Movement Patterns of Juvenile Blacktip Sharks (*Carcharhinus limbatus*) within a Tropical Nursery Habitat

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAIʻI AT HILO IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

TROPICAL CONSERVATION BIOLOGY & ENVIRONMENTAL SCIENCE

May 2025

By

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Keywords: distribution, acoustic telemetry, estuary, environmental parameters, temporal, diel, site fidelity, Hawaiʻi

Abstract

Blacktip sharks (*Carcharhinus limbatus*) are a circumglobal species that rely on nearshore nursery habitats during their early years. Very little is known of the movement patterns and habitat usage of blacktip sharks in the Hawaiian Islands, and no nursery habitats have yet been designated for this species within Hawaiʻi. For this study, juvenile blacktip sharks (n = 29) were caught and tagged in Hilo Bay, Hawaiʻi, USA, using VEMCO V-13 PPM acoustic transmitters. Tracking occurred every 2-5 weeks between July 2022 and January 2024 at 44 stations throughout Hilo Bay using a VR-100 receiver and VH-165 omnidirectional hydrophone. Results showed that juvenile blacktip sharks were present in the Bay year-round with peak occurrence of tagged individuals (41.3-50.0%) between March and August, and more limited occurrence (24.1-30.1%) between October and January. Tagged sharks were detected within Hilo Bay more during the day than at night, likely due to excursions into deeper waters during heightened nocturnal foraging activity. Accordingly, blacktip sharks were detected more frequently in deeper waters at night. Detections were significantly higher in areas where the benthic composition was predominately mud as opposed to coral or rock. Temperature and salinity did not significantly vary among stations, and as such, were not influential factors in habitat use, though DO appeared to limit habitat use during the day when concentrations were lowest. Thus, juvenile blacktip sharks appear to preferentially utilize deeper habitats with mud substrates within Hilo Bay and are limited in these areas by DO. The lowest levels of DO were recorded during the months with the fewest sharks detected in the Bay, suggesting that oxygen requirements may be limiting both spatial and temporal habitat usage. The results presented here are the first to delineate Hilo Bay as a blacktip shark nursery habitat in Hawaiian waters and suggest that this population of blacktip sharks reside predominantly within Hilo Bay for the first few years of their life.

Introduction

In marine ecosystems around the world, sharks influence the structure and stability of food webs (Bascompte et al., 2005). Sharks are predominantly apex predators and help maintain healthy populations through top-down control by preying on weak and injured animals (Motivarash et al., 2020). Reef biodiversity is closely tied to the presence of sharks, and many elasmobranchs are considered keystone species due to their disproportionate influence on ecosystem health (Baum & Worm, 2009; Ruppert et al., 2013). Despite their importance, shark populations have rapidly declined over the last half-century, have become functionally extinct from 20% of reef ecosystems, and the abundance of oceanic sharks has declined by more than 70% (MacNeil et al., 2020, Pacoureau et al., 2021). Elasmobranchs are at severe risk for overexploitation due to low fecundity, heightened fishing pressure, and habitat degradation (Ward-Paige et al., 2012; Dulvy et al., 2021). To increase offspring survivorship, many coastal shark species rely on near-shore nursery habitats (Simpfendorfer & Milward, 1993).

Shark nurseries exist in nearly all tropical to temperate coastal regions and act as essential habitats for young sharks, as well as the coexisting marine life (Castro, 1996; Heupel et al., 2007). Nursery areas exhibit considerable variations in size, benthic features, and species composition, though they are most common in semi-enclosed, shallow areas of high productivity such as estuaries or mangrove marshes (Hoenig & Gruber, 1990; Castro, 1993; Bethea et al., 2004). Following the criteria defined by Heupel et al. (2007), shark nursery habitats are areas in which juvenile (1) shark density is greater inside the area than surrounding areas, (2) sharks exhibit site fidelity and return to the habitat for long periods of time, and (3) sharks repeatedly use the area over several years. Traditionally, the greatest benefits of these areas were thought to be the abundance of small prey and fewer large predators (Branstetter, 1990; Simpfendorfer &

Milward, 1993). However, recent studies have also shown nursery habitats may reduce osmoregulatory stress on marine inhabitants, particularly juveniles (Matich et al., 2021).

Blacktip sharks (*Carcharhinus limbatus*) are a near-shore species found circumglobally in tropical to temperate waters (Garrick, 1982). They maintain residence in shallow coastal regions less than 140 m in depth and are considered one of the most important commercial and recreational shark species in the US (Castro, 1996). These opportunistic predators have a diet primarily of small fish, but will also consume squid, shrimp, and other elasmobranchs if available (Barry et al., 2008; Matich et al., 2021). Life history varies regionally for this species; blacktip sharks reach maturity between 160-210 cm total length (TL), and size at birth can be 38-72 cm TL (Compagno, 1984; Dudley & Cliff, 1993; Crow et al., 1996). Mature females give birth to small litters of 1-11 live young every 2-3 years in the same nursery area they were born in (Branstetter, 1987; Gardiner et al., 2015; Matich et al., 2021). Blacktip shark pupping season occurs at the end of spring; May-June in the Northern Hemisphere, and November-December in the Southern Hemisphere (Heupel & Simpfendorfer, 2002; Harry et al., 2012).

Juvenile blacktip sharks have frequently been the subject of nursery-focused studies due to their high abundance and wide regionality (Capapé et al., 2004; Speed et al., 2010; Passerotti & Baremore, 2012; Tinari & Hammerschlag, 2021). Length of residency within a nursery habitat is closely tied to seasonal shifts, with peak blacktip shark presence in the late spring and summer months (Heithaus, 2007; Legare et al., 2015). In subtropical and temperate regions, blacktip shark pups tend to remain within the nursery until late fall, regardless of site fidelity and the varying rate of return in following summers (Castro, 1996; Heupel, 2007; DeAngelis et al., 2008). In the Gulf of Mexico, mean residence time is 21 weeks from birth, and all young-of-year (YOY) blacktip sharks tend to leave their natal grounds by week 28 (Heupel & Simpfendorfer, 2005). Older juveniles commonly demonstrate philopatry, with olfactory cues guiding them back to their natal nursery the following spring (Gardiner et al., 2015).

Seasonal environmental changes likely influence the movement patterns of juvenile blacktip sharks within and out of their nursery habitats (Chapman et al., 2015; Matich et al., 2021). For example, sudden decreases in water temperature of 4-5°C in the Northeastern Gulf of Mexico have been identified as a cue for blacktip sharks to move to deeper waters, and the juveniles generally begin leaving the nursery areas before temperatures reach 21°C (Heupel, 2007). Conversely, if the water temperature within the nursery remains above 21°C, YOY blacktip sharks may reside for longer than one season. For example, in the US Virgin Islands where shark nurseries have an annual water temperature range of 25-32 ºC, a portion of YOY blacktip sharks are present year-round with some remaining for several years (Legare et al., 2015). This suggests that when nursery habitat availability is not limited by environmental fluctuations, blacktip sharks may preferentially remain in their natal home range for an extended period, likely until they outgrow their food source. Further, temperature has been shown to influence the fine-scale movement patterns of juvenile sharks within a nursery habitat, with blacktip sharks most commonly found in waters close to 26°C (Tinari & Hammerschlag, 2021). Environmental factors such as salinity, dissolved oxygen, depth, and benthic habitat have also been shown to influence habitat usage within shark nurseries (Branstetter, 1990; Tavares, 2008). Moreover, evidence suggests that the narrow range of temperatures and salinities that juvenile sharks inhabit may lower energetic costs of osmoregulation and promote growth (Heupel & Simpfendorfer, 2008).

Diel shifts in activity and movement patterns are a common trend observed in many aquatic species (Speed et al., 2010). Time of day, length of day, and time of sunset have all been shown to influence fine-scale distribution patterns of blacktip sharks (Legare et al., 2015). Heightened nocturnal activity levels are commonly observed, and juveniles tend to make their furthest excursions at night (Legare et al., 2018). For example, in the Caribbean, juvenile blacktip sharks have been observed making rapid movements to the far end of their nursery habitat in the first hour after sunset, then gradually returning to their core area before sunrise (Speed et al., 2010). Since prey fish tend to undergo similar nocturnal journeys to deeper waters, it is believed that this diel trend exhibited by many shark species is due to heightened foraging activity (Holland et al., 1992; Cartamil et al., 2010). Comprehensive coastal management requires a thorough understanding of local marine life and oceanic processes, which can be limited in isolated, lesser-studied regions. No nursery habitats have been delineated for blacktip sharks in Hawaiʻi, and their residency and habitat usage are ambiguous (Garrick, 1982; Crow, 1996).

The aim of this study was to determine how temporal, spatial, and diel shifts influence the distribution and movement patterns of juvenile blacktip sharks in Hawaiian waters. I hypothesized that without the threat of seasonal thermal stress, the sharks would be present in suspected nurseries year-round, with fewer shark detections expected in the fall/winter months than in the spring/summer months. I also expected to observe diel shifts in habitat usage and detection frequency. Lastly, I theorized that environmental parameters (temperature, salinity, dissolved oxygen, depth, benthic composition) would impact the fine-scale distribution of juvenile blacktip sharks, and that the influence of each environmental parameter on shark detection frequency would differ by time of day.

Methods

Site description

This study was conducted in Hilo Bay, Hawai‘i, USA, on the windward side of the Island of Hawai‘i (Fig. 1). Hilo Bay is an estuary partially enclosed by a 3-km breakwater and has a surface area of 6.4 km^2. Depths reach up to approximately 16 m, with the deepest areas in the dredged channel leading from the breakwater opening to the Port of Hilo on the inner east side of the Bay. Benthic habitat is primarily mud and rocky rubble, though patchy coral reefs extend from the breakwater inside and outside Hilo Bay to form Blonde Reef (Paquay et al., 2007) (Fig. 2). The city of Hilo, along the coast of Hilo Bay, is one of the rainiest cities in the United States receiving an average of 300+ cm of rainfall every year (US Department of Commerce, 2023). The Wailuku and Wailoa Rivers are the primary freshwater inputs to the Bay, the former of which is the largest river in the State of Hawai‘i. The flow of both rivers varies significantly, with higher input in the wet season (Oct.-April) and lower input in the dry season (May-Sept.) (Waiki et al., 2025). This location was selected as it has been the site of mark-recapture studies on elasmobranchs via the University of Hawai‘i at Hilo for over a decade (J. Turner, unpublished data).

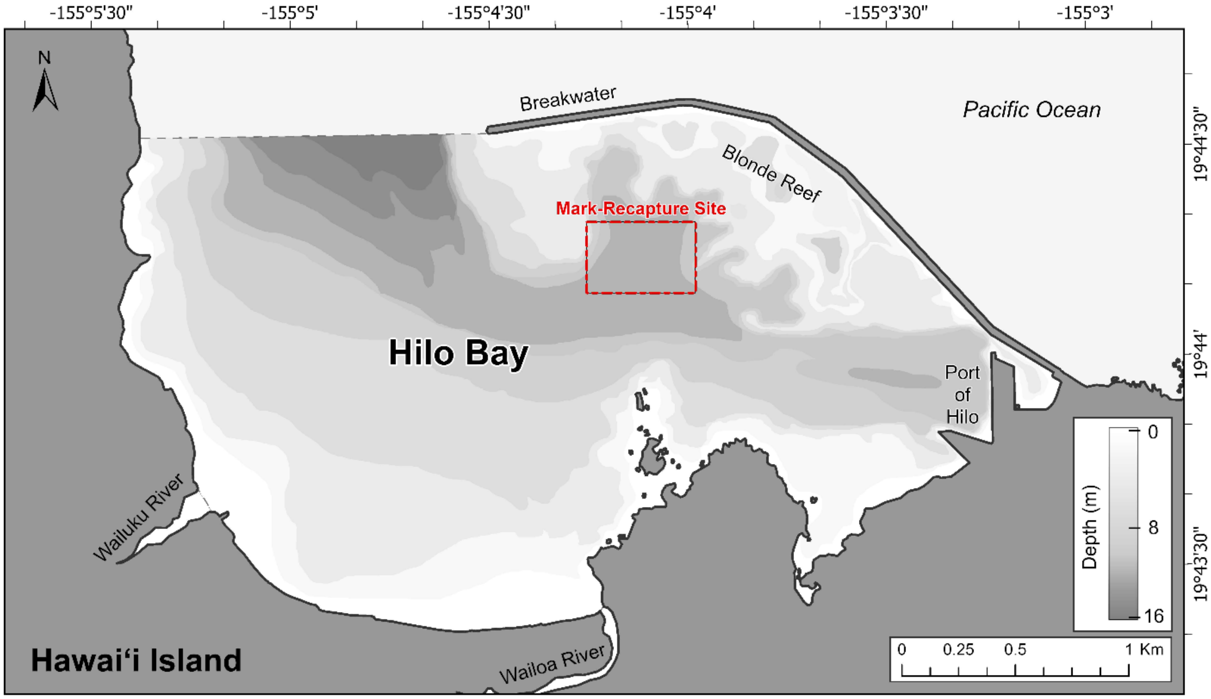


Figure 1. Study site of Hilo Bay, Hawai'i, USA, showing freshwater inputs from the Wailuku and Wailoa River as well as the structured inner Blonde Reef. Bathymetry lines show depths ranging from 0 to 16 m within the Bay, and the grey dashed line shows the entrance to Hilo Bay and the extent of the sampling area. Shark tagging took place within the red box.

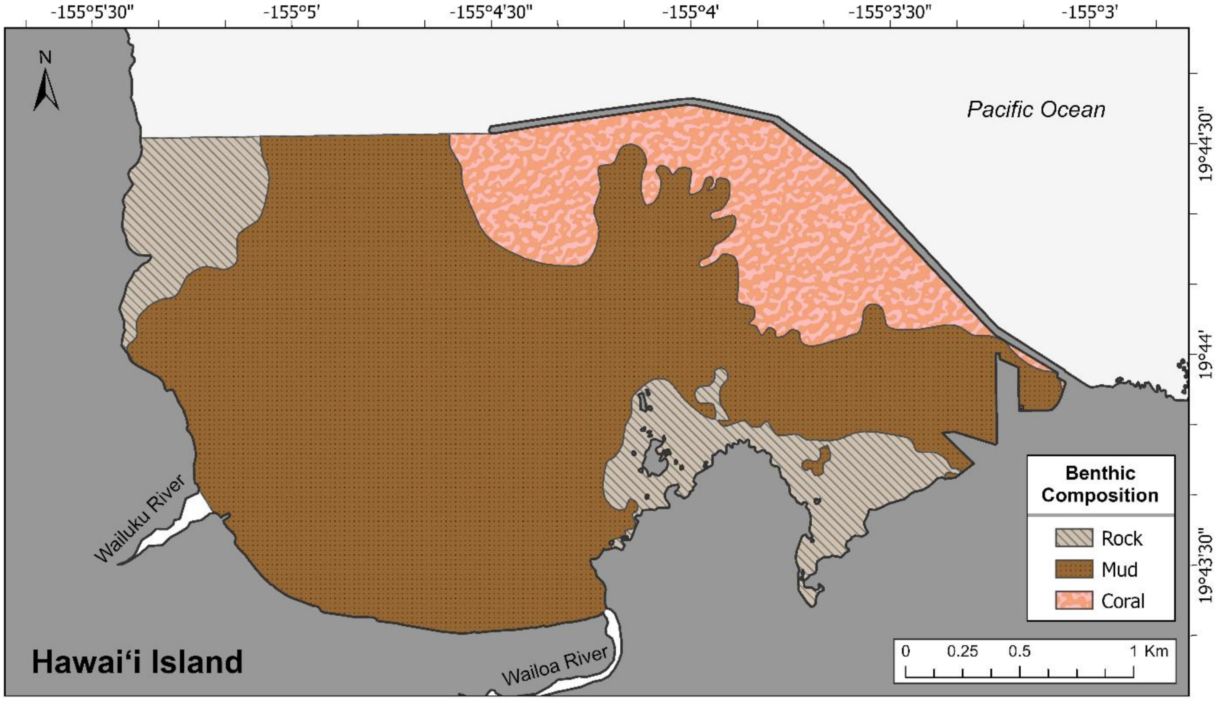


Figure 2. Benthic composition within Hilo Bay, Hawai'i, USA; after Coyne et al. (n.d.) via NOAA's National Oceanographic Data Center (Accession No. 0001329).

Tagging operations were conducted from June 10 to July 6, 2022, and from June 2 to June 30, 2023, between the hours of 17:00-22:00 HST. Two benthic trot lines, 30 m in length, were set and baited with 8-12 Pacific sardines (*Sardinops sagax*) on 13/0 tuna circle hooks using 200 lb. monofilament leaders 60 cm in length. Lines were checked every thirty minutes, and once captured, leaders were transferred from the benthic trot line to a 3 m, 9.52 mm diameter polypropylene rope for assessment and tagging. Sharks were caught and released between the inner Blonde Reef and the dredged channel of Hilo Bay, where depths averaged 13 m. Although juvenile blacktip sharks were primarily caught (average of 3-8 per day), sandbar sharks (*Carcharhinus plumbeus*) and tiger sharks (*Galeocerdo cuvier*) were also caught on occasion. Sharks remained in the water during the entire handling process to reduce stress and limit post-release mortality (Mohan et al., 2020). Umbilical scar presence and sex were recorded, and total length (TL), fork length, girth, dorsal fin height, dorsal fin width, and mouth gape were measured, though only TL was used in the present study. Sharks were designated as YOY or age 1+ based on presence of an open umbilical scar (Debaere et al., 2023).

Overall health and activity were considered prior to selecting individuals for acoustic tagging, and only blacktip sharks were included in the study. VEMCO V-13 pulse position modulation (PPM) transmitters were surgically implanted in the lateral body wall following the methodology of Legare et al. (2018). Incisions were closed with 2-3 0.58 mm diameter surgical staples. Acoustic tag activation was verified during release using a VEMCO VH-165 omnidirectional hydrophone connected to a VR-100 portable receiver. The tags placed in 2022 had a transmission time of 90-150 seconds, and those placed in 2023 had a transmission time of 40-100 seconds. A range test tag was used to verify reception distance, which was measured at

700 m from receiver at the surface. A total of 29 juvenile *C. limbatus* were fit with acoustic transmitters and included in the study: 14 in 2022, and 15 in 2023.

Acoustic telemetry tracking

Forty-four sampling stations were identified in Hilo Bay through spatial gridding, in which stations were set ~500 m apart (Fig. 3). This allowed for significant coverage of the study site and slight overlap of acoustic reception between monitored stations. Biweekly acoustic tracking surveys (n = 16) were conducted between July 20 and October 27, 2022, and approximately monthly surveys (n = 26) from November 2022 to January 2024. No sampling occurred in the months of February or June due to weather conditions and tagging operations. Sampling consisted of paired diurnal (08:00-14:00) and nocturnal (18:00-24:00) surveys in a single 24-hour period. Stations were located using GPS and physical markers, and all were monitored once per survey, twice per sampling day. The order of stations visited was randomized between dates to ensure stations were not sampled at exactly the same time of day or night. Areas outside of Hilo Bay breakwater (≈ 1,000 m) and inside the Wailoa river estuary (< 100 m) were sampled haphazardly throughout the study but not included in the station design.

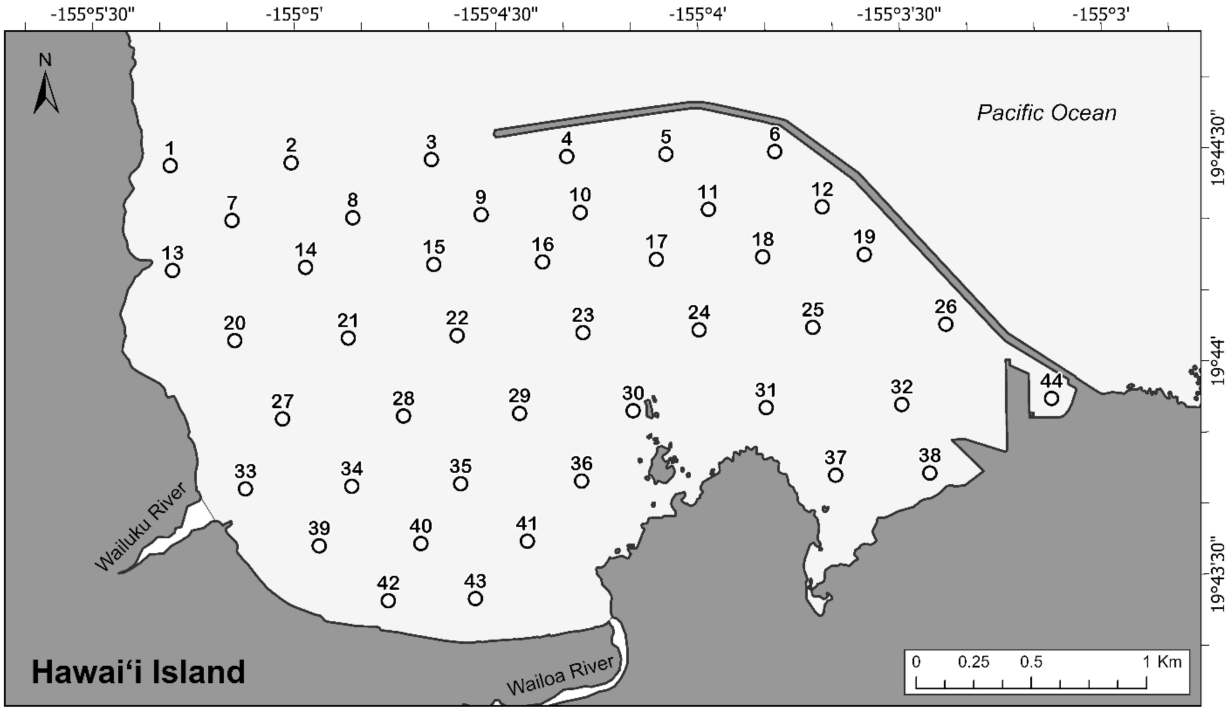


Figure 3. Map of Hilo Bay, Hawaiʻi, USA showing stations 1-44 sampled in juvenile blacktip shark acoustic telemetry tracking surveys (July 20, 2022 – January 28, 2024).

A VEMCO VH-165 omnidirectional hydrophone was connected to a VR-100 portable receiver and deployed at each station from a rigid-hull inflatable boat for five minutes to maximize reception time and was 2-7 times the transmission rate of the tags used in this study. Temperature, salinity, and DO were collected 1 m above the sea floor, midwater, and at the surface at each station using a YSI Pro2030. Depth was measured using a HawkEye DT1H Handheld Depth Finder and converted to meters. GPS position of each station was recorded and later verified using a Garmin handheld GPSMAP 86sc.

Statistical analyses

Five sharks (8825, 8835, 9261, 9265, 9267) were not detected on any tracking cruises post-tagging, but still included in statistical analyses due to the assumption that the animals were active but left the confines of the study area and did not return to be detected. The correlation between TL and detection frequency (proportion of times each shark was detected) was determined using a Kendall's rank correlation due to non-normality and ties, and the correlation between TL and observed residency period was determined through a Spearman's rank correlation. Hours of daylight (US Naval Observatory Astronomical Applications Department) were obtained to examine the temporal association between photoperiod and juvenile blacktip shark presence within Hilo Bay. A Pearson's product-moment correlation test was performed to assess the relationship between daylight duration and the percentage of tagged individuals detected. A two-sided T-test was used to show diel differences in the average shark detections per station. To determine whether stations were being used equally, a chi-square test was performed. Then, a Fisher's Exact Test was conducted to examine whether sharks used the same number of stations on diurnal and nocturnal surveys. Diel shifts in station use were calculated as the difference between the average number of diurnal detections and nocturnal detections at each station, and a spatial analysis of diel changes in habitat use was conducted. Kernel density geoprocessing was used to examine the density of shark detections within Hilo Bay using a ratio of mean detections per station to the number of times each station was sampled.

The water column at each station was characterized using the mean values for 1 m from the sea floor, midwater, and surface on each cruise. The average value from the three sampled depths were calculated for temperature, salinity, and DO, and were used in all statistical analyses. Kruskal-Wallis rank sum tests were performed to determine temporal and spatial variability in temperature, salinity, and DO. Box plots were created to show temporal variability via monthly ranges in water quality, and Empirical Bayesian kriging interpolations were created to show spatial variability in water quality across stations within Hilo Bay. Stations were classified by benthic habitat type using the NOAA National Oceanographic Data Center (Accession No. 0001329) as coral (n = 12), mud (n = 33), and rock (n = 5).

Generalized Additive Models (GAMs) were created to examine the influence of environmental parameters on habitat use. The GAM framework supports repeated station sampling, and additive smoothing functions allow non-linear relationships to be observed. The response variable, shark presence, was the number of individual sharks detected at a station on each survey. Explanatory variables used to develop GAMs included temperature, salinity, DO, depth, benthic habitat, hours of daylight, date, survey time (diurnal/nocturnal), and station. Models used a Poisson distribution with a log link function, which accounted for detection frequency being recorded as count data. A manual backwards stepwise procedure was used to determine the best fit model based on Akaike information criteria (AIC) and deviance explained (DE) following Dance & Rooker (2016). The final model was replicated twice to tease apart diel shifts in influential terms: first, using only diurnal data, then again using only nocturnal data. Statistical analyses were conducted within the program R v.4.3.3 ($\alpha = 0.05$), and GAMs were created using the R packages mgcv and MuMIn. Means are reported with ±SD. ArcGIS Mapping & Analytical Software (Ver. 10.8.2) was used to create maps and analyze spatial data.

Results

The TL of tagged blacktip sharks ranged from 73.1 to 98.4 cm (mean = 81.6 ± 6.32 cm) (Table 1). Only two sharks were considered YOY based on umbilical scar visibility (9264, 9266), and their measured TLs were 75.0 and 74.1 cm, respectively. Due to the small sample size of YOY (n = 2) compared to 1+ year individuals (n = 27) included in the present study, no tests were conducted with age as a variable. TL was expected to be an influential factor in detection frequency, but no significant relationship was observed (z = 1.436, tau = 0.194, p = 0.151) (Fig. 4).

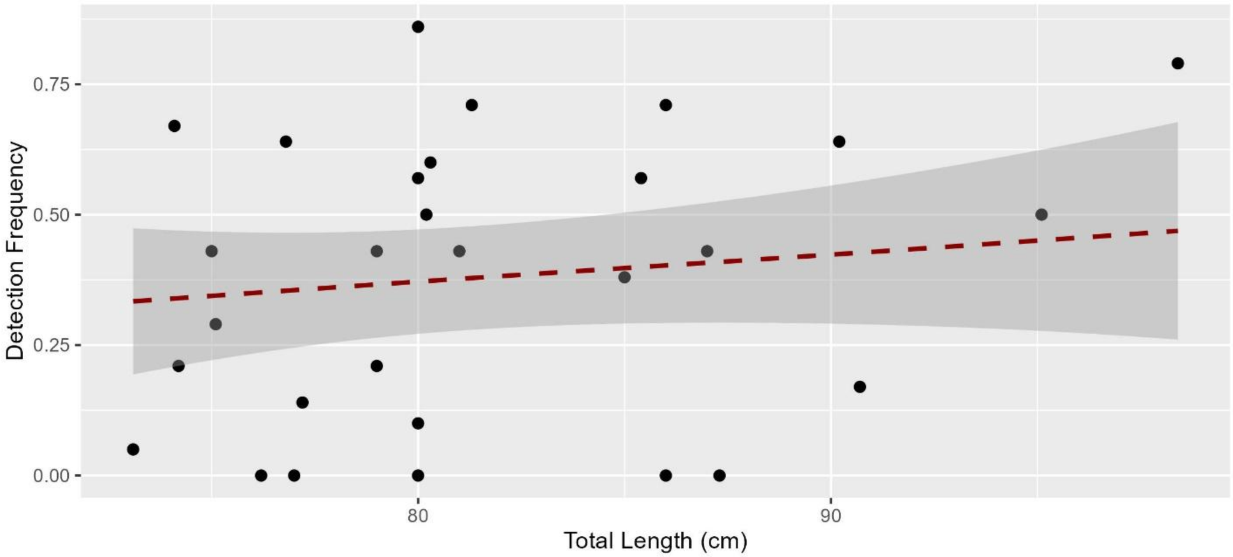


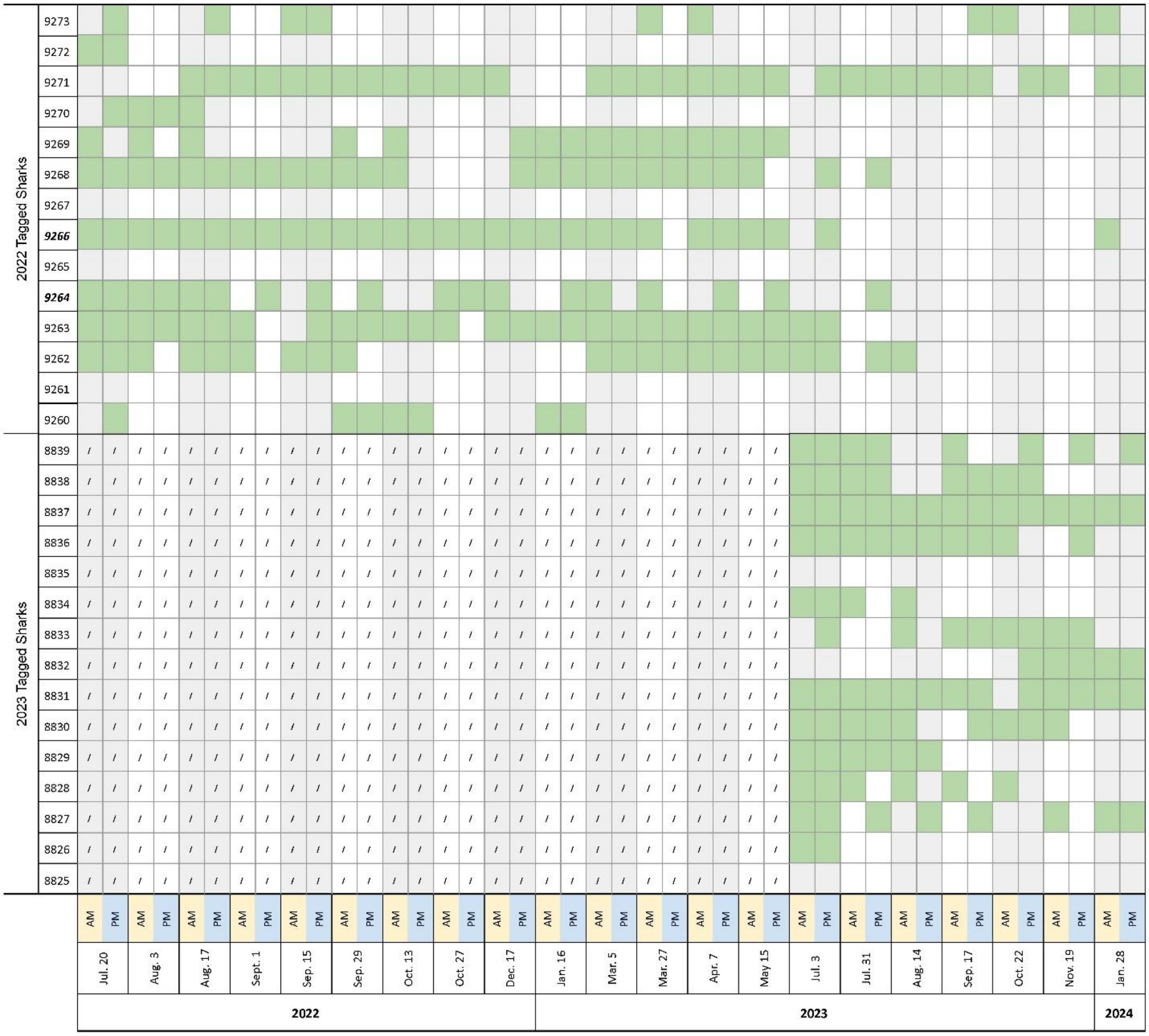
Figure 4. Relationship between total length (TL) and detection frequency (proportion of times detected) for tagged blacktip sharks in Hilo Bay during the survey period of July 20, 2022, to January 28, 2024. Red dashes show GAM regression lines, and the shaded dark grey areas represent 95% confidence intervals.

A total of 820 shark detections were recorded in Hilo Bay across all surveys (n = 42) between July 2022 and January 2024. Each detection represented a unique individual at a given station, such that repeated detections of the same shark at one station were only counted once, while detections at different stations on the same survey were recorded separately. Of the 29 tagged sharks, 24 were detected in at least one survey, and individual detection frequency ranged from 0-0.86 with a mean of 0.38 ± 0.272 (Table 2). Observed residency periods were calculated as the days between the first and last detection, regardless of periodic absences between the two dates. It is important to note that the majority (93%) of individuals were at least a year old at the time of tagging and sharks were still detected on the final day of sampling, meaning the observed residency period reported in this study is the minimum number of days that an individual utilized the nursery habitat. The longest observed residency period of an individual was 598 days, seen in shark 9273 who was present on the first and last day of sampling. The average residency period after tagging for the 2022 cohort (n = 14) was 287 days. There was no correlation between TL and observed residency (S = 3601.1, rho = 0.111, p = 0.567) (Fig. 5).

Table 1. Tag number and total length (TL) for all blacktip sharks included in the study. First and last detection days are listed along with the length of time between them (observed residency), and detection frequency is provided as a ratio of cruises detected to cruises with tag active. YOY tagged shark IDs are bolded and italicized.

Shark ID #	TL (cm)	Date Tagged	Last Date Detected	Observed Residency (days)	Detection Frequency
9260	90.7	Jun 10, 2022	Jan 16, 2023	220	0.17
9262	80.2	Jun 10, 2022	Aug 14, 2023	430	0.50
9270	80	Jun 10, 2022	Aug 17, 2022	68	0.10
9272	73.1	Jun 10, 2022	Jul 20, 2022	40	0.05
9273	74.2	Jun 10, 2022	Jan 28, 2024	598	0.21
9261	86	Jun 17, 2022	Jun 17, 2022	0	0.00
9264	75	Jun 17, 2022	Jul 31, 2023	409	0.43
9268	80.3	Jun 17, 2022	Jul 31, 2023	409	0.60
9265	76.2	Jun 24, 2022	Jun 24, 2022	0	0.00
9271	86	Jun 24, 2022	Jan 28, 2024	584	0.71
9263	90.2	Jul 1, 2022	Jul 3, 2023	367	0.64
9269	85	Jul 1, 2022	May 15, 2023	318	0.38
9266	74.1	Jul 6, 2022	Jan 28, 2024	572	0.67
9267	87.3	Jul 6, 2022	Jul 6, 2022	0	0.00
8825	77	Jun 2, 2023	Jun 2, 2023	0	0.00
8827	81	Jun 2, 2023	Jan 28, 2024	240	0.43
8828	87	Jun 2, 2023	Oct 22, 2023	142	0.43
8829	79	Jun 2, 2023	Aug 14, 2023	73	0.43
8831	98.4	Jun 9, 2023	Jan 28, 2024	233	0.79
8839	95.1	Jun 9, 2023	Jan 28, 2024	233	0.50
8832	79	Jun 26, 2023	Jan 28, 2024	217	0.21
8833	80	Jun 26, 2023	Nov 19, 2023	146	0.57
8834	75.1	Jun 26, 2023	Aug 14, 2023	49	0.29
8826	77.2	Jun 28, 2023	Jul 3, 2023	5	0.14
8836	81.3	Jun 28, 2023	Nov 19, 2023	144	0.71
8837	80	Jun 28, 2023	Jan 28, 2024	214	0.86
8838	85.4	Jun 28, 2023	Oct 22, 2023	116	0.57
8830	76.8	Jun 30, 2023	Nov 19, 2023	142	0.64
8835	80	Jun 30, 2023	Jun 30, 2023	0	0.00

Table 2. Tag detections of blacktip sharks in Hilo Bay on each cruise (AM/PM) from July 20, 2022, to January 28, 2024. Green boxes indicate that an animal was detected, white boxes indicate that the tag was active but the animal was not detected, and crossed boxes indicate that the tag was not active. YOY tagged shark IDs are bolded and italicized.



2022 Tagged Sharks	9273	☐	🟩	☐	☐	☐	🟩	☐	☐	🟩	🟩	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	🟩	☐	🟩	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	🟩	🟩	☐	☐	🟩	🟩	☐
	9272	🟩	🟩	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
	9271	☐	☐	☐	☐	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	☐	☐	☐	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	☐	🟩	🟩	🟩	🟩	🟩	🟩	🟩	☐	🟩	🟩	☐	🟩	🟩
	9270	☐	🟩	🟩	🟩	🟩	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
	9269	🟩	☐	🟩	☐	🟩	☐	☐	☐	☐	☐	🟩	☐	🟩	☐	☐	☐	☐	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
	9268	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	☐	☐	☐	☐	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	☐	☐	🟩	☐	🟩	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
	9267	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
	9266	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	☐	🟩	🟩	🟩	🟩	☐	🟩	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	🟩	☐
	9265	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
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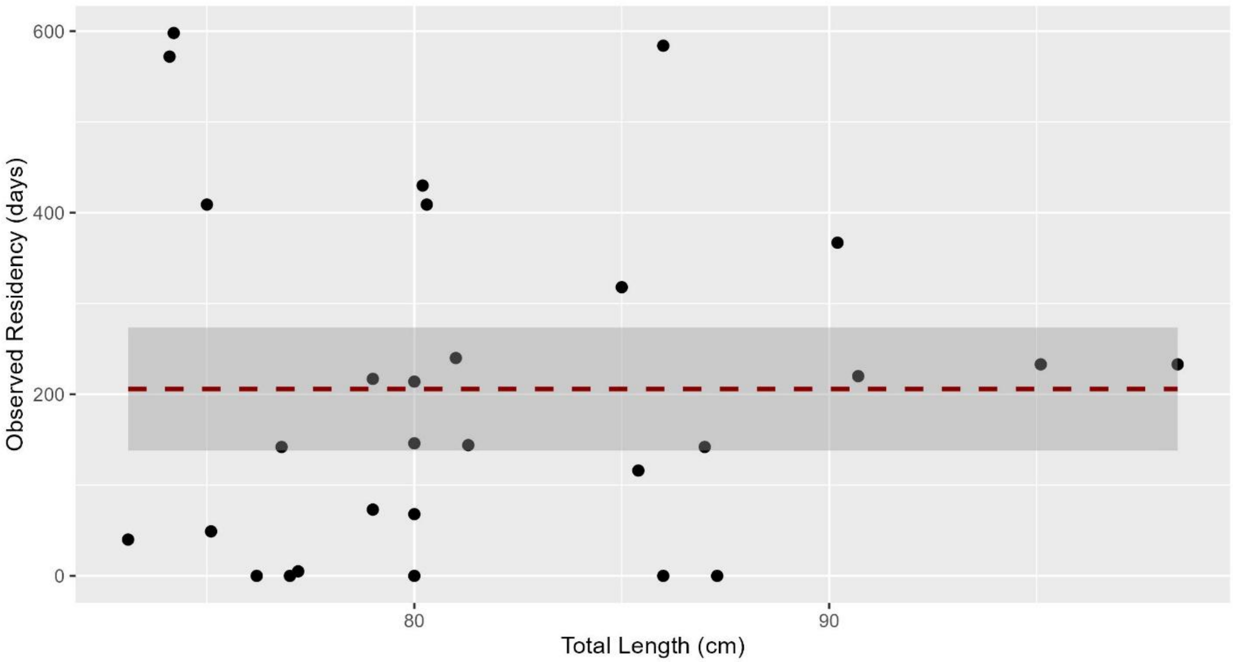

Figure 5. Relationship between total length (TL) and observed residency (number of days between first and last detections) for tagged blacktip sharks in Hilo Bay during the survey period of July 20, 2022, to January 28, 2024. Red dashes show GAM regression lines, and the shaded dark grey area represents 95% confidence intervals.

Peak occurrence was observed between March and August, in which 41.3 to 50.0% of tagged sharks were detected each month, while the fewest sharks (24.1-30.1%) were detected between October and January (Fig. 6). At least 20.7% of tagged sharks were detected on every survey, with a high of 64.3% and a mean of 38.4 ± 11.5%. There was a significant correlation between hours of daylight and individual sharks detected on each day of sampling ($t = 3.576$, $df = 19$, $p = 0.002$), with more juvenile blacktip sharks detected in the Bay on longer days (Fig. 7).

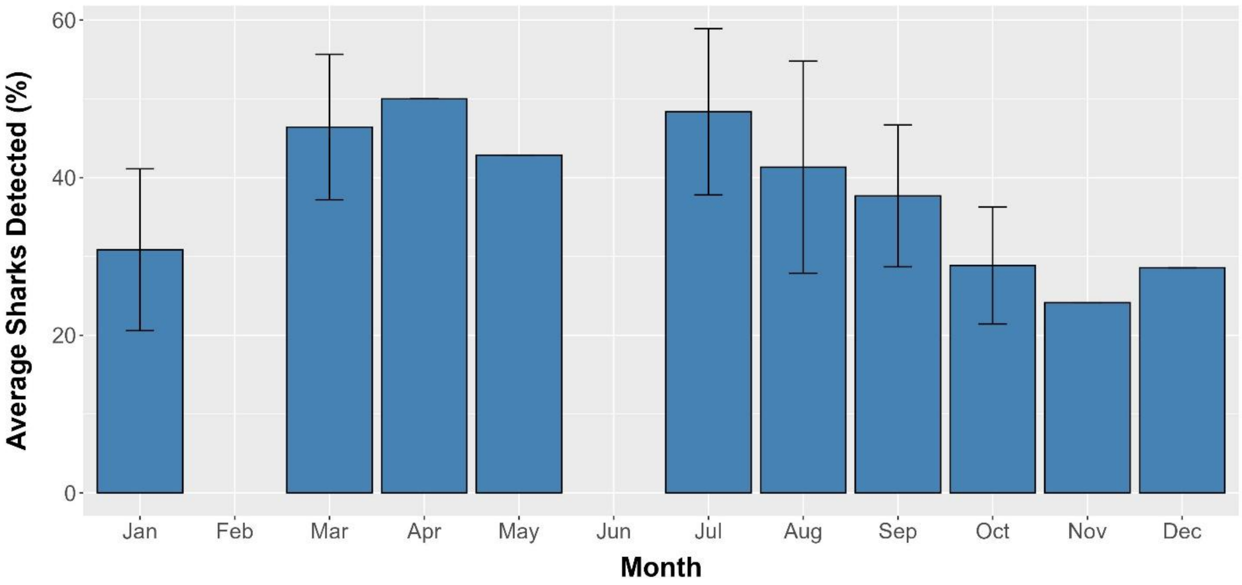

Figure 6. Monthly averages for percentage of tagged blacktip sharks detected each survey (July 20, 2022 - January 28, 2024), with error bars showing standard deviation for months with multiple days of sampling. No surveys occurred in February or June.

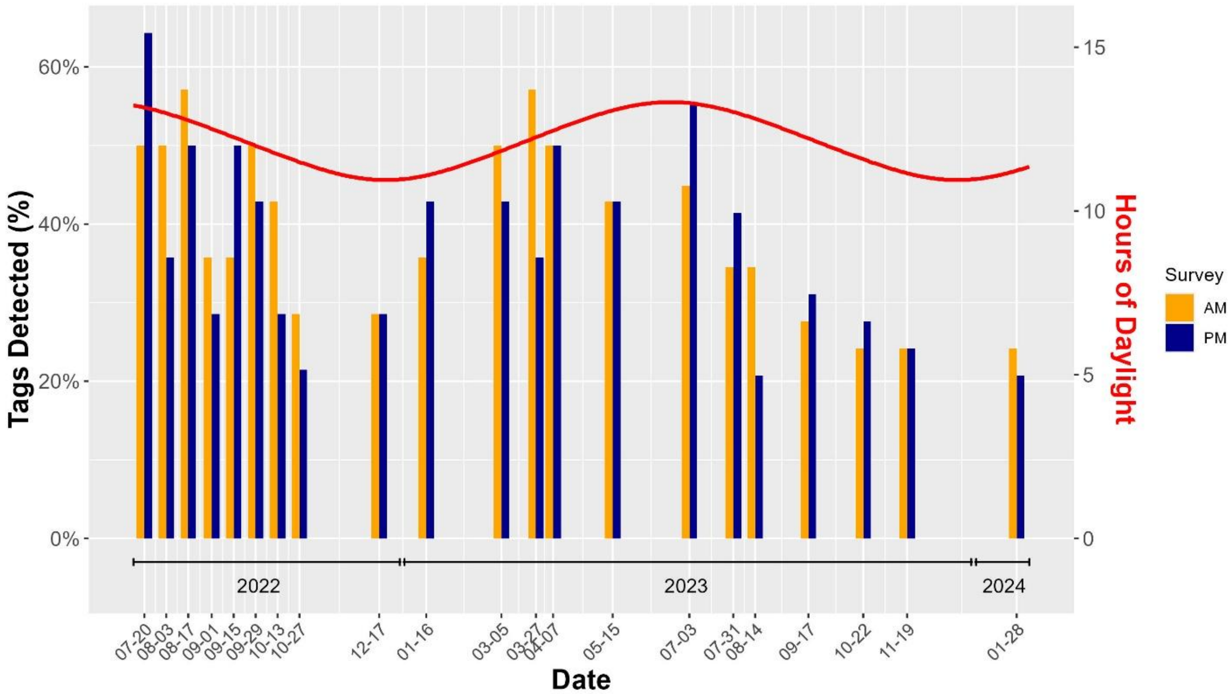

Figure 7. Percentage of tagged blacktip sharks detected on each cruise (orange = diurnal, blue = nocturnal). The red line shows the hours of daylight each day for the duration of the study period (July 20, 2022 - January 28, 2024), which stands to represent seasonality and show the relationship between detection frequency and time of year. No surveys occurred in February or June.

Total detections were greater during diurnal cruises (n = 466) than nocturnal cruises (n = 370). There was a significant difference in average shark detections per station between diurnal and nocturnal surveys (t = 2.704, df = 1801.1, p = 0.007) with more detections during diurnal cruises (0.496 ± 0.889) than nocturnal cruises (0.392 ± 0.758). Results showed that juvenile blacktip sharks do not use all areas within Hilo Bay equally ($X^2 = 516.42$, df = 43, $p < 0.001$). There was no significant diel difference in the number of stations with nonzero detections (Fisher's Exact Test; p = 0.360, odds ratio = 0.24), suggesting the tagged animals utilized the same number of stations during the day as at night. However, statistical and spatial analyses revealed that there was a diel shift in the stations being used (V = 520, p = 0.1399) (Fig. 8).

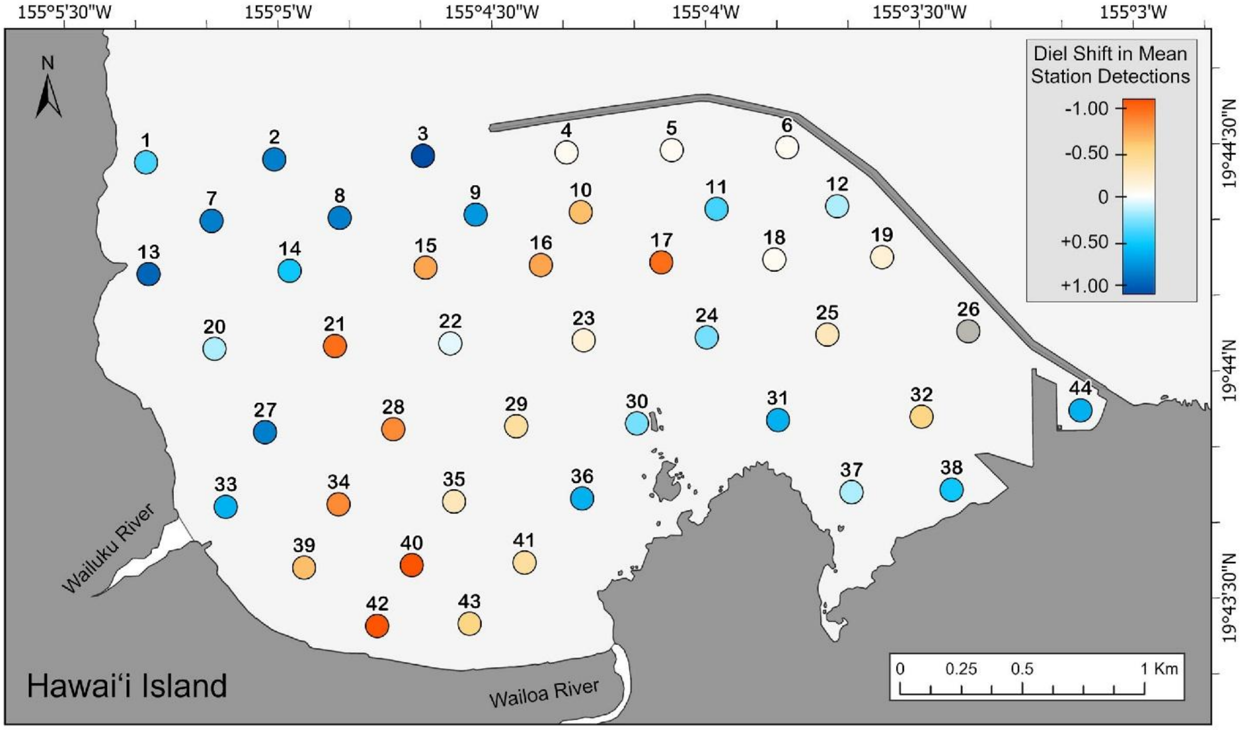

Figure 8. Shift in mean shark detections per station from diurnal to nocturnal surveys. Stations are indicated by labeled circles. A negative shift, indicating more detections on diurnal surveys, is represented by orange circles; a positive shift indicates more nocturnal detections and is represented by blue circles. Station 26 (grey) had no detections.

Kernel density geoprocessing was completed for diurnal detections and nocturnal detections to visually show shifts in habitat usage (Fig. 9). Overall detection density was greatest on the west side of the Bay near the opening in the breakwater. Diurnal detections were most prevalent in the same vicinity, but extended south towards the inner shoreline, whereas nocturnal detections exhibited the opposite trend and were concentrated near the opening of the Bay. Additional sampling occasionally occurred (n = 89) beyond the breakwater > 1000 m from stations 1-3, in which 16 individual detections occurred across 12 of the sampling periods. No detections were identified inside the Wailoa river estuary.

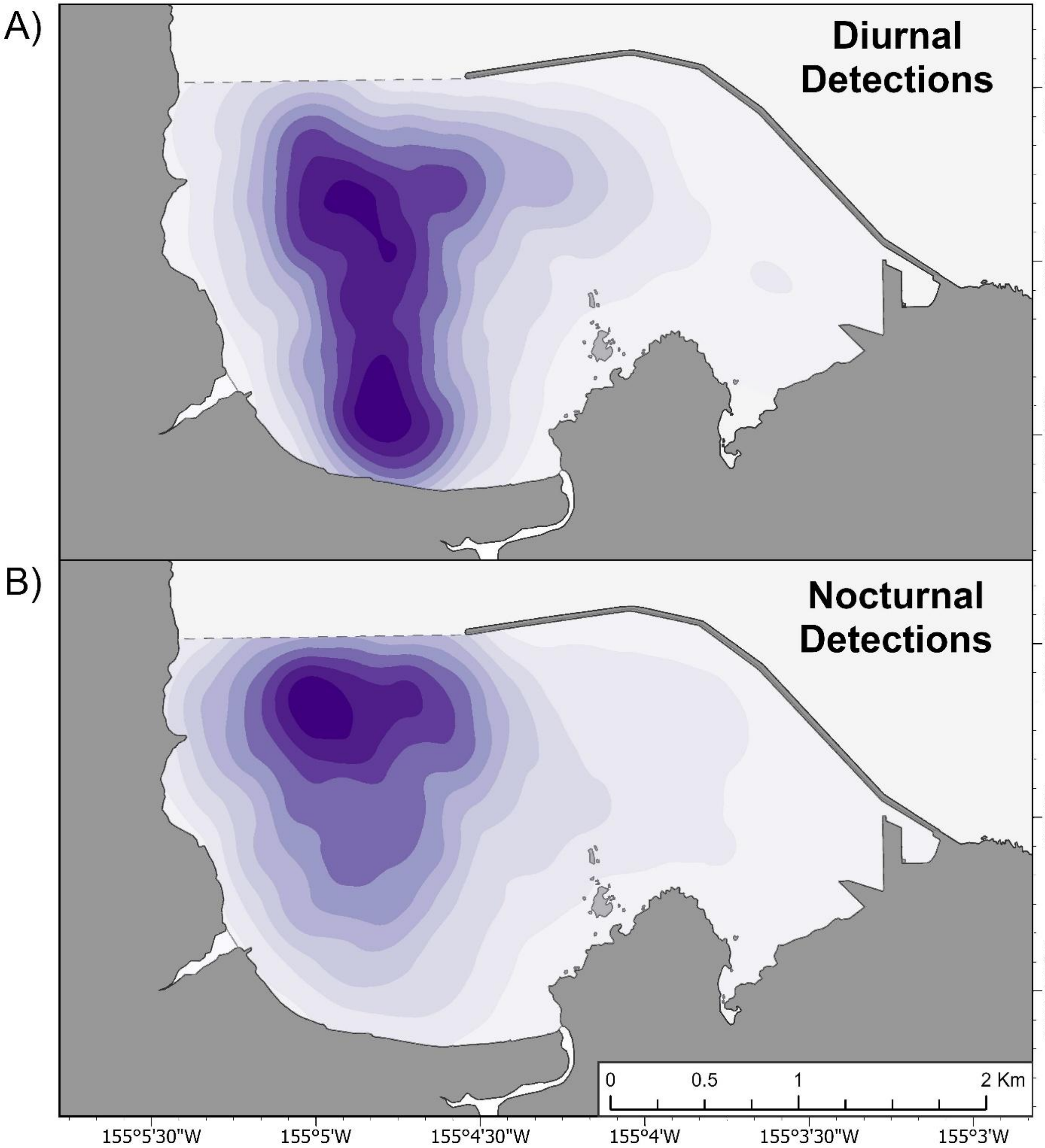

Figure 9. Kernel density of blacktip shark detections by station as a ratio of number of times sampled. Darker purple areas represent higher densities of shark detections. A) Diurnal detections, B) nocturnal detections.

Across the whole sampling site and study length, the average water temperature was 25.56 ± 1.19 ºC, while salinity averaged 32.75 ± 1.96, and DO averaged 6.42 ± 0.68 mg/L. Hilo Bay exhibited significant variability by month for temperature ($X^2 = 1281.3$, $df = 9$, $p < 0.001$), salinity ($X^2 = 357.3$, df = 9, $p < 0.001$), and DO ($X^2 = 425.2$, df = 9, $p < 0.001$) (Fig. 10). Among stations, temperature and salinity were relatively similar but DO varied significantly on both diurnal ($X^2 = 141.7$, df = 43, $p < 0.001$) and nocturnal ($X^2 = 124.4$, df = 43, $p < 0.001$) surveys (Fig. 11).

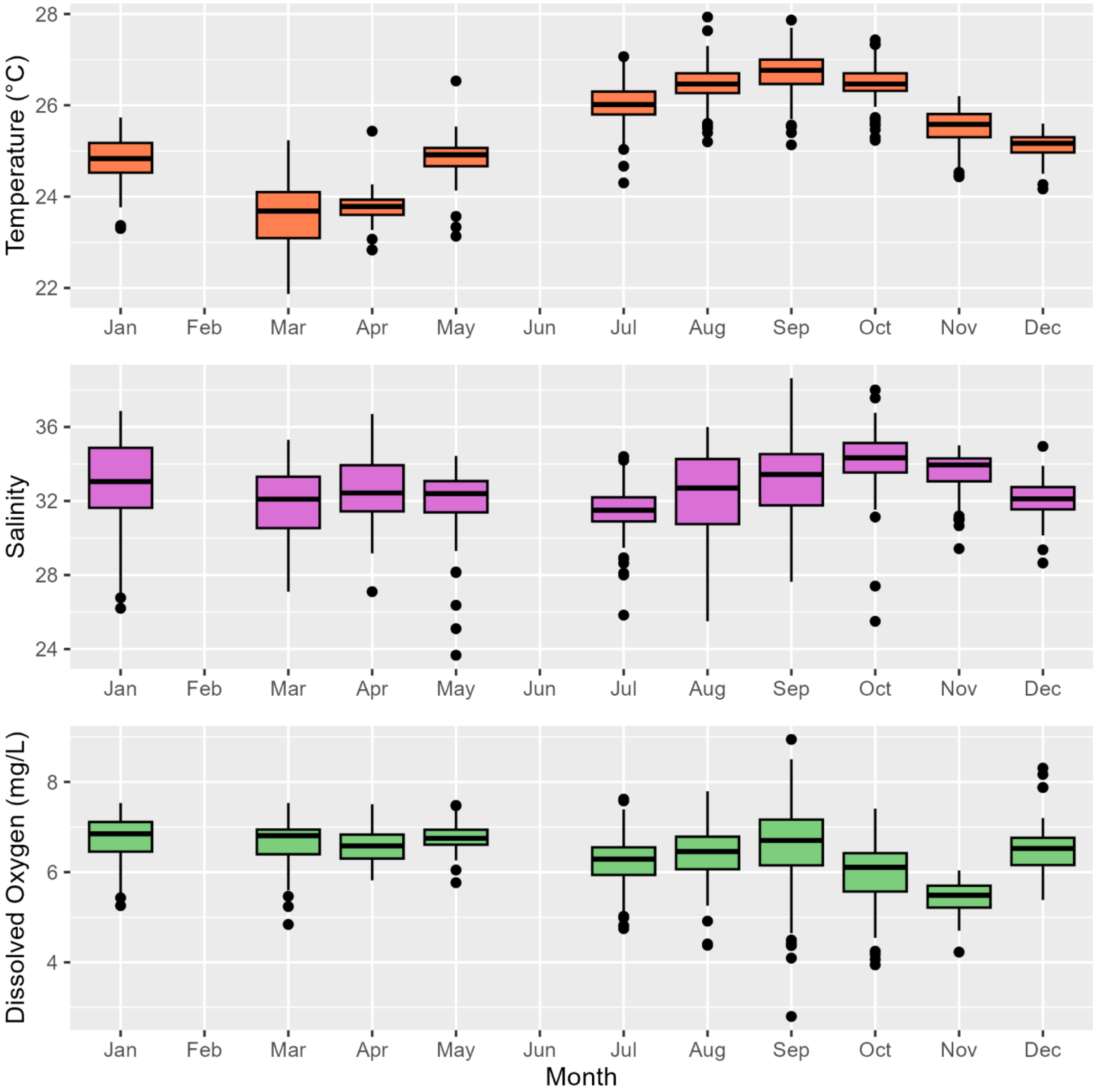

Figure 10. Box plots showing average water temperature, salinity, and DO by month. Boxes span the interquartile range (25th–75th percentiles) and the horizontal line within each box represents the median. Whiskers extend up to 1.5 times the IQR, and dots represent outlier values. No sampling occurred in February or June.

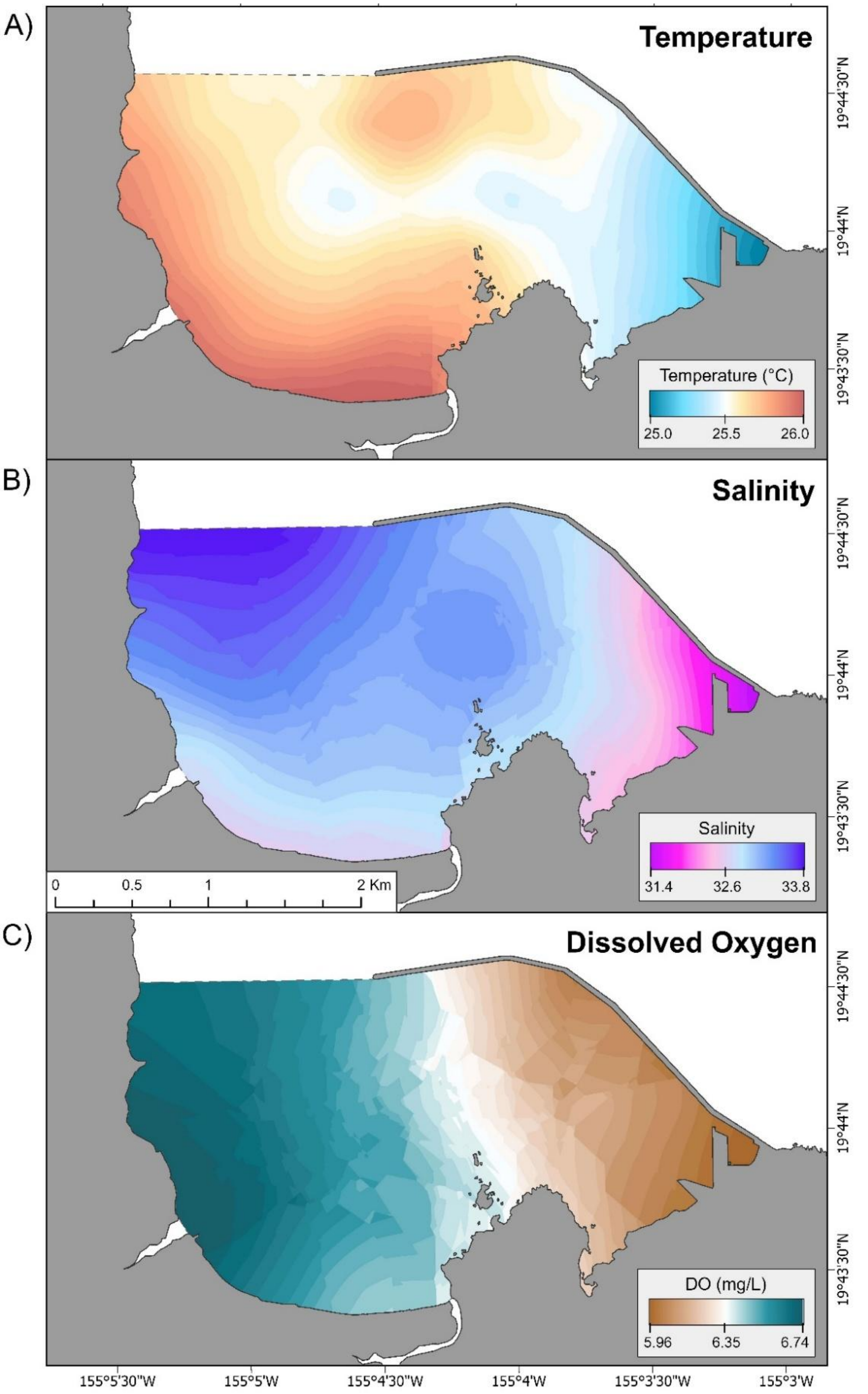

Figure 11. Empirical Bayesian kriging interpolation of the average A) temperature, B) salinity, and C) DO at each station (~500 m apart) within Hilo Bay between July 2022 and January 2024.

The relative influence of each variable on blacktip shark presence was examined using GAMs with Poisson distribution. The full model included the following: benthic habitat as categorical predictor; temperature, salinity, dissolved oxygen, and depth as non-parametric smooth-term fixed effects; and date/daylight hours, survey, and station as smooth-term random effects. Date and hours of daylight both acted as a proxy for time, and since date (AIC = 2371.7, DE = 34.5%) had better explanatory power than daylight hours (AIC = 2425.1, DE = 30%), only date remained in the full model. Manual backwards stepwise procedure and dredging indicated that the strongest model retained all terms. Initial correlation analysis confirmed multicollinearity was not an issue. Basis dimensions were appropriate for the model and indicated that the smooth terms were not overly complex and the model was not at risk of overfitting (Table 3).

Table 3. Basis dimension (k') check for final GAM smooth terms.

Smooth Term	Basis Dimension (k')	Effective Degrees of Freedom (edf)	k-index	p-value
Temperature (°C)	9	2.19	0.89	0.14
Salinity	9	2.56	0.96	0.97
DO (mg/L)	9	1.00	0.92	0.59
Depth (m)	9	1.00	0.89	0.11
Date	19	15.12	-	-
Survey (AM/PM)	2	0.70	-	-
Station	44	31.37	-	-

Diurnal (AIC = 1302.6, DE = 38.4%) and nocturnal (AIC = 1088.4, DE = 38.7%) GAMs were created to examine diel shifts in influential factors of shark presence (Table 4). The same terms from the full model were included (habitat, temperature, salinity, dissolved oxygen, depth, date, station) except for survey, since each model included half of the data and represented all of one survey type. Response plots showed slight variations in the influence of smooth term fixed effects between the final combined model, diurnal model, and nocturnal model (Fig. 12).

Temperature and salinity both had nonsignificant effects on shark presence, aligning with the full model. Dissolved oxygen only had a significant effect during the day, indicating sharks were present at stations with higher DO during the day. Depth had the opposite trend: a nonsignificant effect for the full model and the diurnal model, but a strong significant effect during nocturnal surveys ($p = 0.006$) indicated that blacktip sharks were more commonly detected at stations in deeper parts of the Bay at night. Detections were greatest in muddy areas (Estimate = 1.37 ± 0.31, $p < 0.001$), and sharks only appeared to utilize rocky bottom habitats at night (Estimate = 1.13 ± 0.42, $p = 0.007$).

Table 4. Model summary table for final GAMs fit to combined, diurnal, and nocturnal data. Significant p-values ($p \leq 0.05$) bolded and followed by an asterisk (*).

	Combined	**Diurnal**	**Nocturnal**
AIC	2371.7	1302.6	1088.4
R-sq. (adj)	0.336	0.353	0.383
Deviance explained	34.5%	38.4%	38.7%
p-values			
Parametric Coefficients:			
Habitat	**< 0.001 ***	**< 0.001 ***	**< 0.001 ***
Habitat (Mud)	**< 0.001 ***	**< 0.001 ***	**< 0.001 ***
Habitat (Rock)	0.225	0.650	**0.013 ***
Smooth Terms:			
Temperature (°C)	0.235	0.711	0.267
Salinity (ppt)	0.178	0.333	0.385
DO (mg/L)	**0.018 ***	**0.027 ***	0.701
Depth (m)	0.094	0.454	**0.004**
Date	**< 0.001 ***	**< 0.001 ***	**< 0.001 ***
Survey (AM/PM)	0.069	-	-
Station	**< 0.001 ***	**< 0.001 ***	**< 0.001 ***

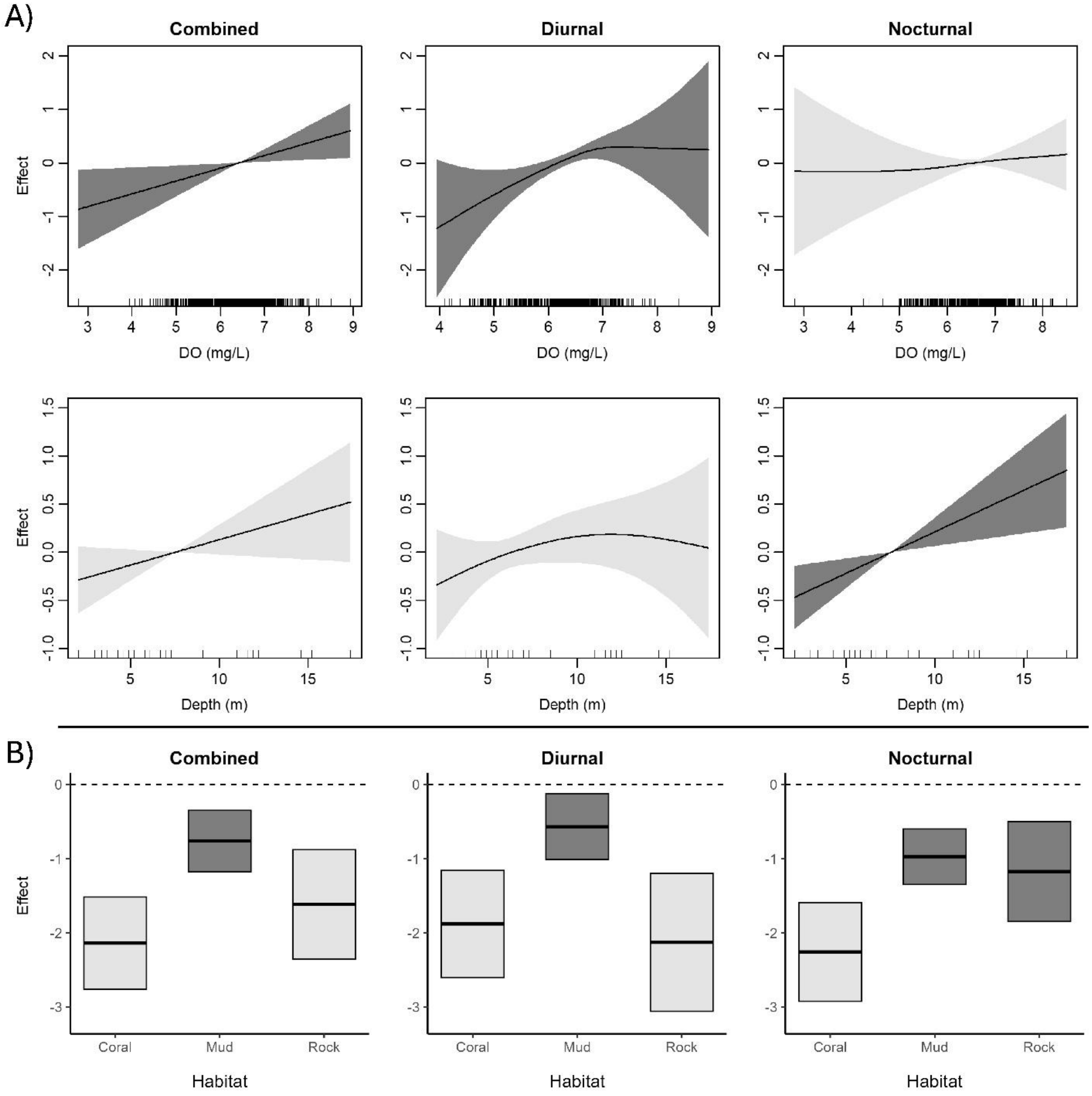

Figure 12. Response plots showing additive effects for final GAMs fit to combined (left), diurnal (middle), and nocturnal (right) data. Dark grey shading indicates significant terms. A) Effect of smooth term explanatory variables (DO, depth) on shark presence; solid lines indicate the smoothed additive effect of each variable, while shaded areas represent 95% confidence intervals. B) Effect of benthic habitat type on shark presence; boxes represent 95% confidence intervals.

Discussion

This study is the first to present in-depth residency patterns for juvenile blacktip sharks in Hawai‘i, and based on our findings and the criteria set forth by Castro (1993) and Heupel et al. (2007), we posit that Hilo Bay meets the definition of a shark nursery habitat for *C. limbatus*. Nearly 25% of tagged individuals maintained year-round residence within the study site, highlighting a continued reliance on their natal grounds. The majority of well-documented and heavily studied blacktip nursery habitats are located in subtropical and temperate regions, where juveniles only maintain residence seasonally (Simpfendorfer & Milward, 1993; Heupel, 2007). This has been linked to water temperature, as YOY blacktip sharks move to deeper waters beyond the nursery habitat to avoid thermal stress in the fall and winter (Heupel & Simpfendorfer, 2002; Chapman et al., 2015; Matich et al., 2021). The results presented here support the hypothesis that tropical nurseries with minimal variability in water conditions (i.e. temperature) allow juvenile sharks to continually take advantage of the protected, shallow-water habitat for much longer than the first few months of life (Tavares, 2008; Chapman et al., 2015). The temporal patterns observed in this study align closely with findings by Legare et al. (2015) in the Caribbean, a tropical climate similar to Hawai‘i, where juvenile blacktip sharks were present year-round with peak residency during the pupping season and declines in the fall-winter.

The 2022 cohort of tagged blacktip sharks had an average observed residency period of 287 days from first to last detection, with one individual (ID or #9273) present periodically from the first to last day of sampling (598 days). Due to the absent umbilical scar during tagging, it was assumed the young shark was 1+ year old at the start of the study, which would suggest at least part-time residency within Hilo Bay of 963+ days. Since only 2 of the 29 sharks included in this study were considered YOY upon tagging, we assume 93% of the tagged individuals were already present within Hilo Bay for a year prior to acoustic tracking. Peak residency (41.3-50.0%) occurred between March and August, while minimal residency (24.1-30.1%) occurred between October and January. These findings imply blacktip sharks exhibit site fidelity and repeatedly use the area over several years. Outside of this study, no species-specific nursery habitats have been confirmed on any of the Hawaiian Islands for blacktip sharks, though it is likely that others exist along the archipelago.

Based on the acoustic detection range and stations we observed, it was assumed that if a tagged animal was present in Hilo Bay during sampling, it would have been detected. Thus, when individuals were not detected during a survey, they were presumed to have left the confines of the study (Heupel et al., 2004; Cooke et al., 2013). Juvenile sharks are commonly observed making periodic ventures beyond their natal grounds (DeAngelis et al., 2008). During the present study, haphazard sampling occurred outside of the Hilo Bay breakwater, in which tagged animals were present 13.5% of the time. As young sharks mature, they often make further and more frequent excursions in search of sufficient food, weighing the benefit of predator avoidance that their shallow-water nursery habitat provides (Chapman et al., 2015). In the present study, we observed more detections of the 2022 cohort in the fall of 2022 than the fall of 2023, indicating that the individuals were likely approaching the threshold in which the nursery habitat was no longer beneficial. This trade-off led to our hypothesis that detection frequency would exhibit an inverse relationship to shark size (TL), but this pattern was not observed as it had been in other studies (Barry et al., 2008; Tavares, 2008).

The age of an animal has historically been shown to influence their movement patterns within a nursery habitat (DeAngelis et al., 2008; Matich et al., 2021). Our hypothesis that detection frequency would directly relate to TL was based on the assumption that shark size could be used as a proxy for age. However, significant variation exists in size at birth for blacktip sharks, with the driving factor being maternal size (Dudley & Cliff, 1993; Baremore & Passerotti, 2013). Additionally, growth rates are highly region- and population-specific; in the Los Roques Archipelago of Venezuela, juvenile blacktip sharks more than double in size and reach maturity in as little as two years (Tavares, 2008), whereas in South Africa the same process takes 6-7 years (Wintner & Cliff, 1995). There was a substantial range in the TL of tagged individuals (73.1-98.4 cm) in the present study, and importantly, the two YOY were not the two smallest, but rather the second and fourth smallest included here. Thus, TL cannot be considered a reliable predictor of age in juvenile blacktip sharks, especially in areas with little to no record of average size at birth or growth rates such as the Hawaiian population (Branstetter, 1987). Since detection frequency was not correlated to TL, we theorize that the length of time an individual spends within a nursery habitat may be more influential than size in predicting when juvenile sharks will leave their natal grounds. Current literature regarding nursery habitat residency as it relates to age versus size at birth is limited, and more research is needed to fully understand the relationship that TL may have on nursery usage (Llerena et al., 2013; Matich et al., 2021).

A greater number of detections occurred during diurnal surveys than nocturnal surveys, suggesting that juvenile blacktip shark excursions beyond the nursery habitat in Hilo Bay were more common at night. Many species of sharks exhibit heightened foraging activity after dusk and move into deeper waters to track prey (Holland et al., 1993; Cartamil et al., 2010; Speed et al., 2010). For example, Legare et al. (2018) found that young blacktip sharks tend to remain in a nearshore "core area" during the day, then travel their furthest distance in the hour after sunset, before working their way back to the core area over the course of the night. A similar pattern can be seen in the current study by comparing detection density maps during the day and at night. Juvenile blacktip sharks were found more frequently in the shallower, inward part of Hilo Bay during the day, then shifted towards the opening of the Bay at night. Since the majority of nocturnal detections were at the edge of the study area, we suspect that many of the nighttime excursions done by tagged animals were only slightly beyond the nursery habitat, such that they could return before sunrise. This trend aligned with the diel GAM results, in which depth was a significant predictor in blacktip shark detections at night, but not during the day.

Benthic composition appeared to be a reliable indicator of blacktip shark distribution within Hilo Bay. Between rocky, muddy, or coral benthic habitat types, the tagged sharks were detected more regularly in muddy areas, but they also preferentially used rocky habitats at night. Spatial analysis showed muddy habitats dominate much of Hilo Bay (66% of stations sampled), including the core area that the blacktip sharks appeared to utilize. The deepest areas within the Bay were all mud, primarily since they were within the dredged shipping channel which runs through the middle of Hilo Bay. Only five stations existed in rocky areas, with three along the entrance of the Bay where detections were concentrated at night. Individuals were rarely detected in areas with coral, which may stem from the structural complexity and hiding spots available for prey. Predatory efficiency of blacktip sharks is comparatively low in their early years, so juvenile sharks who are still learning to hunt may have more success in open muddy flats (Barry et al., 2008). Limited information is available regarding benthic preferences in young *C. limbatus*, though at Palmyra Atoll, juvenile blacktip reef sharks (*Carcharhinus melanopterus*) were found most frequently in sand-flat habitats (Heupel & Hueter, 2002; Papastamatiou et al., 2009).

Temperature and salinity did not appear to influence shark distribution within Hilo Bay, which was unexpected based on the current literature (DeAngelis et al., 2008; Froeschke et al., 2010). Blacktip sharks are typically found in areas where DO is between 5.0-10.0 mg/L (Bubley & Carlson, 2012). The effect that DO has on habitat usage varies by site and study but likely relates to the range of concentrations of DO in the area and the likelihood that certain spots can become hypoxic (Rodil et al., 2020). For example, in one study from the Gulf of Mexico where DO averaged 8.00 ± 1.80 mg/L, researchers found that DO had a small relative influence on blacktip shark movement patterns as opposed to temperature and salinity, which both had ranges extending beyond the suitable parameters for blacktip sharks (Froeschke et al., 2010). Off the Atlantic Coast of South Florida where water temperature and salinity are comparably more stable, a recent study found that DO and depth had a greater influence than temperature and salinity in predicting the distribution of juvenile blacktip sharks (Tinari & Hammerschlag, 2021). Similarly, in the current study, there was little spatial variability in temperature and salinity among stations, and both the lowest and highest recorded values were well within the tolerable range for blacktip sharks. DO, however, was significantly different among stations. In the aforementioned study from South Florida, blacktip sharks were found most commonly in waters where DO averaged 6.97 ± 1.52 mg/L (Tinari & Hammerschlag, 2021). In Hilo Bay, DO averaged 6.42 ± 0.68 mg/L, and the bottom 3.4% of recorded DO concentrations were below 5.00 mg/L, meaning hypoxic conditions were occasionally observed. This suggests that the negligible effect which temperature and salinity had on blacktip shark detection frequency was due to relatively stable and ideal conditions in both parameters across the study site, as opposed to DO, which was highly variable and occasionally limiting in habitat availability. Further, the temporal patterns observed in the current study for DO and shark detections align closely with a study from Australia regarding juvenile pigeye sharks (*C. amboinensis*) in a tropical nursery habitat comparable to Hilo Bay (Knip et al., 2011). In both, a significant decline in DO concentrations occurred at the start of the wet season as the first flooding events took place, which coincided with the fewest nearshore shark detections of the year (Knip et al., 2011).

Diel cycling of DO occurs due to photosynthesis by phytoplankton and algae taking place during the day, followed by respiration dominating during the night (D'Avanzo & Kremer, 1994). Minimum DO concentrations in shallow estuaries typically occur within two hours after sunrise as photosynthesis begins to take place, and daily maximum concentrations are seen two hours prior to sunset (Tyler et al., 2009). For this study, diurnal sampling took place from 08:00 to 14:00, while nocturnal sampling occurred from 18:00 to 24:00. On average, Hilo Bay DO was lower and more variable during diurnal surveys (6.27 ± 0.67 mg/L) than nocturnal surveys (6.58 ± 0.65 mg/L), which may explain why DO significantly influenced detection frequency during the day, but not at night. Even slight reductions in ambient oxygen concentrations can limit aerobic metabolism, energy budgets, and overall fitness (Rodil et al., 2020). The diel fluctuations in DO within Hilo Bay suggest that juvenile blacktip sharks may need to be more selective in diurnal habitat usage to avoid unnecessary physiological stress (Waller et al., 2024).

With rapid declines in shark populations across the world, it is vital that we protect not just the animals, but the environments they rely upon (Dulvy et al., 2021). Since shark nursery habitats are often found in shallow, coastal waters, they are frequently in close proximity to human development and therefore can be significantly influenced by anthropogenic activities (Oh et al., 2017; Crear et al., 2020). The city of Hilo experiences high discharges of surface runoff, which collects in the Wailoa and Wailuku rivers before draining into Hilo Bay. Pollutants from surface runoff have been linked to a variety of health problems in sharks including cancer, liver and kidney damage, immunosuppression, reproductive defects, and endocrine disruption (Letcher et al., 2009). Further, juvenile sharks tend to be more sensitive than adults to environmental and physiological stressors, highlighting the need for a healthy, stable environment in their early years (Froeschke et al., 2010; Tinari & Hammerschlag, 2021). The results presented here indicate that Hilo Bay is a vital developmental area for juvenile *C. limbatus* year-round and therefore is critical to ensuring the stability of the local marine ecosystem. We propose that Hilo Bay be delineated as the first blacktip shark nursery habitat in Hawaiian waters and simultaneously emphasize the need for stronger environmental management plans to support the continued survival of this culturally and ecologically important species.

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