Inferring vertical and horizontal movements of shortfin mako sharks *Isurus oxyrinchus* in the northwestern North Pacific Ocean from electronic tags

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Working document submitted to the ISC Shark Working Group Workshop, 27 January -3 February 2025, Web-meeting. Document not to be cited without author's permission.

Abstract

The shortfin mako shark (*Isurus oxyrinchus*) is an essential component of the pelagic shark community. It is widely distributed across tropical and temperate waters. However, there is still limited knowledge about the stock structure of this highly migratory shark, as movement data from tagging programs are generally not incorporated into stock assessments. In this study, pop-up satellite archival tags were deployed on three shortfin mako sharks (weighing 170 kg, 40 kg, and 50 kg) and remained attached for 117 to 142 days. One tag was physically recovered, providing detailed data for the entire 117 days of liberty. The deepest recorded dive reached 989 meters, with the lowest temperature encountered at 4.7°C. During daylight hours, the sharks spent most of their time above 400 meters, in waters with temperatures ranging from approximately 10°C to 25°C. At night, their movements were primarily confined to the mixed layer, from the surface down to about 200 meters. Daytime vertical movements often traversed the thermocline, likely driven by physiological constraints or rapid directional changes, which potentially optimize foraging strategies and increase prey capture success. The tagged sharks predominantly remained along the continental shelf of the northern Pacific Ocean and did not exhibit seasonal migrations. These findings provide valuable insights to identify fishery and gear vulnerabilities and inform management.

Keywords: mixed-layer depth; mesopelagic; movement patterns; residence time; thermal niche

Introduction

Many large-bodied, highly migratory species are apex predators in marine ecosystems, but there is uncertainty about the current state of many populations (Burgess et al. 2005, Hampton et al. 2005). Generally considered large apex predators, especially sharks, are at the greatest risk vulnerable to overexploitation (Dulvy et al., 2024). Sharks are often caught in various fisheries including commercial and recreational fishing, due to their prolonged life spans, slow maturation, and low rate of reproduction, and are vulnerable to overexploitation (Pratt & Casey 1983, Mollet et al. 2000, Cortés et al. 2010, Block et al. 2011, Francis et al. 2019). Sharks often bycatch in pelagic longline fisheries targeting tuna (*Thunnus* spp.) and swordfish (*Xiphias gladius*) (Mandelman et al. 2008, Petersen et al. 2009). Still, Taiwanese coastal longline and driftnet fisheries primarily target sharks. Especially, shortfin mako sharks (*Isurus oxyrinchus*) are regarded as a desirable and valuable catch in commercial fishing (Campana et al. 2005), due to their high-quality meat and valuable fins (Clarke et al. 2006).

Shortfin mako shark is considered fast-swimming species and distributed throughout the generally tropical, sub-tropical, and temperate warmer waters in coastal and offshore. It is a highly mobile apex predator that feeds diverse diet of many species of teleost and cephalopods and hunts other sharks, tunas, and billfishes of large and fast-swimming prey (Cliff et al. 1990, Maia et al. 2006, Preti et al. 2012). The shortfin mako shark has been categorized as endangered (EN) in the International Union for Conservation of Nature (IUCN) Red List. Knowledge of the movements and habitats of this species is essential for their conservation, rebuilding population and robust assessments (Hays et al. 2019). However, it is very challenging to identify habitat preferences for large-scale pelagic species, because their extensive movement ranges can span many jurisdictional boundaries and areas with varying degrees of protection, which creates a unique management problem (Rooker et al. 2019).

Pop-up satellite archival tag (PSAT) technology is an established fisheries-independent tool attached externally with a tether and various anchoring devices attachment methods to marine animals, especially useful for attaching to highly migratory species because data are retrieved via transmission to the Argos satellite system (Arnold & Dewar 2011, Musyl et al. 2011). PSAT to monitor vertical movement depth (pressure), ambient temperature, and movement track (light levels) on tags attached to animals for extended periods to chronicle both horizontal and vertical movement patterns and habitat preference, as well as provide information on migration routes, possible spawning areas, thermal habitat, exchange rates between areas and post-release mortality (Block et al. 2011, Musyl et al. 2011, Sippel et al. 2015a, Musyl & Gilman 2018, 2019).

Shortfin mako sharks represent a significant portion of the shark bycatch and their life history characteristics make them particularly vulnerable to fishing pressure. Due to the large amount of this species caught by various fisheries, it has been identified as the key shark species by various regional fisheries management organizations (Cortés 2000, Dulvy et al. 2008, Chang & Liu 2009). Recently, many studies examined their behavioral information on vertical, and horizontal movement and swimming behavior (Musyl et al. 2011, Gibson et al. 2021, Saraiva et al. 2023, Waller et al. 2023). However, their behavioral data is still lacking in the northwestern Pacific Ocean. This study uses PSAT to collect scientific data to clarify the movement behavior characteristics of the shortfin mako shark in the northwestern Pacific Ocean. This movement information provides the mismatch between gears deployed in the depth and habitual depth of sharks to possibly minimize bycatch and establish important ecological information on fishery management.

Methods and materials

Study site and tagging techniques and programming

Pop-up satellite archival tags (PSATs)(Wildlife Computers) were deployed off the eastern coast of Taiwan, within the coordinates 23.03° to 23.06°N and 121.32° to 121.38°E, using commercial shark longline gear. The gear consisted of four hooks between floats, baited with frigate tuna (*Auxis rochei rochei* and *Auxis thazard thazard*) or Kawakawa (*Euthynnus affinis*).

The PSATs were programmed to release 150 days after release and collected a complete record of ambient water temperature range of -40 to 60°C (resolution 0.05°C), depth range of 0 to 1,700 m (resolution 0.5 m) and light-level readings. The data were transmitted to the Argos when the tag was released from fish and popped up to the sea surface. PSAT tag heads were constructed from durable harpoon-grade stainless steel, while the tether, made of 300-lb fluorocarbon with stainless steel crimps, matched the diameter of the fishing line. To minimize muscle ulceration at the tagging site, stainless steel ball bearings were used to mitigate torque and precession. The PSATs were attached using a ~2-meter tagging pole. Captured sharks were carefully retrieved alongside the vessel, where the tags were affixed beneath the dorsal fin. Prior to tagging, the tag heads and tethers were treated with a broad-spectrum antibiotic to prevent infections. Following release, the GPS location of tagging was recorded, and the sharks' round weight was estimated by the captain.

Data analysis

After popping up of PSAT, transmitted archived data via Argos including time series data of daily summaries of time-at-depth, time-at-temperature, max depth, mean sea surface temperature (SST) and light level data (using the WC software, DAP Processor). Daily geolocation estimates were generated for each individual using the WC GPE3 software, a discretized hidden Markov model that requires observations of light level, SST, and maximum swimming depth as inputs (Pedersen et al. 2011). Linear displacements from deployment to pop-up locations were determined by great-circle distance and pop-up locations estimated by Doppler shift using Argos messages with location classes of 1 or higher.

Daytime and nighttime partitioned into local times of sunrise and sunset were determined by MPTs (http://aa.usno.navy.mil/). Time series of depth and temperature data were aggregated into 50 m and 1°C bins, respectively, and partitioned into daytime and nighttime were tested for normality using Kolmogorov–Smirnov tests and found to be non-normally distributed and after by using non-parametric Mann–Whitney W-tests compare distributions of differences in depth and temperature between daytime and nighttime (Zar 2010). The greatest vertical distances between cumulative Kolmogorov–Smirnov functions (DN) among months were formatted into an input matrix for UPGMA (unweighted pair-group method using arithmetic averages) clustering using Euclidean distances (Musyl et al. 2011).Vertical swimming speeds for ascents and descents were calculated from the directional changes in swimming patterns by examining the time-series data stored in the PSATs.

Results and Discussion

In total, three shortfin mako sharks (estimated body mass, ~40 to 170 kg) were successfully tagged. These tags transmitted data over 394 tag-days in total (Table 1). One tag was physically recovered, providing fine-scale data archiving contained >3,800,000 data points (depth, temperature) in time series recorded at 3-sec intervals.

Horizontal movements

After their release, the mako sharks exhibited both southern and northern movement trajectories. Mako#227052 traveled a straight-line distance of 883 km from the deployment site to the pop-up location, with a displacement rate of 7.8 km/day over 117 days (Table 1). Based on the most probable tracks (MPTs), its movement was predominantly southeastward, reaching the vicinity of the Philippines (Fig. 1). Mako#254642 initially followed a northern course into the East China Sea, then altered its path, swimming southward back near the tagging area where the tag popped up after 135 days (Fig. 2). Mako#254647 covered 1,886 km from the tagging location to the East China Sea over 142 days, achieving a displacement rate of 8.4 km/day, and approached the Yellow Sea where the tag popped up (Fig. 3).

The tracking data for the mako sharks over several months revealed both southerly and northerly movements. Mako#227052 exhibited southerly movements within sea surface temperatures (SST) ranging from 24.2˚C to 31.4˚C, with a strong preference for SSTs between 24˚C and 30˚C (>90%). Mako#254642 initially traveled northward to the East China Sea before reversing course and swimming southward. Its SST range was 13.7˚C to 28.5˚C, with a preference for SSTs between 19˚C and 26˚C (>80%). Meanwhile, Mako#254647 undertook a northern trajectory, with SSTs ranging from 13.9˚C to 25.6˚C and a preference for SSTs between 15˚C and 19˚C (>70%) (Table 1, Fig. 4).

The movements of mako sharks in the Northwest Atlantic Ocean by use of catch record data, conventional mark–recapture tag returns, and electronic tags were seasonal and largely influenced by SST (Casey & Kohler 1992, Vaudo et al. 2016). Vaudo et al. (2017) indicated mako sharks displayed considerable variability, long-distance and highly directional southern excursions of movement into less productive subtropical/tropical waters. In this study, mako shark did not experience large drops in SST of their tracks instead found experience warmer waters. This movement from cooler to warmer waters have also been observed in the northeastern and southeastern Pacific Ocean (Block et al. 2011, Abascal et al. 2011), and partially in the southeastern Indian Ocean (Rogers et al. 2015), and in the Gulf of Mexico (Gibson et al. 2021). Vaudo et al. (2016) reported that their juvenile mako sharks showed southerly directional movements when SST dropped. Several studies have also reported directional movements related to the size of mako sharks, SST, and area (Abascal et al. 2011, Block et al. 2011, Vaudo et al. 2016). Our data indicates the wide geographic distribution of mako sharks in the northwestern Pacific Ocean, consistent with many previous studies that demonstrated their highly migratory characteristics (Vaudo et al. 2017, Queiroz et al. 2019, Gibson et al. 2021, Santos et al. 2021).

Vertical movements

Three mako sharks showed vertical movements from the surface to mesopelagic waters, with one individual reaching a maximum depth of 993.5 m. The ambient temperatures ranged from 4.7 to 31.6°C (Table 2). Mean depth (±SD) and ambient temperatures experienced during daytime and nighttime were 62.1± 44.4 m, 19. ± 2.4°C and 57.7 ± 44.4 m, 20.1 ± 2.3°C, respectively (Table 2, Figs. 5, 6 and 7).

Mako#227052 reached a maximum depth of 993.5 m, with temperatures ranging from 4.7˚C to 31.6˚C (Table 2, Fig. 5). It spent approximately 80% of its time between the surface and 300 m, within an ambient temperature range of 13°C to 25°C during the daytime, and about 90% of its time in the upper 200 m, where temperatures ranged from 18°C to 25°C during the nighttime (Figs. 8, 9). This mako shark exhibited diel vertical movement, diving deeper during the daytime than at nighttime (Fig. 10). Mako#254642 attained a maximum depth of 507.5 m, with temperatures ranging from 10.2°C to 28.8°C (Table 2, Fig. 6). It spent approximately 90% of its time between the surface and 100 m, with an ambient temperature range of 16°C to 23°C (Figs. 8, 9). No significant differences in depth or temperature were observed between daytime and nighttime (Fig. 10). Mako#254647 reached a maximum depth of 531 m, with temperatures ranging from 6.6°C to 24.6°C (Table 2, Fig. 7). It spent roughly 80% of its time between the surface and 100 m, within an ambient temperature range of 15°C to 23°C (Figs. 8, 9). Similar to #254642, no significant differences were observed between daytime and nighttime depth or temperature patterns (Fig. 10).

The dive patterns of a mako shark are illustrated in Fig. 11 (corresponding to Fig. 2). From January to February, the shark exhibited repetitive deep daytime dives, moving between the surface and approximately 300 meters, while spending most of the daytime at depths of 150 to 200 meters. In March and April, as the shark entered the East China Sea, its behavior shifted to include periods where it spent most of its time, both day and night, near the surface (<100 meters). By May, this mako shark changed course, swimming southward from the East China Sea toward the tagging area. During this period, it made repetitive deep dives, reaching depths of up to 200 meters during the daytime and around 100 meters at night.

The East China Sea primarily consists of a continental shelf and is relatively shallow, but its vertical temperature structure varies seasonally. From late autumn to spring, water mixing occurs, while a strong thermocline develops from late spring through summer. The mixing of different water masses with varying temperature gradients is believed to influence the vertical movements of marine species. Analysis of vertical movement data provides valuable insights into the vertical habitat use of shortfin mako sharks. However, residency was largely confined to the mixed layer from the surface to ~200 m of mako sharks, but sometimes diving deeper. Shortfin mako sharks have regional endothermy, maintain some tissues and organs warmer than ambient temperature by retaining metabolic heat with vascular heat exchangers may also explain their wide range of experienced ambient temperatures and SST. This ability allows them to to exploit food resources in the thermocline more effectively than other fishes (Bernal et al. 2001).

Our results show vertical movement patterns significantly influenced by the time of day (Mako#227052). They occupied greater mean depths during daytime than nighttime. Klimley et al. (2002) postulated that mako sharks occasionally dive deep to sample magnetic gradients, but also need to sample the earth's main dipole field at the surface where it is strongest. The absence of pronounced vertical movements during crepuscular transitions suggests that sun elevations or changes in light intensity may not be critical for navigation (Musyl et al. 2011).

Diel vertical movement is typically characterized by prey species remaining in deep water during the day to avoid visually orientating predators and moving into shallow water at night where they feed before returning to depths at dawn (Andrzejaczek et al. 2022). Many pelagic predators regularly descend to the thermocline to exploit organisms comprising the deep sound scattering layer (SSL) as a food resource. This diel vertical behavior is similar to previous observations of shortfin mako sharks (Vaudo et al. 2016, Nasby-Lucas et al. 2019) as well as other pelagic sharks (Musyl et al. 2011, Coffey et al. 2017, Oliver et al. 2023) and teleosts (Marchal & Lebourges-Dhaussy 1996, Dewar et al. 2011, Lin et al. 2021).

This study presents electronic tagging data on mako sharks in the northwestern Pacific Ocean, revealing their horizontal and vertical movement behaviors over durations of 117 to 142 days. The findings provide valuable insights into mako shark habitat use, migration patterns, and the factors influencing their behavior. Understanding habitat preferences and migratory routes is essential for comprehending the species' ecology and identifying potential critical habitats, such as mating grounds, nursery areas, or regions that could be designated as separate fisheries management units. It also crucial for developing effective management measures and successful conservation strategies.

Acknowledgements

We sincerely thank Captain Jyh-Wen Su and the crew of the shark longline vessel *FV YI-XING NO. 68* for their exceptional skill in catching shortfin mako sharks. Our gratitude also extends to Chi-Hsuan Chang, Wen-Hua Chen, Ba-Zan Macai, and Je-Yu Chiang for their invaluable assistance in tagging sharks and recovering PSATs. This study was partially funded by the Ocean Conservation Administration, Ocean Affairs Council, Taiwan, R.O.C. (grant numbers 11100012465 and 1120001752) and the Fisheries Research Institute, Council of Agriculture, Taiwan (grant numbers 112AS-6.4.2-A2(6) and 113AS-6.4.2-A02(3)), awarded to Wei-Chuan Chiang.

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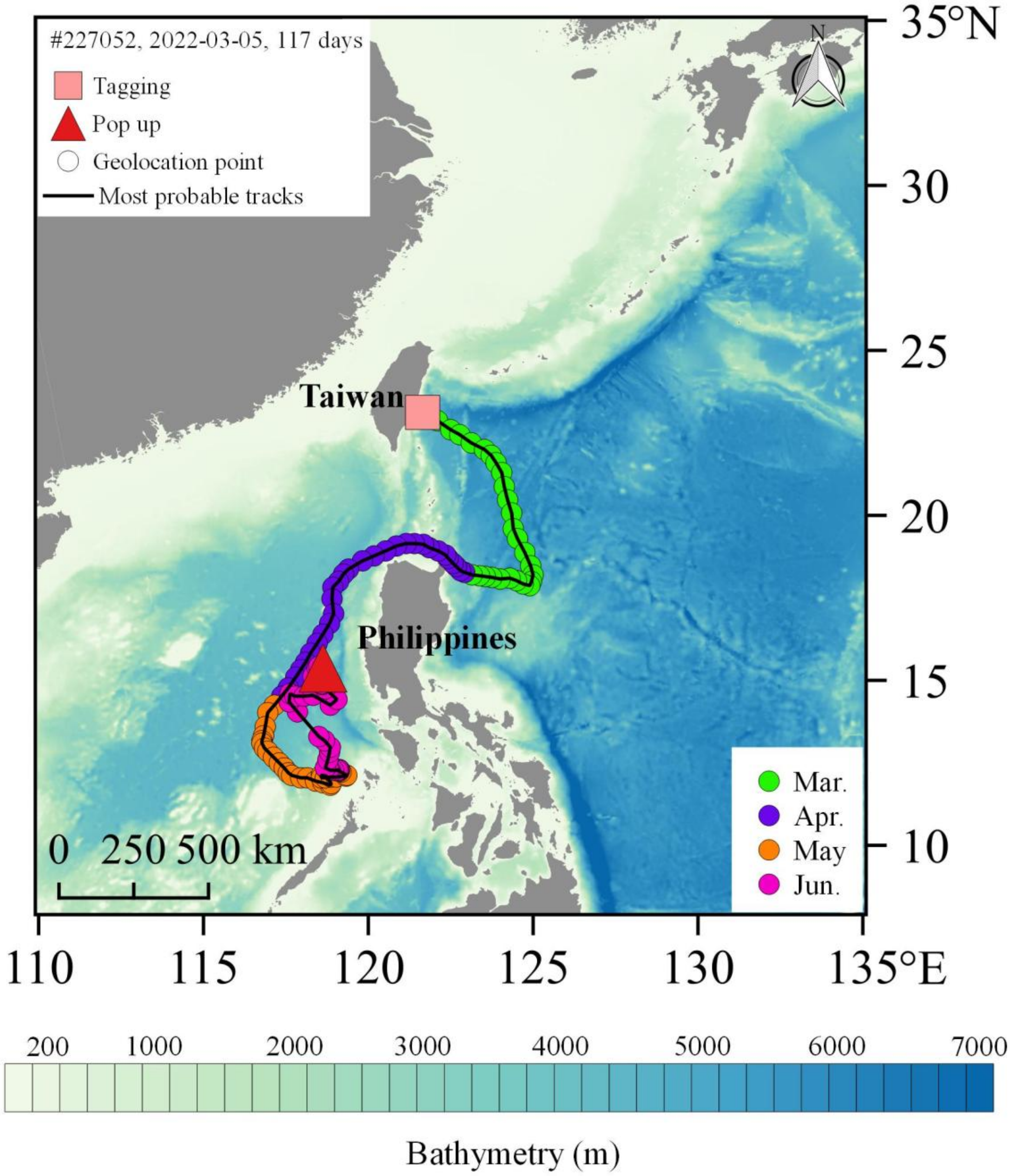

Fig. 1. Map of most probable track (MPTs) of SMA#227052 tagging at 2022/03/05.

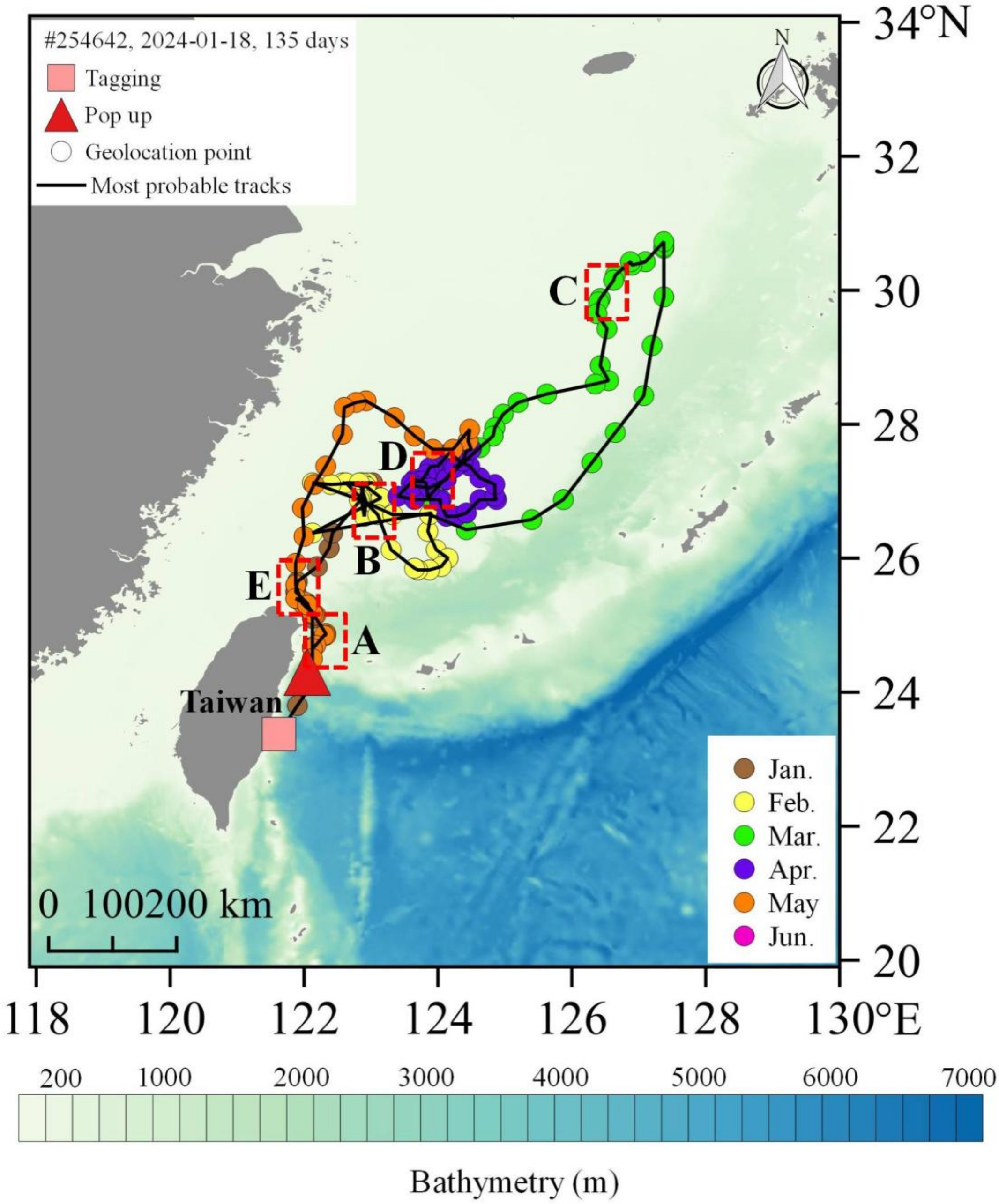

Fig. 2. Map of most probable track (MPTs) of SMA#254642 tagging at 2024/01/08.

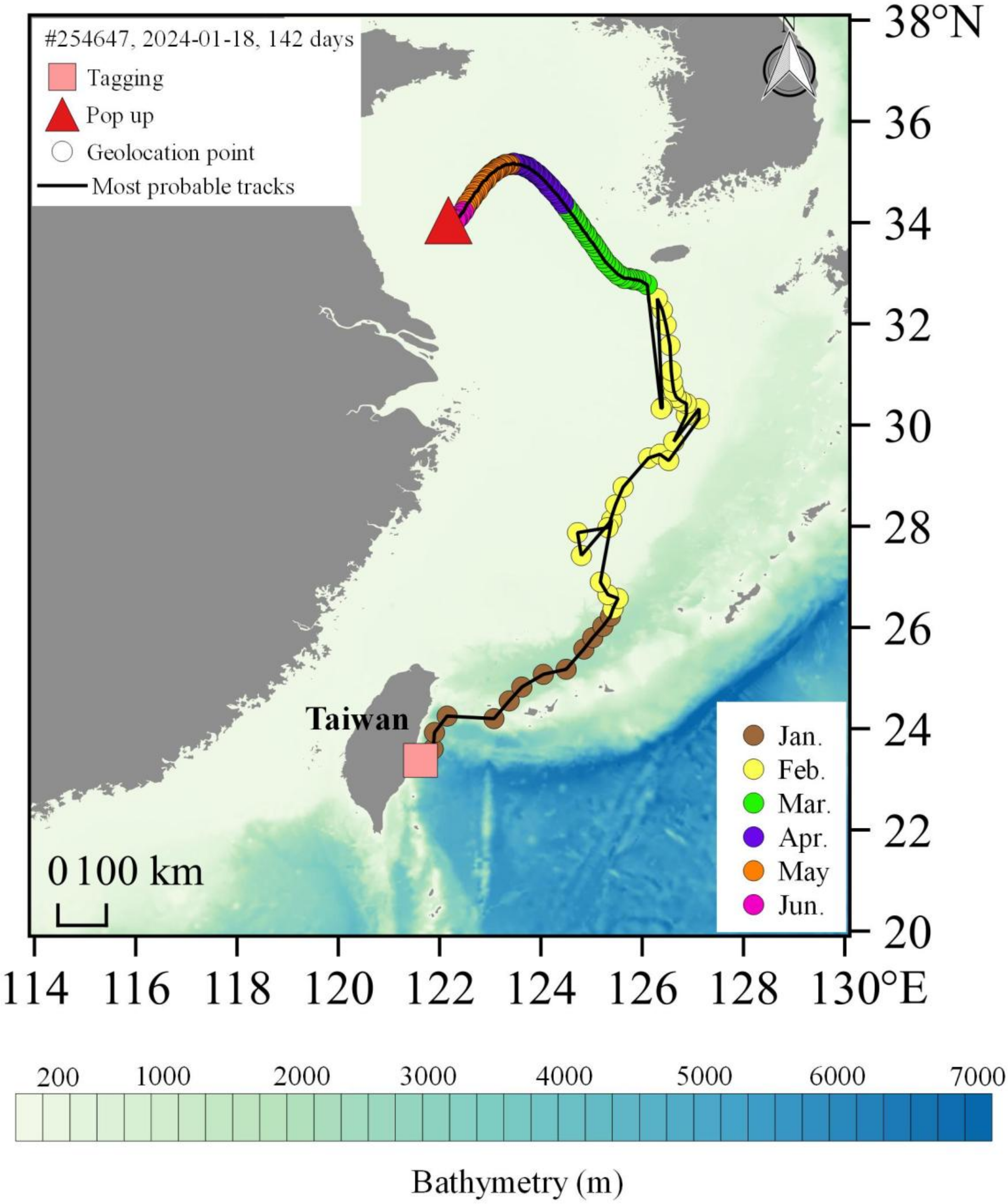

Fig. 3. Map of most probable track (MPTs) of SMA#254647 tagging at 2024/01/08.

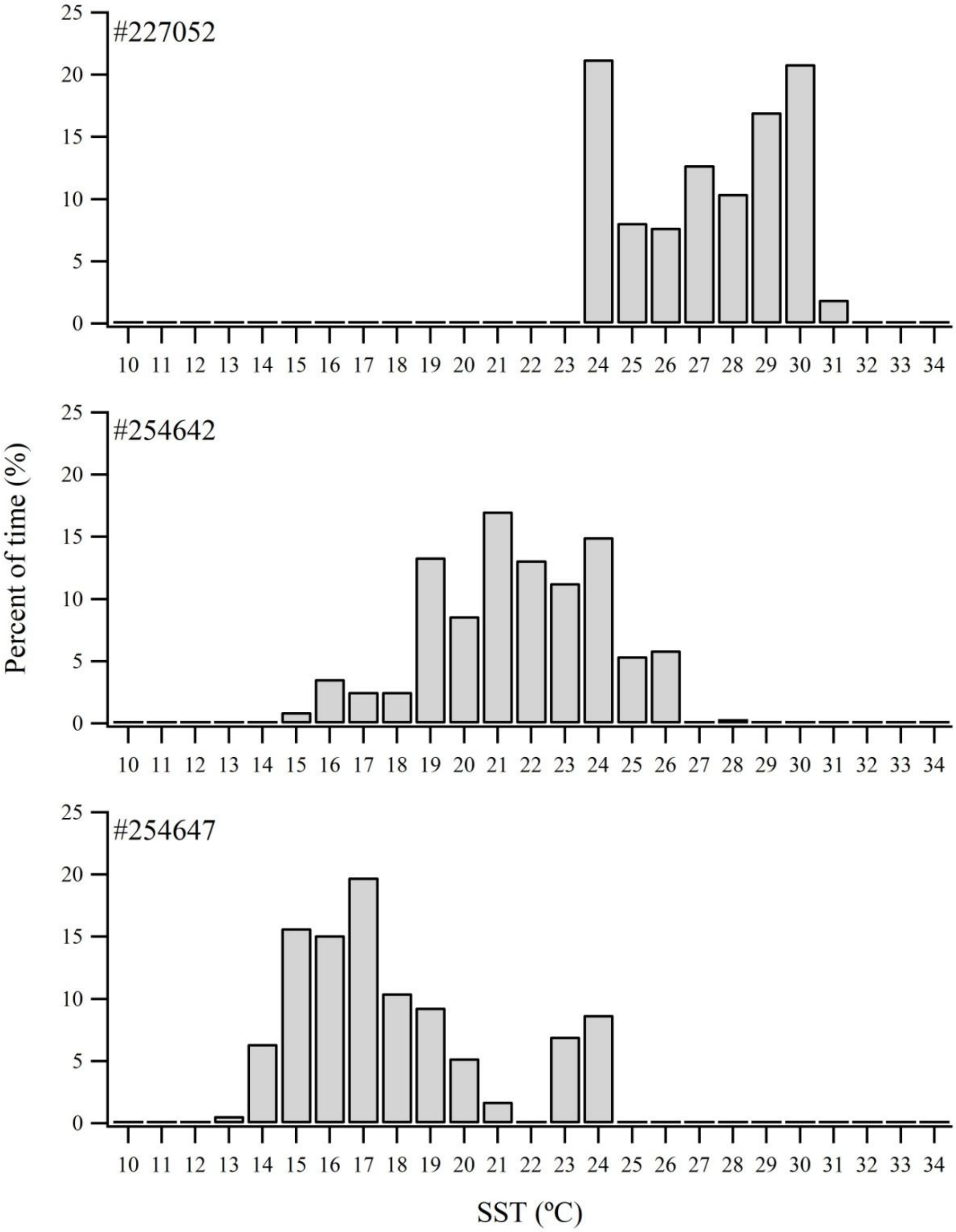

Fig. 4. Histogram of sea surface temperature (SST) experienced by SMA.

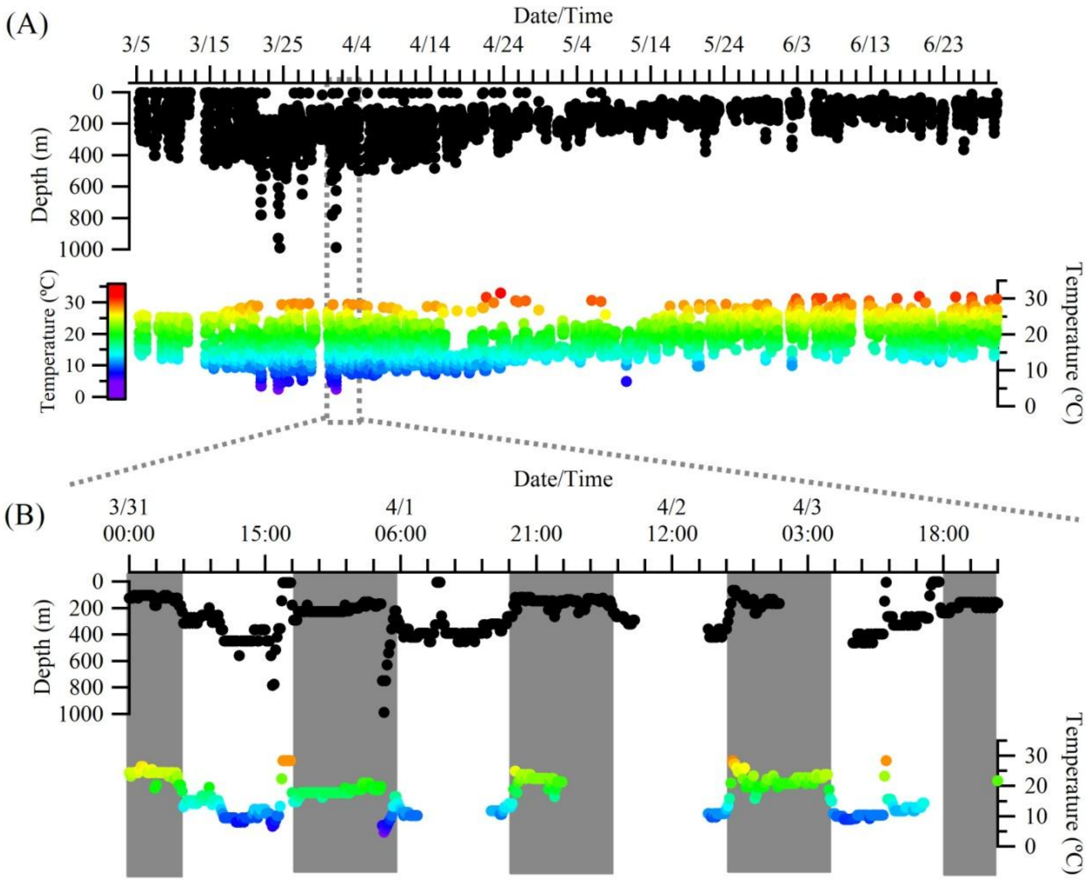

Fig. 5. Depth and temperature series obtained from SMA#227052. The upper panel shows the entire record covering 117 days-at-liberty (A), while the lower panel covers a 4-day period (B). Black vertical bars indicate nighttime.

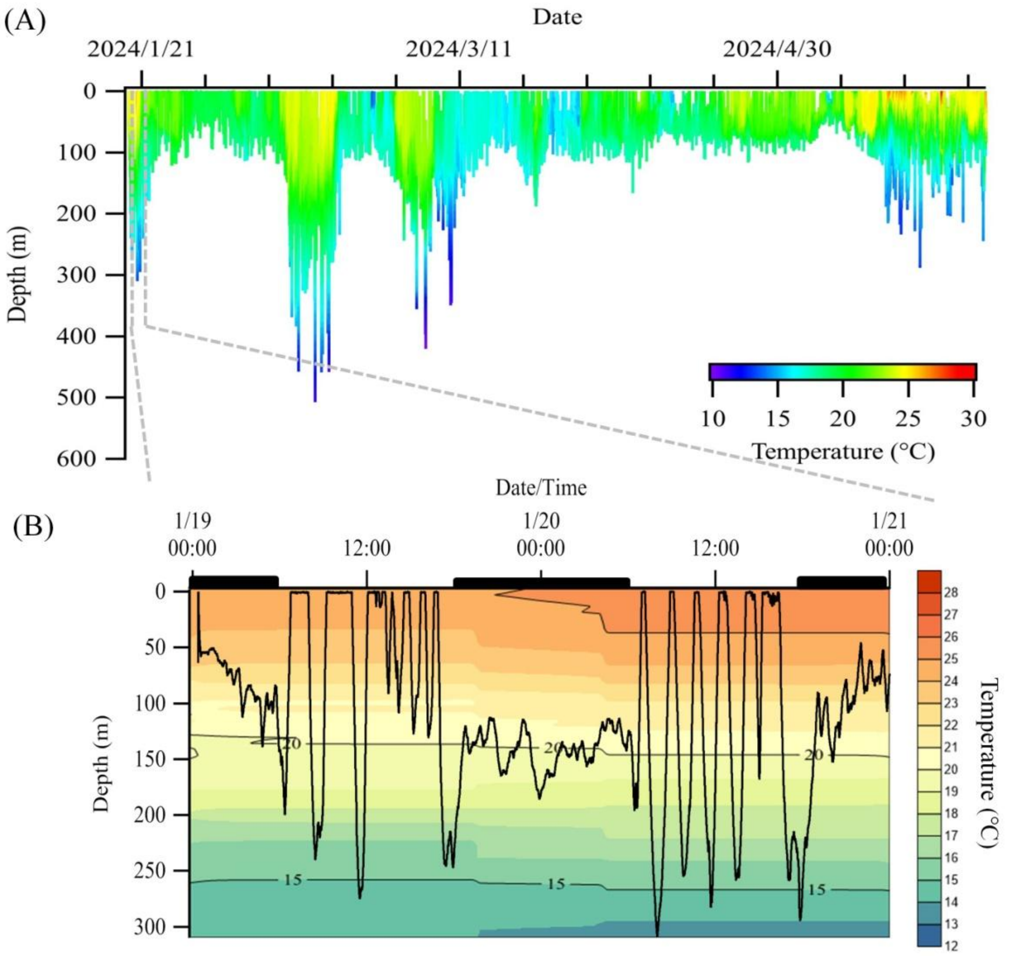

Fig. 6. Swimming depth and temperature panel shows the entire record covering 135 days-at-liberty (A), and panel covers a 3-day period and vertical thermal structure (B) obtained from fish #254642. Horizontal black bars indicate nighttime.

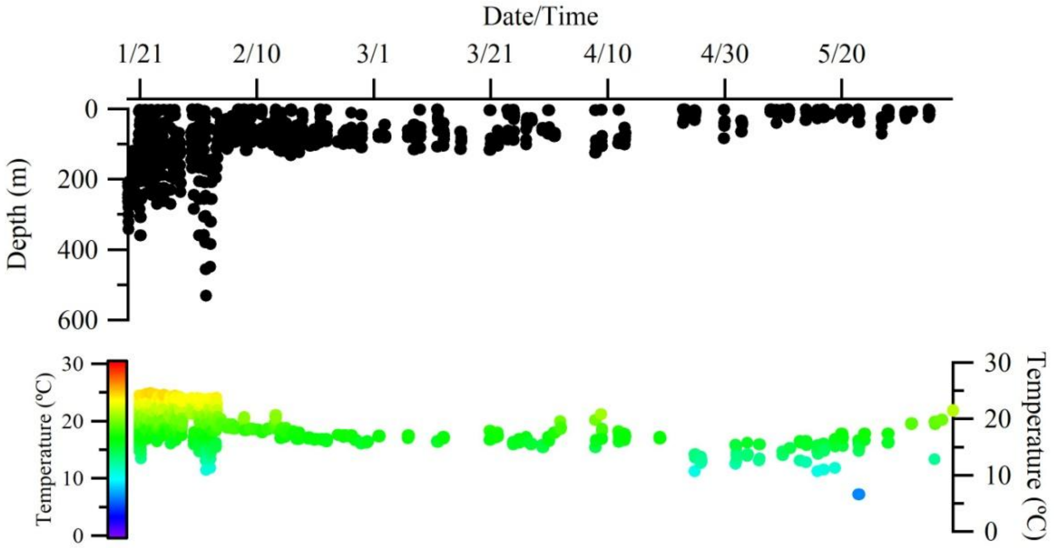

Fig. 7. Swimming depth and temperature of SMA#254647, panel shows the entire record covering 142 days-at-liberty.

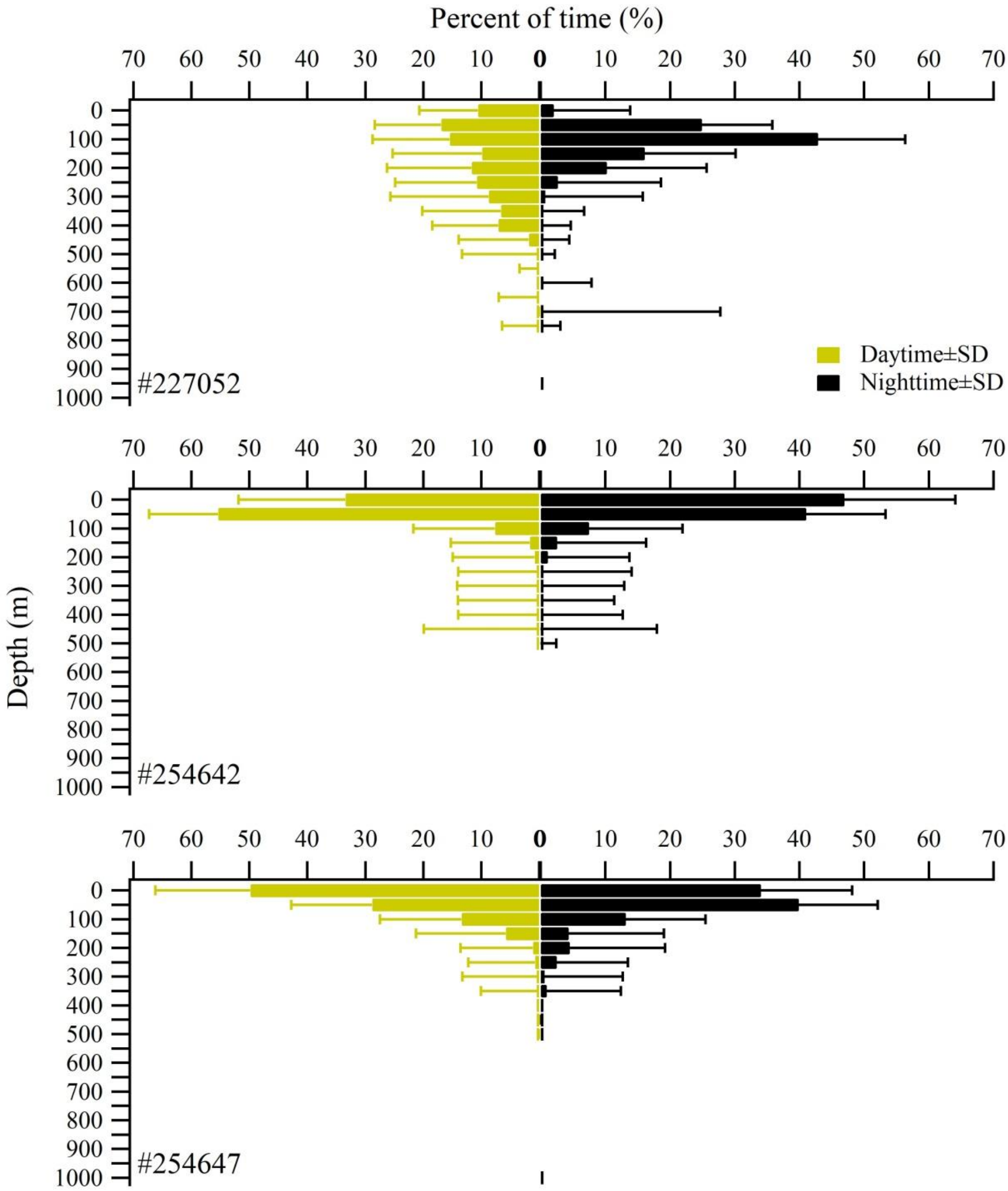

Fig. 8. Depth occupied for shortfin mako shark in the study. Fraction of time during daytime (white bars) and nighttime (black bars) spent in each successively deeper 50 m bin.

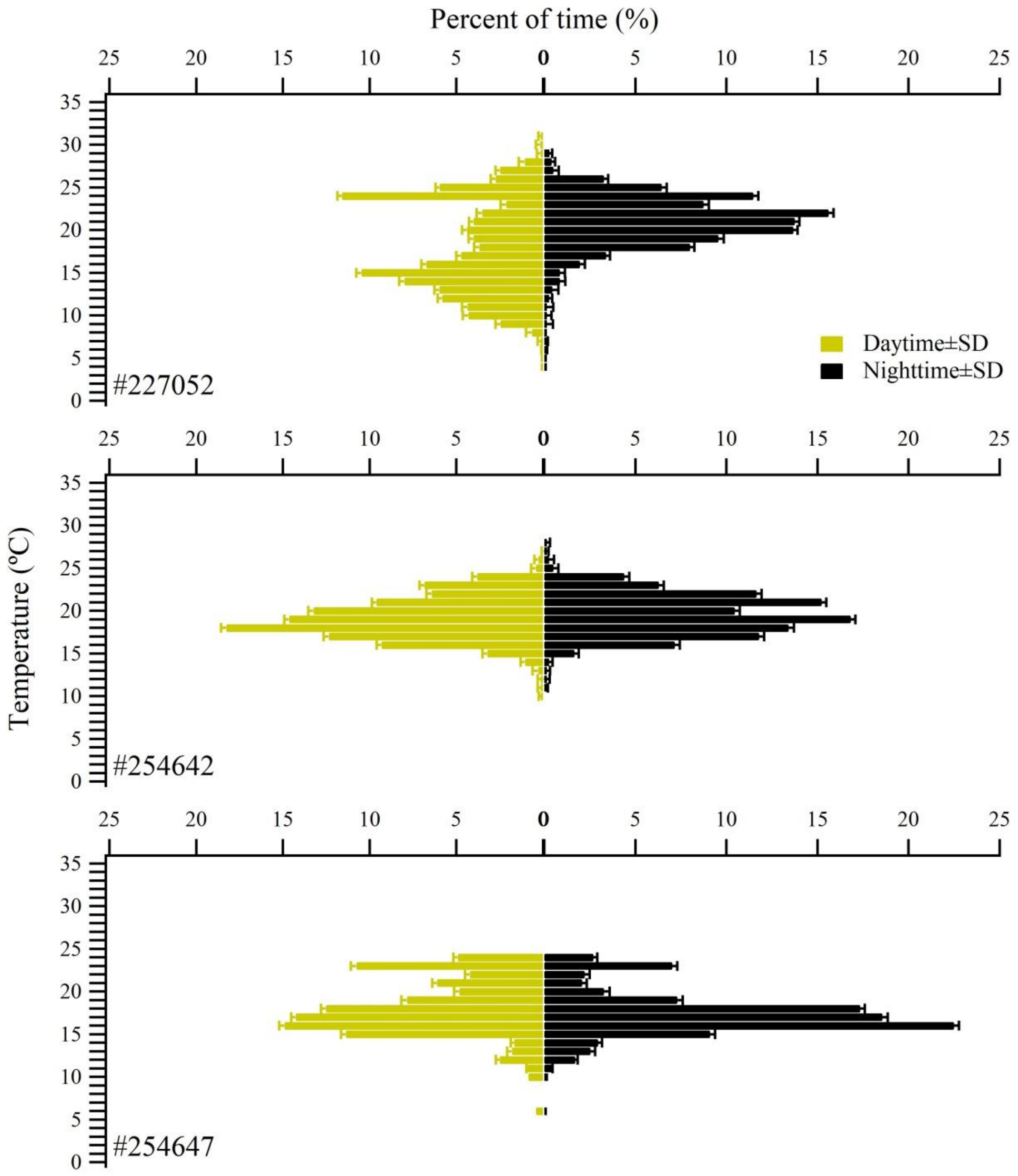

Fig. 9. Temperatures occupied for shortfin mako shark in the study. Fraction of time during daytime (white bars) and nighttime (black bars) spent in each 1℃ temperature bin.

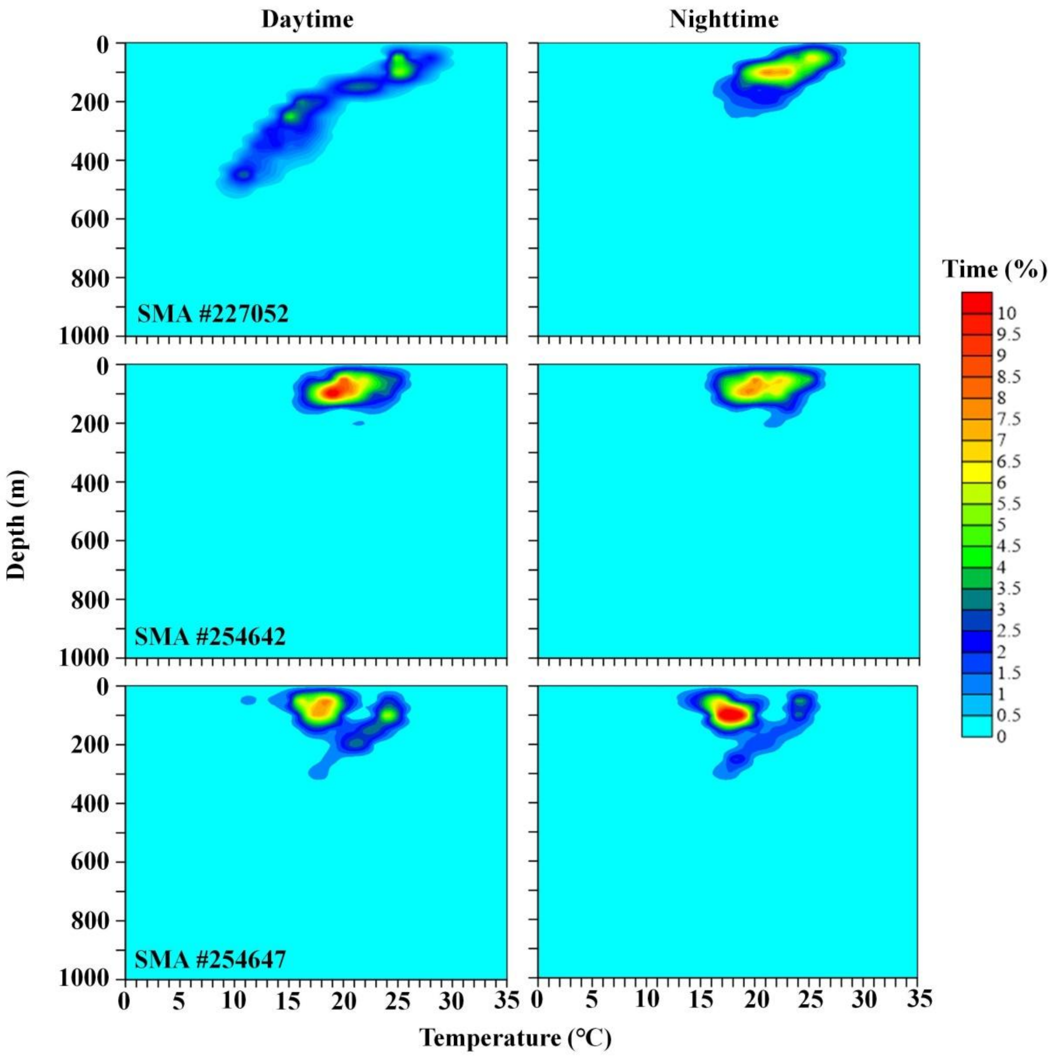

Fig. 10. Aggregated temperature-depth profiles for shortfin mako shark in daytime and nighttime.

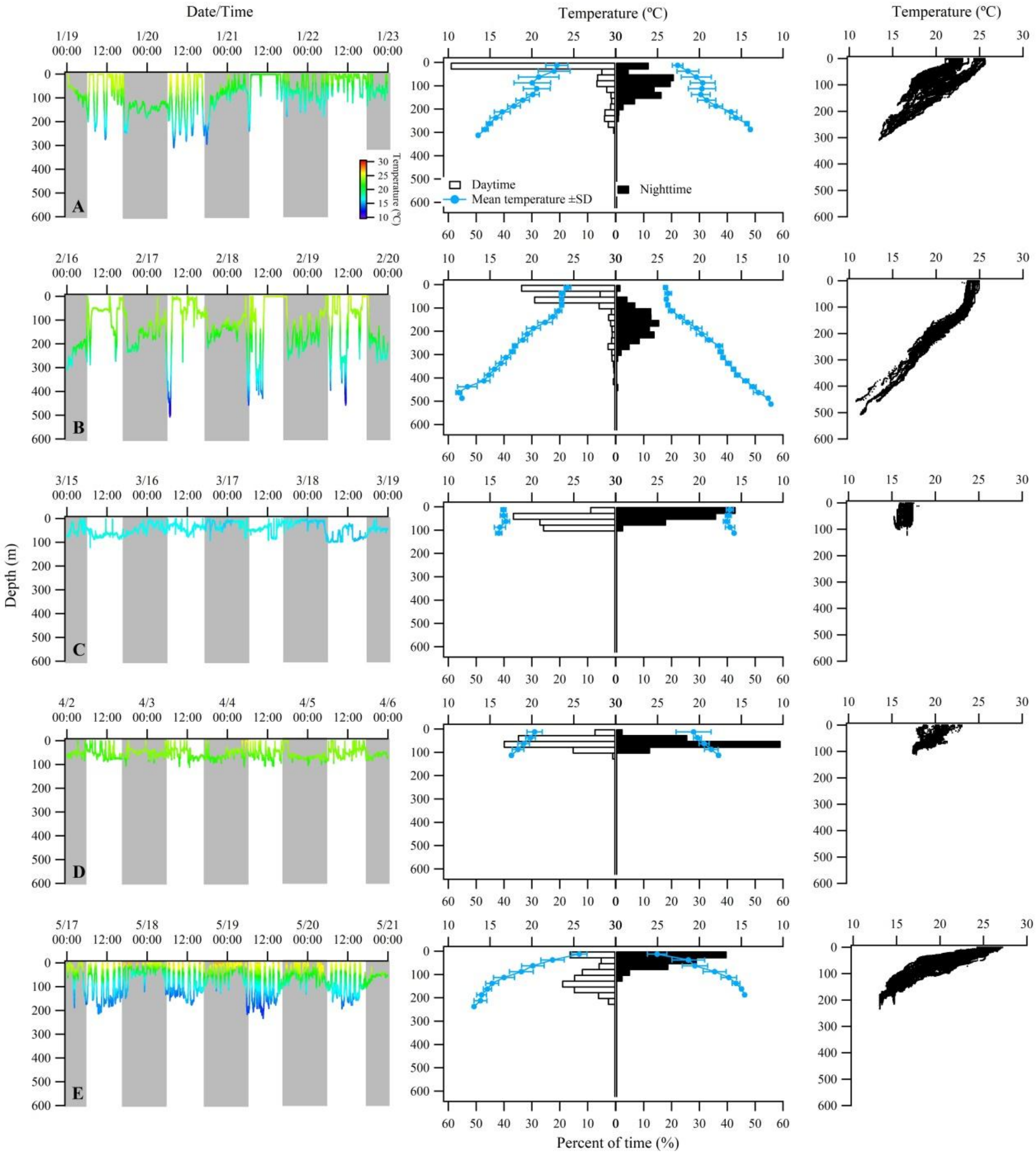

Fig. 11. Vertical patterns from recovered PSAT data from #254642, overlaid with color-coded temperature (shaded regions are nighttime), indicating percent time at depth day and night, and the temperature depth profile. Each plot displays 5 days of data.

Table 1. Details for pop-up satellite archival tags (PSATs) deployed on shortfin mako sharks off eastern Taiwan. Fish PTT (platform transmitter terminal) ID number is provided. Straight-line distance is the linear distance between deployment and pop-up location.

PTT ID	Tagging date	Estimated weight (kg)	Deployment location	Days at liberty	Reporting location	SST (°C)	Straight-line distance (km)	Linear speed (km/day)
Mako#227052	05-Mar-22	170	23°12'N 121°65'E	117	15°38'N 118°63'E	24.2-31.4	883	8
Mako#254642	18-Jan-24	40	23°38'N 121°63'E	135	23°50'N 121°73'E	13.7-28.5	17	0.1
Mako#254647	18-Jan-24	50	23°38'N 121°63'E	142	34°05'N 122°18'E	13.9-25.6	1,886	8

Table 2. Summary of the depth and temperatures obtained for pop-up satellite archival tags (PSATs) deployments on shortfin mako sharks.

PSAT ID	Day depth (m) Min.-max. (mean±SD)	Night depth (m) Min.-max. (mean±SD)	Day temp. (℃) Min.-max. (mean±SD)	Night temp. (℃) Min.-max. (mean±SD)
#227052	0-993.5 (201.6±132.4)	0-989.0 (135.1±62.7)	4.7-31.6 (18.2±5.3)	4.7-29.9 (21.6±2.9)
#254642	0-500 (61.8±43.3)	0-507.5 (57.5±44.1)	10.2-27.8 (19.6±2.4)	11.3-28.8 (20.1±2.3)
#254647	0-531 (62.4±57)	0-531 (81.3±72.3)	6.6-24.6 (18.6±3.3)	6.6-24.6 (17.9±2.7)
Grand Average	0-993.5 62.1±44.4	0-989.0 57.7±44.4	4.7-31.6 19.6±2.4	4.7-29.9 20.1±2.3