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Spatial and temporal use of a tropical nursery habitat by juvenile blacktip sharks (*Carcharhinus limbatus*)

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Blacktip sharks (*Carcharhinus limbatus*) are a circumglobal species that rely on nearshore nursery habitats during their early years. Movement patterns and habitat use of blacktip sharks in the Hawaiian Islands is poorly understood, and no nursery habitats have been discovered within Hawai'i. For this study, juvenile blacktip sharks (n = 29) were caught and tagged in Hilo Bay, Hawai'i, USA with acoustic transmitters. Tracking occurred every 2–5 weeks between July 2022 and January 2024 at 44 stations throughout Hilo Bay using a receiver and omnidirectional hydrophone. Results showed that juvenile blacktip sharks were present in the bay year-round, with the greatest monthly residence (41.3-50.0%) from March through August, and the lowest monthly residence (24.1-30.1%) from October through January. Blacktip sharks were detected within Hilo Bay more during the day than at night, but more frequently in deeper waters at night, which is likely due to excursions into deeper waters during heightened nocturnal foraging activity. Temperature and salinity did not significantly vary among stations, and as such, were not influential factors in habitat use. Dissolved oxygen (DO) appeared to limit habitat use during the day when concentrations were lowest in the bay. The lowest DO concentrations were observed during the months when the fewest number of sharks were detected, suggesting that oxygen requirements may influence habitat use within the bay. The residency patterns presented here support the delineation of Hilo Bay as the first known blacktip shark nursery habitat in Hawaiian waters. Our results suggest that this population of blacktip sharks reside predominantly within Hilo Bay for the first few years of their life, and highlight the effect that environmental changes can have on this species' habitat availability and movement patterns.

KEYWORDS
diel, distribution, Hawai'i, telemetry, temporal

1 Introduction

Sharks affect the structure and stability of food webs throughout marine ecosystems (Bascompte et al., 2005; Roff et al., 2016; Barley et al., 2017; Dulvy et al., 2021). Coral reef biodiversity is closely tied to the presence of sharks, and several species of sharks are considered keystone species due to their disproportionate influence on ecosystem health (Baum and Worm, 2009; Ruppert et al., 2013). Shark populations have rapidly declined over the last half-century; despite their ecological importance, sharks 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). Many shark populations are at risk of 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 and Milward, 1993).

Shark nurseries have been identified in protected areas along the coastline of tropical to temperate waters worldwide and act as essential habitats for young sharks (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 and Gruber, 1990; Castro, 1993; Bethea et al., 2004). Shark nurseries are typically habitats 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 (Heupel et al., 2007). The abundance of small prey and scarcity of predators have traditionally been considered as the greatest benefits of nursery areas for juvenile sharks (Branstetter, 1990; Simpfendorfer and Milward, 1993). Recent studies have shown that the predictable conditions found in these environments may also reduce osmoregulatory stress on marine inhabitants–particularly juvenile sharks (Matich et al., 2022).

Blacktip sharks (*Carcharhinus limbatus*) are a near-shore species found circumglobally in tropical to temperate waters (Garrick, 1982). They reside in shallow coastal regions and are considered one of the most important commercial and recreational shark species in the US (Castro, 1996). Juvenile blacktip sharks have frequently been the subject of nursery-focused studies due to their high abundance and broad geographic distribution (Capapé et al., 2004; Speed et al., 2010; Passerotti and Baremore, 2012; Tinari and Hammerschlag, 2021). 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, young-of-year (YOY) blacktip sharks tend to remain within the nursery until late fall, regardless of site fidelity and with varying rate of return in following summers (Castro, 1996; Heupel, 2007; DeAngelis et al., 2008). Older juveniles commonly demonstrate philopatry, returning to their natal nursery in the spring (Gardiner et al., 2015). Multiple cohorts often inhabit the same nursery grounds until venturing into deeper waters as temperatures drop to avoid thermal stress (Heupel, 2007; Chapman et al., 2015; Matich et al., 2021). In warmer, tropical waters where the water temperature within the nursery remains within the known suitable range for the species year-round, blacktip sharks may reside for longer than one season (Legare et al., 2015). Tavares (2008) showed that in a tropical nursery habitat, juvenile blacktip sharks remained within the central nursery for 14–16 months before egress. Legare et al. (2015) similarly found that in a tropical nursery, the peak residency of blacktip sharks was immediately following the pupping season, with a reduction in shark abundance leading into the fall months.

While in the nursery, several factors have been shown to influence juvenile blacktip shark habitat use and movement, including physiochemical conditions (temperature, salinity, dissolved oxygen), depth, and benthic habitat type (Branstetter, 1990; Tavares, 2008; Tinari and Hammerschlag, 2021). Blacktip shark habitat availability is limited to areas within the suitable range of water quality parameters, and evidence suggests that the narrow range of temperatures and salinities that juvenile sharks inhabit may lower energetic costs of osmoregulation and promote growth (Heupel and Simpfendorfer, 2008). Both habitat use and movement within nurseries also vary as a function of time of day, with diel shifts often linked to foraging activity (Holland et al., 1992; Cartamil et al., 2010; Legare et al., 2015). 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).

Comprehensive coastal management and species protection efforts require a thorough understanding of local marine life and oceanic processes, which can be limited in isolated, lesser-studied regions. No nursery habitats have yet been delineated for blacktip sharks in Hawai'i, and their residency and habitat usage are poorly understood (Garrick, 1982; Crow et al., 1996). The aim of this study was to use acoustic telemetry to determine residency patterns of juvenile blacktip sharks in Hilo Bay, Hawai'i, USA, and examine how environmental variables influence distribution patterns on a spatial and temporal scale. We hypothesized that without the threat of seasonal thermal stress, sharks will be present in Hilo Bay—the suspected nursery habitat—year-round, with fewer shark detections expected in the fall/winter months than in the spring/summer months. We also expected that habitat use and movements would be influenced by environmental parameters (temperature, salinity, dissolved oxygen, depth, benthic composition).

2 Materials and methods

2.1 Site description

This study was conducted in Hilo Bay, Hawai'i, USA, on the windward side of the Island of Hawai'i (Figure 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 a 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

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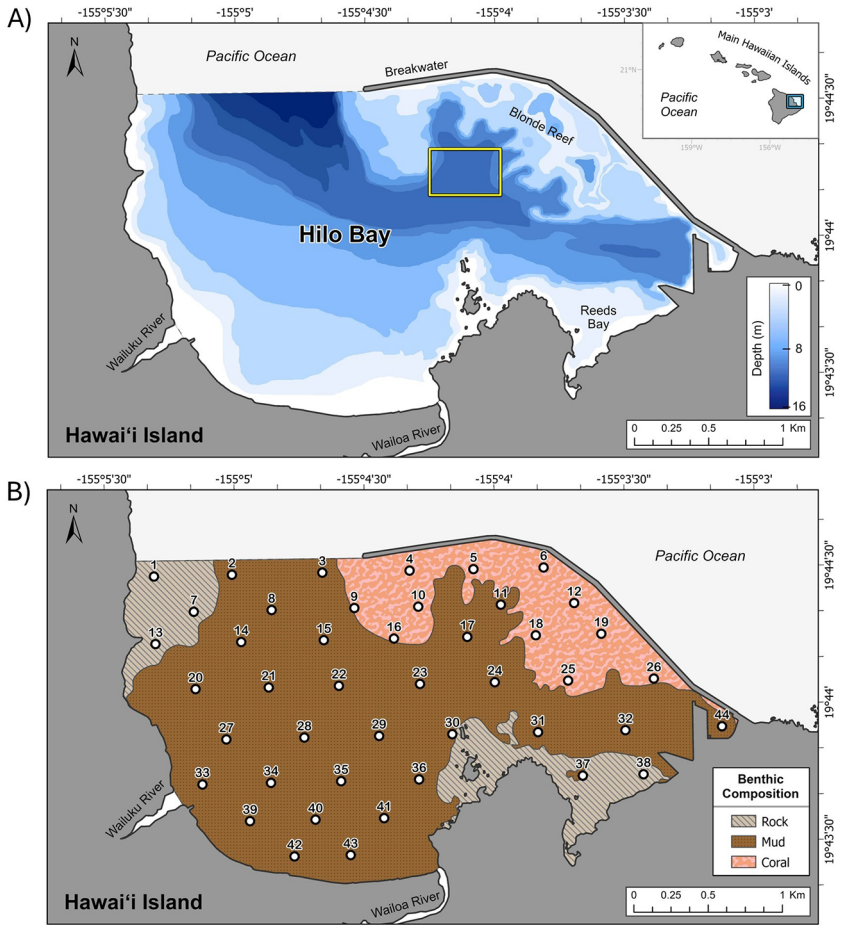

FIGURE 1
Study site of Hilo Bay, Hawai'i, USA, showing freshwater inputs from the Wailuku and Wailoa River as well as the structured inner Blonde Reef. **(A)** Bathymetry lines show depths ranging from 0 to 16 m within the bay, and the gray dashed line shows the entrance to Hilo Bay and the extent of the sampling area. Shark capture, tagging, and release took place within the yellow box. **(B)** Benthic composition after Coyne et al. (n.d.) via NOAA's National Oceanographic Data Center (Accession No. 0001329). White points indicate stations 1–44 sampled in acoustic telemetry tracking surveys (July 2022 – January 2024).

reefs extend from the breakwater inside and outside Hilo Bay to form Blonde Reef (National Centers for Coastal Ocean Science). The city of Hilo, along the coast of Hilo Bay, is one of the rainiest cities in the U.S. receiving an average of 300+ cm of rainfall every year (National Centers for Environmental Information). 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. Freshwater inputs from groundwater are also significant in the area around Reeds Bay. The flow of both rivers varies significantly, with higher discharge in the wet season (Oct.-April) and lower discharge in the dry season (May-Sept.) (Giambelluca et al., 2013). 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).

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, 9.5 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 levels were evaluated 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 deployed in 2022 had a transmission time of 90–150 seconds, and those deployed in 2023 had a transmission time of 40–100 seconds. A total of 29 juvenile *C. limbatus* were fitted with acoustic transmitters and included in the study (14 in 2022, 15 in 2023). Prior to the study, a range test tag with constant transmissions was placed following the same protocol, and the animal was led away from the receiver by swimming on a line alongside a small boat until the transmissions were no longer detected. This process was used to verify reception distance, which was measured at 700 m from receiver at the surface.

2.2 Acoustic telemetry

Forty-four sampling stations were identified in Hilo Bay through spatial gridding, in which stations were set ~500 m apart. This allowed for significant coverage of the study site and slight overlap of acoustic reception between monitored stations. Biweekly acoustic tracking surveys (n = 8) were conducted from a rigid-hull inflatable boat between July 20 and October 27, 2022, and approximately monthly surveys (n = 13) from November 2022 to January 2024. No sampling occurred in the months of February or June due to weather conditions and tagging operations. Surveys consisted of paired diurnal (08:00-14:00) and nocturnal (18:00-24:00) cruises in a single 24-hour period. Stations were located using GPS and physical markers, and all were monitored once per cruise, twice per survey day. The order of stations visited was randomized between dates to ensure stations were not sampled at the same time each survey. 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.

A VEMCO VH-165 omnidirectional hydrophone was connected to a VR-100 portable receiver and deployed at each station 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 measured at 1 m above the sea floor, midwater, and at the surface at each station using a calibrated YSI Pro2030. Depth was measured using a HawkEye DT1H Handheld Depth Finder. GPS position of each station was recorded using a Garmin GPSMAP 86sc.

2.3 Statistical analyses

The relationship 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 relationship between TL and observed residency period (days between initial tagging and final detection) was determined using a Spearman's rank correlation. Five sharks (# 8825, 8835, 9261, 9265, 9267) were not detected 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. Hours of daylight (US Naval Observatory, Astronomical Applications Department) were used to explore 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.

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 cruise were recorded separately. 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 cruises. 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.

On each station and cruise, temperature, salinity, and DO were recorded at three depths (seafloor, midwater, surface). For each variable, these measurements were averaged to obtain a single water column value, which was used in all statistical analyses. Kruskal-Wallis rank sum tests were performed to determine temporal and spatial variability in temperature, salinity, and DO. 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 and 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.

3 Results

A total of 820 juvenile blacktip shark detections were recorded in Hilo Bay across all surveys (n = 21) between July 2022 and January 2024. Of the 29 tagged sharks, 24 were detected in at least

one cruise, and individual detection frequency ranged from 0-0.86 with a mean of 0.38 ± 0.27 (Figure 2). Observed residency periods were calculated as the days between the first and last detection, regardless of periodic absences between the two dates. The residency period calculated is a minimum, since these juveniles may have been present in the bay since birth (especially the YOY), and could have remained beyond the length of this study. 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 and median residency period after tagging for the 2022 cohort (n = 14) was 287 days and 343 days, respectively.

For the 29 tagged juvenile blacktip sharks, the TL 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. TL was expected to be an influential factor in both detection frequency and observed residency, but no significant relationship was observed (Figure 3).

Detections of tagged juvenile blacktip sharks peaked between March and August, with 41.3 to 50.0% of tagged individuals detected each month over the six-month period, while the fewest sharks (24.1-30.1%) were detected from October to January. At least 20.7% of tagged sharks were detected on each individual cruise, with a high of 64.3% and a mean of 38.4 (SD ± 11.5%). There was a significant correlation between hours of daylight and individual sharks detected on each day of sampling (Pearson's correlation; r (19) = .634, p = 0.002), with more sharks detected in the bay on longer days (Figure 4).

Total detections of juvenile blacktip sharks 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 cruises (Welch two sample t-test; t = 2.70, df = 1801, p = 0.007) with more detections during diurnal cruises (0.496 ± 0.889) than nocturnal cruises (0.392 ± 0.758). Juvenile blacktip sharks did not use all areas within Hilo Bay equally (Chi-squared test; X^2 = 516, 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 (Wilcoxon signed rank test; V = 520, p = 0.140).

Kernel density geoprocessing for diurnal detections and nocturnal detections showed shifts in habitat usage by juvenile blacktip sharks (Figure 5). Overall detection density of sharks was greatest on the west side of the bay near the opening in the breakwater. Diurnal detections of sharks were most prevalent in the same vicinity, but extended south toward the inner shoreline, whereas nocturnal detections exhibited the opposite trend and were concentrated near the opening of the bay. Additional station sampling

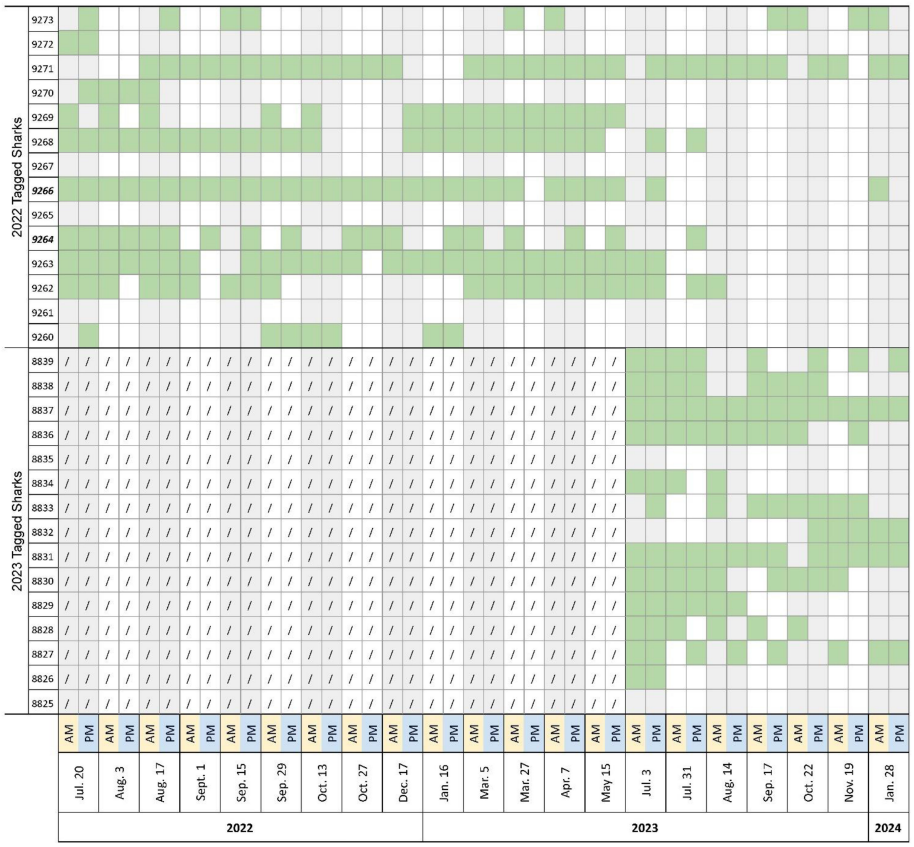

FIGURE 2
Tag detections of blacktip sharks in Hilo Bay on each cruise (AM/PM) from July 20, 2022, to January 28, 2024. Green boxes indicate that an animal was detected, white boxes indicate that the tag was active but the animal was not detected, and crossed boxes indicate that the tag was not active.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

occasionally occurred (n = 89) beyond the breakwater > 1000 m from stations 1-3, in which 16 individual shark detections occurred across 12 cruises. No detections of sharks were identified inside the Wailoa River estuary. Temperature, salinity, and DO varied spatially and temporally within Hilo Bay (Supplementary Figures 1, 2).

The full GAM model included the following: benthic habitat as categorical predictor; temperature, salinity, DO, and depth as non-parametric smooth-term fixed effects; and date/daylight hours, survey type (diurnal/nocturnal), and station as smooth-term random effects (Table 2). Date and hours of daylight both acted as a proxy for time, and since date (AIC = 2372, DE = 34.5%) had better explanatory power than daylight hours (AIC = 2425, DE = 30%), date was selected. 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. Results of the full model indicated benthic habitat and DO were the only significant environmental variables; shark detections were greatest at stations with mud substrate (Estimate = 1.38 ± 0.31, $p < 0.001$), and DO exhibited a significant effect on shark detections ($p = 0.018$). Random terms suggested survey time had no significant effect on shark presence, though substantial variation was captured by date ($p < 0.001$) and station ($p < 0.001$).

Diurnal (AIC = 1302, DE = 38.4%) and nocturnal (AIC = 1088, DE = 38.7%) GAMs were created to examine diel shifts in influential factors of the presence of juvenile blacktip sharks (Table 2). The same terms from the full model were included (habitat, temperature, salinity, DO, 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

TABLE 1 Tag number and total length (TL) for all blacktip sharks included in the study.

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

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. Tagged young-of-the-year sharks have ID # bolded and italicized.

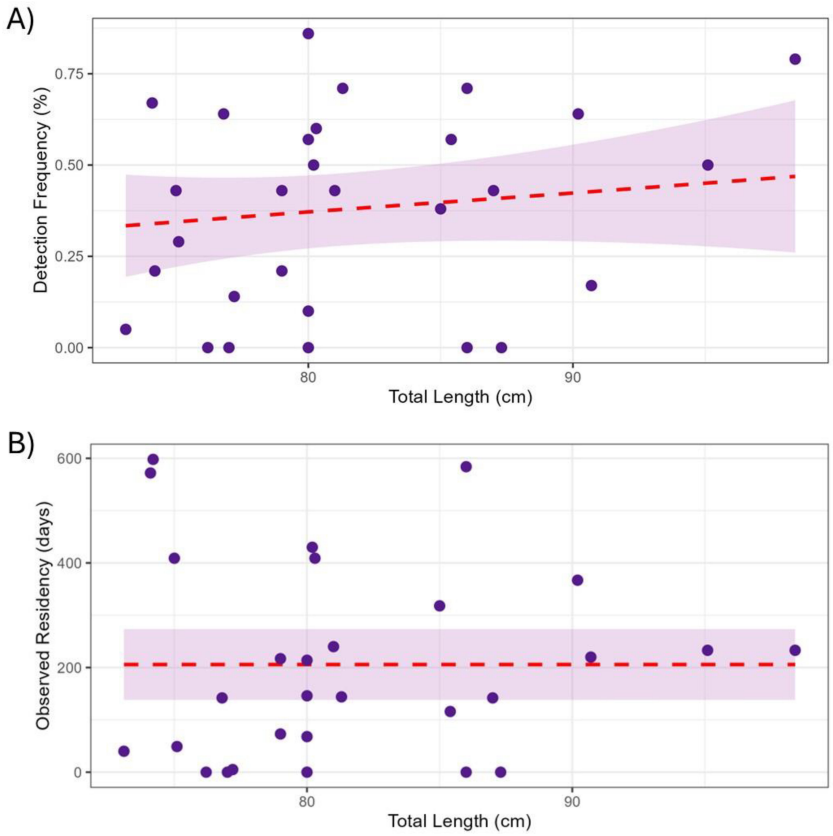

FIGURE 3
Relationship between **(A)** total length (TL) and detection frequency (proportion of times detected), and **(B)** total length (TL) and observed residency (number of days between first and last detections) for tagged blacktip sharks in Hilo Bay during the survey period of July 20, 2022, to January 28, 2024. Red dashes show GAM regression lines, and the shaded purple area represents 95% confidence intervals.

model, diurnal model, and nocturnal model (Figure 6). Detections were consistently greatest at stations with mud substrate, while sharks only appeared to utilize stations with rocky-bottom habitats at night (Estimate = 1.13 ± 0.42, p = 0.007). 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 (p = 0.027), 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 = 0.004) indicated that blacktip sharks were more commonly detected at stations in deeper parts of the bay at night.

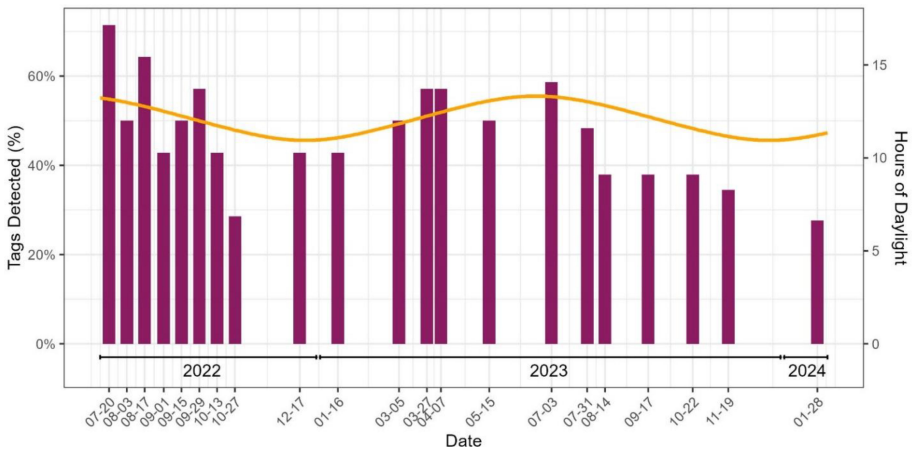

FIGURE 4
Percentage of tagged blacktip sharks detected on each sampling day. The orange line shows the hours of daylight each day for the duration of the study period (July 20, 2022 - January 28, 2024), which represents seasonality and the relationship between detection frequency and time of year.

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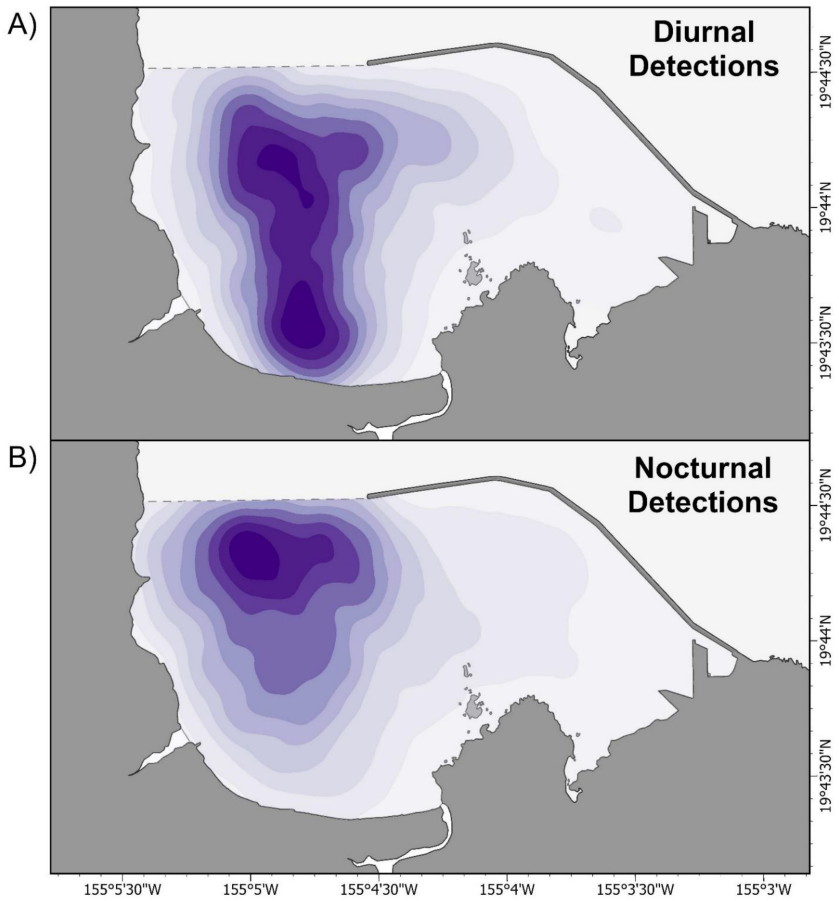

FIGURE 5
Kernel density of blacktip shark **(A)** diurnal detections and **(B)** nocturnal detections by station as a ratio of number of times sampled. Darker purple areas represent greater occurrence of shark detections.

4 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 blacktip sharks. Nearly 25% of tagged individuals maintained year-round residence within the study site, highlighting a continued utilization of their natal grounds. The 2022 cohort of tagged blacktip sharks had an average observed residency period of 287 days from first to last detection, with one individual (# 9273) present periodically from the first to last day of sampling (598 days). Due to the absent umbilical scar during tagging, it was assumed this juvenile 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, it is likely that 93% of the tagged individuals were already present within Hilo Bay for several months to a year prior to acoustic tracking. 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. Previous research showed that blacktip shark nurseries occur in subtropical and temperate regions, where juveniles only maintain residence seasonally (Simpfendorfer and Milward, 1993; Heupel, 2007). For instance, in the Gulf of Mexico, mean residence time is approximately 4–5 months after birth, and all YOY blacktip sharks tend to leave their natal grounds after 6–7 months (Heupel and Simpfendorfer, 2005). Egress from nurseries 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 and Simpfendorfer, 2002; Chapman et al., 2015; Matich et al., 2021). The temporal patterns observed in this study align closely with findings by Legare et al. (2015) in the Caribbean Sea, 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. This suggests that when nursery habitat availability is not limited by environmental fluctuations, blacktip sharks may preferentially remain at natal sites for extended periods of time, possibly until they outgrow their food source (Simpfendorfer and Milward, 1993). The results presented here support the hypothesis that tropical nurseries with minimal variability in water temperature allow juvenile sharks to take advantage of the protected, shallow-water habitat for much longer than the first few months of life (Tavares, 2008; Chapman et al., 2015).

TABLE 2 Model summary table for final GAMs fit to combined, diurnal, and nocturnal data.

	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** *

Significant p-values ($p \leq 0.05$) bolded and followed by an asterisk (*).

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., 2012). 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).

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). 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, and therefore venturing beyond the nursery more regularly (Chapman et al., 2015). We hypothesized that detection frequency would exhibit an inverse relationship to TL, but this pattern was not observed as it had been in other studies (Barry et al., 2008; Tavares, 2008). Significant variation exists in size at birth for blacktip sharks, with the driving factor being maternal size and developmental plasticity (Dudley and Cliff, 1993; Hussey et al., 2010; Baremore and Passerotti, 2013). Thus, TL may not be 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). Therefore, we posit that age may be more influential than size when determining when 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 Hilo Bay were more common at night. Many species of shark 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, in the Caribbean Sea, 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 (Legare et al., 2018). This trend aligned with the diel GAM results, with depth being a significant predictor in blacktip shark detections at night, but not during the day. Since most nocturnal detections were at the edge of the study area, we suspect that many of the nighttime excursions undertaken by tagged animals were only slightly beyond the nursery habitat, such that they could return before sunrise.

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, and 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. 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). Individuals were rarely detected in areas with coral, which may stem from the structural complexity and hiding spots available for prey. Limited information is available regarding benthic preferences in juvenile blacktip sharks, though at Palmyra Atoll, juvenile blacktip reef sharks (*Carcharhinus melanopterus*) were similarly found most frequently in sand-flat habitats (Heupel and Hueter, 2002; Papastamatiou et al., 2009).

Of the physiochemical variables assessed, only DO influenced habitat use, while water temperature and salinity did not appear to influence juvenile blacktip shark distribution in Hilo Bay. 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 potential to drop below the tolerable range (Rodil et al., 2020; Waller et al., 2024). Parsons and Carlson (1998) identified the lower limit of 5.0 mg/L, beyond which obligate ram-ventilators began showing hypoxia responses (wider gape, increased swimming speed). In 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 less variable,

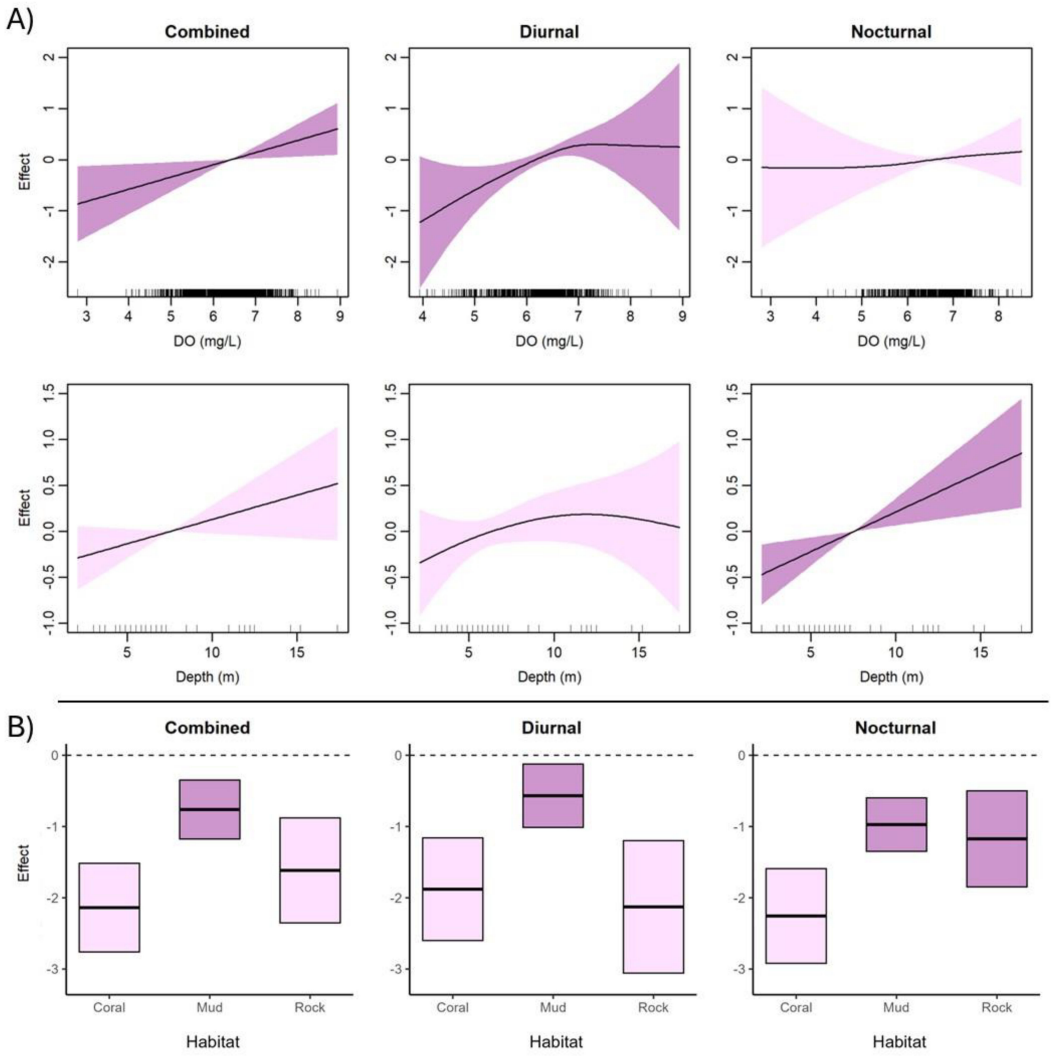

FIGURE 6
Response plots showing additive effects for final GAMs fit to combined (left), diurnal (middle), and nocturnal (right) data. Dark purple shading indicates significant terms; light purple shading indicates non-significant terms. **(A)** Effect of smooth term explanatory variables (DO, depth) 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.

DO and depth had a greater influence than temperature and salinity in predicting the distribution of juvenile blacktip sharks (Tinari and Hammerschlag, 2021). Sharks were found most commonly in waters where DO averaged 6.97 ± 1.52 mg/L (Tinari and 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 (Froeschke et al., 2010). DO, however, was significantly different among stations. In Hilo Bay, DO averaged 6.42 ± 0.68 mg/L, and the lowest 3.4% of recorded DO concentrations were below the normal lower limit of 5.00 mg/L. Further, 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.

With 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 proximity to human development and therefore can be significantly influenced by anthropogenic activities (Oh et al., 2017; Crear et al., 2020). Juvenile sharks tend to be more sensitive than adults to environmental and physiological stressors, highlighting the need for a predictable habitat with minimal pollutants in their early years (Froeschke et al., 2010; Tinari and Hammerschlag, 2021). The results presented here indicate that Hilo Bay is an important developmental area for juvenile blacktip sharks year-round and therefore may be a fundamental part of this local marine ecosystem. We propose that Hilo Bay be delineated as the first known blacktip shark nursery habitat in Hawai‘i and simultaneously emphasize the need for stronger environmental management plans to support the continued survival of this culturally and ecologically important species.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by Institutional Animal Care and Use Committee (IACUC) Texas A&M. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

LM: Software, Investigation, Conceptualization, Funding acquisition, Writing – review & editing, Formal Analysis, Writing – original draft, Project administration, Data curation, Methodology. JT: Methodology, Software, Investigation, Visualization, Project administration, Funding acquisition, Validation, Data curation, Writing – review & editing, Resources, Supervision, Formal Analysis, Conceptualization. JR: Funding acquisition, Conceptualization, Writing – review & editing, Resources, Methodology, Validation, Visualization. RW: Visualization, Conceptualization, Resources, Validation, Funding acquisition, Writing – review & editing, Methodology. SC: Visualization, Data curation, Validation, Writing – review & editing.

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Conflict of interest

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

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Supplementary material

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