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Distribution of the Pacific stingray (*Styracura pacifica*) in the Térraba River Mouth, Térraba Sierpe National Wetland, Pacific of Costa Rica

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Coastal wetlands are vital habitats for elasmobranchs, yet the spatial ecology of many species remains poorly understood, hindering effective conservation. The Pacific chupare ray, *Styracura pacifica*, listed as Vulnerable by the IUCN, is one such data-poor species with virtually unknown feeding habits and limited ecological data. This study aimed to address the spatial ecology of *S. pacifica* within the Térraba-Sierpe National Wetland (HNTS), Costa Rica, providing baseline data for management. We employed a participatory science framework, integrating Local Ecological Knowledge (LEK) from artisanal fishers with over 15 years of experience in the area, to identify key sampling sites in the main river channel and intertidal sand flat pools. Data were collected between 2022 and 2023 using floating longlines and modified cast nets. For each captured ray, sex and disc width (DW) were recorded, alongside environmental variables like temperature and precipitation. Due to non-normal catch per unit effort (CPUE) distributions, non-parametric analyses were applied. Relationships between CPUE, disc width (DW), and environmental variables were assessed using Spearman correlations, and differences between ecosystems, years, and groups were evaluated using a rank-based test. A total of 66 individuals were captured across both habitats. Captures were exclusively composed of immature individuals, with significantly smaller DWs recorded in intertidal pools (19.6–37 cm DW) compared to the main channel (31–55.7 cm DW), confirming strong size-based habitat segregation. CPUE was significantly and inversely correlated with temperature in the main channel and with rainfall in the intertidal pools, suggesting dynamic shifts in

distribution linked to local environmental conditions. Our findings provide empirical evidence that the HNTS functions as a crucial nursery system for juvenile *S. pacifica*. The observed sensitivity to temperature and rainfall highlights the vulnerability of these life stages to climate-driven habitat instability. Methodologies that allow us to track individuals and their movements, adapted to small-sized rays, are recommended for a better understanding of habitat use.

KEYWORDS

elasmobranch, estuary, local ecological knowledge, nursery, sand flat, wetland

Introduction

Costa Rica is a global elasmobranch hotspot, hosting approximately 100 species of sharks and rays, which represents 8% of the world's total diversity (1). Despite this rich diversity, 15% of these species are currently listed as threatened by the International Union for Conservation of Nature (IUCN) (1). Understanding the ontogenic variation at the spatial ecology of elasmobranchs, including their residency, site fidelity, space use, and migratory behaviors, is crucial for assessing their overlap with fishing activities and for developing effective conservation strategies (2, 3).

Shallow marine environments, such as intertidal zones, are highly dynamic, and habitat selection within them is influenced by a combination of physical factors, including temperature, tidal flow, and salinity, as well as biological processes like predation risk and prey availability (4–6). The influence of these factors can vary across different temporal scales, from large-scale seasonal to smaller-scale diel and tidal cycles (e.g., nocturnal habitat shifts or high-tide movements) (7, 8).

Intertidal zones often serve as critical nursery grounds, with studies documenting the presence of neonates, juveniles, and pregnant females in coastal sandbanks (9); the correlation of egg density with sandy, muddy, or rocky substrates for oviparous species (10–12); and high abundances of juveniles in reef lagoons with soft sediments (13).

Studies confirm habitat use segregation, often based on ontogeny (14–16). For instance, a study on the Caribbean Whiptail Stingray (*Styracura schmardae* (Werner, 1904)) found juveniles concentrate in shallow margins, creek mouths, and floodplain lakes, whereas adults are more frequently in deeper channels, central troughs, or more exposed foraging areas; some species forage in channel margins while adults occupy central troughs (17). This pattern is further supported by a particularly evident behavior during high tides, when water depths reach up to 2 meters, when stingrays use shallow sand flats to mitigate predation risk from sharks (18, 19). Sand flats are intertidal coastal ecosystems characterized by fine to medium-grained quartz sand, often situated between mangrove fringes and seagrass beds. At low tide, these flats may feature water-retaining depressions, such as those created by stingray feeding, which can serve as the soft-shore equivalent of hard-shore rockpools (20, 21).

The Térraba-Sierpe National Wetland (HNTS) in Costa Rica has been protected since March 1994, and it is a vital habitat for a

diverse elasmobranch community (22). The area's main economic activity is small-scale artisanal fishing (23). Studies have identified 15 elasmobranch species within the HNTS, with the scalloped hammerhead shark (*Sphyrna lewini* (Griffith & Smith, 1834)) (29%), the Pacific round stingray (*Urotrygon aspidura* (Jordan & Gilbert, 1882)) (19%), and the Pacific chupare ray (*Styracura pacifica* (Beebe & Tee-Van, 1941)) (16%) being the most abundant species in fisheries interactions (24). It's not a fisherman's target species. While *S. pacifica* has been recorded in shallow, muddy habitats along the Pacific coast of Central America (25), specific ecological information remains limited, with recent studies reporting only incidental catches (26).

Despite the Superorder Batoidea comprising a diverse group of elasmobranchs, the vast majority of ecological research has been heavily skewed towards trophic ecology, having extensively documented the diets of 198 ray species. However, this established dietary understanding stands in stark contrast to the significant gaps that remain concerning their true impact on marine systems, particularly for lesser-studied species (15). Specifically, *S. pacifica*, listed as Vulnerable (VU) by the IUCN, epitomizes this knowledge deficit; despite the broad literature on ray diets, the feeding habits of *S. pacifica* itself are still virtually unknown. Therefore, to move beyond simple food web characterization and fully integrate this ecologically important, yet data-poor, species into our models of marine community dynamics, the urgency to address not only the critical questions of how its behavioral ecology influences predator-prey interactions, how its bioturbation affects infaunal communities, and its role in trophic cascades, but must first establish baseline knowledge.

S. pacifica is distributed along the Eastern Pacific coast, ranging from Mexico (e.g., Acapulco Bay) to Panama, with its southern limit confirmed off the Chocó coast of Colombia (26–28). Despite this known range, ecological knowledge of *S. pacifica* remains severely limited. By contrast, a congeneric study on the Atlantic member, *S. schmardae*, revealed long-term site fidelity to mangrove creek systems, which serve as a possible 1 nursery habitats, with over 95% of individuals captured being immature (17). The profound implications of such habitat use for conservation underscore the urgent need to define the spatial ecology of its Pacific counterpart. Therefore, the present study, conducted between 2021 and 2023, focuses on understanding how *S. pacifica* utilizes the HNTS, aiming to fill key knowledge gaps regarding the species' spatial ecology and contribute foundational data for the development of effective conservation strategies.

Materials and methods

Study site

The Térraba-Sierpe National Wetland (HNTS), situated in Costa Rica's South Pacific region, encompasses 16,700 hectares and harbors the largest mangrove ecosystem in Central America (29) (Figure 1). Within this system, *Rhizophora racemosa* and *Pelliciera rhizophorae* are the most spatially extensive or continuously distributed mangrove species, covering 7,670 ha and 5,824 ha, respectively. The substrate supporting the various mangrove species within the HNTS is classified into five textural types based on granulometry, ranging from finest to coarsest: mud, sandy mud, sand, muddy sand, and gravelly mud. Mud and sandy mud substrates collectively constitute 49% and 39% of the HNTS estuarine sector's area (30).

The specific study area was the lower estuarine section of the Térraba River (9°3.841'N, 83°39.151'W) within the HNTS. This area is characterized by an exceptionally high mean annual rainfall of 4,000 mm, with the wettest period occurring in September and October, contributing approximately 13% and 19%, respectively, of the average annual precipitation; correspondingly, the river's discharge fluctuates significantly, ranging between 60 m³/s and 230 m³/s (31). While historically a relatively stable estuarine system sustained by substantial sediment deposition from the Térraba River, the HNTS is currently experiencing pronounced degradation driven by the synergistic effects of sea-level rise and regional tectonic activity (32). The adjacent human communities rely on primary economic activities, including artisanal fishing, extraction of *Anadara*

species mollusks, shrimp aquaculture, and extensive agriculture, further compounding the anthropogenic pressures on this ecosystem (33). Sampling was conducted throughout 2022 and 2023, encompassing the wet, dry, and inter-seasonal periods. Effort was maximized to ensure as many sampling events as possible within each season to capture the temporal variability of the species' occurrence.

Habitat and capture

We employed a participatory science framework that integrated Local Ecological Knowledge (LEK) from artisanal fishers with over 15 years of experience (34). This collaboration identified two key ray aggregation zones: the main river channel and intertidal sand flat tide pools at the river mouth, and also suggested using different sampling gears for each zone, considering the depth. For the deep, fast-flowing main channel, a floating longline with 50 hooks was deployed. In the first year (2022), we used size 6 J-type hooks, while in the second year (2023), we switched to size 7 and 8 circular hooks to minimize harm in captured individuals (35). To avoid bias, we did not standardize or compare CPUE between years (36).

Local fishers reported that stingrays frequently aggregate within intertidal pool formations during low tide. These pools are characterized by highly irregular topography and dynamic depth fluctuations driven by tidal cycles, rendering traditional longline fishing gear unsuitable for sampling. Considering that, the fishers advised adopting another conventional harvesting method: cast nets. This gear is particularly well-suited for these shallow, complex environments, as it does not require significant water-column depth for

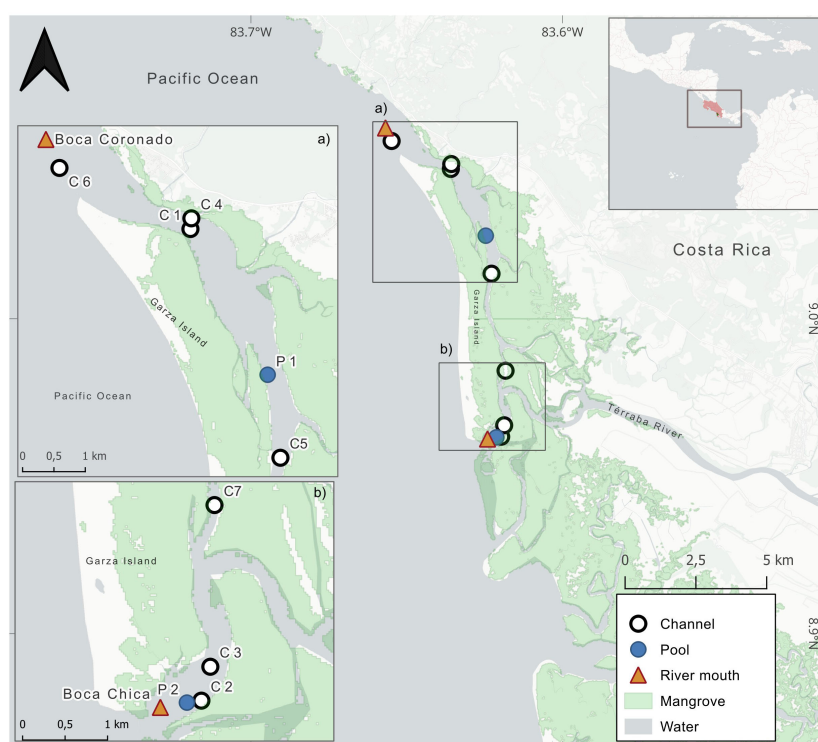


FIGURE 1

Map of the study site, Térraba-Sierpe National Wetland, showing the locations of the sampling to capture rays along the estuary within the channel and pools, close to the river mouth: a) Boca Coronado and b) Boca Chica.

deployment and effectively minimizes the probability of specimen escape, thereby ensuring higher capture success rates. Considering their suggestions, two modified cast nets (*atarrayas*) with a 2.13-meter diameter and 7 mm mesh size were used to capture any rays they observed. During the survey at the pools, two fishermen threw the cast nets consecutively for one hour per pool, starting at low tide. Captured individuals were quickly received in a net or sack for biometric data collection to minimize fishing effort disruption. The sampling took into account the rainy, dry, and transitional seasons, following the fishermen's suggestion, in order to obtain a clearer picture of the animals' behavior.

Data collection

For each captured ray, we recorded sex (based on the presence or absence of claspers) and measured DW using a flexible measuring tape (± 0.1 cm) (Figure 2). Individuals whose sex could not be determined due to small size were classified as "NI" (not identified). Sexual maturity was defined as a DW greater than 71.8 cm for females and 69.0 cm for males (26). Environmental data, specifically precipitation and air temperature, were obtained from the National Meteorological Institute of Costa Rica (37) annual reports. Although salinity is a critical environmental factor influencing the spatial ecology of species within estuarine habitats, this parameter remained unmeasured due to logistical and budgetary limitations regarding the acquisition of a salinity meter.

Calculations of catch per unit effort

For the statistical analysis, two distinct datasets were compiled: one incorporating the values of CPUE and environmental variables, while the second dataset comprised DW measurements of captured

individuals and the same environmental variables. Relative abundance was estimated as CPUE, standardized according to the fishing gear employed. For the longline sampling, CPUE was calculated as the number of individuals captured per 1,000 hooks (38). For the cast net sampling conducted in intertidal pools, CPUE was calculated as the number of individuals captured per hour by two fishermen. Sampling units from pools and channels were analyzed separately to account for differences in habitat, fishing effort, and capture efficiency between study areas.

Multiple linear regression model

To assess the combined influence of environmental conditions on ray relative abundance, multiple linear regression models were fitted separately for each ecosystem (39). The CPUE was used as the response variable, while mean temperature (Tmean) and precipitation (Rain) as explanatory variables.

The general model was expressed as:

$$CPUE_i = \beta_0 + \beta_1(T\beta mean_i) + \beta_2(Rain_i) + \varepsilon_i$$

where $CPUE_i$ is the catch per unit effort recorded during sampling event i , β_0 is the intercept, β_1 and β_2 are regression coefficients associated with temperature and precipitation, respectively, and ε_i represents the residual error term (39, 40).

Separate models were fitted for each ecosystem to account for differences in habitat characteristics and sampling methodology. Model assumptions were evaluated by examining residual distributions and residuals against fitted values to assess homoscedasticity, quantile–quantile (Q–Q) plots to evaluate residual normality, and residual autocorrelation plots to verify independence among observations. No substantial deviations from model assumptions were detected. Regression coefficients, associated significance tests, and



FIGURE 2
Styracura pacifica Disc Width (DW) measurement.

coefficients of determination (R^2) were used to quantify the contribution of environmental variables to observed variation in CPUE. The fitted models were visualized using three dimensional regression surfaces to facilitate interpretation of the joint effects of temperature and precipitation on ray abundance.

Statistical analyses

A non-experimental, observational study design was applied to evaluate spatial, temporal, and environmental drivers influencing the distribution and relative abundance of *S. pacifica* within the Térraba-Sierpe National Wetland between 2022 and 2023. Two estuarine ecosystems, Channel and Pools, were treated as fixed factors in the analyses. The primary response variables were CPUE and DW (cm), while explanatory variables included mean water temperature (Tmean), maximum water temperature (Tmax), precipitation (Rain), year (2022 and 2023), and ecosystem type (Channel and Pools).

Data normality was assessed using the Shapiro–Wilk test because CPUE values showed significant departures from normality ($p < 0.001$), and non-parametric statistical approaches were adopted. Associations between CPUE, environmental variables, and DW were evaluated using Spearman's rank correlation coefficients. Differences in CPUE and individual DW between ecosystems and between years were tested using Wilcoxon rank-sum tests. When more than two groups were compared, Kruskal–Wallis tests were applied, and when significant differences were detected, *post hoc* pairwise comparisons were conducted with Bonferroni correction to control for Type I error.

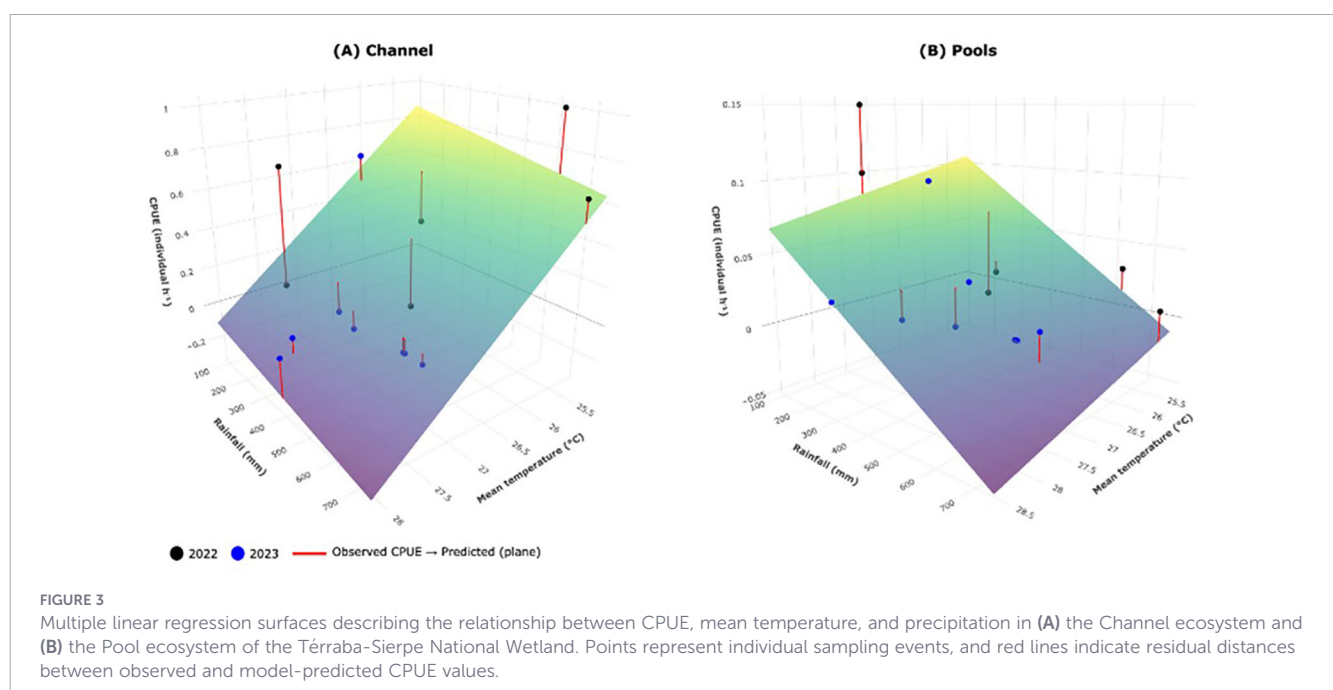
All data processing, calculations, statistical analyses, and figure generation were performed in R software (version 4.5.1). Statistical significance was assessed at $\alpha = 0.05$.

Results

Main channel

During six monitoring events in 2022, a total of six individuals of *S. pacifica* were captured, with two females and four males, with their disc widths (DW) ranging from 31 to 55.7 cm. In contrast, during eight monitoring events carried out in 2023, only two individuals were captured, both males, and both captured prior to the change in hook type. The highest CPUE (1 individual h^{-1}) was obtained during a single set of 50 hooks in June 2022. This particular event also resulted in the capture of a bull shark (*Carcharhinus leucas* (Valenciennes, 1839)), the only other elasmobranch species recorded during the study period.

Spearman correlation analysis revealed a significant negative relationship between CPUE and mean temperature in the Channel ecosystem ($r = -0.642$, $p = 0.013$), whereas no significant association was detected between CPUE and precipitation ($r = -0.03$, $p = 0.93$), suggesting lower ray abundance under warmer conditions. To evaluate the combined influence of environmental variables on ray abundance, a multiple linear regression model was fitted using CPUE as the response variable and mean temperature (Tmean) and precipitation (Rain) as predictors (Figure 3A). The model explained 58.0% of the observed variation in CPUE ($R^2 = 0.580$, $F = 7.59$, $p = 0.008$). Mean temperature had a significant negative effect on CPUE ($\beta_1 = -0.332$, $p = 0.0025$), whereas precipitation was not a significant predictor ($\beta_2 = -0.00034$, $p = 0.351$) (Table 1). The three-dimensional regression surface illustrates a clear decline in predicted CPUE with increasing temperature, whereas variation along the precipitation axis produced comparatively minor changes in model predictions (Figure 3A).



Sand flat intertidal pools

A total of 14 sampling events were conducted at the intertidal pools (6 in 2022, 8 in 2023), resulting in 58 total captures. Their DW range was between 19.6 and 37 cm; the smallest individual was captured in Pool 2 (P2, Figure 1) in March 2022 and represents the shortest size reported up to date. Of the total captures, 26 individuals were females, 13 males, and 18 were too small to determine sex. The highest CPUE (0.15 individuals h^{-1}) was obtained in P2 in March 2022, with 16 individuals captured in one hour. Spearman correlation analysis revealed a moderately strong and significant negative correlation between CPUE and rainfall ($r = -0.532$, $p = 0.041$), whereas no significant association was detected between CPUE and mean temperature ($r = 0.11$, $p = 0.68$), suggesting a decrease in ray captures in the intertidal pools under higher precipitation conditions. The multiple linear regression model explained 57.2% of the observed variation in CPUE ($R^2 = 0.572$, $F = 8.02$, $p = 0.006$; Figure 3B). Precipitation was negative associated with CPUE ($\beta_2 = -0.000178$, $p = 0.0018$), whereas mean temperature was not a significant predictor ($\beta_1 = -0.011$, $p = 0.278$) (Table 1). In contrast, the regression surface for the Pool ecosystem shows a pronounced decline in predicted CPUE as precipitation increases, while temperature had a comparatively limited influence on model predictions (Figure 3B).

Main channel and sand flat intertidal pools

Environmental drivers of CPUE differed between ecosystems. In the Channel ecosystem, variation in CPUE was primarily associated with mean temperature, whereas precipitation emerged as the principal predictor in the Pool ecosystem. The fitted regression models explained a similar proportion of the observed

TABLE 1 Summary of multiple linear regression models describing the relationship between CPUE and environmental variables in the channel and pool ecosystems.

Ecosystem	Variables	Multiple linear regression			
		Coefficient	s.e.	t-Value	p-Value
Channel	Intercept	9.269835	2.328362	3.981	0.0022
	Tmean	-0.332014	0.085249	-3.895	0.0025
	Rain	-0.000339	0.000348	-0.975	0.3505
Pools	Intercept	0.404063	0.268679	1.504	0.1585
	Tmean	-0.011072	0.009751	-1.135	0.2783
	Rain	-0.000178	0.000045	-4.002	0.0018

variation in relative abundance in both ecosystems (Channel: $R^2 = 0.580$; Pools: $R^2 = 0.572$).

From 2022 to 2023, a significant decrease was observed in both CPUE and the average disk width (DW) of captured individuals, coinciding with a moderate increase in mean temperature (Figure 4). Spearman correlation analysis revealed a moderately strong and statistically significant negative correlation between CPUE and mean temperature ($r = -0.642$, $p = 0.013$), whereas precipitation showed no significant association ($r = -0.03$, $p = 0.93$). Furthermore, an analysis of local precipitation data indicated that 2023 was characterized by distinct conditions compared to 2022; specifically, the precipitation patterns did not follow typical dry or wet season thresholds. Consequently, due to this lack of inter-annual consistency, we could not classify sampling events by season, and thus, data were analyzed as an integrated temporal set. Consistent with these findings, the multiple regression model

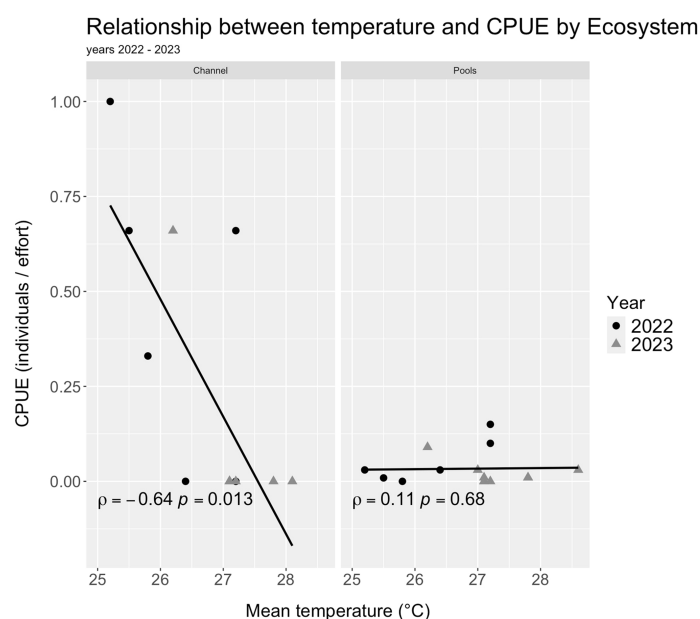


FIGURE 4

The relation between mean air temperature and CPUE by ecosystems in the years 2022 and 2023. The black dots represent the 2022 and the blue ones the 2023 year.

identified temperature as the only significant predictor of CPUE in the channel ecosystem ($\beta_1 = -0.332$, $p = 0.0025$).

In contrast, in the Pool ecosystem, the correlation between CPUE and mean temperature was weak and not statistically significant (Spearman, $r=0.11$, $p=0.68$), but showed a significant negative correlation with precipitation ($r = -0.532$, $p = 0.041$). The regression analysis similarly identified precipitation as the only significant environmental predictor of CPUE in this ecosystem ($\beta_2 = -0.000178$, $p = 0.0018$).

The rays captured in the Channel and Pool ecosystems showed significant differences in DW (Wilcoxon, $p < 0.001$), indicating marked size structuring between habitats (Figure 5). A clear ontogenetic segregation of *S. pacifica* was observed between ecosystems, with distinct size distributions characterizing each ecosystem. Pools were dominated by smaller individuals, with lengths primarily ranging between 19 and 38 cm, whereas larger individuals were more frequently recorded in the channel, with one individual reaching a disc width exceeding 50 cm, while the remaining seven captured individuals ranged between 31 and 42 cm. Differences in DW between ecosystems were statistically significant in 2022 ($p = 0.0003$), in 2023 ($p = 0.0236$), and in the pooled dataset ($p = 1.1 \times 10^{-5}$). None of the captured individuals reached the reported sizes at sexual maturity for males (69 cm) or females (71.8 cm), indicating that the study area was predominantly occupied by juvenile individuals.

Discussion

This study reveals clear spatial and environmental structuring in the occurrence, size distribution, and catchability of *S. pacifica* across adjacent coastal habitats, highlighting the functional role of shallow intertidal pools and mangrove-associated environments as

juvenile-dominated systems. Across both years, captures were exclusively composed of immature individuals, with significantly smaller disc widths recorded in intertidal sand flat pools compared to the main channel, indicating strong size-based habitat segregation. This size distribution is consistent with findings for its congener, *S. schmardae*, where field surveys have documented a high number of small-sized individuals within mangrove creeks, suggesting that these habitats serve as nurseries (41). Empirical surveys and physiological studies of stingrays consistently link juveniles to shallow nursery and growth areas in rivers and creeks, as these environments offer reduced predation risk and stable foraging opportunities (42).

Further support for this segregation comes from stable-isotope analyses on *S. schmardae*, which indicate that smaller rays utilize mangrove-derived and sulfide-rich creek habitats. This not only highlights a distinct dietary niche separate from larger, sympatric stingrays but also implies spatial segregation based on both size and diet. The observed pattern aligns with broader life history models for non-marine elasmobranchs, which describe progressive habitat shifts as individuals mature and their dietary needs and salinity tolerance change. These shifts reflect the multifunctional role of channels, which are used for foraging, resting, masting, and parturition in elasmobranchs (43). This includes a transition from nursery habitats to marginal areas and eventually to main river channels or coastal zones as they grow (21). Although this study was not able to demonstrate higher relative densities compared with surrounding areas, nor residency time, or animals' return behavior, the consistent presence of juveniles within the intertidal sand flats and mangrove creeks, combined with observed size-based distribution patterns, suggests this ecosystem works as a recruitment and refuge area. While these data are not exhaustive, they underscore the high probability that the T rraba-Sierpe National Wetland is important for the early life stages of the species. These results reinforce the ecological relevance of the existing protected status of

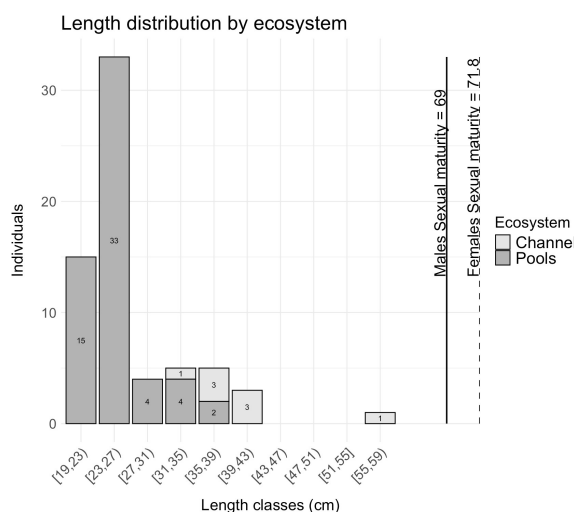


FIGURE 5

Frequency distribution of disc width (cm) of *Styracura pacifica* in the Channel and Pool ecosystems of the T rraba-Sierpe National Wetland. Bars represent the number of individuals per size class and ecosystem. Dashed lines indicate estimated sizes at sexual maturity for males (69 cm) and females (71.8 cm). The light gray color represents individuals captured at the main channel, while the dark gray color represents those captured at the sand flat pools.

the Térraba-Sierpe National Wetland and underscore the need for targeted, long-term monitoring to fully characterize its role in the life cycle of this species.

While the statistical data associates the lower 2023 catch rate with the use of circle hooks, several studies indicate that observed differences in CPUE between J-style and circle hooks in elasmobranch longline fisheries are typically ascribed to mechanical factors post-bait ingestion, rather than to hook-induced variations in initial attraction or feeding behavior (44, 45). Considering this, any significantly higher catch rates recorded for circle hooks should result solely from their superior performance in two key metrics: a reduced probability of the shark avoiding being hooked after taking the bait, or a greater capacity to retain the animal once hooked, thus minimizing escape prior gear retrieval (44, 46, 47). Also, previous studies demonstrated that changes in hook types (J-hook to circle hooks) have shown no significant effect on CPUE of other pelagic stingray (48), any gear-related transition in our study would be biased against detecting a decline in CPUE, as circle hooks are more effective in reducing bycatch mortality but increase catch rates on sharks (49–51).

The negative correlation revealed between CPUE and temperature at the main channel (a value of an environmental variable), showing a reduction in catchability or presence during warmer periods. This inverse relationship suggests that spatial distribution shifts when the habitat changes, particularly due to temperature. As well, pools are buffered environments, allowing the presence of the species even under thermal fluctuations, and supports the hypothesis that *S. pacifica* responds differentially to temperature depending on habitat type, which is key for understanding its spatial use within the Térraba-Sierpe National Wetland. The ectothermic nature of elasmobranchs means that temperature, in particular, can have a significant impact on physiological and biological aspects, such as growth, metabolism, parturition, and the rate of digestion (19). Such an inter-annual decline is consistent with findings that the temperature increase produces thermal stress and prey availability, causing temporary habitat displacement. This behavior suggests that, as sea surface temperature rises and the frequency of El Niño events increases, elasmobranch communities will likely exhibit more fluctuations in abundance and habitat preference (52). Long-term shifts in the distribution of species and phenology have already been changing for more than 40 years, which is parallel with ocean warming (7). Consequently, the observed decline in CPUE, despite switching to a potentially more efficient gear type, suggests that higher average water temperature may affect *S. pacifica* capture more than gear variability alone.

The inverse correlation between CPUE and rainfall in the intertidal pools (Spearman $r = -0.53$, $p = 0.041$) suggests that freshwater input may influence presence of juvenile *S. pacifica* in the HNTS. This is consistent with salinity being the primary abiotic driver of elasmobranch abundance in estuarine systems, as demonstrated across multiple estuaries worldwide. (53, 54). Although direct salinity measurements were unavailable in our study, precipitation constitutes a proxy for freshwater discharge in the HNTS system, given the local coupling between rainfall and river discharge (31). In similar tropical and subtropical estuaries, juvenile rays occupy low-salinity areas within a narrow tolerance ranges, and the

extent of these suitable areas depends directly on freshwater input (3).

Our results provide empirical evidence that the studied estuaries function as a nursery system for *S. pacifica*, with intertidal pools and mangrove-influenced habitats supporting smaller individuals and higher relative abundances than deeper channel environments. The observed sensitivity of CPUE to temperature and rainfall highlights the dynamic nature of habitat use and suggests that even moderate environmental variability can alter juvenile distribution, detectability, or habitat suitability at short temporal scales. These findings are particularly relevant in the context of ongoing climate-driven warming and changing precipitation regimes, which are expected to intensify habitat instability in tropical coastal systems (55).

From a conservation and fisheries-management perspective, the reliance of juvenile rays on shallow, nearshore habitats emphasizes the vulnerability of these life stages to habitat degradation, hydrological alteration, and coastal development. Protecting and managing these nursery habitats should therefore be considered a priority for sustaining *Styracura* populations and maintaining the ecological function of tropical coastal ecosystems more broadly.

In conclusion, this study addresses a critical knowledge gap regarding the spatial ecology of the Pacific chupare ray, *S. pacifica*, within the Térraba-Sierpe National Wetland (HNTS). By providing the first dedicated assessment of its distribution and habitat use in this key Central American ecosystem, our findings provide empirical evidence for the functional role of the HNTS—specifically its shallow intertidal areas—as a possible nursery habitat.

Our data reveal a high degree of environmental sensitivity: relative abundance (CPUE) showed a significant inverse correlation with temperature in the main channels and with precipitation in intertidal pools. Such dynamics suggest that the spatial distribution and detectability of these rays are governed by fluctuating local conditions. While this research establishes a necessary ecological baseline for ecosystem-based management, it also underscores the urgent need for expanded research within estuarine environments.

Critically, the integration of LEK was fundamental to the design of this research; the insights provided by local fishermen's communities were instrumental in identifying key sampling sites and designing catch strategies, which confirmed strong size-based habitat segregation that might otherwise have been overlooked. LEK is strongly recommended for a better understanding of habitat use.

We believe that there are limitations to comparing CPUE between the pools and the channel due to this difference in hooks and cast nets. However, according to the guidance of experienced fishermen who participated in the LEK, the difference in environments would have had a greater impact on CPUE than the type of fishing gear, if the one indicated for each environment is not used.

Future studies must prioritize the implementation of environmental and physicochemical variables monitoring would improve understanding of how hydrological variability mediates juvenile persistence in this tropical wetland. Also, specialized tracking and marking methods for small-bodied elasmobranchs, such as Passive Integrated Transponder (PIT) tags, to longitudinally monitor individual site fidelity and recruitment. Advancing these fine-scale telemetry techniques will be essential to quantifying the

physiological thresholds and residency patterns that drive the environmentally linked shifts observed in this vulnerable species.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was approved by Sistema Nacional de Áreas de Conservación (SINAC) Área de Conservación Osa (ACOSA), approved resolution numbers SINAC-ACOSA-DT-PI-R-008-2023 and SINAC-ACOSA-DASP-PI-INV-037-2021. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

GP: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. FT: Investigation, Methodology, Project administration, Resources, Visualization, Writing – review & editing. OB: Funding acquisition, Investigation, Methodology, Writing – review & editing. M-PB: Data curation, Formal analysis, Investigation, Resources, Software, Validation, Visualization, Writing – review & editing. RD-O: Resources, Software, Validation, Writing – review & editing. HB-G: Conceptualization, Data curation, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. FM: Conceptualization, Data curation, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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