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Evidence of shifts in habitat use of two snappers (Lutjanidae) in a tropical estuarine bay subjected to seasonal upwelling

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ABSTRACT: Biological and environmental conditions are drivers of fish habitat use, making it essential to understand how fish move and use specific areas to inform effective fisheries management and conservation. This study quantified the residency and habitat use patterns of the juveniles and early adults of 2 commercially exploited snappers (Lutjanidae) in Santa Elena Bay, a tropical estuarine embayment influenced by a seasonal upwelling in the north Pacific coast of Costa Rica. Using an array of 28 acoustic receivers, we monitored 14 Colorado *Lutjanus colorado* (28.8–48.9 cm) and 16 Pacific dog *L. novemfasciatus* (22.5–49.3 cm) snappers over 22 mo. Both species were detected inside the bay over 60% of the monitoring days, showing higher relative abundance in mangrove and transitional estuarine habitats. Throughout the study, a shift in habitat use was observed for both species. Individuals moved from mangrove and transitional habitats to the outer reef habitat and exhibited a decreasing occurrence probability over time, suggesting they leave the bay as they mature. Season and environmental variables, e.g. temperature, had minimal or no effect on the occurrence of the tracked snappers in the bay. However, roaming varied seasonally, increasing during upwelling periods. These results suggest that habitat connectivity facilitates gradual life stage transitions, indicating that Santa Elena Bay likely supports essential fish habitat for commercially important species, particularly for *L. novemfasciatus*. Results also highlight the importance of integrating knowledge of the complex interplay of biological components (e.g. developmental and intra- and interspecific interactions) and seasonal habitat dynamics into conservation and management strategies.

KEY WORDS: Lutjanidae · Spatial ecology · Upwelling · Costa Rica · Eastern Tropical Pacific · Fisheries management

1. INTRODUCTION

Understanding where and when fish move and why they use specific habitats has direct application to spatial management and conservation (Moffitt et al. 2009, Allen et al. 2018). Movement patterns of fish are shaped by diverse biological and environmental drivers across different spatial and temporal scales (Nathan et al. 2008). For instance, the time fish spend in a specific area, i.e. reflecting their residency and habitat use, depends greatly on the availability of essential resources like food and shelter (Dahlgren & Eggleston 2000, Murray & Sandercock 2020, Appert et al. 2023). These resource requirements can vary across different life stages (Allen et al. 2018). In addition, climate-driven environmental conditions such

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*Corresponding author: vargas.lucia1810@gmail.com as temperature, dissolved oxygen and pH can influence fish movement and habitat selection (Pörtner et al. 2017, Woodson et al. 2019, Pinsky et al. 2020). Fish may need to seek optimal conditions for survival and to meet energy requirements based on their physiological limits (Brett & Groves 1979, Keefer et al. 2009, Fey et al. 2019). Therefore, environmental variability may trigger movements to regions with more suitable temperatures (Topping & Szedlmayer 2011a, Piraino & Szedlmayer 2014) as a thermoregulatory strategy (Fey et al. 2019), or to accelerate digestion (Bacheler et al. 2021). Moreover, the effect of different environmental and biological drivers can be life-stage dependent (Erisman et al. 2020). For example, for red snapper *Lutjanus campechanus*, habitat quality, competition and predation have a different impact on juveniles than on adults (Erisman et al. 2020).

Environmental variability can also trigger shifts in ecosystem dynamics and biological interactions that can influence the spatial ecology of a species (Allan et al. 2015, Kämpf & Chapman 2016). Therefore, by quantifying the effects of biological and environmental drivers on fish movement across different spatio-temporal scales and life stages, it is possible to define their critical habitats (e.g. nursery, feeding, or reproductive areas) and, ultimately, predict how species may respond to environmental change (Hussey et al. 2015, Crossin et al. 2017). This information is key to effectively managing populations of important targeted fish species, such as snappers, under the pressure of fishing, habitat degradation and climate change (Hussey et al. 2015, Crossin et al. 2017, Barange et al. 2018, Rilov et al. 2019).

Coastal upwellings are natural oceanographic phenomena that influence marine ecosystem dynamics (Kämpf & Chapman 2016, Pinsky et al. 2020). During coastal upwellings, cool, nutrient-rich water emerges to the surface, resulting in high productivity and sharp fluctuations in oceanographic conditions (e.g. temperature, dissolved oxygen, pH) (Kämpf & Chapman 2016). Given their contrasting fluctuating conditions, seasonal upwellings in tropical regions can increase our understanding of how fishes may respond to environmental variability. Within the Eastern Tropical Pacific, there are 3 main wind-driven seasonal coastal upwellings: the Tehuantepec Bowl in Mexico, the Bay of Panama and Papagayo, between Nicaragua and northern Costa Rica (Fiedler & Lavín 2017). The Papagayo upwelling largely influences the dynamics of local reefs and their associated reef fish assemblages on the northern Pacific coast of Costa Rica (Jimenez & Cortés 2003, Dominici-Arosemena & Bnignoli 2005, Roth et al. 2015), suggesting that some species readjust their space use in response to changing environmental conditions (Eisele et al. 2020).

Snappers (Lutjanidae) are economically important reef fish that typically exhibit ontogenetic patterns in movements and habitat use (Gillanders et al. 2003, Martinez-Andrade 2003). Juveniles of estuarine-dependent snappers usually remain near mangroves and shallow estuarine areas with abundant food and refuge (Reis-Filho et al. 2019), whereas adults use a wider range of habitats including rocky and coral reefs and periodically migrate to offshore habitats to spawn (Sadovy de Mitcheson et al. 2008). Thus, the degree of connectivity between estuarine and reef habitats is key to supporting the transition of many snapper species to mature life stages (Gillanders et al. 2003, Pimentel & Joyeux 2010, Vasconcelos et al. 2011, Dance & Rooker 2015, Reis-Filho et al. 2019) and to enhancing fishery production as they leave their nursery grounds (Kramer & Chapman 1999, Grüss et al. 2011). However, continuous tracking data on the early life-stages of snappers remains scarce, making it difficult to accurately identify their essential habitats.

Snappers are the main target of local artisanal fishers in the north Pacific coast of Costa Rica and are also important in recreational fisheries (Villalobos-Rojas et al. 2014, SINAC 2017). However, overfishing and habitat degradation have negatively impacted the populations of snappers in this region (Villalobos-Rojas et al. 2014, Alvarado et al. 2018, Beita-Jiménez et al. 2019, Arias-Godínez et al. 2019, 2021). Previous studies using underwater visual surveys and catch records of small individuals suggest that Santa Elena Bay, a relatively large embayment on the northern Pacific coast of Costa Rica, functions as a nursery area for several species of snappers (Arias-Zumbado 2021, Espinoza et al. 2022). However, knowledge of how snappers are using this area is still lacking or restricted to sighting records. Santa Elena Bay was declared a Marine Management Area (MMA) in 2018, which means that specific zones of the bay are protected from fishing and others are restricted to low-impact fishing gears (SINAC 2017). The unique conditions of the bay (i.e. diverse habitats available ranging from mangrove to coral and rocky reefs), coupled with the management zoning and the influence of a seasonal upwelling, provide an ideal opportunity to investigate the spatial ecology of early life stages of snappers in relation to multiple environmental drivers.

This study quantified the residency and habitat use patterns of the Colorado *L. colorado* and the Pacific dog *L. novemfasciatus* snappers in the Santa Elena Bay MMA. These are 2 common species that are known to be estuarine-dependent, particularly in their early life stages, and are expected to use mangroves as nurseries and transition to reef environments as they grow larger, particularly *L. novemfasciatus*, as *L. colorado* is known to be highly associated with both environments at mature life stages as well (Martinez-Andrade 2003, Vega et al. 2015). Therefore, our objectives were to (1) determine the residency time and movement extent of individuals of both species within the bay, (2) quantify the use of mangrove, transitional and reef habitats within Santa Elena Bay, (3) investigate temporal shifts associated with movements across habitats over time and (4) determine the effect of biological and environmental drivers on the probability of fish occurrence in the bay over time. Given the variety of habitats found in the bay and that different species of snappers in Santa Elena Bay are often found in small sizes (Arias-Zumbado 2021), we expected *L. colorado* and *L. novemfasciatus* to exhibit high residency to Santa Elena Bay, spending a significant proportion of days within the bay compared to days spent outside of it through the study period. Furthermore, we expected particularly high use of areas with high mangrove cover, as these habitats are believed to offer an abundant source of food and shelter for growth and survival (Martinez-Andrade 2003). In addition, environmental drivers play a key role in fish movement; therefore, we expected that changes in water temperature from the seasonal upwelling may influence the movements in and out of the bay and between habitats of *L. colorado* and *L. novemfasciatus* within Santa Elena Bay.

2. MATERIALS AND METHODS

2.1. Study site

Santa Elena Bay MMA is a ~728 ha, semi-enclosed estuarine embayment located on the north Pacific coast of Costa Rica (Fig. 1). Nearshore habitats along the entire coastline are shallow (<10 m deep), while the middle and outer areas of the bay can reach maximum depths of 35 m (Lizano & Alfaro 2015). The bay is subjected to a semidiurnal tidal cycle with an average daily amplitude of 228 cm (Lizano 2006). Some chan-

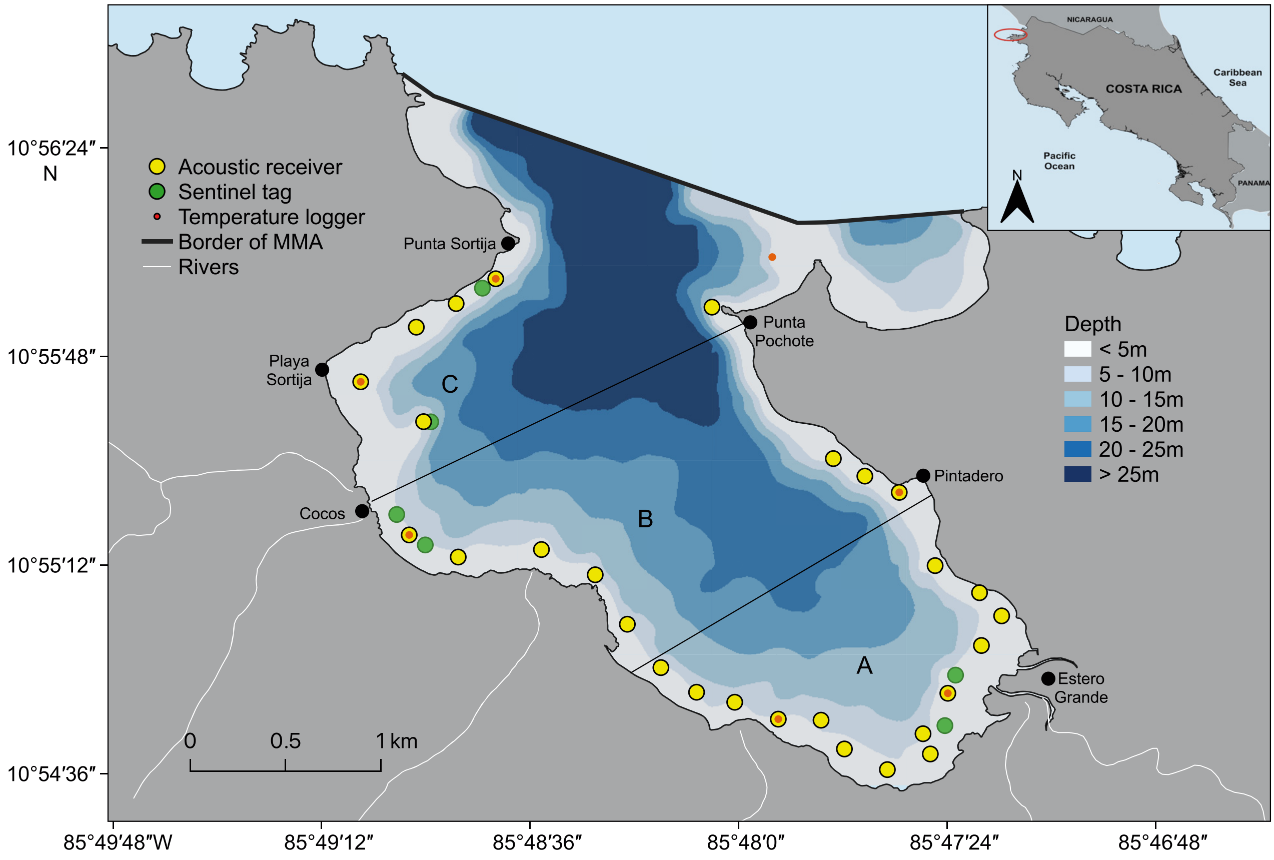

Fig. 1. Acoustic array at the Santa Elena Bay Marine Management Area, northwestern Pacific coast of Costa Rica. Regions of the bay are classified as Mangrove (A), Transitional (B) and Reef (C)

nels of the inner mangrove (Estero Grande) and some fringing mangrove roots are only inundated during high tide. The bottom in the innermost areas of the bay is composed of silt, sand and some submerged rocks with dense mangrove cover. The seascape gradually transitions outwards to sparse mangrove patches and to sandy and rubble beaches with rocky outcrops (BIOMARCC-SINAC-GIZ 2012, 2013).

During the wet season (May–November), small rivers discharge into the inner and middle regions of the bay (BIOMARCC-SINAC-GIZ 2012, 2013), whereas the dry season (December–April) is influenced by the Papagayo upwelling, a result of intensification of the north trade winds that leads to the cooling and enrichment of the water in the region (Amador et al. 2006, Alfaro & Cortés 2015, Stuhldreier et al. 2015). Although long-term oceanographic characterization of the bay is not available, in adjacent coastal waters from the Gulf of Santa Elena, water temperature is known to fluctuate from 28° to 34°C during non-upwelling season (May to November) to minimum temperatures of ~15°C during upwelling months (Alfaro & Cortés 2015, Stuhldreier et al. 2015). Water temperatures inside Santa Elena Bay are more stable than in coastal areas outside the bay (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m752p149_supp.pdf).

Santa Elena Bay is surrounded by Sector Murciélago, which is part of the Santa Rosa National Park, providing land protection since 1980 (Decreto Ejecutivo 12062-A 1980). Moreover, in 2018, Santa Elena Bay was declared a MMA with a zoning plan (Fig. S2) that delineates 4 areas based on the human activity level permitted, ranging from very low (i.e. no-take zones) to high (i.e. commercial fishing only with handline, recreational catch-release, or free diving extraction) intervention (SINAC 2017). Over 50% of the bay was designated as no-take (very low to low intervention), covering mostly the innermost areas of the bay and the coastline contour. Fishing is only allowed in the outer deeper areas of the bay that have medium and high intervention, which comprises about 42% of the MMA (SINAC 2017).

2.2. Acoustic array and fish tagging

L. colorado and *L. novemfasciatus* were monitored inside Santa Elena Bay from November 2020 to August 2022 (665 d) using an array of 28 acoustic receivers (180 kHz VR2W, Vemco, Innovasea). Receivers were deployed at 4–10 m depths across different habitats (Fig. 1). The average detection range of receivers at 25% detection efficiency placed in the mangrove area was ~141 m; ~181 m in the estuarine region and 22 m in the reef (Matley et al. 2022). Therefore, receivers were spaced 150–400 m from each other, following a linear array along the coast to cover the entire bay and optimize the monitoring area along the coast. The receivers were covered with electric tape and panty hoses to reduce biofouling (Heupel et al. 2008). The receivers were positioned on mooring systems consisting of concrete blocks connected to a buoy by a 1.5–2.5 m long rope or stainless iron rod, to which receivers and stationary sentinel transmitters or reference tags programmed to emit a signal every 600s were attached ~1 m above the ocean bottom. During August and September 2021, approximately 6 receivers located in the different habitat types of the bay were inactive for a few days due to dead batteries.

Snappers were captured using rod and reel near the inner and middle of the bay and held in a floating net cage near the boat. Fish were then transferred into a water-holding bin with a dissolved clove-oil-based solution to anesthetize them before surgery (Topping et al. 2005). Each fish was surgically implanted with coded acoustic transmitters (Vemco, V9-2x-180k-1, 180 kHz, code intervals: 70–110 s, battery life: 730 d). These high-frequency transmitters are typically smaller than lower frequency types and are ideal for tracking smaller individuals. This tag frequency also proved to be effective within the study system after acoustic receiver performance tests (Matley et al. 2022). The acoustic transmitter, covered with liquid povidone-iodine as an antiseptic, was implanted inside the peritoneal cavity of each individual through a small (~1 cm) incision above the ventral midline (Wagner et al. 2011). The incision was closed by 1 or 2 square knot sutures using absorbable monofilament material (Sutuvet sutures, size 3-0, tapered-point, 25 mm long needle). Subsequently, total length (TL, cm) and weight of fish (g) were measured. Additionally, a plastic dart tag (Floy Tag, FT-2-94 Dart tag) with a unique code number was inserted into the dorsal musculature near the base of the dorsal fin to obtain reports of recapture events. Fish were held in a floating net pen until complete recovery (~20–40 min) and then released back into their capture site. The stage of maturity was determined by comparing measured lengths with available published length at maturity for *L. colorado* (25.0 cm TL) (Rojas 1997, Ángel Pérez 2011, Vega et al. 2015) and *L. novemfasciatus* (58 cm TL) (Sala et al. 2003, Duncan et al. 2011, Vega et al. 2015). These lengths were also compared to their approximate maximum lengths (91 cm for

L. colorado and 170 cm for *L. novemfasciatus*) to obtain a relative measure of life stage (Froese & Pauly 2024).

To assess the potential fate of each tagged fish, detection plots were used to examine movement patterns between receivers following criteria suggested by Klinard & Matley (2020). Given that acoustic transmitters did not have an acceleration or pressure sensor, we based our conclusions about the fate of our fish mainly on the cessation of detections. Similarities in behaviors between conspecifics were assessed to identify potentially atypical behaviors, particularly the timing of cessation of detection. We also considered that our acoustic equipment configuration could bias the interpretation, as there were no receivers in the centre of the bay (typically deeper ~25–30 m, soft-mud habitats with low oxygen levels) or in a curtain at the entrance to the bay. Ultimately, the cessation of detections was considered to be potential fish mortality (natural predation or fishing mortality) or emigration from the bay. The monitoring period of our study was shorter than the battery life of the transmitter and while transmitter failures cannot be completely ruled out, they are rare. Individual detection plots also allowed an assessment of intra- and interspecific variability and the identification of movement patterns for each species. All data processing and analyses were carried out in R version 4.3.2 (R Core Team 2023).

2.3. Data analysis

2.3.1. Residency and roaming in the bay

Prior to analysis, we filtered the acoustic data to remove potential false positive detections by removing sole transmitter detections in a 24 h period (Speed et al. 2011, Udyawer et al. 2013, Papastamatiou et al. 2015). To determine the mean proportion of time each species spent within the array over the course of the monitoring period, we calculated the residency index (RI) of each fish in the bay by dividing the number of days an individual was detected in the array by the number of days between the tagging day and the last day of the study. The RI is a value between 0 and 1, with 1 indicating that a fish was present within the acoustic array every day of the entire monitoring period. We selected an RI that quantified the presence in the array throughout the entire study period rather than specific detection periods (time between the first and last detection of each individual). This decision was based on the observation that all monitored individuals were tagged within 2 consecutive days and that multiple individuals were observed to return after long absences spanning weeks or even months. Including the entire monitoring period thus provided a more comprehensive measure of residency, accounting for potential long-term absences rather than assuming that individuals were permanently absent after their last detection (Appert et al. 2023, Kraft et al. 2023). To test for differences in the RI between the upwelling and non-upwelling seasons, the seasonal RI for each individual was estimated. Given the non-parametric nature of the data, a Kruskal-Wallis test was applied.

To investigate the extent to which individual fish of both species used the entire bay, a roaming index (RoI) was used. The RoI was calculated for each individual by dividing the number of receivers with detections by the total number of receivers in the array. The range of the RoI is from 0 to 1, with a value of 1 indicating that the individual was present at all receivers. The mean RoI was calculated for each species across the entire study period. To test for differences in the RoI between the upwelling and non-upwelling seasons, the seasonal index was estimated for each individual fish. Given the non-parametric nature of the data, a Kruskal-Wallis test was applied. To assess temporal shifts in movement extent at a finer temporal scale, the mean monthly RoI was estimated for each species, similar to Matley et al. (2016). Despite the deployment of receivers at greater densities in certain areas (e.g. mangroves), the majority of receivers were spaced at similar distances along the coast, thereby encompassing all available habitats bordering the bay. This approach provided an effective method to quantify the relative space use of snappers.

2.3.2. Spatial and temporal patterns of habitat use

The detections at each region of the bay, hereafter referred to as habitat type (i.e. mangrove, transitional and reef), were estimated for each species to explore the relative importance of different habitats. To assess potential biases related to the differences in habitat availability, i.e. area of coverage of each habitat, we estimated the number of detections relative to the area covered by each habitat (Table S1). We measured relative habitat availability by creating a buffer ring of 250 m from the bay's coastline using a QGIS buffer tool and then estimating the area corresponding to each habitat type. Additionally, to assess differences in habitat use across the bay and seasons, we calculated a standardized receiver-specific metric quantifying detections by dividing the number of detections by the number of individuals detected at each corresponding station and habitat, i.e. as an average. This approach reduced the potential bias of a single individual or a few individuals inflating presence at certain locations, which might be misleading.

To evaluate movement across habitat types over time (i.e. how the abundance of individuals shifted over time across habitat types), we applied a generalized additive model (GAM) with a Poisson distribution, with the number of snappers detected across the 3 habitats each day as the response variable. Habitat type was included as a categorical predictor and the month of study was used as a temporal predictor, ranging from 1 (January 2021) to 21 (September 2022). Data from November and December 2020 was excluded to start the analysis from January 2021 to ensure a complete and consistent data set for the entire year. To assess model performance, the null and full models (M_{FULL}: Number of individuals ~s(month, by = habitat) + habitat) were compared with each other using Akaike's information criterion (AIC). The model with the lowest AIC value was selected. The analysis was conducted using the 'gam' function from the 'mgcv' package in R (Wood 2011).

2.3.3. Drivers of snapper occurrence patterns

Generalized additive mixed models (GAMMs) with binomial distribution were used to evaluate the effect of biological (fish size), environmental (water temperature, wind speed, moon illumination, rainfall) and temporal (day of year [DOY] and season) predictors on the occurrence of both species within the bay on any given day (Table 1). The response variable, 'occurrence', represented the presence (coded as 1) or absence (coded as 0) of fish individuals. The binomial distribution included in the model transforms the binomial response variable (presence–absence) to a probability scale (i.e. probability of occurrence in this case) (Zuur et al. 2009). Predicted probabilities close to 0 indicate a low probability of fish occurrence, while probabilities close to 1 suggest a high probability of occurrence within the acoustic array on a given day. Additive models were selected to incorporate smooth functions to model predictor variables with non-linear relationships with the response variable. A mixed model approach was used to treat individual fish as a random factor. All environmental variables were estimated for each day to match the temporal scale of the daily presence–absence estimations. Water temperature near the seafloor was obtained from 5 *in situ* temperature loggers deployed at specific receivers (see Fig. 1), programmed to record every 10 min and then averaged for the entire bay for each day. To analyze temporal patterns of fish occurrence, we incorporated the DOY (0–365), season (upwelling and non-upwelling) and study year (2021 and 2022) into the models. The use of the DOY and the daily environmental measures allows for the observation of fine-scale seasonal dynamics and transitions. The study time overlapped with 3 calendar years; however, data from 2020 was excluded to reduce biases in the models, as it was sampled for less than 2 mo. Additionally, data exploration suggested that probability of occurrence patterns differed across habitats; therefore, habitat was included as an inter-

Table 1. Environmental and temporal predictor variables considered as fixed effects for probability of occurrence in generalized additive mixed models

Variable	Data source	Splines
Environmental		
Water temperature (°C)	Temperature loggers *in situ* (HOBO U22 Water Temp Pro v2; Onset Computer)	Cubic regression
Rainfall (mm)	Weather station: 72153 Santa Elena, La Cruz (Instituto Meteorológico Nacional)	Cubic regression
Wind speed (m s^{-1})	Weather station: 72191 Asada La Cruz Guanacaste (Instituto Meteorológico Nacional)	Cubic regression
Moon illumination (%)	R package 'lunar' (Lazaridis 2022)	Cubic regression
Temporal		
Day of the year	Calendar	Cyclic cubic regression
Season	Based on approximate upwelling (Dec–Apr) and non-upwelling months (May–Nov)	Cubic regression
Year	Calendar	Cubic regression

action term with day of year to account for the variability between years.

Models were developed for each species separately. The full model for both species included all selected predictors (M_{Full}: Occurrence ~ 1 + (1|tag) + fish length + s(DOY, by = habitat) + habitat + season + year + s(temperature) + rain + s(wind speed) + moon illumination), and further candidate models were developed by removing 1 predictor at a time. These combinations of explanatory variables were compared using AIC to assess model performance. The model with the lowest AIC value was selected. If 2 models had very similar AIC values, the one with the most degrees of freedom and weight was selected. The selected model was assessed by calculating the marginal R^2, which represents the variation explained by fixed effects, and the conditional R^2, which accounts for the variation explained by both fixed and random effects. The GAMMs were fitted using the 'gamm4' function in the 'gamm4' R package (Wood & Scheipl 2020).

3. RESULTS

3.1. Residency and movement extent

Fish were tagged on 2 consecutive days in November 2020 and monitored for 645 d inside Santa Elena Bay (Fig. 2, Table 2). The sizes of all 14 individuals of *Lutjanus colorado* (range: 28.8–48.9 cm, mean: 35.5 cm) were above reported lengths at maturity (~25 cm) and thus were classified as mature. All 16 individuals of *L. novemfasciatus* were considered immature, as they were below the reported size at maturity of 58 cm (range: 22.5–49.3 cm, mean: 35.5 cm). During this period, we recorded a total of 1 891 411 detections for both species (1 017 852 detections of *L. colorado* and 873 559 detections of *L. novemfasciatus*). Over 50% of the tagged individuals were detected regularly for at least 1 yr of the study and 30% were still present within the study site by the conclusion of the monitoring period. The shortest period of detection was approximately 5 mo for 1 individual. Consistent detections over extended periods indicated successful tag implantation and normal post-surgery behavior up to the date of their last detection. Both species were detected inside Santa Elena Bay for over 60% of the monitoring days, showing a high mean (±SD) RI (*L. colorado*: 0.64 ± 0.31; *L. novemfasciatus*: 0.65 ± 0.29). Some *L. colorado* individuals exhibited periodic absences of weeks at times (Fig. 2 & Fig. S3). The largest *L. colorado* (ID: T-55368) showed the longest absence, leaving in May 2021 and returning 9 mo later in January 2022. In the case of *L. novemfasciatus*, absences occurred across a variety of sizes (Fig. 2 & Fig. S4). Detection plots showed that individuals of both species stayed close to specific groups of neighboring receivers for the first few weeks or months after being tagged. Over time, however, they were detected in receivers farther away (Figs. S3 & S4). Detection of some individuals decreased or ceased completely over the course of the study (Fig. 2). Cessation of detections could have been indicative of emigration or mortality events. The tagged fish did not exhibit either stationary behavior in specific receivers, indicating mortality events, or sudden, rapid movements, indicative of predation or fishing (Figs. S3 & S4). Therefore, mortality events could not be confirmed. There was no significant difference in the RI between seasons for *L. colorado* or *L. novemfasciatus* (χ^2 = 1.7205, df = 1, $p > 0.05$ and χ^2 = 1.4556, df = 1, $p > 0.05$, respectively).

On average, both species used a large proportion of the receiver array, with *L. colorado* detected on up to 24 receivers (RoI: 0.85 ± 0.15) and *L. novemfasciatus* detected on up to 22 receivers (RoI: 0.79 ± 0.16) (Table 2). The RoI showed temporal variation over the study period, with both species exhibiting significantly higher roaming values during the upwelling season (*L. colorado*: χ^2 = 9.5477, df = 1, p = 0.01; *L. novemfasciatus*: χ^2 = 7.0938, df = 1, p = 0.01) (Fig. S5). The mean monthly RoI values indicated that higher RoI occurred during specific months of upwelling (Fig. 3). For *L. novemfasciatus*, a peak in roaming was particularly evident during months of upwelling in the second study year (Fig. 3).

3.2. Habitat use patterns

All 14 *L. colorado* individuals were detected in mangroves, with 13 observed in transitional and 12 in reef habitats. For *L. novemfasciatus*, all 16 individuals were present in all habitats. The number of detections standardized by available habitat area was higher for both species in mangroves, followed by the transitional and reef environments. The highest number of detections for *L. colorado* was recorded in mangrove habitats, with 59 970.1 detections standardized by habitat area (number of detections per km^2), representing 66.1% of the total detections. In contrast, transitional habitats yielded 24 906.5 detections (6.4%) and reef habitats contributed only 5854.1 detections (27.4%). Similarly, *L. novemfasciatus* exhibited a higher use of mangrove habitats, with 41 265.5 detections standardized by habitat area (60.3%). Transitional hab-

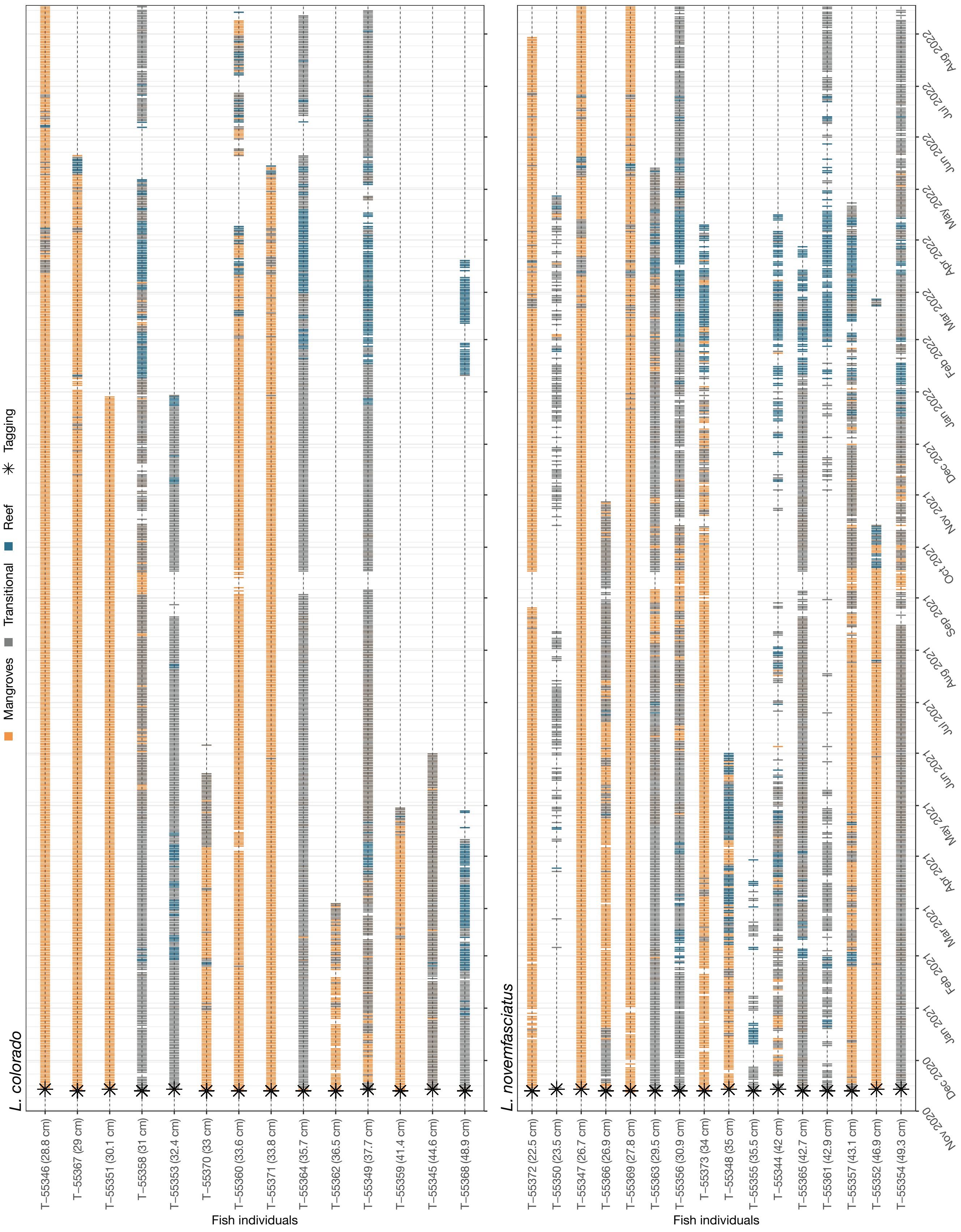

Fig. 2. Detection plot for Colorado snapper *Lutjanus colorado* and Pacific dog snapper *L. novemfasciatus* monitored between November 2020 and August 2022. Fish tags are on the vertical axis with total lengths in parentheses. Background vertical grey lines: each calendar week and month of study

Table 2. Colorado snapper *Lutjanus colorado* (LCO) and Pacific dog snapper *L. novemfasciatus* (LNO) monitored in Santa Elena Bay, north Pacific coast of Costa Rica, from November 2020 to August 2022. RI: residency index (number of days detected relative to the number of days monitored); RoI: roaming index (number of receivers that detected the individual relative to the total number of receivers available for monitoring); I: immature; M: mature

Species	Tag ID	Total length (cm)	Weight (g)	Stage of maturity	Date tagged (dd/mmm/yy)	No. of days monitored	No. of days detected	No. of detections	RI	No. of receivers	RoI
LCO	55346	28.8	460	M	14/Nov/20	644	643	148153	1.00	23	0.82
LCO	55367	29	480	M	13/Nov/20	645	552	106584	0.86	23	0.82
LCO	55351	30.1	545	M	14/Nov/20	644	411	62377	0.64	12	0.43
LCO	55358	31	500	M	13/Nov/20	645	588	59813	0.91	27	0.96
LCO	55353	32.4	650	M	14/Nov/20	644	387	36969	0.60	23	0.82
LCO	55370	33	660	M	13/Nov/20	645	190	39952	0.29	25	0.89
LCO	55360	33.6	630	M	13/Nov/20	645	565	148255	0.88	28	1.00
LCO	55371	33.8	640	M	13/Nov/20	645	549	131024	0.85	25	0.89
LCO	55364	35.7	850	M	13/Nov/20	645	603	95003	0.93	26	0.93
LCO	55362	36.5	700	M	13/Nov/20	645	101	14894	0.16	21	0.75
LCO	55349	37.7	910	M	14/Nov/20	644	605	86519	0.94	28	1.00
LCO	55359	41.4	900	M	13/Nov/20	645	169	40262	0.26	23	0.82
LCO	55345	44.6	450	M	14/Nov/20	644	199	26961	0.31	23	0.82
LCO	55368	48.9	1500	M	13/Nov/20	645	202	24264	0.31	28	1.00
LNO	55372	22.5	250	I	13/Nov/20	645	596	179638	0.92	21	0.75
LNO	55350	23.5	280	I	14/Nov/20	644	188	3403	0.29	23	0.82
LNO	55347	26.7	270	I	14/Nov/20	644	643	113640	1.00	24	0.86
LNO	55366	26.9	270	I	13/Nov/20	645	342	48365	0.53	23	0.82
LNO	55369	27.8	NA	I	13/Nov/20	645	637	66543	0.99	23	0.82
LNO	55363	29.5	440	I	13/Nov/20	645	538	41476	0.83	28	1.00
LNO	55356	30.9	500	I	13/Nov/20	645	611	60503	0.95	26	0.93
LNO	55373	34	350	I	13/Nov/20	645	469	55670	0.73	27	0.96
LNO	55348	35	400	I	14/Nov/20	644	197	35134	0.31	16	0.57
LNO	55355	35.5	790	I	13/Nov/20	645	50	805	0.08	13	0.46
LNO	55344	42	1000	I	14/Nov/20	644	292	28719	0.45	25	0.89
LNO	55365	42.7	1000	I	13/Nov/20	645	458	37965	0.71	22	0.79
LNO	55361	42.9	1100	I	13/Nov/20	645	288	28770	0.45	14	0.50
LNO	55357	43.1	1100	I	13/Nov/20	645	493	42031	0.76	25	0.89
LNO	55352	46.9	1100	I	14/Nov/20	644	339	46896	0.53	25	0.89
LNO	55354	49.3	1600	I	14/Nov/20	644	606	86200	0.94	20	0.71

itats accounted for 18 085.7 detections (13.3%) and reef habitats showed a comparable number of detections at 9124.0 (26.4%).

Overall, regardless of season, both species were predominantly detected at receivers positioned in mangrove habitats (Fig. 4A). However, there was an increase in detections at receivers located in transitional and reef habitats during the upwelling season compared to the non-upwelling season. Seasonal shifts in the proportion of detections across habitats were observed (Fig. 4B). During non-upwelling periods, *L. colorado* exhibited 75.5% of detections in mangroves, 24% in transitional and 0.5% in reef habitats, whereas *L. novemfasciatus* exhibited 77.8% of detections in mangroves, 19.8% in transitional and 2.2% in reef habitats. In the upwelling season, *L. colorado* exhibited a slight increase in detections in the reef habitat (11.5%) compared to the non-upwelling season. Similarly, *L. novemfasciatus* showed increased detections in transitional and reef habitats, 22.2 and 21.2%, respectively, during the upwelling relative to non-upwelling periods.

Based on GAMs, the number of individuals detected for both *L. colorado* ($R^2 = 0.882$, deviance explained = 84.4%) and *L. novemfasciatus* ($R^2 = 0.792$, deviance explained = 78.6%) varied significantly between habitats and months (Table 3; see model selection summary in Table S2). The number of individuals detected was significantly higher in mangroves than in transitional and reef habitats. The predicted number of individuals detected in mangroves and the transitional habitats decreased over time. There was a slight increase in the number of individuals detected in reef habitats between December 2021 and May 2022, which was more evident for *L. novemfasciatus* than for *L. colorado* (Fig. 5).

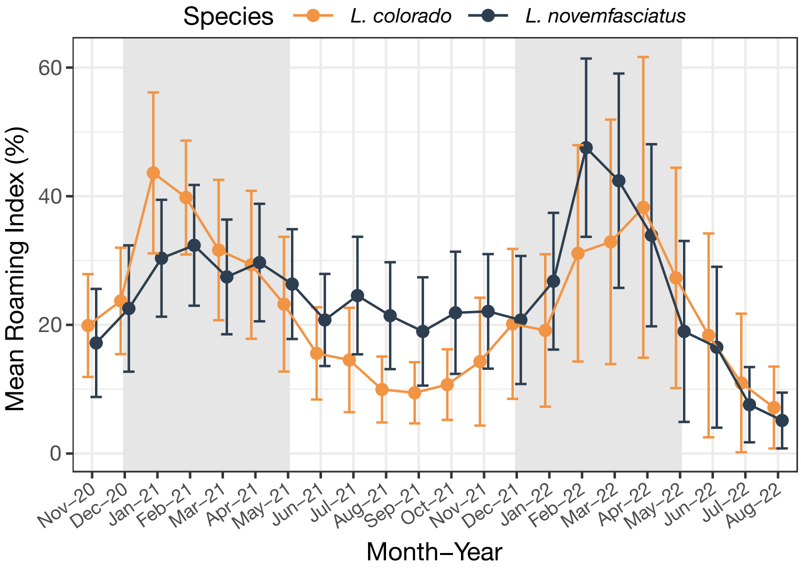

Fig. 3. Monthly roaming index as the mean percentage of receivers with detections of the Colorado snapper *Lutjanus colorado* and the Pacific dog snapper *L. novemfasciatus*. Shaded regions: approximate upwelling season. Error bars: 95% confidence intervals of the mean

3.3. Drivers of the probability of fish occurrence

For *L. colorado*, the selected model (see candidate models in Table S3) included DOY, year, season, TL, temperature, rain and moon illumination, habitat and its interaction with DOY and explained 21% of the variation in probability of occurrence (Table 4). The conditional R^2 for the selected model was 0.54 and the marginal R^2 was 0.42, indicating that fixed effects accounted for 42% of the variation in the model and the random effects (i.e. ID) accounted for 12%. The probability of occurrence was higher in the mangroves, followed by the transitional and reef habitats throughout the monitoring period. Overall, the probability of occurrence was lower in 2022 than in 2021 (Fig. 6) and season had no significant effect. There was a significant negative relationship between TL and probability of occurrence, with larger individuals having a lower probability of occurrence. Although the effect sizes of environmental drivers were small, there was a slight positive relationship between moon illumination and probability of occurrence.

One *L. novemfasciatus* detected for only 55 d was removed from the GAMMs to reduce biases in long-term occurrence patterns. For *L. novemfasciatus*, the selected model (see candidate models in Table S3) included DOY, year, temperature, wind speed, habitat and the interaction between DOY and habitat (Table 5). The model explained 18% of the variation in probability of occurrence of this species. The conditional R^2 for the selected model was 0.43 and the marginal R^2 was 0.36, indicating that fixed effects accounted for 36% of the variation in the model and the random effects (i.e. ID) accounted for 7%. The probability of occurrence was higher in the mangroves, followed by the transitional and reef habitats throughout the monitoring period. Overall, probability of occurrence decreased by the second monitoring year (Fig. 7). Water temperature and wind speed had significant but relatively weak effects on fish occurrence. Overall, probability of fish occurrence was slightly higher at lower temperatures and at intermediate wind speeds (~7–12 m s^{-1}).

4. DISCUSSION

Understanding the spatial ecology of commercially exploited fishes is crucial for identifying critical habitats that improve species survival and population connectivity (Allen et al. 2018), which has direct application to fisheries and spatial management planning. Our study demonstrated how habitat-use patterns of young individuals of Colorado *Lutjanus colorado* and Pacific dog *L. novemfasciatus* snappers within Santa Elena Bay are influenced by seasonality and ontogenetic shifts. Specifically, we found that acoustically tagged snappers (1) spent significant time within Santa Elena Bay, using all available habitats along its entire coastline, (2) exhibited higher use of the mangrove habitat compared to other available habitats, (3) underwent habitat shifts from inner estuarine to outer reef habitats over time, (4) exhibited a gradual decline in probability of occurrence in the bay over the study period, suggesting increased movements to deeper regions and outside the bay, (5) had their probability of occurrence only slightly influenced by environmental drivers and (6) expanded their space use within the bay during upwelling compared to the non-upwelling season.

Multiple studies have shown that different snapper species exhibit high residency to specific coastal habitats for extended periods, including rocky or coral reefs (Williams-Grove & Szedlmayer 2020) and estuarine environments (Hammerschlag-Peyer & Layman 2010). Both of our study species spent most of their monitoring time within Santa Elena Bay using all available habitats, with a higher frequency of detections recorded in mangroves relative to transitional

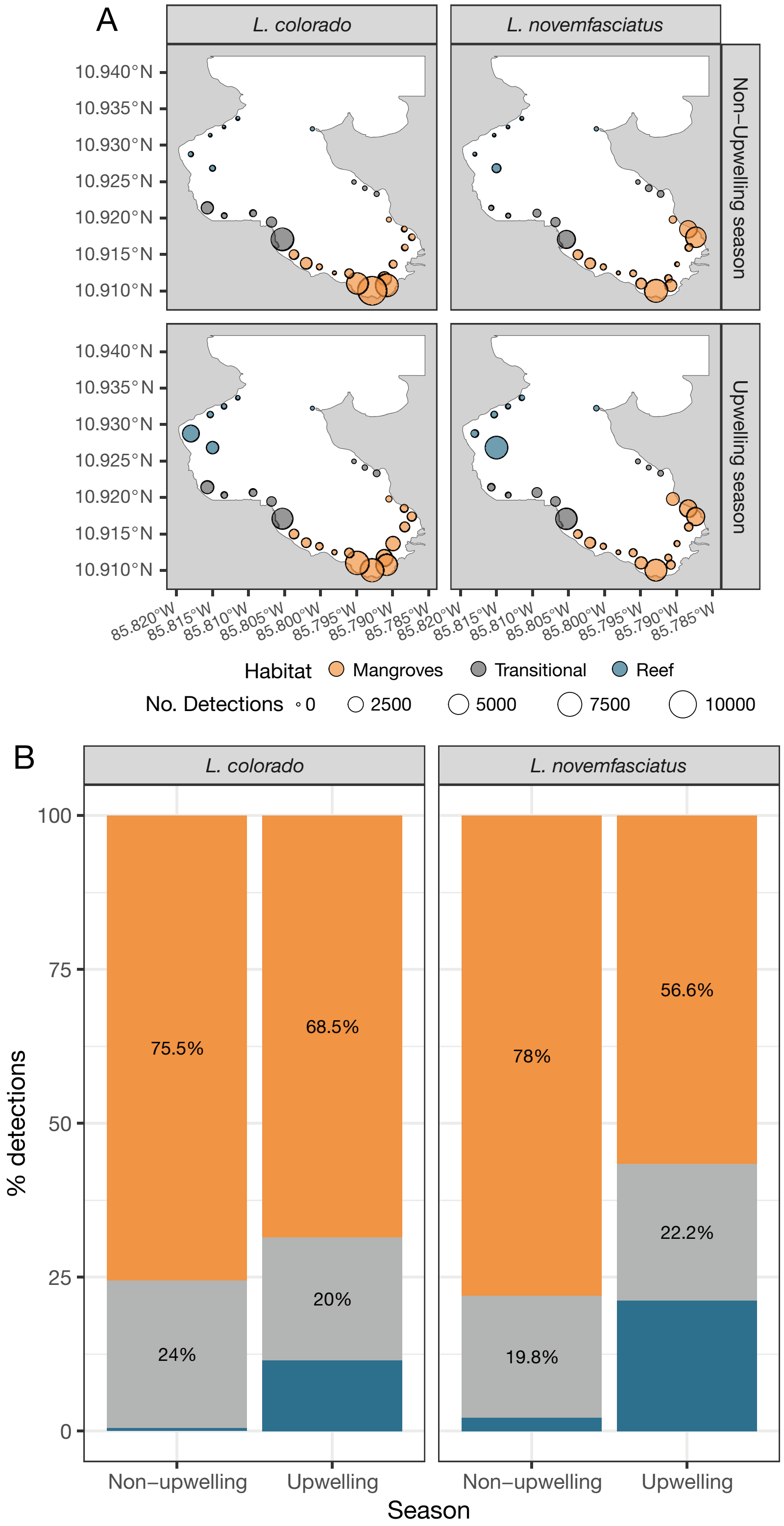

Fig. 4. (A) Standardized number of detections at the different receivers in Santa Elena Bay and (B) standardized percentage of detections for the colorado *Lutjanus colorado* and pacific dog snapper *L. novemfasciatus* during upwelling and non-upwelling months. Standardized number of detections: average for each species at each station or habitat

estuarine and reef habitats. Mangroves have been identified as essential fish habitat for several aquatic species, including snappers at early life stages (Martinez-Andrade 2003), as they provide food and refuge from predators. This was expected based on previous studies highlighting the relevance of estuarine habitats for *L. novemfasciatus*, particularly at early life stages, and for *L. colorado* at both immature and early adult life stages (Martinez-Andrade 2003, Vega et al. 2015). It is important to consider that the lack of receivers in the centre of the bay may have underestimated the RI and RoI. However, the centre of the bay is also a deep (25—30 m) soft-mud area with relatively low water circulation and oxygen levels (A. Tisseaux pers. comm.). Therefore, our initial receiver configuration along the entire coastline of Santa Elena Bay was intended to maximize areas of high snapper use. Permanent movements outside of the bay over time must also be interpreted with caution, as it is possible that individuals that were no longer detected died in an area without receiver coverage.

Our study showed that most of the monitored snappers were consistently detected at receivers located in the innermost areas of Santa Elena Bay, but many individuals also exhibited intermittent movements away to adjacent or more distant receivers, or even detection gaps of varying durations. Snappers may exhibit high residency to specific locations, while occasionally expanding movements to explore other areas (e.g. Topping et al. 2005, Topping & Szedlmayer 2011b, Piraino & Szedlmayer 2014, Heidmann et al. 2021). Tidal and diel-related changes and their interplay can also determine habitat selection (Hartill et al. 2003, Dorenbosch et al. 2004, Ramirez-Martínez et al. 2016). Indeed, the same individuals tracked for this study were found to use intertidal mangrove habitats during high tide, especially at night (Tisseaux-Navarro et al. 2024). These natural fluctuations can help

Table 3. Summary of generalized additive model used to evaluate differences in abundance across habitats and months for the Colorado *Lutjanus colorado* and Pacific dog *L. novemfasciatus* snappers monitored inside Santa Elena Bay, north Pacific coast of Costa Rica

Parameter	Estimate ± SE	95% CI	*z*	df	p
Colorado snapper *Lutjanus colorado*					
Mangroves	1.69 ± 0.02	[1.65, 1.72]	89.67	1480.38	<0.001
Transitional	−0.29 ± 0.03	[−0.34, −0.23]	−10.31	1480.38	<0.001
Reef	−1.18 ± 0.08	[−1.34, −1.03]	−15.08	1480.38	<0.001
s(month-year) × mangroves			616.47	5.09	<0.001
s(month-year) × transitional			200.25	5.53	<0.001
s(month-year) × reef			45.96	5.01	<0.001
n = 1499, R^2 = 0.882, deviance explained = 84.4%					
Pacific dog snapper *L. novemfasciatus*					
Mangroves	1.92 ± 0.02	[1.88, 1.95]	119.19	1537.89	<0.001
Transitional	−0.25 ± 0.02	[−0.30, −0.20]	−10.4	1537.89	<0.001
Reef	−1.33 ± 0.1	[−1.51, −1.14]	−13.89	1537.89	<0.001
s(month-year) × mangroves			551.15	5.32	<0.001
s(month-year) × transitional			182	8.49	<0.001
s(month-year) × reef			219.59	8.3	<0.001
n = 1563, R^2 = 0.792, deviance explained = 78.6%					

explain why most snappers were present in all habitat types at different times despite their preference for mangroves and their periodic short absences from monitored regions.

The absence of multiple individuals for long periods (weeks or months) suggests that some individuals likely utilize nearby rocky or coral reef habitats to disperse outside Santa Elena Bay. Prolonged absences of snappers from their residency areas may be triggered by unsuitable weather conditions like storms (Topping & Szedlmayer 2011b, Matley et al. 2019, Bacheler et al. 2021) or by offshore spawning aggregations (Luo et al. 2009, TinHan et al. 2014, Heidmann et al. 2021). In this study, most *L. colorado* were considered mature. Detection gaps in which multiple *L. colorado* individuals were not detected for extended periods partially coincided with reported spawning peak seasons of other snapper species along the Pacific coast of Costa Rica and Panama, from March–May and September–October (Vega & Maté 2016, Soto-Rojas et al. 2018). However, detailed information on the spawning sites, timing, frequency and duration of *L. colorado* is limited. The extended absences of mature *L. colorado* may indicate spawning migrations, but further research is needed to confirm this hypothesis. The lack of receivers in deeper areas of the bay limits our ability to determine if absences were due to movement out of the bay or if the fish remained in deeper regions where no receivers were placed. Previous studies indicate that deeper regions of the bay have low habitat complexity and oxygen levels (BIOMARCC-SINAC-GIZ 2012, Lizano & Alfaro 2015), making it unlikely that tagged individuals would remain there for long periods. While the use of deeper regions of the bay cannot be completely discarded for short-term gaps, the long-term presence of smaller individuals and the return of some fish after extended absences, sometimes of weeks or months, were likely indicative of movements outside the bay.

In this study, we observed a shift in habitat use over time for both studied species, with individuals transitioning from inner and middle bay mangrove and transitional habitats to outer reef habitats. This shift was accompanied by a gradual decrease in the probability of occurrence within the bay. We hypothesize that both these shifts occurred as the snappers grew: they gradually moved towards the reef and outside the bay. Snappers typically remain in estuarine and mangrove habitats, seeking sheltered refuges for safety from predation (Hammerschlag-Peyer & Layman 2010) before transitioning to rocky or coral reefs as they grow (TinHan et al. 2014, Williams-Grove & Szedlmayer 2020). Most fish, including snappers, exhibit rapid growth rates at early life stages (Beverton & Holt 1959, Ángel Pérez 2011, Duncan et al. 2011, Soto Rojas et al. 2013). Therefore, our study period may have been long enough for them to exhibit habitat use changes related to their growth and the associated gradual shifts in space use behavior.

For *L. colorado*, the negative effect of fish size on occurrence probability further supports the observed ontogenetic shift, indicating that larger individuals were more likely to be outside the bay or in deeper

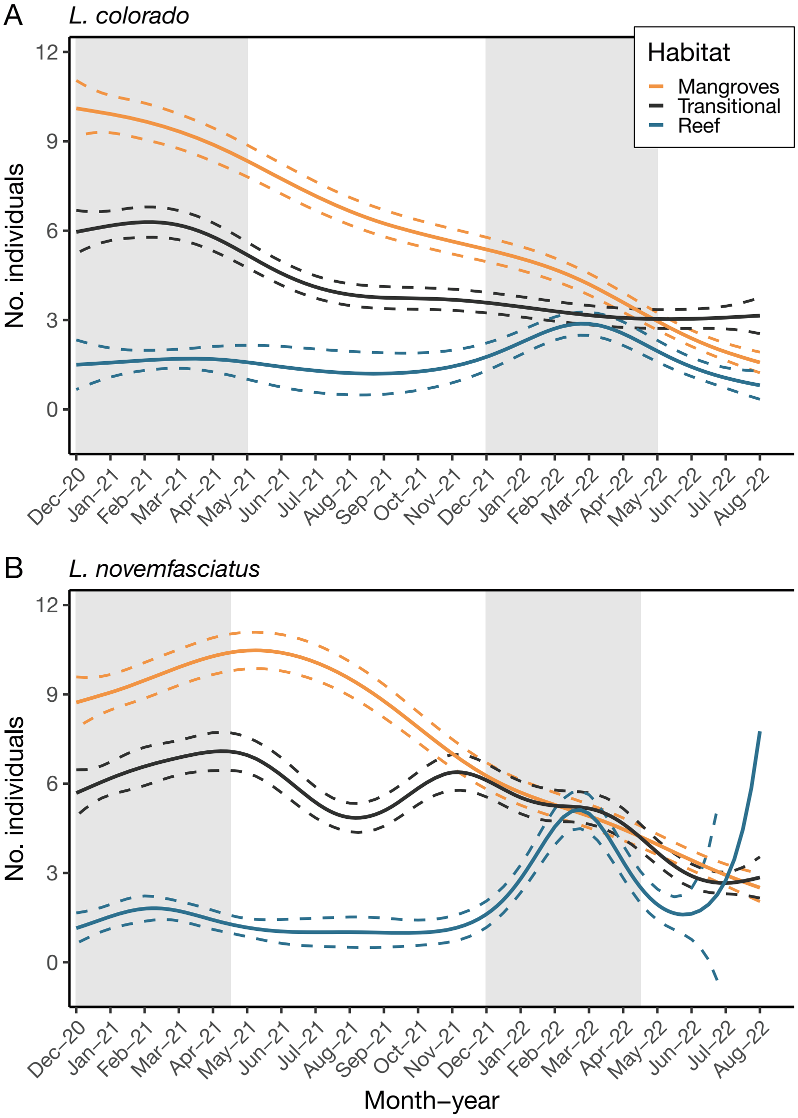

Fig. 5. Predicted number of individuals detected across habitats over time in Santa Elena Bay based on generalized additive models for (A) Colorado *Lutjanus colorado* and (B) Pacific dog snapper *L. novemfasciatus*. Shaded regions: approximate upwelling season

regions out of detection range, at least for short periods of time, where their presence is considered rare as noted before. Some studies have reported an increase in the size of *L. novemfasciatus* with increasing distance from mangrove habitats (Lyons & Schneider 1990, Vega et al. 2015). However, in our study of *L. novemfasciatus*, no relationship between size and probability of occurrence was found, likely due to our sample including only immature individuals (Luo et al. 2009, Hammerschlag-Peyer & Layman 2010, Duncan et al. 2011). According to Duncan et al. (2011), even under optimal growth conditions, it can take over 2 yr for *L. novemfasciatus* to reach maturity. Given the size of the individuals tagged in this study, it is probable that they doubled or quadrupled in size without reaching maturity (Duncan et al. 2011) by the end of the 2 yr tracking period. This limitation affects our ability to detect strong ontogenetic shifts in terms of residency within the bay for *L. novemfasciatus*.

In Santa Elena Bay, Arias Zumbado (2021) found a higher biomass of snappers in the outer region than in the inner mangrove region, also suggesting ontogenetic habitat use differences between inner and outer areas of the bay. Our results potentially provide evidence for when and how this ontogenetic transition occurs. Estuaries with fringing mangrove forests or with continuums of adjacent heterogenous habitats facilitate ontogenetic transitions for snappers (Faunce & Serafy 2007). The connectivity of diverse habitats from fringing mangrove patches and rocky outcrops within transitional habitats of the bay potentially facilitates ontogenetic shifts of our study species and their eventual migrations to other coastal habitats. The extent to which juvenile and adult fish habitats are interconnected is a key process in maintaining viable populations (Gillanders et al. 2003) and should be further investigated in the north Pacific coast of Costa Rica.

Climate-driven environmental variability can lead to changes in fish habitat use (Topping & Szedlmayer 2011b, Piraino & Szedlmayer 2014). Temperature changes during processes like the El Niño—Southern Oscillation or upwellings can induce relocations of fish as they search for more suitable conditions (Woodson et al. 2019). Given that Santa Elena Bay is generally warmer than the surrounding waters, it may offer physiological advantages during the cold upwelling months (Fey et al. 2019). Contrary to expectations, environmental factors and season were not significant drivers of occurrence probability for *L. colorado* or *L. novemfasciatus* within the bay. However, a slight increase in the occurrence probability of *L. novemfasciatus* with lower temperatures could support the idea of the bay serving as a thermal refuge. Wind speed also mar-

Table 4. Summary of selected generalized additive mixed model of the effects of multiple drivers on probability of occurrence for the Colorado snapper *Lutjanus colorado* in Santa Elena Bay, Costa Rica, from January 2021 until August 2022. DOY: day of year

Parameter	Estimate ± SE	95% CI	*z*	df	p
R^2 = 0.21; R^2 marginal = 0.42; R^2 conditional = 0.54					
Intercept	2.68 ± 0.29	[2.12, 3.25]	9.30	24958.89	<0.001
Total length	−0.08 ± 0.00	[−0.08, −0.07]	−25.29	24958.89	<0.001
Habitat: transitional	−0.73 ± 0.04	[−0.82, −0.64]	−16.44	24958.89	<0.001
Habitat: reef	−3.65 ± 0.04	[−3.73, −3.56]	−82.26	24958.89	<0.001
Season: upwelling	−0.15 ± 0.11	[−0.36, 0.07]	−1.32	24958.89	0.19
Year 2022	−1.09 ± 0.20	[−1.47, −0.70]	−5.57	24958.89	<0.001
Rain	−0.003 ± 0.001	[−0.01, 0.00]	−1.93	24958.89	0.05
Moon illumination	0.13 ± 0.05	[0.03, 0.23]	2.50	24958.89	0.01
s (DOY) × habitat mangroves			39.38	5.76	<0.001
s (DOY) × habitat transitional			35.01	6.81	<0.001
s (DOY) × habitat reef			325.41	7.49	<0.001
s (temperature)			7.71	3.04	0.05

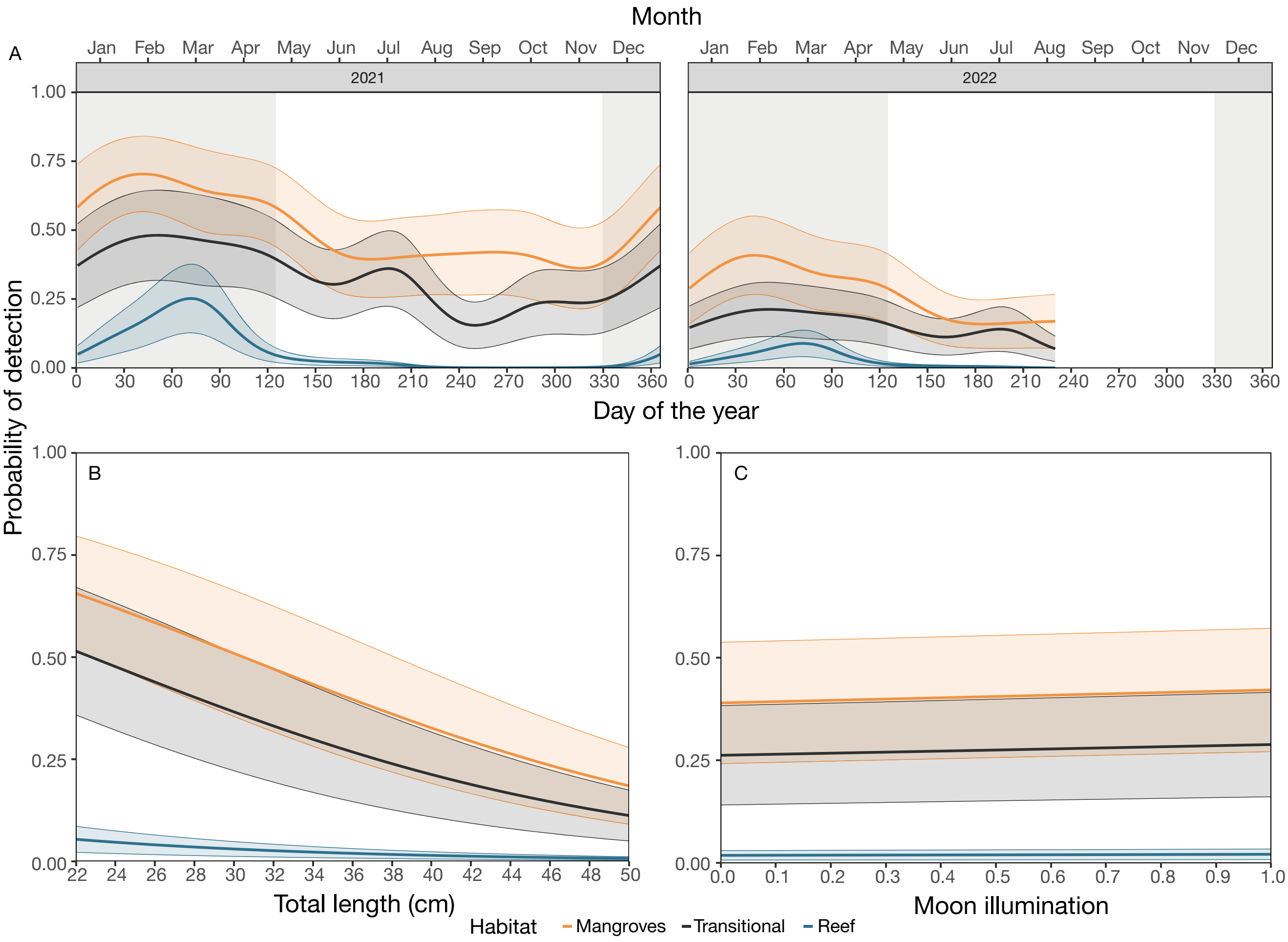

Fig. 6. Predicted effect of (A) day of the year for years 2021 and 2022, (B) total length, and (C) moon illumination on probability of occurrence for the Colorado snapper *Lutjanus colorado* for each habitat (mangroves, transitional and reef) fitted from selected generalized additive mixed model. Shaded areas: 95% CIs

Table 5. Summary of selected generalized additive mixed model of the effects of multiple drivers on probability of occurrence for the dog snapper *Lutjanus novemfasciatus* in Santa Elena Bay, Costa Rica, from January 2021 until August 2022. DOY: day of year

Parameter	Estimate ± SE	95% CI	z	df	p
n = 26775; R^2 = 0.18; R^2 marginal = 0.36; R^2conditional = 0.43					
Intercept	016 ± 0.19	[−0.21, 0.53]	0.86	26743.34	0.39
Habitat: transitional	−0.65 ± 0.04	[−0.72, −0.57]	−17.06	26743.34	<0.001
Habitat: reef	−3.18 ± 0.04	[−3.25, −3.10]	−84.02	26743.34	<0.001
Year 2022	−0.87 ± 0.17	[−1.20, −0.54]	−5.21	26743.34	<0.001
s (DOY) × habitat mangroves			46.01	7.24	<0.001
s (DOY) × habitat transitional			45.18	6.96	<0.001
s (DOY) × habitat reef			306.73	7.18	<0.001
s (temperature)			14.94	3.14	0.002
s (wind speed)			28.29	3.14	<0.001

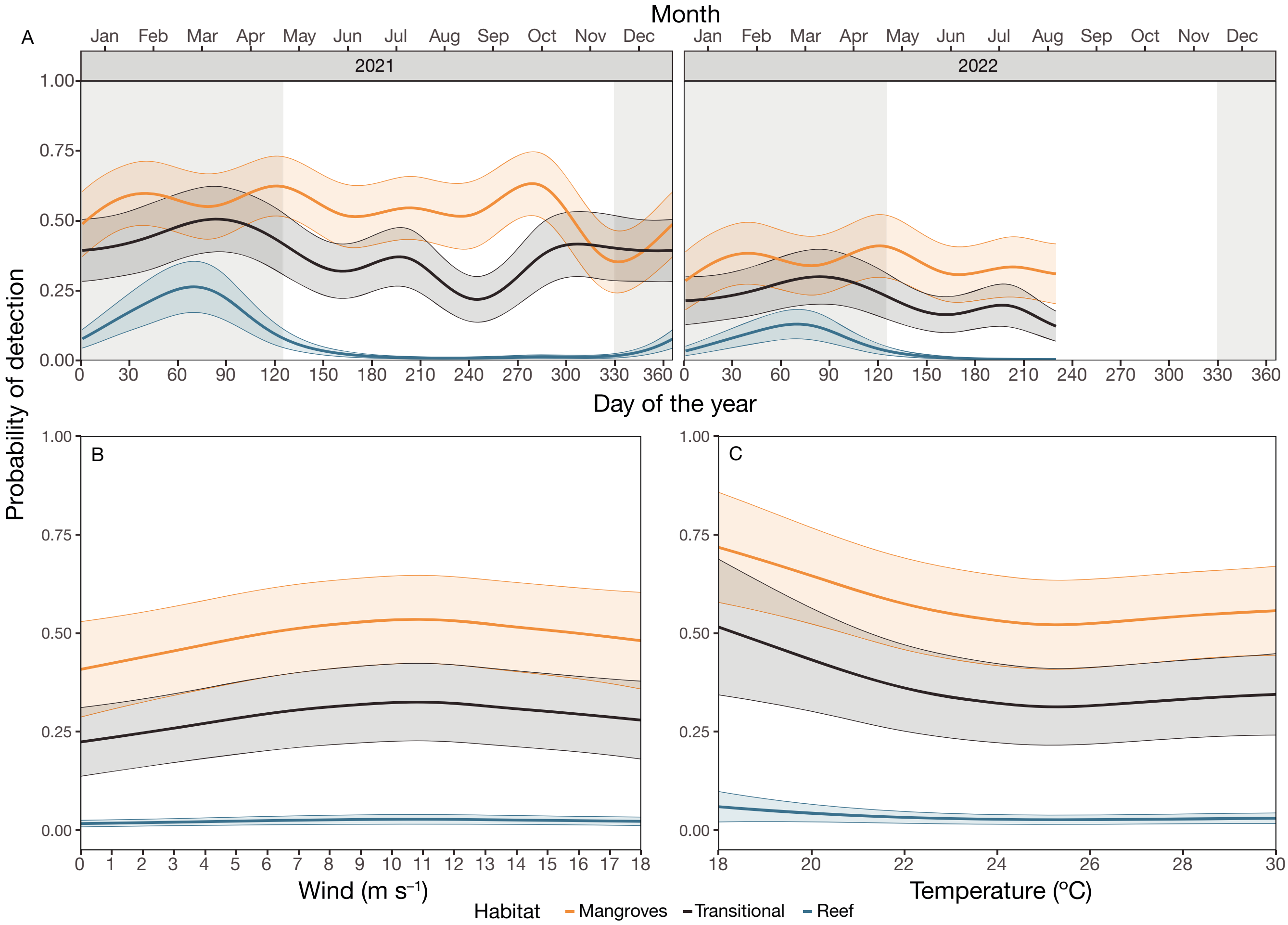

Fig. 7. Predicted effect of (A) day of the year for years 2021 and 2022, (B) wind speed, and (C) temperature on probability of occurrence for the Pacific dog snapper *Lutjanus novemfasciatus* for each habitat (mangroves, transitional and reef). Fitted from selected generalized additive mixed model. Shaded areas: 95% CIs

ginally affected the occurrence of *L. novemfasciatus*, likely due to the lack of more locally specific wind speed data or the fact that wind intensity was not as relevant as the duration of sustained wind speeds (Bohaboy et al. 2022). It is also unlikely that the wind hindered receiver detection efficiency, as previously tested (Matley et al. 2022). Environmental drivers not accounted for in this study could also influence space use by our study species; for example, hypoxia, which has been reported near the mouth of the bay (Lizano & Alfaro 2015, Stuhldreier et al. 2015). Short-term temperature fluctuations can affect space use of snappers due to physiological mechanisms like digestion (Williams-Grove & Szedlmayer 2017, Bacheler et al. 2021, Bohaboy et al. 2022). Therefore, analyses at finer temporal scales may clarify how environmental variability shapes the snappers' use of the bay. A meta-analysis by Erisman et al. (2020) indicated that density-dependent mechanisms, particularly competition, predation, habitat quality and availability, may be more significant drivers of red snapper *L. campechanus* densities than physical environmental variables, particularly for juveniles. Thus, the low effect of environmental variables in our study suggests that biological condition and interactions may play a more critical role in shaping the spatial behavior of the studied snappers within Santa Elena Bay. The lack of significant effects from temperature or wind may indicate some level of resilience to environmental change. However, other variables like oxygen concentration should also be considered to assess how changes in habitat suitability affect them.

Studies in the bay and region have revealed shifts in the spatial assemblages of fish between upwelling and non-upwelling periods (Eisele et al. 2020, Arias Zumbado 2021). In our study, although occurrence probability did not exhibit clear seasonal patterns, movement extent did. During upwelling, snappers roamed more widely and utilized habitats they typically did not frequent often, particularly outer reef areas, more extensively. Upwelling alters both the biomass and assemblages of fishes as a cascading effect along with the physical conditions that influence habitat suitability (Kämpf & Chapman 2016). Thus, this seasonal shift in space use could be attributed to either biological factors, such as changes in resource availability and intra- or interspecific interactions, or physiological reasons due to the mosaic of oceanographic conditions in the bay.

On the one hand, Arias Zumbado (2021) carried out a study of the assemblages of different trophic levels of fish and described an increase in planktivorous fish within Santa Elena Bay during the first 2 mo of the upwelling and a lagged increase in carnivorous fish in the following months. Fish biomass in the bay, particularly of piscivores, peaked around March and April. This increase in the biomass of planktivorous fish likely provides more prey availability and ultimately influences their movement patterns (Arias-Zumbado 2021). On the other hand, a study conducted during non-upwelling months showed that heterogenous conditions across the bay may occur given its geomorphology and water circulation patterns (Tisseaux-Navarro et al. 2021). The reefs are where a higher abundance of snappers occurred, particularly in the case of *L. novemfasciatus*, during upwelling months. This was more evident during the second year, coinciding with a stronger La Niña index (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php), which intensifies upwelling conditions (Leung et al. 2019). Thus, the change in the movement extent of snappers between seasons could potentially be explained by the combined effects of environmental variability and resource availability. Based on previous studies on other snapper species where densities were mostly shaped by density-dependent mechanisms rather than physical environmental conditions (Erisman et al. 2020), we consider that the evidence of our study suggests mostly a seasonal pattern related to changes in resource availability. However, a deeper examination of the conditions within Santa Elena Bay coupled with trophic ecology may help elucidate if shifts are driven by changes in habitat suitability conditions or due to density-dependent mechanisms.

The findings of this study have important implications for fisheries management, particularly in estuarine tropical bays. Our results suggest that Santa Elena Bay may act as a nursery for *L. novemfasciatus* and for transitional stages for early adult *L. colorado*, which likely contributes to their adult populations and fisheries through spillover as the snappers grow. Apart from contributing to the adult populations, the key to confirming Santa Elena Bay as a nursery ground is to compare its relative importance to other sites in terms of juvenile density and contribution (Beck et al. 2001). Since we focused on single life stages for each of our tagged species, further demographic studies coupled with movement analyses on a variety of life stages at different sites could help confirm the nursery ground function of Santa Elena Bay. Although we initially expected environmental variables to significantly influence the movement and habitat use of our study species due to upwelling, the behavior of the young snappers tracked in Santa Elena Bay appeared to be primarily driven by a complex interaction among ontogenetic, biological and environmental dynamics. Longer-term monitoring across multiple years that includes other environmental variables like oxygen levels would provide a more comprehensive understanding of how snappers respond to environmental change. Implementing spatial protection measures in similar settings that protect habitats suitable for snapper populations at different life stages and ensuring connectivity between them to support growth and reproduction can benefit snapper populations. Additionally, our results suggest that further evaluation and attention to seasonal patterns is key to guiding potential seasonally dynamic management measures, as the occurrence of snappers in the bay may vary across habitats between upwelling and non-upwelling months. Further research is essential to unravel the dynamics driving the spatiotemporal patterns of fish within the bay. This involves investigating trophic ecology and the coexistence of snapper species inhabiting the bay and the degree of connectivity between Santa Elena Bay and other habitats along the coast. Additionally, a finer-temporal-scale examination of snapper spatial behavior, accounting for environmental drivers of habitat use not considered in this study, should be carried out. Increasing our understanding of these patterns would contribute substantially to more accurate predictions.

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