Seasonal distribution and environmental predictors of the movement of male blacktip sharks *Carcharhinus limbatus* off the US East Coast

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ABSTRACT: Migrations of many marine species have shifted poleward in response to global climate change. It is imperative to gather baseline distribution data on migratory species so that these shifts can be measured and overexploitation can be avoided. Migratory species can be tracked over great distances using acoustic telemetry within cooperative networks. We reconstructed tracks from acoustic telemetry data using movement modeling and determined the seasonal distribution of male blacktip sharks *Carcharhinus limbatus* along the US East Coast using hot spot analyses. In addition, we modeled the environmental drivers of blacktip shark movement. We show that male blacktip sharks exhibit partial migration, and that individual migration patterns vary. The migrating population frequently migrates farther than what has been described in the scientific literature; several individuals migrated from Palm Beach County, FL, in the winter to as far north as Long Island, NY, in the summer. A smaller proportion of the population remains off southeastern Florida year-round. Male blacktip shark movements correlated with chlorophyll *a* and sea surface temperature in spring, photoperiod in autumn, and chlorophyll *a* and photoperiod in winter. Variable migration patterns likely concealed reliable predictors of movement during the summer. Like many other migratory species, the blacktip shark may have adapted photoperiod as a forecaster of environmental changes. Global climate change will affect many environmental processes but photoperiod will remain unchanged. If sharks use photoperiod as a migratory cue, they may encounter unfavorable conditions more often under climate change scenarios, which could impose stress on individuals and the population.

KEY WORDS: Migration · Hot spot · Acoustic telemetry · Climate change · Continuous-time correlated random walk

1. INTRODUCTION

Migration is defined as repeated movements between regions in which environmental conditions alternate between favorable and unfavorable (Dingle 2014). The commonality that all migratory animals share is that some unfavorable conditions motivate their relocation efforts. These motivational factors are often abiotic and, as global climate change progresses, the migratory patterns and subsequent distributions of many species are expected to change (Wilcove &

Wikelski 2008). Compared to terrestrial ectotherms, marine ectotherms will likely experience a greater effect from climate change (Pinsky et al. 2019). The distributions of many marine ectotherms have already shifted poleward as a result of rising sea surface temperatures (SST) (Cheung et al. 2009, Sorte et al. 2010). Many shark species are ectothermic and behaviorally thermoregulate by traveling latitudinally away from unfavorable temperatures; thus, their migratory movements are often correlated with temperature (Weng et al. 2008, Sequeira et al. 2012, Speed et al. 2012).

Climate change is projected to cause dynamic changes in the environment, including ocean warming (Pachauri et al. 2014), and these dynamic changes could alter the distributions of shark species (Diaz-Carballido et al. 2022). The rate of ocean warming varies across the globe (Saba et al. 2016). For example, the Northwest Atlantic Shelf is projected to warm at a rate that is 3 times that of the global average (Saba et al. 2016) and some areas along the shelf are warming more than others (Pershing et al. 2015). Mixed-layer depths will become shallower, limiting nutrient supplies to phytoplankton (Boyce et al. 2010). Increases in upper sea level temperatures can cause changes in ocean circulation (Manabe & Stouffer 1994), which could reroute the migrations of many fish species that meso- and top predators rely on for food (Goldenberg et al. 2017). Prey abundance can be approximated through lower trophic level measurements such as chlorophyll concentrations (Blackburn et al. 1970, Fiedler et al. 1991, Drymon et al. 2013), and as a result, the movements of many shark species are linked to primary productivity (Weng et al. 2008, Papastamatiou et al. 2013, Rohner et al. 2018). Ocean pH is expected to decrease by 0.1–0.4 by 2100 (Pachauri et al. 2014). Whereas ocean acidification alone would increase primary productivity, the accompanying increases in SST will negate this positive effect as predators will exhibit an increased metabolism in warmer conditions and consume more prey (Goldenberg et al. 2017). Thus, prey abundance is projected to decrease under global climate change conditions (Goldenberg et al. 2017). As a consequence of these broad-scale, rapid changes, it is hypothesized that global climate change will dramatically affect the migrations and ranges of many shark species (Diaz-Carballido et al. 2022).

Although global climate change scenarios forecast a dynamic marine environment, many migratory animals have evolved preemption, which enables them to leave the area before unfavorable conditions become too poor (Dingle & Drake 2007). Through preemption, environmental changes are forecasted by a surrogate such as photoperiod (Dingle & Drake 2007), and as a result, photoperiod often serves as a cue to migrate (Eriksson et al. 1982). Many animals, including birds, mammals, insects, and fishes, have evolved the ability to perceive changes in photoperiod (Dingle 1972, 1974, Caldwell 1974, Aidley 1981, Rees 1982, Post & Forchhammer 2008, Smith et al. 2021). This sensitivity to photoperiod may afford advantages to an animal by ensuring that it acquires enough fuel to relocate before habitat quality declines, allowing it to become an initial colonizer of newly favorable hab-

itat, where it can take advantage of resources before competition increases and ensure that reproduction occurs at a time of year when the offspring will have access to favorable conditions just after birth (Dingle & Drake 2007, Winkler et al. 2014). In Atlantic salmon, photoperiod, along with water temperature, triggers smolt migration (Teichert et al. 2020). The movements and presence of many shark species are also correlated with photoperiod (Grubbs et al. 2007, Kneebone et al. 2012, Nosal et al. 2014). Photoperiod initiates fall migrations of juvenile sandbar sharks *Carcharhinus plumbeus* emigrating from Chesapeake Bay, USA (Grubbs et al. 2007), juvenile sand tiger sharks *Carcharias taurus* emigration from Massachusetts and Rhode Island, USA (Kneebone et al. 2012), and correlates with male leopard shark *Triakis semifasciata* abundance off Del Mar, California, USA (Nosal et al. 2014). However, it is possible that shark movements are motivated by the movements of prey species that are driven by photoperiod, which is difficult to investigate separately (Kajiura & Tellman 2016). Like many other shark species, the migration of blacktip sharks *Carcharhinus limbatus* off the US East Coast may be influenced by temperature, prey abundance, and/or photoperiod. Striped mullet *Mugil cephalus* migrate southward off the US mid-Atlantic coast during autumn (Peterson 1976) to eastern Florida (Chagaris et al. 2014, Myers et al. 2020) and it is hypothesized that blacktip sharks follow this movement (Kajiura & Tellman 2016, Bowers & Kajiura 2023). The southern migration of the US East Coast blacktip shark currently terminates off the coast of Palm Beach County, Florida, where blacktip sharks overwinter in densities of up to 803 sharks km^{-2} (Fig. 1) (Kajiura & Tellman 2016). When day and night lengths are equal (i.e. the vernal equinox), and SST exceeds 25°C, blacktip sharks emigrate from Palm Beach County and travel northward toward Georgia and South Carolina (Castro 1996, 2011, Kajiura & Tellman 2016). Along the coast, blacktip sharks inhabit waters between 18 and 25°C (Castro 1996, 2009, 2011, Ulrich et al. 2007).

The blacktip shark migration revolves around their synchronous reproductive cycle (Bigelow & Schroeder 1948, Dodrill 1977), in which mating occurs in specific locations at the same time each year (Castro 1996, 2009). Female blacktip sharks exhibit a biennial reproductive cycle whereby one year of reproduction is followed by a year of rest; males are thought to reproduce annually (Castro 1993, 2009). Reproduction is synchronous, in that females that are in their reproductive year ovulate around 1 June (Castro 1996, 2009, Baremore & Passerotti 2013). Mating grounds have been identified near nursery grounds in

Fig. 1. Aerial view of massive blacktip shark aggregations off the coast of Palm Beach County, FL. Each dark speck is a shark

Georgia and South Carolina (Castro 1996, Gurshin 2007, Swift et al. 2023). There is some evidence of a nursery in northeastern Florida (McCallister et al. 2013, Bowers & Kajiura 2023); however, nursery grounds have been confirmed only in inshore and estuarine regions of Georgia and South Carolina (Castro 1996, Abel et al. 2007, Gurshin 2007, Ulrich et al. 2007, Bowers & Kajiura 2023, Swift et al. 2023).

Seventy-five years ago, it was thought that only stray blacktip sharks traveled north of Cape Hatteras, North Carolina (Bigelow & Schroeder 1948). However, in the early 1900s, blacktip sharks were landed off the coast of Massachusetts and Long Island, New York, on at least 6 occasions (Helmuth 1916, Thorne 1916, Bigelow & Schroeder 1948), although the reliability of the species identity in these accounts is questionable (Bowers & Kajiura 2023). In recent years, blacktip sharks were tagged and recaptured as far north as Delaware Bay (Kohler & Turner 2019) and have been caught regularly as far north as New Jersey and New York (E. Cortes unpubl. data, T. Curtis unpubl. data). However, the distance that individuals travel and the proportion of the adult population that relocates during an annual migration remain unclear.

Given the recently recorded blacktip shark presence north of Cape Hatteras in Delaware Bay, New Jersey, and New York, we hypothesize that (1) blacktip sharks off Palm Beach County migrate to Delaware Bay, north of Cape Hatteras. Given that the migration cycle is reproduction-driven, we hypothesize that (2) all adult male blacktip sharks perform an annual latitudinal migration. Since peak densities in blacktip shark abundance at the southern terminus of the migration correlate with SST > 25°C, we hypothesize that (3) blacktip shark distribution will shift northward in the warmer seasons and southward in the cooler seasons and that (4) SST will correlate with the latitudinal movement of blacktip sharks in each season.

2. MATERIALS AND METHODS

2.1. Study site

Blacktip sharks were captured in the meteorological winter (December, January, and February) and/or spring (March, April, and May) of 2014−2017 off Palm Beach County. This area was chosen because it is thought to be the southern terminus of the blacktip shark migration and has a great density of blacktip sharks (up to 803 ind. km^{-2}), which occurs during winter (Kajiura & Tellman 2016). Nearly all sharks were caught and released off Singer Island, Florida (n = 51), the easternmost point of the state. One shark was caught and released off Boynton Beach, Florida, approximately 25 km south of the primary release site (Fig. 2). Both release sites were in shallow, clear
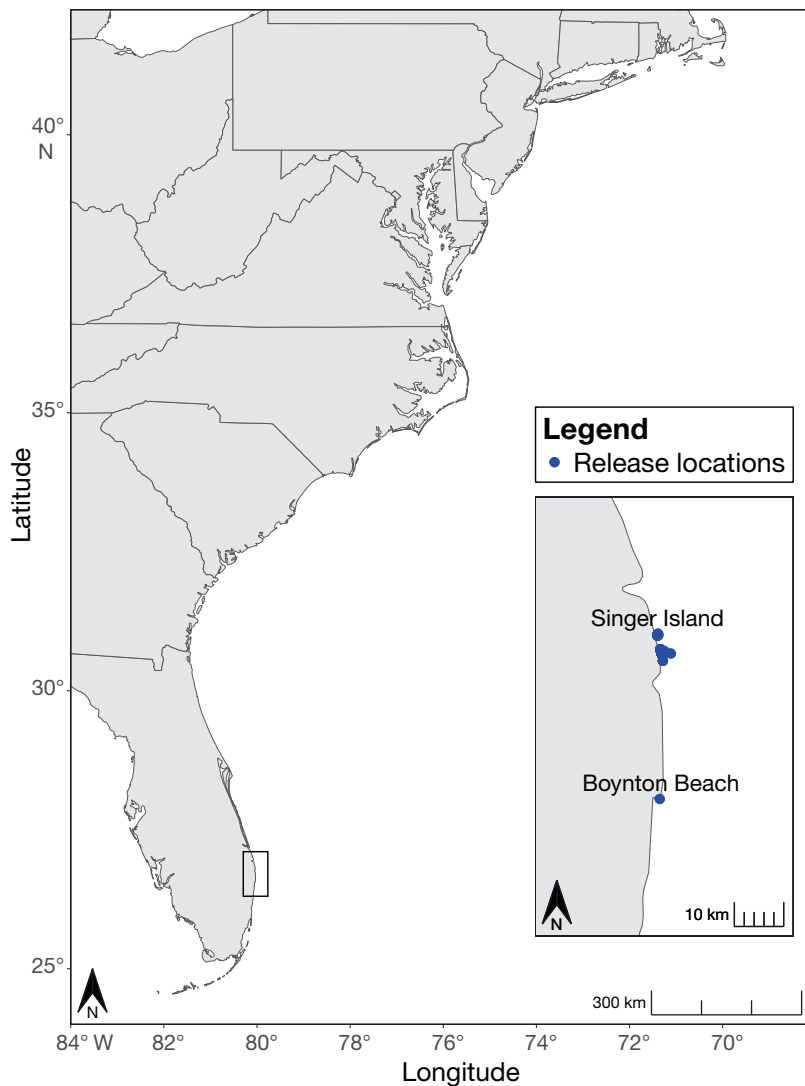
Fig. 2. Release sites of blacktip sharks (n = 53) instrumented with acoustic transmitters

clasper length was measured from the tip of the clasper to the insertion of the pelvic fin. The clasper lengths and calcification of captured blacktip sharks suggest that all were reproductively mature males (Clark & Von Schmidt 1965, Castro 1996).

2.3. Acoustic telemetry

Captured sharks were surgically implanted with V16-5L acoustic transmitters (signal delay: 60–180 s; VEMCO) in the coelom, and released. Acoustic telemetry is a cost-effective electronic tagging method that allows researchers to track animals over great distances within cooperative acoustic telemetry networks (Crossin et al. 2017, Bangley et al. 2020, Young et al. 2020). Briefly, animals are instrumented with acoustic transmitters, and the date, time, and presence of these tagged animals is recorded by an acoustic receiver when they enter within range (400–1200 m) (Espinoza et al. 2011, Huveneers et al. 2016, Innovasea 2020). In addition to the authors' own receiver array, these transmitter data were recorded on receivers owned by other researchers, and those data were shared with the authors (i.e. transmitter owners), in accordance with the Ocean Tracking Network, Atlantic Cooperative Telemetry Network, and FACT Network data sharing agreements (The FACT Network 2018, Pye et al. 2018, Young et al. 2020, The Atlantic Cooperative Telemetry Network 2021). As a result of these collaborative networks, the sharks were detectable along much of the US East Coast, which included broad longitudinal coverage in some regions (Bangley et al. 2020, Young et al. 2020).

Unfortunately, funding for permanent baseline infrastructure of US national acoustic telemetry assets is lacking, which often causes irregular receiver coverage within these networks and results in sporadic spatial and temporal data. This irregular coverage can skew cluster analyses that are performed over broad spatial scales and lead to fragmented ecological results (Bowers & Kajiura 2024). To regularize the temporal and spatial components of the current detection data and define seasonal distributions of adult male black-

waters of 4 m depth or less, and the Singer Island location contained natural limestone structure that was present on an otherwise sandy bottom seafloor.

2.2. Morphometrics

Total length was measured dorsally from the tip of the snout along the body midline to the orthogonal intersection of the posterior end of the caudal fin in its natural state (not stretched). Fork length was measured dorsally from the tip of the snout to the fork of the caudal fin. Inner and outer clasper lengths were measured to infer male maturity (Clark & Von Schmidt 1965). Inner clasper length was measured from the tip of the clasper to the insertion of the cloaca, and outer

tip sharks along the US East Coast, we used methods tested in Bowers & Kajiura (2024). Through these methods, a movement model is applied to average daily locations (derived from detection data) to predict locations in between daily locations and subsequently close gaps in the detection data caused by non-uniform receiver coverage (Bowers & Kajiura 2024).

Of the 52 sharks instrumented with transmitters, 47 were subsequently detected. Detections were filtered using the false detection analysis in the 'glatos' R package (v.0.4.0) (Holbrook et al. 2019) with a 3600 s time interval, which is 30 times the maximum nominal delay of the transmitters (Pincock 2012). After false detection analysis, 1% of 136 250 total detections were removed and 41 individuals remained in the analysis. In a previous study, sharks were fed acoustic transmitters and the longest verified retention time was 34 d (Brunnschweiler 2009). Thus, predation was classified by speeds that exceeded the average volitional swimming speed of a blacktip shark (Porter et al. 2020) that was not detected 34 d or more beyond the initial date of this excessive speed. For sharks that were classified as depredated, all detections after the predation date were removed. After a predation filter was applied, 4% of 134 853 total detections were removed from 8 individuals. Detections beyond 34 d in the current study represent a tag that was retained longer than verified tag retention times that were identified in the aforementioned study (Brunnschweiler 2009); therefore, these detections were unlikely to have been the result of a tag that was ingested by a predator but instead could have resulted from tag collisions, which are caused by the ID ping sequence of the tags of 2 animals overlapping in time and thereby interfering with one another as they are recorded on a receiver (Innovasea 2021). A speed filter was used to identify detections that suggest an individual swam faster than the average volitional swimming speed of blacktip sharks (0.76 body lengths s^{-1}) previously recorded (Porter et al. 2020), which could indicate tag signal collisions (Nielsen et al. 2009). Detections that corresponded to speeds greater than 0.76 body lengths s^{-1}, given a 650 m buffer around receivers, tallied 0.08% of 129 439 total detections and were subsequently removed. To minimize the disproportionately high number of detections near the release site, sharks that were not detected later than 1 mo beyond the date of instrumentation were assumed to have lost the ability to be detected (e.g. due to predation, post-release mortality, transmitter malfunction) and all detections of these individuals were removed from further analysis. After this 1 mo detectability criterion was applied,

0.2% of 129 325 total detections were removed and 30 individuals remained in the analysis. The maximum and minimum latitudes across all study years were calculated per individual for sharks that were tracked for at least half of a migration cycle, or 183 d, which were initially traveling northward by default since they were tagged at the southern terminus of the migration.

2.4. Statistics

To quantify the percentage of the adult male blacktip population that traveled north of Cape Hatteras (35.5° N), to Delaware Bay (38.8° N), to Long Island (40.5° N), and repeatedly to Long Island, binomial probabilities were calculated within a 95% confidence interval using the 'exact' method in the R package 'hmisc' (v.4.6-0) (Harrell 2021).

2.4.1. Detection data and hot spot analyses

Direct locations (daily averaged detections) were calculated from the detection data to obtain a maximum of one location per day per individual, and a continuous-time correlated random walk model (ct-CRW) was applied to impute predicted locations at a chosen time interval that fill in gaps in detection data (Johnson et al. 2008, McClintock & Michelot 2018, Bowers & Kajiura 2024). Given that a ct-CRW leverages velocity autocorrelation to predict locations in between direct locations (Johnson et al. 2008), it may be especially useful in reconstructing tracks of obligate ram ventilators like the blacktip shark that maintain a relatively consistent cruising speed (Bowers & Kajiura 2024). The ct-CRW does not discriminate against boundaries; therefore, locations that were predicted on land were re-routed using the 'pathroutr' (v.0.2.1) package in R (London 2020) after being separated by season. A 15 min temporal imputation interval was used in the ct-CRW model, as it was the coarsest temporal resolution that allowed for paths to remain in water after land intersections were re-routed (Bowers & Kajiura 2023). Meteorological season was chosen over astronomical season because it aligns with the blacktip shark's synchronous reproduction cycle, in which mating occurs around 1 June (Castro 1996, 2009). The ct-CRW models were constructed using the 'momentuHMM' R package (v.1.5.5) (McClintock & Michelot 2018).

To determine the seasonal distributions of blacktip sharks, a 50 × 50 km resolution grid was overlain on

the re-routed, reconstructed shark tracks, and distinct counts of blacktip sharks were taken in each grid cell and subsequently used to run an optimized hot spot analysis in ArcMap (v.10.6) (Environmental Systems Research Institute 2017). Given that blacktip sharks travel an average of 111 km d^{-1} (Porter et al. 2020), the grid size allows for twice the sampling rate of blacktip shark travel per day, as 50 km is less than half the daily travel distance (Bowers & Kajiura 2024). Daily blacktip shark travel was calculated by multiplying the mean total length by the previously recorded average velocity (1.71 m mean total length × 0.76 body lengths s^{-1} × 86 400 s d^{-1}; Porter et al. 2020). The optimized hot spot analysis uses Z-scores that are produced by the Getis-Ord Gi* statistic to identify clusters of grid cells that contain a significantly large number of individuals (hot spots) and clusters of grid cells that contain a significantly small number of individuals (cold spots) (Ord & Getis 1995, Getis & Ord 2010) and corrects for spatial dependence and multiple testing using the false discovery rate method (Caldas de Castro & Singer 2006). To ensure that each seasonal hot spot analysis was comparable to the others, the optimal fixed distance bands that are determined by Arc-Map and based on peak clustering (Mitchell & Griffin 2005) were averaged across each season and applied to each seasonal cluster analysis, resulting in a scale of analysis of 224.5 km.

2.4.2. Environmental predictors of movement

Predicted locations that intersected land were removed from further analysis since the uncertainty associated with re-routing these locations cannot be readily calculated. To avoid pseudoreplication, the predicted locations that did not intersect land were averaged to obtain a daily location. The response variable, latitudinal velocity, was calculated by dividing a change in latitude between the current and preceding location of an individual by the number of days between these locations (i.e. a change in latitude normalized by the number of days between locations; km of latitude per day) (Secor et al. 2024).

To gather the environmental conditions that may be associated with migratory movement, each shark location was used to find the corresponding environmental data in the NOAA ERDDAP server (Simons & John 2022) using the R package 'rerddapXtracto' (v.1.1.2) (Mendelssohn 2019). Environmental data consisted of SST (5 d composite) (Brown et al. 1999) and sea surface chlorophyll a (chl a; weekly composite) (O'Reilly et al. 1998) averaged within 0.05 dec-

imal degrees (about 5.5 km) of the direct and predicted locations, and photoperiod based on day of year and latitude from the 'geosphere' R package (v.1.5-14) (Hijmans 2021). To identify individual variation in SST and latitude ranges, the maximum and minimum latitude per individual were determined from direct locations. The SST ranges, like the latitude ranges, were only calculated for individuals that were tracked for at least half of a migration cycle (183 d).

To determine which environmental conditions are correlated with male blacktip shark migratory movement, a model was fit using backward selection by p-value. Given that time-series data generally exhibit autocorrelation, which is a correlation between the current location and lagged versions of itself, a generalized least squares (GLS) model with an AR1 autocorrelation structure within individuals was fit by maximizing the restricted log-likelihood with the R package 'nlme' (v.3.1-155) (Pinheiro et al. 2022). The AR1 represents an autocorrelation structure of order 1, which specifies a decrease in the correlation between repeated measures over time (Pinheiro & Bates 2006, Box et al. 2015). In the context of this study, the autocorrelation structure helps to describe the variance within sharks and correlates locations that are closer in time higher than those further apart in time by raising the phi coefficient to a power that is equal to the number of days between locations. The GLS model also accommodates weighted structures and repeated measures (Pinheiro et al. 2022). Fixed variances (e.g. weights) were assigned to a variance function based on relative certainty of location. These fixed variances weigh the covariates for each location corresponding to the relative distance from a direct location. For each shark, a direct location had the highest certainty (i.e. greatest weight: 1) and the predicted location that represented the midpoint between 2 subsequent direct locations that were farthest from one another had the lowest certainty (e.g. smallest weight: 0.001). Chl a, SST, and photoperiod from the preceding location were included as main effects in the GLS model in addition to meteorological season, study year, and interaction terms between both season and study year for each main effect, and an interaction term between the categorical variables, season and study year. The preceding location rather than the current location was chosen because the unfavorable environmental conditions at the preceding location are likely the driver behind the movement associated with the current location. Study years were separated on 1 June, or the 152nd day of the year during leap years, rather than 1 January as for the hot spot analyses.

Outliers were defined as locations in which the days between locations were greater than 1.5 times their third interquartile range (Tukey 1983). These outliers are caused by land intersections in the movement model that were omitted from the GLS models due to immeasurable uncertainty associated with re-routing. They represent a gap in time between the environmental measurement and the response variable. It is important to remove them because the greater the time difference is between locations, the less likely it becomes that the environmental condition at the preceding location influenced the latitude of the succeeding location. After removing 514 outliers, 21 171 locations remained with 1 d between each location. Rows of data that lacked any environmental data value (e.g. because of cloud cover, a gap in satellite sensor coverage) were subsequently removed. After removing every row where environmental data were absent and removing Year 1, which lacked sufficient data in each season, 17 260 locations remained among 29 individuals.

To interpret the hierarchical GLS model, the year and season factors were releveled for each combination of year and season to create a reference category (e.g. spring of study year 2). The main effects were examined for each reference category, and the significance and the relationship of coefficient estimates to the response variable (e.g. direct or inverse) of each coefficient for each season were compared across study years. Main effects that had a significant, consistent relationship across all years per season (e.g. always direct) were considered reliable in that they could predict the movement of blacktip sharks during a season regardless of annual variation in environmental conditions. Multicollinearity was examined using the generalized variance inflation factors (GVIF) of the main effects that were calculated and reduced to a linear level with $GVIF^{(1/2 \times df)}$, where df is the degrees of freedom of the model term (Fox & Monette 1992) using the 'car' package (v.3.0-11) (Fox & Weisberg 2019) in R.

3. RESULTS

All instrumented blacktip sharks were adult males that measured 141.1 ± 7.1 (mean ± SD) in fork length and 171.1 ± 8.8 in total length (Table 1). Of the 30 individuals tracked, 24 traveled north of Cape Hatteras, 20 traveled as far north as Delaware Bay, and 10 traveled as far north as Long Island, of which 4 individuals did so repeatedly (Fig. 3). Three individuals traveled to Long Island during 2 different migration cycles and one individual traveled to Long Island during 3 different migration cycles. Of individuals tracked for at least half of a migration cycle (n = 26), the latitudinal range among individuals varied from 182 to 1591 km, SST ranged from 15.5 to 31°C across all individuals and study years, and the variation of SST inhabited by individuals spanned 5.4—12.1°C (Fig. 4).

3.1. Hot spot analyses

Seasonal hot spot analyses showed northward latitudinal movements along the US East Coast in the spring and summer and southward latitudinal movement patterns in the winter and autumn. Hot spots suggest that great quantities of blacktip sharks occur in different areas depending on the season, whereas cold spots suggest low quantities of blacktip sharks. Blacktip shark hot spots were between southeastern Florida and southern North Carolina in the spring and cold spots were north of Cape Hatteras (Fig. 5). During summertime, blacktip shark hot spots were off the coast of south-central North Carolina up to central New Jersey and cold spots occurred off Georgia, Florida, and New England (Fig. 5). As blacktip sharks traveled southward in the fall, hot spots occurred off Maryland to South Carolina and cold spots occurred off New Jersey northward and southeastern Florida (Fig. 5). Hot spots occurred from South Carolina to southeastern Florida and cold spots occurred from New England to south-central North Carolina during winter (Fig. 5).

3.2. Environmental conditions

Multicollinearity was evaluated for the environmental variables used as main effects in the model and all $GVIF^{(1/2 \times df)}$ values were less than 3 for all continuous variables. Collinearity existed between photoperiod and season, which was expected. Given that the greatest $GVIF^{(1/2 \times df)}$ was attributable to a categori-

Table 1. Morphometrics of captured blacktip sharks. All individuals were male (n = 48)

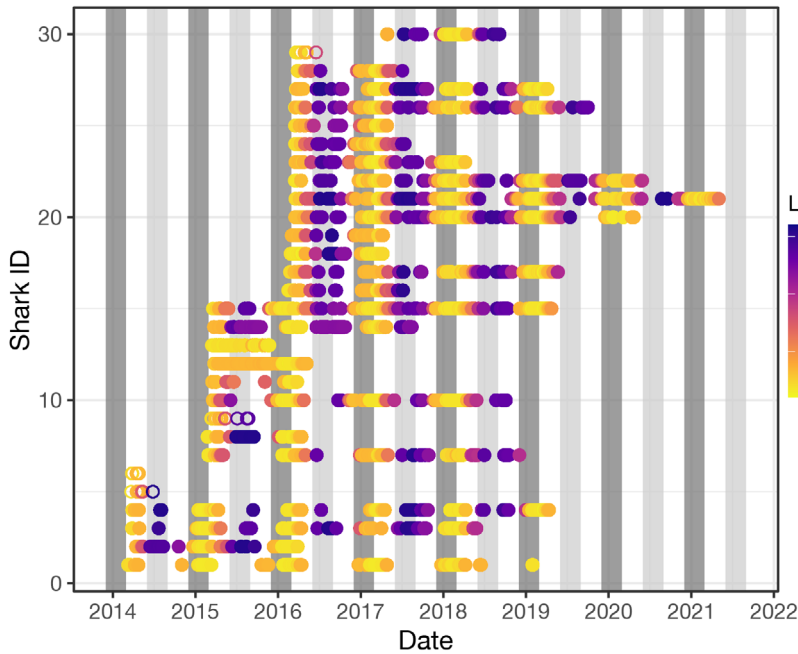|	Min.	Mean ± SD	Max.
Total length (cm)	145	171.1 ± 8.8	186
Fork length (cm)	121	141.1 ± 7.1	153
Inner clasper length (cm)	17	19.1 ± 1.0	21
Outer clasper length (cm)	12	13.9 ± 0.8	15

Fig. 3. Male blacktip shark detections over time by latitude (n = 30 tracked sharks, n = 129 066 detections) filtered for false detections, speed, predation, and detectability criterion. Each row corresponds to an individual shark. Light grey shaded regions: summer; dark grey shaded regions: winter. Warmer colors on the color bar represent lower latitudes; cooler colors represent higher latitudes

cal variable that was an indicator variable, and was less than 3, that variable (season) was retained in the model. When season was removed from the multicollinearity model, the greatest GVIF$^{(1/2 \times df)}$ dropped from 3 to 1.1 for photoperiod. The low GVIF$^{(1/2 \times df)}$ values indicated that it was not necessary to include interaction terms between main effects (e.g. chl a × SST) in the GLS model (Fox & Monette 1992). The final model included the correlation structure and all terms: study year, season, chl a, SST, photoperiod; interaction terms between season and study year, chl a, SST, and photoperiod; and interaction terms between study year and chl a, SST, and photoperiod. The phi coefficient of the AR1 correlation structure was 0.89. The residual standard error was 13.3 km in latitude per day.

For clarity, the relationships between explanatory variables and response variables are reported in terms of direct and inverse relationships, rather than positive and negative, because a direct relationship could indicate a

sped-up northward movement (positive latitudinal velocity) or a sped-up southward movement (negative latitudinal velocity; Table 2). In all study years, SST had a direct relationship with spring latitudinal velocity (p < 0.001) and chl a had an inverse relationship with spring latitudinal velocity (p < 0.001). Photoperiod had an inverse relationship with spring latitudinal velocity in Years 2 through 5 (max. p = 0.01) and a direct relationship in Year 6 (p < 0.001; Table 2). As we are seeking reliable environmental drivers, they must exhibit consistent relationships with latitudinal velocity across all years for a given season. Thus, SST and chl a were the only reliable predictors of movement during spring. For every 1°C increase in SST, male blacktip shark latitudinal velocity increased about 0.7–4.4 km d^{-1}. For every 1 mg m^{-3} decrease in chl a, northward latitudinal velocity increased by about 0.3–1.1 km d^{-1}.

During summer in Year 2 and Years 4–6, SST was inversely related to latitudinal velocity (p < 0.001). Chl a had a direct relationship with summer latitudinal velocity in Years 3 and 4 (p < 0.001) and an inverse

Table 2. Quantitative results of generalized least squares model. Coefficients for each main effect are listed for each season of each year. SST: sea surface temperature. Asterisks indicate significance: *p < 0.05; **p < 0.01; ***p < 0.001

| Effect	Year						
	2	3	4	5	6	7	8
During spring							
SST	0.7***	1.7***	1.1***	0.8***	0.7***	1.3***	4.6***
Chl a	−0.5***	−0.3***	−0.5***	−0.6***	−0.6***	−0.6***	−1.3***
Photoperiod	−2.4**	−3.5***	−2.3***	−4.1***	3.4***	1.6	3.7
During summer							
SST	−1.0***	0.0	−0.5***	−0.9***	−0.9***	−0.3	2.9***
Chl a	0.0	0.3***	0.1***	0.0	0.0	0.0	−0.8*
Photoperiod	−3.2***	−4.3***	−3.1***	−4.9***	2.6***	0.7	2.8
During autumn							
SST	0.0	1.0***	0.5***	0.1	0.0	0.7**	3.9***
Chl a	0.0	0.3***	0.1*	0.0	0.0	0.0	−0.8*
Photoperiod	5.1***	4.1***	5.2***	3.5***	10.9***	9.1***	11.2**
During winter							
SST	−0.8***	0.3*	−0.3**	−0.6***	−0.7***	−0.1	3.2***
Chl a	0.2*	0.5***	0.2**	0.2**	0.2*	0.2*	−0.6
Photoperiod	17.3***	16.3***	17.4***	15.7***	23.2***	21.3***	23.4***
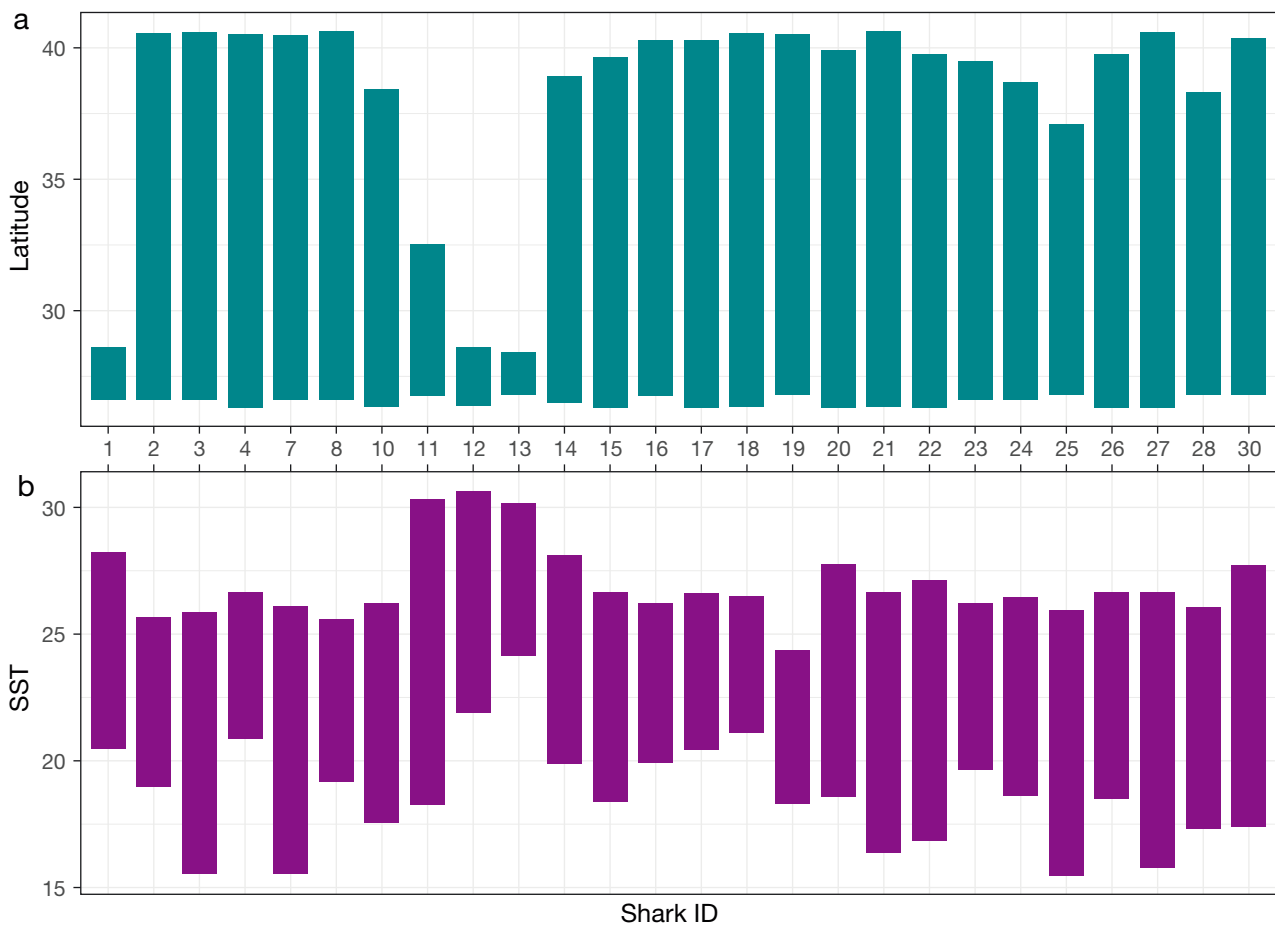
Fig. 4. (a) Latitudinal and (b) sea surface temperature (SST) range of adult male blacktip sharks by individual across all study years. Based on detection data, there is great variability in the migratory extent and thermal preference among individuals in the male US East Coast population. Shark IDs 5, 6, 9, and 29 were removed because they were not tracked for at least half of a migration cycle

relationship in Year 8 (max. p = 0.031). Photoperiod had an inverse relationship with summer latitudinal velocity in Years 2—5 and a direct relationship during Year 6 (p < 0.001; Table 2). None of the examined environmental predictors were reliable indicators of movement during the summer, as no predictors had consistent effects across study years.

During autumn in Years 3, 4, 7, and 8, SST was directly related to latitudinal velocity (max. p = 0.005). Chl *a* was directly correlated with autumn latitudinal velocity in Years 3 and 4 (max. p = 0.03) and inversely correlated in Year 8 (p = 0.03). Photoperiod was directly related to autumn latitudinal velocity in all years (max. p = 0.004; Table 2). During autumn, photoperiod was the only reliable predictor of latitudinal movement. For every 1 h of daylight reduction, southward latitudinal velocity increased by about 3.4—11.2 km d^{-1}.

In Years 2, 4, 5, and 6, SST was inversely correlated with winter latitudinal velocity (max. p = 0.006) and directly correlated in Years 3 and 8 (max. p = 0.011).

Chl *a* was directly related to winter latitudinal velocity in Years 2—7 (max. p = 0.046). Photoperiod was directly related to winter latitudinal velocity in all years (p < 0.001; Table 2).

During winter, chl *a* was consistent across all years, except Year 8, which consisted of locations from a single individual. Thus, chl *a* was considered reliable during winter. For every 1 mg m^{-3} decrease in chl *a*, southward latitudinal velocity increased by 0.2—0.4 km d^{-1}. In addition, photoperiod was a reliable predictor of latitudinal movement during winter. This effect was stronger in winter than in autumn, when southward latitudinal velocity increased by about 15.7—23.4 km d^{-1} for every 1 h of daylight reduction.

4. DISCUSSION

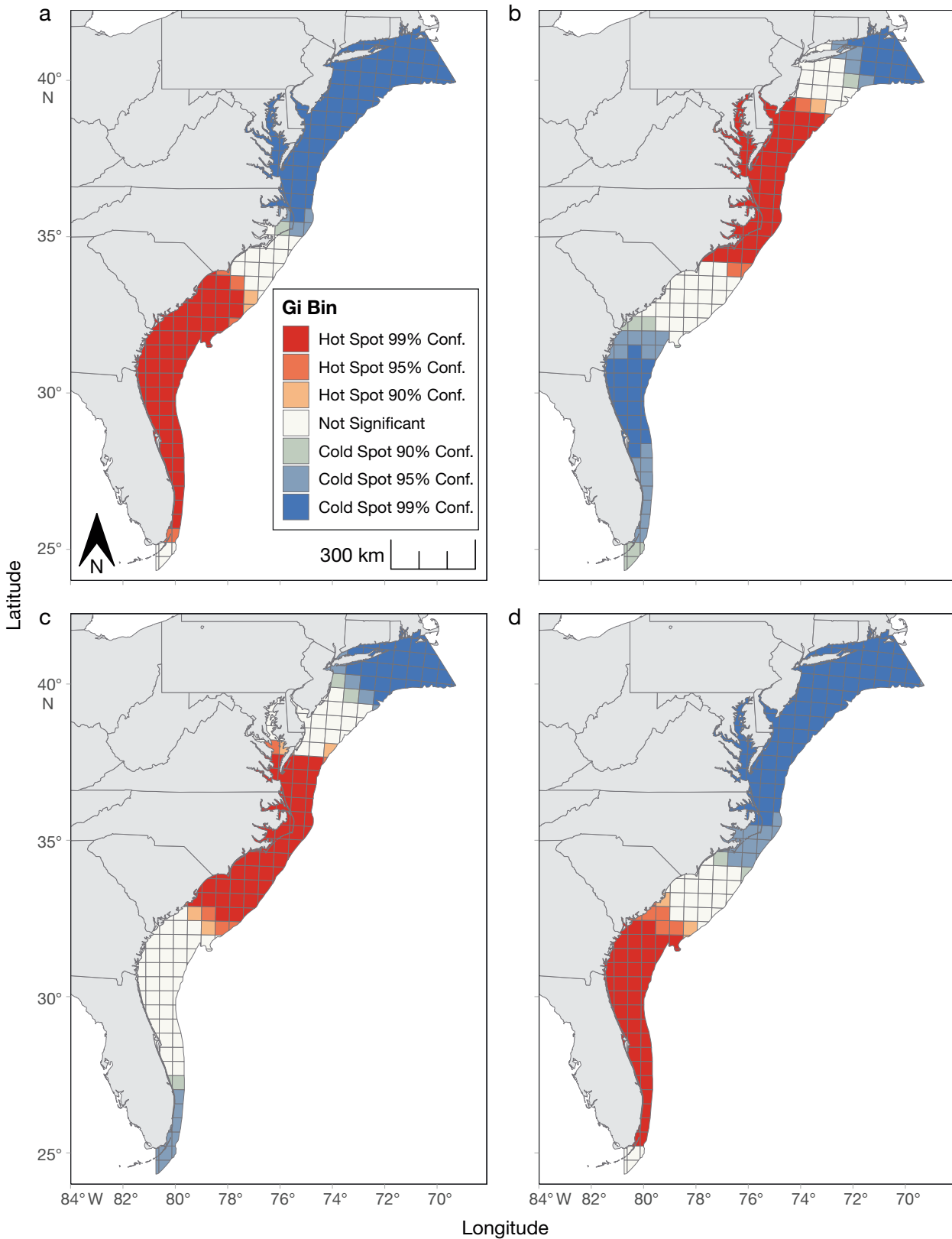Blacktip sharks that aggregate at the southern terminus of the migration are primarily male. This male

Fig. 5. Seasonal optimized hot spot analysis of blacktip sharks aggregated to 2500 km^2 during (a) spring, (b) summer, (c) autumn, and (d) winter. Warm colors: significant hot spots of blacktip shark distribution; cool colors: significant cold spots. Confidence interval of the Gi* statistic is represented by the intensity of warm and cool colors

sex bias may be a result of sexual segregation, a difference in male and female spatial distributions that is seen in many shark populations (Klimley 1987, Economakis & Lobel 1998, Sims 2005, Mucientes et al. 2009, Drymon et al. 2020), including blacktip sharks in the Gulf of Mexico (Drymon et al. 2020). Further investigation is being conducted to determine the seasonal distributions and migratory drivers of females as well as sexual segregation between blacktip sharks off the US East Coast (authors' unpubl. data).

Earlier studies have documented the occurrence of blacktip sharks at least as far north as Long Island (Helmuth 1916, Thorne 1916, Bigelow & Schroeder 1948); however, this study is the first to demonstrate that blacktip sharks off the US East Coast regularly migrate from the southern terminus in southeastern Florida (Kajiura & Tellman 2016) to almost the northernmost extent of the range in Long Island (Helmuth 1916, Thorne 1916, Bigelow & Schroeder 1948, Bowers & Kajiura 2023). If the northern migratory limit of blacktip sharks defined by Bigelow & Schroeder (1948) was accurate, then it has shifted poleward over the past 70 yr, with a large proportion of the male population of blacktip sharks now traveling north of Cape Hatteras. The 95% confidence interval calculated in the binomial probabilities indicated that between 61 and 92% of the adult male US East Coast blacktip shark population migrates north of Cape Hatteras (35.5° N) and between 47 and 83% of the population migrates to at least Delaware Bay (38.8° N), as we predicted. Blacktip sharks that surpass Cape Hatteras during their migratory route do so relatively consistently from year to year (Fig. 3). Thus, our first hypothesis, that the northern terminus of the blacktip shark migration is located north of Cape Hatteras in Delaware Bay, appears to be supported, but individuals traveled farther than we expected. Between 17 and 53% of male blacktip sharks migrate as far north as Long Island (40.5° N). Given that blacktip sharks were previously caught off Long Island and Buzzards Bay, Massachusetts (Helmuth 1916, Thorne 1916, Bigelow & Schroeder 1948), albeit on rare occasions and with questionable species identification (Bowers & Kajiura 2023), the current findings do not constitute a range expansion. Instead, these annual northward migratory tracks indicate that individuals that surpass Cape Hatteras are not 'strays' that drift in the Gulf Stream never to return as was described by Bigelow & Schroeder (1948), given that between 4 and 31% repeatedly migrate to Long Island. Long Island may be the northernmost extent of the US East Coast blacktip shark distribution at this time.

The Sustainable Fisheries Act of 1996 mandated that fishery management councils establish Essential Fish Habitat (EFH) for managed fish species that includes all habitats in which a species spawns, breeds, grows to maturity, or feeds (NOAA 2002). Currently, the National Marine Fisheries Service (NMFS) EFH does not include the northern extent of the migratory range of blacktip sharks that we have documented here. The northern boundary of the current Atlantic blacktip shark EFH extends to only the southern border of Maryland (National Marine Fisheries Service 2017). At least 20 of the 30 individuals remained north of Delaware Bay from $1-126$ d yr^{-1}, which suggests that at least 66% of these tagged male blacktip sharks may rely on regions outside of the EFH to feed. If management decisions are made based on the current EFH, migratory adult male blacktip sharks may be vulnerable to overfishing during summer and autumn months when they inhabit waters north of Delaware Bay.

The overall latitudinal migration range varies greatly among individuals (Fig. 4). All males traveled to some extent during migration cycles, although individual migration range varied from 182 to 1591 km in latitude. For perspective, that is the difference between migrating from Palm Beach to Cape Canaveral versus Palm Beach to Long Island. Thus, our second hypothesis, that all adult male blacktip sharks travel latitudinally during the migratory cycle, is weakly supported. The blacktip shark migration may be a partial migration, as there are individuals in the adult male population that remain south of Cape Canaveral year-round. Partial migration occurs in mammals, birds, fish, and invertebrates (Chapman et al. 2011) and has been documented in a variety of other shark species, including nurse sharks *Ginglymostoma cirratum* (Pratt et al. 2018), tiger sharks *Galeocerdo cuvier* (Papastamatiou et al. 2013), and female bull sharks *Carcharhinus leucas* (Espinoza et al. 2016). Predation vulnerability, arrival time at breeding grounds, intraspecific food competition, and thermal tolerance are a few hypothesized drivers of partial migration in animal species (Ketterson & Nolan 1976, Gauthreaux 1982, Chapman et al. 2011, Skov et al. 2011).

Predation vulnerability may drive partial migration in this population. Blacktip sharks are prey to many larger shark species (Kajiura & Tellman 2016, Doan & Kajiura 2020) and it is hypothesized that aggregating behaviors, such as those that blacktip sharks exhibit in the winter, are used to confuse predators (Ruxton et al. 2007). Remaining in southern latitudes may increase the risk of predation, as the resident blacktip sharks have sparser aggregations to confuse predators. Thus, it may be advantageous for individuals to migrate in groups away from predator habitat and to maintain these aggregations along the coast to minimize predation vulnerability.

Arrival time at breeding grounds may motivate partial migration in this population. Male blacktip sharks exhibit regional philopatry (Swift et al. 2023), and migrating males may benefit from arriving early to the mating grounds to maximize their probability of mating, as is hypothesized in other animals (Ketterson & Nolan 1976). However, individuals may fail to contribute to the breeding population by remaining resident. Shark 1 exhibited sporadic location data throughout the years and could have traveled to the mating grounds but remained undetected, whereas 2 individuals (Sharks 12 and 13) remained south of Cape Canaveral with relatively consistent detections, and therefore did not travel to the mating grounds in Georgia and South Carolina. These individuals may not have reproduced, although this contrasts with foundational assumptions in evolutionary biology. Instead, there may be additional blacktip shark mating grounds on the US East Coast that have yet to be identified. Female blacktip sharks with fresh mating wounds were observed off Melbourne Beach, Florida, in a previous study (Dodrill 1977), which may indicate that additional mating grounds exist between Cape Canaveral and Palm Beach County, where these residents remain year-round.

Alternatively, partial migration may occur in this population as a result of intraspecific competition for food, in which individuals migrate to avoid competing for limited resources (Gauthreaux 1982). Blacktip shark movements were inversely correlated with chl *a* in spring. At lower chl *a* concentrations, blacktip sharks migrated more quickly northward. This suggests that food availability is an important factor as these males relocate to the mating grounds. There are energetic costs associated with spermatogenesis and travel to the mating grounds. The 2 confirmed residents were tracked for only 254 and 409 d each, so they may skip reproductive years. This skipped spawning phenomenon occurs in some male bony fishes, such as Northwest Atlantic cod *Gadus morhua* and winter flounder *Pseudopleuronectes americanus* (Burton 1991, Maddock & Burton 1994, Burton et al. 1997), but it is more often studied in female bony fishes, perhaps because it is easier to measure in females (Rideout & Tomkiewicz 2011). Skipped spawning can be induced in male (and female) winter flounder *P. americanus* by restricting food availability (Burton 1991). This phenomenon has not been observed in male elasmobranchs, although it is possible that the residents remain south to take advantage of decreased competition for food and mate every other year. However, it is also possible that these individuals are not representative of the population and are simply behavioral outliers.

Finally, partial migration may occur because of differences in thermal tolerance. As we predicted in Hypothesis 3, most blacktip sharks migrate northward during warmer seasons and southward during cooler seasons, but the individual variation in male blacktip migratory behavior that we observed may be an indicator of diverse thermal tolerance within the population. The range of temperatures inhabited by blacktip sharks tracked during this study was relatively broad (15.5—31°C) but is corroborated by the temperature ranges previously documented in the scientific literature (Dodrill 1977, Castro 1996, Ulrich et al. 2007). The residents may have a greater thermal tolerance, through which they are able to tolerate higher temperatures than the migrating population, which may suggest resilience under global climate change conditions.

Hypothesis 4, that SST will affect movement during each season, was not supported. It may seem that this could be due to the broad thermal range observed in the study, but the model trends remained the same when residents were removed. Spring was the only season during which SST was a reliable predictor of movement, which is consistent with conclusions from a previous study that determined blacktip sharks head northward from the southern terminus of the migration when SST rises above 25°C in mid-March (Kajiura & Tellman 2016). We expected that SST would influence the movement of blacktip sharks in summer, yet no reliable predictors of movement were identified. Although this population is commonly described as coastal (Compagno 1984, 1988, Castro 1996, Ebert et al. 2013), it is possible that blacktip sharks seek out cooler temperatures by utilizing microhabitats such as deeper water, like the grey reef shark *Carcharhinus amblyrhynchos* (Vianna et al. 2013) and the oceanic whitetip *Carcharhinus longimanus* (Howey-Jordan et al. 2013). These changes in microhabitat would not be observed in the surface temperature variable used in this study. It is also possible that temperatures are more uniform during summer, and the spatial constraints experienced during cooler seasons are effectively removed during this time of year.

In addition to SST, latitudinal movements of blacktip sharks were correlated with chl *a*. High chlorophyll concentrations are linked to high concentrations of phytoplankton (Visser et al. 2011) and could indirectly reflect prey abundance such as Atlantic menhaden *Brevoortia tyrannus* (Lynch et al. 2010) or other fish species (Chassot et al. 2010). During spring, blacktip sharks migrate faster northward as prey

abundance decreases. This suggests that food availability is important while (most) male blacktip sharks travel to the mating grounds. Blacktip sharks sped up southward travel during winter as chl *a* decreased. The timing of the southward blacktip winter migration corresponds to anecdotal accounts of mullet *Mugil* spp. occurrence, which are part of blacktip shark diets in addition to other species that co-occur with mullet such as jacks (Carangidae), flounders *Paralichthys* spp., bluefish *Pomatomus saltatrix*, and ladyfish *Elops saurus* (Dodrill 1977, Castro 1996, Karl's Bait & Tackle 2017, Olander 2018, Sukhdeo 2018, Bowers & Kajiura 2023). During their southward winter trek, it is likely that blacktip sharks follow these prey species that follow primary productivity, as many fishermen have suggested (Bowers & Kajiura 2023).

Photoperiod was a reliable indicator of blacktip shark movement during autumn and winter, but it may become an unreliable forecaster of a changing environment under global climate change conditions. Photoperiod can also predict the movements of blacktip conspecifics and other shark species (Grubbs et al. 2007, Kneebone et al. 2012, Nosal et al. 2014, Ayres et al. 2021). This zeitgeber relies on the rhythmicity of seasonal changes in the surrounding environment (Gwinner 1989). Photoperiod forecasts changes in temperature and prey movements and may represent a cue for blacktip sharks to preemptively move southward before conditions become too unfavorable. Preemption may afford an evolutionary advantage to blacktip sharks by allowing them to consume enough energy to relocate before prey decreases and to colonize new habitats before competition increases (Tilman 1982, Bradshaw & Holzapfel 2007, Dingle & Drake 2007). However, it is also possible that prey species exhibit preemption and that blacktip sharks follow the prey species as they migrate. The 2 scenarios are difficult to investigate separately (Kajiura & Tellman 2016). In either case, photoperiod will remain unchanged as global climate change progresses, which may lead to cue mismatches between photoperiod and the environmental conditions it forecasts, such as temperature and food abundance (Post & Forchhammer 2008, Walker et al. 2019).

The hot spot analyses indicated that blacktip sharks could be distributed from the shore out to the 500 m isobath. Although at least 4 blacktip sharks have made short-distance transits across open water, including crossing the Gulf Stream current (Gledhill et al. 2015, Kohler & Turner 2019, Legare et al. 2020, Bowers & Kajiura 2023), the blacktip shark is likely more prevalent closer to shore (Bigelow & Schroeder 1948, Compagno 1984, 1988, Castro 1996, Ebert et al.

2013, Kajiura & Tellman 2016, Bowers & Kajiura 2023). Further research using satellite telemetry is being conducted to determine the extent to which blacktip sharks utilize the continental shelf along the migratory route (I. Tuszynski et al. unpubl. data). A previous study tested the bias incurred from the movement models used here and determined that the accuracy heavily depends on the placement of receivers (Bowers & Kajiura 2024). The results of that study (Bowers & Kajiura 2024) should serve as a guide with respect to the reliability of the distribution results in the current study.

Although a GLS model type was chosen to account for the correlation of these time-series data in determining what environmental parameters predict male blacktip shark latitudinal velocity, the model may still be biased. The model included a first-order autocorrelation structure by individual, which accounted for the likeness of explanatory variables that are closer in time (and intrinsically, space) to one another and the random variability associated with repeated measures recorded from the same individual. Even though weight was assigned based on relative certainty of location, due to the relatively high certainty associated with direct locations (average daily detections), imputed locations of animals will concentrate near receivers, especially in cases where there were fewer daily detections to create an average location. Conversely, the midpoint between these direct locations will be more variable because it possesses the least certainty. Collectively, the imputed locations of multiple individuals will often inherently be in closer proximity to direct locations, more so when there are sparse daily detections; thus, the weights of abiotic factors are still skewed towards those measured at or near receiver stations.

5. CONCLUSIONS

Male blacktip sharks regularly surpass Cape Hatteras as they travel northward from Palm Beach County to as far as Long Island, which is outside the current designated NMFS EFH. The observed variation in migration distance, SST range, and seasonal migratory drivers may be an indication of resilience, as this population will respond to increasing temperatures in diverse ways. However, if individuals rely on preemption via photoperiod as a migratory cue, mismatches between the environment and photoperiod under climate change conditions may induce stress on this population (Post & Forchhammer 2008, Walker et al. 2019).

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