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Pacific nurse sharks *Ginglymostoma unami* exhibit yearly patterns of site fidelity to a tropical embayment subjected to seasonal upwelling

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ABSTRACT: Seasonal upwelling in tropical coastal regions can create dynamic oceanographic conditions similar to temperate systems, which are known to influence the distribution and movement of marine species. Mobile marine species may seek warmer environments (i.e. exhibit behavioral thermoregulation) in response to stronger winds during the upwelling season, which cause cold, nutrient-rich waters to rise and cool shallower environments. Pacific nurse sharks *Ginglymostoma unami* are present in the upwelling regions of the Eastern Tropical Pacific coastline, serving as an ideal model species to study the effects of changing water temperatures on movement behavior. In this study, we analyzed 4 yr of passive acoustic telemetry data to quantify the movement, residency, and habitat use of *G. unami* in Santa Elena Bay, north Pacific coast of Costa Rica, located within the Papagayo upwelling system. A total of 28 sharks (15 males and 13 females) ranging from 85 to 256 cm total length were monitored inside the bay. The mean (±SD) residency index (i.e. number of days detected relative to the number of days monitored) of individual sharks was 37 ± 28%. Generalized additive mixed models revealed seasonal and diel patterns of *G. unami* use of Santa Elena Bay that were associated with water temperature and wind speed changes during the upwelling season. *G. unami* likely uses the warmer waters of Santa Elena Bay as a thermal refuge during the upwelling season to avoid colder adjacent waters. This research will serve as a baseline to understand the movement behavior of this species as climate change alters upwelling patterns.

KEY WORDS: Tropical upwelling system · Movement behavior · Water temperature · Behavioral thermoregulation · Protected areas

1. INTRODUCTION

Site fidelity, an animal's tendency to return to previously visited locations, is a common behavior across mobile taxa and is key to understanding the movement ecology of a species (Matthiopoulus et al. 2005, Pratt et al. 2022). Understanding what drives a species' recurring preference for a particular site and identifying areas of high site fidelity is necessary to define important habitats for threatened species and predict how anthropogenic impacts may alter species distributions in the future (Jones et al. 2013, Chapman et al. 2015). Many elasmobranchs (sharks and rays) are known to exhibit varying degrees of site

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*Corresponding author: sergiomadrigalmora@gmail.com fidelity (e.g. Chapman et al. 2015, Anderson et al. 2021, Pratt et al. 2022) that is often seasonal, whereby species return to certain areas when environmental conditions are more favorable or when resources are seasonally available (Schlaff et al. 2014, Doherty et al. 2017, Logan et al. 2020).

Movements of elasmobranch species in the tropics are not typically influenced by seasonality since tropical marine systems present generally stable environments. However, some regions are exposed to seasonally changing conditions associated with upwelling systems that could affect the behavior of elasmobranchs (Ryan et al. 2017, Eisele et al. 2021). During the upwelling season, stronger winds cause nutrient-rich cold water to rise from the seafloor to the surface, creating seasonal patterns that are uncommon in the tropics and more similar to temperate systems (O'Dea et al. 2012, Alfaro & Cortés 2021). Since tropical upwelling regions are relatively uncommon and more often adjacent to data-poor countries, the effects of seasonal upwelling conditions on mobile marine fauna in the tropics have not been well studied (Eisele et al. 2021). In certain tropical areas like Yucatan (Mexican Caribbean), the Gulf of Tehuantepec (Mexican Pacific), the Costa Rica Thermal Dome/Gulf of Papagayo upwelling system, and the Gulf of Panamá, wind-driven upwelling may influence the behavior of resident and wide-ranging species (O'Dea et al. 2012, Ruiz-Castillo et al. 2016). For example, whale sharks *Rhincodon typus* routinely return to sites in the Yucatán Peninsula, Mexico, when intensified upwelling conditions drive seasonal plankton, which in turn is closely coupled with mass fish spawning events (Cárdenas-Palomo et al. 2015). Additionally, the movements of whale sharks in the Eastern Tropical Pacific (ETP) have also been shown to be closely coupled to seasonal changes in water temperatures and plankton availability (Ryan et al. 2017).

Water temperature changes that occur during upwelling likely influence the movements and site fidelity of coastal elasmobranchs, as the selection of sites with optimal water temperature may be favored to better suit their metabolic requirements (Papastamatiou et al. 2015, Whitney et al. 2016, Lear et al. 2017). Individuals may move to waters that are thermally beneficial for foraging during the night and return to sites with temperatures beneficial for digestion during the day, or vice versa, to maintain optimal physiological benefits (e.g. Matern et al. 2000, Papastamatiou et al. 2015, Meese & Lowe 2020). These behaviors may also vary between sexes, as females can be more thermally selective as a result of their higher energy requirements associated with reproductive development and gestation (Hight & Lowe 2007, Jirik & Lowe 2012, Gong et al. 2023). Thermoregulatory movement behavior of elasmobranchs in tropical upwelling systems is of particular importance based on climate change scenarios where alterations in upwelling intensity may influence movement patterns, distributions, and overall fitness (Diaz-Carballido et al. 2022, Vilmar & Di Santo 2022).

The north Pacific of Costa Rica is part of the Papagayo upwelling system (Cortés 2016), and there is limited knowledge of the influence of seasonal upwelling on the distribution and movements of elasmobranch species in this area (Eisele et al. 2021, Madrigal-Mora et al. 2024). Pacific nurse sharks *Ginglymostoma unami* are frequently observed in these regions and serve as an ideal model species to study the effects of changing water temperatures on movement behavior. This species is found throughout the coastline from Mexico to Peru, inhabiting all 3 upwelling systems of the ETP. *G. unami* is currently listed as Endangered by the International Union for the Conservation of Nature's (IUCN) Red List given ongoing population declines in some areas, interactions with coastal fisheries, and loss of critical habitats (Pollom et al. 2021). Little is known about the biology of *G. unami*, as most research on nurse sharks comes mostly from its sister species the Atlantic nurse shark *Ginglymostoma cirratum* in the Caribbean (Castro 2000, Carlson et al. 2021). So far, only 2 studies have focused exclusively on *G. unami*: the description of the species (Del Moral-Flores et al. 2015) and a short report of the species' long-distance movements (Madrigal-Mora et al. 2024). However, no detailed research on the movement ecology of *G. unami* and the influence of environmental conditions has been published prior to this study.

Populations of *G. unami* in relatively undisturbed conditions still exist; for example, in the Santa Elena Bay Marine Management Area (MMA) along the North Pacific of Costa Rica where they are not directly targeted by fisheries (Villalobos-Rojas et al. 2014, López-Garro & Zanella 2015, Espinoza et al. 2022). In addition, the Gulf of Santa Elena, which includes Santa Elena Bay, was recently identified as an Important Shark and Ray Area (ISRA) by the IUCN Shark Specialist Group based on its overall importance as a critical area for the conservation of a wide range of threatened elasmobranch species (Jabado et al. 2023). In Santa Elena Bay and the adjacent Gulf of Santa Elena, *G. unami* is exposed to seasonal upwelling from December to April, when water temperatures can decrease to as low as 16°C (Alfaro & Cortés 2012, Eisele et al. 2021), becoming considerably colder than the lowest temperature (25°C) at which *G.*

cirratum have been reported in the Atlantic (Wiley & Simpfendorfer 2007, Ferreira et al. 2013). Understanding the influence of these environmental changes on *G. unami* in Santa Elena Bay will be valuable for the management and conservation of this species, particularly in the tropical upwelling systems they inhabit (López-Garro & Zanella 2015, Pollom et al. 2021).

In this study, we investigated the site fidelity and movement of *G. unami* to Santa Elena Bay, a tropical estuarine embayment subjected to seasonal upwelling. Specifically, we (1) quantified the site fidelity of *G. unami* to Santa Elena Bay and whether it varied between sexes and different areas of the bay; (2) determined whether the site fidelity of *G. unami* varies throughout the year as a result of changing environmental conditions (wind speed and water temperature), and (3) determined whether *G. unami* exhibits diel patterns in the use of the bay and whether these are affected by changes in water temperature during upwelling seasons.

2. MATERIALS AND METHODS

2.1. Study site

Santa Elena Bay is a relatively large embayment (7.3 km^2) located in the Gulf of Santa Elena, north Pacific coast of Costa Rica (Fig. 1), comprising a wide variety of habitats including mudflats, subtidal sand and rocky reef substrata, and mangroves (Cortés 1996, Espinoza et al. 2022). The bay is relatively shallow (<15 m) but can reach up to 30 m depth near the mouth and in the center. Santa Elena Bay also functions as a seasonal reverse estuary, where the salinity inside the bay can be higher than the surrounding waters of the Gulf of Santa Elena (Tisseaux-Navarro et al. 2021). There is also yearly seasonality, with a dry season (average daily rainfall: 0.2 mm) from December to April characterized by the strengthening of the trade winds (average wind speed: 13.2 m s^{-1}) (data obtained from Costa Rican National Meteorological Institute, IMN). Stronger winds during the dry season drive upwelling events that reduce water temperatures from an average of 28° to as low as 16°C and draw nutrients to the surface waters, increasing productivity (Alfaro & Cortés 2021). The rainy season lasts from May to November, when winds decrease (median wind speed: 7.5 m s^{-1}) and average daily rainfall increases to 32.6 mm (data obtained from Costa Rican National Meteorological Institute, IMN).

In May 2018, Santa Elena Bay was designated an MMA (Law Decree No. 41171; SINAC 2017), allowing for some eco-tourism, sport angling, snorkeling, and diving. More intensive fishing methods, including trawling, longline, and gillnet, are prohibited (SINAC 2017). This is beneficial for threatened species including elasmobranchs and sea turtles that may be captured as by-catch by artisanal fisheries operating along the Pacific coast of Costa Rica (Villalobos-Rojas et al. 2014, López-Garro & Zanella 2015, Clarke et al. 2016).

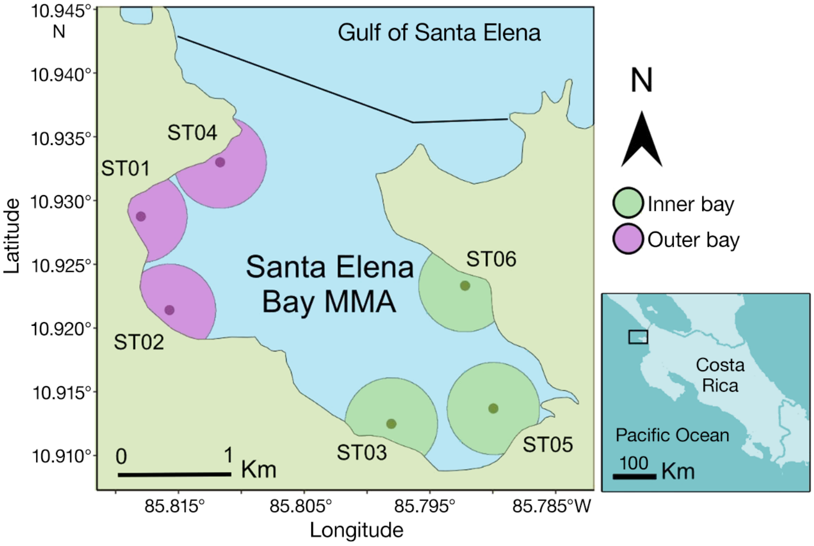

Fig. 1. Acoustic receiver locations in Santa Elena Bay Marine Management Area (MMA), north Pacific coast of Costa Rica. Receivers monitor 28% of Santa Elena Bay MMA

2.2. Shark tagging

Scientific bottom longline surveys were conducted in various sites of Santa Elena Bay to capture and tag *Ginglymostoma unami*. Longlines (~1 km long) were deployed with 19–54 hooks of sizes 13-0 and 14-0 and then soaked for ~1 h. Hooked sharks were brought to the side of the boat to be sexed, measured, and fitted with Innovasea V16 coded acoustic transmitters (16 mm diameter, 98 mm length, 69 kHz, power output: 150–162 dB, 100–300 s pulse interval, 10 yr battery life). Transmitters were surgically implanted into the peritoneal cavity through a small incision (~2 cm) along the abdomen, and wounds were closed with 2–3 interrupted PDS sutures. Tagging procedures were performed under and approved by California State University Long Beach Institutional Animal Care and Use Committee (IACUC), protocol no. 364.

2.3. Acoustic telemetry array

An array of 6 acoustic telemetry receivers (Innovasea VR2W and VR2Tx, 69 kHz) were used to monitor the movement and site fidelity of acoustically tagged sharks in Santa Elena Bay (Fig. 1). Receivers were moored 1–2 m above the sea floor at depths ranging from 4–9 m, with OnSet HOBO Water Temperature Pro v2 Data Loggers attached to each receiver to record bottom water temperature with a resolution of 0.1°C every 30 min.

To determine if there are spatial differences in habitat use within Santa Elena Bay, we divided the bay into 2 zones (outer and inner bay) based on habitat composition and abiotic conditions present in each area that may provide certain advantages for *G. unami*. In July 2018, 3 of these receivers (ST01, ST02, ST04) were deployed in the outer section of the bay, and an additional 2 (ST03, ST05) in the inner section (hereafter referred to as the outer and inner bay; Fig. 1), with a third (ST06) added to the inner bay in June 2021. The outer bay (the area closer to the mouth of the bay) is characterized by rocky reefs, gravel substratum, and sandy beaches where shallow waters are exposed to direct sun during the day, whereas the inner bay is composed mostly of muddy flats and mangrove forest. The inner bay tends to have generally calmer waters, as it is isolated from swells and wind action, and is characterized by mangrove forest which may provide greater prey availability.

Acoustic receivers were deployed predominantly around the perimeter of some portions of the bay where sharks have previously been observed to aggregate (M. Lara pers. comm.). Receivers detected 50% of transmissions at an average range of 400 m (V. Valverde et al. unpubl. data). The outer bay receivers (ST01, ST02, ST04) covered 12.4% of the area of Santa Elena Bay MMA, while the 2 initial inner bay receivers (ST03, ST05) covered 11.8%. The addition of ST06 increased the coverage of the inner bay receivers to 16.1% of the bay. Hence, a total of 24.2% of the MMA was monitored when all 5 receivers were present, and the monitored area increased to 28.5% when ST06 was added (Fig. 1). The positions of the receivers were chosen based on reported observations of *G. unami* by local fishers and divers (ST01, ST05) and to monitor Santa Elena Bay MMA as evenly as possible with the limited equipment available (ST02, ST03, ST04, ST06).

2.4. Site fidelity of *Ginglymostoma unami* to Santa Elena Bay

To quantify the site fidelity of *G. unami* in Santa Elena Bay, we used detection data collected from January 2019 to December 2022. The presence or absence of tagged sharks at each acoustic receiver was determined for each day of the monitoring period. A tagged shark was considered to be present in the bay at any receiver if 2 or more detections were recorded on the same day. We calculated the residency index (RI), the total percentage of days when a shark was detected, for all of Santa Elena Bay as well as independently for the inner and outer zones of the bay. Although we calculated RI, the primary purpose of this analysis was to quantify site fidelity to each area of the bay since these sharks were not expected to be permanent residents of the bay (Chapman et al. 2015). RI is defined as:

$$\text{RI}\,(\%) = \left(\frac{\text{Number of days detected}}{\text{Total days since tagging}}\right) \times 100$$

To determine the variation among individual sharks' use of Santa Elena Bay, we calculated RI separately for each tagged shark as well and compared overall site fidelity between the inner and outer zones of the bay. An analysis of covariance (ANCOVA) was used to determine if RI varied between individuals of different sexes and total lengths and between the zones of the bay.

2.5. Yearly changes in use of Santa Elena Bay

Generalized additive mixed models (GAMMs) with a binomial error distribution were used to predict changes in the daily probability of detection of *G. unami* using the 'mgcv' package (Wood 2017). GAMMs are able to model non-linear patterns from multiple continuous variables while considering interactions with categorical predictors and can also account for the variation of random effects such as individual behavior (Wood 2017). GAMMs were used to determine if there were inter- and intra-annual patterns in the daily probability of detection of *G. unami* and whether they were related to environmental variables associated with upwelling (Table 1). GAMMs were compared with the Akaike information criterion (AIC) using stepwise selection

Table 1. Generalized additive mixed models (GAMMs) used to predict the daily probability of detection of Pacific nurse sharks *Ginglymostoma unami* in Santa Elena Bay, Costa Rica. The list of variables and their descriptions included in the saturated models was used as a starting point for stepwise selection using Akaike's information criterion

Variable	Description	Type
Detection probability	Calculated from a binomial variable of presence or absence (1 or 0) of each tagged shark at each zone of the bay for each day of the study	Dependent variable
Days of the year (DOY)	Discrete variable for days of the year. Interactions for categorical variables sex and zone were included	Smoothed effect
Water temperature (°C)	Median water temperature for each day of monitoring was calculated at each receiver station from the data recorded by HOBO loggers. Interactions for categorical variables sex and zone were included	Smoothed effect
Wind speed ($\mathrm{m\ s^{-1}}$)	Daily median wind speed data was obtained from the nearest meteorological station in La Cruz, Guanacaste, from the Costa Rican National Meteorological Institute (IMN). Interactions for categorical variables sex and zone were included	Smoothed effect
Sex	Categorical variable for male and female	Parametric effect
Zone	Categorical variable for zone of Santa Elena Bay (outer bay and inner bay)	Parametric effect
Year	Categorical variable for years of the study (2019–2020)	Random effect
Individual shark	Categorical variable for transmitter ID of each tagged shark	Random effect
Error distribution	Binomial	

to find a best-fit model. We built models that treated day of the year (DOY) as a cyclical response variable; however, these were not significantly different from models that treated this variable linearly. We decided to keep the models that did not include cyclical parameters, as adding these resulted in significantly lower p-values when checking basis dimensions (*k*) and, hence, worse models.

2.6. Diel patterns in use of Santa Elena Bay

To assess whether *G. unami* showed diel patterns associated with the use of different zones of Santa Elena Bay, we calculated the number of sharks detected at each receiver for each hour of the monitoring period. A 2-way ANOVA was used to test for differences between hours, zones, and interactions between both variables. A second 2-way ANOVA was conducted to test whether mean hourly water temperatures in Santa Elena Bay varied between hours, zones of the bay, and upwelling and non-upwelling seasons.

To determine how much time each individual spent in each zone during the hours it was detected, we calculated the mean detections per individual present per hour of the day and then used GAMMs with the package 'mgcv' (Wood 2017) to generate predictions for this variable (Table 2). GAMMs were used to determine if there were diel patterns in the hourly mean detections per individual and whether these were related to water temperature changes associated with upwelling (Table 2). Stepwise selection of GAMMs based on AIC was again used to find a best-fit model. We built models with hours treated as a cyclical response variable; however, these were not significantly different from models that treated this variable linearly. Models that did not include cyclical parameters were used, as significantly lower p-values when checking *k* resulted from the addition of these parameters. All data analysis was conducted in R version 4.2.3 (R Core Team 2023).

3. RESULTS

3.1. Site fidelity to Santa Elena Bay

A total of 28 individuals were tagged during 2 major tagging events, including 13 female and 15 male sharks ranging from 85–256 cm total length (Table 3, Fig. 2). *Ginglymostoma unami* was detected in Santa Elena Bay 1298 d out of a total of 1461 d monitored (88% of days detected); however, the mean (±SD) RI of individual sharks was 37 ± 28%, showing considerable variation among individuals (Table 4, Fig. 2B,C). There was no association between RI and sex or size (total length) according to the ANCOVA ($F = 0.91$, df = 1, p = 0.34). However, mean residency was significantly higher in the outer bay, where sharks were detected 31 ± 28% of the days, than in the inner bay (12 ± 10% of days) ($F = 7.959$, df = 1, p = 0.007).

Table 2. GAMMs used to predict hourly number of individual *G. unami* detected in Santa Elena Bay, Costa Rica. The list of variables and their descriptions included in the saturated models were used as a starting point for stepwise selection using Akaike's information criterion

Variable	Description	Type
Mean detections per individual present	Mean detections per individual present in that hour were calculated for each hour of the monitoring period	Dependent variable
Hour	Discrete variable for hours of the day. Interactions for categorical variables sex and zone were included	Smoothed effect
Water temperature (°C)	Median water temperature per hour for the monitoring period was calculated at each receiver station from the data recorded by HOBO loggers. Interactions for categorical variables sex and zone were included	Smoothed effect
Zone	Categorical variable for zone of Santa Elena Bay (outer bay and inner bay)	Parametric effect
Season	Categorical variable for season when a measurement occurred (upwelling and non-upwelling season)	Parametric effect
Year	Categorical variable for years of the study (2019–2020)	Random effect
Month	Categorical variable for transmitter ID of each tagged shark	Random effect
Error distribution	Gaussian	

Table 3. Pacific nurse sharks captured and tagged internally with acoustic transmitters in Santa Elena Bay, Costa Rica

Transmitter ID	Sex	Total length (cm)	Date tagged (yyyy-mm-dd)	No. of days at liberty	No. of days detected
8916	Male	176	2018-09-07	1576	126
8917	Female	194	2018-09-07	1576	669
8918	Male	234	2018-09-07	1576	234
8915	Female	238	2018-09-07	1576	623
8592	Female	85	2018-09-08	1575	63
7321	Female	190	2019-05-17	1324	7
7327	Male	202	2019-06-08	1302	365
7322	Male	225	2019-06-08	1302	177
7326	Male	232	2019-06-08	1302	81
7325	Male	242	2019-06-08	1302	348
7323	Male	195	2020-01-29	1067	104
7324	Female	249	2020-01-29	1067	612
6121	Female	130	2022-05-28	217	164
4321	Male	188	2022-05-28	217	31
4323	Female	220	2022-05-28	217	136
6119	Female	209	2022-07-11	173	155
56657	Male	215	2022-07-11	173	99
10043	Male	217	2022-07-11	173	24
56656	Male	221	2022-07-11	173	115
10041	Male	256	2022-07-11	173	36
10042	Female	170	2022-07-14	170	135
56654	Female	219	2022-07-14	170	61
10044	Male	102	2022-07-18	166	114
10045	Male	205	2022-07-18	166	119
56655	Female	226	2022-07-19	165	7

3.2. Inter and Intra-annual patterns of detection

The GAMM best-fit model showed that the probability of detecting sharks in Santa Elena Bay changed by DOY, with different patterns between males and females and between the inner and outer zones (Table 5, Fig. 3). A higher overall probability of detection for both sexes was observed in the outer bay compared to the inner bay. There was no difference in the probability of detection between sexes, but males and females had varying probabilities of detection throughout the year. Shark probability of detection varied between monitoring years, with 2020 having the highest probability of detection, followed by 2022, 2019, and then 2022 (Table 5, Fig. 3).

Probability of detection was also influenced by water temperature and wind speed (Table 5). Overall, the detection probability of male and female *G. unami* increased with lower water temperatures and dropped sharply after 29°C (Fig. 4A). Higher wind speeds were linearly correlated with higher detection probabilities for both males and females (Fig. 4B). Lower temperatures and higher wind speeds occurred during the upwelling months, from December to April (Fig. 4C,D). The model also found significant random effects, indicating variation in the probability of detection among individuals (Table 5).

3.3. Diel patterns in habitat use

Sharks were disproportionately detected during certain hours of the day within each zone of Santa Elena Bay ($F = 14.65$, df = 23, $p < 0.001$). There was also a significant interaction between the hours of the day and zones of the bay, which influenced shark detection probability ($F = 32.49$, df = 23, $p < 0.001$) (Fig. 5A). More sharks were detected in the outer bay during the night, while more were detected in the inner bay during the day (Fig. 5D). There was no significant difference in water temperature across diel periods ($F = 0.69$, df = 23, $p = 0.86$); however, water temperature in the outer bay was significantly warmer than in the inner bay ($F = 22.46$, df = 1, $p < 0.001$), and the upwelling season was significantly colder than the non-upwelling season ($F = 1841.16$, df = 1, $p = 0.86$) (Fig. 5B,C). The model indicated that diel patterns in mean detections per individual occurred during upwelling seasons and were more pronounced than in non-upwelling seasons (Fig. 5E). Additionally, mean detections per individual per hour changed across the water temperature regimes of each season (Fig. 6). More detections occurred at water temperatures between 18° and 20°C during the upwelling season (Fig. 6A), while the non-upwelling season had more detections at water temperatures near 23°–26°C (Fig. 6B). Additionally, there were more detections of sharks in the outer bay when temperatures were lower, while there were more detections in the inner bay as water temperatures increased (Fig. 6C). At temperatures above 29°C, *G. unami* individuals showed low detections per hour throughout the bay. The model found the random effect of year of the study to be significant.

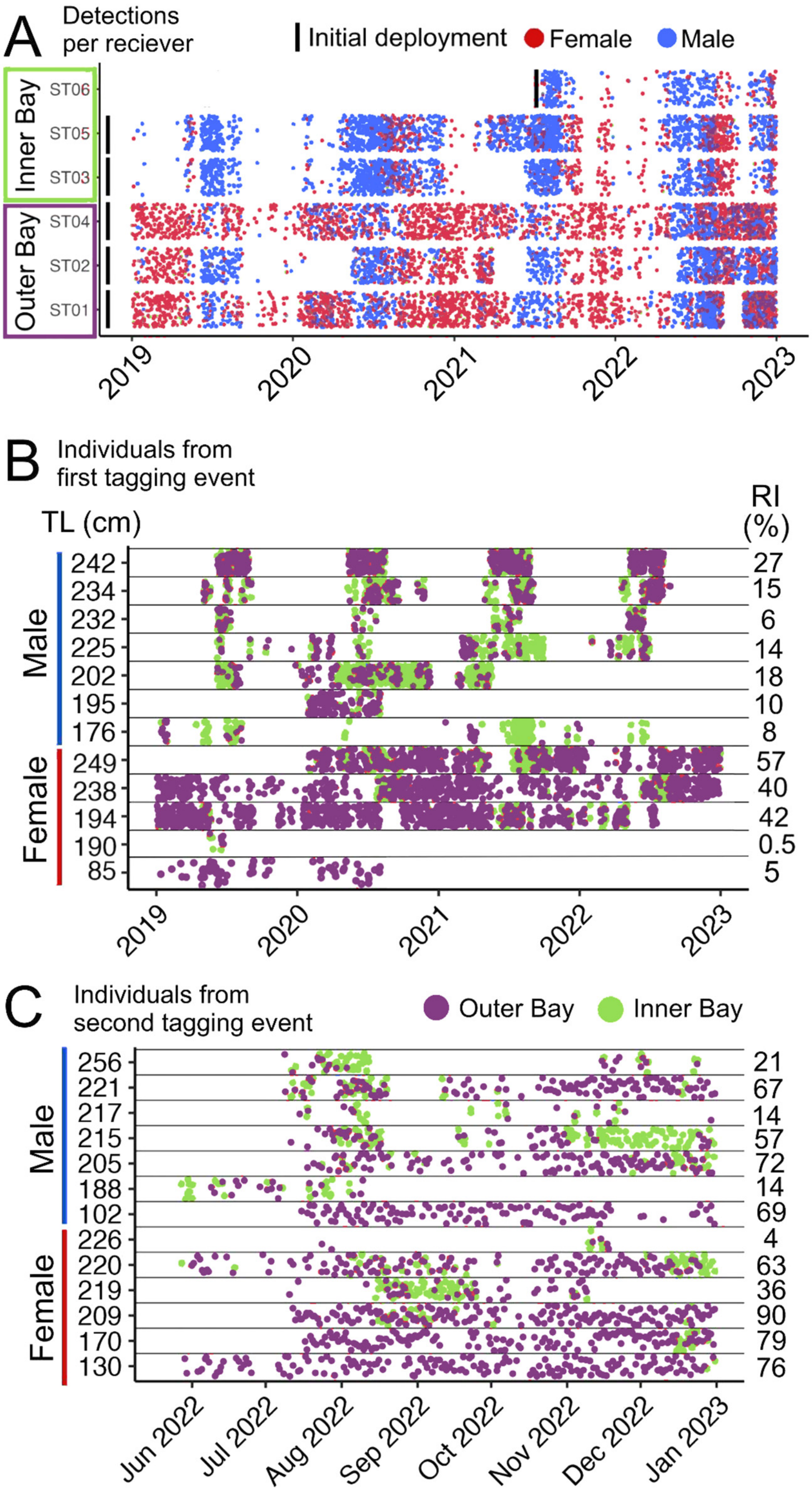

Fig. 2. Detections of Pacific nurse sharks *Ginglymostoma unami* tagged with acoustic transmitters (A) at each acoustic receiver station on (B) the first tagging event (September 2018–January 2020) and (C) the second tagging event (May–July 2022). The total length at the time of tagging (TL) and the residency index (RI) is displayed for each tagged individual

4. DISCUSSION

Our study reveals some of the first data on the movement ecology of the recently described Endangered *Ginglymostoma unami* in the ETP. Study sites such as Santa Elena Bay offer some degree of protection from extractive activities and are exposed to seasonally changing environmental

Table 4. Results of best-fit GAMM predicting daily probability of detection of *G. unami* through days of the year (DOY) in Santa Elena Bay from 2019 to 2022. Model uses a binomial error distribution and had an adjusted R^2 of 0.28 and explained 27% of the deviance

Parametric terms	Estimate	SE	*z*
(Intercept)	−2.804181	0.337483	−8.309
Wind speed	0.033316	0.007402	4.501
Zone (outer bay)	1.343107	0.045501	29.518
Year (2020)	0.886447	0.076397	11.603
Year (2021)	0.425510	0.077564	5.486
Year (2022)	−0.181811	0.082213	−2.211
Smooth terms	edf	Ref. df	*F*
DOY by sex (female)	7.728	8.390	83.107
DOY by sex (male)	6.829	7.468	295.372
DOY by zone (inner bay)	7.466	7.892	604.211
DOY by zone (outer bay)	1.003	1.003	20.502
DOY by year (2019)	1.000	1.000	8.188
DOY by year (2020)	7.889	8.533	70.404
DOY by year (2021)	8.177	8.702	86.548
DOY by year (2022)	6.638	7.576	54.919
Temperature by sex (female)	4.723	5.848	14.345
Temperature by sex (male)	3.911	4.900	13.059

Table 5. Results of best-fit GAMM predicting mean detections per *G. unami* individual present per hour in Santa Elena Bay from 2019 to 2022. Model uses a Gaussian error distribution and had an adjusted R^2 of 0.18 and 18.2% of the deviance explained

Parametric terms	Estimate	SE	*t*
(Intercept)	2.850	1.390	2.040
Smooth terms	edf	Ref. df	*F*
Hour by Zone (Inner Bay)	0.204	0.268	0.004
Hour by Zone (Outer Bay)	6.915	7.941	15.49
Hour by Season (Non-Upwelling)	8.124	8.740	8.015
Hour by Season (Upwelling)	3.659	4.498	4.41
Temperature by Zone (Inner Bay)	1.000	1.000	9.79
Temperature by Zone (Outer Bay)	8.253	8.777	25.285
Temperature by Season (Non-Upwelling)	5.591	6.136	29.61
Temperature by Season (Upwelling)	7.202	7.771	30.02
Random effects	edf	Ref. df	*F*
Year	2.997	3.000	1772.44
Month	4.999	5.000	8301.34
Station	10.972	11.000	1013.425

conditions, providing a unique opportunity to unravel the behavioral movement patterns of *G. unami*.

4.1. Site fidelity to Santa Elena Bay during upwelling months

As ectotherms, *G. unami* individuals may behaviorally thermoregulate by moving to microhabitats where more energetically suitable temperatures are available (Fitzgerald & Nelson 2011, Spurgeon et al. 2022). The probability of detecting *G. unami* in Santa Elena Bay was higher on days with water temperatures below 20°C and high wind speeds (up to 20 m s^{-1}), which typically occurred during the upwelling season. Additionally, *G. unami* individuals showed higher detections per hour in the outer bay during the upwelling season when temperatures were between 18° and 20°C, spending considerably more time here than in the inner bay. During the non-upwelling season, when water temperatures were warmer than 25°C, more detections were observed in the inner bay, with sharks spending less time at the outer bay at these temperatures. *G. unami* may use the outer bay less frequently and spend more time in the inner bay when available waters are warmer and the outer bay no longer provides thermal benefits over the inner bay (Matern et al. 2000, Hight & Lowe 2007, Papastamatiou et al. 2015).

The shallow, sun-exposed waters of the outer bay and its geographic position (facing the incoming trade winds) possibly warm up faster due to solar warming of the substrata, forming pockets of warmer water that provide a temporary thermal benefit (Hight & Lowe 2007, Papastamatiou et al. 2015, Madrigal-Mora et al. preprint doi:10.2139/ssrn.4956621). A study with unoccupied aerial vehicle (drone) surveys and *in situ* temperature loggers deployed in higher density found evidence that these pockets provide refuge to *G. unami* from the cooler waters in other

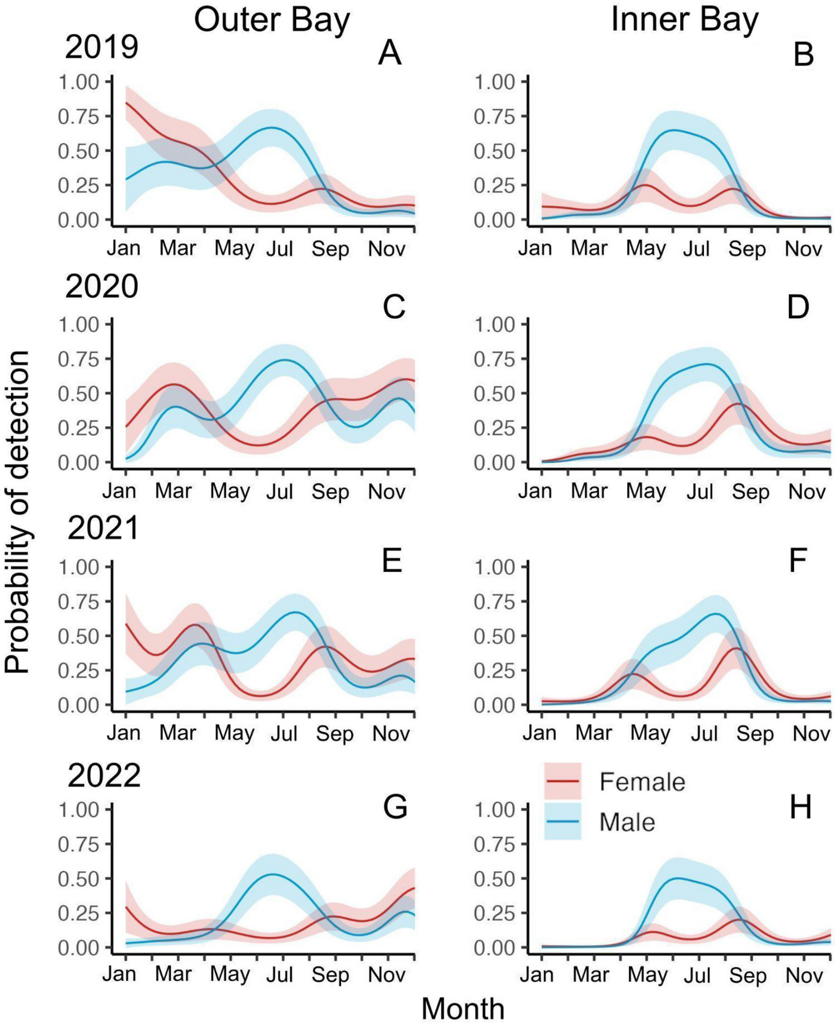

Fig. 3. Detection probability of male and female *G. unami* from 2019–2022 in the (A), (C), (E), and (G) outer and (B), (D), (F), and (H) inner regions of Santa Elena Bay, Costa Rica, predicted by a generalized additive mixed model (GAMM)

areas of the bay during upwelling season (Madrigal-Mora et al. preprint doi:10.2139/ssrn.4956621). These warmer-water pockets may not be reflected in the coarser-scale measurements of average water temperature from the limited number of temperature loggers used for this study, as they occur at finer scales in the outer bay's shallow waters (Madrigal-Mora et al. preprint doi:10.2139/ssrn.4956621). The higher detection probability of *G. unami* at lower temperatures is contradictory to studies on *G. cirratum*, which are known to select habitats with temperatures above 25° but not higher than 30°C (Ferreira et al. 2013). This is likely due to the distinct conditions of the seasonal upwelling that the *G. unami* in this study are exposed to as opposed to the more seasonally stable environments where *G. cirratum* have been studied.

As they sought warmer pockets of water in these shallow areas, sharks of both sexes were likely to be detected in the outer bay during the upwelling season, when water temperatures are generally colder (Alfaro & Cortés 2012). Yet females had a higher probability of detection than males during the upwelling season. Females may be more selective than males in their thermal preferences, as optimal temperatures can make reproductive processes more efficient (Hight & Lowe 2007, Jirik & Lowe 2012). For example, in other elasmobranchs such as the spotted eagle ray *Aetobatus narinari* and the round stingray *Urobatis halleri*, females have been shown to have shorter gestation periods at optimal water temperatures (Jirik & Lowe 2012, Swider et al. 2017). Furthermore, leopard shark *Triakis semifasciata* females are more selective of temperatures than males, forming aggregations in warmer shallow waters (Hight & Lowe 2007, Nosal et al. 2014).

4.2. Diel patterns in habitat use

G. unami showed diel patterns in which they spent more time in the inner bay during the day and showed more detections in the outer bay during late night. The diel detection patterns are not likely a response to hourly temperature changes, since we found that water temperatures did not vary significantly throughout diel periods. However, the outer bay was consistently warmer than the inner bay; hence, the pockets of water *G. unami* use in the outer bay are warmed by the sun during the day and remain warm through the night because of the slow circulation of Santa Elena Bay (Tisseaux-Navarro et al. 2021). Warmer temperatures resulting from solar warming might not persist in the shallow areas of the inner bay because various creeks carry cooler freshwater into this zone. *G. unami* do not show a preference for a thermal refuge during the day as they spend more time in the colder inner bay during these hours but remain for longer periods of time in the warmer outer bay at night.

These patterns may indicate that *G. unami* has varying thermal requirements for different behaviors

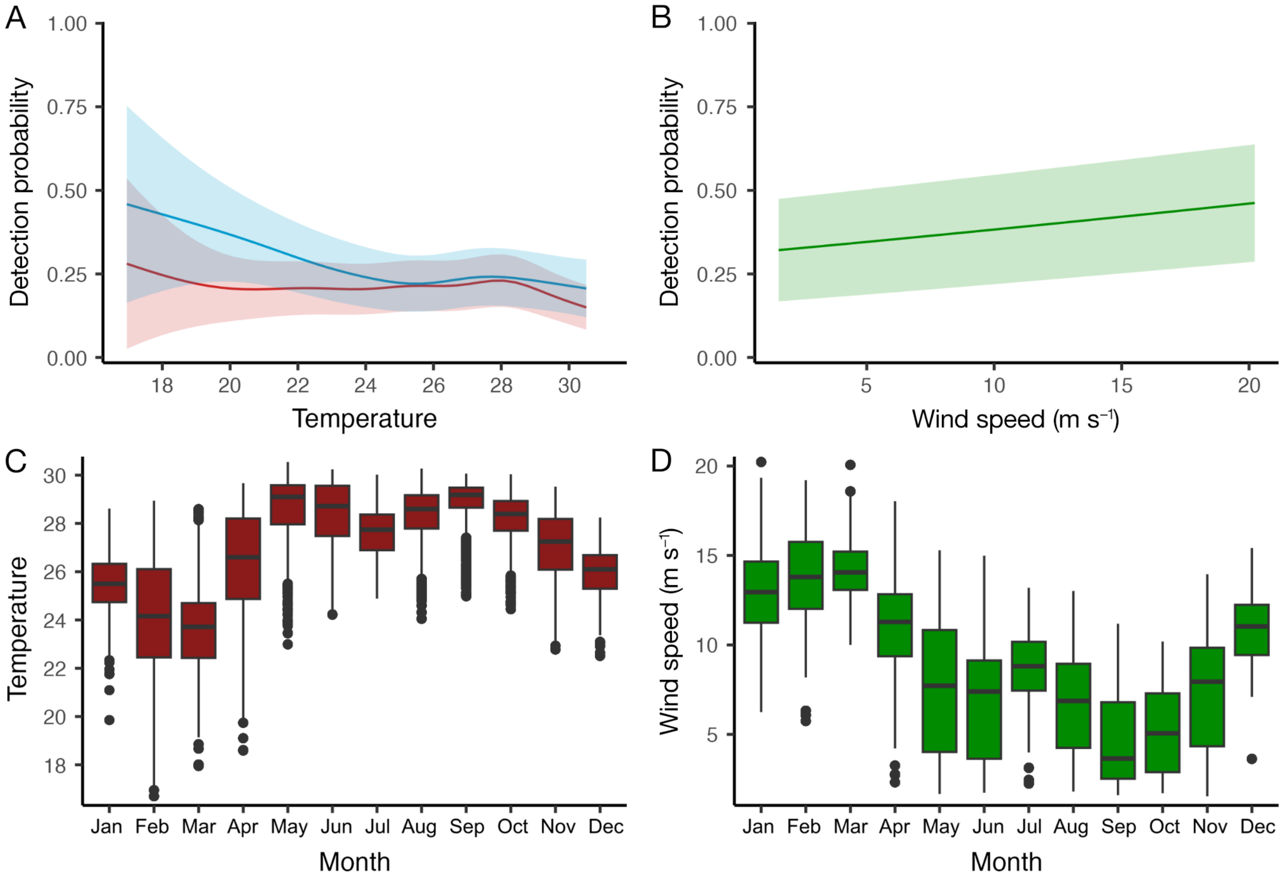

Fig. 4. Effect of (A) water temperature (°C) and (B) regional wind speed, a metric for upwelling, on detection probability of male and female *G. unami* in Santa Elena Bay, Costa Rica, predicted by a GAMM and (C) mean daily water temperature (°C) and (D) mean daily wind speed per month, using data from 2019–2022. Horizontal line in box: median; top and bottom of box: 25th and 75th percentiles; whiskers: 10th and 90th percentiles; black dots: outliers

throughout diel periods (Meese & Lowe 2020). Behavioral thermoregulatory strategies have been described in elasmobranchs where some species rest at water temperatures warmer than where they forage to improve digestion efficiency (i.e. blacktip reef sharks *Carcharhinus melanopterus*, Papastamatiou et al. 2015; California horn sharks *Heterodontus francisci*, Meese & Lowe 2020). Species like *H. francisci* have been found to tolerate less suitable water temperatures in order to forage in areas known to have profitable and predictable prey availability (Meese & Lowe 2020). *G. unami* may display similar behavior of foraging in the less thermally suitable waters of the inner bay during the day, returning to the outer bay at night to rest in the warmer waters available in this zone. Even though waters throughout the bay are significantly warmer in the non-upwelling season, these diel patterns persist, albeit with less variation in detections between day and night. It is possible that some *G. unami* may still use the outer bay as a known central refuging point to aid with navigation to other areas, even when there are no thermal benefits, as has been observed for scalloped hammerhead sharks (Klimley & Nelson 1984, Hearn et al. 2010) and *C. melanopterus* (Papastamatiou et al. 2018).

4.3. Midyear variation probability of detection between males and females

As the dry season ended (late April to early May), the probability of detecting male *G. unami* peaked throughout the bay. Between June and July, male sharks appear to use the inner and outer bay with similar frequency, suggesting that the outer bay no longer provides the thermal benefits that were available to sharks during upwelling. Upwelling events during the dry season can have a bottom-up effect, increasing the primary productivity in the area (Stuhldreier et al. 2015); therefore, the increase in male

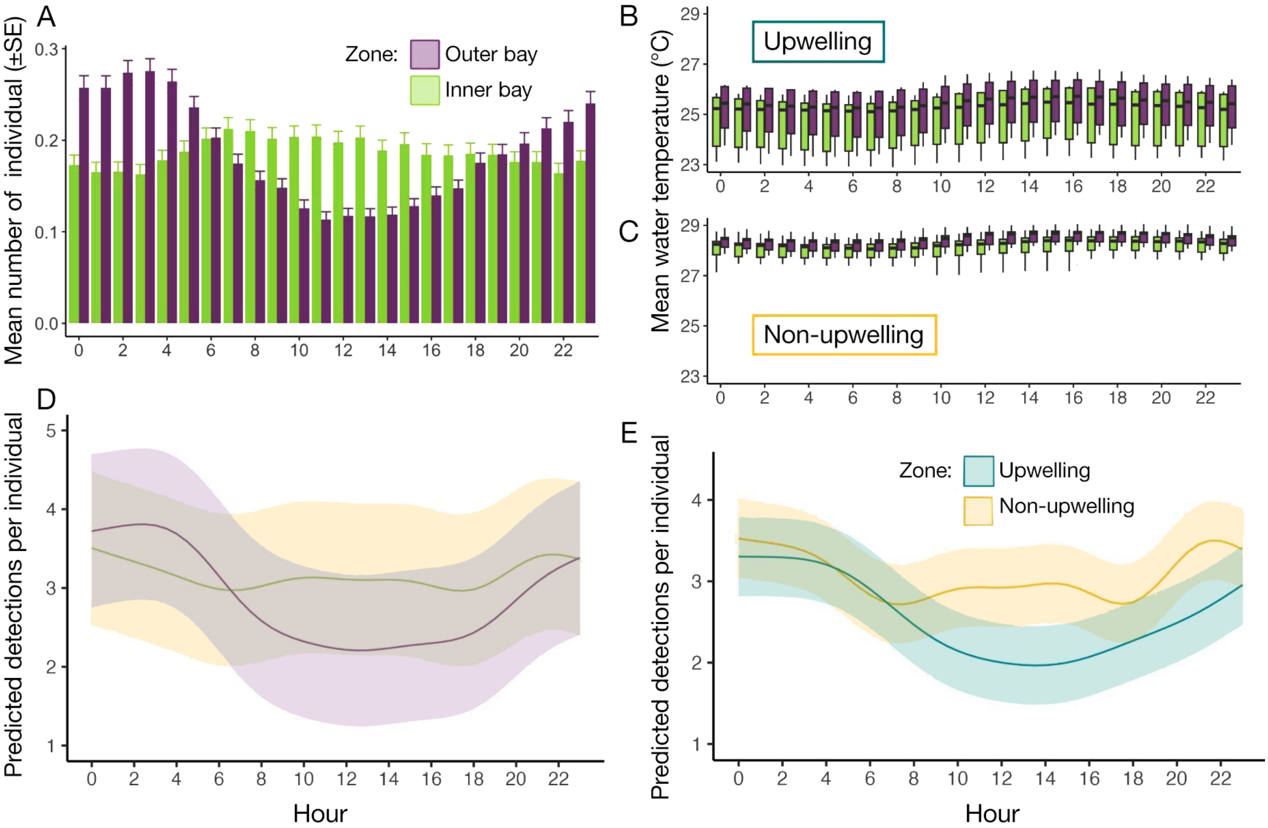

Fig. 5. Diel patterns in (A) number of acoustically tagged *G. unami* detected per hour in 2 zones (inner and outer bay) of Santa Elena Bay, Costa Rica. Mean hourly water temperature available throughout the day in the 2 zones of the Bay during the (B) upwelling (December to April) and (C) non-upwelling seasons (May to November). GAMM predictions for mean detections per individual present per hour in (D) the 2 zones of Santa Elena Bay and (E) during the upwelling (December to April) and non-upwelling seasons (May to November)

detections may be associated with prey availability remaining after the upwelling season combined with the generally warmer waters now available. Concurrently, the probability of detecting females decreased significantly in the outer bay and remained low in the inner bay. During this time, the outer bay may no longer function as a warmer water refuge for females as wind speeds decrease and water temperature rises again throughout the region. Females may also be mostly absent at this point due to male avoidance during these months of high male presence, returning after the decrease in male detections after August (observed in 2020 and 2022). Female avoidance of males has been reported for *G. cirratum* in the Atlantic, where sexual segregation occurs throughout the year except for the breeding season (Afonso et al. 2016). So far, *G. unami* courtship behavior has not been observed in Santa Elena Bay, and the breeding season has not been reported for the species anywhere in its distribution. Since the early months of the year are the only period during which high detections of males and females coincide, courtship and reproduction may be playing an important role in patterns of site fidelity (Afonso et al. 2016, Pratt et al. 2022).

4.4. Influence of other environmental factors

The selected GAMMs for probability of detection by DOY and number of sharks per hour explained only 27 and 21% of the variance, respectively, suggesting that factors that were not considered in our study may influence the behavior and long-term patterns of *G. unami* occurrence in Santa Elena Bay. The model found variation between years, which could be a result of some unmeasured environmental conditions that changed through the study period. The pattern in detection probability observed during 2019, 2020, and 2021 was not evident in 2022. This year had the lowest overall probability of detection, which could be associated with the frequent occurrence of algal blooms (red tides) inside the bay during

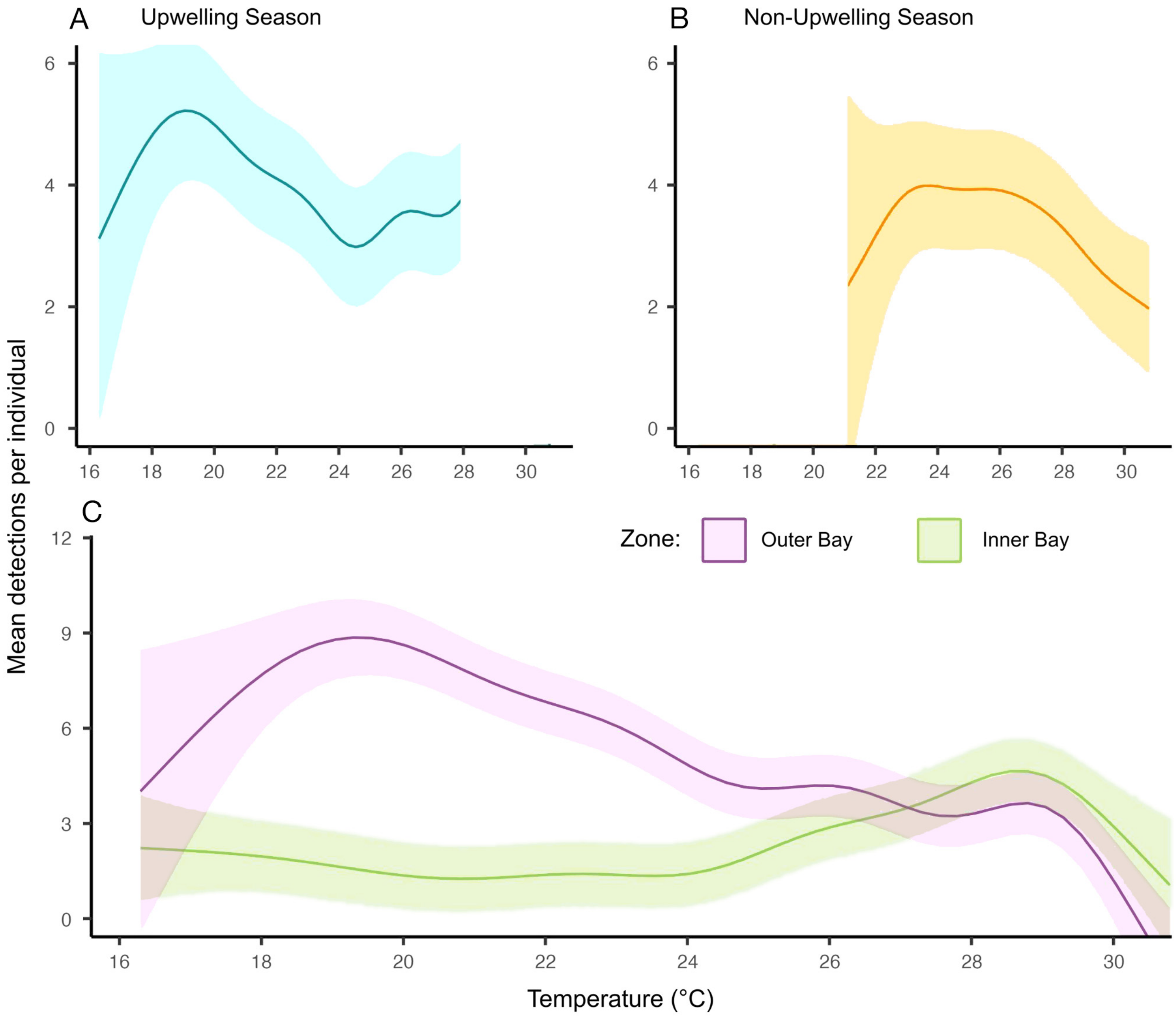

Fig. 6. GAMM predictions for the effect of water temperature on mean detections per *G. unami* individual present per hour during the (A) upwelling (December to April) and (B) non-upwelling seasons (May to November) and (C) 2 zones (inner and outer bay) of Santa Elena Bay, Costa Rica

2022 (M. Lara pers. comm.). Algal blooms have been studied in other areas of the Costa Rican Pacific (Gulf of Nicoya, Gulf of Papagayo, Caño Island), yet the causes of these blooms in these areas are poorly understood and have not been studied in Santa Elena Bay (Hargraves & Víquez 1981, Gocke et al. 1990). The low detection probability of *G. unami* in 2022 may have been associated with large algal bloom events, as they are known to drastically reduce dissolved oxygen concentrations in the affected areas (Gocke et al. 1990). In other regions, such as the Gulf of Mexico, seasonal red tides and hypoxic conditions can influence the distribution of demersal fish that seek adjacent waters with suitable oxygen levels (Craig et al. 2001, Driggers et al. 2016). In areas also subjected to seasonal upwelling, such as the Gulf of Oman, pronounced red tide events are correlated with periods of strong upwelling, although these also occur outside of the upwelling season (Al Gheilani et al. 2011), hence upwelling may intensify this phenomenon in Santa Elena Bay as well. The observation of red tides in Santa Elena Bay coincided with periods of the lowest probability of detection early in 2022.

Although variation between individuals was included as a random effect in the model, some unexplained variance may still be related to the high individual variation in shark movement. Variation between the propensity of dispersal of different individuals within a population is commonly observed in many species of fish (Dodson et al. 2013, Gillanders et al. 2015), including bull sharks *Carcharhinus leucas* (Matich & Heithaus 2015) and Australian blacktip sharks *Carcharhinus tilstoni* (Munroe et al. 2016). Both resident and transient individuals may be present within a population, where more transient movement patterns may be beneficial by increasing access to prey items or accessibility to mates (Matich & Heithaus 2015, Munroe et al. 2016), while residents ensure greater chances of survival by avoiding the risks of travel and reducing energetic costs of movement if other areas are more devoid of resources (Dodson et al. 2013).

4.5. Forays outside Santa Elena Bay MMA

This is the first study to describe annual patterns and quantify the effects of changing environmental conditions on the site fidelity of *G. unami*, yet the extent and frequency with which these sharks move beyond Santa Elena Bay is still poorly understood. Although at least one tagged shark was detected in the bay on 88% of the days of our study, these were generally not the same individuals. When examining the detections of each tagged shark, we found that, on average, individuals were present in the bay less than half of the days monitored (37%), indicating that they frequently exit the boundaries of the MMA. A previous study showed that a single *G. unami* tagged in Santa Elena Bay could travel over 200 km along the north Pacific coast of Costa Rica before returning to the bay (Madrigal-Mora et al. 2024). Though *G. unami* is not directly targeted by artisanal fisheries in Costa Rica, they are occasionally caught as bycatch in gillnets, as individuals with fishing nets tangled on their fins and dead juveniles have been occasionally found by recreational divers in the Gulf of Santa Elena (M. Lara pers. comm.).

Frequent forays outside Santa Elena Bay expose *G. unami* to these risks and suggest that relatively small and isolated MMAs such as Santa Elena Bay are likely ineffective for the conservation of mobile species like this one, particularly in regions subjected to stronger fishing pressure (Pollom et al. 2021).

4.6. Potential influence of climate change

Climate change is expected to warm ocean waters and alter regional patterns of upwelling (Sydeman et al. 2014, Johnson & Lyman 2020). We expect warming ocean waters to reduce the amount of time *G. unami* individuals spend inside the MMA during the non-upwelling season (Caughman et al. 2024), as our data shows that the sharks are less likely to visit the bay when water temperatures are at or above 30°C. On the other hand, strengthening trade winds are likely to intensify upwelling events, increasing the surface water cooling that occurs in this region during the upwelling season (Sydeman et al. 2014, Latif et al. 2023). With an increasing necessity to behaviorally thermoregulate during colder and more intense upwelling events, we expect that *G. unami* will visit Santa Elena Bay more frequently during the upwelling season. During the non-upwelling season, sharks may spend less time in the MMA, leaving for deeper waters or higher latitudes when waters get too warm (Latif et al. 2023, Caughman et al. 2024). These trends suggest that other ectothermic elasmobranchs could also use tropical upwelling regions as thermal refuges in warming oceans, as has been suggested for mobile fish species (Angeles-Gonzalez et al. 2024) as well as sessile invertebrates such as corals (Randall et al. 2020).

5. CONCLUSIONS

Santa Elena Bay MMA is located within the Gulf of Santa Elena, a larger region that was recently identified by the IUCN Shark Specialist Group as an IUCN ISRA; hence, we provide a fundamental baseline for informing management and spatial planning strategies for this ISRA (Jabado et al. 2023). Additionally, the minimal fishing pressure experienced by *Ginglymostoma unami* in the north Pacific coast of Costa Rica allows us to study a practically undisturbed population without substantial interference from the anthropogenic factors (e.g. fishing or habitat degradation) that are prevalent throughout its restricted distribution range, yielding valuable insights to inform management and conservation (Pollom et al. 2021).

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LITERATURE CITED

Afonso AS, Cantareli CV, Levy RP, Veras LB (2016) Evasive mating behaviour by female nurse sharks, *Ginglymostoma cirratum* (Bonnaterre, 1788), in an equatorial insular breeding ground. Neotrop Ichthyol 14:e160103

Al Gheilani HM, Matsuoka K, AlKindi AY, Amer S, Waring C (2011) Fish kill incidents and harmful algal blooms in Omani waters. J Agric Mar Sci 16:23–33

Alfaro EJ, Cortés J (2021) Forzamiento de los eventos cálidos y fríos del agua subsuperficial del mar en Bahía Salinas, Costa Rica. Rev Biol Trop 69(Suppl 2):127–127

Anderson JM, Burns ES, Meese EN, Farrugia TJ and others (2021) Interannual nearshore habitat use of young of the year white sharks off Southern California. Front Mar Sci 8:645142

Angeles-Gonzalez LE, Torrejón-Magallanes J, Escamilla-Aké A, Osorio-Olvera L, Avendaño O, Díaz F, Rosas C (2024) Can upwelling regions be potential thermal refugia for marine fishes during climate warming? J Therm Biol 123:103893

Cárdenas-Palomo N, Herrera-Silveira J, Velázquez-Abunader I, Reyes O, Ordoñez U (2015) Distribution and feeding habitat characterization of whale sharks *Rhincodon typus* in a protected area in the north Caribbean Sea. J Fish Biol 86:668–686

Carlson J, Charvet P, Blanco-Parra MP, Briones Bell-lloch A and others (2021) *Ginglymostoma cirratum*. The IUCN Red List of Threatened Species 2021: eT144141186A3095153. https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T144141186A3095153.en

Castro JI (2000) The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahama Islands. Environ Biol Fishes 58:1–22

Caughman AM, Gaines SD, Bradley D (2024) Climate change reduces long-term population benefits from no-take marine protected areas through selective pressures on species movement. Glob Change Biol 30:e17240

Chapman DD, Feldheim KA, Papastamatiou YP, Hueter RE (2015) There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. Annu Rev Mar Sci 7: 547–570

Clarke TM, Espinoza M, Ahrens R, Wehrtmann IS (2016) Elasmobranch bycatch associated with the shrimp trawl fishery off the Pacific coast of Costa Rica, Central America. Fish Bull 114:1–17

Cortés J (1996) Comunidades coralinas y arrecifes del Área de Conservación Guanacaste, Costa Rica. Rev Biol Trop 44:623–625

Cortés J (2016) The Pacific coastal and marine ecosystems. In: Kappelle M (ed) Costa Rican ecosystems. University of Chicago Press, Chicago, IL, p 97–138

Craig JK, Crowder LB, Gray CD, McDaniel CJ, Kenwood TA, Hanifen JG (2001) Ecological effects of hypoxia on fish, sea turtles, and marine mammals in the northwestern Gulf of Mexico. In: Rabalais NN, Turner RE (eds) Coastal hypoxia: consequences for living resources and ecosystems. Coastal and Estuarine Studies, Vol 58. American Geophysical Union, Washington, DC, p 269–291

Del Moral-Flores LF, Ramírez-Antonio E, Angulo A, León G (2015) *Ginglymostoma unami* sp. nov. (Chondrichthyes: Orectolobiformes: Ginglymostomatidae) una nueva especie de tiburón gata del Pacífico oriental tropical. Rev Mex Biodivers 86:48–58

Diaz-Carballido PL, Mendoza-González G, Yañez-Arenas CA, Chiappa-Carrara X (2022) Evaluation of shifts in the potential future distributions of carcharhinid sharks under different climate change scenarios. Front Mar Sci 8:745501

Dodson JJ, Aubin-Horth N, Thériault V, Páez DJ (2013) The evolutionary ecology of alternative migratory tactics in salmonid fishes. Biol Rev Camb Philos Soc 88:602–625

Doherty PD, Baxter JM, Gell FR, Godley BJ and others (2017) Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the northeast Atlantic. Sci Rep 7:42837

Driggers WB III, Campbell MD, Debose AJ, Hannan KM, Hendon MD, Martin TL, Nichols CC (2016) Environmental conditions and catch rates of predatory fishes associated with a mass mortality on the West Florida Shelf. Estuar Coast Shelf Sci 168:40–49

Eisele MH, Madrigal-Mora S, Espinoza M (2021) Drivers of reef fish assemblages in an upwelling region from the Eastern Tropical Pacific Ocean. J Fish Biol 98:1074–1090

Espinoza M, Arias-Zumbado F, Chaves-Zamora I, Farías-Tafolla B (2022) Comparación de cuatro métodos para contar peces en una bahía tropical: el caso del Área Marina de Manejo Bahía Santa Elena en el Pacífico de Costa Rica. Rev Biol Trop 70:235–249

Ferreira LC, Afonso AS, Castilho PC, Hazin FH (2013) Habitat use of the nurse shark, *Ginglymostoma cirratum*, off Recife, Northeast Brazil: a combined survey with longline and acoustic telemetry. Environ Biol Fishes 96:735–745

Fitzgerald LA, Nelson RE (2011) Thermal biology and temperature-based habitat selection in a large aquatic ectotherm, the alligator snapping turtle, *Macroclemys temminckii.* J Therm Biol 36:160–166

Gillanders BM, Izzo C, Doubleday ZA, Ye Q (2015) Partial migration: growth varies between resident and migratory fish. Biol Lett 11:20140850

Gocke K, Cortés J, Villalobos C (1990) Effects of red tides on oxygen concentration and distribution in the Golfo de Nicoya, Costa Rica. Rev Biol Trop 38:401–407

Gong AY, Nosal AP, Cartamil DP, Anderson JM and others (2023) Migration, aggregation, and philopatry of two nearshore elasmobranch species in the Southern California Bight. Mar Ecol Prog Ser 724:111–125

Hargraves PE, Víquez R (1981) The dinoflagellate red tide in Golfo de Nicoya, Costa Rica. Rev Biol Trop 29:31–38

Hearn A, Ketchum J, Klimley AP, Espinoza E, Penaherrera C (2010) Hotspots within hotspots? Hammerhead shark movements around Wolf Island, Galapagos marine reserve. Mar Biol 157:1899–1915

Hight BV, Lowe CG (2007) Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: evidence for behavioral thermoregulation? J Exp Mar Biol Ecol 352:114–128

Jabado RW, García-Rodríguez E, Kyne PM, Charles R and others (2023) Central and South American Pacific: a regional compendium of important shark and ray areas. IUCN SSC Shark Specialist Group, Dubai

Jirik KE, Lowe CG (2012) An elasmobranch maternity ward: female round stingrays *Urobatis halleri* use warm, restored estuarine habitat during gestation. J Fish Biol 80:1227–1245

Johnson GC, Lyman JM (2020) Warming trends increasingly dominate global ocean. Nat Clim Chang 10:757–761

Jones MC, Dye SR, Fernandes JA, Frölicher TL, Pinnegar JK, Warren R, Cheung WW (2013) Predicting the impact of climate change on threatened species in UK waters. PLOS ONE 8:e54216

Klimley AP, Nelson DR (1984) Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central-position social system. Behav Ecol Sociobiol 15:45–54

Latif M, Bayr T, Kjellsson J, Lübbecke JF and others (2023) Strengthening atmospheric circulation and trade winds slowed tropical Pacific surface warming. Commun Earth Environ 4:249

Lear KO, Whitney NM, Brewster LR, Morris JJ, Hueter RE, Gleiss AC (2017) Correlations of metabolic rate and body acceleration in three species of coastal sharks under contrasting temperature regimes. J Exp Biol 220:397–407

Logan RK, Vaudo JJ, Sousa LL, Sampson M, Wetherbee BM, Shivji MS (2020) Seasonal movements and habitat use of juvenile smooth hammerhead sharks in the western North Atlantic Ocean and significance for management. Front Mar Sci 7:566364

López-Garro A, Zanella I (2015) Sharks and rays caught by artisanal bottom line in Golfo Dulce, Costa Rica. Rev Biol Trop 63:183–198

Madrigal-Mora S, Chávez EJ, Arauz R, Lowe CG, Espinoza M (2024) Long-distance dispersal of the endangered Pacific nurse shark (*Ginglymostoma unami*, Orectolobiformes) in Costa Rica revealed through acoustic telemetry. Mar Freshw Res 75:MF23162

Matern SA, Cech JJ, Hopkins TE (2000) Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: evidence for behavioral thermoregulation? Environ Biol Fishes 58:173–182

Matich P, Heithaus MR (2015) Individual variation in ontogenetic niche shifts in habitat use and movement patterns of a large estuarine predator (*Carcharhinus leucas*). Oecologia 178:347–359

Matthiopoulos J, Harwood J, Thomas LEN (2005) Metapopulation consequences of site fidelity for colonially breeding mammals and birds. J Anim Ecol 74:716–727

Meese EN, Lowe CG (2020) Active acoustic telemetry tracking and tri-axial accelerometers reveal fine-scale movement strategies of a non-obligate ram ventilator. Mov Ecol 8:8

Munroe SEM, Simpfendorfer CA, Heupel MR (2016) Variation in blacktip shark movement patterns in a tropical coastal bay. Environ Biol Fishes 99:377–389

Nosal AP, Caillat A, Kisfaludy EK, Royer MA, Wegner NC (2014) Aggregation behavior and seasonal philopatry in male and female leopard sharks *Triakis semifasciata* along the open coast of southern California, USA. Mar Ecol Prog Ser 499:157–175

O'Dea A, Hoyos N, Rodríguez F, Degracia B, Gracia C (2012) History of upwelling in the Tropical Eastern Pacific and the paleogeography of the Isthmus of Panama. Palaeogeogr Palaeoclimatol Palaeoecol 348–349:59–66

Papastamatiou YP, Watanabe YY, Bradley D, Dee LE, Weng K, Lowe CG, Caselle JE (2015) Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? PLOS ONE 10:e0127807

Papastamatiou YP, Watanabe YY, Demšar U, Leos-Barajas V and others (2018) Activity seascapes highlight central place foraging strategies in marine predators that never stop swimming. Mov Ecol 6:9

Pollom R, Avalos C, Bizzarro J, Burgos-Vázquez MI and others (2021) *Ginglymostoma unami*. The IUCN Red List of Threatened Species 2021: e.T144151831A144151864. https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T144151831A144151864.en

Pratt HL Jr, Pratt TC, Knotek RJ, Carrier JC, Whitney NM (2022) Long-term use of a shark breeding ground: three decades of mating site fidelity in the nurse shark, *Ginglymostoma cirratum*. PLOS ONE 17:e0275323

R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Randall CJ, Toth LT, Leichter JJ, Maté JL, Aronson RB (2020) Upwelling buffers climate change impacts on coral reefs of the Eastern Tropical Pacific. Ecology 101:e02918

Ruiz-Castillo E, Gomez-Valdes J, Sheinbaum J, Rioja-Nieto R (2016) Wind-driven coastal upwelling and westward circulation in the Yucatan shelf. Cont Shelf Res 118:63–76

Ryan JP, Green JR, Espinoza E, Hearn AR (2017) Association of whale sharks (*Rhincodon typus*) with thermo-biological frontal systems of the eastern tropical Pacific. PLOS ONE 12:e0182599

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev Fish Biol Fish 24: 1089–1103

SINAC (Sistema Nacional de Áreas de Conservación) (2017) Plan General de Manejo del Sitio de Importancia para la Conservación Bahía Santa Elena. Área de Conservación Guanacaste, ACG. SINAC, San José

Spurgeon E, Anderson JM, Liu Y, Barajas VL, Lowe CG (2022) Quantifying thermal cues that initiate mass emigrations in juvenile white sharks. Sci Rep 12:19874

Stuhldreier I, Sánchez-Noguera C, Roth F, Cortés J, Rixen T, Wild C (2015) Upwelling increases net primary production of corals and reef-wide gross primary production along the Pacific coast of Costa Rica. Front Mar Sci 2:113

Swider DA, Corwin AL, Kamerman TY, Zimmerman SL, Violetta GC, Davis J, Janse M (2017) Reproduction of spotted eagle rays, *Aetobatus narinari*, in aquaria. In: Smith M, Warmolts D, Thoney D, Hueter R, Murray M, Ezurra J (eds) The elasmobranch husbandry manual II: recent advances in the care of sharks, rays and their relatives. Special publication of the Ohio Biological Survey, Columbus, OH, p 433–442

Sydeman WJ, García-Reyes M, Schoeman DS, Rykaczewski RR, Thompson SA, Black BA, Bograd SJ (2014) Climate change and wind intensification in coastal upwelling ecosystems. Science 345:77–80

Tisseaux-Navarro A, Salazar-Ceciliano JP, Cambronero-Solano S, Vargas-Hernández JM, Marquez X (2021) Reverse circulation in Bahía Santa Elena, North Pacific of Costa Rica. Reg Stud Mar Sci 43:101671

Villalobos-Rojas F, Herrera-Correal J, Garita-Alvarado CA, Clarke T, Beita-Jiménez A (2014) Actividades pesqueras dependientes de la ictiofauna en el Pacífico Norte de Costa Rica. Rev Biol Trop 62:119–137

Vilmar M, Di Santo V (2022) Swimming performance of sharks and rays under climate change. Rev Fish Biol Fish 32:765–781

Whitney NM, Lear KO, Gaskins LC, Gleiss AC (2016) The effects of temperature and swimming speed on the metabolic rate of the nurse shark (*Ginglymostoma cirratum*, Bonaterre). J Exp Mar Biol Ecol 477:40–46

Wiley TR, Simpfendorfer CA (2007) The ecology of elasmobranchs occurring in the Everglades National Park, Florida: implications for conservation and management. Bull Mar Sci 80:171–189

Wood SN (2017) Generalized additive models: an introduction with R, 2nd edn. Chapman and Hall, Boca Raton, FL

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