977. However, blacktip shark catch increased in late May and June and again in November and December, which suggests that the blacktip sharks are migrating through this region at those times (Dodrill 1977). The biannual increase in abundance in central Florida described by Dodrill (1977) is temporally consistent with the single increase in abundance observed off Palm Beach County, FL, during the intervening months, January through March (Kajiura and Tellman 2016). The timing of the two adult spinner sharks caught in the Dodrill (1977) study do temporally coincide with winter distributions of *C. brevipinna* in southeastern Florida (Bigelow and Schroeder 1948; Compagno 1984) and it is possible that spinner sharks were more abundant in depths that were outside the Dodrill (1977) study site. However, it is also possible that Springer (1963) misidentified these spinning sharks and that spinner sharks are rare in Melbourne Beach, FL, as Dodrill (1977) concluded. Aggregations of blacktip sharks occur off Daytona Beach, FL, in mid-March to late April (Castro 2011), which is consistent with Kajiura and Tellman (2016), but slightly inconsistent with Dodrill (1977) as the first annual increase in abundance off Melbourne Beach, FL, occurred after April in late May and June. Bigelow and Schroeder (1948) also note the occurrence of *C. brevipinna* off the northeastern coast of Florida in the spring, which corresponds with the spring distribution of *C. limbatus* in Castro (2011) in addition to recent observations of *C. limbatus* off Jacksonville at that time of year (McCallister et al. 2013). It is possible that many of the accounts around Florida that Bigelow and Schroeder (1948) attributed to *C. brevipinna* were actually *C. limbatus*. In any case, these discrepancies justify the need for further investigation of the seasonal distributions of blacktip sharks off the U.S. East Coast.

#### Mating and nursery grounds

One consistent claim in most western North Atlantic blacktip shark movement ecology literature is that the migration revolves around the synchronous reproductive cycle, during which mating occurs around May and June (Springer 1938; Bigelow and Schroeder 1948; Dodrill 1977; Castro 1996). In April and May, adult blacktip sharks reach South Carolina (Castro

1993a, 1996). Ulrich et al. (2007) observed female and male adult blacktip sharks in South Carolina estuarine waters during May and June. By late May and early June, some blacktip sharks reach North Carolina (Castro 2011).

Every other year, females give birth during May and June in habitat that will serve as a nursery to the neonates (Castro 1993a, 1996). Primary shark nursery grounds are characterized by the birthplace of sharks, whereas secondary nursery grounds are areas that are inhabited by sharks that are pre-adolescent but older than neonates (Bass 1978). Castro (1993a) argued that identification of primary nursery grounds requires the observations of both free-swimming neonates and gravid females. Heupel et al. (2007) proposed that a nursery should be defined as a repeatedly used area where neonates and young-of-year sharks remain for weeks or months in greater densities as compared to overall density.

No nursery grounds have been confirmed in Florida, but it is likely that a primary nursery site exists relatively close to Melbourne Beach, FL. Dodrill (1977) caught many gravid female blacktip sharks off Melbourne Beach, FL, during all months except May, June, and July (Dodrill 1977). The catch of postpartum and newly mated females increased in late May and early June, when parturition occurs in this species, but no neonates were caught (Dodrill 1977). Thus, no direct evidence of a nursery ground in Melbourne Beach, FL, can be derived from this study as no gravid females or neonates were caught at the time of parturition (Bass 1978; Castro 1996, 2009; Heupel et al. 2018). However, it is likely that a birthing area exists relatively close by as parturition occurs in May through mid-June (Castro 1996, 2009) and gravid female blacktip sharks were caught in April and postpartum females were caught in the same location in late May (Dodrill 1977). Although Dodrill states that identification keys and descriptive material were used to identify the sharks, it is possible that misidentification existed in the Dodrill (1977) study. Multiple individuals identified the shark specimens and 16% (73/445) of the specimens were not examined by Dodrill himself. Dodrill (1977) referenced fisher non-compliance in logging information on the conditions and times of the catch and so it is possible that fishers were lackadaisical in properly identifying the species as well. Aubrey and Snelson (2007) identified secondary nursery grounds in Cape Canaveral

and Cocoa Beach, FL for spinner sharks (Aubrey and Snelson 2007), which would coincide with the findings in Dodrill (1977) if gravid spinner sharks were falsely identified as blacktip sharks. Four spinner sharks were reported in Dodrill (1977), two adults, one unsexed during February and a gravid female during April, and two juveniles, a pre-adolescent during May and a neonate during June that possessed an umbilical scar, and so, it is possible that at least some gravid females recorded as blacktip sharks were spinner sharks. Gurshin (2007) incorrectly cited Castro (1996) as stating that gravid female blacktip sharks in the southeastern U.S. migrate to Florida to birth pups in shallow coastal habitats. However, McCallister et al. (2013) later documented evidence of young of year and juvenile blacktip sharks in Cumberland and Nassau Sounds in northeastern Florida, making these areas both potential primary and secondary nurseries, according to Bass' (1978) definition.

Mating and nursery grounds used by the U.S. East Coast blacktip shark have been confirmed in Georgia and South Carolina (Castro 1996; Abel et al. 2007; Gurshin 2007; Ulrich et al. 2007). Primary nursery habitat for blacktip sharks has been identified in the Middle and Lower Duplin River and Doboy Sound, GA (Gurshin 2007), and the estuarine waters of Port Royal Sound, St. Helena Sound, North Edisto, Charlestown Harbor, and Bulls Bay, SC (Ulrich et al. 2007). Juvenile blacktip sharks were caught off Georgia from July to September (Dahlberg and Heard 1969; Castro 1996). Secondary nursery habitat for blacktip sharks has been observed in estuarine waters of Georgia (Gurshin 2007) and both estuarine and nearshore waters of South Carolina (Ulrich et al. 2007). Castro (1996) stated that southern North Carolina served as both a primary and secondary nursery for blacktip sharks because neonates, juveniles, and breeding adults spent the summer there. However, data from a more recent 2-year study sampling from May to September suggest that neonate blacktip sharks inhabit southern North Carolina infrequently (Thorpe et al. 2004). During that study, only one neonate blacktip shark was caught, and adult female blacktip sharks were not caught during May and June, when parturition occurs (Thorpe et al. 2004). Blacktip shark neonates were also absent in other routine nearshore surveys in North Carolina (F. Schwartz, University of North Carolina Institute of Marine Sciences, pers. comm. from Thorpe et al. 2004; Jensen

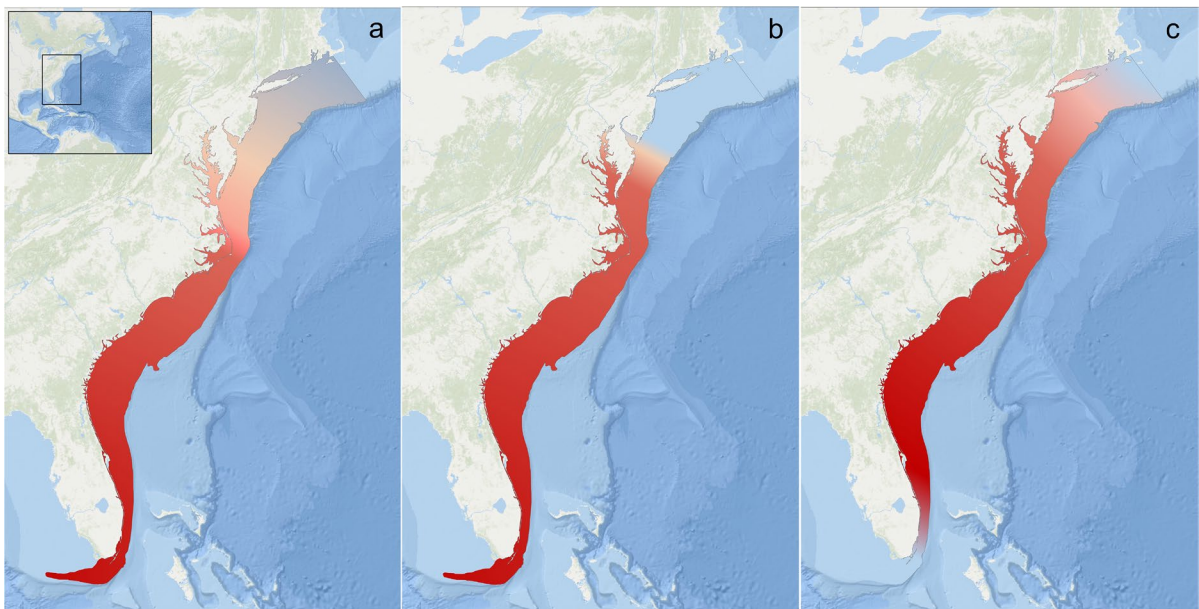


and Hopkins 2001) and Virginia (D. Grubbs, Virginia Institute of Marine Sciences, pers. comm. from Thorpe et al. 2004). By the definition proposed by Heupel et al. (2007), North Carolina is not a nursery at all. Taken together, this evidence suggests that both primary and secondary blacktip shark nurseries exist in Georgia and South Carolina in the western North Atlantic Ocean. However, according to the proposed nursery definition in Heupel et al. (2007), the densities of neonates and young-of-year in these pre-established nursery habitats should be statistically compared to the density of blacktip neonates and young-of-year in neighboring marine waters (Heupel et al. 2018), which suggests that the potential for Georgia and South Carolina waters to support a nursery for this species still requires confirmation. In addition, Florida waters should be evaluated as both primary and secondary blacktip shark nursery habitat.

Bigelow and Schroeder (1948) note that blacktip sharks occur north of Cape Hatteras, NC “only as a stray.” However, recent work has demonstrated that blacktip sharks occur at least as far north as Delaware Bay (Fig. 2b) (Kohler and Turner 2019). Whereas Bigelow and Schroeder (1948) stated that blacktip

sharks rarely surpassed Cape Hatteras, NC, Kohler and Turner (2019) demonstrated that blacktip sharks travel from northeastern Florida as far north as Delaware Bay and from southeastern Florida (around Jupiter, FL) to Virginia. Blacktip sharks occurred north of Cape Hatteras, NC, during summer and autumn (Kohler and Turner 2019).

There have been some accounts of blacktip sharks caught off Long Island, NY. One adult male blacktip shark was taken in Great South Bay, Long Island, NY, in July of 1910, but it may have been misidentified (Nichols 1916; Thorne 1916). J.T. Nichols identified the species (Thorne 1916), but only by the jaw, which is very similar to that of *C. brevipinna* (Naylor and Marcus 1994), with the exception of a notch on the posterior trailing edge of the mandible in *C. limbatus* (F. Crooke from Branstetter 1982). This morphological distinction was not published until 1982 and thus, it is unlikely that Nichols or Thorne were aware of this distinction in 1910. Moreover, it is almost certain that this individual was misidentified as *C. limbatus* as the length of the shark (9' 2", 279.4 cm) exceeds the maximum documented in the scientific literature (260 cm) by 7.5% (Tester 1969), the global catch



**Fig. 2** Distribution of United States East Coast blacktip shark population based on various interpretations from the literature. **a** Blacktip shark distribution based on Helmuth (1916), Thorne (1916), Bigelow and Schroeder (1948), Wright (1983), and

Castro (1996). **b** Blacktip shark distribution based on Kohler and Turner (2019). **c** Blacktip shark distribution based on our current interpretation of all available literature

record for the species (245 cm) by 14% (International Game Fish Association (IGFA) 2022), and the maximum size caught off the U.S. East Coast (202 cm TL) by 38%. Based on age and growth data from a previous study, which found that 50% of the male population in the South Atlantic Bight, USA, are mature at 5 years of age, at around 116.7 cm FL (132 cm TL) and a growth rate of 6.5 cm year<sup>-1</sup> from 0 to 12 years of age (Carlson et al. 2006), this potentially misidentified blacktip shark would have been about 28 years old. Currently, the maximum observed age of blacktip sharks is 15.5 years, which was a female (Carlson et al. 2006). In this same study, the maximum age of males observed in the South Atlantic Bight was 13.5 years (Carlson et al. 2006). In addition, this harvest of a potentially misidentified *C. limbatus* was only one of 350–400 sharks harvested by Thorne in Great South Bay, Long Island (Thorne 1916). Although it is possible that increased fishing efforts and other anthropogenic effects have decreased the maximum age of this population, it is likely that this individual was not a *C. limbatus* specimen. However, two blacktip sharks were landed off Easthampton, Long Island, in 1916. One was female and the size was approximated at 7' (213 cm) and the other was male, measured at 6' 4" (193 cm) (Helmuth 1916). The female was approximated at a size 5.4% larger than the maximum size recorded for this species off the U.S. East Coast (202 cm) (Castro 1996). Although it is possible that this was a record size blacktip shark for this region, it is more likely that this specimen was misidentified or that the size of the female blacktip shark was overestimated. Helmuth (1916) examined four other blacktip sharks harvested off Montauk Point “some days before” September 1st [1916]. No measurements for these four sharks were reported and Helmuth (1916) declares that *C. limbatus* is rare on Long Island. These rare reports are consistent with Bigelow and Schroeder (1948), which states that blacktip sharks reach “the southern New England coast in unusual numbers at rare intervals” (Fig. 2a). This same rare occurrence in New York and New England is referenced in secondary literature (McCormick et al. 1963).

Bigelow and Schroeder (1948) also cite two instances in which at least 20 small blacktip sharks were caught in a pound net off Buzzards Bay, near Woods Hole, MA, during the summers of 1878 and 1916 and state “Nor is it unusual to see Black-tipped

Sharks in the warm oceanic waters off this sector of the continental shelf in summer” (Bigelow and Schroeder 1948). The authors hypothesize that these stray individuals drift north into the Gulf Stream and never return (Bigelow and Schroeder 1948). These accounts in Bigelow and Schroeder (1948) have been used to establish Massachusetts (or New England) as the northern range for *C. limbatus* (e.g., Castro 1996, 2011; Compagno 1984; Compagno et al. 2005; Ebert et al. 2013; Rigby et al. 2021) (Fig. 2a). However, Bigelow and Schroeder (1948) explain that the occurrence of blacktip sharks in the western North Atlantic Ocean could only be “outlined within broad limits” because of the possibility that published records referred to spinner sharks, *C. brevipinna* (Valenciennes in Müller and Henle, 1839), formerly *C. maculipinnis* (Poey, 1865), and not *C. limbatus* (Bigelow and Schroeder 1948). Thus, there exists uncertainty in the account that “at least twenty small ones were taken in pound nets” due to potential misidentification and in the statement that it is not unusual to see “Black-tipped Sharks” in this northern region, as this could refer to either *C. limbatus* or *C. brevipinna* since the authors refer to these species as Small and Large Black-tipped sharks, respectively, and since *C. brevipinna* was reported as *C. limbatus* until about 1938 (Springer 1938; Bigelow and Schroeder 1948). It is possible that the *C. limbatus* landings data used in Bigelow and Schroeder (1948) contain inaccurate accounts, and thus, it is also possible that the range of *C. limbatus* never reached the Massachusetts coast. Therefore, we contend that the northern extent of the *C. limbatus* range north of Long Island, NY, should be referenced with caution and that the seasonal distribution of U.S. East Coast blacktip shark warrants further investigation prior to the evaluation of any climate change effects on this population.

Interindividual variability in the northern extent seems to exist within this population. The distribution of blacktip sharks off the U.S. East Coast during fall spans from Delaware to southeastern Florida (Kohler and Turner 2019). In South Carolina, however, adult blacktip sharks occur in abundance through September (Castro 1993a, 1996) and at least a portion remains in South Carolina waters until October (Ulrich et al. 2007; Castro 2011). Blacktip sharks leave the mating and nursery grounds in the Carolina(s) and Georgia between late September to mid-October, which coincides with a drop below

21 °C in sea surface temperatures (Castro 1996, 2011). However, Ulrich et al. (2007) observed both male and female adult blacktip sharks in nearshore waters from June through November. A second increase in abundance of blacktip sharks off Melbourne Beach, FL, occurs in November and December (Dodrill 1977). By winter, the blacktip shark distribution off the U.S. East Coast contracts and encompasses the eastern coast of Florida (Kohler and Turner 2019). The variability of blacktip shark distribution found in the literature forms a basis for future research to work towards closing the gaps in the blacktip shark movement ecology knowledge.

#### Potential climate change effects

Climate variability may be the cause of inconsistencies in the northern extent described throughout the blacktip movement ecology literature. Bigelow and Schroeder (1948) and Castro (1996) agree that only stray blacktip sharks surpass Cape Hatteras, NC. However, assuming no misidentification, multiple studies have observed blacktip sharks north of Cape Hatteras, NC, in Virginia (Peterson et al. 2017) through Delaware (Kohler and Turner 2019), off Long Island, NY, albeit rare (Helmuth 1916; Thorne 1916; Bigelow and Schroeder 1948) and potentially Massachusetts (Bigelow and Schroeder 1948). Peterson et al. (2017) speculated that blacktip sharks may adjust their northern migratory limit according to unfavorable environmental conditions associated with the Atlantic Multidecadal Oscillation Index, which is closely associated with sea surface temperatures. These rare sightings off Long Island, NY, and Massachusetts may have coincided with sea temperature anomalies. The results from the long-term study by Kohler and Turner (2019) suggest that blacktip shark occurrence north of Cape Hatteras, NC, is no longer as rare as what Bigelow and Schroeder (1948) suggested. Given the temperature changes that continue to occur in the western North Atlantic Ocean because of climate change (Pershing et al. 2015; Saba et al. 2016; NOAA (National Oceanic and Atmospheric Administration 2021), a greater number of individuals may be thermoregulating behaviorally to adapt to warming oceans. However, behavioral thermoregulation has not been proven in this population and the environmental drivers of U.S. East Coast

blacktip shark migratory movements need to be further investigated.

#### Sexual segregation

Rather than misidentification or environmental variability caused by climate change, the inconsistent descriptions of the spatiotemporal distribution of the blacktip shark could be a result of sexual segregation. Information on the sexual segregation of the U.S. East Coast blacktip shark is lacking. Many descriptions of the blacktip shark migratory pattern do not distinguish between male and female movements (e.g., Springer 1938, 1963; Bigelow and Schroeder 1948; Castro 1996, 2011). Yet, sexual segregation is common in elasmobranch species (e.g., Klimley 1987; Economakis and Lobel 1998; Pratt and Carrier 2001; Sims et al. 2001; Sims 2005; Mucientes et al. 2009; Dell’Apa et al. 2014; Haugen et al. 2017), was documented in blacktip sharks in the northern Gulf of Mexico (Drymon et al. 2020), and was hypothesized for the blacktip shark population off Melbourne Beach, FL (Dodrill 1977). Dodrill (1977) stated that an increase in the abundance of blacktip sharks off Melbourne Beach, FL, occurred in late May through June and was comprised primarily of female blacktip sharks ( $n=88$ ), the most abundant shark in depths less than 10 m off Melbourne Beach, FL. While very few male blacktip sharks were caught during the Dodrill (1977) survey ( $n=3$ ), adult male blacktip sharks were regularly landed in late March to mid-May off Melbourne Beach, FL, outside of the survey period, slightly earlier than the increase in female blacktip shark abundance. Ebert et al. (2013) specified that female blacktip sharks are seasonally migratory in addition to stating that this species often segregates by age and sex. It is possible that male and female blacktip sharks occupy the same space at different times, outside the mating period.

In shark populations, male aggression can promote sexual segregation due to the energetic burden that the female incurs from mating associated injuries (Sims 2005). In the act of copulation, the male uses its teeth to grasp the trunk or pectoral fin of the female in its mouth and the female often incurs physical damage as a result (Stevens 1974; Pratt 1979; Gilmore et al. 1983; Schwartz 1984; Castro 1993b, 1996, 2000; Pratt and Carrier 2001). During the mating season, reproductive female blacktip sharks are

characterized by fresh, deep lacerations that sometimes penetrate the musculature almost to the peritoneum (Castro 1996). Blacktip sharks in the northern Gulf of Mexico segregate by sex but remain in similar temperatures (Drymon et al. 2020). This may suggest that sex-specific differences in reproductive strategies, such as females seeking out refugia from predators for their offspring, are responsible for spatial segregations in that population (Drymon et al. 2010).

Female blacktip sharks carry the energetic burden of gestation and may exhibit different reproductive strategies that cause migratory patterns to differ from that of the males (Andersson 1994). The rate of embryonic development in live-bearing ectotherms has been shown to be directly proportional to the internal temperature of the mother (Precht 1958). Thus, gravid females may preferentially inhabit warmer waters to increase embryonic growth rates and shorten the gestation period of their embryos (Harris 1952; Wallman and Bennett 2006; Hight and Lowe 2007). When female blacktip sharks dominated the catch off Melbourne Beach, FL, water temperatures ranged from 15.5 to 29.5 °C (Dodrill 1977). Approximately half (35/76) of the female blacktip sharks landed were gravid during any given month, with the exception of June, which had zero gravid females as the timing was just after parturition (Dodrill 1977). However, temperatures that corresponded to the catch rates of gravid and non-gravid females were not differentiated by Dodrill (1977) and so it does not provide evidence that female blacktip sharks seek out warmer waters to increase the gestational growth rate of their embryos. Further research is necessary to determine whether temperature affects blacktip shark sexes differently and whether females inhabit warmer temperatures during the gestation period.

It is possible that blacktip shark females prefer different prey items than males, similar to what has been observed in scalloped hammerhead sharks, *Sphyrna lewini* (Klimley 1987), to restore the lipid-rich nutrients that are relinquished from the liver during the gestation year to sustain developing embryos. In addition, the diet requirements of females exhibiting resting years may differ from those exhibiting gestation years. Many fishers believe that mullet (*Mugil* spp.) runs drive the southward migration of blacktip sharks (multiple members of the West Palm Beach Fishing Club, pers. comm.). Given that the blacktip shark diet

is comprised of multiple species of teleosts, elasmobranchs, and crustaceans, and no sex-specific diet differences can be found in the scientific literature (Clark and Von Schmidt 1965; Dodrill 1977; Wright 1983; Castro 1996, 2011), there is currently no evidence that suggests that the large-scale movements of a particular prey type drives migratory movements or the sexual segregation of these sharks. Mulletts are accompanied by a variety of meso-predators during the north/south migration that have also been found in blacktip shark stomach contents (e.g., bluefish (*Pomatomus saltatrix*), ladyfish (*Elops saurus*), jacks (*Carangidae*), flounders (*Paralichthys* spp.)) (Dodrill 1977; Castro 1996; Karl's Bait & Tackle: By the Catch Company 2017; Olander 2018; Sukhdeo 2018). While the timing of the southward blacktip shark migration described in the literature may coincide with the mullet run in some areas, this phenomenon coincides with the appearance of many other prey types that could motivate the movements of blacktip sharks (Kajiura and Tellman 2016). However, it is also possible that these ectotherms (blacktip sharks and teleosts) are motivated by changing temperatures and that the coincident appearance of predator and prey occurs as the predators travel southward to avoid decreasing ocean temperatures (Kajiura and Tellman 2016). Further research on the environmental correlates of movement, and their relation to sex, should be pursued for this population.

### Conservation implications

As climate change continues to rapidly alter habitats that are integral to the proliferation of certain species, it becomes imperative to record accurate baselines in movement behavior and occurrence. These baselines allow for future comparison as migratory patterns, seasonal distributions, and ranges shift due to climate change. Misinformation and inconsistencies due to misidentification, such as the presence of spinner sharks and absence of blacktip sharks from southeastern Florida in December through February (Bigelow and Schroeder 1948) or the uncertain accounts of potentially misidentified blacktip sharks off the Long Island and New England coasts described by Bigelow and Schroeder (1948) and Helmuth (1916) during summer, may obscure changes that occur in the distribution of this species under future climate change conditions. Due to these inconsistent accounts, we



may need to rely on more recent baseline information, as opposed to historical range, to measure changes caused by climate change. It is also possible that nursery grounds will shift as environmental conditions are altered by climate change, as recently documented in the congeneric *C. leucas* (Bangley et al. 2018a, b). Thus, potential, and pre-established nursery grounds should be confirmed so that these areas can also be monitored for future shifts and exploitation.

Sexual segregation of blacktip sharks may cause one sex to enter waters that are more frequently fished, thereby creating a sex-biased fishery, where one sex is more heavily exploited than the other (Mucientes et al. 2009; Dell’Apa et al. 2014; Haugen et al. 2017). It has been suggested that the tendency of sharks to segregate by sex may offer resource managers a mechanism to avoid rapid stock depletion by directing fishing efforts away from mature, breeding females (Gilbert et al. 1967; Hoey and Casey 1986; Speed et al. 2010). The blacktip shark is fished commercially and is often bycatch in other commercial fisheries (Hoey 1983; Hoey and Casey 1986; Morgan and Burgess 2007; Whitney et al. 2017a). In addition to commercial fishing, many recreational anglers target blacktip sharks (Guay et al. 2021) for their characteristic strong fight (McCormick et al. 1963; Bullbuster Team 2017; Tamarindo Fishing 2019; Saffan n.d.). Blacktip sharks may endure a greater post-release mortality than many other elasmobranchs due to their strong fight (Gallagher et al. 2017; Mohan et al. 2020; Binstock et al. 2023) and relatively high physiological stress response when angled (Mandelman and Skomal 2009; Whitney et al. 2017b). This stress response, and subsequent post-release mortality, may be exacerbated by warmer water temperatures (Whitney et al. 2017a) and the physiological stress experienced by mating and postpartum females. Researchers have proposed that long-term fishery independent monitoring should be prioritized to further investigate the role that sex-specific migratory patterns play in effective management (Drymon et al. 2020). It is necessary to understand the variability and environmental correlates of blacktip shark migratory movements by sex and reproductive state (i.e., resting or gravid) to fully comprehend the risk of mortality to which this population is subjected along its annual migratory routes. This information can facilitate the development of an effective management strategy to minimize fishery interactions with mature, breeding

females, as has been previously suggested (Hoey and Casey 1986).

## Conclusions

Review of current and historic literature suggests that the blacktip shark off the U.S. East Coast is one stock that ranges from Palm Beach County, FL, to (at least) Long Island, NY (Fig. 2c). The blacktip sharks that inhabit the Florida Keys are not likely part of the U.S. East Coast population as their movement behavior is more similar to the Gulf of Mexico blacktip shark population, although Biscayne Bay may represent a region of spatial overlap between the U.S. East Coast and Gulf of Mexico stocks. However, further investigation is warranted to identify to which population the Florida Keys blacktip shark inhabitants belong, or if they are genetically distinct from neighboring populations.

Inconsistencies in the migratory pattern descriptions of the U.S. East Coast blacktip shark may have occurred because of misidentification, environmental variability caused by climate change, and/or sexual segregation. Future studies should determine the environmental correlates of migratory movement and whether sexual segregation exists in the U.S. East Coast blacktip shark population. One prey item, like mullet, is likely not the sole driver of migratory movement or sexual segregation as blacktip sharks off the U.S. East Coast have been shown to consume a variety of teleost species, elasmobranchs, and crustaceans (Dodrill 1977; Compagno 1984; Castro 1996). Further research is required to determine the sex-specific motivational drivers of blacktip shark movement off the U.S. East Coast.

Indirect evidence of potential nursery habitat in eastern Florida (e.g., Dodrill 1977; McCallister et al. 2013) should be explored further. Fishery managers may benefit from the quantitative analysis of baseline nursery habitat (e.g., Heupel et al. 2018), which could utilize data that are currently being collected through the National Marine Fisheries Service Cooperative Atlantic States Shark Pupping and Nursery Habitat Survey (i.e., COASTSPAN). As climate change continues to rapidly alter the marine environment, it is imperative that we develop reliable baselines by which we can compare future changes.



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**Data availability** Any data referenced in this review manuscript were obtained from the scientific literature.

## Declarations

**Ethics approval** This is a literature review, and therefore, it did not require ethics approval.

**Competing interests** The authors declare no competing interests.

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