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Habitat use and movement patterns of adult male and juvenile scalloped hammerhead sharks *Sphyrna lewini* throughout the Hawaiian archipelago

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ABSTRACT: Scalloped hammerhead sharks *Sphyrna lewini* are a circumglobal species found in tropical and subtropical waters. Globally, populations of *S. lewini* have undergone dramatic declines in recent decades, and 4 of 6 distinct population segments are at risk of extinction and listed under the United States Endangered Species Act. Despite this, limited data exist on movement behavior or habitat use requirements of *S. lewini*, especially in the Central Pacific region. In this long-term (2009–2020) telemetry study, 27 *S. lewini* (24 males [22 adults, 2 juveniles], and 3 juvenile females) ranging in size from 106 to 310 cm (total length) were tagged with a combination of acoustic and/or satellite tags in a known nursery area, Kāneʻohe Bay, Hawaiʻi. Acoustic data revealed repeated movements of adult male *S. lewini* to Kāneʻohe Bay between May and September across multiple years. Horizontal movements away from the Bay indicate these individuals are highly associated with the Hawaiian Archipelago (i.e. Northwestern and main Hawaiian Islands), while vertical movements were dynamic, with repeated, nocturnal deep dives to depths beyond 800 m and temperatures as low as 5.0°C. We conclude that adult male and juvenile *S. lewini* tagged in Kāneʻohe Bay exhibit fairly restricted movements throughout the Hawaiian Archipelago, and mature males specifically exhibit strong seasonal site fidelity to Kāneʻohe Bay. These data add crucial baseline information on habitat preferences of *S. lewini* around the Hawaiian Islands, and can be used to help structure conservation strategies for a portion of the Central Pacific population.

KEY WORDS: Archival tag · Elasmobranch · Nursery · Species distribution · Telemetry · Threatened species

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1. INTRODUCTION

The scalloped hammerhead shark *Sphyrna lewini* is a large coastal and semi-oceanic pelagic shark, with a circumglobal distribution in warm-temperate and tropical waters (Compagno 1984, Miller et al. 2013). *S. lewini* are highly mobile and are likely the most abundant of the hammerhead species, although robust data on population sizes is limited (Maguire et al. 2006, Miller et al. 2013). *S. lewini* life history traits such as a long lifespan (~30 yr), relatively slow growth rates, and a late age at maturity (Cortés 2000, Piercy et al. 2007, Hayes et al. 2009) make them susceptible to overfishing. Regionally, indicators of abundance have shown decreasing trends in catch rates (Sabarros et al. 2022), evidence of overfishing

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(Hayes et al. 2009, Jiao et al. 2011, Pacoureau et al. 2021), and population declines across ocean basins (Miller et al. 2013, Rigby et al. 2019). While traditional stock assessments of scalloped hammerhead sharks have not been possible because catch is often reported at the genus level (*Sphyrna* spp., Rice et al. 2015), an assessment of large hammerhead sharks, which includes *S. lewini*, in the Gulf of Mexico found an 83–85% decrease in abundance between 1981 and 2005 (Hayes et al. 2009). These declines are attributed to both targeted fishing to supply the shark fin trade, where the fin rays of hammerhead sharks are considered highly valuable (Clarke et al. 2006), and high bycatch mortality in a wide range of fisheries (i.e. artisanal, longline, purse seine, gill net) in every ocean (Miller et al. 2013).

As a result of documented population declines, *S. lewini* were determined to be at risk of extinction in 4 of 6 distinct population segments (DPSs) and listed under the United States Endangered Species Act (ESA) in 2014 (Title 16 United States Code [U.S.C.] § 1531 et seq.). The analysis concluded that there was sufficient evidence to support the existence of 6 DPSs based on genetic differentiation, movement behavior, life history data, and differences in international regulatory management mechanisms (Miller et al. 2013). The 6 DPSs and associated ESA listing status are: Northwest Atlantic and Gulf of Mexico DPS — not warranted, Central and Southwest Atlantic DPS — threatened, Eastern Atlantic DPS — endangered, Indo-West Pacific DPS — threatened, Central Pacific DPS (which includes the main [MHI] and Northwestern Hawaiian islands [NWHI]) — not warranted, and Eastern Pacific DPS — endangered (Miller et al. 2013). *S. lewini* were also listed under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and in 2018, *S. lewini* were listed as Critically Endangered globally by the International Union for Conservation of Nature (IUCN; Rigby et al. 2019). Despite their global vulnerability and associated international regulations, effective conservation of hammerhead sharks remains challenging due in part to our limited understanding of their biology and ecology across regions (Gallagher et al. 2014a,b, Gallagher & Klimley 2018).

In general, current knowledge of the biology, movement patterns, diet and life history of *S. lewini* in the Pacific Ocean is largely derived from studies around isolated seamounts off the Central and South American Pacific coasts in the Eastern Tropical Pacific (Hearn et al. 2010, Bessudo et al. 2011a,b, Ketchum et al. 2014a,b, Lara-Lizardi et al. preprint doi:10.1101/2020.03.02.972844). These studies show strong habitat selectivity and site fidelity to oceanic seamounts or atolls where adult *S. lewini* routinely form aggregations in the upper layers of the water column (Klimley & Nelson 1981, 1984, Hearn et al. 2010, Bessudo et al. 2011a, Ketchum et al. 2014a,b). These aggregations have been linked to foraging, reproduction, thermoregulation, and refuging (Bessudo et al. 2011a, Ketchum et al. 2014a,b, Jacoby et al. 2022), although the underlying processes driving this behavior are less understood. Away from islands or seamounts, *S. lewini* are known to exploit large ranges of vertical habitat to the epi- and mesopelagic environments (>1000 m in some cases, Bessudo et al. 2011b, Anderson et al. 2022). These excursions likely facilitate the exploitation of deepwater prey (Jorgensen et al. 2009, Bessudo et al. 2011b, Hoffmayer et al. 2013, Hoyos-Padilla et al. 2014, Spaet et al. 2017) and avoidance of interspecific prey competition (Jorgensen et al. 2009). The horizontal movement patterns of *S. lewini* vary spatially and temporally, and are often related to abiotic factors such as temperature and habitat type as well as stage of ontogeny (Klimley & Butler 1988, Galvan-Magana et al. 1989, Holland et al. 1993, Bessudo et al. 2011b, Ketchum et al. 2014b, Hussey et al. 2015). *S. lewini* pups are generally born during warmer months in shallow, turbid embayments which serve as nursery areas where they remain resident for up to 2 yr (Bush & Holland 2002, Duncan & Holland 2006, Corgos & Rosende-Pereiro 2022). Adult *S. lewini* have been shown to undertake seasonal movements between sheltered coastal and open oceanic habitats (Klimley & Butler 1988, Galvan-Magana et al. 1989, Holland et al. 1993). Conservation management plans tend to concentrate on *S. lewini* 'hotspots', such as isolated aggregation sites, for marine protected areas, but the species' regionally specific use of both coastal and pelagic habitats makes effective conservation management planning particularly complex. Consequently, more data are required on movement behavior and habitat use preferences of *S. lewini* across their range and throughout various stages of ontogeny (Gallagher & Klimley 2018).

S. lewini that occupy waters around Hawai'i are considered part of the Central Pacific DPS. Adult female *S. lewini* enter sheltered coastal areas and embayments during warmer months for parturition, with peak numbers arriving between May and September (Clarke 1971, Holland et al. 1993, Duncan & Holland 2006). Adult male *S. lewini* are also present in these inshore areas at the same time, possibly for mating or feeding opportunities (Clarke 1971).

Kāneʻohe Bay on the island of Oʻahu is a known nursery area for *S. lewini*, and the most recent estimates from the early 2000s suggest that 180–660 adult females give birth to 7700 (±2240) pups yr^{-1} (Duncan & Holland 2006). Although fluctuations in population size since then are likely, the importance of the Bay throughout all stages of ontogeny for *S. lewini* is unequivocal (Clarke 1971, Holland et al. 1993, Duncan & Holland 2006). Thus, Kāneʻohe Bay is an essential habitat and could be considered a critical habitat for *S. lewini* in Hawaiʻi, if the Central Pacific DPS gets listed under the ESA. A critical habitat is defined as 'a habitat or resource that is essential to the conservation of a species' (ESA, 16 U.S.C. § 424.01) and is important for preventing populations from being threatened or endangered with extinction in the future. Although some information exists on the small-scale movements and specific habitat preferences of juvenile *S. lewini* around Oʻahu, Hawaiʻi (Clarke 1971, Holland et al. 1993, Duncan et al. 2006), to date, no studies have focused on the broader-scale, long-term movement patterns of both juvenile and adult *S. lewini* throughout the Hawaiian Archipelago (i.e. NWHI and MHI) and the Central Pacific, with the exception of a 180 d tag deployment from 1 adult female tagged near Kona, Hawaiʻi (Anderson et al. 2022). Wide-ranging movements may increase *S. lewini* exposure to open-water fisheries (Pikitch et al. 2008), although if individuals or populations choose to remain within restricted areas, there is potential for increased vulnerability to both local fishing pressure and habitat degradation (Mucientes et al. 2009). Therefore, in order to structure effective conservation strategies for this highly mobile species throughout the Central Pacific, it is important to understand both larger-scale and localized movement patterns within the DPS.

Here we combine more than a decade (2009–2020) of acoustic and satellite telemetry data to investigate diel, seasonal, and long-term movement patterns and habitat use of adult male and juvenile *S. lewini* captured and tagged around a known nursery area, Kāneʻohe Bay, Hawaiʻi. Our objectives were to: (1) elucidate the overall scale and patterns of movement for adult male and juvenile *S. lewini* around the Hawaiian Archipelago, (2) determine connectivity and temporal patterns of inter-island movements, (3) elucidate offshore deep diving activity, and (4) evaluate the seasonal and interannual use of Kāneʻohe Bay as an essential habitat for *S. lewini* around Hawaiʻi. These data are crucial for providing baseline information for effective conservation and management of this iconic species in the Central Pacific.

2. MATERIALS AND METHODS

2.1. Electronic tags overview

We used 3 types of electronic telemetry tags to quantify the horizontal and vertical movements of *Sphyrna lewini*: (1) surgically implanted, acoustic transmitters provided long-term presence–absence data at locations monitored by underwater acoustic receivers, (2) pop-up archival tags (PATs) recorded horizontal (light-level geolocation) and vertical movements (depth and temperature) to document how *S. lewini* use shallow inshore and offshore deep water habitats, and (3) dorsal fin-mounted satellite tags provided a broad overview of horizontal movements outside the detection range of the acoustic receiver array. Some of the dorsal fin-mounted satellite tags were equipped with depth and/or temperature sensors to provide additional insight into shark vertical behavior and thermal environmental preferences.

2.2. Acoustic monitoring system

An archipelago-wide acoustic monitoring array (Fig. 1A) was used to track the long-term movements of acoustically tagged sharks (refer to Meyer et al. 2010 for more details). VR2 and VR2W acoustic receivers (Innovasea) were deployed throughout the archipelago from 2009 to 2020. In the NWHI, receiver stations were installed at Kure Atoll (Hōlanikū), Maro Reef (Kamokuokamohoaliʻi), Laysan Island (Kamole), Lisianski Island (Kapou), Midway Atoll (Kuaihelani), Pearl & Hermes Atoll (Manawai), and French Frigate Shoals (FFS; Lalo). Around the MHI, receiver stations were deployed around Oʻahu (where all *S. lewini* were tagged), Maui-Nui, Niʻihau, and Hawaiʻi Island (Fig. 1). Although the numbers of receivers at each island varied over time, receivers were deployed at different times, and a number of receivers were lost or removed throughout the span of the study to accommodate additional research needs, there was capacity to detect *S. lewini* around the MHI and NWHI archipelago from 2009 to 2020. Acoustically monitored habitats included atoll fore reefs, atoll lagoons, shallow (2–15 m) embayments, coastal fringing reefs of high islands (depth 10–30 m), mariculture cages (depth 50–70 m), harbor entrance channels, a submerged pinnacle, and moored buoys anchored 5–25 km offshore in 150–2480 m of water (Fig. 1).

Acoustic detection ranges were empirically determined by deploying transmitters on a weighted line

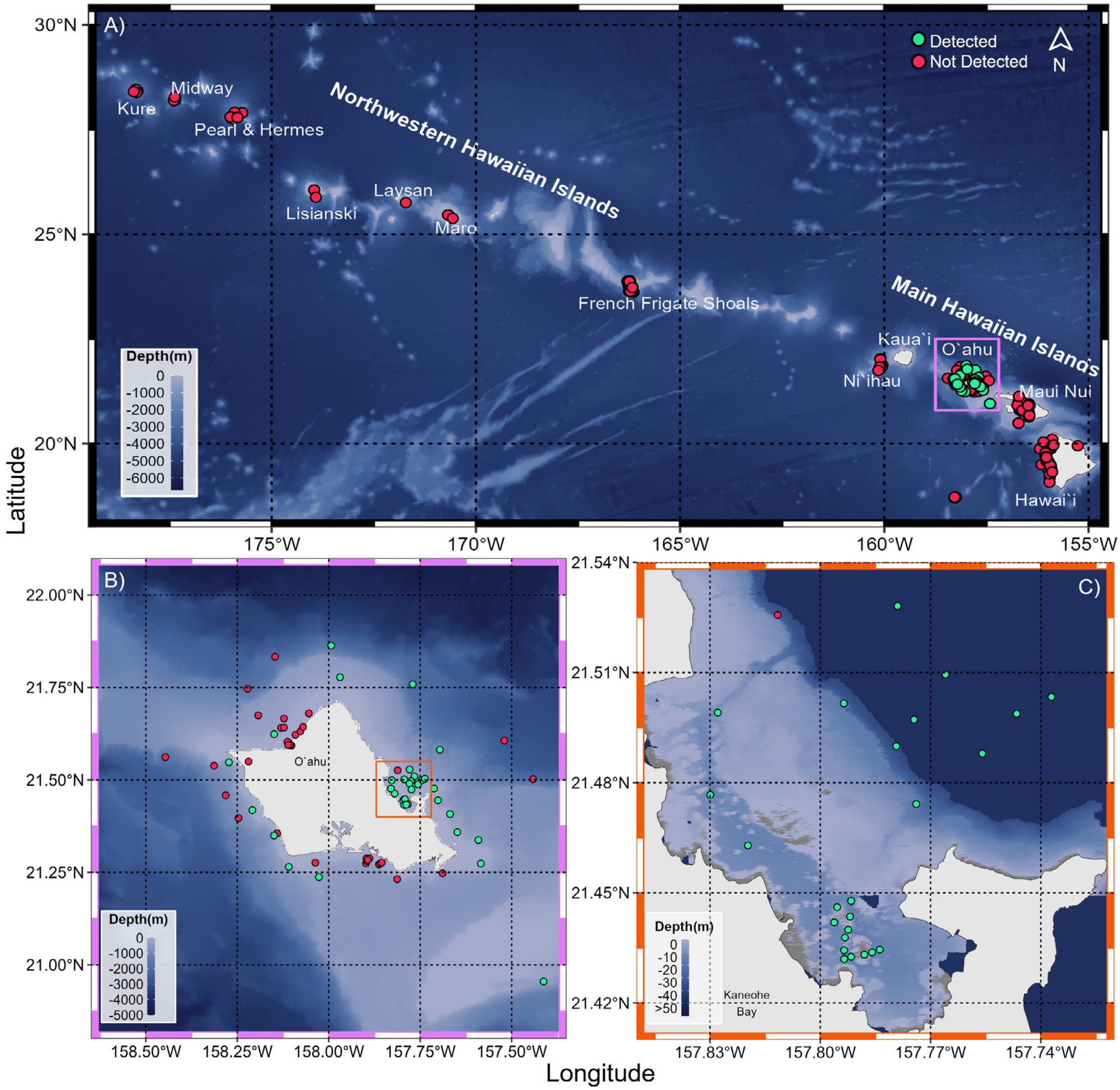


Fig. 1. Extent of the receiver array over the course of the study (March 2009–August 2020), including receiver stations that did (green circles) and did not (red circles) detect hammerhead sharks. (A) All receivers covering the main and Northwestern Hawaiian Islands, (B) receivers around O‘ahu and (C) zoom-in of receiver stations in Kāne‘ohe Bay

from a skiff equipped with an on-board GPS-equipped Vemco VR100 receiver and hydrophone. The transmitter was first deployed directly over each receiver and allowed to transmit 10 times before recovery. This process was repeated at 100 m intervals beyond the receiver to a maximum distance of 1.5 km. Detection range estimates were up to 900 m, but varied with sea state, weather conditions, and local topography (open water with calm, low-swell conditions had the largest detection ranges).

2.3. Satellite transmitters

Two different types of PATs were used in this study: (1) mk10 PATs and (2) miniPATs (both: Wildlife Computers). PATs collect and store temperature, depth and irradiance time series data during the course of a pre-programmed deployment period. Tags were programmed to detach from the shark 80, 100 or 250 d after deployment. Released PATs floated to the surface, where they transmitted archived data to the Argos satellite array.

Two different types of dorsal-fin mounted satellite transmitters were attached to *S. lewini*: (1) SPOT tags (SPOT5, 106 × 45 × 19 mm, 53 g, Wildlife Computers), which yield Argos-quality location estimates for tagged sharks, and (2) SCOUT Fastloc-GPS tags (SCOUT-Temp-361A, 107 × 57 × 20 mm, 90 g, Wildlife Computers), which are data-archiving, event-driven tags combining Fastloc GPS technology with high accuracy temperature and depth sensors for animal-borne oceanographic profiling. Once a dive is deep enough and a Fastloc GPS snapshot is taken after the dive, it is considered an 'event', so the tag creates the profile and transmits the data package through Argos. In this study, the 3 SCOUT tags were programmed to trigger an 'event' if depth exceeded 90 m and only if 10 min had elapsed since the last event. All dorsal-fin mounted tags only transmitted when the animal was at the surface and the dorsal fin was out of the water.

2.4. Shark capture and tag deployments

All *S. lewini* were captured between March and August in Kāneʻohe Bay (Oʻahu) between 2009 and 2017 (see Table 1). Even though shark fishing in the Bay took place relatively consistently year-round, no adult females were ever captured, such that only adult male and juvenile *S. lewini* were captured and tagged. Individuals were captured using demersal longlines baited with market squid, mackerel or fish scraps and soaked for <3 h in depths of 8–10.5 m (see Holland et al. 1999 for additional details of longline fishing methods). Captured sharks were brought alongside a 6 m skiff, where they were tail-roped and inverted to initiate tonic immobility. Sharks were manually restrained at the side of the vessel, measured, sexed, and assessed for maturity (based on calcification of the claspers), and remained in the water to allow irrigation of the gills. Later in the study, a pump was used as a ventilator to improve irrigation over the gills while animals were restrained in the water at the side of the vessel. Sharks remained in this position while an acoustic and/or satellite tag was attached. Acoustically tagged *S. lewini* were tagged with either a V13 (13 × 42 mm) or a V16 (16 × 94 mm) transmitter (Innovasea). These coded sonic transmitting tags provide a time stamp when they are within range of a receiver. Each tag was programmed to randomly emit a unique coded signal every 20–130 s and had expected battery lives of 622–3650 d (see Table 1 for more details). Acoustic tags were surgically implanted into the body cavity through a small incision in the abdominal wall (as per Holland et al. 1999). Following transmitter insertion, the incision was closed with uninterrupted sutures, and each shark was tagged with an external identification tag (Hallprint stainless steel dart 'wire through' tags). The PATs were inserted into the dorsal musculature with a nylon Wilton anchor and tether (Wildlife Computers), and the fin-mounted satellite tags were attached to the dorsal fin of each shark by plastic or steel surgical screws secured through 2–3 small holes drilled through the fin. The hook was then removed, and the shark released. The entire handling process took <15 min, and all sharks swam away vigorously on release.

2.5. Statistical analysis: acoustic telemetry

Transmitter data collected from the acoustic receiver array were used to analyze patterns associated with residency, frequency of detections, and diel movements. For all analyses, only individuals that were detected ≥25 times and for ≥5 d were included, to avoid individuals with low or erroneous detections biasing outputs (e.g. mortality events or moving outside the receiver detection range). If mortality events were apparent during exploratory analysis (e.g. continuous repeated detections at a single receiver for an extended period of time), the affected portion of data were removed. In total, detections from 13 *Sphyrna lewini* from 2010 to 2020 were used in the acoustic telemetry analysis. All analyses were completed in R v.4.0 (R Core Team 2021).

2.5.1. Presence and residency indices

Trends relating to the presence of *S. lewini* within the receiver array were investigated using residency indices (RIs). Monthly RIs were calculated by dividing the number of days an individual was detected on any receiver each month by the total number of days in that month. This index provided an estimate of presence and repeated annual movements at a large temporal scale (i.e. across years). RIs range from 0 to 1, where values of 1 indicate an individual was detected on all receivers (i.e. 100% of the time) and values of 0 indicate an individual was not detected at all. Exploratory analysis of the data determined that sharks were primarily detected on receivers inside and immediately outside Kāneʻohe Bay. However, for residency analyses, values were calculated only from receivers deployed inside Kāne‘ohe Bay (see Fig. 1, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n052p041_supp.pdf).

Repeated-measures ANOVAs (RM-ANOVAs), with individual as the random effect, were applied with month, season (winter: Dec-Jan-Feb, spring: Mar-Apr-May, summer: Jun-Jul-Aug, fall: Sep-Oct-Nov), and year (2010–2020) to determine temporal differences in RIs. RIs were tested for normality and arcsine-transformed prior to analysis. Planned contrasts with Tukey's adjustments were then carried out to determine which categories (i.e. month, season, year) differed from each other using the R package *emmeans* (Lenth 2021). Interactions among explanatory variables were not analyzed.

2.5.2. Diel movements

To determine diel movement patterns of *S. lewini* around Kāne‘ohe Bay, detections from receivers deployed inside and directly outside the Bay were used. The number of detections for each individual (after grouping in 1 h intervals) were grouped in four 6 h bins based on time of day (00:00–05:59, 06:00–11:59, 12:00–17:59, 18:00–23:59 h, Hawaiian Standard Time) as a percentage of total detections to allow for standardization among individuals. Only detections between April and September were included in the analysis because these were the months with the highest number of detections. Models were checked for overdispersion, and an RM-ANOVA (with individual as the random effect) was used to determine the influence of time of day and location of the receiver (either inside or outside Kāne‘ohe Bay) on the frequency of detections (arcsine-transformed) using the R packages *metafor* (Viechtbauer 2010) and *lme4* (Bates et al. 2015). Planned contrasts with Tukey's adjustments were then carried out to determine which categories (i.e. time of day and location) differed from each other using the *emmeans* package (Lenth 2021).

2.6. Statistical analysis: satellite telemetry

2.6.1. Horizontal movement patterns

The entire transmitted and recovered satellite tagging datasets, including the first 24 h following release, were decoded with the manufacturer's (Wildlife Computers) cloud-based tagging data portal (https://my.wildlifecomputers.com/). Sampling frequency for transmitted and archival tags varied from 3 to 300 s, but recovered data were down-sampled to a resolution of 150 s to facilitate the comparability of the time series data between archived and transmitted datasets (see Table S1). Location estimates for PAT-tagged sharks were constructed using the geolocation processing software WC-GPE3 (Wildlife Computers). The software uses gridded hidden Markov models with 0.25° × 0.25° grid spacing to estimate maximum likelihood locations (MLLs) which are then interpolated to a 0.025° × 0.025° grid and smoothed with a cubic spline. The accuracy of MLL is improved by constraining the model by: (1) omitting points on land, (2) implementing a speed filter which is the standard deviation of the half-normal distribution of diffusion for each shark, (3) matching observed to reference sea surface temperature and weighting the probability of the fit, and (4) estimating the fit between observed twilight and theoretical twilight at that location. The model was also anchored using known positions which included: deploy position, pop-up location, SPOT/SCOUT positions, and locations of acoustic detections for double-tagged individuals. For the model, a user-defined speed setting of 1.5 or 2 times the average traveling speed (Wildlife Computers pers. comm.) was required to regulate the allowable distance moved per day. To calculate the average daily traveling speed for *S. lewini*, we used Argos (location classes 0, 1, 2 or 3) and Fastloc GPS position data ($n = 125$ position records) from 3 SPOT and SCOUT tags. This yielded 26 daily speed estimates with an overall average traveling speed of 0.57 ± 0.5 m s^{-1} (mean ± SD). Therefore, 1 m s^{-1} was used as the speed parameter in the GPE3 geolocation models. Each model generated the tags' MLLs as well as the related probability surfaces that were subsequently analyzed and visualized via the *RchivalTag* package (Bauer et al. 2015) in R Statistical Program (version 4.0).

Finally, we conducted a supplementary analysis in the form of a Wilcoxon signed-rank test with a limit of 1000 m distance from shore, on the speed data derived to determine any variation in traveling speed of *S. lewini* between inshore and offshore areas.

2.6.2. Vertical depth diving behavior

Depth time series (DepthTS) data were used to analyze depth preferences and characteristic dive patterns of *S. lewini*. To highlight diel differences in vertical behavior, we used daily geolocation estimates to split the DepthTS data into day and night (including dawn and dusk) based on algorithms provided by the National Oceanic and Atmospheric Administration (NOAA) via the *RchivalTag* package (Bauer 2020). Individual and monthly depth preferences were further analyzed via time-at-depth profiles (TAD) and 24 h boxplots, based on daily (day and nighttime) datasets with data coverage of ≥75%. DepthTS data were also used to identify and analyze characteristic dive patterns in relation to the thermal stratification of the water column. To analyze and quantify the deep diving behavior of *S. lewini*, we classified sequences of ≥3 consecutive DepthTS records below the 200 m isobath, which marks the boundary between epipelagic and mesopelagic zones (see Howey et al. 2016). The start of a deep dive was represented by the last depth record above 200 m, and the end of a deep dive was identified as the first depth record above 200 m, resulting in ≥5 DepthTS records dive^{-1}. Based on exploratory analysis, repetitive deep dives were identified as those dives that were within 90 min of one another and exceeded a maximum depth of 325 m (i.e. to exclude relatively short deep dives). Only DepthTS records with 100% data coverage in a single dive (i.e. no gaps in transmitted depth measurements) were used to avoid sampling bias; though, we acknowledge there are inherent biases in different sampling rates (e.g. 150 vs. 300 s; Table S1). Any deep dive that did not meet these criteria were omitted from the analysis, and based on this, only repetitive deep dives from 4 *S. lewini* were included (see Table 2). Days when no repetitive deep diving occurred were also excluded from the analysis (i.e. summary statistics calculated using non-zero values only).

3. RESULTS

In total, 27 (24 male [22 adult, 2 juvenile], 3 juvenile female) *Sphyrna lewini* ranging in size (total length, TL) from 106 to 310 cm (227.92 ± 64.63; mean ± SD) were tagged with only acoustic (n = 6 [1 adult male, 5 juveniles]) or satellite (n = 2 adult males) transmitters or both (n = 19 adult males) between March 3, 2009 and June 9, 2017 (Table 1). On average, between 4 and 5 *S. lewini* were tagged per year, except for the years 2009, 2010, 2013 and 2016, in which 1, 2, 0, and 1 sharks were tagged respectively. Of all tagged individuals, HH4 (241 cm TL) and HH7 (238 cm TL) were ingested by another animal (based on PAT temperature and light level data), and HH8˜ either died or shed its acoustic tag near a receiver immediately after tagging. Six acoustically tagged individuals either moved out of the acoustic receiver array detection range or were only detected for 1 d, and 4 double-tagged individuals (i.e. combination of acoustic and satellite tags) did not successfully transmit data from either tag (Table 1; see Text S1 for additional information on tag coverage). Therefore, 14 individuals were excluded from further analysis, resulting in 13 *S. lewini* (10 adult males, 2 juvenile females, and 1 juvenile male; 8 of these 13 were double-tagged individuals) with sufficient data for analysis (see Table 1 for more details). Thus, our results pertain to adult male and juvenile *S. lewini* habitat use and movement patterns.

3.1. Acoustic tags

Of the 23 animals that were acoustically tagged, 5 were juveniles, and 3 of these were the only female *S. lewini* tagged in this study (Table 1). Two juvenile *S. lewini* (1 male; HH14$^{\mathrm{JM}}$ and 1 female; HH15$^{\mathrm{JF}}$) were only detected on the acoustic array for 1 d after tagging. The juvenile male (HH13$^{\mathrm{JM}}$) was detected for 13 d and then recaptured by a fisherman on the west side of Oʻahu 22 d after tagging. The 2 juvenile females (HH12$^{\mathrm{JF}}$ and HH16$^{\mathrm{JF}}$) were detected for 21 d across a 538 d period (HH12$^{\mathrm{JF}}$) and 12 d across a 484 d period (HH16$^{\mathrm{JF}}$) respectively (see Table 1 for details about track lengths and detection periods of all individuals). Thus, after filtering out all detections that were <25 times and/or <5 d, 13 individuals (10 adult males, 2 juvenile females, and 1 juvenile male) were included in the acoustic analyses (Table 1), lending these results to be heavily skewed toward adult male *S. lewini* movement behavior. In total, individuals were detected for 13–397 d between July 24, 2010 and June 6, 2020 (Fig. 2, Table 1). The number of sharks detected varied throughout the study and depended on tagging effort and receiver coverage (Fig. S1), such that months or years when more sharks were tagged and more receivers were in the water invariably led to higher detections.

3.1.1. Presence and residency of adult male and juvenile female *S. lewini* in Kāneʻohe Bay

Of the 237 acoustic receiver stations deployed between 2009 and 2020 across the Hawaiian Archipelago (Fig. 1A), acoustically tagged *S. lewini* were almost exclusively detected on receivers around Oʻahu (Fig. 1B); however, 1 adult male (HH10, 219 cm TL) was detected at Penguin Banks, a topo-

Table 1. Tagging metadata for every *Sphyrna lewini* (HH) tagged during this study. ‡: Mortality; ^{JM}: juvenile male; ^{JF}: juvenile female; $^{\sim}$: erroneous detections. PAT: pop-up archival tag; *tag was recovered and full archive available for analysis; **tag that communicated with satellites but did not transmit any usable data; floater: tag that came off early due to attachment failure; ND: no data (tag that did not transmit); ingested: tag that was determined to have been ingested by another animal due to changes in light levels (indicates a mortality); CD: completed deployment or the tag initiated detachment after the programmed deployment period; sitter: tag that was at a consistent depth before initiating pop-off (indicates a mortality); sinker: tag that sank below a critical depth threshold of 1400 m before initiating pop-off (indicating mortality); pin broke: tag that came off prematurely due to a manufacturer error. SPOT, SCOUT and SPLASH tags that have transmission dates but 0 detection days are tags that communicated with satellites but did not transmit any data. Dates are mm/dd/yyyy

Individual	Tagging date	Sex	Total length (cm)	Tag type	Tag number	Tag fate (PAT)/ last transmission date (SPOT/SCOUT/ Acoustic)	Deployment period (d) (PATs)/days detected (SPOT/SCOUT)/ detection period (d) (days detected, Acoustic)
HH1	03/03/2009	M	265	mk10PAT	07A0935	Floater	42
				Acoustic	367	03/15/2009 19:30	12 (5 days detected)
HH2	06/22/2010	M	257	SPOT	05S0573	ND	0
				Acoustic	54784	08/05/2014 19:48	1506 (224 days detected)
HH3	07/09/2010	M	242	SPOT	06S0055	ND	0
				Acoustic	60804	ND	0
HH4‡	06/28/2011	M	241	miniPAT	09P0279	Ingested	1
				Acoustic	61946	ND	0
HH5	06/28/2011	M	238	SPOT	08S0715	ND	0
				Acoustic	62846	08/16/2015 02:40	1511 (397 days detected)
HH6	07/27/2011	M	252	miniPAT	10P0191	Floater	77
				Acoustic	61953	07/28/2011 02:59:14	1
HH7‡	08/25/2011	M	238	miniPAT	10P0210	Ingested	1
				SPOT	08S0713	ND	0
				Acoustic	61963	ND	0
HH8$^{\sim}$	04/18/2012	M	260	miniPAT	10P0196	ND	0
				Acoustic	61964	05/20/2013 03:02	398 (293 days detected)
HH9	05/02/2012	M	246	miniPAT	11P0257*	Floater	11
				Acoustic	54789	08/25/2013 18:55	481 (139 days detected)
HH10	05/11/2012	M	219	miniPAT	11P0205	ND	0
				Acoustic	54785	11/23/2012 06:05	197 (9 days detected)
HH11	05/16/2012	M	215	miniPAT	11P0216	CD**	100
				Acoustic	61979	04/18/2014 03:49	703 (280 days detected)
HH12^{JF}	09/08/2014	F	106	Acoustic	38672	04/12/2016 16:05	538 (21 days detected)
HH13^{JM}	09/08/2014	M	117	Acoustic	38667	09/25/2014 16:51	18 (13 days detected)
HH14^{JM}	09/08/2014	M	116	Acoustic	18795	09/09/2014 05:21	1
HH15^{JF}	09/08/2014	F	117	Acoustic	18796	09/09/2014 00:44	1
HH16^{JF}	09/08/2014	F	128	Acoustic	18797	01/04/2016 02:26	484 (12 days detected)
HH17‡	06/16/2015	M	252	miniPAT	11P0100	Sitter	0.13
				Acoustic	7918	ND	0
HH18‡	06/16/2015	M	247	miniPAT	11P0207*	Sitter	37
HH19	07/08/2015	M	248	SPOT	13S0704	07/10/2016	361
				Acoustic	7919	07/01/2017 18:39	725 (82 days detected)
HH20	07/14/2015	M	267	SPOT	09S0208	08/20/2016	432
				Acoustic	7917	06/06/2020 16:56	1790 (160 days detected)
HH21	07/14/2015	M	281	Acoustic	50332	ND	0
HH22	06/22/2016	M	233	SCOUT-Temp-361A	15A0905	12/26/2016	188
HH23‡	04/28/2017	M	254	miniPAT	13P0054	Sinker	11
				SPOT	16U0444	06/17/2017	0
HH24	05/10/2017	M	310	miniPAT	10P0102	CD	250
				SCOUT-Temp-361A	15A0942	01/17/2018	252
				Acoustic	20965	06/13/2017 22:19	35 (22 days detected)
HH25	06/05/2017	M	209	miniPAT	10P0098	CD**	250
				Acoustic	20964	06/29/2020 06:47	1121 (154 days detected)
HH26	06/05/2017	M	243	miniPAT	11P0160*	Pin broke	1
				Acoustic	20966	05/19/2020 09:07	1079 (149 days detected)
HH27	06/09/2017	M	241	miniPAT	10P0097	Floater	186
				SCOUT-Temp-361A	15A0970	08/01/2017	0

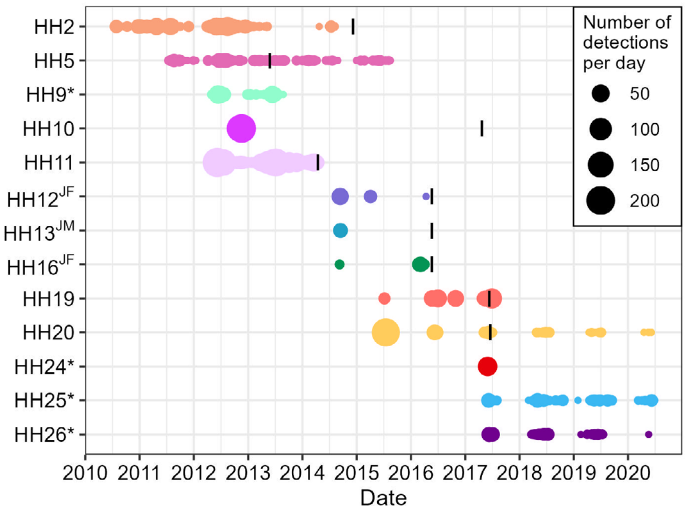


Fig. 2. Number of daily acoustic detections for 13 *Sphyrna lewini* across the study period from 2010 to 2020. Vertical black lines: estimated tag-battery life end dates. *Tag that should still be transmitting after 2020; ^{JF}: juvenile female; ^{JM}: juvenile male

graphic feature approximately 28 miles (45 km) southeast of Oʻahu (Figs. 1B & 3A). Overall, there were between 1 (in 2010) and 6 (in 2014) individuals detected inside Kāneʻohe Bay annually between 2010 and 2020, with an average of 3.3 *S. lewini* detected yr^{-1} (Fig. 3). Monthly RIs pooled across all individuals between 2010 and 2020 indicate increased presence of *S. lewini* in Kāneʻohe Bay between May and September (Fig. 4A). Presence of *S. lewini* was consistently highest throughout the summer months (i.e. June–August) across all years (RI: 0.48 ± 0.35, mean ± SD), with values peaking in June (RI: 0.57 ± 0.35, Tables S2 & S3). In contrast, there was consistently low presence of *S. lewini* during winter (i.e. December–February) across the study period (RI: 0.04 ± 0.01), with the lowest RIs in January and February (0.03, mean) (Fig. 4A, Tables S2–S4), although 5 individuals (HH2, HH5, HH11, HH25 and HH26) were detected in Kāneʻohe Bay during winter in 2012 (n = 1), 2013 (n = 2), 2014 (n = 1) and 2019 (n = 2, Fig. 4B). *S. lewini* were relatively consistently present in the Bay during the fall between 2010 and 2014; however, after 2014, no individuals were detected within the Bay during the fall (Fig. 4B). This result may be an artifact of sampling design rather than absence of *S. lewini* in the area (see Fig. S1 for details on receiver coverage). Overall, RI did not differ substantially between years, due to the large inter-annual variation in RI (Fig. 4A, Table S4).

Of the 13 acoustically tagged *S. lewini* that provided sufficient data, 7 adult males made repeated seasonal movements to Kāneʻohe Bay throughout the study period (Fig. 4B). On average, adult male

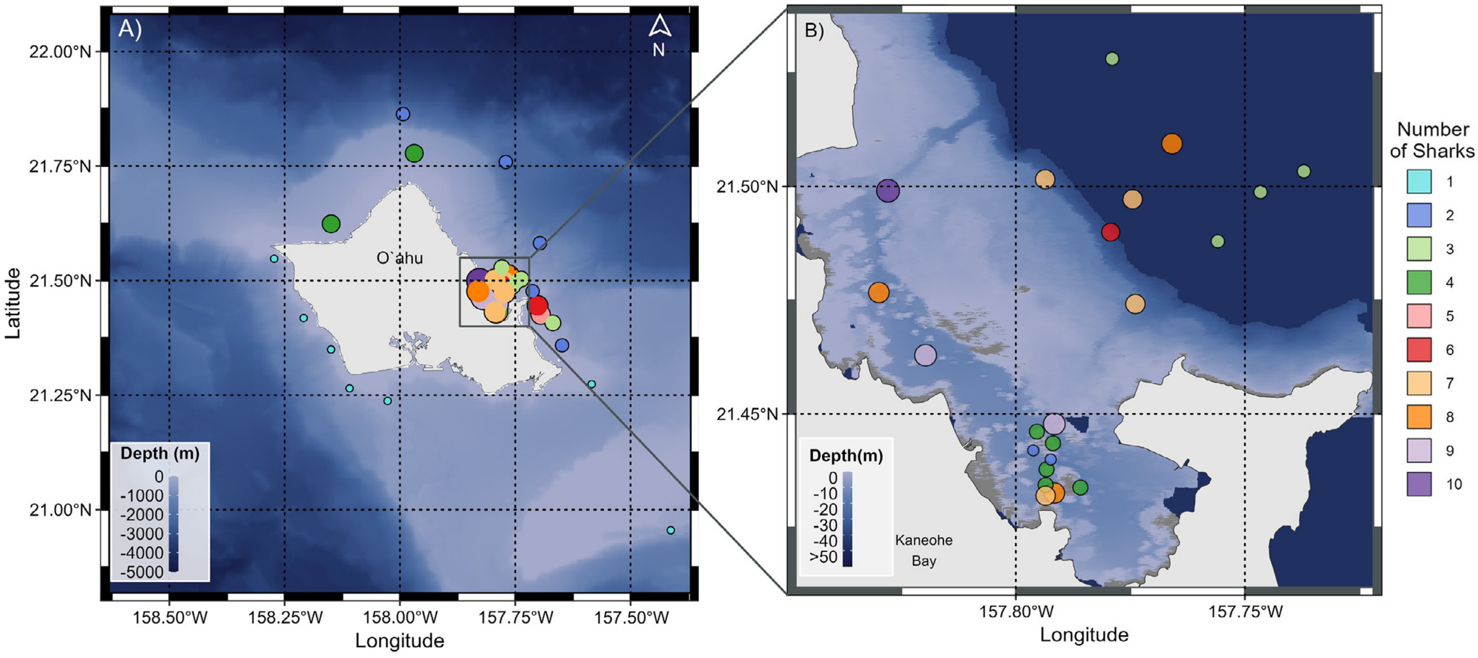


Fig. 3. (A) Bubble plot showing number (circle color and size) of acoustically tagged *Sphyrna lewini* detected on Oʻahu receivers across the detection period 2010–2020 and (B) a zoom-in of number of *S. lewini* detected on receivers inside and outside of Kāneʻohe Bay

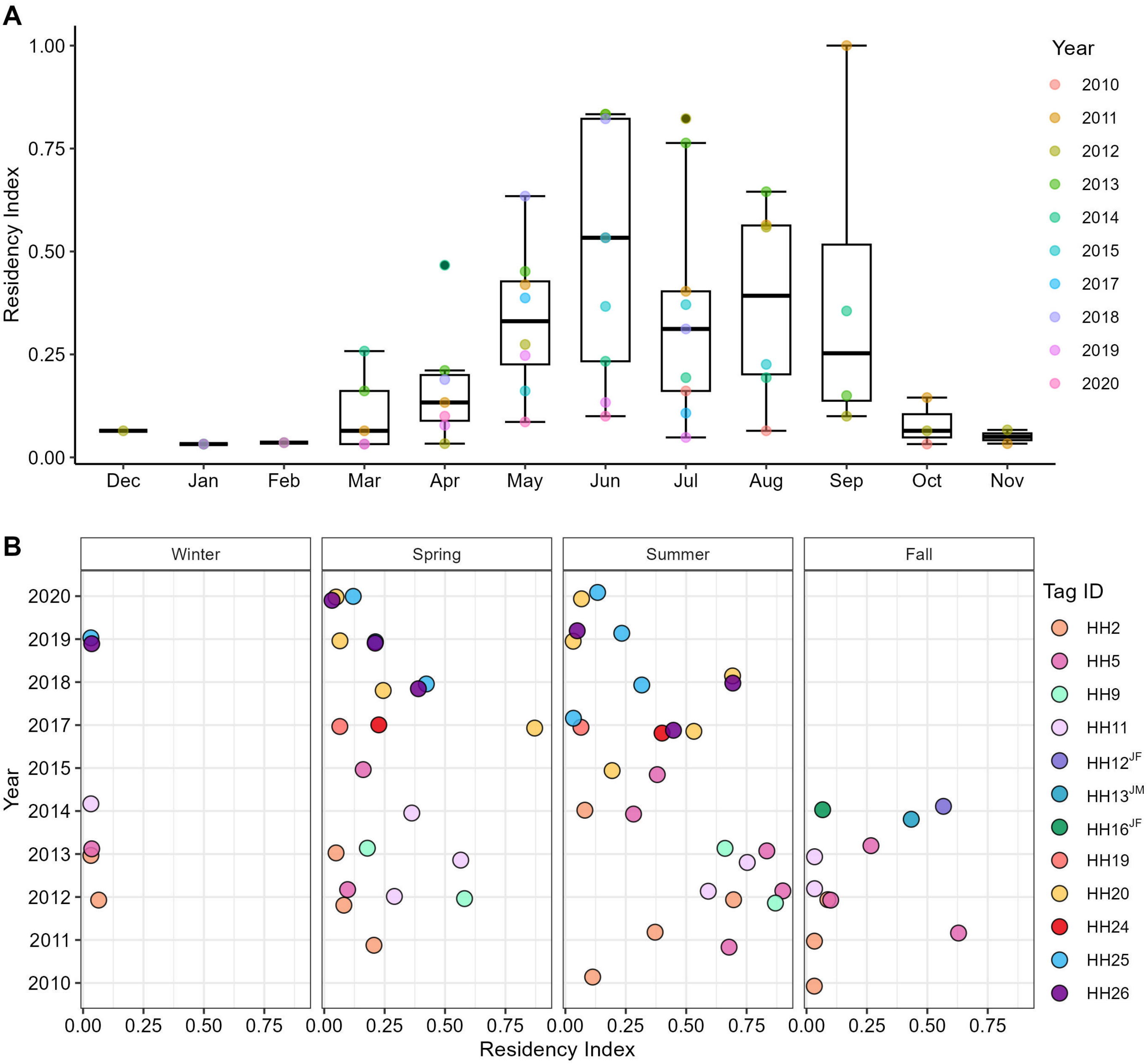


Fig. 4. Residency indices (RIs) for acoustically tagged *Sphyrna lewini* (n = 13) across the detection period 2010–2020. (A) Monthly RI for all individuals combined between 2010 and 2020. Each colored circle represents mean RI for 1 year. Box-and-whisker plots: lower 25th percentile, median and upper 75th percentile monthly RI for each year, with whiskers extended to extreme values. (B) Seasonal mean RI for n = 12 *S. lewini* across years. Repeated annual movements of individuals into Kāneʻohe Bay represented by the same colored circle. ^{JF}: juvenile female; ^{JM}: juvenile male. NB: Data for winter and fall of 2020 are not included

S. lewini returned to Kāneʻohe Bay across 3 years (not necessarily consecutively) and mainly during spring and summer (Fig. 4B), although there was a large amount of individual variation in repeated annual movements. Moreover, 2 individuals were detected inside Kāneʻohe Bay for 5 consecutive years between 2010 and 2015 (HH2) and between 2011 and 2016 (HH5), and 2 other individuals (HH25 and HH26) returned to the Bay across 4 consecutive years between 2017 and 2020 (Fig. 4B).

Interestingly, the 2 juvenile females (HH12^{JF} and HH16^{JF}) were only detected in the Bay after tagging in September 2014 and did not make repeated movements back to the Bay across years (Fig. 4B).

HH12^{JF} was detected on receivers just outside of Kāneʻohe Bay over 2 d in spring 2015 and 1 d in spring 2016. HH16^{JF} was undetected for 2 yr after leaving the Bay, before being detected on the North Shore of Oʻahu over 9 d in winter and spring of 2016.

3.1.2. Acoustic diel movements of adult male and juvenile female *S. lewini*

Diel movement patterns of adult male and juvenile female *S. lewini* (calculated from receivers inside and directly outside Kāneʻohe Bay) showed an increase in the proportion of detections inside the Bay during the night between 18:00 and 05:59 h compared with the daytime from 06:00 to 17:59 h (Fig. S2, Table S5). However, consistently higher detections on receivers outside the Bay suggest that *S. lewini* spent the majority of their time outside the Bay but made brief, intermittent movements into the Bay during nighttime in the summer months.

3.2. Satellite tags

3.2.1. Data coverage

Only adult male *S. lewini* were tagged with satellite tags. In total, 15 individuals were tagged with PATs, but only 7 tags provided sufficient data for analysis, due to mortality events and tag malfunctions (see Table 1, Fig. S3, and Text S1). *S. lewini* with PATs had track durations ranging from 11 to 250 d. Average daily data transmission rates for the non-recovered PAT tags were poor, and ranged from 0 to <5% for tags with longer deployment periods (Fig. S3), drastically reducing the number of days with usable data for vertical behavior and habitat use analyses. Of the 10 dorsal-fin mounted satellite transmitters (SPOT and SCOUT tags), only 3 adult male *S. lewini* (HH20, HH22, HH24) yielded usable data, of which HH24 was double-tagged with a PAT (see Table 1 for more details). The 3 SPOT and SCOUT tags with sufficient data generated intermittent position data for periods of 188–432 d and were at liberty for a total of 870 d (Table 1). There were average data gaps of 4.6–39 d (maximum data gaps: 47–155 d) between subsequent (exploitable) records, corresponding to a data coverage of only 3% (excluding the 7 non-reporting-SPOT and SCOUT tags, see Text S1).

3.2.2. Horizontal movement behavior of adult male *S. lewini*

Horizontal movements of adult male *S. lewini* tagged in Kāneʻohe Bay were variable yet highly associated with the Hawaiian Archipelago (Figs. 5, 6 & S4–S12). All of the adult male *S. lewini* left the Bay within 1 d after tagging. HH1 moved north and was later acoustically detected at a shark tourism location on the north shore of Oʻahu prior to moving into deeper offshore habitats between Oʻahu and Kauaʻi, where the tag came off after 47 d (Figs. 5A & S4). HH6 moved due east after tagging, towards Molokai, and then continued east and off the shelf into deep water before turning south and then directly west towards the north side of Maui, where the tag came off 77 d later (Figs. 5A & S5). HH9 stayed close to shore and moved around to the northern tip of Oʻahu, where the tag was shed 11 d later (Figs. 5A & S6). HH18 moved away from Kāneʻohe Bay after tagging and headed directly offshore and then east to the northern side of Maui, where the animal died 37 d later (Figs. 5A & S7). HH23 headed offshore and northeast, where it also died 11 d later (Figs. 5A & S8). The longest PAT deployment period of 252 d was for HH24, which left the Kāneʻohe Bay area a month after tagging and swam northwest along the archipelago until reaching FFS in the NWHI, where it remained until the tag ceased reporting (Figs. 5A,B & S9). HH27 spent 241 d in the deep offshore habitats north of Oʻahu, swimming back and forth between the east side of Oʻahu and northwest of Molokai before heading south through the Kaʻiwi Channel to the southern tip of Penguin Banks, where the tag detached (Figs. 5A,B & S10).

For the 3 adult male *S. lewini* with usable fin-mount tag (SPOT/SCOUT) data, 2 remained in waters around Oʻahu for 50 (HH20, until September 2015) and 39 (HH24, until June 2016) days after tagging respectively, prior to swimming northwest along the archipelago towards FFS (Figs. 5, 6, S9C & S11). HH20 took approximately 115 d and HH24 took 38 d to reach this area. HH20 was subsequently detected in the general vicinity of FFS (mean ± SD distance to FFS of 55.9 ± 15.5 km, n = 3 locations) 3 times over the course of 43 d (Fig. S11). HH20 was next detected around Oʻahu 6 mo later and then intermittently detected by acoustic receivers around Oʻahu for an additional 160 d. In contrast, HH24 remained within close proximity of FFS for 183 d (44.4 ± 29 km, mean ± SD), until the PAT released as programmed after 250 d and the SCOUT stopped transmitting after 251 d (Figs. 6 & S9). HH24 was

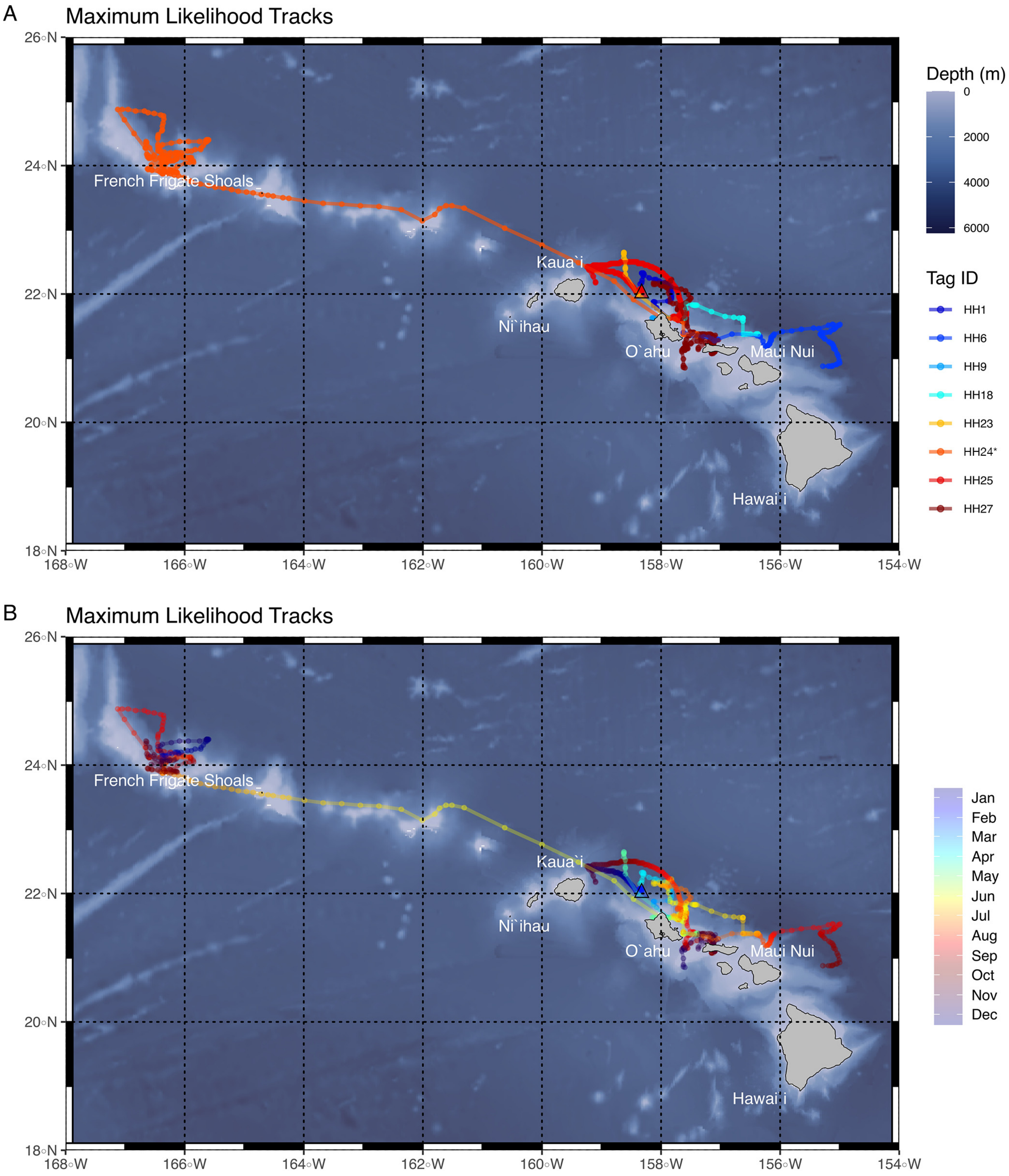


Fig. 5. The Hawaiian archipelago with (A) overall maximum likelihood tracks of 8 satellite-tagged *Sphyrna lewini*, and (B) the same tracks colored by month of deployment period. Triangles: pop-off locations of the tags. The * next to HH24 denotes that this individual was triple-tagged

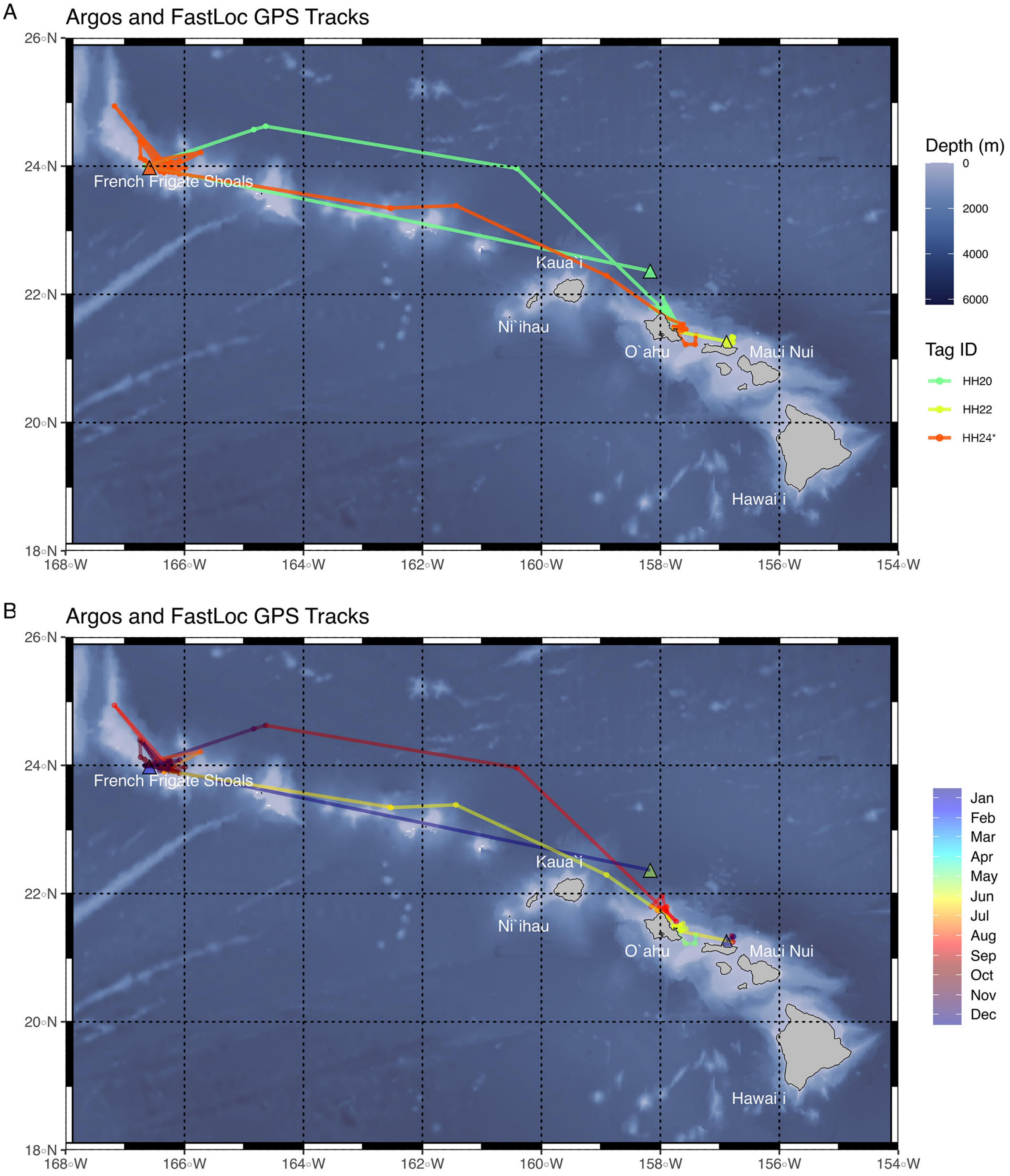
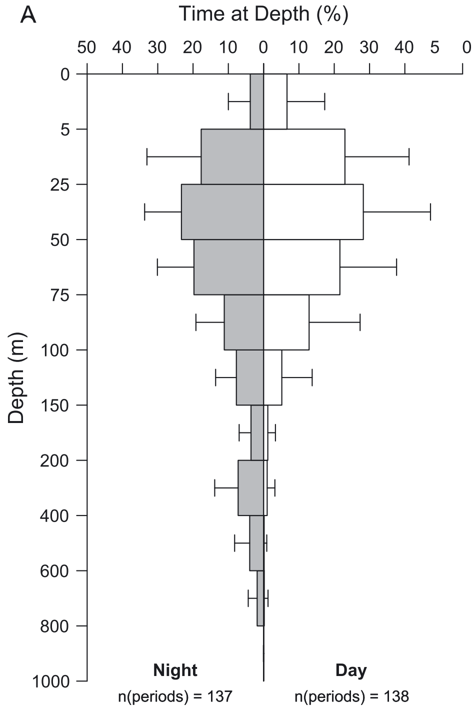


Fig. 6. Bathymetric maps of the Hawaiian archipelago with: (A) the transmitted Argos and Fastloc GPS positions of 3 fin-mount satellite-tagged *Sphyrna lewini* that moved away from O'ahu, and (B) the same tracks colored by month of deployment period. Tracks have been overlaid onto bathymetry for the region. Triangles: pop-off locations of the tags. The * next to HH24 denotes that this individual was triple-tagged

never detected on the acoustic array after leaving Kāneʻohe Bay post tagging. Unlike these 2 individuals, HH22 remained between Oʻahu and Maui (mean ± SD distance to shore of 8.6 km ± 7.67 km; n = 6 locations) throughout the duration of its tag deployment (188 d from mid-June until the end of December 2016; Figs. 6 & S12). The estimated overall average traveling speed of these individuals (HH20, HH22, HH24) was 0.57 ± 0.5 m s^{-1}, and these animals exhibited higher traveling speeds in offshore (0.69 ± 0.5 m s^{-1}, n = 17 daily speed estimates) compared with inshore areas (0.33 ± 0.4 m s^{-1}, n = 9 daily speed estimates).

3.2.3. Vertical movement behavior of adult male *S. lewini*

Diel vertical movements. Five adult male *S. lewini* (HH6, HH9, HH18, HH23, HH27) yielded sufficient data (transmission coverage ≥75% in a 24 h period) for analysis of diel vertical movements and habitat use. On a 24 h scale, tags from these individuals provided 125 d of data, whereas the day and nighttime datasets returned 138 and 137 periods for TAD data analysis respectively (Figs. 7 & S13). After tagging, depth use



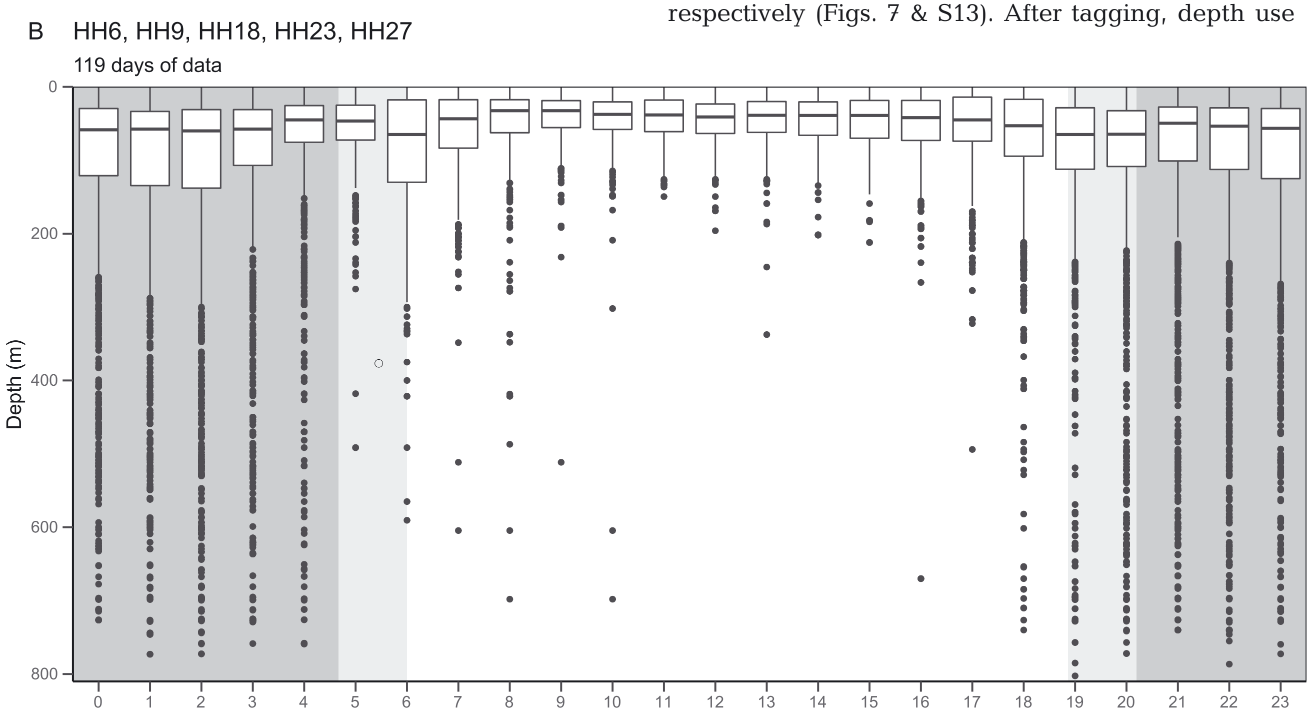


Fig. 7. (A) Daytime and nighttime depth use of 5 satellite-tagged *Sphyrna lewini*. Error bars: SD across all records. (B) Lower (25th percentile), median and upper (75th percentile) diel vertical movement patterns across hours of the day of the same individuals. Whiskers extend to minimum and maximum values. Dark gray and light gray: average night and twilight periods, respectively. Data from HH1 not shown here because the tag was an early version that did not return time series data. Data from HH24 not shown here because it did not meet the criteria of depth time series (DepthTS) data transmission coverage ≥75% in a 24 h period. HST: Hawaiian Standard Time

was restricted to the upper mixed layer (100 m) of the water column, with only short dives beyond 200 m for periods ranging from 1 to 12 d post tagging. Fig. 7 shows variation in diel movement patterns across all individuals, but generally, *S. lewini* spent the majority of their time in the upper 100 m, with higher frequencies during the day (92.4 %) than during nighttime (75.7 %) (Figs. 7 & S13). We were unable to make inferences regarding seasonal patterns in diving behavior; however, at a monthly scale, vertical movements appeared to be more dynamic between July and October compared with May and June (Fig. S14), although this could be an artefact of small sample sizes and insufficient data coverage.

Deep-diving behavior. Four of the adult male *S. lewini* (HH6, HH18, HH24 and HH27) that exhibited deep, repetitive diel diving behavior had sufficient data coverage (i.e. DepthTS records with 100 % data coverage in a single dive with no gaps in transmitted depth measurements) for analysis of dive patterns. Time periods from tagging to the onset of deep diving ranged from 7 to 22 d (Table 2). The typical deep repetitive dive patterns began with shorter-duration dives (i.e. an initial excursion to ~300 m) during the twilight periods, followed by a series of deep dives (i.e. dives to the mesopelagic layer beyond 325 m occurring within 90 min of each other) during the night (Table 2). In total, the adult male *S. lewini* made between 44 and 407 (depending on deployment period and transmission coverage) nocturnal repetitive deep dives to depths between 330 and 802 m (Table 2). These individuals made between 2 and 14 repetitive deep dives night^{-1}, with a single dive taking anywhere from 6 to 105 min. The range of water temperatures experienced during a deep dive was between 5.0 and 13.9°C. Fig. 8 provides a clear illustration of the deep-diving behavior for HH18 (recovered PAT) across a period of 1 mo (June 17 to July 22, 2015, Fig. 8A). After tagging on June 17 until July 1, this individual remained primarily within the upper 150 m of the water column, but made sporadic, infrequent dives down to ~300 m during the day and at night (Figs. 8B & S13). On July 7, 2015, the diving behavior shifted to very consistent nocturnal deep dives beyond 500 m (Fig. 8C,D), which was characteristic of the deep diving behavior also exhibited by HH6, HH24 and HH27. Unfortunately, the dates and times of the SCOUT locations and deep-diving behavior did not overlap for the double-tagged sharks (HH24 and HH27), so we were unable to pinpoint exact locations of these deep dives.

3.4. Tag reliability and performance

Finally, excluding the individuals that died (based on tag signatures), 6 of the 23 acoustically tagged animals were either detected for 1 d or remained undetected within the acoustic array. It is not uncommon for tagged sharks or fish to go undetected because they either never moved into the detection range of the receiver (Meyer et al. 2007), or more likely, ventured to other locations where there were no receiver stations. Similarly, and excluding the finmount tags on animals that died, 9 of 25 satellite tags did not transmit data. Unfortunately, tag hardware, software, user issues and limited Argos satellite coverage (only 6–12 min h^{-1} in Hawai'i) as well as tag retention time on animals resulted in shorter deployment durations than expected and limited data availability for analysis (see Text S1 for more information).

Table 2. Comparison of vertical deep diving behavior of 4 *Sphyrna lewini* (HH6, HH18, HH24 and HH27) that exhibited repetitive deep dives below 325 m and within 90 min of one another. +: temperature data not available; *: archived data available. DVM: diel vertical migration; NA: not available; temp.: temperature

Shark ID	Tag number	Days from tagging to DVM	Total deep dives	Total repetitive deep dives	Mean ± SD (range)					
					Deep dives night^{-1}	Dive duration (min)	Maximum depth (m)	Min. temp. (°C)	Time since previous dive (min)	Temp. since previous dive (°C)
HH6+	10P0191	16	393	387	7 ± 2 (2–11)	30 ± 7 (20–105)	622 ± 104 (330–802)	NA	38 ± 12 (15–85)	NA
HH18*	11P0207	22	68	61	4 ± 2 (2–6)	19 ± 5 (6–32)	569 ± 63 (352–741)	6.2 ± 0.7 (5.0–10.4)	52 ± 11 (32–79)	25.4 ± 0.3 (24.6–25.8)
HH24	10P0102	11	44	19	3 ± 1 (2–4)	29 ± 4 (20–38)	707 ± 66 (504–801)	5.6 ± 0.5 (5.1–6.7)	64 ± 7 (55–78)	25.9 ± 0.5 (25.0–26.5)
HH27	10P0097	7	428	407	6 ± 3 (2–14)	27 ± 5 (20–45)	564 ± 75 (374–758)	6.7 ± 0.8 (5.3–13.9)	40 ± 10 (25–90)	25.3 ± 0.6 (22.4–26.8)

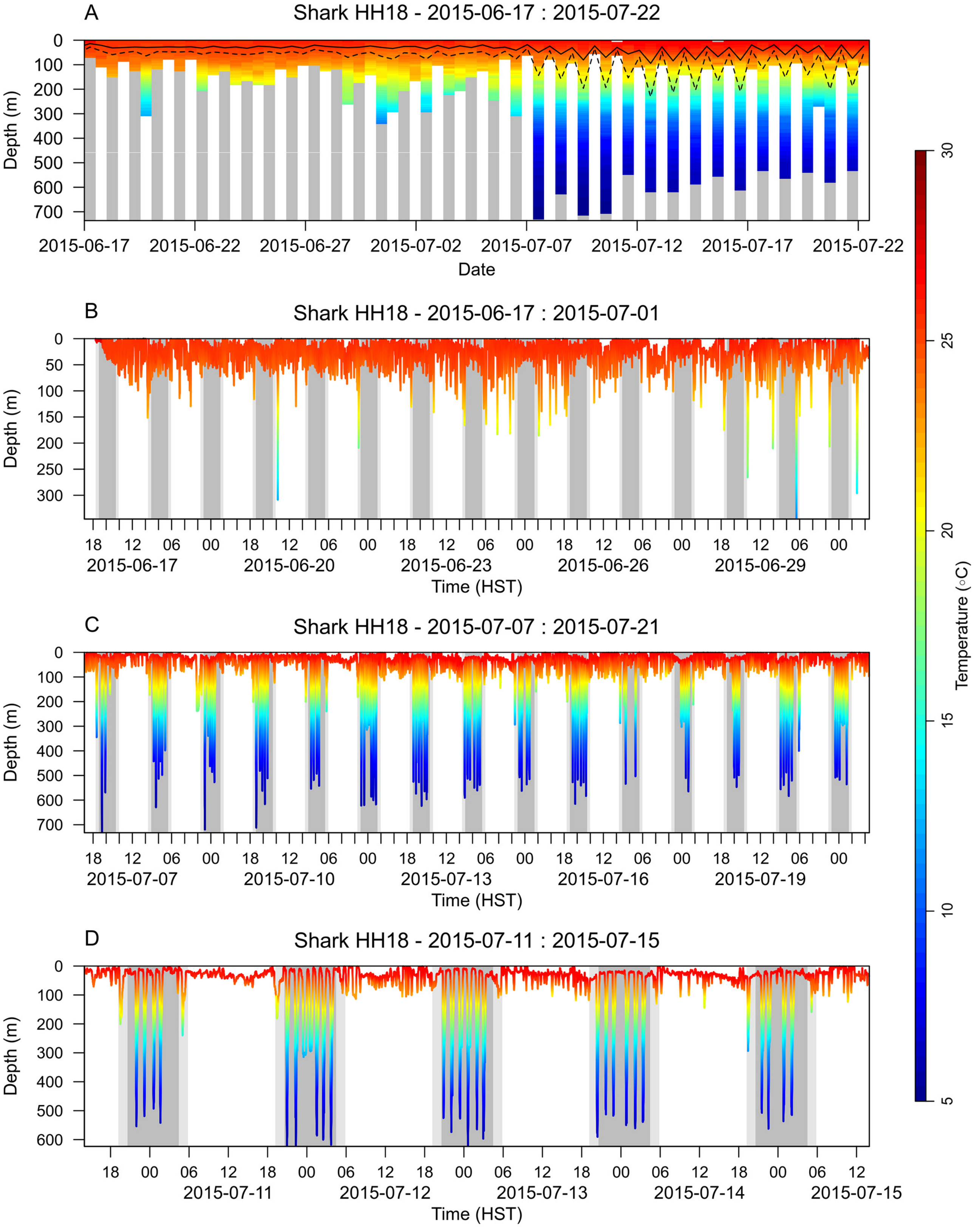


Fig. 8. Archival time series of depth–temperature profiles from a *Sphyrna lewini* (HH18) during a 37 d deployment. (A) Daily interpolated depth–temperature profiles, with average depths (black solid line) and SD (black dashed line) during day (white bars) and night periods (gray bars). Depth–temperature profiles are color-coded by water temperature (*y*-axis), where the lowest temperatures denote the daily maximum depth. (B,C) Depth–temperature time series during the (B) first and (C) last 2 wk of the deployment respectively. (D) Repetitive deep-diving behavior over a 4 d period. HST: Hawaiian Standard Time

4. DISCUSSION

Provision of effective global conservation and management measures for shark populations has become increasingly important on a global scale (Schiffman & Hammerschlag 2016, Queiroz et al. 2019, Dulvy et al. 2021). Ultimately, successful measures depend upon accurate assessment of population status, which is often constrained by limited and unreliable catch, life history, and habitat use data (Clarke 2013). The present study provides timely and crucial information on the spatial and temporal movement patterns of adult male and juvenile scalloped hammerhead shark *Sphyrna lewini* throughout the Hawaiian Archipelago and the Central Pacific.

4.1. Seasonal residency of adult male and juvenile *S. lewini* in Kāneʻohe Bay (identifying important habitats for conservation)

Here, we show that adult male *S. lewini* tagged in Kāneʻohe Bay, Oʻahu, exhibit very strong site fidelity specifically during the warmer months (i.e. April–September), with >50% (7 of 13) of acoustically tagged individuals making repeated visits back to the Bay across multiple years. These specific and repeated uses of Kāneʻohe Bay confirm previous studies suggesting this location would likely be considered a critical habitat, containing 'physical or biological features essential to the conservation of the species', if the Central Pacific DPS is ever listed under the US ESA (Holland et al. 1993, Lowe 2001, 2002, Duncan & Holland 2006) (ESA, 16 U.S.C. § 424.01). Kāneʻohe Bay is the largest semi-enclosed body of water (16 mi^2, or 41 km^2) in the MHI (Smith et al. 1973). The Bay is sheltered, shallow (<20 m), and consists of a network of fringing, barrier and patch reefs providing foraging opportunities and shelter from predators for *S. lewini* across all life stages. High site fidelity, especially seasonal residency to specific locations, is a common behavioral characteristic of *S. lewini* (e.g. Klimley & Nelson 1984, Hearn et al. 2010, Bessudo et al. 2011a,b, Ketchum et al. 2014a,b), often indicating movements to parturition areas (Clarke 1971, Duncan & Holland 2006), feeding sites (Boelhert & Genin 1987, Barton 2001, Dewar et al. 2008) or places of refuge (e.g. Hamilton & Watt 1970, Klimley & Nelson 1984, Ketchum et al. 2014b). An estimated 7700 (±2240) pups are born in Kāneʻohe Bay each year (Duncan & Holland 2006), and reproductive aggregations of female *S. lewini* have been observed traveling into and around the Bay annually between April and September (authors' pers. obs.). These ecological attributes create an increase in both reproductive and feeding opportunities for male *S. lewini* in the Bay during specific times of the year, particularly as *S. lewini* pups are a known prey item for adult *S. lewini* and other larger sharks (Clarke 1971). Repeated use of the Bay may also vary with stage of ontogeny. Our results show that the 2 juvenile females (HH12^{JF} and HH16^{JF}) were not re-detected in Kāneʻohe Bay after tagging, indicating that once juvenile *S. lewini* leave the Bay, they may not return until they are mature. However, habitat use and movement behavior for juvenile (>2 yr old) and subadult *S. lewini* is unknown. Considering then, the enormous importance of Kāneʻohe Bay throughout the life cycle of *S. lewini*, we suggest that management strategies should explicitly consider temporal closures of Kāneʻohe Bay, and other known hammerhead shark nurseries, to unmonitored fishing methods (e.g. gillnets, throw/surround nets) particularly during April–September, when local fishing pressure in the Bay is highest (Everson & Friedlander 2004).

Conservation management plans should ensure the protection of ecosystem health and integrity of known nursery areas, particularly as climate change and other anthropogenic impacts are predicted to disproportionately affect shallow inshore reef ecosystems (Wooldridge 2009, Giddens et al. 2022, IPCC 2022). Duncan & Holland (2006) found that *S. lewini* pups in Kāneʻohe Bay lost weight over a short period of time (<60 d) and that high estimated natural mortality rates of the young-of-the-year pups were likely due to starvation. The most current research suggests that *S. lewini* pups forage on small benthic infauna such as Gobiidae and alpheids (Bush & Holland 2002, Bush 2003); however, diets of juvenile *S. lewini* were previously dominated by scarid species (Clarke 1971). These dietary shifts that occurred within Kāneʻohe Bay between 1971 and 2000 could be due to changes in prey availability with changing water quality and increased fishing pressure within the Bay. Nevertheless, given the limited nutritional margin on which hammerhead pups appear to survive in their nursery grounds, it is advisable to adopt holistic approaches that ensure the health of the whole ecosystem for effective conservation of this and other species.

4.2. Horizontal movements of adult male and juvenile *S. lewini*

Our horizontal movement results are largely biased towards the movements of adult male *S.*

lewini around Oʻahu. Of the 5 juveniles tagged, only 3 (2 females, 1 male) were detected for >5 d, and all 3 remained on the east and northern side of Oʻahu. Wide-ranging horizontal movements for mature male *S. lewini* showed that this demographic undertook long-distance movements throughout the Hawaiian Island chain, and conducted large offshore excursions but demonstrated a strong affinity for and remained in association with the Hawaiian Archipelago. One of the most surprising findings of this study was that once acoustically tagged *S. lewini* (both adult male and juveniles) left Kāneʻohe Bay, they were only detected at receiver stations around Oʻahu, primarily on the east and north east sides, with only 1 individual detected at a topographic feature, Penguin Banks, 28 miles (45 km) south of Oʻahu.

S. lewini were not detected on any other station throughout the archipelago-wide acoustic array despite satellite-tagged animals revealing horizontal movements up and down the archipelago and visits to other islands where acoustic receivers were *in situ*. This suggests that *S. lewini* tagged on the island of Oʻahu exhibit strong affinity for the inshore coastal habitats of this island specifically. Additionally, our satellite tag data shows that once they moved away from the coastal areas of Oʻahu, *S. lewini* tended to remain in offshore oceanic waters, moving between the windward waters (eastern sides) of the MHI, with only 2 individuals traveling significant distances up the island chain to the NWHI. Individual variation in movement patterns of *S. lewini* is common (Bessudo et al. 2011b, Gallagher & Klimley 2018), and may be driven by resource limitation, intraspecific competition, food–predation risk trade-offs and spatial overlap of food webs (Matich et al. 2011), although these specific mechanisms warrant further investigation for this species. Irrespective of individual variation, our data show that although some *S. lewini* make large-scale movements up and down the island chain, in general, the species does appear to be restricted in range to the Hawaiian Archipelago (i.e. NWHI and MHI). Previous studies of *S. lewini* have also documented that the species exhibits restricted movements and shows a high degree of residency (e.g. Ketchum et al. 2014a,b, Heupel et al. 2020) to specific habitats, supporting the delineation of DPSs for *S. lewini* across Oceania.

A DPS is the smallest division of a taxonomic species permitted to be protected under the US ESA (16 U.S.C. § 1531 et seq.). For designation as a DPS, a population needs to be discrete or markedly separate (i.e. spatially) from other populations, contain different genetic characteristics, and demonstrate that loss of this segment would result in a significant gap in the range of a taxon (ESA, 16 U.S.C. § 1532). Advances in genetic tools and a recent study using 3 marker types (mitochondrial DNA, SNP, microsatellites) have updated our understanding of *S. lewini* connectivity across the Indo-Pacific, and suggest that neither sex crosses ocean basins, and gene flow occurs along well-connected habitat (Green et al. 2022). This negates the previous theory of male-mediated gene flow between Hawaiʻi, the Indo-Pacific and the Seychelles populations (Daly-Engel et al. 2012), and instead demonstrates that there are distinct populations across at least 3 regions. Further, evidence suggests that the Eastern Tropical Pacific population may be distinct and that strong population structure exists amongst animals sampled from the central Indo-Pacific (Green et al. 2022). More research is required to determine genetic connectivity between apparent population segments in the Pacific Ocean. However, if connectivity is low between distinct populations, high-intensity removal or harvesting of sharks may result in local extirpations (Chin et al. 2017, Pinhal et al. 2020). Taken together, the movement data presented in the present study in combination with the genetic differentiation of the Hawaiʻi population show that it is isolated from other populations by the remoteness of the Hawaiian Islands, and management strategies should be tailored to incorporate the available science, including any unique threats affecting the Central Pacific.

4.3. Sexual segregation

The differential exploitation of segments of a population is an extremely important consideration for conservation and management, particularly for species that exhibit sexual segregation. In this study, our sample size was heavily skewed towards males, with juvenile females comprising only 3 of 27 tagged individuals. Notably, despite year-round fishing efforts, we did not catch or tag any mature or sub-adult female *S. lewini* within Kāneʻohe Bay, which may indicate limited use of the habitat by mature females outside of peak reproductive season. Similarly, specific fishing methods used may have induced a bias within season and selectively targeted males, as females were most likely using the Bay to give birth and not searching for food (or taking baited hooks). Nevertheless, there were no detections of our acoustically tagged adult male *S. lewini* (or juvenile females) around the island of Hawaiʻi, where persistent aggregations of adult females are known to form seasonally (J. Anderson pers. obs.). These patterns could suggest potential sex-segregated habitat preferences for *S. lewini* across Hawaiʻi (Klimley 1987), although more data from female *S. lewini* are required to explicitly confirm this. The lack of data from adult females hinders our ability to draw definitive conclusions on any potential delineations of segregation by sex for this species. Therefore, in order to successfully manage an entire population of *S. lewini* across the Hawaiian Archipelago, we suggest it is important to consider both temporal (i.e. Kāneʻohe Bay during the summer months), spatial (i.e. island-specific to identify other important nursery habitats) and sex-segregated movement patterns. Although the potential role of sexual segregation in the overexploitation of shark populations remains uncertain (but see Mucientes et al. 2009), complex sex-related structuring coupled with region-specific fishing activities may have disproportionate effects on different components of shark populations (Sims 2005, Mucientes et al. 2009). Again, we emphasize that future research and tagging studies should specifically focus on mature female *S. lewini* around the Hawaiian Islands to determine any sex-related differences in movement patterns and habitat use, providing crucial information for effective management of this species.

4.4. Vertical movements of adult male *S. lewini*

In addition to spatial, temporal and sex-related movement patterns, depth data revealed vertical habitat preferences for *S. lewini.* After tagging, individuals exhibited restricted depth use <100 m in the warmer mixed layers of the water column for up to 12 d. This could have been due to habitat selection of shallow coastal waters during the summer months (the animals were captured in shallow depths), or it could have been indicative of a recovery period after the capture and tagging event prior to engaging in physiologically taxing deep dives (Klimley 1987, Hoffmayer et al. 2013). When away from coastal habitats, 4 of the 5 satellite-tagged individuals made repetitive nocturnal dives down to 802 m where temperatures were as low as 5°C. Similar deep-diving behavior in the species has been observed in Hawaiʻi down to 1240 m (Anderson et al. 2022), in the Gulf of Mexico to 964 m (Hoffmayer et al. 2013), the Red Sea to 971 m (Spaet et al. 2017), the Gulf of California to 980 m (Jorgensen et al. 2009), and in the Eastern Tropical Pacific to 1000 m (Bessudo et al. 2011b). Nocturnal deep dives to the mesopelagic layer may be related to navigation (Ketchum et al. 2014a,b, Braun et al. 2022), but in this study are most likely related to foraging opportunities (Jorgensen et al. 2009, Hoffmayer et al. 2013, Hoyos-Padilla et al. 2014). High proportions of meso- and bathypelagic prey species are often found in the stomachs of adult *S. lewini* (Clarke 1971, Klimley & Nelson 1984, Smale & Cliff 1998, Vaske Júnior et al. 2009). As cold, deep-water prey move slowly compared to surface-dwelling *S. lewini*, ease of capture may also motivate deep-diving behavior (Childress et al. 1990, Childress 1995, Seibel et al. 1997, Drazen & Seibel 2007). Around Hawaiʻi, the diel vertical migrations of mesopelagic species are delineated into 2 layers: the shallow scattering layer (SSL) which extends down to an average depth of 200 m and is only prominent at night, and the deep scattering layer (DSL, Domokos et al. 2010). The DSL consists of 2 layers: daytime (600–750 m) and nighttime (450–575 m) (Domokos et al. 2010). Active acoustics have shown that the region between the SSL and DSL (200–400 m depth) is relatively devoid of organisms, except during dawn and dusk transition times (Domokos et al. 2010). Thus, nighttime dives beyond 575 m exhibited by *S. lewini* in this study may not have been to forage on midwater species but foraging excursions to the seafloor. Unfortunately, the resolution of the geolocation estimates prevented our ability to overlay deep diving locations on ocean floor bathymetry to assess where in the water column they may be foraging. However, recent empirical observations of *S. lewini* show increased activity and burst swimming events indicative of active pursual of prey at depths below 800 m (Royer et al. 2023), and *S. lewini* have also been observed near the seafloor at depths >1000 m via remotely operated vehicles (Moore & Gates 2015). *S. lewini* are known to be generalist feeders, and stomach content analyses from adults have revealed a variety of prey items, including the beaks of cephalopods and other mesopelagic species as well as shallower, reef-associated fish (*Naso* sp., milk fish) and octopus (Clarke 1971). Stable isotope analyses from *S. lewini* in other regions suggest that this species forages at a high trophic level in adulthood across a broad trophic range (Hussey et al. 2015). *S. lewini* do exhibit ontogenetic changes in diet, where juveniles feed mostly on benthic infauna in coastal nursery habitats and shift to pelagic prey as they mature and move away from inshore areas (Bush & Holland 2002, Torres-Rojas et al 2014). The combination of movements across broad depth and habitat gradients highlights the potential for *S. lewini* to act as nutrient conduits transferring nutrients and energy between shallow coastal and meso-pelagic environments (Meyer et al. 2007, Papastamatiou et al. 2015). However, when *S. lewini* were not in the deep-diving phase, they spent up to ~93% of their time during the day and 76% of time during the night in the mixed upper layers <100 m. Undoubtedly, repetitive deep diving is likely to be extremely metabolically costly, particularly as *S. lewini* have been found to suppress gill function to maintain warm muscle temperature while undertaking deep dives (Royer et al. 2023). Thus, inter-dive periods in the upper 100 m may serve as physiological recovery events to 're-warm' (Klimley 1987, Carey et al. 1990, Hoffmayer et al. 2013, Royer et al. 2023) or for social interactions with conspecifics (Klimley & Nelson 1984, Klimley & Butler 1988). This preference for shallower depths, however, may lead to increased capture vulnerability in some fisheries.

4.5. Vulnerability

Over the past decade, it has become increasingly apparent that hammerhead species are in general more sensitive (physically and physiologically) to capture stress than other shark species (Gallagher et al. 2014a, Butcher et al. 2015, Gulak et al. 2015, Drymon & Wells 2017, Jerome et al. 2018). In the present study, 4 individuals died within 11 d of tagging, and another animal died after 37 d, evident from unique depth profiles associated with the satellite tags. Obviously, there is uncertainty in the fates of the acoustically tagged individuals that were not detected and we cannot ascertain whether HH8 shed its acoustic tag or died near a receiver. This information not only has important implications for future scientific research, and the improvement of post-release survivorship from catch and release shark fisheries, but also highlights the fact that no retention measures for hammerhead sharks may not effectively reduce mortality in commercial fisheries (i.e. longline, gillnet, and purse seine) where they are captured as bycatch. Capture and restraint elicit profound physiological and biochemical responses from hammerhead sharks and estimates of at-vessel mortality in longline fisheries range between 60 and 100% (Morgan & Burgess 2007, Morgan & Carlson 2010, Gulak et al. 2015, Butcher et al. 2015), with 50% mortality predicted after soak times of >3 h (Gulak et al. 2015) and 87.5% mortality after 7 h (Butcher et al. 2015). There are several potential reasons for this. Firstly, the gape relative to body size of hammerhead sharks may restrict the amount of water flowing into the mouth and over the gills (Gulak et al. 2015). Consequently, captured hammerhead sharks may have to exert additional energy to ensure sufficient oxygen flow over their gills, resulting in elevated stress levels and eventual mortality (Gulak et al. 2015). Secondly, a recent study of 5 coastal shark species determined the great hammerhead to be most susceptible stress caused by fishing due to high lactate levels (a proxy for stress response, Gallagher et al. 2014c). It is unequivocal that avoidance of fishery interactions is the best option for reducing mortality to hammerhead sharks. Although avoidance is undeniably challenging, there have been some advances in bycatch reduction devices specifically focused on hammerhead sharks (e.g. O'Connell et al. 2015). Therefore, studies such as this one, that delineate the environmental, spatial and temporal factors of potential biological hotspots, are crucial. Hammerhead sharks are known to aggregate in large numbers (Klimley & Nelson 1981, 1984, Hearn et al. 2010, Bessudo et al. 2011a, Ketchum et al. 2014a,b), greatly increasing vulnerability to some fishing gears and illegal, unreported and unregulated fishing at critical life stages. Identifying potential *S. lewini* aggregation sites around the Hawaiian Archipelago is an important avenue for future research to improve local conservation efforts.

5. CONCLUSIONS

In conclusion, the overexploitation of sharks is a global environmental issue in need of an urgent, comprehensive, and flexible management response. Through a combination of acoustic and satellite electronic tracking, this study has provided baseline information on the spatial and temporal movement patterns of the Central Pacific scalloped hammerhead shark *Sphyrna lewini* around Hawaiʻi. We acknowledge our dataset is highly skewed towards adult males; however, our findings show that adult male and juvenile *S. lewini* alternate between the use of coastal and pelagic zones, and that individuals tagged in Kāneʻohe Bay exhibit extremely high site fidelity, making repeated annual movements to the Bay between April and September consistently across seasons and years. These data provide strong evidence that Kāneʻohe Bay is most likely an essential habitat for *S. lewini* throughout all life stages, and time-area closures to unmonitored fishing gears may prove effective in the sustainable management for a portion of the Central Pacific population. Additionally, our data show that broader movements away from Kāneʻohe Bay were restricted in their range to the Hawaiian Archipelago, supporting the delineation of the Central Pacific population as distinct from the Indo-Pacific and Eastern Tropical Pacific populations. Future research on female *S. lewini* movements around the Hawaiian Islands is crucial to determine sex-related differences in habitat preferences for this species which will help to inform effective conservation strategies. Additional avenues for future research should also include the degree to which environmental factors influence *S. lewini* movements across habitats, particularly as climate change is predicted to impact nearshore ecosystems to a large degree (Giddens et al 2022). Management authorities of each DPS would benefit from conducting similar studies to investigate the sexually explicit spatial and temporal movement patterns and habitat use of *S. lewini* throughout ontogeny (Hazen et al. 2018) in each region. Finally, the high post-tagging mortality rates for this species suggests that *S. lewini* are particularly vulnerable to tagging and capture. We suggest future tagging studies work on protocols to limit soak times of baited hooks and handling times for tagging and release. In this study, we found the use of a ventilator during the tagging process to ensure sufficient oxygen flow across the gills greatly improved survival rates. Taken together, this study provides critical baseline information on the spatial and temporal movement patterns of *S. lewini* around the Hawaiian Archipelago, which can be directly used to understand the conservation needs of this species and inform future management scenarios.

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