Variable migration patterns of whitespotted eagle rays *Aetobatus narinari* along Florida's coastlines

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Abstract

Basic distribution and movements of elasmobranch species, particularly mesopredatory rays, remain relatively unknown. This is especially true for the whitespotted eagle ray (*Aetobatus narinari*), a protected species in Florida with poorly described migratory and habitat use patterns. Passive acoustic telemetry was used to reveal multi-scale spatial patterns of *A. narinari* in Florida waters. Between 2016 and 2018, 54 rays were fitted with acoustic transmitters and tracked via collaborative telemetry networks. Movement patterns between the Atlantic and Gulf coast individuals were distinct; a majority of Gulf coast tagged *A. narinari* exhibited migratory or transient behaviors while most Atlantic coast tagged individuals remained resident in the Indian River Lagoon (IRL). On both coastlines, water temperatures during times when *A. narinari* were present were significantly warmer (mean = 27.8 °C) compared to temperatures when *A. narinari* were absent (mean = 24.9 °C), suggesting temperature may be a major abiotic factor influencing migration patterns. Ontogenetic shifts in habitat use were evident along the Atlantic coast in the IRL, but not along the Gulf coast. Immature rays spent significantly more time (mean = 91.5%) inside the IRL compared to mature counterparts (mean = 60.2%). This is the first multiyear study to examine large-scale movements of *A. narinari* in U.S. waters and results may be important for adaptive management strategies throughout this species' range. Importantly, our work suggests potential sub-population structuring of *A. narinari* may be occurring more than previously considered within Florida, which has significant conservation implications for this species.

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Introduction

Elasmobranchs (sharks and rays) contain speciose lineages of predators, some of which play ecologically important functions in the top-down control of coastal and oceanic ecosystems (Stevens et al. 2000; Heithaus et al. 2012). As such, the decline of elasmobranchs could lead to complex marine community changes including declines in commercial fisheries, mesopredatory release, trophic cascades, and novel interactions among food web components resulting in a new state of organization (Ferretti et al. 2010; Navia et al. 2016). Based on their trophic position as both predator and prey, rays represent an ecologically important component of marine ecosystems (Barnett et al. 2010; Serrano-Flores et al. 2018). Yet, spatial distribution patterns are unknown for many of these species, which limits our understanding of seasonal or long-term residency and movements, ultimately impeding our ability to understand the ecological roles of rays over multiple scales. Although studies of batoid movement have increased in recent years (e.g., Davy et al. 2015; Brinton and Curran 2017; DeGroot et al. 2020), information

on large-scale movements over expansive coastal corridors (100 s of km) and across multiple years is lacking for most species.

A wide range of taxa is known to undertake long-distance migrations to secure optimal conditions and resources (Doherty et al. 2017). For many elasmobranchs, these movements are often driven by abiotic factors, with the animal seeking out or remaining within preferred environmental conditions (Schlaff et al. 2014). For example, previous studies have documented temperature to be a major abiotic driver of movement in elasmobranchs (Sims et al. 2006; Hight and Lowe 2007; Cartamil et al. 2010) as it often regulates physiological processes like digestion, reproduction, and growth, which ultimately affect survival. However, biotic factors such as prey availability, predator abundance, and presence of conspecifics have also been shown to structure movements of these species (e.g., Collins et al. 2007; Heithaus et al. 2009; Jaine et al. 2012). The complexity of these movements is typified by results from tracking cownose rays (*Rhinoptera bonasus*) in the northern Gulf of Mexico, which is suspected to be triggered below water temperatures of 15.5 °C (Neer 2005); however, tagging off the southwest coast of Florida showed *R. bonasus* remained resident to estuarine waters of Charlotte Harbor throughout all seasons (Collins et al. 2007, 2008; Poulakis 2013). Contrastingly, movement of *R. bonasus* off the Atlantic coast of the U.S. was driven by both biotic and abiotic factors (Omori and Fisher 2017). Satellite tracking of cownose rays revealed both sexes migrated south out of Chesapeake Bay and New England waters, respectively, to overwinter in warmer waters off east-central Florida (Omori and Fisher 2017). Acoustic telemetry further identified movement behaviors during this migration, which were classified as resident or ranging in summer and winter, and migratory in fall and spring with strong inter-annual site fidelity to tagging locations (Ogburn et al. 2018). Although cownose ray migration has been studied throughout the Gulf and Atlantic coasts, the migration of other pelagic rays with respect to drivers of movement and ontogenetic shifts, has yet to be explored in these regions.

Mature and immature conspecifics require different resources for survival, which often manifest as ontogenetic changes in habitat use for many elasmobranchs (Grubbs 2010). Due to the smaller size of immature elasmobranchs, habitat use is an important factor for reducing predation risk (Grubbs and Musick 2007; Heithaus et al. 2009). To avoid predators, immature elasmobranchs typically occupy shallow-water nursery habitats (Heupel and Hueter 2002; Matich and Heithaus 2012) before shifting to more productive but predator dense areas as they mature (Werner and Hall 1988; Ajemian and Powers 2016; Heupel et al. 2018). These shallow-water nursery habitats also provide immature animals with an abundance and diversity of food and environmental conditions required for rapid growth (e.g., warmer

temperatures). Conversely, mature conspecifics have less risk of predation due to their larger size; therefore, habitat selection in adults may be driven by competitors, behavioral thermoregulation, prey availability, or the presence of mates (Matern et al. 2000; Heithaus et al. 2002; Jacoby et al. 2010). These distribution and habitat use differences over ontogeny have been documented for cownose rays in the northern Gulf of Mexico, where young rays are observed in the upper reaches of the estuary and adults are typically located further downstream (Ajemian and Powers 2016), but these patterns have not been described for other pelagic rays in the region.

Aetobatus narinari is a benthopelagic ray with a wide distribution throughout the warm temperate to tropical waters in the western North Atlantic Ocean (Sales et al. 2019). The species has a muscular body morphology adapted for long-distance travel, including large pectoral fins suited for oscillatory swimming behavior (Parson et al. 2011). These physical aspects of *A. narinari*, as well as its occurrence in remote islands such as Bermuda, have led to assumptions of highly migratory behavior in this species (Bigelow and Schroeder 1953). While multiple tagging studies have been conducted on *A. narinari* in Bermuda and The Bahamas (Silliman and Gruber 1999; Ajemian et al. 2012; Ajemian and Powers 2014), these have been limited in temporal scale (< 3 months). Lacking information on long-term individual movements impedes our ability to understand how the species responds to wide ranging environmental conditions that occur over annual cycles. Further, large-scale movements and migrations could lead to decreased survival if *A. narinari* travels through multiple management jurisdictions where fishing pressures increase (Lascelles et al. 2014). This is a distinct possibility in the Gulf of Mexico, where *A. narinari* is protected in multiple state waters of the U.S., but is fished in Cuba and Mexico (Cuevas-Zimbrón et al. 2011; Tagliafico et al. 2012; Serrano-Flores et al. 2018). Information on migratory routes, seasonality, and habitat use are thus essential for the successful conservation and management of this species and the ecosystems it inhabits (Webster and Marra 2005; Lascelles et al. 2014), yet these remain undescribed in U.S. waters.

In this study, we assessed residency, seasonality, and large-scale movements of *A. narinari* in Florida to provide insight into the spatial and temporal dynamics of this mobile species. Animals were acoustically tagged along both the Gulf of Mexico and Atlantic coasts of Florida, which differ in environmental characteristics, and tracked via collaborative passive acoustic monitoring arrays. Although the seasonality of *A. narinari* has been described from aerial and boat-based surveys on the Gulf coast, the study was restricted to visual surveys and occurred on a small spatial scale (Bassos-Hull et al. 2014). A 6% recapture rate in Sarasota Bay across multiple years also suggests that although these rays migrate seasonally, they may exhibit some

philopatry to the area (Bassos-Hull et al. 2014), which can structure their populations over fine geographical scales and allow for conservation and management strategies (Sellas et al. 2015; Flowers et al. 2016).

Similarly, the dynamics of *A. narinari* occurrence are poorly understood along the entire Atlantic coast of Florida. A recent active acoustic telemetry study examined short-term movements and habitat use of *A. narinari* in the Indian River Lagoon (IRL), which identified use of modified habitats such as inlets and channels and up to week-long affinities for the general region (i.e., < 12 km², DeGroot et al. 2020). The study only occurred between April and August of 2017 and 2018; rate of movement significantly increased with temperature, suggesting rays are more active during warmer periods. However, the species' long-term seasonal migration patterns have not been examined in the area. Furthermore, although an initial genetic study suggested a single population of *A. narinari* between the two coastlines of Florida (Newby et al. 2014), no comparative study examining migration between the two coastlines has been conducted. Based on this previous research on the species as well as findings of estuarine residence in related cownose rays in southwest Florida waters (Collins et al. 2007, 2008; Poulakis 2013), we hypothesized that *A. narinari* would similarly occupy estuaries for periods of several months (seasonally resident), but that these would be interspersed with migrations coincident with a temperature threshold of 23 °C as reported from previous boat based, aerial survey data, and genetic studies (Bassos-Hull et al. 2014; Sellas et al. 2015).

Study locations

Due to animal accessibility in both Sarasota Bay (Bassos-Hull et al. 2014) and the Indian River Lagoon (DeGroot et al. 2020), we chose to concentrate our tagging efforts within these two distinct locations across Florida. These locations widely differ in regional bathymetry, currents, wave forces, and biological influences. Sarasota Bay consists mainly of fringing barrier islands, passes, and inlets (200–2500 m wide, up to about 10 m in depth) that provide a crucial link between the interior bay waters and the Gulf. Henceforth, the terms pass and inlet are used interchangeably. The shallow estuary of Sarasota Bay, averaging 1.5 m deep, contains large beds of seagrasses that house invertebrates that are potential prey for *A. narinari* (Stephenson et al. 2013). On average, tidal fluctuations in this area are less than 1 m. Additionally, the west Florida shelf is expansive, extending to 250–300 km offshore. In general, the Gulf coast is a low-energy environment due to a gently sloping continental shelf with a < 1:2000 gradient (Hine et al. 2003).

Much like Sarasota Bay, the IRL on Florida's Atlantic coast encompasses a shallow estuarine lagoon that averages 1.5 m depth, extends for 253 km north to south, and is protected by barrier islands (Gilmore 1977). However, the adjacent offshore region is largely influenced by regional currents and steeper bathymetric gradients. For example, the Florida Current (which includes the Gulf Stream) runs parallel to the east coast of Florida, mediating water temperatures resulting in a more stable year-round water temperature regime than the Gulf coast (Gilmore 1995). The shelf width in this area varies, but remains relatively narrow, around 30 km wide. The nearshore benthos is composed of 2–3 distinct reef tracts that lie parallel to the coastline with interspersed hard-bottom and sand deposits. Tidal fluctuations in this area are microtidal with a 0.8 m range; however, ranges are dependent on proximity to the inlets where the tidal amplitude force within a few kilometers of the inlets increases two- to threefold compared to the center of the lagoon (Steward et al. 2005). The IRL is connected to the Atlantic Ocean by several inlets ranging from 234 to 575 m wide and up to 10 m deep. Historically, the IRL was designated as the most biologically diverse estuarine system in the continental U.S.; it was supported by ample benthic habitats of seagrasses and mangroves which maintained a wide diversity of fishes and invertebrates (Dybas 2002). However, in recent years, the IRL has been a primary topic of discussion among environmental groups and policy-makers due to the altered freshwater flow and deteriorating benthic environments (Steward et al. 1994).

Materials and methods

Animal collection

All rays were caught in the coastal nearshore waters of Florida, U.S.A. (Fig. 1). On Florida's Gulf coast in Sarasota Bay and occasionally on the Atlantic coast in the IRL (N = 12), rays were targeted with a nylon seine net (500 m long × 4 m deep). Two additional methods of capture were used in the IRL, (1) a 200-m long × 3-m-deep gillnet (one 100 m panel of 15.24-cm stretch monofilament and one 100 m panel of 20.32-cm stretch monofilament) (N = 8) or (2) a 35.56-cm stretch braided nylon tangle net (200 m long × 3 m deep; N = 6). In targeted seine and tangle net sets, rays were sighted from the boat after which the nets were rapidly set in an approximately 50 m diameter circle around the animal. Once the animal was onboard, it was placed in a live well with a running ambient water flow-through system, and a series of measurements (disc width [DW], standard length, and total length), tissue samples (for genetics and stable isotope analysis), and the animal's

Fig. 1 Map of tagging locations on Florida's coastlines (Gulf coast in Sarasota Bay and Atlantic coast in the Indian River Lagoon). Water quality station locations, the state waters boundary line, and bathymetric contours are displayed. Water depth increases from light blue (< − 200 m) to dark blue (> − 800 m) by increments of 200 m
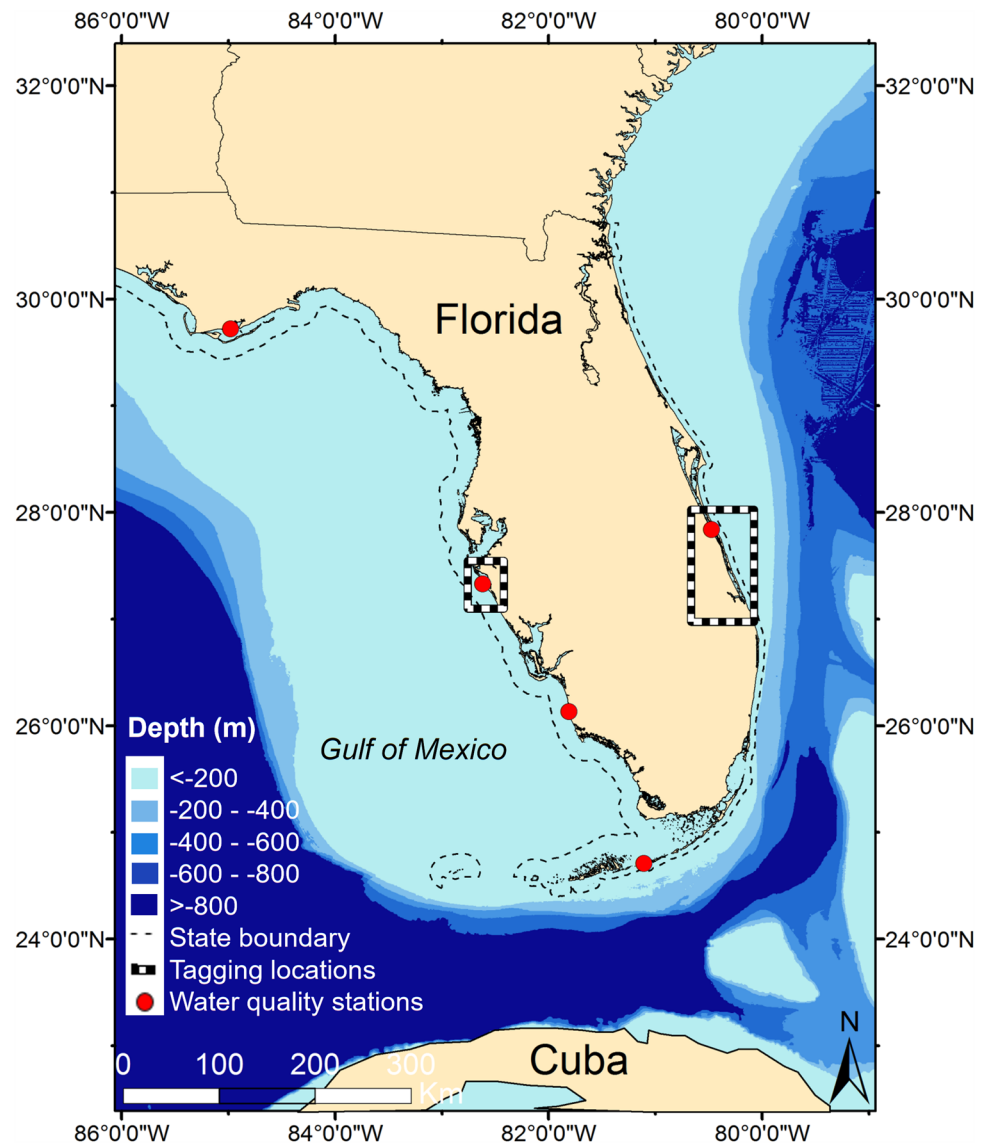
weight was collected as described by Bassos-Hull et al. (2014).

Animal tagging

Prior to tagging, rays were rotated onto their dorsum to induce tonic immobility (Kessel and Hussey 2015). Before an incision was made, animals were swabbed with a 10% povidone-iodine swab stick. To avoid potential damage to reproductive organs located on the animal's left side, a 2–3 cm incision was made to the right of the animal's midline in the peritoneal cavity. An acoustic V16-4H (24 g, 158 dB) or V13-1H (11 g, 152 dB) coded transmitter (Vemco Innovasea, Halifax, Nova Scotia) was placed in the peritoneal cavity so that it lay lateral to the internal organs. The V16 acoustic transmitters randomly transmitted unique coded signals every 30–90 s (60 s nominal delay)

and standard battery life was 1350 days. The V13 acoustic transmitters randomly transmitted unique coded signals every 60–180 s (120 s nominal delay) and standard battery life was 502 days. All tag weights were < 2% of the body mass for all individuals tagged (Smith 2012). Incisions were closed using braided absorbable sutures coated with polyglactin 910 (OS-6, 36 mm 1/2C, reverse cutting coated VICRYL Plus antibacterial needle) using two interrupted sutures, each secured with a surgeon's knot. After surgery, rays were monitored for 3 min in the live well to ensure full recovery prior to release. Animals were tagged using organization-approved animal use protocols (Gulf coast, Mote APU #17-11-PH1; Atlantic coast, FAU APU #A16-16) and handling permits (Gulf coast, FWC SAL-16-1140-SRP; Atlantic coast, FWC SAL-16-1785-SRP).

General movements

Arrays of Vemco Innovasea acoustic receivers (VR2W, VR2Tx) were deployed (Gulf = 37, Atlantic = 10) to monitor tagged *A. narinari* movements around our core tagging areas (Figs. 2, 3, 4). Additional detections were provided by two collaborative acoustic telemetry networks: (1) iTAG (Integrated Tracking of Aquatic Animal in the Gulf of Mexico) and (2) the FACT Network. The iTAG array spanned from the Florida Keys to south Texas with most of the receivers concentrated in coastal areas. The FACT Network spanned from the Carolinas through the Florida Keys and The Bahamas. This network included over 1900 unique stations. Marine acoustic receivers have a typical detection range from 350 to 900 m; however, given environmental heterogeneity, the range is unlikely to

be constant over the period of the study and between locations (Kessel et al. 2014). Movement analyses included data from 25 April 2016 to 16 June 2019 on the Gulf coast and from 20 September 2016 to 10 August 2019 on the Atlantic coast. All statistical analyses were conducted in R V4.0.2 (R Core Team 2020) and all data presented are in means ± SD. To facilitate our descriptive migration analyses and influence of temperature on movement, detection data were grouped by 1° of latitude starting at 24°N in the Florida Keys and ending at 30°N in north Florida for each coastline (Fig. 2). Detection data collected by study arrays, as well as by iTAG and FACT, were compiled and analyzed using time-series plots to determine general movements and affinity to Sarasota Bay and the IRL.

To examine whether there were differences in dispersal by coastline, the minimum distance between the two furthest detection points (minimum coastal range) was

Fig. 2 Location of acoustic receivers on which whitespotted eagle rays (*Aetobatus narinari*) were detected within the collaborative acoustic telemetry networks (iTAG and FACT). Receivers were grouped by 1° latitude as represented by unique colors. The receivers in Sarasota and Sebastian, where the majority of *A. narinari* were captured and tagged are bracketed
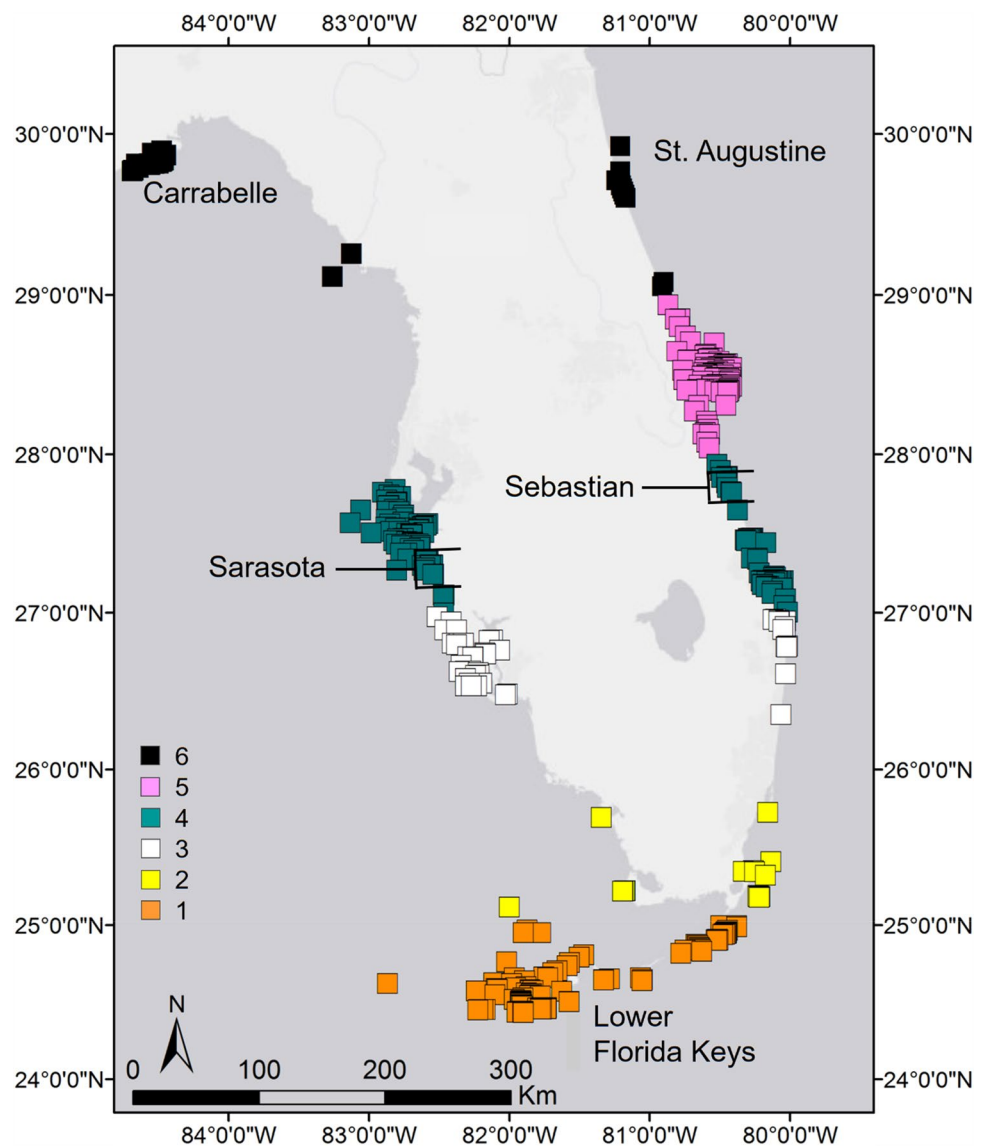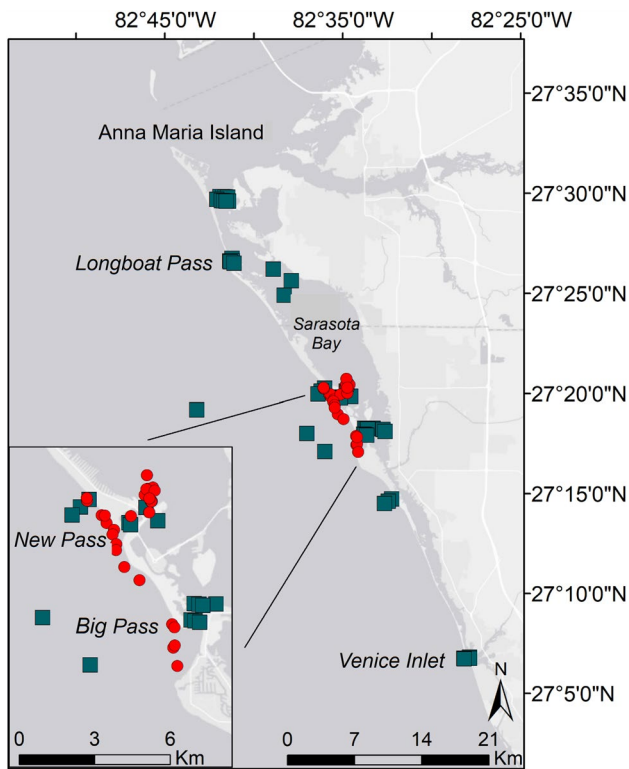
Fig. 3 Author owned receiver stations (squares) and release locations (circles) of 34 whitespotted eagle rays (*Aetobatus narinari*) tagged in Sarasota Bay. Additional iTAG network receivers were also located nearby although not displayed. The passes connecting Sarasota Bay to the Gulf of Mexico are labeled. The inset shows detail of the primary Gulf coast tagging area

Fig. 4 Acoustic receiver stations (squares) and release locations (circles) of 26 whitespotted eagle rays (*Aetobatus narinari*) tagged in the Indian River Lagoon. The passes connecting the Indian River Lagoon to the Atlantic Ocean are labeled. The inset shows detail of the primary Atlantic coast tagging area

calculated for each tagged animal using the Haversine formula, which converts geographic units of each receiver (degrees latitude and longitude) to metric units (i.e., km).

Haversine formula:

$$a = \sin^2\left(\frac{\Delta\varphi}{2}\right) + \cos\varphi_1 \times \cos\varphi_2 \times \sin^2\left(\frac{\Delta\lambda}{2}\right),$$

$$c = 2 \times a\tan 2\left(\sqrt{a}, \sqrt{(1-a)}\right),$$

$$d = R \times c,$$

where φ is position latitude, λ is position longitude, R is earth's radius (6371 km), d is minimum coastal range, and angles are in radians. Tracks that intersected land were manually redrawn to better estimate minimum coastal range. To examine factors that may influence the minimum coastal range for animals tagged along both coasts, two-way analysis of variance (ANOVA) was conducted with factors of maturity (immature or mature) and sex (including sex:maturity) for each coastline. Rays were classified as immature or
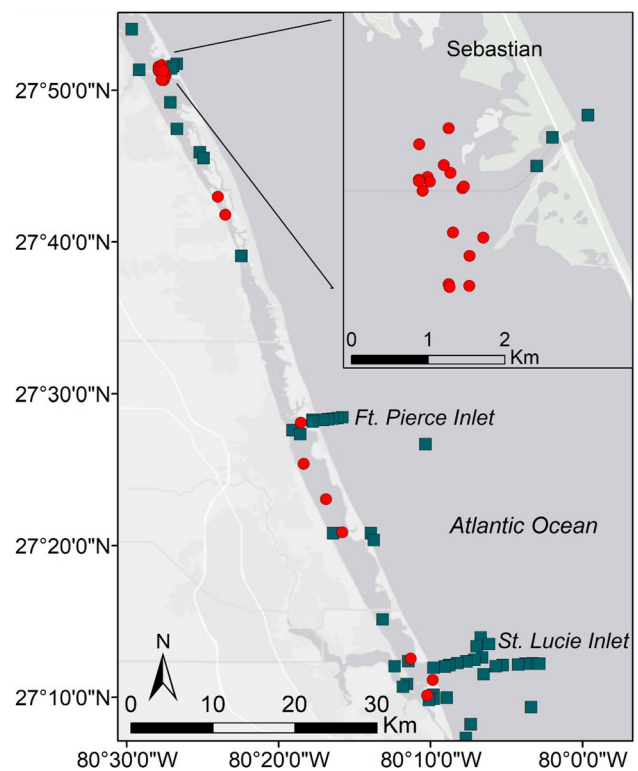
mature based on disc width (mature $= \geq 127$ cm DW for males and ≥ 135 cm DW for females) and clasper condition at time of capture (Tagliafico et al. 2012; Bassos-Hull et al. 2014). Only those animals that were detected at least once, 21 days after release, were included in all analyses.

Residency time

Residency time within the two study sites was assessed by subtracting egress and ingress per individual. Residency time in other latitudinal areas was not assessed as there was either insufficient receiver coverage to assess egress and ingress or there was not a clear entrance to a bay or estuary (i.e., the Florida Keys). All inlets from Sarasota Bay (Anna Maria, Longboat, New Pass, Big Pass, and Venice, Fig. 3) and the southern portion of the IRL (Sebastian, Ft. Pierce, and St. Lucie, Fig. 4) were equipped with sufficient receiver coverage to track ingress and egress. In Sarasota Bay, receiver range testing was conducted on 80% of the inlet passes. Receivers were placed at an average of 134 m apart and had a detection efficiency > 70%. Each inlet was gated such that at least one receiver was located near the outside of the inlet (maximum distance of 0.5 km from

the outer edge of the pass) and a minimum of one receiver located in the middle or on the inside of the inlet. Egress was defined as movement from inside the system (lagoon or bay) to the Gulf or ocean and was marked at the last detection in the inlet before the animal was detected at the outermost receiver in the inlet. Ingress was determined by the movement from the Gulf or ocean to inside of the system and was marked at the last detection in the inlet before the animal was detected at the innermost receiver. Due to the potential for inconsistent detection ranges of the acoustic receivers throughout the study period, the data were manually scanned and missed ingress or egress movements were interpolated. In cases where one of the receivers within the inlet gate presumably missed an ingress or egress, a straight line trajectory (accounting for land when necessary) to the next detecting receiver was manually drawn in ArcGIS (ESRI 2018). A constant rate of movement was assumed along this path and the time at which the non-detecting receiver should have detected the tag was estimated. Egresses and ingresses on both coastlines were interpolated for <5% of total movements. Once egress and ingress were determined, the time spent inside and outside of the system was estimated and summed by individual to determine overall residency time (Ajemian et al. 2012). The proportion of time spent inside or outside the estuarine systems was analyzed until the last detection date, regardless of location, for each individual. The proportion of time spent inside the system by each individual was then analyzed using a nonparametric Kruskal–Wallis test and post hoc Dunn's test to determine if differences occurred by maturity or sex within and between coastlines. In addition, we explored the effect of disc width on residency time in both systems using linear regression. Lastly, we also investigated the variability in continuous residency time (i.e., the number of consecutive days an individual was detected) within the two core monitoring areas to better understand the dynamics of inshore use by tagged individuals.

Residency index

Two Residency Index (RI) values were calculated for each receiver grouping within the array (Fig. 2). A monthly RI defined as the number of days each ray was detected within a month at a designated area as a fraction of the total number of days in that month (Reubens et al. 2013) and a total RI defined as the number of days each ray was detected at a designated area within the study as a fraction of the total number of possible days in the study for each ray (Udyawer et al. 2018). Analysis of monthly RI only included detections from receiver grouping 4 on both coastlines. These regions were chosen for monthly RI analysis due to the limited number of detections in other regions of the coast. All RI values ranged from 0, meaning an individual was not detected on any days,

to 1, indicating the fish was detected every day. Monthly RI values on both coasts were compared by sex, maturity, and season using a nonparametric Kruskal–Wallis test due to the failure to fit ANOVA assumptions for normality and equal variance (Shapiro–Wilk test, $P < 0.05$, Brown–Forsythe equal variance test, $P < 0.05$) followed by a Dunn's test using a Bonferroni correction. Season was delineated by 3-month groupings (Table 1).

Temperature analyses

To examine potential drivers of movement, data were collected from local environmental monitoring stations and examined in association with detection data. On the Gulf coast, water column temperatures for receiver groupings 1, 3, and 6 were extracted from NOAA's National Data Buoy Center (Fig. 1). Temperature data for receiver grouping 4 was extracted from Mote Marine Laboratory's in situ probe in New Pass (Fig. 1). Temperature data from receiver groupings 2 and 5 were not analyzed due to minimal detections or lack of receivers. In receiver groupings 1, 3, and 6, temperature data were averaged into mean daily temperatures, which were compared between periods when rays were present and absent from the arrays using Wilcoxon rank-sum tests. It was assumed that mean conditions were representative of the environmental conditions for a given receiver grouping.

For the Atlantic coast, water temperatures were collected from the nearest Land Ocean Biogeochemical Observatory (LOBO) deployed in Sebastian (LOBO 2019) and averaged by day (Fig. 1). The temperature analysis was conducted only for receiver grouping 4, as a large majority of detections occurred in this receiver grouping, temperature data from all other receiver groupings were not analyzed. It was assumed that mean daily temperature reported by the LOBO was representative of the environmental conditions experienced by all individuals detected in that group. A Wilcoxon rank-sum test was used to compare temperatures *A. narinari* experienced during detection in Sebastian compared to temperatures recorded when *A. narinari* were absent.

Table 1 Mean seasonal water temperature and standard deviation for latitudinal block 4 over the entire study period

Season	Months	GC temperature (°C)	AC temperature (°C)
Winter	1–3	19.4 ± 2.9	20.9 ± 2.6
Spring	4–6	26.9 ± 2.4	26.6 ± 1.8
Summer	7–9	30.3 ± 1.3	29.4 ± 1.0
Fall	10–12	23.3 ± 3.3	23.7 ± 2.9

GC Gulf Coast, *AC* Atlantic coast

Results

Tagging

All rays on the Gulf coast ($N=30$) and 88% of the rays on the Atlantic coast ($N=22$) were tagged within 5 km of an inlet. The remaining four rays were tagged between 10 and 20 km from an inlet. In Sarasota Bay and nearshore Gulf waters, 34 *A. narinari* (111.2–191.6 cm DW) of mixed sexes were tagged between April 2016 and May 2018 (Fig. 3). Due to insufficient detections of four rays (no detections throughout the entire array ≥ 21 days after tagging), only 30 animals were included in the movement analyses (Table 2). Of these, 80% were mature with a mature sex ratio of 1:1 (females:males) and an overall sex ratio of 8:7. Sex ratios

did not differ from 1:1 (χ^2 test, X30$=0.535$, $P=0.464$). In the IRL, 26 *A. narinari* (55–203.8 cm DW) were tagged between September 2016 and August 2018 (Fig. 4). However, only 24 animals had enough detections to be included in the movement analyses (Table 3). Of these, 66% were mature with a mature sex ratio of 7:9 and the overall sex ratio of 9:15. Sex ratios did not differ from 1:1 (χ^2 test, X24$=1.434$, $P=0.231$).

On the Gulf coast, a total of 221,296 detections were recorded by 248 receivers, 10 of which were located in federal waters (i.e., > 14.48 km from the shoreline). Receivers spanned from Carrabelle (29.8°N) to the lower Florida Keys (24.4°N; Fig. 2). On the Atlantic coast, a total of 368,991 detections were recorded by 258 receivers, 61 of which were located in federal waters (i.e., > 4.82 km from the shoreline). Receivers spanned from St. Augustine (29.9°N) to the

Table 2 Summary of tag and biological data of 30 whitespotted eagle rays (*Aetobatus narinari*) in Sarasota Bay, Florida

Ray ID	Tag date	Last detection date	Detection period (days)	DW (cm)	Sex	Weight (kg)
R2	26-Apr-16	18-Jul-17	448	170.8	M	90.4
R3	27-Apr-16	13-Aug-18	838	167.4	M	73.4
R4	27-Apr-16	22-Sep-18	878	176	F	77.4
R5	28-Apr-16	2-Jun-16	35	175.4	F	77.2
R6	28-Apr-16	10-Dec-18	956	179	F	83.6
R7	29-Apr-16	16-Jun-19	1143	112	F	18.0
R8	29-Apr-16	15-Nov-16	200	112.4	M	20.0
R9	12-May-16	16-Jun-19	1130	150.4	F	48.4
R10	12-May-16	1-Jun-19	1115	146.6	F	47.2
R11	12-May-16	16-Jun-19	1130	148.4	M	48.6
R13	20-Jun-16	16-Jun-19	1091	172	F	88.2
R14	21-Jun-16	16-Jun-19	1090	124.6	F	33.8
R15	21-Jun-16	16-Jun-19	1090	123.8	M	24.0
R16	21-Apr-17	16-Jun-19	786	179	M	80.8
R17	21-Apr-17	10-Aug-18	476	170.2	F	73.6
R18	15-May-17	12-Jul-18	423	170	M	72.0
R19	16-May-17	16-Jun-19	761	157.8	M	49.2
R20	16-May-17	16-Jun-19	761	156.2	F	61.8
R21	17-May-17	28-Apr-19	711	176	F	88.6
R22	19-May-17	16-Jun-19	758	176.8	M	78.8
R23	30-May-17	16-Jun-19	747	168.8	M	68.0
R24	31-May-17	16-Jun-19	746	157.4	F	67.8
R25	24-Apr-18	16-Jun-19	418	165.2	F	70.7
R26	03-May-18	16-Jun-19	409	156.2	M	56.6
R27	03-May-18	16-Jun-19	409	130.0	M	36.7
R28	04-May-18	31-May-18	27	114.0	F	21.4
R29	04-May-18	29-May-18	25	111.2	F	20.3
R30	09-May-18	16-Jun-19	403	147.1	M	48.6
R31	09-May-18	16-Jun-19	403	165.7	F	64.6
R32	09-May-18	16-Jun-19	403	154.2	M	56.6

R1 and R12 were not included in data analyses

DW disc width

Table 3 Summary of tag and biological data of 24 whitespotted eagle rays (*Aetobatus narinari*) in the Indian River Lagoon

Ray ID	Tag date	Last detection date	Detection period (days)	DW (cm)	Sex	Weight (kg)
R1	20-Sep-16	10-Jun-18	628	184	F	96.4
R2	20-Sep-16	10-Aug-19	1054	153	M	53.6
R3	21-Sep-16	10-Aug-19	1053	118.6	F	23
R4	21-Sep-16	10-Aug-19	1053	124	M	33.8
R5	2-Mar-17	23-Sep-17	205	56.8	M	2.4
R7	10-Mar-17	11-Jan-18	307	65	M	2
R8	19-Apr-17	06-Feb-19	658	106	M	17
R9	12-May-17	05-Jul-18	419	56.9	M	2.6
R11	6-Jul-17	03-Dec-17	150	55	M	NA
R12	7-Jul-17	08-Apr-18	275	83	F	NA
R13	25-Jul-17	21-Oct-18	453	151	M	52.8
R14	25-Jul-17	10-Aug-19	746	127.2	M	34.4
R15	25-Jul-17	10-Aug-19	746	156.4	F	58.4
R16	26-Jul-17	10-Aug-19	745	195	F	109.4
R17	26-Jul-17	10-Aug-19	745	203.8	F	133
R18	26-Jul-17	25-Oct-18	456	182	F	111.4
R19	26-Jul-17	15-May-19	658	186	F	109.1
R20	26-Jul-17	15-May-19	658	151.8	M	52.2
R21	27-Jul-17	15-May-19	657	128.4	M	33.6
R22	5-Apr-18	10-Aug-19	492	133.8	M	42
R23	26-Jun-18	10-Aug-19	410	147.8	M	43.7
R24	25-Jul-18	10-Aug-19	381	145.2	F	38.8
R25	13-Aug-18	10-Aug-19	362	119	M	22.9
R26	21-Aug-18	10-Aug-19	354	146	M	48

R6 and R10 were not included in data analyses

DW disc width

lower Florida Keys (Fig. 2). Additionally, some receivers (particularly those receivers in the Keys) were part of both iTAG and FACT.

General movements

On the Gulf coast, all rays were detected after tagging ($N=34$), although rays 1 and 12 were not included in the following analyses due to minimal detections. Detection period ranged from 25 to 1115 days (660 ± 351 d). Daily detections revealed consistent seasonal movements throughout the study (Fig. 5b). Rays were primarily located in latitudinal blocks 3 and 4 throughout the spring and summer (April–September) although detections spanned the entire Gulf coastline (blocks 1–6). Overwintering habitats were located south in blocks 1–3; however, much of the overwintering habitat was not captured or reported by the existing acoustic array. Gulf coast tagged rays were not detected on Atlantic coast receivers apart from those receivers located in block 1 (Florida Keys).

On the Atlantic coast, all but one *A. narinari* (203.8 cm DW female) remained in the lagoon or nearshore ocean

waters of the IRL ($N=25$) throughout the study (Fig. 5c). Rays 6 and 10 were removed from analyses due to limited detections. There were no distinct seasonal movements and *A. narinari* primarily remained in the same latitudinal block in which they were originally tagged; our results highlight residency to block 4 in the IRL.

To examine general use of the coastline by Gulf and Atlantic coast rays, the minimum range for each coastline was compared by sex and maturity using a two-way ANOVA. For the Gulf coast, coastal range did not differ significantly with maturity [ANOVA, $F(1,26)=2.048$, $P=0.164$], sex [ANOVA, $F(1,26)=1.120$, $P=0.300$], or the interaction of sex and maturity [ANOVA, $F(1,26)=1.473$, $P=0.236$]. The lack of a relationship between maturity on coastal range was further confirmed by comparing disc width and coastal range (Linear regression, $r^2=-0.010$, $P=0.409$; Fig. 6a). However, for the Atlantic coast, coastal range differed significantly by sex [ANOVA, $F(1,20)=7.903$, $P=0.011$] but not maturity [$F(1,20)=0.760$, $P=0.394$] or the interaction of sex and maturity [ANOVA, $F(1,20)=1.446$, $P=0.243$]. However, the relationship between disc width and coastal range
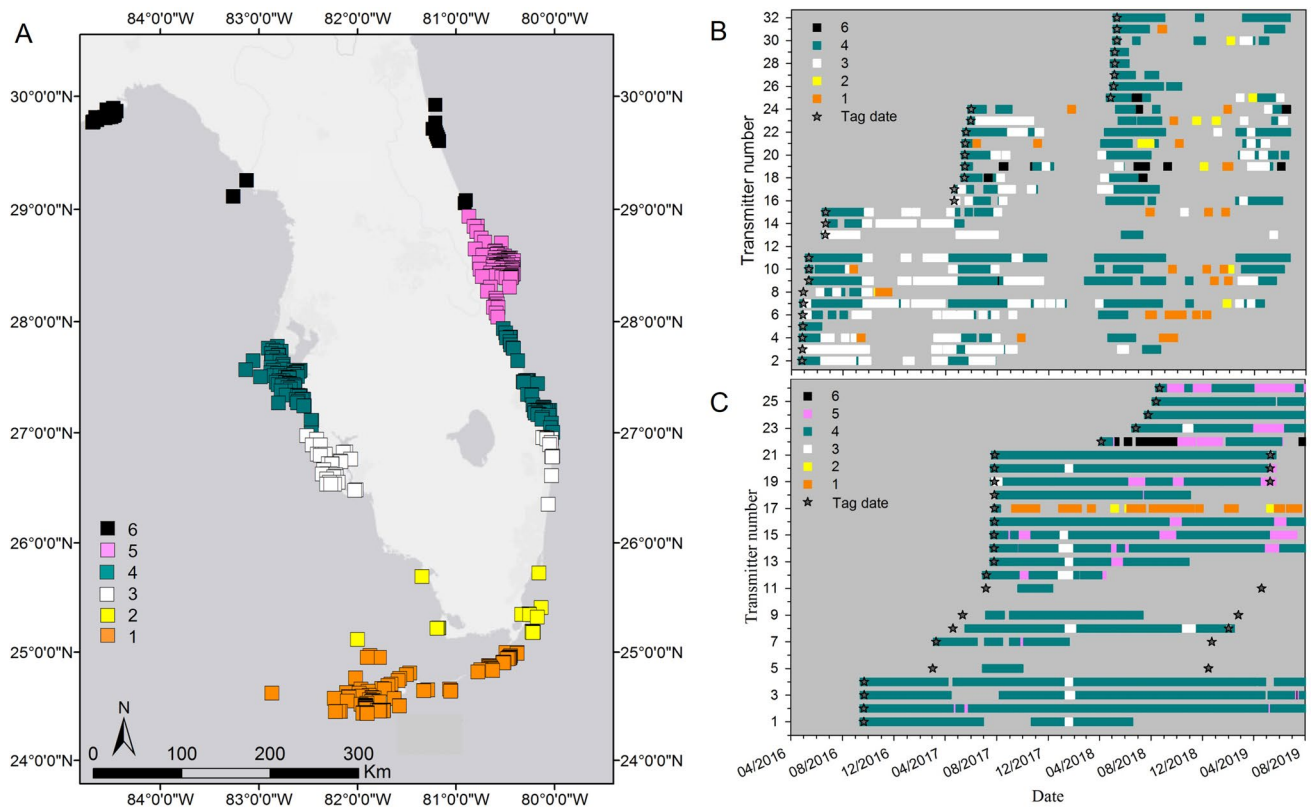
Fig. 5 **a** Acoustic receiver coverage in each latitudinal grouping for both the Gulf and Atlantic coastlines of Florida. **b** Gulf coast whitespotted eagle rays (*Aetobatus narinari*) abacus graph through 16 June 2019. R1 and R12 were not included in data analyses. **c** Atlantic coast *A. narinari* abacus graph through 10 August 2019. R6 and R10 were not included in data analyses

was significant (Linear regression, $r^2 = 0.300$, $P = 0.003$; Fig. 6b), where coastal range increased linearly with increasing disc width. Female *A. narinari* traveled considerably further distances (253.1 ± 29.3 km) than males (160.5 ± 29.1 km).

Residency time

Residency time inside the estuaries was different between the coastlines (Kruskal–Wallis test, $H1 = 30.30$, $P < 0.001$). On average, regardless of size, Atlantic coast rays spent a larger percentage of time inside the estuary ($71.9\% \pm 23.8\%$) than Gulf coast rays ($13.3\% \pm 18.6\%$). Residency time within Sarasota Bay was not influenced by maturity (Kruskal–Wallis test, $H1 = 3.93$, $P = 0.139$) or sex (Kruskal–Wallis test, $H1 = 0.92$, $P = 0.340$). Continuous residency time inside the Bay ranged from < 1 to 65 days with a majority of *A. narinari* continuously resident for < 7 days (Fig. 7a).

Residency time inside the IRL was not variable by sex (Kruskal–Wallis test, $H1 = 1.22$, $P = 0.269$), but was significantly influenced by maturity (Kruskal–Wallis test, $H1 = 13.97$, $P < 0.001$). Immature individuals spent a larger percentage of time inside the lagoon ($88.1\% \pm 10.4\%$)

compared to mature individuals ($58.2\% \pm 23.5\%$; Fig. 6). This relationship was confirmed by linear regression, where residency time was shown to decrease with increasing disc width ($r^2 = 0.498$, $P < 0.001$). Continuous residency time inside the IRL ranged from < 1 to 320 days with a large majority of *A. narinari* continuously resident for up to 60 days (Fig. 7b).

Residency index

On the Gulf coast, total RI values were highest in latitudinal block 4 (0.091 ± 0.072) and lowest in block 2 (0.001 ± 0.003; Table 4) apart from block 5 where there were no receivers present during the time of this study. Monthly RI values showed a seasonal effect in latitudinal block 4 (Kruskal–Wallis test, $H3 = 127.57$, $P < 0.001$) but no effects of maturity (Kruskal–Wallis test, $H1 = 0.524$, $P = 0.469$) or sex (Kruskal–Wallis test, $H1 = 2.43$, $P = 0.119$). Pairwise comparisons by season (winter, RI = 0.03 ± 0.10, spring, RI = 0.27 ± 0.25, summer, RI = 0.11 ± 0.16, fall, RI = 0.02 ± 0.06) revealed significant differences in all comparisons except fall to winter. Monthly RI was highest in the spring and the lowest in the fall.
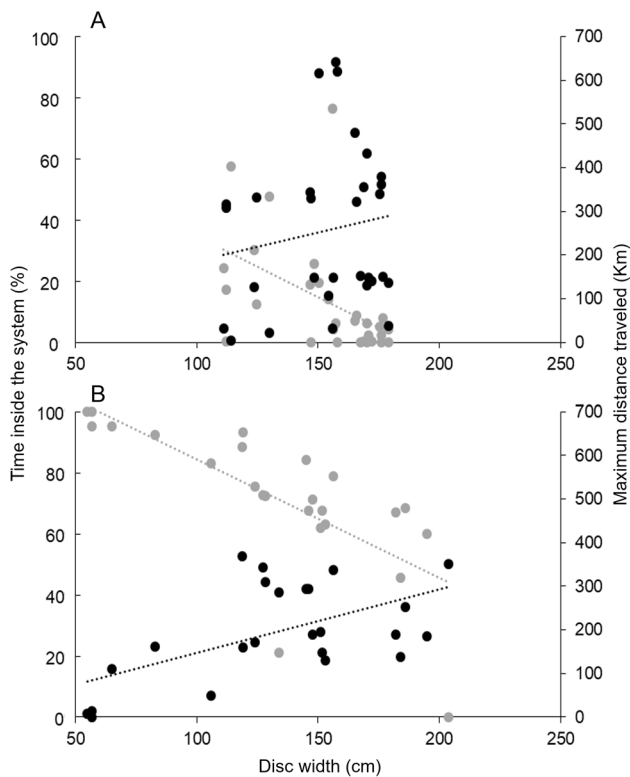
Fig. 6 a Percentage of time Gulf coast whitespotted eagle rays (*Aetobatus narinari*) spent within Sarasota Bay (grey circles) and maximum distance traveled (black circles) in relation to disc width. **b** Percentage of time Atlantic coast rays spent within the Indian River Lagoon (grey circles) and maximum distance traveled (black circles) in relation to disc width

Fig. 7 a Continuous residency time Gulf coast whitespotted eagle rays (*Aetobatus narinari*) spent within Sarasota Bay by maturity. **b** Continuous residency time Atlantic coast rays spent within the Indian River Lagoon by maturity. For both panels, the grey bar represents the number of immature rays and black bar represents the number of mature rays detected within each time period

On the Atlantic coast, total RI values were the highest in latitudinal block 4 (0.344 ± 0.241) and lowest in block 2 (0.003 ± 0.002, Table 5). Monthly RI values showed there were significant differences among season (Kruskal–Wallis test, $H3 = 8.71$, $P = 0.033$) but not between maturity (Kruskal–Wallis test, $H1 = 0.14$, $P = 0.709$) or sexes (Kruskal–Wallis test, $H1 = 0.403$, $P = 0.526$). Pairwise comparisons by season (winter, RI = 0.46 ± 0.32, spring, RI = 0.33 ± 0.32, summer, RI = 0.38 ± 0.36, fall, RI = 0.48 ± 0.36) revealed that the source of variation stemmed from the comparison of fall and spring, in which spring had a lower monthly RI.

Response to temperature

On the Gulf coast, there were distinct temperature ranges used by *A. narinari* in latitudinal block 4 (Fig. 8). Significant differences in temperature were found between periods when *A. narinari* were present within the study array compared to temperatures when they were absent (Wilcoxon signed-ranks test, $T = 1,114,429$, $N = 4371$, $P < 0.001$) within Sarasota Bay (Kruskal–Wallis test, $H1 = 56.31$, $P < 0.001$) and
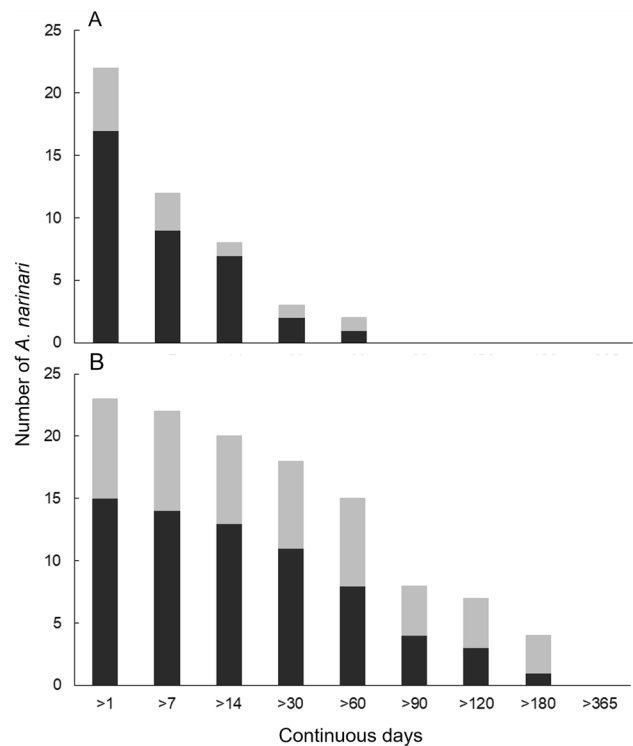
with receiver grouping (Kruskal–Wallis test, $H3 = 381.76$, $P < 0.001$, Fig. 9). The average temperature for receiver groupings 1, 3, 4, and 6 during times when *A. narinari* were present was compared to the average temperature when rays were absent (Table 6). Overall, temperature was significantly warmer when *A. narinari* were present (27.6 ± 3.3 °C) compared to when they were absent (24.8 ± 5.1 °C). The average temperature in each latitudinal grouping progressively warmed as they moved south. Grouping 1 had the warmest average annual temperature (27.4 ± 3.7 °C) and grouping 6 had the coldest average annual temperature (23.2 ± 5.8 °C). Additionally, temperatures when rays were present were significantly warmer in each receiver grouping than when they were absent, except for block 1 where temperature did not influence ray presence (Table 6).

On the Atlantic coast, there were significant differences in temperature between periods when *A. narinari* were present or absent in the Sebastian area (Wilcoxon signed-ranks tests, $T = 24,741$, $N = 1043$, $P < 0.001$). The average temperature recorded by the Sebastian LOBO when *A. narinari* were detected was warmer (25.2 ± 3.7 °C) than when rays were absent (21.9 ± 4.6 °C).

Table 4 Total residency index values (%) for 30 whitespotted eagle rays (*Aetobatus narinari*) tagged in Sarasota Bay, Florida

Ray ID	Total days	Block 6	Block 5	Block 4	Block 3	Block 2	Block 1
2	1147	0	0	7	7	0	0
3	1146	0	0	6	7	0	0
4	1145	0	0	9	2	0	1
5	1145	0	0	0	0	0	0
6	1144	0	0	7	3	0	2
7	1144	0	0	30	6	0	0
8	1143	0	0	1	1	0	1
9	1143	0	0	16	5	0	0
10	1130	0	0	9	0	0	0
11	1130	0	0	25	1	0	0
13	1130	0	0	2	5	0	0
14	1101	0	0	2	2	0	0
15	1091	0	0	10	1	0	0
16	1090	0	0	6	0	0	0
17	1090	0	0	10	2	0	0
18	786	2	0	8	0	0	0
19	786	1	0	3	0	0	0
20	762	0	0	12	1	0	0
21	761	0	0	6	0	1	0
22	761	0	0	22	1	0	0
23	760	0	0	4	4	1	0
24	758	1	0	5	0	0	0
25	747	0	0	5	0	0	0
26	746	0	0	12	0	0	0
27	418	0	0	7	0	0	0
28	409	0	0	6	0	0	0
29	409	0	0	6	0	0	0
30	408	0	0	2	0	0	0
31	408	0	0	13	0	0	0
32	403	0	0	19	0	0	0
Mean	875	0	0	9	2	0	0

Latitudinal block 6 is the most northern block of acoustic receivers and block 1 is the most southern. R1 and R12 were not included in data analyses

Discussion

Acoustic telemetry data provided the first insights into multiyear migration patterns of the whitespotted eagle ray, throughout Florida. Rays tagged on the Atlantic and Gulf coasts of Florida overlapped in sizes, sexes, and maturity, but revealed striking differences between the Gulf and Atlantic coast movements. Gulf coast rays conducted repeated southward migration patterns from Sarasota Bay starting in late fall and returned to the area beginning in spring of the following year. Seasonal detection patterns off Sarasota corroborate boat-based and aerial survey findings of Bassos-Hull et al. (2014). This study documented that *A. narinari* on the Gulf coast have the highest monthly RI values in spring and summer and lower values in fall and winter, indicative of seasonally resident and migratory behavior. Although the southernmost extent of the winter habitat is still unclear, northward return migration patterns were evident beginning in spring and rays were detected at the mid-latitudes by summer. During summer, the warmer thermal habitat expands, which may account for a widespread use of the coastline by Gulf coast tagged rays as far north as Carrabelle, which was exclusively used during June through October with < 15% of detections occurring outside of June and July. Average temperature in this northernmost location in June and July when rays were detected was 29.53 °C ± 0.61 °C. The general decline of monthly detections in November–January suggests these rays do not reside in the coastal nearshore waters, where receiver arrays are concentrated, for the entire winter season. It is hypothesized that rays move to an offshore location or continue the exhibited southward movement in coastal waters where receivers are not present. Rays

Table 5 Total residency index values (%) for 24 whitespotted eagle rays (*Aetobatus narinari*) tagged in the Indian River Lagoon

Ray ID	Total days	Block 6	Block 5	Block 4	Block 3	Block 2	Block 1
1	1054	0	0	33	0	0	0
2	1054	0	12	67	0	0	0
3	1053	0	2	44	0	0	0
4	1053	0	0	65	0	0	0
5	652	0	0	4	0	0	0
7	652	0	0	18	0	0	0
8	652	0	59	2	0	0	0
9	652	0	0	18	0	0	0
11	652	0	0	3	0	0	0
12	764	0	4	12	1	0	0
13	746	0	7	40	0	0	0
14	746	0	14	50	1	0	0
15	746	1	25	40	0	0	0
16	745	0	0	11	62	0	0
17	745	0	0	0	0	1	9
18	745	0	1	42	0	0	0
19	652	0	20	49	1	0	0
20	652	0	8	80	0	0	0
21	652	0	1	60	0	0	0
22	492	12	8	12	0	0	0
23	410	0	19	64	1	0	0
24	381	1	1	53	0	0	0
25	362	0	2	45	0	0	0
26	354	1	59	14	0	0	0
Mean	694	1	10	34	3	0	0

Latitudinal block 6 is the most northern block of acoustic receivers and block 1 is the most southern. R6 and R10 were not included in data analyses

may travel to Cuba or Mexico during these winter months when seasonal abundance is highest in these areas (Cuevas-Zimbrón et al. 2011). Further, a microsatellite and nuclear mitochondrial study showed mixing of Sarasota and Cuba samples with more limited mixing of Sarasota and Mexico samples (Sellas et al. 2015). Although additional receivers are needed to capture the full extent of the overwintering portion of the migration, the northern extent of the winter habitat in this species is likely determined by water temperature as has been shown for other species such as cownose rays (Ogburn et al. 2018). Contrastingly, on the Atlantic coast, the vast majority of rays remained near the tagging location, suggesting that the IRL can sustain year-round populations of *A. narinari*. As males and females were equally resident to the Sebastian portion of the IRL, this area is likely an important feeding ground, nursery habitat, mating location, pupping ground, or serves a combination of these roles. To establish that the Sebastian region provides these various functions, additional life history studies (e.g., diet, reproductive biology) and tagging of young rays (< 90 cm DW) are needed in the area.

As with many other studies on fishes, including elasmobranchs, abiotic factors such as temperature, salinity, and dissolved oxygen have been documented to drive movements (Ubeda et al. 2009; Belcher and Jennings 2010; Poulakis et al. 2013; Ward-Paige et al. 2015). Available and used thermal conditions in Sarasota Bay suggest rays only use a portion (23–31 °C) of the available temperature regime (13–33 °C). Available and used thermal conditions throughout the Gulf coast showed a similar trend; rays only used a portion (18–34 °C) of the available temperature regime (8–34 °C). Additionally, the average temperature during ray presence was warmer than ray absence throughout all receiver blocks apart from block 1. This restricted temperature use pattern was also shown in reef manta rays (*Manta alfredi*) tagged off the coast of Australia in which > 98% of detections occurred in water temperature between 21 and 25 °C (Armstrong et al. 2020). In Atlantic stingrays (*Hypanus sabinus*), seasonal residency patterns have been attributed to changes in temperature, although it is unlikely to be the sole driver of movement (Ramsden et al. 2017). Additional drivers may include salinity and dissolved oxygen, which have been shown to affect the abundance and
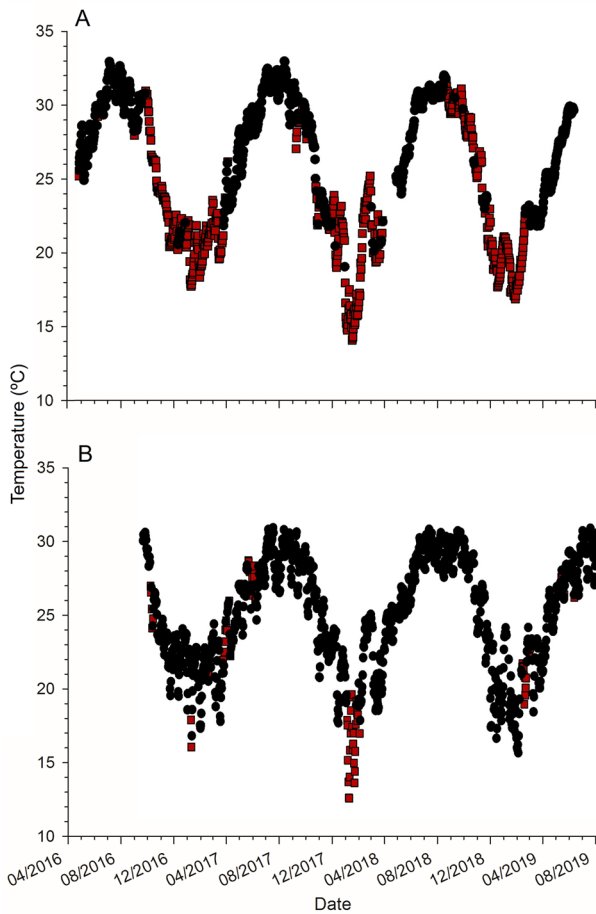
Fig. 8 a Water temperatures whitespotted eagle rays (*Aetobatus narinari*) were detected in (black circles) and not detected in (red squares) in Sarasota Bay on Florida's Gulf coast. **b** Water temperatures rays were detected in and not detected in in the Indian River Lagoon on Florida's Atlantic coast

distribution of several elasmobranchs (Schlaff et al. 2014). For example, juvenile smalltooth sawfish (*Pristis pectinata*) and cownose rays tagged in the Caloosahatchee River exhibited similar trends in movement; rays moved upriver as salinity increased and downriver as salinity decreased (Collins et al. 2008; Scharer et al. 2017). As with salinity, dissolved oxygen has also been documented to affect the abundance and distribution of elasmobranchs (Schlaff et al. 2014). The distribution of several species of juvenile and adult sharks in the Gulf of Mexico was negatively correlated with dissolved oxygen (Drymon et al. 2013); however, the role dissolved oxygen plays in the distribution of many elasmobranch species has not been thoroughly evaluated. Due to the limited freshwater input from rivers that minimally affect the salinity of Sarasota Bay, migration out of the Bay by *A. narinari* is not likely influenced by salinity in this area although further investigation is needed.

While temperature is hypothesized to be the primary environmental factor driving migration patterns, additional variables may play roles in movements. For example, multiple species of coastal elasmobranchs have been documented to vacate coastal waters in response to short-term, major changes in atmospheric pressure (Heupel et al. 2003; Udyawer et al. 2013; Strickland et al. 2020). Additionally, the presence of toxic harmful algal blooms (> 100,000 cells L^{-1}) may prompt more mobile species, such as *A. narinari,* to depart bodies of water or risk morbidity (Flewelling et al. 2010). Toxic blooms typically occur in patches that may further enable *A. narinari* to reside in areas devoid of toxic blooms after short-term exposure. During the study years, Florida's Gulf coast experienced several blooms of red tide (*Karenia brevis*) (Weisberg et al. 2019), which consequently reduced dissolved oxygen levels. These blooms often occurred in the fall, when water temperature was naturally decreasing, making it difficult to determine if departure of

Fig. 9 Median water temperature and interquartile range during times when whitespotted eagle rays (*Aetobatus narinari*) were present and absent on Florida's Gulf coast in latitudinal blocks 1, 3, 4, and 6. Acoustic receiver block 6 is the most northern and block 1 is the most southern. Different letters above the data represent significantly different temperatures both between and among latitudinal blocks
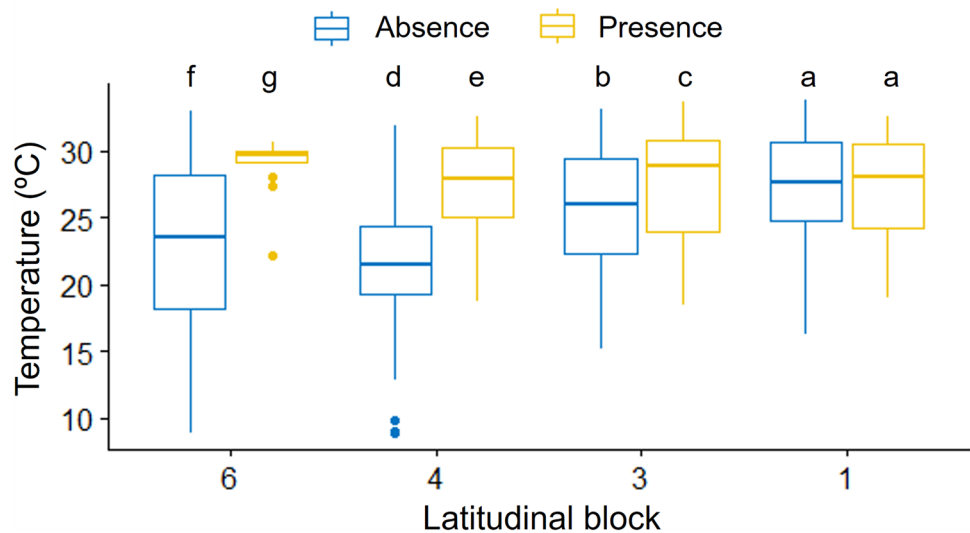
Table 6 Mean water temperature and standard deviation during whitespotted eagle rays (*Aetobatus narinari*) presence and absence for latitudinal blocks 1, 3, 4, 6 on Florida's Gulf coast

Latitudinal block	TP (°C)	TA (°C)	W	*P* value
6	29.3 ± 1.4	22.9 ± 5.8	5968	< 0.001
4	27.5 ± 3.0	22.0 ± 4.3	33,668	< 0.001
3	27.5 ± 3.7	25.5 ± 4.3	106,321	< 0.001
1	27.0 ± 4.1	27.4 ± 3.7	31,814	0.428

Latitudinal block 6 is the most northern block of acoustic receivers and block 1 is the most southern. Data were analyzed using a series of Wilcoxon signed-ranks sum

TP temperature when rays were present, *TA* temperature when rays were absent

A. narinari from receiver block 4 was in response to changes in temperature, harmful algal cell concentrations, dissolved oxygen, or a combination of these factors. Storms and *K. brevis* blooms likely affect how the migration occurs, but may also cue the migration itself. Further examination of harmful algal blooms as it relates to *A. narinari* movements is needed to determine how the species responds to such events.

As with the Gulf coast, temperature was significantly warmer while rays were detected in the IRL than when the rays were absent. Although temperature likely played a role in movements, the range of thermal habitats used by *A. narinari* on the Atlantic coast encompassed more (15–31 °C) of the available thermal range (12–31 °C). It is hypothesized that water temperatures below 15 °C approached the lower limit of the species' thermal tolerance as rays synchronously departed from the IRL into the deeper, nearshore waters of the Atlantic Ocean when temperatures dropped below this lower threshold in winter 2018. Rapid and extreme changes in the environment (with regard to temperature, salinity, and dissolved oxygen) can lead to both short and long-term alterations in the size and structure of populations (Daufresne et al. 2007), which can result in shifts of habitat use and prey availability (Lea et al. 2009). Thermally driven shifts in habitat use was previously documented in juvenile bull sharks (*Carcharhinus leucas*) in the Florida Everglades (Matich and Heithaus 2012) and by juvenile smalltooth sawfish in the Caloosahatchee River (Scharer et al. 2017) and common snook (*Centropomus undecimalis*) in the IRL (Young et al. 2014) during a similar cold snap in 2010. In addition to temperature, salinity may also result in shifts of habitat use (Schlaff et al. 2014). This is of particular concern for the IRL as this area can experience sharp declines in both salinity and dissolved oxygen due to large pulses of freshwater input from lock and dam systems (Hanisak and Davis 2018). Understanding how extreme weather events and fluctuations in environmental factors may impact ecologically

important large-bodied mesopredators, such as *A. narinari*, is needed as the frequency of these events is predicted to increase (Easterling et al. 2000; IPCC 2007) yet the potential alterations on the ecosystem are unknown.

Comparing minimum coastal range within coastlines showed no significant differences in range by sex or maturity for Gulf coast rays. These results parallel genetic findings of *A. narinari* sampled off Sarasota, which found no evidence of sex-biased dispersal (Sellas et al. 2015). Minimum coastal range for the Gulf coast rays was variable across individuals, which may contribute to the lack of significance between sex and maturity. However, coastal range on the Atlantic coast differed between sexes. Although females had a larger coastal range than males, the monthly RI values were not significantly different, suggesting female rays were making short-term movements to distant locations before returning. This larger coastal range exhibited by females may be driven by R17, which was the largest female tagged on the Atlantic coast (203.8 cm DW) and traveled the second furthest distance on this coastline (350.29 km). The need for females to locate pupping grounds or the need to locate more productive feeding grounds during pregnancy may contribute to this difference by sex, although the possibility of males being intrinsically more resident cannot be discounted. While the results were not statistically significant, male bull sharks had a higher residency index and traveled shorter distances than their female counterparts in southern Mozambique (Daly et al. 2014). As such, male residency may be more common in elasmobranchs than previously considered.

Aetobatus narinari on Florida's Atlantic coast exhibited ontogenetic shifts in habitat use, moving from estuarine to offshore-dominated habitats with size. Immature rays spent a significantly larger proportion of time inside the confines of the IRL compared to mature counterparts. During the first years of life, estuaries provide a low risk of predation as shallow, brackish systems restrict large predators from using these habitats (Duncan and Holland 2006; McElroy et al 2006; Peterson et al. 2017). Additionally, these inshore waters often provide higher abundance of smaller prey and warmer waters which assist in faster growth rates for young animals (Knip et al. 2011; Heupel et al. 2018). Ontogenetic shifts in habitat use may also reduce intraspecific competition and may ultimately increase population success (Spina 2000; Knip et al. 2011). Larger, mature adults experience decreased vulnerability from attack by marine predators (i.e., larger sharks) in conjunction with an increased energetic need may drive mature rays to use more productive offshore habitats (Grubbs 2010).

Although ontogenetic shifts in habitat use were evident on the Atlantic coast, comparing the proportion of time Gulf coast rays spent inside the estuary did not reveal any differences by sex or maturity. The lack of ontogenetic effects with Gulf coast *A. narinari* may be attributed to a more

restricted size range of tagged individuals compared to the Atlantic coast. The smallest Gulf coast ray tagged was 111.2 cm DW, whereas there were three rays tagged on the Atlantic coast < 60 cm DW. Clearly, additional tagging of smaller individuals along the Gulf coast is needed. Additionally, despite tagging occurring within 5 km of inlets for 100% of Gulf coast rays and 88% of Atlantic coast rays, the proportion of time *A. narinari* spent inside the estuaries (Sarasota Bay or the IRL) was drastically different. Atlantic coast rays spent greater than five times the amount of time inshore, regardless of maturity or sex, than Gulf coast rays. Although the IRL and Sarasota Bay have similar numbers of inlets, the IRL is a much larger system both latitudinally and with respect to aerial coverage. Therefore, time spent inside the IRL may be inherently higher than in Sarasota Bay due to the larger inter-inlet distance. The striking difference in residency time between coastlines provides further evidence to support the migratory behavior of rays on the Gulf coast and resident behavior of rays on the Atlantic coast.

The extensive continental shelf in the Gulf of Mexico may allow for increased abundance of prey in the shallow waters extending nearshore and offshore feeding habitat, expanding *A. narinari's* use of offshore habitats. Alternatively, the bivalve population on Florida's Gulf coast may be negatively affected by regular red tide blooms, which can concentrate brevetoxins in habitats where flushing is limited (such as estuaries), resulting in fish kills, hypoxic conditions, and, therefore, less productive inshore habitats (Brand and Compton 2007). The increased proportion of time spent inside the IRL by Atlantic coast rays compared to the proportion of time Gulf coast rays spent inside Sarasota Bay suggests the IRL can support all size classes of *A. narinari.* Additionally, the higher proportion of time adults spend inside the IRL compared to Sarasota Bay may increase their risk to persistent anthropogenic impacts in this area (Sime 2005; Lapointe et al. 2015). This is disconcerting, especially for immature rays, which spend the most time in the IRL with no evidence of neonate or young-of-the-year rays leaving the lagoon throughout the study.

Shark nursery criteria established by Heupel et al. (2007) and modified by Martins et al. (2018) to fit batoids requires: (1) newborn or young-of-the-year individuals are more commonly encountered there than in other areas, (2) newborn or young-of-the-year individuals have a tendency to remain or return for extended periods and (3) newborn or young-of-the-year individuals repeatedly use the area or habitat across years. Based on these criteria, the IRL is hypothesized to be a nursery habitat for *A. narinari* due to the encounter rate, duration of detections, and use of the area across the study. However, additional tagging of newborns or young-of-the-year rays and additional receivers in habitats likely to support these animals is necessary to provide defined nursery habitats within the IRL.

When following the 2016 mature cohort of tagged *A. narinari* on the Gulf coast, fidelity was consistent between sexes. Inter-annual site fidelity, a type of philopatry (as defined by Flowers et al. 2016), may structure populations over fine geographical scales (Chapman et al. 2015; Flowers et al. 2016). The restricted use of estuarine waters during warmer temperatures has been documented in other batoids throughout the U.S., including Atlantic stingrays and cownose rays (Ramsden et al. 2017; Ogburn et al. 2018). Female elasmobranchs may seek out warmer waters to help speed gestation and thus base their presence and movements on availability of warm water (Hight and Lowe 2007; Knip et al. 2012). This hypothesized benefit of warm water for gestation may account for the inter-annual site fidelity of females to Sarasota Bay and is often a precursor to documenting natal philopatry (Chapman et al. 2015).

Habitat use and location of pupping grounds are likely driven by temperature as has been shown by opposing movements of cownose rays in the northern (Neer 2005; Ajemian and Powers 2016) and eastern Gulf (Collins et al. 2007, 2008). Alternatively, fidelity to Sarasota Bay may be indicative of an aggregation, mating, pupping, feeding site, or combination of these roles (Speed et al. 2010). Although aggregations of large (> 130 cm DW) *A. narinari* (up to 60 individuals) and pups (< 60 cm DW) have been documented from aerial and boat-based sightings data (Bassos-Hull et al. 2014), the role Sarasota Bay plays in the life history of the species remains unresolved.

The estuarine waters in Sarasota Bay may be capable of serving as a nursery ground for the species. This coastal estuary is shallow (1–7 m deep) and the benthos consists primarily of seagrass beds and sandy shoals. The invertebrate community is diverse and abundant, it consists of gastropods (whelks and conch) and bivalves (scallops and clams) (Estevez and Bruzek 1986; Stephenson et al. 2013), which have been documented as prey for *A. narinari* (Ajemian et al. 2012; Serrano-Flores et al. 2018). The habitat and abundance of prey may support and protect *A. narinari* pups. Additionally, Bassos-Hull et al. (2014) documented sightings of young rays (< 80 cm DW) to be highest during October and November. The smallest pups (< 50 cm DW) were captured starting in early August, which corresponds to the reproductive cycle of female *A. narinari* (Bassos-Hull unpubl data).

In addition to Sarasota Bay, *A. narinari* exhibited an affinity for Charlotte Harbor (receiver block 3) across seasons. The elevated use of Charlotte Harbor by cownose rays (Collins et al. 2007; Poulakis 2013), smalltooth sawfish (Norton et al. 2012), and *A. narinari* suggests Charlotte Harbor may act as an additional feeding or mating ground capable of supporting multiple batoid species. Based on both the documentation of pregnant females in summer and the presence of pups in late summer and early fall in Sarasota Bay

(Bassos-Hull et al. 2014; Bassos-Hull unpubl data), these rays may be using the area as a parturition ground; however, the possibility of Charlotte Harbor fulfilling a similar role cannot be discounted. To test this hypothesis, a concerted effort should be taken to examine the reproductive status of mature females (> 150 cm DW) in Sarasota Bay and Charlotte Harbor, particularly during the late summer months (July–August). Additional acoustic tagging of young individuals in Sarasota Bay and Charlotte Harbor is also needed to determine if these areas fit established batoid nursery criteria (Martins et al. 2018).

Implications for management

Our results showed modest evidence of migration outside of Florida state waters by *A. narinari*; however, R15 was detected in the nearshore waters off the eastern Yucatán Peninsula in Mexico in July 2019. While these findings suggest current statewide protections may be sufficient, our analysis of *A. narinari* distribution was limited to the extent of participating acoustic telemetry arrays. Expanded monitoring in areas like Cuba and Mexico where genetic analysis has shown mixing with Florida populations (Sellas et al. 2015) is needed. Future studies would also benefit from additional receivers in latitudinal block 2 on the Gulf coast to further understand migratory corridors. Further, this study was limited by the inherent designs of the participating collaborative acoustic telemetry networks, which only provided locations for receivers that rays were detected on. This may have artificially deflated RI calculations in areas where rays were not detected due to lack of receiver coverage. Future research would benefit from knowledge of all receiver locations to determine critical habitats and migratory corridors as well as provide more representative RI values.

Many rays from this study were resident to Florida waters, where habitats are degrading rapidly. Conservation and management of essential habitats, particularly in areas where *A. narinari* is resident such as the IRL, is crucial to sustain local populations. These habitats could be affected by local anthropogenic threats such as altered freshwater flow, harmful algal blooms, pollutants, fishing activities, and dredging of inlets. Such threats are likely to influence rays in the IRL, which our data show are continuously resident in this estuary for several months at a time and can thus prolong their exposure to these activities. Disruptions to natural habitats have altered the distribution and abundance of elasmobranch populations in other systems outside the United States (Edgar et al. 2000; Lotze et al. 2006; Stump 2013; Schlaff et al. 2014; Barash et al. 2018). Due to the predicted rise of coastal human populations, anthropogenic impacts on coastal ecosystems, such as Sarasota Bay and the IRL, are expected to increase (IPCC 2007). This highlights the urgency to understand resident populations of ecologically important elasmobranchs, such as *A. narinari*, that could be negatively affected by these activities.

Although *A. narinari* is considered a single population in the southeast USA (Newby et al. 2014), our findings of residency along the Florida east coast suggests some sub-population structuring may be occurring, which was considered a possibility by Newby et al. (2014) given the coarse-scale nature of their genetic analyses. However, the overlap of Gulf and Atlantic tagged *A. narinari* in the Florida Keys suggest that this region may facilitate genetic mixing. Thus, further genetic research is recommended to better understand fine-scale population dynamics of this species.

Conclusion

This study provides the first analyses of large-scale and inter-annual movements of *A. narinari* along both coastlines of Florida. Although the need for large, marine ecosystem-scale data is clear in this time of changing oceans, obtaining these data for large mobile species remains challenging. Two means currently exist, both with limitations. One is to use satellite tracking, but currently, this costly technique results in low spatial resolution data. The other approach is to use integrated acoustic tracking networks. Although these networks are only as good as their spatial coverage and are hampered by areas without monitoring coverage or changing coverage over time (Lowerre-Barbieri et al. 2019), due to the increasing coverage of acoustic networks throughout the U.S., high spatial resolution, and relatively inexpensive long-lasting acoustic transmitters (up to 10 years), acoustic telemetry is preferred for coastal species where coverage is likely. Although tagged at similar latitudes, *A. narinari* exhibited coastline-specific movements. *Aetobatus narinari* on the Gulf coast conduct repetitive annual migration patterns, heading south from Sarasota starting in fall and returning to the area in early spring. This behavior is likely driven by a combination of environmental factors, but most notably temperature. Additionally, the expansive, shallow shelf on the Gulf coast may provide additional habitat, enabling *A. narinari* to move over larger distances along nearshore migratory corridors and lessen their reliance on inshore estuaries. In contrast, most of the rays tagged on Florida's Atlantic coast were resident in the same area in which they were originally tagged. This residency pattern can not only increase susceptibility to local stressors, but also structure populations on spatial and temporal scales, justifying the need for adaptive management and conservation of these crucial habitats. The consistent presence of rays in the IRL throughout the 3-year study allows for the development of several hypotheses, but most importantly that the IRL serves as parturition grounds and nursery habitat for *A. narinari*.

Compliance with ethical standards

Conflict of interest The submitted work was not carried out in the presence of any personal, professional, or financial relationships.

Ethical approval All applicable institutional guidelines for the care and use of animals were followed. Animals were acoustically tagged using university-approved animal use protocols (Gulf coast, Mote AUP #17-11-PH1; Atlantic coast, FAU AUP #A16-16) and handling permits (Gulf coast, FWC SAL-16-1140-SRP; Atlantic coast, FWC SAL-16-1785-SRP).

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