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# Multi-year movements of adult and subadult bull sharks (*Carcharhinus leucas*): philopatry, connectivity, and environmental influences

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**Abstract** Understanding the movement ecology of marine species is important for conservation management and monitoring their responses to environmental change. In this study, adult and subadult bull sharks (*Carcharhinus leucas;* $n = 16$) were acoustically tagged in Biscayne Bay, Florida (USA), where they were tracked locally via an array of 40 passive acoustic receivers, as well as regionally via cooperative acoustic telemetry networks, with individuals tracked up to 4.5 years. Detection data were used to assess philopatry, regional connectivity, and environmental correlates of shark habitat use. Spatial range varied per individual; however, most individuals displayed high residency to Biscayne Bay, exhibiting strong philopatric behavior to the tagging area. A generalized linear mixed model revealed a seasonal pattern in habitat use, with mature females displaying high residency in Biscayne Bay during the colder dry season (November to February) and lower residencies during the warmer wet season (June to October). These seasonal patterns were supported by catch data from long-term fishery-independent shark surveys in the study area. During summer months when residencies of *C. leucas* declined in Biscayne Bay, their residencies increased in other regions (e.g., Florida Gulf Coast), demonstrative of seasonal migrations. Connectivity between areas of high use (Biscayne Bay and Florida Gulf Coast) was demonstrated by some individuals traveling between these areas. Results from generalized additive mixed models suggest that these movement patterns could be partially driven by seasonal changes in environmental variables as well as an individual's life stage, including reproductive status.

**Keywords** Movement ecology · Acoustic telemetry · Philopatry · Tracking · Highly migratory species · *Carcharhinus leucas*

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## Introduction

Determining the spatial ranges and movement patterns of mobile species is critical for conservation management, including establishing effective place-based management (Hays et al. 2019) and predicting species responses to environmental change (Birkmanis et al.

2020; Niella et al. 2020). This is particularly important for threatened and vulnerable species, where an understanding of their spatial use can inform effective spatial protections (Knip et al. 2012; Graham et al. 2016; McDonnell et al. 2020), enable population recovery (Speed et al. 2018), and track their responses to climate change (Birkmanis et al. 2020). Understanding habitat use and residency patterns can shed light on both short- and long-term space use and may even highlight differences in environmental preferences (Bangley et al. 2020), social networks (Jacoby et al. 2016), foraging behaviors (Bailey et al. 2012), and predator–prey interactions (Hammerschlag et al. 2012).

Studying the movements of highly migratory species within the marine environment is inherently challenging, as it can be difficult to differentiate between populations and to delineate precise residencies and areas of core use. Over the last decade, however, advances in biotelemetry have enabled researchers to more effectively remotely track the movements of wide-ranging marine animals, such as large sharks (Cooke 2008; Hammerschlag et al. 2011; Hussey et al. 2015). These technologies have allowed marine scientists to determine specific movement metrics, including spatial range, connectivity, and activity levels (e.g., Howey-Jordan et al. 2013; Guttridge et al. 2017; Skubel et al. 2020).

Bull sharks (*Carcharhinus leucas*) are large marine predators that occupy tropical and warm temperate waters around the globe (Castro 2010). To date, most movement studies of this species within U.S. waters have focused on juvenile life stages within specific nursery areas (e.g., Simpfendorfer et al. 2005; Ortega et al. 2009; Curtis et al. 2011; Drymon et al. 2013), with only a few evaluating habitat use of adult and subadult life stages (e.g., Carlson et al. 2010; Hammerschlag et al. 2012). Such studies have generally revealed preference for shallow (< 20 m) and warm (26 °C–33 °C) coastal waters by mature and maturing *C. leucas*, largely restricted to inshore areas, with relatively low mobility. These findings have implications for conservation and management of adults as the core use areas of tagged individuals have rarely spanned multiple jurisdictions (Graham et al. 2016; Calich et al. 2018). However, tracking periods of these previous studies were relatively short (median tracking periods less than 3 months). Additionally, recent evidence indicates poleward shifts in *C. leucas* nursery grounds along the U.S. eastern seaboard due to warming (Bangley et al. 2018), suggesting the possibility of range shifts in adults due to climate change. Therefore, there is a need to further examine movement patterns of adult and subadult life stages of *C. leucas* over longer time periods (i.e., years) to determine potential philopatric behavior to specific locations, possible regional connectivity, and if and how changes in environmental conditions, particularly temperature, influence these movement patterns.

Acoustic telemetry has been previously used to track long-term movements of adult *C. leucas*, for example in South Africa and Australia, pinpointing important aggregation sites, highlighting seasonal residency patterns (Daly et al. 2014), and even predicting responses to environmental change (Niella et al. 2020). Moreover, the rise in cooperative acoustic telemetry networks permits researchers to track their acoustically tagged animals outside of their own arrays, enabling them to answer important research questions over a wider spatial scale (Crossin et al. 2017; Friess et al. 2020; Bangley et al. 2020). These networks and their associated data-sharing policies can facilitate the examination of movement patterns of wide-ranging demersal species, like *C. leucas* over larger spatial and temporal scales.

In this study, we used passive acoustic telemetry data to investigate potential philopatric behavior, regional connectivity, and environmental correlates of habitat use by adult and subadult *C. leucas* tagged in Biscayne Bay (Florida). Spanning multiple years of tracking (up to 4.5 years), acoustic detection data were obtained through our own local array in Biscayne Bay and from four cooperative acoustic tracking networks covering coastal areas of the U.S. eastern seaboard and Gulf of Mexico. These data were supplemented with fishery-independent shark abundance surveys in Biscayne Bay. We used these data to address the following three questions: (1) What is the spatial extent of *C. leucas* tagged in Biscayne Bay to other coastal regions covered by acoustic receivers within the U.S. Atlantic and Gulf of Mexico? (2) What role do these regions serve in *C. leucas'* seasonal migrations (end point or pathway), and is there any evidence of philopatric behavior within any of them? (3) Do any relationships exist between key environmental variables measured within regions and the number of days *C. leucas* were detected there per month?

## Methods

### Study species

Bull sharks (*Carcharhinus leucas*) are common to tropical and subtropical coastal waters. Along the Atlantic Coast of the United States, they range from Massachusetts to the Gulf of Mexico (Castro 2010). Among the top marine predators in South Florida waters (Shipley et al. 2019), *C. leucas* consumes a wide variety of fishes and small elasmobranchs and occurs in considerably high numbers during the winter and spring (Castro 2010).

These sharks are born at approximately 60 cm–75 cm total length (TL) (Branstetter and Stiles 1987) and use inshore estuaries as nursery areas as juveniles until reaching approximately 190 cm TL (Curtis et al. 2011), after which they expand their range to adjacent coastal areas as subadults. Reaching lengths of up to 285 cm, *C. leucas* become sexually mature at lengths greater than 225 cm TL for females and between 210 cm–220 cm TL for males (Branstetter and Stiles 1987). Accordingly, here we defined juvenile *C. leucas* as those below 190 cm TL, subadult (maturing) sharks as those between 190 and 210 cm TL, and adult (mature) sharks as those greater than 210 cm TL for males and 225 cm TL for females.

This species can inhabit waters as deep as 150 m, but are primarily found in shallower areas inshore, especially during the juvenile life stage (Ortega et al. 2009). *C. leucas* is euryhaline and inhabits low salinity environments such as rivers and estuaries, achievable via osmoregulation (Thorson 1972). The relationship between *C. leucas* movement and water temperature has been examined in previous studies, with mixed results (Ortega et al. 2009; Daly et al. 2014; Calich et al. 2018; Altobelli and Szedlmayer 2020). For example, one study found that juveniles' movements within a Florida estuary were significantly related to water temperature, with individuals occurring between surface temperatures of 27.0 and 37.3 °C (mean = 30.4 °C) (Ortega et al. 2009). On the other hand, a recent study conducted in the Gulf of Mexico found no significant effect of temperature on *C. leucas* residency, despite observing significant seasonal effects on residency patterns (Altobelli and Szedlmayer 2020).

### Study site

All *C. leucas* individuals considered for this study were originally caught in Biscayne Bay, Florida. This bay is a clear water barrier island lagoon that spans the coastline from the city of Miami to the beginning of the Florida Keys (~ 56 km by ~ 13 km). It is primarily a benthic-based ecosystem containing communities of seagrasses and corals and is also characterized by areas of estuarine habitats (Browder et al. 2005), similar to those known to attract *C. leucas* at younger life stages (Wiley and Simpfendorfer 2007). The northern part of Biscayne Bay borders the city of Miami, subjecting waters in this area to effects of urbanization, including but not limited to chemical and noise pollution, coastal development, and a high level of human recreation (Rider 2020).

In Biscayne Bay, an array consisting of 40 Innovasea VR2W receivers (Amirix Inc., Bedford, NS, Canada) were deployed along and within the Bay's boundaries beginning in July 2015 (Online Resource 1). At each site, the receivers were anchored to the substrate using a concrete stand. Receivers were retrieved for maintenance every six months and their data were downloaded prior to being redeployed. To determine the effective detection range of the receivers, range testing was performed at three separate stations using similar methods described by Kessel et al. (2014b). At these three receiver stations, six Innovasea sentinel range testing tags (Amirix Inc., Bedford, NS, Canada) with nominal delays of one minute were deployed at 100, 200, 400, 600, 800, and 1000 m for a total of 24 h. After the range testing period, receiver detection data were downloaded and the number of detections per hour from each transmitter tag were divided by the total number of hourly detections a receiver could have theoretically received (in this case, maximum $N = 60$). These proportions were plotted against their associated distance and a logistic regression curve was fitted to these data points and used to derive the 50 and 5% detectability range of the receiver station. The receiver stations selected for range testing were representative of the differing habitats and substrates that are represented in Biscayne Bay.

### Capture and tagging

To monitor movements of *C. leucas*, sharks were caught and acoustically tagged between February 2015 and December 2017 using standard sets of 10 drumlines with baited C-hooks (described in Gallagher et al. 2014). Drumlines were deployed and left to soak for approximately one hour, usually three times per day. Typical bait included great barracuda (*Sphyraena barracuda*) and false albacore (*Euthynnus alletteratus*). Once caught, hooked *C. leucas* were secured alongside the boat and total length (TL; the straight-line length from the tip of the snout to the tip of the upper tail lobe) was measured. All sharks were tagged with a plastic ID dart tag into the dorsal musculature at the base of the dorsal fin to permit re-identification if encountered again. We selected to acoustically tag a subset of *C. leucas* that were caught in different parts of Biscayne Bay to reduce any potential spatial biases, but we did not follow any sex or size-specific criteria in selecting these individuals. Bull sharks were affixed with individually coded Innovasea V16-4X internal acoustic transmitters (Amirix Inc., Bedford, NS, Canada), with a nominal delay of 60 to 90 s. Tags were inserted through an incision into the body cavity following the same protocol described in Hammerschlag et al. (2017). Once the transmitter was inserted, the incision was closed promptly with one to two sutures. All caught sharks were released in good condition.

As described by Griffin et al. (2018), detection data from the Biscayne Bay array were used in conjunction with data gathered from four cooperative networks: Integrated Tracking of Aquatic Animals in the Gulf of Mexico (Coast of Florida and Gulf of Mexico), Florida Atlantic Coast Telemetry (Florida Coast), Mid-Atlantic Acoustic Telemetry Observation System (East Coast, United States), and Ocean Tracking Network (East Coast, United States) (Cooke et al. 2011; Currier et al. 2015). Each network consists of various organizations that utilize Innovasea acoustic receivers to track different marine species, facilitating data sharing among them. The detection data were filtered to remove any false detections – defined as a single detection that occurred alone within a one-hour period (Kessel et al. 2014a) using the R package 'GLATOS' (Holbrook et al., 2017). Additionally, any shark that was not detected on more than 10 individual days among the arrays within the four cooperative networks was removed (Kessel et al. 2014a).

### CPUE analysis

Catch data used to compute CPUE were gathered using the same fishing methods described in the previous section. Sampling efforts occurred in Biscayne Bay during both the dry (November–April) and wet (May–October) seasons from 2015 to 2018. CPUE was calculated as the number of *C. leucas* caught divided by the total number of drumlines deployed per month (Bangley et al. 2018). To normalize these data, CPUE values were log-transformed. A linear model examined the effects of season, sex, life stage (based on TL, as described in Study Species) and their interactions on the log-transformed CPUE. Model predictions were used to estimate the percent change of CPUE between seasons for different combinations of sex and life stage.

### Residency

Receiver stations where *C. leucas* was detected were divided up into 7 different regions (Northern Gulf of Mexico, Florida Gulf Coast, Florida Keys, Biscayne Bay, Central Florida Atlantic Coast, Northern Florida to South Carolina, and Chesapeake Bay to Maryland Coast) to analyze the residency patterns within each region. There were no available detection data between South Carolina and Chesapeake Bay, and therefore these areas were not assigned to a region within our analyses. A monthly residency index (RI) for each individual within each region was calculated as the number of total days detected per month divided by the number of days at liberty per month (Bond et al. 2012; Altobelli and Szedlmayer 2020). As we did not have detection range data for any array outside of Biscayne Bay, we moved forward with our calculations of residency assuming that the 50 and 5% detection probability distances were similar across all regions. Additionally, our calculations were limited to presence-only data since we did not have metadata for receiver stations outside of our own array on which sharks were not detected.

Monthly RIs were compared within the Biscayne Bay array (where all acoustic metadata was available) using a generalized linear mixed model (GLMM) with a Poisson distribution where the explanatory variable was the days detected per month, the fixed effects were month and an offset of days in month, and the random effect was the transmitter ID to account for individual variation. The GLMM was carried out using the 'lme4′ package in RStudio (Bates et al. 2014). A least square means *post-hoc* test was performed using the 'emmeans' package in R (Lenth et al. 2019) to determine significant contrasts between all months. Sea surface temperature data were extracted from NOAA's ERDAPP data server (coastwatch.pfeg.noaa.gov), using the R package 'rerddapXtracto' (V.0.4.5) for the Biscayne Bay area using NOAA's Multi-scale Ultra-high Resolution SST Analysis (MURSST) monthly product between the years of 2015–2020.

### Connectivity and range

Connectivity was determined for individuals that moved between Biscayne Bay and any of the other six regions. Round trips were counted per individual based on the farthest region traveled to on each coast before returning to Biscayne Bay. For example, if an individual left the Bay, moved to the Northern Gulf of Mexico, visited the Central Florida Atlantic Coast, and then returned to the Bay, the round trip would be to both the Northern Gulf of Mexico region and the Central Florida Atlantic Coast region. Range was measured as the farthest region each individual traveled to from Biscayne Bay on both the Atlantic and Gulf Coasts of the United States.

### Environmental effects

To explore potential influences of temperature and productivity on shark residency patterns, satellite-derived gridded datasets' values were obtained from NOAA's ERDAPP data server using the 'rerddapXtracto' package to match environmental values to each receiver location at the time of shark detection. The SST data were extracted to positions within 0.01° latitude/longitude of receiver location using the NOAA Multi-scale Ultra-high Resolution SST Analysis (MURSST) daily (https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41.html). Chlorophyll *a* (chl *a*) levels (mg/m$^3$) were extracted within 0.05° latitude/longitude using AQUA MODIS 5-day composite product (https://upwell.pfeg.noaa.gov/erddap/griddap/erdMBchla5day_LonPM180.html). Depth was also assigned to each point using NOAA's topography ETOPO1 dataset, with a resolution of 0.01°. High-resolution salinity data were only available for a fraction ($\sim$ 10%) of receiver locations, therefore, this environmental variable was not included in our analyses. The lack of data may be due to the receivers' proximity to the coast and the paucity of daily remotely sensed and high-resolution sea surface salinity data available in these areas (Medina-Lopez and Ureña-Fuentes 2019).

To understand the effect of SST and chl *a* on the number of days sharks were detected per month, we employed a generalized additive mixed model (GAMM) with a Poisson distribution for each region using the 'mgcv' package in RStudio (Wood 2004). Depth was originally included as an effect in the GAMMs, however, this factor did not meet the assumptions of the tests, nor did it pass diagnostic tests for any of our models. Upon further review, this is likely due to the very small range of depth measured in areas with the highest residencies (e.g., Biscayne Bay, where all receivers occur in waters less than 10 m deep). Therefore, this variable was removed from the models. GAMMs were employed for every region except the Northern Gulf of Mexico and Chesapeake Bay, as individuals were only detected in these regions on one day. As receiver coverage did not span the regions in their entirety, it would be impossible to accurately identify if an individual was truly absent. Therefore, datasets analyzed for each region contained only the months during which sharks were detected (*i.e.*, days detected per month $> 0$). Fixed effects included mean monthly SST and chl *a*, while animal ID was a random effect, accounting for individual variation and adding predictive power. A smoothing function was applied to both SST and chl *a* to model the relationship between these fixed environmental effects and monthly days detected. Model diagnostics were analyzed to verify the number of basis functions as well as to check for concurvity.

## Results

### Acoustic tagging summary

Between February 2015 and December 2017, a total of 22 individual bull sharks (*Carcharhinus leucas*) (4 males and 18 females) were caught and acoustically tagged in Biscayne Bay, ranging from 188 to 270 cm

**Table 1** Summary of acoustically tagged *C. leucas* individuals, detected more than 10 days within the four cooperative networks

| Transmitter ID # | Date tagged (mm/dd/yyyy) | Tagging latitude | Tagging longitude | Sex | Total length (cm) | Life stage | Days detected | Days at liberty |
|---|---|---|---|---|---|---|---|---|
| 24655 | 02/24/2015 | 25.7480 | −80.1890 | F | 263 | Adult | 161 | 1616 |
| 24660 | 02/27/2015 | 25.7262 | −80.1577 | F | 219 | Subadult | 362 | 1616 |
| 24661 | 02/24/2015 | 25.7262 | −80.1577 | F | 250 | Adult | 88 | 1616 |
| 58396 | 08/11/2015 | 25.7051 | −80.0868 | F | 211 | Subadult | 267 | 1616 |
| 58403 | 01/21/2016 | 25.6220 | −80.1790 | F | 202 | Subadult | 282 | 1588 |
| 13487 | 12/12/2017 | 25.7294 | −80.1581 | F | 196 | Subadult | 233 | 897 |
| 16325 | 03/10/2017 | 25.7289 | −80.2322 | F | 244 | Adult | 240 | 1174 |
| 16324 | 08/13/2017 | 25.6921 | −80.0850 | F | 261 | Adult | 17 | 1018 |
| 16328 | 02/07/2017 | 25.7145 | −80.2082 | M | 196 | Subadult | 21 | 1205 |
| 18401 | 09/11/2016 | 25.6176 | −80.1500 | M | 188 | Juvenile | 15 | 1354 |
| 18413 | 10/17/2016 | 25.6126 | −80.1410 | F | 242 | Adult | 30 | 1318 |
| 18415 | 10/22/2016 | 25.6380 | −80.1968 | F | 191 | Subadult | 268 | 1313 |
| 18419 | 1/20/2017 | 25.6016 | −80.0907 | F | 236 | Adult | 61 | 1223 |
| 18421 | 02/04/2017 | 25.6223 | −80.0980 | F | 242 | Adult | 31 | 1208 |
| 20563 | 12/04/2015 | 25.7002 | −80.9900 | F | 256 | Adult | 90 | 1636 |
| 20773 | 02/16/2016 | 25.7051 | −80.0868 | F | 245 | Adult | 119 | 1562 |

TL. Of the 22 sharks originally tagged, 16 individuals (2 male and 14 female) were detected on 10 days or more; these were retained for further analyses (Table 1). Based on TL, one of the males and five of the females were classified as subadult, while the remaining females were classified as mature, and the other male was classified as juvenile (Table 1). Range testing in Biscayne Bay revealed a 50% detection rate at ∼ 250 m and 5% detection rate closer to 1000 m for each of the three receiver stations tested.

Sharks were detected between March 2015 and June 2020 on a wide range of individual receivers ($N = 504$) spanning the U.S. coastline from the Alabama-Mississippi Shelf to the Maryland coast (Fig. 1). However, most of the receivers (43%) that detected tagged *C. leucas* were located in the Florida Keys. The total number of days detected per individual ranged from 15 to 362 days with a median of 88 days (mean = 120.5 days), while the total days at liberty ranged from 897 to 1636 days (2.46–4.43 years) with a median of 1336 days (3.66 years) (mean = 1372 days, or 3.76 years) (Table 1).

## CPUE analyses

The linear model used to understand differences in CPUE between seasons for different combinations of sex and life stage was significant ($p < 0.009$, $R^2 = 0.162$) (Table 2). The model predicted a 96% increase in the CPUE of mature female *C. leucas* during the dry season compared to the wet ($t = 2.527$, $p = 0.013$). In contrast, the model predicted a 21% decrease in the CPUE of subadult females ($t = -0.906$, $p = 0.367$). Both CPUE of mature and subadult males were predicted to decrease by 32% ($t = -1.360$, $p = 0.177$) and 39% ($t = -1.47$, $p = 0.146$), respectively, from the wet season to the dry season.

## Residency

During spring and summer months, when Biscayne Bay RI was lowest, RIs in other array locations, including the Florida Keys, Florida Gulf Coast, and North Florida to South Carolina peaked (Fig. 1). It should be noted that while peaks were observed in these areas during the spring/summer, the respective average RI within these arrays was overall lower (*e.g.,* mean RI = 0.0190, max RI = 0.0444 in Florida Keys, mean RI = 0.0057, max RI = 0.0158 in Florida Gulf Coast) compared to values observed in Biscayne Bay (mean RI = 0.0621, max RI = 0.1304) (Fig. 1).

Overall, the highest RIs were observed in Biscayne Bay during the dry season (November–April) (Fig. 2).

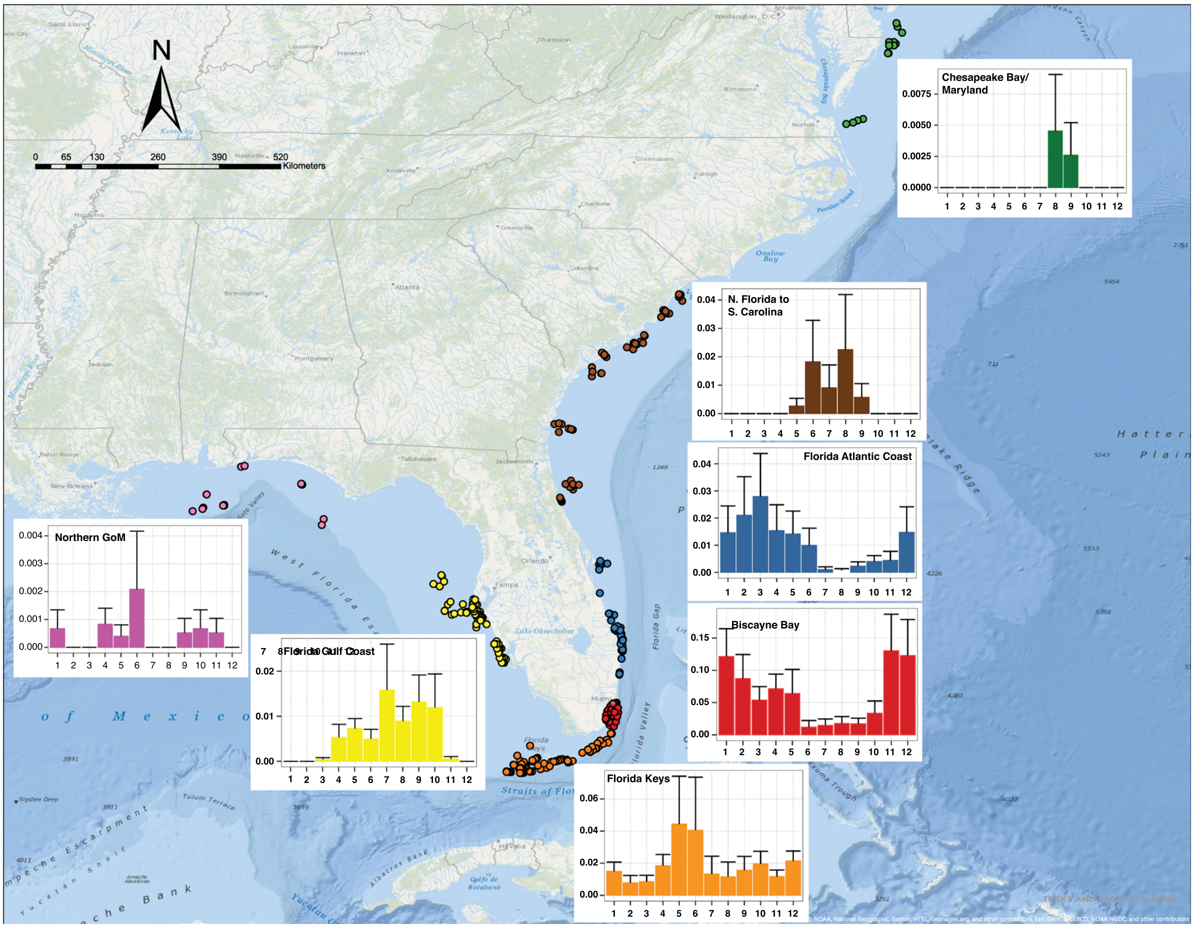


**Fig. 1** Locations of receivers (colored by region) with detections of *C. leucas* originally tagged in Biscayne Bay. Mean residency indices of these sharks (y-axis) are plotted as bars + S.D. over months (x-axis) (January–December, 1–12). Each of the 6 general areas considered in this study are displayed: Northern Gulf of Mexico (pink), Florida Gulf Coast (yellow), Florida Keys (orange), Biscayne Bay (red), Florida Atlantic Coast (blue), Northern Florida to South Carolina (brown) and Chesapeake Bay, Maryland (green)

**Table 2** Results of the general linear model (GLM) testing the effects of season, sex, and life stage on the catch per unit effort (CPUE) of *C. leucas* with wet, female, and mature as the respective reference levels. * represents significance at the alpha = 0.05 level

| | Estimate | Std. error | *t* value | Pr( >\|t\|) |
|---|---|---|---|---|
| (Intercept) | −4.07 | 0.23 | −17.62 | < 0.001* |
| Season: Dry | 0.67 | 0.27 | 2.53 | 0.01* |
| Sex: M | 0.50 | 0.29 | 1.75 | 0.08 |
| Life stage: Subadult | 0.30 | 0.31 | 0.96 | 0.34 |
| Season: Dry, Sex: M | −1.06 | 0.39 | −2.72 | 0.01* |
| Season: Dry, Life stage: Subadult | −0.91 | 0.37 | −2.43 | 0.02* |
| Sex M, Life stage: Subadult | −0.62 | 0.41 | −1.51 | 0.14 |
| Season: Dry, Sex: M, Life stage: Subadult | 0.81 | 0.58 | 1.40 | 0.17 |

Residency indices here were significantly higher between the months of November and February (inclusive) than in all other months (Table 3). Biscayne Bay residency was significantly lower in June through October than in all other months (Table 3, Fig. 2). Mean monthly SST also varied throughout the months, peaking in June and July at 30.3 °C and 30.5 °C, respectively (Fig. 2).

## Connectivity and range

Of the 16 tagged sharks that were retained for analyses, 14 were detected within Biscayne Bay's acoustic receiver array after visiting at least one of the other six regions, with many returning multiple times (Table 4). Specifically, sharks displayed strong connectivity to the Gulf of Mexico, with 11 individuals performing round trips from Biscayne Bay to either the Florida Gulf Coast or the North Gulf of Mexico near Mobile, Alabama. In many cases, individuals performed multiple round trips between these two regions, with one completing four trips (Table 4). Two other individuals did travel from Biscayne Bay to the Gulf but did not return. Only four individuals were detected farther north than the Central Florida Atlantic Coast, three of which made only a single round trip back to the Bay. Of those four individuals, only one was not detected in the Gulf of Mexico, but was, however, detected in the Florida Keys. We observed high connectivity to the Florida Keys: 44% of individuals ($N = 7$) tagged in Biscayne Bay undertook at least one round trip to this region, with two individuals undertaking at least four trips each. All but one individual was detected in this array (shark #13487).

The total range covered by individuals that were detected outside Biscayne Bay ($N = 15$) varied. One individual's detections ranged from the Bay to the Florida Keys, whereas another individual's detections ranged from Ocean City, Maryland to the Mississippi-Alabama shelf. Most individual ranges spanned the Florida Atlantic Coast/Biscayne Bay and the Florida Gulf Coast/Northern Gulf of Mexico (Table 4).

Large scale seasonal movement patterns of *C. leucas* differed by sex. Notable seasonal migrations were undertaken by mature females to and from the

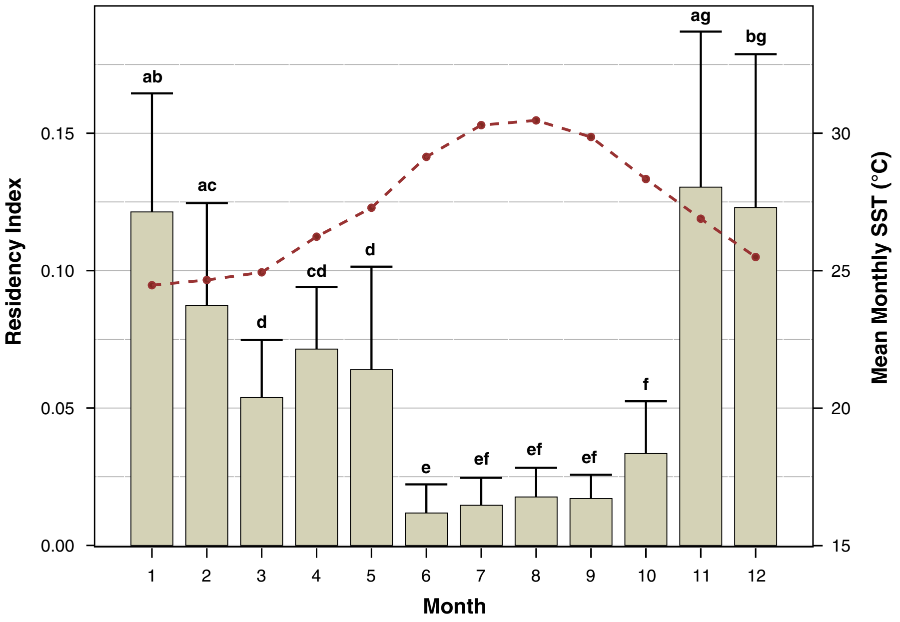


**Fig. 2** Mean monthly residencies of *C. leucas* and mean monthly sea surface temperatures (SST) in Biscayne Bay. Bars represent mean monthly residencies (+ 1 s.d.) within the Biscayne Bay receiver array between June 2015 and June 2020. Monthly residency indices were compared using a generalized linear mixed model (GLMM) and post hoc tests revealed significant contrasts between months: bars with the same letter do not significantly differ from one another ($P > 0.05$). Mean SST within the study site are represented along the dashed red line, averaged between 2015 and 2020

**Table 3** Results from the generalized linear mixed model (GLMM) testing the effect of month on the residency index of acoustically tagged *C. lecuas* within the Biscayne Bay acoustic array with January as the reference level. Tukey's post hoc results are listed in Fig. 2

| Fixed Effects | | | | |
|---|---|---|---|---|
| | Estimate | Std. error | *Z* value | Pr( >\|z\|) |
| (Intercept) | −3.68 | 0.65 | −5.69 | < 0.001* |
| February | −0.31 | 0.11 | −2.92 | < 0.001* |
| March | −0.81 | 0.12 | −6.83 | < 0.001* |
| April | −0.56 | 0.11 | −5.16 | < 0.001* |
| May | −0.85 | 0.13 | −6.67 | < 0.001* |
| June | −2.79 | 0.30 | −9.45 | < 0.001* |
| July | −2.15 | 0.22 | −9.65 | < 0.001* |
| August | −1.84 | 0.19 | −9.49 | < 0.001* |
| September | −1.93 | 0.20 | −9.49 | < 0.001* |
| October | −1.45 | 0.16 | −8.90 | < 0.001* |
| November | 0.02 | 0.10 | 0.25 | 0.8 |
| December | 0.06 | 0.10 | 0.67 | 0.5 |
| Random effects | | | | |
| Groups | Name | Variance | Std. Dev | |
| Transmitter ID # | (Intercept) | 6.197 | 2.489 | |

* represents significance at the alpha = 0.05 level

tagging location (Biscayne Bay) following a similar pattern. Most mature females remained within Biscayne Bay during the colder dry season and migrated to other regions during the warmer wet season (Table 4, Fig. 1). The only mature female that did not follow this pattern (shark #20773) moved consistently between Maryland and Alabama for almost three years before returning to Biscayne Bay during the dry season for three months (Fig. 3; Online Resource 2). The two tagged males exhibited more varied seasonal movements; one subadult and one juvenile, albeit close in length (196 and 188 cm, respectively), displayed strong differences in migration patterns (Table 4). One male made round trips from both the North Gulf of Mexico and the Florida Atlantic Coast, while the other moved from Biscayne Bay to the Florida Keys, and did not return.

Movement patterns also differed among life stages. Of the five subadult females, only one was detected solely in Biscayne Bay. The remaining four made long-range round trips from Biscayne Bay, however some trips did not occur until several years after tagging. For example, sharks #58396 (TL: 211 cm), #58403 (TL: 202 cm), and #18415 (TL: 196 cm) were tagged in August 2015, January 2016, and October 2016, respectively, but were not detected beyond Biscayne Bay or the Florida Keys until November 2017, August 2019, and May 2018, respectively (Fig. 3). The nine mature females all completed long-range round trips; each of them moved between the Gulf of Mexico and Biscayne Bay at least once during their time at liberty (Table 4, Fig. 3).

## Environmental effects

Sea surface temperature and chl *a* data were matched to 93 percent of all detections ($N = 102{,}592$) and this subset was used in the GAMMs. Both environmental variables significantly affected the number of days *C. leucas* were detected per month in different regions (Table 5, Fig. 4). Chlorophyll *a* was significant in all models, whereas SST was significant in all regions except for in the Florida Keys (Table 5, Fig. 4).

The differences in residencies observed in Biscayne Bay during the wet season coincided with shifts in sea surface temperature. Significantly lower residences measured between June and September overlapped with the highest mean monthly SST (29.1—30.5 °C, Fig. 2). The highest residencies occurred between November and February, when mean monthly temperatures were considerably lower (24.5 °C–26.8 °C, Fig. 2). Similarly, the GAMM model for this region revealed that temperatures above 27 °C had a negative effect on *C. leucas* presence (Fig. 4c). The effect of SST was significant in every other region tested except for the Florida Keys (Table 5). There was a positive

**Table 4** Number of round trips between Biscayne Bay and the other six designated regions. Round trips were counted per individual based on the farthest region traveled to on each coast before returning to Biscayne Bay. Half numbers indicate that the shark was last detected in that region after traveling from Biscayne Bay

| Transmitter ID # | Tag date | Florida Keys | Florida Gulf Coast | Northern GoM | Florida Atlantic Coast | Northern Florida to S. Carolina | Chesapeake Bay/ Maryland |
|---|---|---|---|---|---|---|---|
| 24655 | 02/24/2015 | 0 | 3 | 1.5 | 0 | 0 | 0 |
| 24660[b] | 02/27/2015 | 1 | 3 | 0 | 2 | 0 | 0 |
| 24661 | 02/24/2015 | 0 | 0 | 1 | 0.5 | 0 | 0 |
| 58396[b] | 08/11/2015 | 6 | 1 | 0 | 3 | 1 | 0 |
| 58403[b] | 01/21/2016 | 5 | 1 | 0 | 0 | 0 | 0 |
| 13487[b] | 12/12/2017 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16324 | 08/13/2017 | 0 | 0 | 1 | 0 | 1 | 0 |
| 16325 | 03/10/2017 | 1 | 2 | 0 | 0 | 0 | 0 |
| 16328[a] | 02/07/2017 | 0 | 0 | 1 | 1.5 | 0 | 0 |
| 18401[a] | 09/11/2016 | 0.5 | 0 | 0 | 0 | 0 | 0 |
| 18413 | 10/17/2016 | 0 | 0.5 | 0 | 0 | 0 | 0 |
| 18415[b] | 10/22/2016 | 1 | 0 | 0 | 0 | 2 | 0 |
| 18419 | 01/20/2017 | 1 | 1 | 1 | 0 | 0 | 0 |
| 18421 | 02/04/2017 | 0 | 0.5 | 0 | 0 | 0 | 0 |
| 20563 | 12/04/2015 | 3 | 2 | 0 | 0 | 0 | 0 |
| 20773 | 02/16/2016 | 0 | 1 | 2 | 3 | 1 | 1 |

[a] Represents males

[b] Represents subadult females

effect of SST on monthly residencies below ~ 28 °C from North Florida to South Carolina and ~ 26 °C along the Florida Atlantic Coast. In contrast, there was a positive effect of SST above ~ 28 °C along Florida Gulf Coast (Fig. 4).

There was also a positive effect of chl *a* concentration between 4 and 12 mg $m^{-3}$ on shark presence in Biscayne Bay, while values beyond this range had a negative effect (Fig. 4c). These chl *a* levels, measured at the receiver location close to the time of shark detection, are high compared to the mean monthly values in this region during the study period (0.6 mg $m^{-3}$–1.1 mg $m^{-3}$, Online Resource 3). Chlorophyll *a* concentration was significant in all other regions, though its relationship with *C. leucas* presence varied. For example, in the Florida Atlantic and Gulf Coast regions, chl *a* concentration had a positive effect on shark presence between ~ 0.5–1.5 and ~ 2–5 mg $m^{-3}$, respectively (Fig. 4b and e),

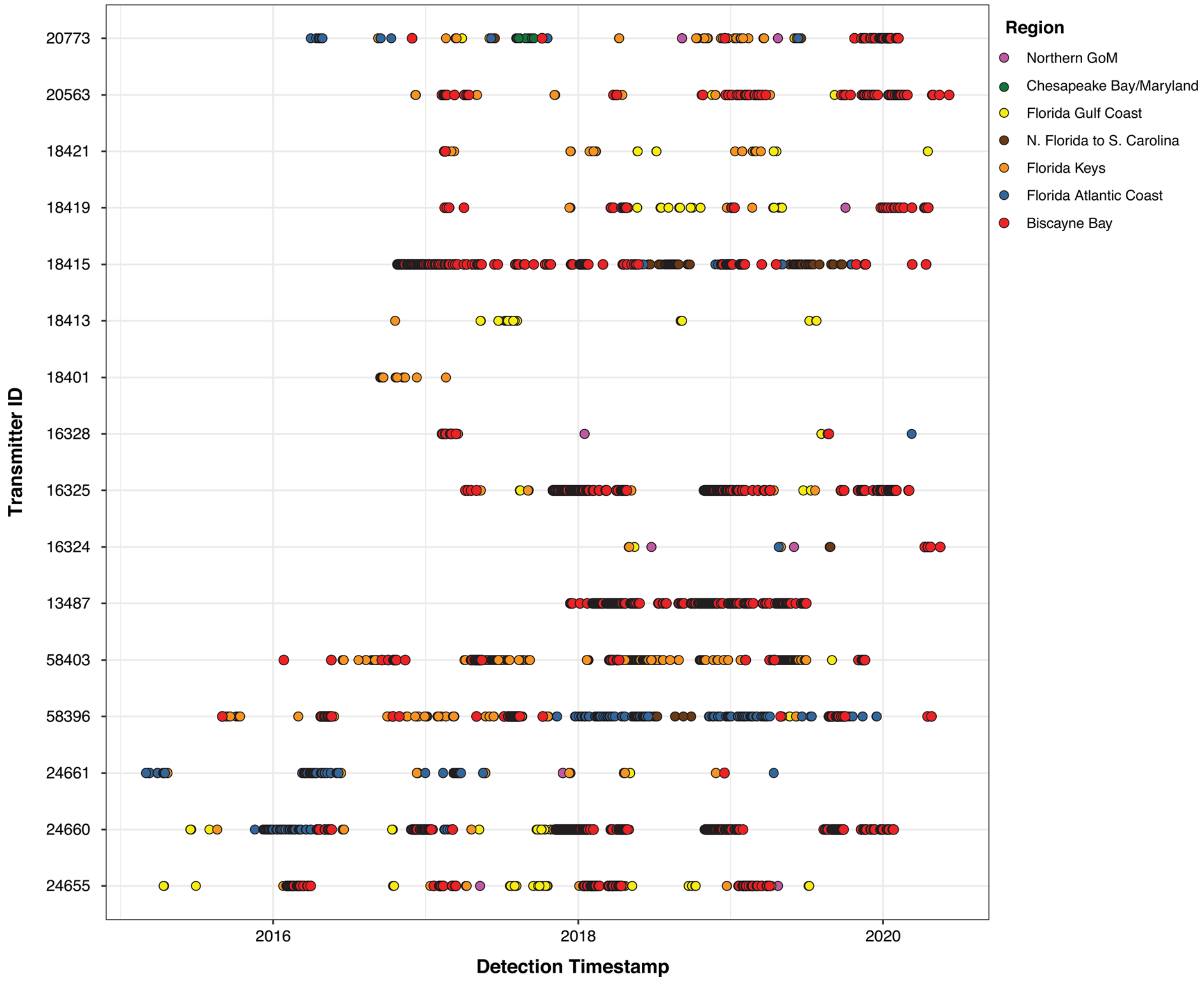


**Fig. 3** Abacus plot depicting detections of each acoustically tagged individual (transmitter ID #) across all 6 regions: Northern Gulf of Mexico (pink), Florida Gulf Coast (yellow), Florida Keys (orange), Biscayne Bay (red), Florida Atlantic Coast (blue), Northern Florida to South Carolina (brown) and Chesapeake Bay, Maryland (green). Each discrete detection within a specific region is represented by a point

while in the Florida Keys, a similar positive effect was observed between ∼ 2–3.5 mg $m^{-3}$ (Fig. 4d).

## Discussion

Our study combined acoustic telemetry, catch, and environmental datasets to examine the temporal and spatial presence and movements of adult and subadult bull sharks (*Carcharhinus leucas*) within Biscayne Bay as well as along the U.S. Atlantic Coast and Gulf of Mexico. Based on multi-year tracking data, with some individuals tracked up to 4.5 years, we provide insights into the spatial extent of their large-scale movements and provide evidence of seasonal patterns and potential philopatry to Biscayne Bay. We also explore the potential drivers of their occurrences within different regions, including sex, life stage, SST, and chl *a* concentration. These findings are of high relevance, as *C. leucas* occupies shallow coastal habitats where they are subjected to significant fluxes in environmental conditions, but also increasing urbanization and considerable overlap with human users of the marine system.

**Table 5** Results from generalized additive mixed models (GAMMs) carried out for each region to determine environmental effects on residency of *C. leucas*

| Region | N | $R^2$ | P | edf | F |
|---|---|---|---|---|---|
| *Biscayne Bay* | 13 | 0.231 | | | |
| SST | | | < 0.001* | 3.732 | 8.324 |
| chl *a* | | | < 0.001* | 3.506 | 25.916 |
| *N. Florida to S. Carolina* | 4 | 0.532 | | | |
| SST | | | 0.010* | 1.00 | 9.249 |
| chl *a* | | | 0.001* | 1.00 | 16.479 |
| *Florida Gulf Coast* | 13 | 0.337 | | | |
| SST | | | 0.020* | 1.00 | 5.911 |
| chl *a* | | | < 0.001* | 2.151 | 9.672 |
| *Florida Atlantic Coast* | 7 | 0.281 | | | |
| SST | | | < 0.001* | 1.000 | 22.371 |
| chl *a* | | | < 0.001* | 3.553 | 9.427 |
| *Florida Keys* | 14 | 0.313 | | | |
| SST | | | 0.090 | 1.00 | 2.925 |
| chl *a* | | | < 0.001* | 4.68 | 11.599 |

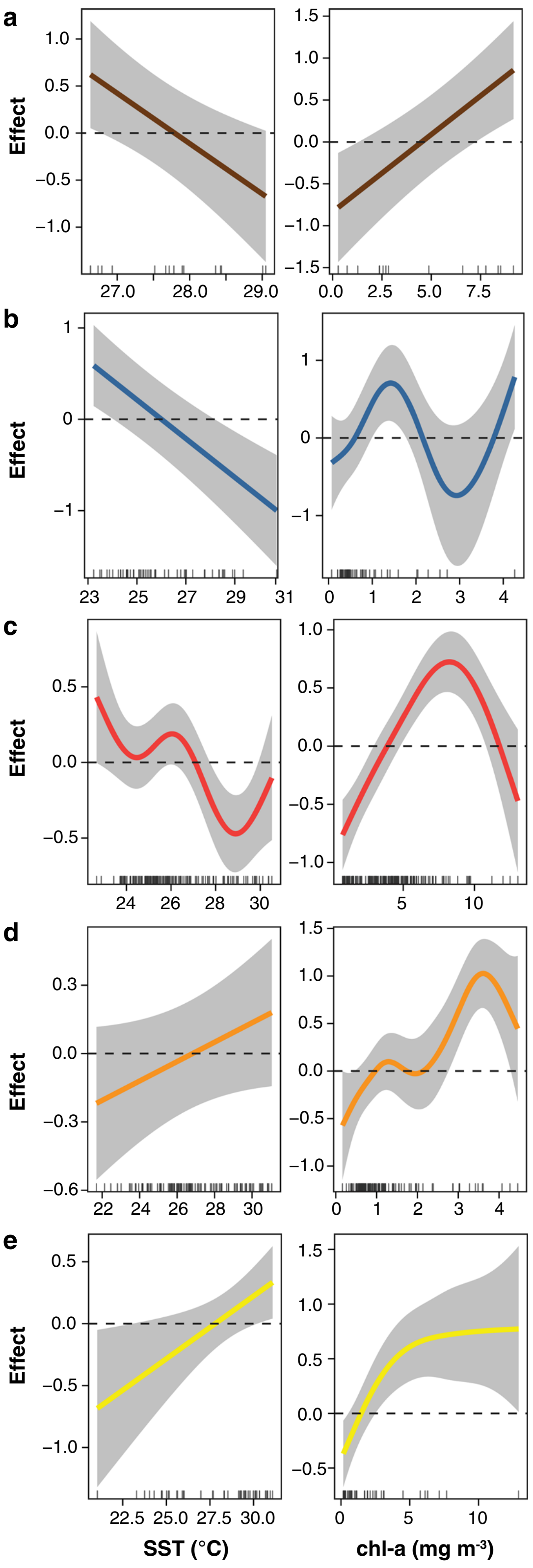
* represents significance at the alpha = 0.05 level

### Biscayne Bay

Life stage played an important role in predicting *C. leucas* presence in Biscayne Bay. Subadult *C. leucas* females only began to initiate seasonal migratory patterns several years after being tagged, presumably once attaining sexual maturity. While movements beyond the acoustic array detection limits cannot be determined for these individuals, our results show that, unlike females tagged at maturity, subadult females were only detected outside of southeast Florida after several years. Interestingly, one female (shark #24660, 219 cm TL), classified as subadult at the time of tagging, did migrate to the Florida Gulf Coast within four months of being tagged. However, unlike other tagged subadults, this individual was very close to the published length of maturity for females at the time of tagging (~ 225 cm, Branstetter and Stiles 1987) and thus could be recently matured.

Similar to the pattern observed in acoustically tracked *C. leucas*, the catch data-derived model showed a significant increase in mature females in Biscayne Bay from the wet to dry season. Previous studies have also demonstrated seasonal patterns in CPUE of adult *C. leucas* in Southwest Florida, with increasing abundance in Florida Bay during the dry season (Hammerschlag et al. 2012). The combined catch and acoustic telemetry results in our study reveal that the Bay may serve an important role in the life history of mature female *C. leucas* that may prompt philopatric behavior. It is plausible that movements into Biscayne Bay during cold months, which were only observed in adult females, could be related to gestation. As an ectothermic species, warm water would reduce gestation period and accelerate embryo development. Indeed, several studies have reported gravid elasmobranchs migrating into warmer water areas during gestation (e.g., Bansemer and Bennett 2009; Jirik and Lowe 2012; Nosal et al. 2014; Sulikowski et al. 2016). Situated in Southeast Florida, the waters of Biscayne Bay are considerably warmer than other areas within their northern range during the cold months. The Bay's waters are also elevated compared to the adjacent ocean waters during colder months since the Bay is semi-enclosed and shallow.

Philopatry has not been previously documented in *C. leucas* within Biscayne Bay; our results are among the first to suggest this behavioral pattern in this species in this area. However, other studies have recognized *C. leucas* philopatry in South Africa (Daly et al. 2014), Australia (Tillett et al. 2012), and most recently in the Gulf of Mexico (Altobelli and Szedlmayer 2020). In contrast to our results, Daly et al. (2017) observed both male and female adults display relatively higher residencies in lower latitudes during the austral summer and fall and migrations to higher latitudes during the winter and spring. While these sharks displayed opposing seasonal residency patterns to those in the present study, the mean monthly temperature during months of relatively higher



◀**Fig. 4** Effect plots from generalized additive mixed models (GAMMs) of sea surface temperature (SST) and chlorophyll *a* (chl *a*) on days detected in each of five regions: North Florida to South Carolina (a, brown), Florida Atlantic Coast (b, blue), Biscayne Bay (c, red), Florida Keys (d, orange), Florida Gulf Coast (e, yellow). Effect values $> 0$ are predictive of increased occurrences, while effect values $< 0$ are predictive of reduced occurrences

residency was similar to that of Biscayne Bay (24 °C–27 °C) providing further evidence of strong thermal preference and subsequent temperature-driven movements. Results from Altobelli and Szedlmayer (2020) were comparable to ours in terms of seasonal philopatry as *C. leucas* ($N = 6$) acoustically tagged in the northern Gulf of Mexico migrated as far as Key West during the dry season before returning to the original tagging area in the wet season.

## Connectivity and range

We provide evidence of *C. leucas'* large scale movements to six other regions from Biscayne Bay, most frequently to the Florida Keys and sites within the Gulf of Mexico. This species has demonstrated use of the Florida Keys in other studies. For example, Altobelli and Szedlmayer (2020) found that two female *C. leucas* (one adult and one subadult), originally tagged in the Northern Gulf of Mexico, frequented the Florida Keys with regularity, though the winter timing of the visits opposed the summer visits observed in the present study. It is possible that the purpose of travel to the Keys differs between these groups. For example, sharks tagged in the Gulf were not detected east of Key West (Altobelli and Szedlmayer 2020), suggesting that this region could be a migratory end point for this group, a possible different or sub-population. On the other hand, despite moving through the Keys regularly, sharks tagged in our study had low residence indices here throughout the year, demonstrating that they likely use the Keys as a migration corridor between the Atlantic and Gulf of Mexico for the population we tagged.

We also observed strong connectivity between Biscayne Bay and the Florida Gulf Coast. Interestingly, there was considerable movement between the Bay and areas that are known *C. leucas* nursery habitats located along the Florida Gulf Coast: Charlotte Harbor (Laurrabaquio-A et al. 2019), Caloosahatchee River, and San Carlos Bay (Simpfendorfer et al. 2005). Additionally, there was notable connectivity between Biscayne Bay and a known nursery habitat along the Florida Atlantic Coast: the Indian River Lagoon (Curtis et al. 2011). Therefore, it is possible that Biscayne Bay serves an important role in the reproduction cycle of *C. leucas*, possibly as a gestation ground for females during colder months as discussed earlier. During warmer months, females' migration out of Biscayne Bay to these known nursery areas could be related to parturition. On the other hand, a lack of catches or detections of neonatal or early juvenile *C. leucas* in Biscayne Bay suggest that the area likely does not serve as a nursery ground for this species. This is not due to gear bias, as our drumline surveys produce catches of bonnethead (*Sphyrna tiburo*), Atlantic sharpnose (*Rhizoprionodon terraenovae*), and blacknose sharks (*Carcharhinus acronotus*), which are of similar sizes to neonate and juvenile *C. leucas*. The seasonal mismatches in peak catch rates and detections of adult males and adult females also suggests that Biscayne Bay is not a mating ground. To further explore Biscayne Bay's potential as a *C. leucas* gestation ground, future studies could measure serum concentrations of different reproductive hormone levels in this species (Manire et al. 1995) combined with ultrasonography (Hammerschlag and Sulikowski 2011) to determine seasonal variation in reproductive state in female *C. leucas* as a non-lethal method to test this hypothesis.

It is possible that sharks' connectivity to regions outside of Biscayne Bay is associated with increased foraging opportunities elsewhere. For example, satellite tracking of *C. leucas* tagged in the Florida Keys showed high use of Florida Bay (Hammerschlag et al. 2012). Here, densities of *C. leucas* were highest near the northwest edge of the Bay, at the opening to the Gulf of Mexico, where fish prey were most abundant within the Bay at the time (Torres et al. 2006; Hammerschlag et al. 2012).

We measured large spatial ranges for the individuals tagged in Biscayne Bay. The *C. leucas* ranges reported by Daly et al. (2014) in South Africa spanned 433 km–703 km. In our study, tagged individuals moved as far as ~ 800 km into the Gulf of Mexico and ~ 1600 km along the Atlantic Coast. This study is among the first to document such large ranges in this species along the East Coast of the United States without the use of satellite tags. This large-scale spatial information is key to adapting management plans to include protection for these species along their migratory routes.

## Environmental correlates

Our results show that *C. lecuas'* preferred temperature range within Biscayne Bay is between 24 and 26 °C, encompassing the thermal preferences recorded for this species previously (Bangley et al. 2018; Lee et al. 2019). Other regional models revealed linear effects of SST on *C. leucas* presence (Fig. 4), which could be indicative of specific seasonal use of these locations. For example, there was a positive effect of SST above 27.5 °C on monthly days detected in the Florida Gulf Coast region (Fig. 4e). A previous study in the Gulf region found that juveniles' movements within a Florida estuary were significantly related to water temperature and documented a preference for high temperatures (range = 27.0–37.3 °C, mean = 30.4 °C, Ortega et al. 2009). In contrast, days detected were significantly negatively correlated with increasing temperature in both the North Florida to South Carolina region (Fig. 4a) and the Florida Atlantic coast region (Fig. 4b). This is likely a result of the overall differences in seasonal SST ranges between the Gulf of Mexico and the Atlantic Ocean, with the latter encompassing a lower temperature range. The Florida Keys was the only region for which there was no significant trend between shark presence and SST, suggesting it may serve as a migration corridor rather than a migratory end point, which is also consistent with the movement data as described earlier.

We observed significant relationships between *C. leucas* residency and chl *a*, a variable often used as a proxy for primary productivity (and food abundance) but also as an indicator of excess nutrient loading in nearshore environments. The effects of increasing chl *a* levels and subsequent eutrophication on fish communities, including top predators like *C. leucas*, are of considerable conservation interest. Monthly median chl *a* levels in Biscayne Bay have been shown to be higher in early spring (February, March) and fall (October and November) (Caccia and Boyer 2005), a period during which we observed high residencies. Specifically, *C. leucas* residency in Biscayne Bay was the highest in November, coinciding with the highest mean monthly chl *a* value (1.12 mg $m^{-3}$). It is possible that these comparatively high levels of chl *a* attract *C. leucas* due to increased fish abundance as a result of higher productivity. Our findings seemingly contrast with those of a recent study which found that chl *a* concentrations contributed the least to *C. leucas* habitat suitability models (Calich et al. 2018). However, this past study utilized chl *a* values averaged over longer periods (seasonal and year-round) in their models, which may have weakened the signal of short-term variability in chl *a* that we detected in the present study (using daily and monthly mean values). This emphasizes the importance of measuring small-scale shifts in this environmental variable (e.g., during algal blooms) as these could significantly influence shark presence, as detected here.

Overall, steadily increasing chl *a* levels have been recorded over the past two decades in Biscayne Bay, with the largest increases observed in shallow nearshore and semi-enclosed environments (Millette et al. 2019), encompassing preferred *C. leucas* habitat and also areas with high acoustic receivers coverage. This trend is indicative of high eutrophication of these waters driven by run-off from land-based sources and is especially apparent in the northern part of the Bay, subject to other effects of urbanization (Caccia and Boyer 2005; Rider 2020). The increased chl *a* values observed in nearshore areas along the western coast of Florida are often close to river discharges and may also be partly driven by run-off (Krueger and Jose 2018). Algal blooms are a major concern in many of Florida's coastal areas, as they decrease light penetration and lead to hypoxic and/or acidified waters, which can negatively affect fish communities (Rudnick et al. 2005). Additionally, there are numerous cyanobacterial toxins associated with algal blooms previously documented in Biscayne Bay that can bioaccumulate through the food web (Brand et al. 2010). Future studies examining the effects of such increases on *C. leucas* in Biscayne Bay are of interest. For example, *C. leucas* sampled in Biscayne Bay were found to have high tissue concentrations of β-N-methylamino-l-alanine (BMAA), a cyanobacterial toxin linked to neurodegenerative diseases (Hammerschlag et al. 2016). Another reason for increased chl *a* levels along the western coast of Florida, especially in August and October, is the Loop Current, a warm-water upwelling that spreads nutrient-rich waters toward the coast (Krueger and Jose 2018). Indeed, we observed the highest residencies in this region between these months.

It is possible these shifts in SST and chl *a* concentration may serve as environmental cues to initiate movements related to life-history events. Past studies have highlighted *C. leucas* nursery grounds in the Gulf of Mexico, where the highest abundance of young of the year occurred at approximately 29 °C (Simpfendorfer et al. 2005). Similarly, Bangley et al. (2018) observed increased CPUE of juvenile *C. leucas* during summer months in a warm temperate estuary along the coast of North Carolina, with presence strongly linked to temperature and salinity measures. It is possible that increased temperature may help stoke the parturition process of *C. lecuas*, prompting large females to leave Biscayne Bay and enter the Gulf of Mexico to use nursery sites for pupping, a pattern that is reflected in their seasonal movements, connectivity between, and residencies in these two areas.

## Limitations and conclusions

One major limitation to this study was the sole use of presence data in our analyses. Since we did not have access to metadata from acoustic arrays where sharks were detected or even arrays where sharks were not detected, our analyses did not account for absence data. Additionally, this study only had detection range data for Biscayne Bay; as such we assumed that the detection range across all regions was similar and therefore that a given shark had an equal chance of being detected on any given array included in this study. This assumption could lead us to overlook receiver arrays with lower detection ranges but to which *C. leucas* may be more philopatric. In addition, it is worth noting that the detection range within Biscayne Bay is quite low (50% detectability at 250 m distance) and therefore it is possible that our measures of residencies are lower, conservative estimates of actual *C. leucas* presence in the area. As with all acoustic tracking studies, these findings represent a snapshot of *C. leucas* presence in these regions but cannot provide specific migratory routes or inform space use outside of the arrays' detection limits. While acoustic tagging methods have proven useful in many previous studies to examine small-scale movements within individual arrays, studies that examine movements between multiple arrays are far fewer. This work highlights the utility of collaborative networks to contribute to our understanding of both long and short-term movements of wide-ranging marine predators that are not optimally suited to satellite tracking (Altobelli and Szedlmayer 2020).

The use of remotely sensed environmental data is also associated with a set of inherent limitations. Since the gridded environmental data used in this study were relatively coarser in spatial resolution, the environmental data extracted to the acoustic receiver positions were more general to the area than that of a specific receiver station. Ideally, future studies should implement the use of sensors, attached to stations, to study fine scale environmental fluctuations at each and relate this to detection data. Gridded salinity data was only available for a small subset of receiver locations and therefore was not used in analyses. However, salinity is known to influence this species and its distributions, especially at younger life stages (Froeschke et al. 2010). Seasonal salinity trends within Biscayne Bay have been outlined in a previous study, in which researchers divided the Bay into five regions (Caccia and Boyer 2005). Authors measured seasonal differences in salinity, but the magnitude and nature of these changes was region-dependent within the Bay. As remote sensing and ocean observation methods continue to progress, future studies carried out in nearshore areas with this species should incorporate salinity measures, where available. This will be especially relevant in south central Biscayne Bay, where freshwater restoration efforts continue to be carried out, which are likely to considerably alter salinity along the coast (USACE 2019).

Our results show that adult and subadult *C. leucas* tagged in Biscayne Bay display seasonal philopatry to the area and undertake long migrations along the Atlantic and Gulf coasts of the United States. Significant relationships between shark presence and environmental variables were region-dependent, but temperature and chl *a* concentration were pinpointed as potential important movement drivers. Placing our results within those from previous studies (e.g., Carlson et al. 2010; Drymon et al. 2013; Laurrabaquio-A et al. 2019; Altobelli and Szedlmayer 2020), more in-depth questions about *C. leucas* space use throughout ontogeny within and between these regions should be addressed in future work. In summary, the findings presented here may help to inform the development, design, and updates to protective measures for this species, by identifying space use patterns over various temporal and spatial scales and environmental gradients. Moreover, these movement data also provide a baseline from which to predict and monitor for future range shifts from climate change as has been suggested for this species (Bangley et al. 2018; Niella et al. 2020).

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**Authors' contributions** Conceptualization: MR; Methodology: MR and LM; Formal analysis and investigation: MR and LM; Writing – original draft preparation: MR and LM; Writing – review and editing: MR, LM, and NH; Funding acquisition: NH; Supervision: NH.

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**Data availability and online material** Raw acoustic tracking data are archived and is available at the Ocean Tracking Network's data warehouse website: https://members.oceantrack.org/.

**Code availability** The code used for data preparation, manipulation, and analysis can be found on Github at this link: https://github.com/lauramcdonnell/UMsharktagging/blob/master/manuscripts/bullshark/bull_script.R.

## Compliance with ethical standards

**Conflict of interest** The authors have no conflict of interest to declare that are relevant to the content of this article.

**Consent for publication** All authors consent to the publication of all material presented in this manuscript.

**Ethics approval** This work was conducted under permits from Florida Fish and Wildlife Conservation Commission, the Florida Keys National Marine Sanctuary, the US National Marine Fisheries Service, and the University of Miami Animal Welfare and Care Committee (Protocol 18–154).

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