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Combining acoustic telemetry with biochemical tracers reveals habitat use by a demersal mesopredator, *Hypanus sabinus*

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ABSTRACT: Knowledge of mesopredator habitat use and trophic ecology is crucial for identifying essential habitat and understanding community and food web dynamics. Defining functional roles of resting elasmobranchs is especially important, as they can influence benthic community dynamics by residing in an area for a considerable amount of time. This study combines acoustic telemetry, bulk stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$), and carbon isotope analysis of essential amino acids ($\delta^{13}C_{EAA}$) to investigate the habitat use and trophic ecology of Atlantic stingrays *Hypanus sabinus* within a subtropical estuary. Diel period, tide height (m), moon illumination, and water temperature (°C) significantly influenced hourly presence of stingrays. Stingray presence increased in water temperatures ranging from 15 to 25°C, and they were more likely to be absent when temperatures were <10 and >30°C. Bulk $\delta^{13}C$ and $\delta^{15}N$ values from stingray tissues exhibited spatial gradients throughout the estuary, likely due to isotopic variability in baseline resource channels (e.g. macroalgae) and dietary differences between individual stingrays. Linear discriminant analysis of $\delta^{13}C_{EAA}$ values indicated trophic assimilation of macroalgal essential amino acids, demonstrating that the observed spatial gradient in bulk $\delta^{13}C$ values may be driven by differential ^{13}C fractionation in macroalgae across space due to environmental conditions, or potentially different species of macroalgae occurring throughout the estuary. These findings provide key insight into the relationship between habitat use and trophic ecology of stingrays, revealing potential responses of vulnerable elasmobranch consumers to future physical and biogeochemical changes within estuarine environments.

KEY WORDS: Estuary · Carbon sources · Compound-specific stable isotope analysis · Amino acids · Trophic ecology · Residency · Environmental drivers · Atlantic stingray

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1. INTRODUCTION

Understanding habitat use and trophic ecology of mesopredators is crucial for assessing food web dynamics, as these consumers provide vital energetic links between lower trophic levels and apex predators (Myers et al. 2007, Prugh et al. 2009, Ritchie & Johnson 2009). By regulating prey populations that are not directly consumed by apex predators, mesopredators facilitate ecosystem structure and energy flow (Nishijima et al. 2014, Tambling et al. 2018). However, mesopredators may also influence ecosystem function through their use of habitat and movement patterns (Vaudo & Heithaus 2011, Bauer & Hoye 2014). Gathering information on the complex interaction between habitat use and trophic ecology of mesopredators is particularly valuable for evaluating the resilience of coastal communities under anthropo-

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genic and climatic stress, such as estuaries (Lotze et al. 2006, Vinagre et al. 2019). While estuarine environments are some of the most threatened due to historical human development and climate change (e.g. storms, warming, hypoxia, etc.) (Elliott & Whitfield 2011), they are often characterized by high productivity and having a diverse range of habitats that may offer essential foraging and refuging opportunities (Beck et al. 2001, Dahlgren et al. 2006, Sheaves et al. 2006). Because of these characteristics, estuaries commonly serve as nursery habitat for a wide range of fishes, including elasmobranchs (sharks, skates, and rays) (Beck et al. 2001, Heupel et al. 2007, Martins et al. 2018, Plumlee et al. 2018, Swift & Portnoy 2021).

Elasmobranchs that commonly display resting behaviors, such as batoids (skates and rays) may reside within a habitat for considerable amounts of time depending on the quality and quantity of foraging and refuging opportunities and whether environmental conditions support 'optimal' physiological performance (Semeniuk & Dill 2006, Martins et al. 2018, Meese & Lowe 2019, Flowers et al. 2021). Because of the dynamic physical and biogeochemical nature of shallow-water estuaries, batoids likely have to balance tradeoffs between physiologically demanding environmental conditions with foraging opportunities and protection from predators (Bernal & Lowe 2015). Water temperature is considered a key determinant of batoid distributions, movements, and feeding behaviors due to its direct effect on physiological performance (Schmidt-Nielsen 1997, Schlaff et al. 2014, Bernal & Lowe 2015). For example, many batoid species exhibit varying 'shuttling' behaviors to thermoregulate and maintain optimal physiological performance (e.g. metabolism, muscle activity). For instance, some batoids forage in warmer waters with plentiful prey while digestion is increased, then move to rest in comparatively cooler waters to slow down metabolism and increase benefits from digestion (Hopkins & Cech 1994, Matern et al. 2000, Di Santo & Bennett 2011a).

Atlantic stingrays *Hypanus sabinus* (previously *Dasyatis sabina*) are sedentary, demersal batoids distributed in marine and coastal waters from the Chesapeake Bay, USA, to Campeche, Mexico (Bigelow & Schroeder 1953, Snelson et al. 1988). Individuals commonly prey on small fishes and invertebrates including commercially important decapods (e.g. penaeid shrimps and callinectid crabs) (Snelson et al. 1988). As bioturbators, their foraging behavior plays an important role in benthic community dynamics through oxygenation, nutrient cycling, and structuring sediments into feeding pits (Thrush et al. 1991, Cross & Curran 2000, Peterson et al. 2001, Crook et al. 2022). Individuals are known to aggregate in shallow (<1 m depth), coastal sand and seagrass areas, and previous work has determined that this species has an exceptional tolerance to warm water temperatures (up to 43°C) and salinities (up to 41 psu), while potentially being limited by cold water temperatures (Fangue & Bennett 2003, Wallman & Bennett 2006). While Atlantic stingrays are currently listed as Least Concern on the IUCN Red List (Carlson et al. 2020), the population is becoming severely fragmented throughout its geographical range due to coastal development, sea level rise, and unfavorable conditions (Dulvy et al. 2017, Jorgensen et al. 2022). However, despite their wide distribution, abundance, and trophic significance, little work has been done in natural environments to quantify Atlantic stingray habitat use and trophic ecology.

Combining acoustic telemetry and biochemical tracer techniques can reveal relationships (or lack thereof) between habitat use and trophic ecology of consumers (Papastamatiou et al. 2015, TinHan et al. 2018, Brownscombe et al. 2022). Carbon and nitrogen stable isotope analysis of bulk tissues ($\mathrm{SIA_{bulk}}$) is a well-established approach that provides time-integrated (e.g. months, seasons) measures of trophic variation and habitat use based on predictable isotopic consumer-diet differences (Fry & Sherr 1984, Peterson & Fry 1987, Post 2002, Petta et al. 2020). Nitrogen isotope values (δ^{15}N) are typically used to estimate the trophic position of a consumer, since they naturally increase by ~2–5‰ per trophic level due to isotopic discrimination associated with the excretion of ^{14}N in nitrogenous waste (e.g. urea and uric acid) (McMahon & McCarthy 2016, Stephens et al. 2023). Comparatively, carbon isotope values (δ^{13}C) exhibit lower discrimination (~0–2‰) between diet and consumer and reflect major carbon sources supporting consumer biomass (e.g. primary producers, heterotrophic bacteria, and fungi). However, isotope values in local habitats are dependent on baseline primary producer (i.e. basal organism) values that often vary both spatially and temporally (Post 2002, Graham et al. 2010), leading to potential confounding interpretations about the habitat use and diet sources of a consumer unless the baseline values are thoroughly quantified.

Carbon stable isotope analysis of individual essential amino acids ($\delta^{13}\mathrm{C_{EAA}}$) has emerged as a reliable technique for tracing molecular resources (i.e. amino acids, AAs) that are synthesized by molecular organisms (e.g. plants, algae, etc.) and assimilated into the tissues of higher trophic level consumers (McMahon & Newsome 2019, Whiteman et al. 2019, Vane et al. 2025). Consumers cannot synthesize the carbon skeleton of EAAs and instead must obtain them from their diet (McMahon et al. 2010, 2015b, Larsen et al. 2013).

This direct 'routing' is associated with minimal isotopic discrimination, such that $\delta^{13}C_{EAA}$ values of consumers can be traced back to their original biosynthetic origin (i.e. the basal resources) (Larsen et al. 2012, McMahon et al. 2015a, Shipley et al. 2023, Vane et al. 2025). Since varying groups of basal resources have evolved their own pathways to synthesize carbon skeletons, they each have different isotopic effects resulting in unique $\delta^{13}C_{EAA}$ fingerprints (Larsen et al. 2012). The fingerprints that are observed between large groups of basal organisms (e.g. plants, algae, etc.) as well as within those groups (e.g. microalgae) can contribute to an understanding of habitat use by consumers, particularly if there is some preliminary knowledge of the spatial heterogeneity of basal organisms within the study area (Elliott Smith et al. 2022, Stahl et al. 2023).

This study combines acoustic telemetry with SIA_{bulk} and $\delta^{13}C_{EAA}$ to investigate drivers of habitat use and identify potential basal organisms supporting Atlantic stingrays. Since estuaries are constantly facing challenges of anthropogenic and natural disturbances, distributions and behaviors of predators and prey often fluctuate in response. Therefore, by establishing baseline data on the habitat use and trophic ecology of Atlantic stingrays within a major bay system, the present study sheds new light on the relationships between habitat use and trophic ecology for vulnerable elasmobranchs and estuarine communities. Specifically, the objectives of this study were to (1) quantify stingray habitat use, estuarine residency, and site fidelity; (2) identify potential environmental drivers of habitat use; and (3) trace possible basal resource use by Atlantic stingrays with $\delta^{13}C_{EAA}$ values.

2. MATERIALS AND METHODS

2.1. Study location

This study was conducted in Matagorda Bay, Texas, USA (Fig. 1A). Matagorda Bay is the second largest estuary along the Texas coastline (1092 km^2). Local

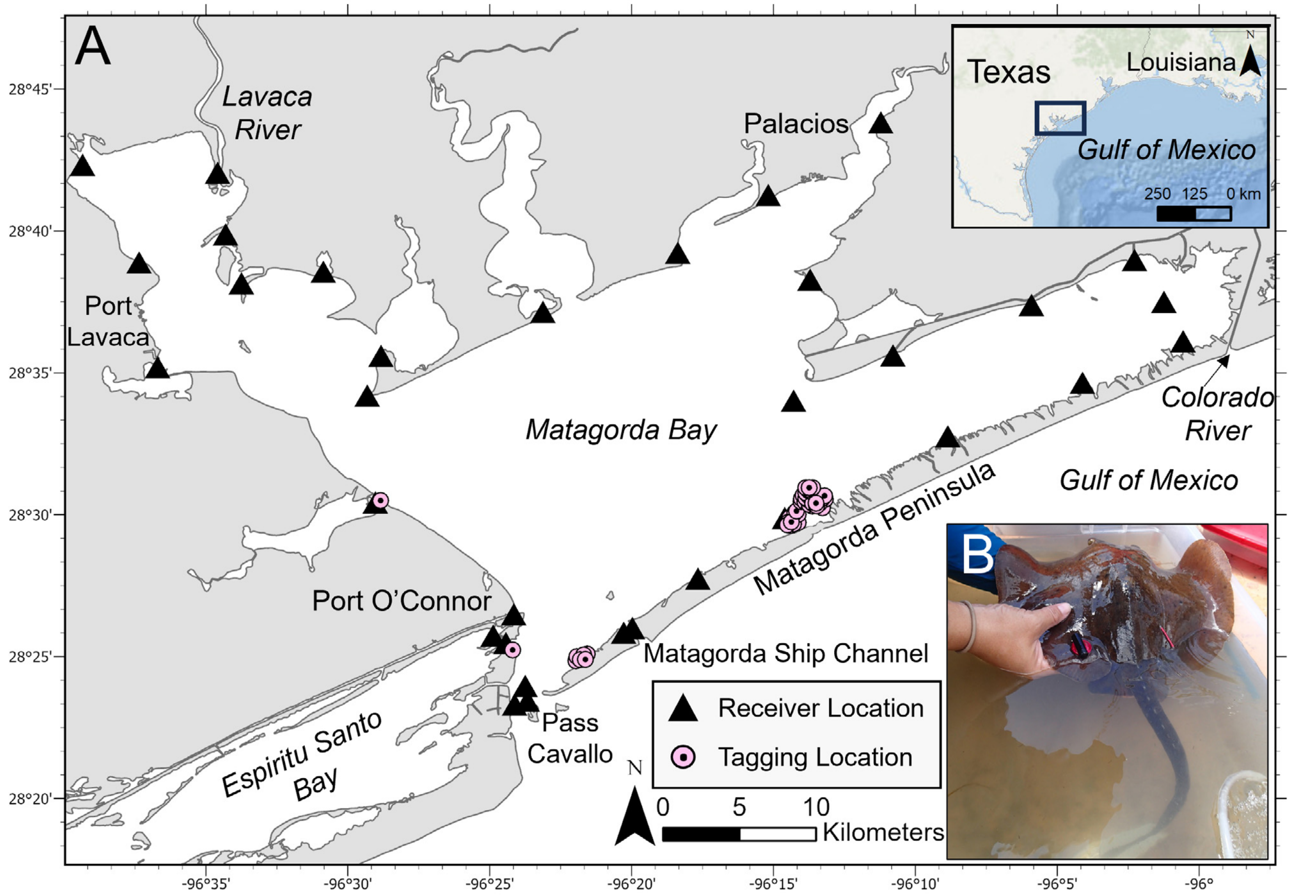

Fig. 1. (A) Acoustic receiver array with Atlantic stingray *Hypanus sabinus* tagging locations in Matagorda Bay, Texas, USA. Tagging locations have been spread out for visualization purposes using the 'disperse' tool in ArcGIS. (B) Atlantic stingrays were externally fitted with temperature sensing acoustic transmitters (V9T-2x, 69 kHz, Innovasea)

water levels and currents are dominated by winds (meteorological tide dominating the astronomical tide), often producing steep, large waves (1–2 m) with turbid conditions. Matagorda Bay is tidally influenced by marine water entering through the Matagorda Ship Channel (maximum depth of 12 m) (Ward et al. 1980). Freshwater enters the bay from the Colorado River outflow in the far eastern arm of the bay, and from the Lavaca River in the northwestern corner. Matagorda Bay is mostly bordered by unaltered saltmarsh habitat and has extensive seagrass beds that are nursery habitat to many recreationally and commercially important invertebrates and fishes. This bay system has a mean depth of 2 m and experiences annual water temperatures ranging on average from 16 to 20°C during the cold season (November–April), and 28 to 35°C during the warm season (May–October) (Ward et al. 1980).

2.2. Sample collections and tagging methods

Atlantic stingrays (n = 71) were collected throughout Matagorda Bay using a variety of capture methods including cast nets, experimental gill nets, entanglement nets, and benthic sleds (Fig. 1; Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m760p117_supp1.xlsx). Upon capture, stingrays were placed into a bin of aerated local bay water to reduce the effects of physiological stress. Stingrays were measured to the nearest 0.1 mm for disc width (DW), sexed, and biopsied in the wing musculature (2 or 4 mm disposable biopsy plug). Muscle biopsies were immediately put on ice until being processed in the lab. A subset of stingrays (n = 50) were fitted externally with acoustic transmitters (V9T-2x, 69 kHz, low power, 180 s delay, estimated battery life = 414 d; Innovasea) that were marine epoxy-glued to a Peterson disc (1.3 cm diameter; Floy Tag) and a nickel alloy pin, similar to tagging methods described by Cartamil et al. (2003) and Burns et al. (2019). Acoustic transmitters were externally attached to the stingrays by piercing the nickel pins on the posterior dorsal side of the left wing (Fig. 1B). Nickel pins were secured on the ventral side using a second disc, excess pin was trimmed ~2.5 cm away from the body, and needle-nose pliers were used to coil the remaining pin inward against the ventral disc to avoid any skin irritation. Stingrays were additionally tagged with a small spaghetti tag (3.5 cm; Floy Tag) with contact information. All stingrays were released at the location of capture.

Acoustic receivers (VR2W and VR2Tx-69 kHz; InnovaSea) were strategically placed throughout Matagorda Bay by the Harte Research Institute (Texas A&M University — Corpus Christi) to record stingray movements (Fig. 1A). Receivers were anchored to the bay floor by attaching them with cable ties to bases constructed from a concrete block and a vertical PVC pipe, with the hydrophone oriented upward, ~0.6 m above the benthos. When tagged individuals came into detection range (estimated ~200 m) of a stationed acoustic receiver, the receiver recorded the date, time, identification code of the individual, and the water temperature (°C) as sensed by the externally placed transmitter. Acoustic receivers were downloaded and maintained twice a year.

2.3. Stable isotope analysis

Stingray muscle samples were kept on ice until being catalogued and frozen at −20°C upon returning to the lab. When ready to process, samples were thawed, thoroughly rinsed in deionized water to remove urea (Carlisle et al. 2017), examined under a dissecting microscope for cleanliness (i.e. removal of skin, connective tissue, and any debris), oven dried at 60°C for 48 h (Heratherm OGS180 drying oven, ThermoScientific), and then homogenized into a fine powder with an agate mortar and pestle. Cleaned muscle samples were not lipid extracted since preliminary bulk isotope analysis (n = 6) confirmed that C:N ratios were near the proposed threshold of 3.5 (3.6 ± 0.2), and lipid extraction is not necessary for AA_{SIA} (Post et al. 2007, Skinner et al. 2016, Yarnes & Herszage 2017). All samples were processed for bulk $\delta^{13}C$ and $\delta^{15}N$ by weighing out 1 mg of homogenized tissue into 9 × 5 mm tin capsules that were shipped to the Stable Isotopes for Biosphere Science (SIBS) Laboratory at Texas A&M University, College Station, Texas, USA. Samples were analyzed using a Costech Elemental Combustion System coupled to a Thermo Scientific Delta V Advance stable isotope ratio mass spectrometer (EA-IRMS). Stable isotope values are reported in delta (δ) notation (‰) which compares the ratio of the heavy to light isotope ($^{13}C/^{12}C$, $^{15}N/^{14}N$) in the sample and the ratio of the heavy to light isotope derived from accepted international standards. These were Vienna PeeDee Belemnite (VPDB) for carbon and atmospheric N_2 (air) for nitrogen via 2-point calibration with USGS40 and USGS41a, with precision $\leqslant 0.2$‰ for both $\delta^{13}C$ and $\delta^{15}N$.

A subset of 10 individuals were selected for $\delta^{13}C_{EAA}$ and prepared by weighing approximately 10 mg of homogenized tissue into 2 ml glass vials, then shipped to the University of California Santa Cruz (UCSC)

Stable Isotope Laboratory, Santa Cruz, California, USA. Dried samples were hydrolyzed (6 N HCl for 20 h at 110°C), and the resulting hydrolysate was purified using cation exchange chromatography (Dowex 50WX8-400 ion exchange resin; Metges et al. 1996). Isopropyl-trifluoroacetate derivatives were prepared following Silfer et al. (1991). Derivatized samples were analyzed by a Thermo Trace Ultra gas chromatograph (GC) coupled to a Thermo-Finnigan Delta Plus XP IRMS (oxidation furnace at 940°C, reduction furnace at 630°C). Individual AAs were separated for $\delta^{13}C$ analyses using a DB-5 column (50 m × 0.32 mm, 0.52 µm film thickness; Agilent Technologies). The 6 EAAs measured included isoleucine (Ile), leucine (Leu), lysine (Lys), phenylalanine (Phe), threonine (Thr), and valine (Val). The average standard deviation (after carbon correction) for the samples across all AAs was ±0.2‰. Norleucine (Nle) was used as an internal standard with an average standard deviation of ±0.2‰. The AA $\delta^{13}C$ values were determined from the measured values of the AA derivatives following the approach of Silfer et al. (1991), and the corrections were based on an AA mixture standard that had been separately determined by conventional EA-IRMS. The injector temperature was 250°C with a split He flow rate of 2 ml min^{-1}. The GC temperature program started at 75°C, held for 2 min, and heated at 4°C min^{-1} to 90°C and held for 4 min; followed by 4°C min^{-1} to 185°C and held for 5 min; then 10°C min^{-1} to 250°C and held for 2 min; and finally 20°C min^{-1} to 300°C and held for 5 min. All samples were analyzed in triplicate.

2.4. Statistical analyses

Acoustic detections were downloaded and managed in VUE (v. 2.7.0; InnovaSea). Detection data were sorted to remove possible false detections, identified as a single detection within a 24 h period. All statistical analyses were conducted in R (v. 4.3.2; R Core Team 2024) and ArcGIS (v. 10.7.1; ESRI).

2.4.1. Residency, site fidelity, and environmental drivers

Residency of Atlantic stingrays to Matagorda Bay was calculated using a residency index (RI) as the number of days that an individual was present within the bay relative to its total days at liberty (tagging date until end of tag life). An individual was considered present if it had at least 2 detections on a given day (Wolfe & Lowe 2015). RI values ranged between 0 and 1, with values close to 1 indicating that an individual stayed within the bay for its entire tracking duration (Burns et al. 2019).

Site fidelity was assessed using a zonal selection index (ZSI) to compare the number of days an individual was present (at least 2 detections) within a zone, divided by the total number of days that individual was detected within any zone (Kessel et al. 2014). We defined each receiver as a zone for the present study. ZSI values range between 0 and 1, with values close to 1 indicating that an individual spent all of its time in that zone (i.e. nearest that receiver), and values close to 0 indicating the individual spent no time in that zone (i.e. near that receiver). Generalized linear models (GLMs) assessed whether ZSI was different across available zones, and if ZSI was specific to the site in which the stingrays were tagged and released. ZSI (value of 0 to 1) was the response variable (Gaussian family), with zone (i.e. receiver ID) and whether the stingray was tagged at the site (i.e. 'yes' or 'no') as the predictor variables. The unit of replication for this model was individual stingray in each zone in which an individual was detected.

Hourly presence/absence of Atlantic stingrays in Matagorda Bay was modeled using generalized additive models (GAMs) in the 'mgcv' library in R (Wood 2017). To determine what environmental factors influenced the presence of Atlantic stingrays in Matagorda Bay, binary values of presence (1) and absence (0) of stingrays were categorized in hourly bins based on detections following TinHan et al. (2018). Environmental factors included diel period, tide height (m), moon illumination (proportion), and water temperature (°C). Diel period was categorized to include twilight dawn, day, twilight dusk, and night based on local sunset, sunrise, and civil twilight times using the 'suncalc' package in R (Thieurmel 2022). Tide height (m) was derived from the local NOAA data buoy (National Data Buoy Center; Port O'Connor Station #8773701; 28° 27.1' N, 96° 23.3' W). Moon illumination (proportional: 0, new moon, to 1, full moon) was retrieved using local sunset and sunrise times with the 'lunar' package in R (Lazaridis 2022) and modeled as a cyclic cubic regression (bs = 'cc'). Water temperature (°C) was the hourly mean based on the NOAA buoy data, measured 0.73 m below the mean lower-low water. While salinity likely plays an important role in Atlantic stingray movements and distribution within estuaries, salinity data at the desired temporal resolution (hourly) and in appropriate spatial proximity to resulting detections were unavailable. GAMs were fit using a binomial distribution, and with individual stingray included as a random effect (bs = 're'). Stepwise backward selection was used to select the most parsimonious model explaining stingray hourly presence based on AIC with a threshold value (ΔAIC) of 2 (Anderson & Burnham 2002, TinHan et al. 2018).

To determine how Atlantic stingrays were using available local water temperatures, water temperatures of the stingrays' geolocations (measured by the acoustic transmitters) were compared with available local water temperatures derived from the NOAA data buoy. Temperatures from detections were then paired to the nearest time available for NOAA buoy temperatures (measured every 6 min) to calculate differences to determine (i.e. proportionally) if stingrays were generally located in waters relatively warmer or cooler to what may have been available.

2.4.2. Spatial patterns of isotope values and diet source fingerprinting

Kruskal-Wallis tests were used to compare differences in bulk $\delta^{13}C$ and $\delta^{15}N$ values across sampling sites (n = 8), as the data did not meet assumptions of normality or homoscedasticity (Shapiro-Wilk test, $p < 0.05$; Levene's test $p < 0.05$). Significant differences were further evaluated with pairwise Wilcoxon rank-sum tests using the Benjamini-Hochberg correction to adjust the p-values to control for the increased risk of Type I errors due to multiple comparisons (Benjamini & Hochberg 1995). Values across sampling sites (n = 8) were assessed for significant differences to inform the selection of individuals for $\delta^{13}C_{EAA}$ by maximizing the spatial spread and the variance in bulk $\delta^{13}C$ values.

$\delta^{13}C_{EAA}$ was used to trace possible basal resources supporting Atlantic stingrays. We identified 3 basal resource groups that were most likely to support food-web biomass within the study system: green macroalgae, phytoplankton, and seagrass. $\delta^{13}C$ values of 6 EAAs (Ile, Leu, Lys, Thr, Phe, Val) from sources that reflect these basal organisms, namely green macroalgae (e.g. *Ulva* sp.), phytoplankton (e.g. diatoms, dinoflagellates), and seagrass (e.g. *Zostera*, *Phyllospadix*), were derived from published data sets (Table S2 in Supplement 1) (Larsen et al. 2013, Elliott Smith et al. 2018, Stahl et al. 2023, Yun et al. 2024). Deriving a basal organism library was deemed appropriate here for several reasons. Firstly, recent work has suggested that spatial variation in basal organism sampling does not significantly impact the uniqueness of isotopic fingerprints across broad basal sources (Liew et al. 2019, Elliott Smith et al. 2022, Shipley et al. 2023, Stahl et al. 2023). In other words, basal organisms sampled from different geographical locations may exhibit similar isotopic fingerprints because $\delta^{13}C_{EAA}$ fingerprinting relies on the relative multivariate spacing between $\delta^{13}C$ values of EAAs, not just the measured $\delta^{13}C$ values. However, as the library-derived data set was created by compiling multiple studies, these results should be taken as suggestive rather than conclusive. Secondly, selected $\delta^{13}C_{EAA}$ values were limited to basal organisms within climates and ecosystems most similar to our study system in the northern Gulf of Mexico. Additionally, this study prioritized including library sources with measured $\delta^{13}C$ values for all 6 EAAs measured in stingray tissues. Finally, this approach was used as a general guide for informing whether the bulk $\delta^{13}C$ values varied because of different basal organism use, versus differences in carbon isotope values of the same basal resources across a spatial gradient.

Both the basal resource library and the stingray $\delta^{13}C_{EAA}$ values were normalized to their means to allow for comparisons of EAA $\delta^{13}C$ patterns across groups and to account for possible temporal variation in food sources or environmental conditions (McMahon et al. 2015a, Fox et al. 2019, Larsen et al. 2020) (Fig. S1 in Supplement 2 at www.int-res.com/articles/suppl/m760p117_supp2.pdf). Principal component analysis (PCA) was performed on basal organism $\delta^{13}C_{EAA\text{-norm}}$ values to initially explore patterns of group membership, and to assess whether the $\delta^{13}C_{EAA}$ patterns in basal organism groups were distinctive (Fig. S2 in Supplement 2) (Stahl et al. 2023). We used linear discriminant analysis (LDA) to probabilistically assign stingrays to basal resource groups based on their multivariate $\delta^{13}C_{EAA}$ fingerprints (Larsen et al. 2009, 2013). The LDA used the $\delta^{13}C_{EAA\text{-norm}}$ values and implemented leave-one-out cross validation to examine classification error rates (Larsen et al. 2009).

3. RESULTS

A total of 71 individual Atlantic stingrays were sampled for the present study (46 females, 24 males, 1 unclassified). Sampled stingrays had a mean ± SD DW of 310.1 ± 63.8 mm (range: 185–542 mm) (Table S1).

3.1. Residency, site fidelity, and environmental drivers

Atlantic stingrays (n = 50) were acoustically tagged from August 2021 to August 2022 at various locations within Matagorda Bay, Texas, USA, to quantify bay-specific movements (Fig. 1A). We tagged 37 females and 13 males with a mean ± SD DW of 300.4 ± 34.17 mm (range: 235–385 mm; Table S1). The majority of stingrays (n = 42) were tagged in the middle of the Matagorda Peninsula near Receiver M14 (Fig. 2A), due to the likelihood of locating stingrays within this region and having optimal conditions where individuals could be visually spotted and targeted. We prioritized having as many tags as possible out at once due to the relatively short battery life of the tags (~414 d) as opposed to evenly distributing tagging efforts throughout the bay. All tagged stingrays were considered to be sexually mature (>220 mm DW; Johnson & Snelson 1996).

We recorded a total of 65 218 detections across 10 receivers over the course of the study period (Fig. 2A). No detection data were excluded immediately after tagging because previous studies have noted a return to normal behavior within minutes of tagging in Atlantic stingrays and other dasyatids (Cartamil et al. 2003, Brinton & Curran 2017). Of the 50 stingrays acoustically tagged, 25 (50%) were detected (Fig. 2B). One stingray (SR-927) exhibited behavior indicative of mortality (i.e. consistent detections at 1 receiver station for 259 d) and was removed from further analyses, resulting in 24 stingrays for further analyses.

Individual stingrays were detected in Matagorda Bay for a range of 1–98 cumulative days (16.3 ± 25.5 d) (Fig. 3). The residency index (RI) was significantly higher in males (0.12 ± 0.09; n = 4) than females (0.02 ± 0.04; n = 20) (Wilcoxon rank sum test, $W = 8$, $p = 0.01$), but we found no significant relationship between RI and DW (GLM, $R^2 = 0.04$, $p = 0.35$). Due to the limited receiver coverage in the mid-bay, RIs for stingrays tagged in the bay should be interpreted as minimum residency values, as individuals that were detected could move in and out of detection range of receivers or were never detected post tagging. Additionally, there were no detections at receivers placed within the bay inlets (e.g. Matagorda Ship Channel and Pass Cavallo), indicating no evidence of stingrays leaving Matagorda Bay during the study.

Most individuals did not travel between receivers, and most individuals were detected near the receiver at which they were tagged (Fig. 2B). Additionally, all stingrays tagged nearest Receivers M18 and M21, located in the southwest corner of the bay, were never detected on any receivers during the study. The receiver in the middle of the peninsula where most tagging had occurred (Receiver M14) identified 22 of

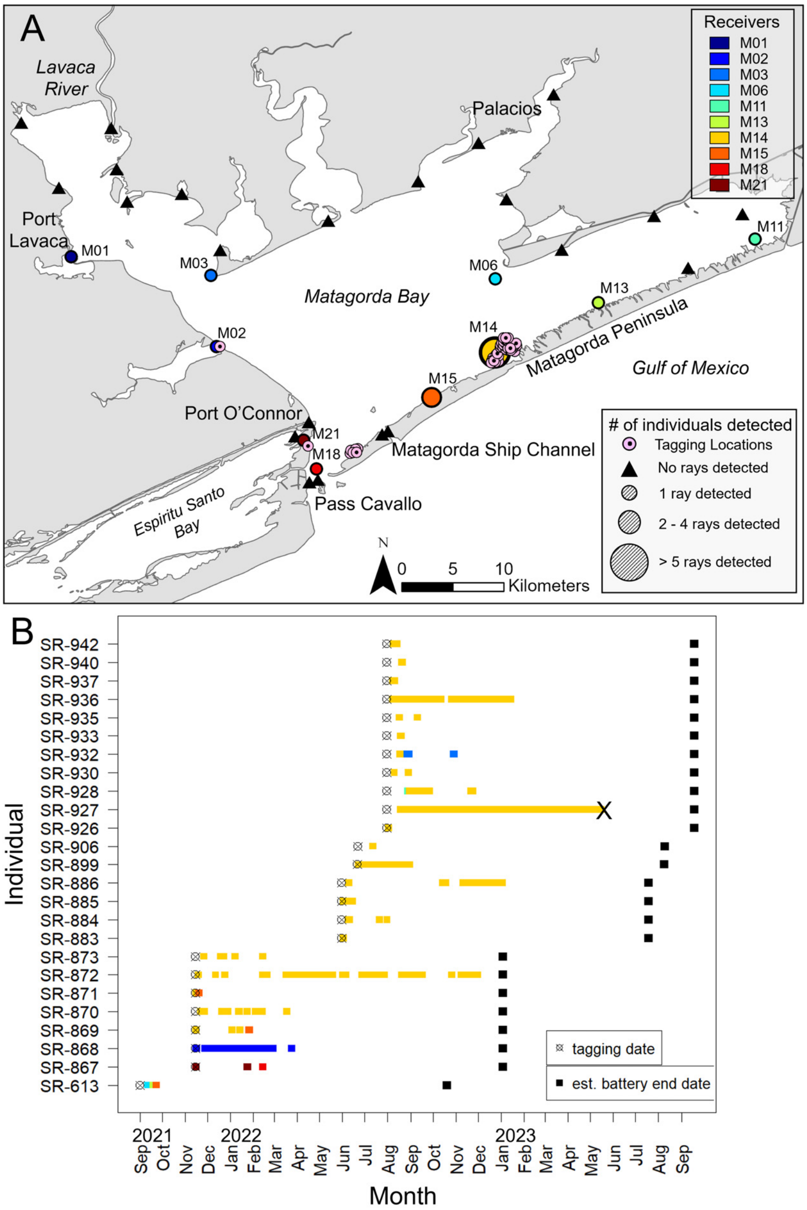

Fig. 2. (A) Number of Atlantic stingrays detected per acoustic receiver in Matagorda Bay. Tagging locations (small pink circles) are referenced on the map. (B) Atlantic stingray detections during the entire study duration. The color(s) of the line correspond to the receiver(s) on the map in (A). The 'X' for SR-927 denotes behavior indicative of mortality (see Section 3.1); est: estimated

the 25 stingrays detected (Fig. 2A). Detected stingrays ($n = 24$) had a mean ZSI of 0.75 ± 0.34. GLM results indicated a significantly higher ZSI in the zones in which individuals were tagged compared to zones in which individuals were not tagged ($p = 0.01$). Specifically, the receiver in the middle of the Matagorda Peninsula (Receiver M14) had a significantly larger ZSI compared to other zones ($p < 0.001$).

All potential environmental drivers for predicting stingray presence were retained in the final GAM, which explained 23.8% of the total deviance. Diel period, tide height, moon illumination, and water temperature were significant predictors of hourly presence of Atlantic stingrays in Matagorda Bay (Fig. 4A–D). Occurrence was higher during nighttime compared to daytime, twilight dawn, and twilight dusk hours ($p < 0.001$; Fig. 4A). Stingray presence was positively related to tide height, but decreased beyond tide heights >0.8 m ($p < 0.001$; Fig. 4B). Moon illumination values >0.8 (~ full moon) were associated with higher presence ($p < 0.001$; Fig. 4C). Water temperatures between 15 and 25°C were associated with higher presence, while individuals were rarely detected at temperatures <10 and >30°C ($p < 0.001$; Fig. 4D).

Water temperature recorded by externally fitted acoustic transmitters ranged from 5.7 to 31.5°C (20.5 ± 6.6°C) (Fig. S3 in Supplement 2). The local water temperature of Matagorda Bay recorded by NOAA Buoy #8773701 during the extent of potential detections (first tagging date until final battery end date) ranged from 2.1 to 36.1°C (26.2 ± 7.0°C). Daily ranges in Matagorda Bay were on average 2.3 ± 1.8°C (range: 0–12.2°C). Atlantic stingrays were recorded present in water temperatures disproportionately to what was available (i.e. NOAA Buoy) ($\chi^2 = 1807.3$, df = 7, $p < 0.001$) (Fig. 4E). Specifically, there was a relatively high density of temperatures greater than 30°C available during the study, but a comparatively reduced density of detections occurred in those temperatures (Fig. 4E). When each detection was matched with local NOAA Buoy time, stingrays were present in temperatures approximately 3.2 ± 1.6°C cooler than what was available (range: 7.8°C cooler to 3.9°C warmer) (Fig. 4F). Cooler temperatures were recorded for ~95% of the total detections, whereas only 5% of stingray detections occurred in temperatures warmer than those available (Fig. 4F).

3.2. Stable isotope analysis

A total of 68 individuals (44 females, 23 males, 1 unidentified) were biopsied for bulk $\delta^{13}C$ and $\delta^{15}N$ throughout Matagorda Bay, with a mean DW of 312.3 ± 64.1 mm (range: 185.0–542.0 mm) (Fig. 5A; Table S1). $\delta^{13}C_{bulk}$ values ranged from −20.1 to −12.8‰ (mean ± SD: −15.8 ± 1.6‰) (Fig. 5B,C; Table S1). There was a significant difference in $\delta^{13}C_{bulk}$ values across sampling sites within Matagorda Bay (Kruskal-Wallis: $\chi^2 = 42.37$, $p < 0.001$; Fig. 5C). Generally, $\delta^{13}C_{bulk}$ values were higher (i.e. more enriched in ^{13}C) for sites located along the Matagorda Peninsula, and comparatively lower (i.e. more depleted in ^{13}C) at sites in the northeast (i.e. towards the Colorado River and Palacios) and nearest Port O'Connor (Fig. 5C).

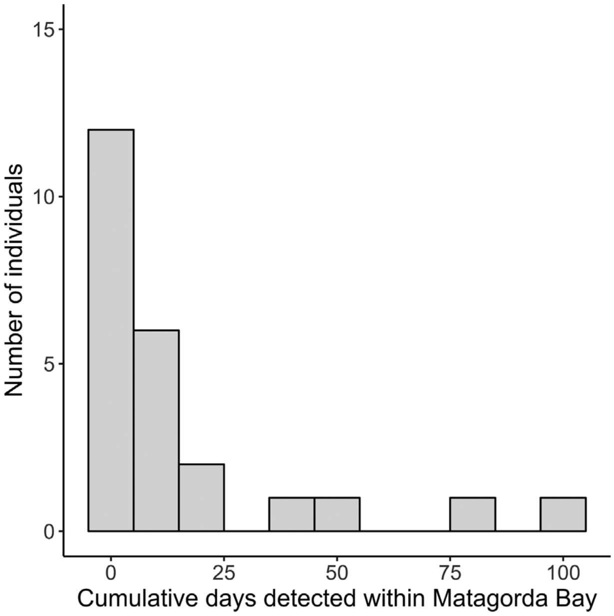

Fig. 3. Frequency distribution of the cumulative days (total number of days during the study) on which individual Atlantic stingrays were detected by Matagorda Bay acoustic receivers

$\delta^{15}N_{bulk}$ values ranged from 10.2 to 18.0‰ (mean 13.0 ± 1.4 SD ‰) (Fig. 5B,D; Table S1). There was no observed pattern with size (DW) and $\delta^{15}N_{bulk}$ ($R^2 = 0.0003$, $p = 0.884$). However, $\delta^{15}N_{bulk}$ values were higher in the northern site nearest Palacios (Site 8), and lower in sites nearest the Matagorda Ship Channel (Sites 1 and 2) (Fig. 5D) (Kruskal-Wallis: $\chi^2 = 26.06$, $p = 0.0005$; Fig. 5D).

To assess whether the gradient of $\delta^{13}C_{bulk}$ values was due to stingrays using distinct basal organism sources, or due to chemical differences that drive variability in $\delta^{13}C$ within the same basal organism, 10 individuals were selected for $\delta^{13}C_{EAA}$ analysis (Fig. 6A; Table S3 in Supplement 1). Six EAAs measured across all individuals included Ile, Leu, Lys, Phe, Thr, and Val for a mean of −17.9 ± 2.3‰ (Table S3). Across individuals, there was expected

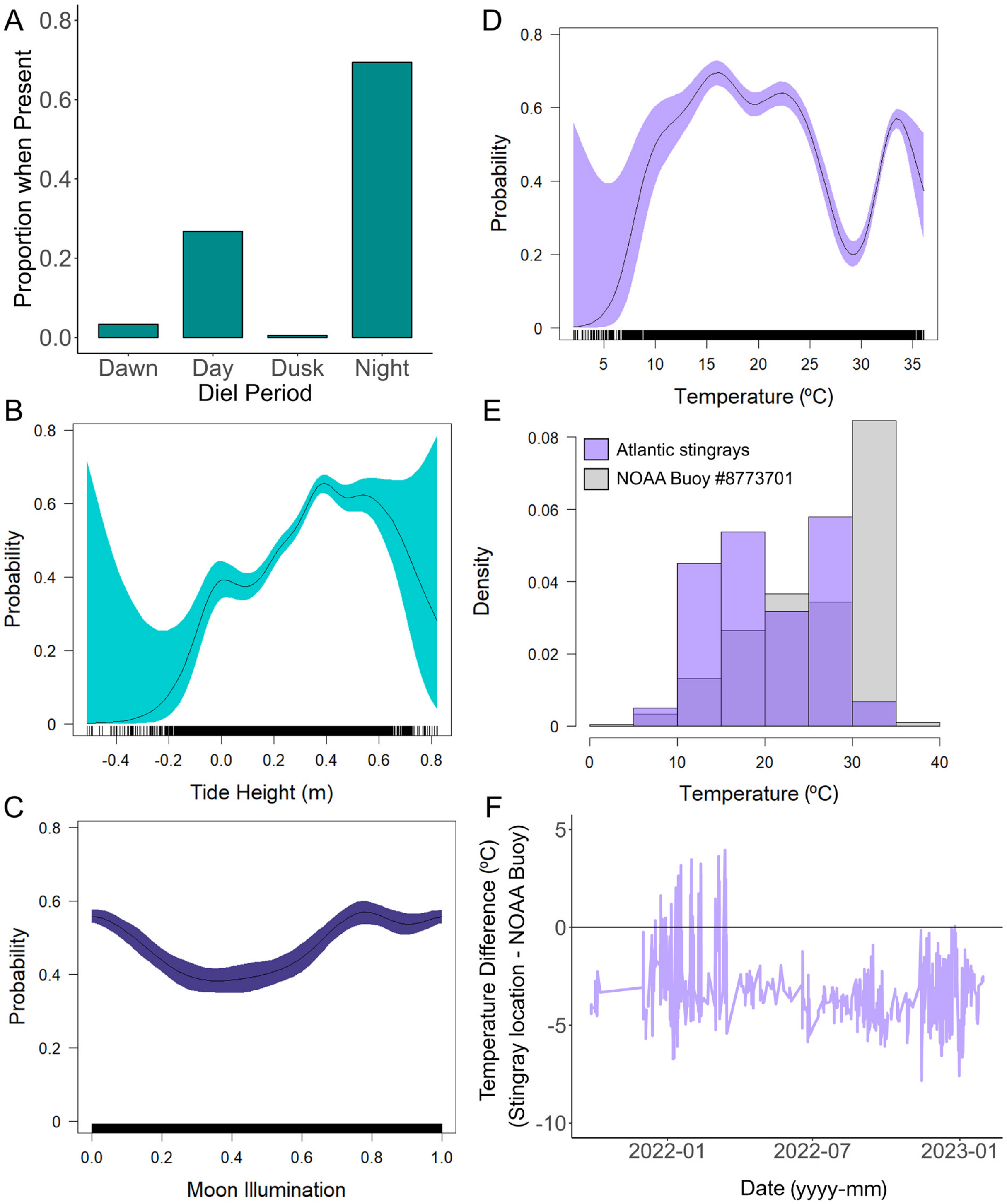

Fig. 4. Influence of environmental variables on Atlantic stingray presence in Matagorda Bay revealed by generalized additive models. Variables retained in the final model included (A) diel period, (B) tide height (m), (C) moon illumination, and (D) water temperature (°C). The *y*-axis for continuous variables (panels B, C, and D) is represented as the probability of stingray presence for the binomial fitted models, and the *x*-axis includes a rug plot to show the distribution of available data. The shading in B, C, and D represents the 95% confidence interval for the mean shape of the effect. (E) Distributions of available water temperature in Matagorda Bay as recorded by NOAA Buoy #8773701, versus as recorded by acoustic transmitters externally fitted to Atlantic stingrays for the entire study duration. (F) Difference in water temperature as sensed by the acoustic transmitters versus the NOAA buoy for each detection from the study duration. Differences above (below) 0 indicate stingrays being detected in comparatively warmer (cooler) waters than what was available

variability in $\delta^{13}C_{EAA}$ values (Fig. 6A). Thr (mean −9.1 ± 2.3 SD ‰) and Lys (mean −13.3 ± 2.1 SD ‰) were the highest, and Leu (mean −22.5 ± 2.2 SD ‰) and Phe (mean −25.0 ± 2.5 SD ‰) were the lowest (Fig. 6A). Ile had the smallest range of $\delta^{13}C_{EAA}$ values (range: 6.2) and Lys had the greatest range of $\delta^{13}C_{EAA}$ values (range: 8.2) (Fig. 6A).

For llinear discriminant analysis of $\delta^{13}C_{EAA}$ (Fig. 6B), reclassification rates were 100, 96, and 100% for green algae, phytoplankton, and seagrass, respectively, indicating effective separation among basal organism groups (Fig. 6C). Variation in LD1 (proportion of trace = 56.6%) inferred via discriminant coefficients was primarily driven by the $\delta^{13}C$ values of Leu (0.704) and Val (−0.575). Variation in LD2 (proportion of trace = 43.3%) was primarily driven by the $\delta^{13}C$ values of Ile (−0.844) and Lys (−0.513). EAA fingerprinting of stingray tissue indicated trophic assimilation of green algae EAAs (Fig. 6C).

4. DISCUSSION

This study found that Atlantic stingrays are highly resident to Matagorda Bay, with their presence in shallower areas driven by diel period, tide height, moon illumination, and water temperature. Stingrays were predominantly supported by macroalgal EAAs, suggesting that the observed spatial gradient in bulk $\delta^{13}C$ values is not related to the use of distinct basal

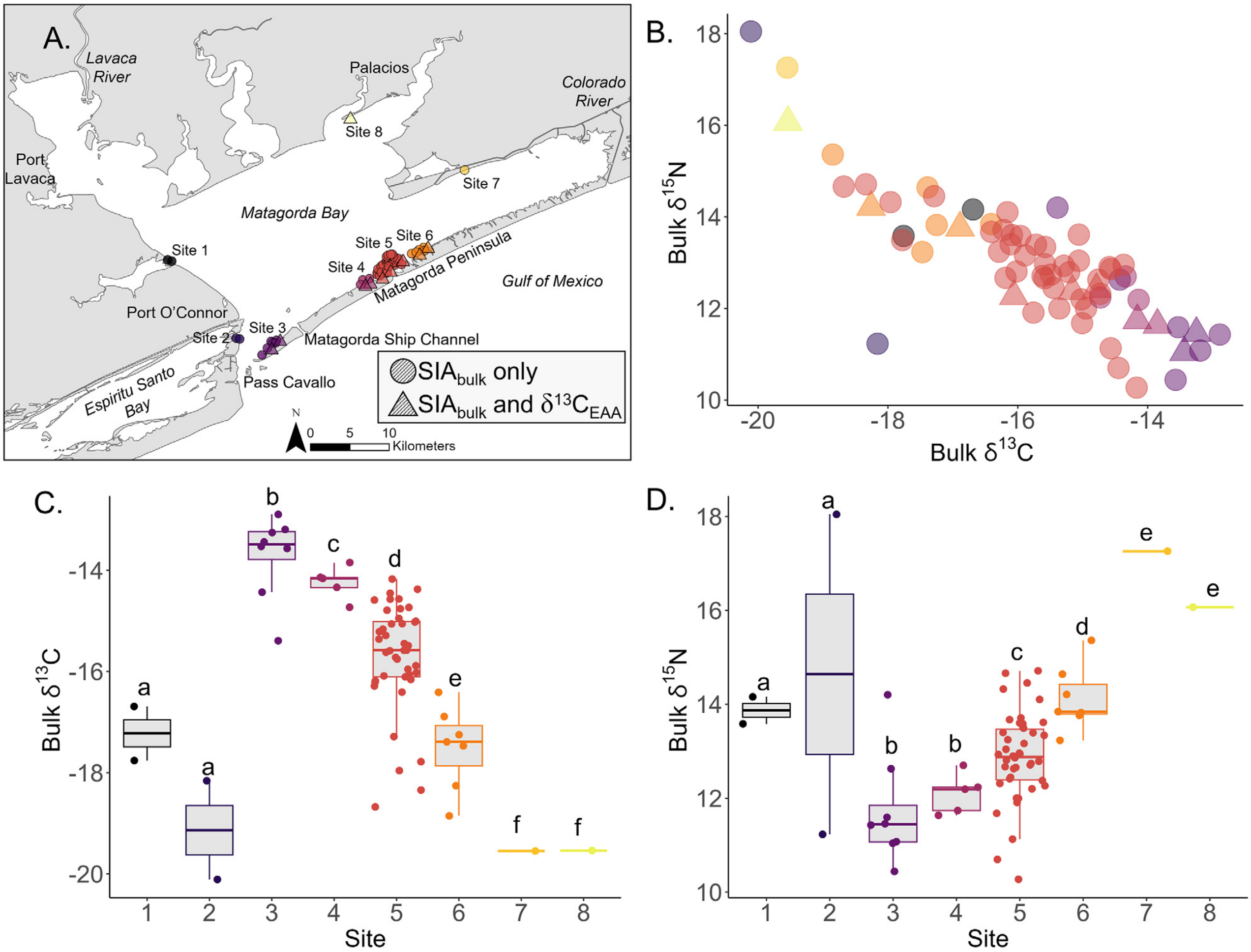

Fig. 5. (A) Locations of Atlantic stingrays biopsied for stable isotope analysis within Matagorda Bay. Circles denote stingrays selected for bulk stable isotope analysis (SIA_{bulk}) only, and triangles denote stingrays selected for essential amino acid $\delta^{13}C$ analysis ($\delta^{13}C_{EAA}$) in addition to SIA_{bulk}. Colors of symbols represent specific sites (n = 8) where sampling occurred. Locations have been spread out for visualization purposes using the 'disperse' tool in ArcGIS. (B) Isoplot of $\delta^{13}C$ and $\delta^{15}N$ SIA_{bulk} values. (C) $\delta^{13}C_{bulk}$ values across sampling sites, and (D) $\delta^{15}N_{bulk}$ values across sampling sites. Box and whisker plots in panels (C) and (D) represent group medians (horizontal lines) with boxes representing the interquartile range and whiskers extending to the minimum and maximum values. Jittered points for individuals show the spread of data. Letters above boxes denote significant differences in pairwise comparisons

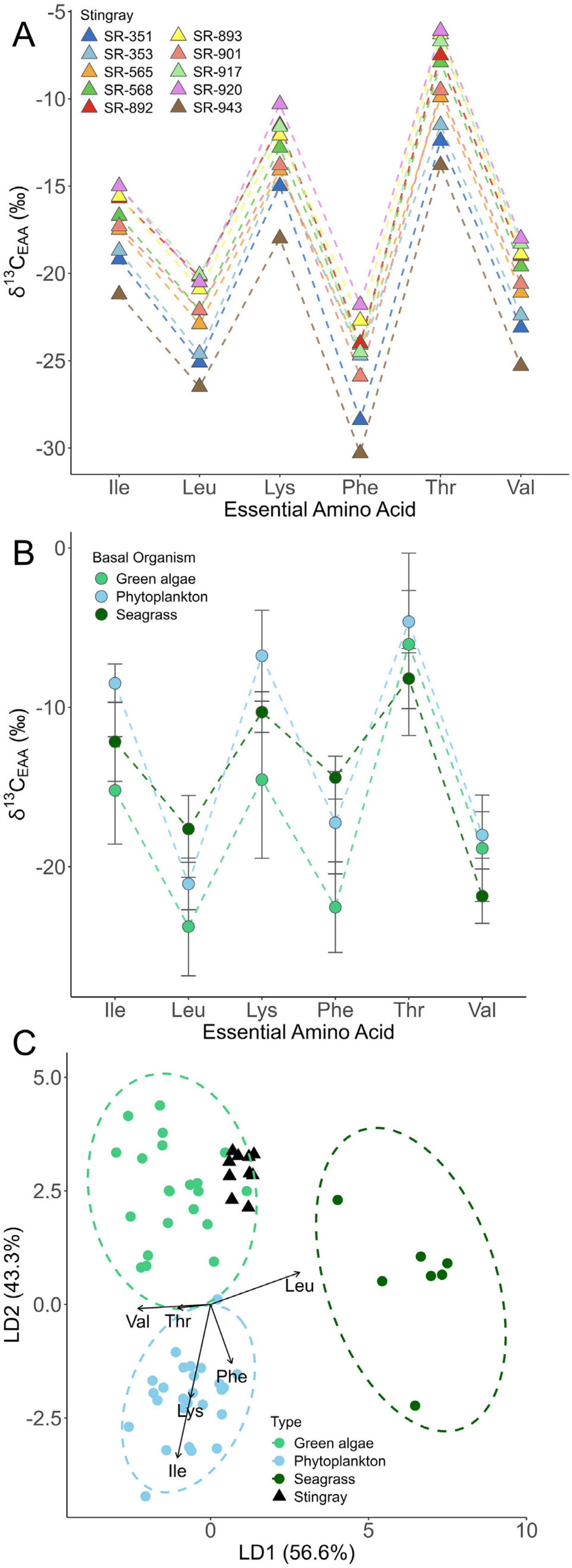

Fig. 6. Essential amino acid δ^{13}C ($\delta^{13}C_{EAA}$) patterns (mean ± SD) of (A) Atlantic stingrays (consumers, n = 10) and (B) library-derived basal organism sources: green macroalgae (n = 21), phytoplankton (n = 27), and seagrass (n = 7). (C) Linear discriminant (LD) analysis based on $\delta^{13}C_{EAA\text{-norm}}$ values of Atlantic stingrays from this study (black triangles) and library-derived basal organisms. Ellipses represent 95% confidence intervals of each basal organism. Arrows represent the relative weightings of the independent variables (amino acids) for creating the discriminant function. The 6 EAAs shown are isoleucine (Ile), leucine (Leu), lysine (Lys), phenylalanine (Phe), threonine (Thr), and valine (Val)

organism sources. Rather, we propose that environmental conditions may drive differential ^{13}C fractionation in green algae across space, or that there are potentially different species of green algae spatially distributed throughout the bay. Ultimately, these findings illustrate the importance of adopting complementary methods for elucidating the causes and consequences of habitat use and trophic ecology for Atlantic stingrays, further contributing to our knowledge of vulnerable elasmobranchs in estuarine environments.

4.1. Residency and site fidelity

We did not detect stingrays at the inlet of the bay (i.e. Matagorda Ship Channel), suggesting that individuals are highly resident within the studied estuarine system. Ramsden et al. (2017) found this species to be resident year-round in an estuary in Savannah, Georgia, USA, and data for our study site also support this. It is possible that stingrays move to deeper waters in the estuary during unfavorable conditions (e.g. too warm, stormy, etc.); however, we had no receiver coverage in mid-bay waters to confirm this. There were very few detections in the Lavaca region of the bay, which may indicate that stingrays utilize deeper shipping channels (e.g. Matagorda Ship Channel, Intracoastal Waterway). The few individuals tagged in the southwestern corner of the bay were never detected on any receivers, despite that area having some of the highest receiver coverage. It is possible those individuals may have moved into the neighboring bay system, Espiritu Santo Bay, characterized by extensive, shallow (<1 m), dense seagrass beds, which leads into San Antonio Bay. While stingrays may remain resident to estuarine habitat, they may also be using multiple estuaries easily accessible in this region of the Texas coast.

Several other factors may have affected our detection efficiency throughout the array. A possible explanation for the loss of detections from individuals over time and for only detecting ~50% of tagged individuals is that Atlantic stingrays are captured by recreational fishers and commercial shrimp trawlers in Gulf coast estuaries and are often used as bait in shark and crab fisheries (Adams et al. 2003). However, we did not receive any fisher reports of captured individuals despite deployment of external spaghetti tags. Another plausible explanation is that this species exhibits a significant use of tidal creek systems (Brinton & Curran 2017), which are readily abundant past the saltmarsh edge in Matagorda Bay. If tagged stingrays were in fact using tidal creek systems, they would have likely been outside of the detection range (estimated 200 m) of our acoustic array.

We observed stingrays exhibiting specific site fidelity within Matagorda Bay. The receiver in the middle of the Matagorda Peninsula (Receiver M14) that detected the most individuals (22 of the 25) was also where most tags were deployed. It is possible, although it may be inflated through our tagging locations, that this could represent a core habitat use area (e.g. hotspot) of this species. The benthos comprises a mixture of seagrass beds, saltmarsh edge, patchy oyster reef, and finer sediments, which together provide suitable refuge habitat and plentiful foraging opportunities. Additionally, this area may serve as nursery habitat for this species, particularly for females. We caught several pregnant females during sampling in July 2022, and we did observe sexual segregation where it was more common to find females at this site compared to neighboring sites <1 km away. Female Atlantic stingrays are known to ovulate during spring, with pups being born in mid- to late summer (Snelson et al. 1988, Johnson & Snelson 1996). Furthermore, sexual habitat segregation is common in elasmobranch species and can arise through a variety of factors including predation risk, competitive exclusion, seasonal resource requirements, and dietary or reproductive requirements (Sims 2005, Wearmouth & Sims 2008). Small-bodied stingrays have previously been found forming large unisex (female) aggregations during months of peak summer water temperatures, where pregnant females may derive a thermal reproductive benefit (i.e. maternal thermophily) by using warm, shallow habitats (Mull et al. 2010, Jirik & Lowe 2012). Therefore, it is possible that some females in this study were using this habitat for some physiological benefit, indicative of this area being a productive nursery area for this species that should be considered in conservation and management decisions (Heupel et al. 2007).

4.2. Environmental drivers of presence/absence

All measured environmental factors significantly influenced the presence of stingrays in Matagorda Bay. Presence increased during nighttime compared to other diel periods (day, twilight dawn, and twilight dusk). In contrast, Brinton & Curran (2017) found that Atlantic stingrays in Savannah, Georgia, moved most at dusk, followed by night. Atlantic stingrays may have been responding to prey populations, as increased nighttime activity has been seen in prey species including blue crabs *Callinectes sapidus* (Clark et al. 1999). We also found that stingray presence increased with positive tide heights, but decreased with negative tide heights and with tide heights >0.8 m. Atlantic stingrays often move with the direction of the tides (Teaf 1980, Brinton & Curran 2017). Because there was essentially no movement of individual stingrays between receivers, and because we were focused on estuarine habitat use, we could not analyze the directionality of movements with respect to tidal direction. It is possible that stingrays were moving in the direction of tidal movement since the probability of presence increased with higher tide heights, indicating that stingrays may be moving closer towards receivers (placed in shallow waters <1 m deep, located <100 m from the saltmarsh edge) during those times. There may be an energetic benefit to using tidal currents for movement for many species including pleuronectid flounders (Wirjoatmodjo & Pitcher 1984) and prey species including white shrimp *Litopenaeus setiferus* (Wenner et al. 1998, Brinton & Curran 2017). For generalist mesopredators like Atlantic stingrays, they may not only receive the energetic benefits of following the tides, but also following potential prey species (e.g. daggerblade grass shrimp *Palaemon pugio*; Welsh 1975) (Rozas & Odum 1987). Since tides also affect turbidity, salinity, and temperature, prey populations may be the first to move in response to tide changes to remain in suitable habitat and conditions (Rountree & Able 2007). The reduced probability of presence with negative tide heights can likely be explained by water levels simply not reaching the saltmarsh edge habitat, thus not providing as many benefits for stingrays to be within detection range. The reduced probability of presence with extreme positive tide heights may be explained by stingrays moving into the dense tidal creek systems as demonstrated in estuarine habitats on the US Atlantic coast (Brinton & Curran 2017, Ramsden et al. 2017).

Diel and tidal patterns may also influence movements and behaviors of stingray predators in Matagorda Bay, including carcharhinid sharks such as bull sharks *Carcharhinus leucas*, Atlantic sharpnose sharks *Rhizoprionodon terraenovae*, and blacktip sharks *C. limbatus* (Hoffmayer & Parsons 2003, Plumlee & Wells 2016, TinHan & Wells 2021). These species are typically nocturnal foragers, suggesting that predation risk may be greater for Atlantic stingrays at night, and provide reasoning as to why they may be present in shallow waters near the saltmarsh edge. Bull sharks are also known to move with tidal directions (Ortega et al. 2009), and to exhibit distinct seasonality by using estuarine habitats during spring, summer, and fall seasons, but egressing out of estuaries during the winter months (TinHan 2020, Matich et al. 2024). Higher probabilities of presence with increased values of moon illumination may relate to the light penetrating further into estuarine waters during these times, so stingrays may move to shallower waters (i.e. within detection range) to take refuge from predators that may be more restricted to relatively deeper (>1 m) waters.

Stingray presence increased in temperatures ranging from 15 to 25°C, but they were more likely to be rare or absent in temperatures <10 and >30°C. Additional confirmation with local NOAA buoy data showed that stingrays were detected in water temperatures disproportionate to a wider range of temperatures observed within the estuary, with a notable decrease in detections at temperatures >30°C. During times of unfavorable water temperatures (<10 and >30°C) it is unclear whether they move to mid-bay waters or to tidal creeks past the saltmarsh edge. Wallman & Bennett (2006) found that Atlantic stingrays in parturition experiments exhibited a range of preferred temperatures between 24.0 and 29.0°C. They also found significant differences, with pregnant females and males preferring temperatures of ~26.1 and 25.9°C, respectively, compared to non-pregnant females, which preferred 25.3°C. Fangue & Bennett (2003) identified 35.1°C as the highest survival temperature for Atlantic stingrays with prolonged and constant exposure and found that this species can take advantage of a wider range of resources than other competing fishes by exploiting extreme thermal gradients (particularly cold, ~7–11°C) as possible refuges from predators to optimize temperature-dependent physiological processes. This supports the notion that Atlantic stingrays remain in the estuary during colder months (i.e. resident year-round) as they would be able to tolerate the cold, wind-driven conditions, yet potentially reside in deeper, cooler, and more protected areas that were outside of our acoustic detection range. Ramsden et al. (2017) found Atlantic stingrays to be year-round residents of estuarine waters in Savannah, Georgia, revealing that this species may not need to take refuge from colder water temperatures and instead prioritize seeking out areas of higher food abundance and refuge from predators. Interestingly, Atlantic stingrays in the Indian River Lagoon in Florida were often found in deeper channels in the winter that were 2–5°C warmer than surrounding shallower waters (Snelson et al. 1988). Furthermore, the reduced detections of stingrays in water temperatures >30°C may be explained by stingrays potentially avoiding shallower, warmer areas, and instead using deeper waters outside of the detection range. Ultimately, the tolerance of Atlantic stingrays to dynamic environmental conditions likely contributes to the wide distribution and success of this species in shallow, inshore habitat. This species may be able to behaviorally optimize temperature-dependent physiological processes (i.e. feeding, reproduction) while taking refuge from higher trophic ordered predators (i.e. carcharhinid sharks, dolphins) (Snelson et al. 1988, Di Santo & Bennett 2011a,b).

Alternatively, instead of seeking a thermal refuge since they are considered thermally tolerant, they may have been influenced by other abiotic (i.e. salinity) or biotic (i.e. prey populations) factors. While our model did not evaluate salinity due to the desired resolution of data being unavailable, it is important to note the influence this environmental variable may have on stingray presence, movements, and behaviors within Matagorda Bay (Froeschke et al. 2010, Plumlee et al. 2018). Salinities in Matagorda Bay can range from 0 to ~40 ppt. Recent studies have shown long-term trends in increasing salinity in Matagorda Bay, likely due to the growing water demand in watersheds opposed to natural climate variability (Bugica et al. 2020). While Atlantic stingrays are relatively tolerant of salinities up to 41 ppt (Fangue & Bennett 2003), prey populations likely do not have the same tolerance, suggesting stingray movements and behaviors may be following food sources. Additionally, we had little evidence of detections in the northern areas of Matagorda Bay that are typically characterized by freshwater salinities and reduced seagrass cover.

4.3. Linking trophic ecology to habitat use

Bulk $\delta^{13}C$ and $\delta^{15}N$ values exhibited spatial gradients throughout Matagorda Bay that aligned with the habitat use patterns identified using acoustic telemetry. Generally, individuals sampled in the southwestern corner of Matagorda Bay exhibited higher $\delta^{13}C$ and lower $\delta^{15}N$ values compared to those sampled in the northeastern region of the bay. The southwestern region of the bay is characterized by having dense seagrass beds. Seagrass cover declines moving east along the Matagorda Peninsula (i.e. towards the Colorado River) where waters become less saline and more turbid, often resulting in ^{13}C-depleted waters. The northeastern region of the bay was characterized by having little to no saltmarsh edge, no seagrasses, and sandy beach habitat. Freshwater and anthropogenic inputs, such as those in the northeastern region of the bay, can decrease δ^{13}C values (as reduced salinity changes the phytoplankton community structure) and increase δ^{15}N values (via nutrient enrichment) of primary producers in coastal ecosystems (Palmer et al. 2011, Marshall et al. 2021). While there would be inherent community composition differences based on differences in available habitat (Yeager et al. 2011, Clarkson & Beseres Pollack 2021), it is not likely that the diets of individual stingrays differ significantly depending on sampling location because they are mobile, generalist foragers. Thus, the differences in $\mathrm{SIA_{bulk}}$ values are likely due to variability in isotopic baseline compositions between the different sampling sites. While isotopic turnover for muscle in elasmobranchs is expected to be relatively long (>1 yr, Logan & Lutcavage 2010, Kim et al. 2012, Malpica-Cruz et al. 2012), sites relatively close in proximity (<2 km) demonstrated significant differences in $\mathrm{SIA_{bulk}}$ values across individuals, indicative of long-term foraging at respective sampling sites. Dale et al. (2011) found similar patterns for brown stingrays *Dasyatis lata* sampled for $\mathrm{SIA_{bulk}}$ within a bay on Oahu, Hawaii, USA, where there were significant differences across sampling sites based on water residence times. Sampling of different tissues with comparatively faster turnover rates (e.g. liver, blood plasma) may provide more insight into temporal patterns of stingray foraging ecology (Hussey et al. 2012). Additionally, while our methods were highly complementary, future work should focus on incorporating mixing models (e.g. MixSIAR) to assess differing contributions of estuarine diet sources (using basal organism data from within the study site) to elucidate spatiotemporal variation in foraging.

Our approach highlights the importance of quantifying spatial variability of baseline values when assessing habitat use and trophic ecology (Matich et al. 2021), and ultimately validates incorporating $\delta^{13}\mathrm{C_{EAA}}$ values to gain insight into the underlying causes of $\delta^{13}\mathrm{C_{bulk}}$ variation. $\delta^{13}\mathrm{C_{EAA}}$ analysis of stingrays selected along the gradient of $\mathrm{SIA_{bulk}}$ values allowed us to trace possible basal resource use by Atlantic stingrays without the need to quantify basal organism $\delta^{13}\mathrm{C_{EAA}}$ values from Matagorda Bay. Applying a library-derived basal organism data set that included δ^{13}C values from 6 EAAs revealed that stingrays were largely supported by green algae. As stingrays are benthic feeders on grazing invertebrates (Funicelli 1975, Cross & Curran 2000), this is not surprising and likely demonstrates the importance of green algae to the broader food web. Incorporating brown algae to exploratory iterations of the LDA did not produce reliable results (33% reassignment rates), likely due to relatively low amounts of brown algae in the study system. Additionally, most available brown algae $\delta^{13}\mathrm{C_{EAA}}$ values were from Laminariaceae samples and were therefore omitted for simplicity in interpretation of the LDA results to align with our study objectives. While previous studies have mentioned that Atlantic stingrays feed on smaller planktivorous teleosts (Snelson et al. 1988), we found little evidence for a significant contribution of phytoplankton-derived energy. This could be because Atlantic stingrays consume grazers or detritivores instead of planktivores, or the stingrays in Matagorda Bay are eating negligible amounts of prey fishes. Therefore, the variability in bulk SIA values was likely due to environmental and biogeochemical conditions, rather than a variety in basal resources being utilized across stingrays. While seagrass seemed to have no dietary contributions to stingrays, it is still considered an important habitat providing the foundation for the existing food web in Matagorda Bay as well as protective habitat for many species, including Atlantic stingrays.

5. CONCLUSIONS

This study contributes to the emerging literature using $\mathrm{SIA_{bulk}}$ and $\delta^{13}\mathrm{C_{EAA}}$ values for elasmobranch species to identify relationships between habitat use and trophic ecology. Understanding habitat use by mesopredators and making direct links to their trophic ecology is an essential first step for effective ecosystem-based management strategies. Specifically, because batoids are often found in aggregations, their combined roles of mesopredator and ecosystem engineer through bioturbation may have impacts on estuarine communities worth considering when implementing management and conservation action. As anthropogenic impacts to coastal environments continue to alter baselines both in food webs and in species-specific behaviors and distributions, studies like this have become critical for resource managers to understand how changing conditions will influence the distribution and behaviors of key estuarine taxa such as elasmobranchs. Even though much has been learned about the Atlantic stingray, more field-based studies are warranted, especially those using higher-resolution techniques (e.g. biologging approaches).

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