Movements and vertical habitat of black marlin (*Istiompax indica*) and swordfish (*Xiphias gladius*) in the northwestern Pacific Ocean

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Abstract

Understanding the movements and ecology of billfish is critical to improving management and understanding the basic life history of these migratory predators. The traditional harpoon and longline gears were utilized to deploy pop-up satellite archival tags (PSATs) on black marlin (*Istiompax indica*) and swordfish (*Xiphias gladius*) in the waters of southeastern Taiwan (Taitung) to examin their movement patterns. Pop-up satellite archival tags (PSATs) recorded depth, temperature and ambient light data. In total, 14 black marlin and 3 swordfish were tagged from December 2008 to November 2021 and PSATs remain affixed on the animals ranging from 13 to 360 days. Linear displacements ranged from 279 to 1,605 km from deployment to pop-up locations with average speeds of 3 to 107 km/day. Black marlin exhibit discernible seasonal movement patterns, as evidenced by the analysis of horizontal movement tracks obtained via Kalman filter calculation. Specifically, fish tagged during spring and summer displayed a tendency to move northwards towards the East China Sea, whereas those tagged during winter exhibited a southerly direction of movement towards the South China Sea. However, swordfish did not exhibit clear seasonal movement patterns, as indicated by the analysis of tagging locations in eastern Taiwan and subsequent pop-up locations spanning a range that extended northwards to the East China Sea, southwest to the South China Sea, and southeast of the Philippines. Diving depths (water temperature) ranged from the surface to ~258 m (14.5°C to 30.3°C) for black marlin, and surface to ~915 m (4.9°C to 32.9°C) for swordfish. The distributions of time spent at depth significantly differ between daytime and night-time diving activity. Tagged black marlin spent the majority of daytime in the surface mixed-layer to ~50 m and exhibited basking behaviour, and at nighttime they were confined exclusively to the surface. Swordfish demonstrated pronounced diel vertical movement patterns reaching daytime of depths >400 m and occupying the surface mixed layer <100 m at night-time. Like the other istiophorid billfish, black marlin is susceptible to surface fishing gears due to their preference for surface water and diving behavior. Swordfish spent considerable time in the mesopelagic zone during the day, and the duration of time grows with the size of the fish. Because of their unique physiological and morphological adaptations (such as vascular counter-current heat exchangers), swordfish can search for food resources more effectively in cooler temperatures and exploit more water column resources than other fishes.

Keywords: basking behaviour; diel vertical movement; electronic tagging; epipelagic and mesopelagic; seasonal movement

Introduction

Marine top predators play a significant role in oceanic and coastal ecosystems, including regulating food webs, cycling nutrients, and supporting fisheries and tourism (Estes et al. 2016) . There is considerable disagreement about the current state of large pelagic fish populations. Still, the species at greatest risk are large apex predators, particularly sharks and istiophorid billfish, because their slow life-history parameters, such as slow growth rates, late maturity, and low reproductive rates, make them susceptible to overexploitation (Kitchell et al. 2006, Collette et al. 2011). Billfishes are economically significant to commercial fisheries for targeted catch (Su et al. 2011, Braun et al. 2019) and are incidentally caught as bycatch (Sharma et al. 2018). Additionally, they are also targeted for recreational fishing (Nakamura 1985, Williams et al. 2016, Kerstetter and Schratwieser 2018). High market values of these species often lead to overexploitation beyond the sustainable level, which ultimately increases the risk of stock collapse (Collette et al. 2011). To achieve improved management of these species, it is crucial to gain a more comprehensive understanding of their ecology (Braun et al. 2015, Collette and Graves 2019). This entails the identification of distinct stocks through the determination of size and distribution of management units, as well as an assessment of their vertical habitat use and diving behavior to gauge their susceptibility to various fishing gears (Rohner et al. 2022).

Multiple techniques have been employed to describe the geospatial movements of marine animals. These advances provided unprecedented ecological insights by connecting animal movements to measures of their physiology and environment (Block et al. 2011, Hussey et al. 2015). Electronic tags in marine wildlife have become a powerful tool for reducing uncertainty in scientific knowledge (Block 2019, Watanabe and Papastamatiou 2023). Pop-up satellite archival tag (PSAT) technology is an established fisheries-independent tool to monitor ambient depth (pressure), temperature, and light levels (used to calculate daily positions or geolocations) on tags attached to animals to chronicle both horizontal and vertical movement patterns (Block et al. 1998). PSATs can offer many benefits to studying vertical dive behaviors, as well as providing information on migration routes, possible spawning areas, thermal habitat, exchange rates between areas, post-release mortality, and climate change impact on the habitat (Musyl and Gilman 2019, Griffiths 2020, Andrzejaczek et al. 2021, Chang et al. 2021, Dale et al. 2022, Freitas et al. 2022, Andrzejaczek et al. 2023). It is crucial to develop a comprehensive understanding of the factors that drive movement patterns at different scales, particularly with regard to fishing activities and climate change, in order to differentiate between these processes.

The aim of this study was to analyze the vertical movements and habitat preference of black marlin and swordfish using PSATs, which were concurrently tagged with off eastern Taiwan. Specifically, our objectives were to (1) investigate seasonal patterns of horizontal movements, (2) gain a better understanding of their diel vertical movement, including the precise depths and temperatures they occupy, and (3) determine their habitat preferences in the northwestern Pacific Ocean.

Methods and materials

Tagging operation

PSATs were deployed from harpoon boat and commercial longline fishing gear out of Taitung (southeastern Taiwan) targeting billfish on the southeastern coast. On the harpoon vessel, the harpooner waited in a bow-mounted platform with a 5 m (~15 kg) pole rigged with the PSAT. See Chiang et al. (2015) for more details on tag setup and deployments for black marlin. Swordfish were using commercial tuna longline gear (i.e., four hooks between floats, green chemical light sticks attached above the hooks baited with squid (*Loglio* spp.) and Pacific saury (*Cololabis saira*). By catch swordfish in good condition were selected to affix PSATs and tags were placed at the base of dorsal fin between spaces of the interneural and neural spines using a ~2 m tagging pole. PSAT tag heads were made of surgical grade nylon and augmented with opposable flopper blades (Musyl et al. 2011a). The tether was made of ~123 kg fluorocarbon with stainless steel crimps matching the diameter of the line and a stainless steel ball bearing (Sampo no. 6, Barneveld, NY, USA) was placed ~10 cm from the tag head to reduce torque and precession. Tagging location (GPS) and estimated body mass were recorded at the time of tagging. All research was conducted under the Fisheries Research Institute on Institutional Animal Care and Use Committee or Panel (IACUC/IACUP) permission.

Data collection

PSATs included in this study were deployed between 2008 and 2021 and included models from Microwave Telemetry (MT, versions PTT-100 and X-Tag) and Wildlife Computers (WC, MK10 and miniPAT). PSATs were programmed to sample pressure, ambient light levels, ambient temperature, and to detach after periods ranging from 180 to 360 days. Depending upon tag manufacturer, tags would also detach if a constant depth reading (signifying mortality or shedding) was recorded for 72 hours. Depth and temperature data were summarized into 24-hour histograms and/or transmitted as time series at minute-hourly intervals. PSATs were equipped with automatic release and fail-safe emergency depth release features whereby the procedure was initiated when a constant depth was detected or if the tag descended below the emergency depth threshold (Musyl et al. 2011b). On the programmed date or if the release mechanism is initiated; the tag releases, surfaces, and uploads archived data to the Argos constellation of polar orbiting satellites.

Data processing

After pop-up, the tag relayed archived data via Argos, including daily maximum depths, archived pressure (depth) and temperature readings, and raw light-based geolocations post-processed from the manufacturer (http://www.microwavetelemetry.com/fish/popupTag.cfm). The raw geolocations were further post-processed with an unscented, state-space Kalman filter augmented with sea surface temperature (SST) (Lam et al. 2008) to calculate most probable tracks (MPTs) for MT PSATs. Data received from the WC PSATs were processed using the WC software (DAP Processor), which provided daily summaries of time-at-depth, time-at-temperature, max depth, mean SST and light level. 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).

Pop-up locations were estimated by Doppler shift with Argos messages with location classes of 1 or higher and linear displacements from deployment to pop-up locations were determined using the Great Circle Distance. Time-at-depth and time-at-temperature data were aggregated into 50 m and 1℃ bins, respectively and were separated into daytime and nighttime periods by calculating times of local sunrise and sunset time (https://www.cnmoc.usff.navy.mil/usno). To further explore daytime and nighttime differences, the data provided by the PSATs were divided into six data streams by parsing depth data into day depth (DD) and night depth (ND). Temperature data were partitioned into day temperature (DT) and night temperature (NT). Because data distributions were not normally distributed (Kolmogorov–Smirnov and Lillifors tests, $P < 0.01$), non-parametric Mann–Whitney W (MW) tests and two-sample Kolmogorov–Smirnov (KS) tests were used to compare quality of medians and distributions for daytime and nighttime diving behaviour (i.e. DD v. ND, DT v. NT) within individuals (Zar 2010). Thermal habitat distributions were expressed as differences (ΔSST) from average daily SST estimates and individual temperature readings in the tags (Brill et al. 1993, Musyl et al. 2011a).

Results and Discussion

In total, 17 PSATs were deployed on 14 black marlin with estimated weights of 80−190 kg (mean ± SD= 117.9 ± 40.2 kg) and 3 swordfish (130.0 ± 62.0 kg), respectively. These tags transmitted data over 1,493 tag-days (black marlin) and 264 tag-days (swordfish) (Table 1).

Horizontal movements

The black marlin and swordfish tracked off southwestern Taiwan displayed wide-ranging movements. The geographic range of movements encompassed Taiwan in the East and South China Seas for tagged 14 black marlin. Linear displacements ranged from 279 to 1,231 km from deployment to pop-up locations with displacement rates of 3.1-31.3 km/day and a mean displacement per day of 11.9±40.2km/day (based on a conservative measure of straight-line distance) (Fig. 1; Table 1). There were three seasonal movement patterns for black marlin (Fig. 1): (1) Northern– black marlin tagged in spring moved into the Kuroshio and continued northwards into the East China Sea (black marlin #59208, 59210, 59242, 102722, 102724, 210626 and 224432); (2) Southwestern–black marlin tagged in winter moved in a southwesterly direction and against the Kuroshio into the South China Sea (black marlin #59267, 59269, 59271 and 224433); (3) Circular movement –black marlin #59262 tagged in summer moved northerly to the East China Sea. The black marlin then went back towards eastern Taiwan in winter and moved in a southerly direction towards the South China in spring. These circular patterns were then repeated by moving northwards the following summer back towards the East China Sea (Figs. S1-1-5). The maximum recorded straight-line distance travelled between tag deployment and pop-up locations for black marlin was 1,231 km, recorded by a ~90 kg individual (#55576) tracked for 155 days from southeastern Taiwan to the coast of Hai-Nan Island in the South China Sea (Fig. S1-1).

Three Swordfish PSATs popped-up prematurely after 15 to 229 days-at-liberty. Linear displacements ranged from 392 to 1,605 km from deployment to pop-up locations with displacement rates of 5.3-19.6 km/day and a mean displacement per day of 44.0 ± 55.1km/day. Based on the MPTs, swordfish #143509 undertook a southeasterly course of ~1,204 km east of the Philippines and #45922 underwent a southwestern course of ~1,605 km to the

South China Sea. #45924 undertook a northwards course ~392 km to the East China Sea (Fig. S2).

The Kuroshio flows in a north-east direction along the East China Sea shelf slope and generates a convergence zone at the boundary between the Kuroshio and a countercurrent system produced by bottom shelf water (Andres et al. 2008). The Kuroshio of eastern Taiwan ranged from 85 to 135 km, and the thickness varied from 400 to 600 m (Jan et al. 2015). This creates upwelling, bringing nutrients and abundant food resources (Ito et al. 1995). The horizontal movements of black marlin tagged in Taiwan appear to be closely associated with the Kuroshio. Horizontal movement tracks also suggest black marlin undergoes distinct seasonal movement patterns. Black marlin tagged in spring and summer moved in a northerly direction to the East China Sea, and those tagged in the winter season moved in a southerly direction to the South China Sea. The sea surface temperature off eastern Taiwan is around 25-27°C from October to November, and tagged black marlin #59262 followed the 24-26°C isotherm while traversing to the South China Sea.

The PSATs used in our study functioned essentially as fisheries-independent data for black marlin and swordfish (Dewar et al. 2011). The rapid speeds for all tagged individuals suggested natural movement away from the deployed location. Many large marine predators (LMPs) are highly migratory and therefore require well-developed abilities to navigate large swaths of open ocean (Braun et al. 2022). Swordfish often conduct annual migrations from tropical spawning grounds to productive temperate feeding habitats (Braun et al. 2019) and presumably possess advanced navigational skills. Given the relatively low sample size and short days-at-liberty of swordfish the utility for examining migratory patterns or stock structure is limited.

Diel vertical movements

Tagged black marlin and swordfish demonstrated diel vertical movement (DVM), with deeper diving during the daytime than at nighttime. MW and KS tests indicated significant differences between daytime and nighttime depth patterns for most tagged individuals. For all fish combined during night-time, tagged black marlin spent ~80% of their time from the surface to ~10 m and 90% of the time in the upper 50 m. By contrast, during daytime, less than 53% of time was spent above 10 m, and only about 75% of time was spent in the upper 50 m (Fig. 3A). Tagged swordfish spent ~50% of their time from the surface to ~100 m and 75% of the time in the upper 200 m during night time. By contrast, during the daytime, less than 20% of time was spent above 200 m, and about

75% of the time was spent in 400-600 m (Fig. 4A).

Tagged blue marlin displayed strong patterns of normal diel vertical movement (nDVM); diel episodes of diving behavior were recorded throughout the entire track (Fig. S3). The W-shaped movement patterns displayed in black marlin and swordfish during daytime are an optimal search strategy to increase prey encounters (Sims et al. 2008). The W-shaped movement pattern involves rapid directional changes, presumably increasing prey encounter rates without extensively increasing linear travel distance (Horodysky et al. 2007). These behaviors have been considered a foraging strategy for many pelagic fishes and sharks (Musyl et al. 2003, Sims et al. 2005, Gleiss et al. 2019).

Vertical movements extended to 258 m, and ambient temperatures ranged from 14.5 to 30.2°C. Mean depth (±SD) and ambient temperatures experienced during daytime and nighttime were 27.9 ± 38.9 m, 14.8 ± 30.2°C and 12.6 ± 27.4 m, 25.0 ± 2.3°C, respectively (Fig. 3; Table 2). Vertical movements for swordfish extended to 914.5 m, and ambient temperatures ranged from 4.9 to 32.9°C. Mean depth (±SD) and ambient temperatures experienced during daytime and nighttime were 419.4 ± 173.4 m, 12.9 ± 5.5°C and 105.5 ± 101.4 m, 23.4 ± 3.9°C, respectively (Fig. 4; Table 3). Dusk and dawn periods more closely resembled daytime depth distributions rather than night.

They revealed a deeper distribution during dawn than dusk for black marlin and swordfish (Figs. 5). There is a consensus that the diel vertical movements of swordfish and other large pelagic predators are associated with foraging in the deep scattering layer (DSL)(Dagorn et al. 2000, Schaefer and Fuller 2002, Musyl et al. 2003, Gilly et al. 2006). Deep diving may serve as a probing behavior by which LMPs can better detect gradients in a diverse suite of environmental cues useful for navigation (Braun et al. 2022). (Abid et al. 2018) indicated swordfish diet composition varied significantly among season and significant correlation was found between the body length of predators and prey sizes. Because of its unique physiological and morphological adaptations (such as vascular counter current heat exchangers), swordfish can maintain their body temperature on an ephemeral basis below the thermocline.

Swordfish occupy during the day and night vary geographically (Fig. S4). Other than while basking, daytime depths are linked to light attenuation, increasing as lightweight penetrates deeper into the water column (Dewar et al. 2011). The diel activity patterns exhibited by swordfish reported herein were similar to what other researchers have reported (Dewar et al. 2011, Sepulveda et al. 2018) and matches the general behavior of bigeye tuna (Musyl et al. 2003, Matsumoto et al. 2013, Lam et al. 2014, Schaefer et al. 2015, Lin et al. 2021) and some pelagic sharks (Musyl et al. 2011a, Andrzejaczek et al. 2022) to the extent allowed by their respective physiological tolerances and limitations. The main driver of diel vertical migration is assumed to be prey species avoiding visual predators in surface waters during the day (Brierley 2014). Vertical movement patterns could include season, geographic region, and physical variables such as mean SST and dissolved oxygen (Andrzejaczek et al. 2023). Movement patterns appear to be consistently driven, at least in part, by temperature, dissolved oxygen, and light level (Braun et al. 2015, Carlisle et al. 2017, Vedor et al. 2021, Dale et al. 2022). However, the extent to which marlin are reacting to their own physiological tolerances or dynamic prey distributions responding to these physical variables is less well resolved.

Habitat use

Tagged black marlin has thermal preferences on the surface to 50 m and temperature from 24°C to 26°C. Vertical shifts were associated with temperature shifts, and during the daytime, black marlin stayed mainly from the surface to 100 m and at nighttime from the surface to 50 m at ambient temperatures from 22°C to 30°C (Fig. 6A). Two thermal preferences for swordfish were from surface to 100 m and 400-600 m, temperature from 24°C to 28°C and 8°C to12°C. Vertical shifts were associated with temperature shifts, and during the daytime, tagged swordfish stayed mainly from 300 to 600 m and at nighttime from 10 to 200 m at ambient temperatures from 8°C to 14°C and 20°C to 28°C, respectively (Fig. 6B). Tag recorded temperature data indicated that the SST experienced by black marlin were about 80% in 24-29 °C, and 90% in 24-29°C for swordfish (Fig. 7).

Given the routes taken by each fish (Figs. 1 & 2), The aggregated temperature-depth profile indicated the bottom of the mixed-layer depth appears to be ~150 m, and black marlin seldom crosses the thermocline (200 m) (Fig. 8A). Black marlin often made deep, short-duration dives that took them into relatively cold environments, and two dives (by two fish) below 250 m were observed (Table 2). Swordfish diving depths were deeper than thermocline (Fig. 8B; Table 3). The △SST analysis indicated black marlin spend most of their time in the uniform temperature surface mixed layer and vertical movements appeared to be limited by a temperature change of ≦-8°C (Table 4). For swordfish, daytime and nighttime vertical movements were restricted by temperature changes of ≦-18° and ≦-6°C, respectively (Fig. S5).

Black marlin is cold-blooded, but they do possess brain and eye heater tissue that support the functionality of these organs as ambient temperatures decrease for short periods (Block 1986). The habitat of istiophorid billfish is largely confined to the surface mixed layer; they seldom cross the thermocline, and do not stay in water 5–10◦C cooler than the mixed layer for extended periods (Holland et al. 1990, Block et al. 1992, Pepperell and Davis 1999, Chiang et al. 2011, Stramma et al. 2012, Chiang et al. 2015). The mixed surface layer is also the warmest part of the local habitat, which may have some metabolic significance (Brill 1996). Swordfish have evolved a set of visual, locomotory, circulatory, and neural adaptations that give them a distinct advantage over many potential prey items in the cold, dark waters of the deep pelagic ocean (Carey 1982, De Metrio et al. 1997, Fritsches et al. 2003). However, there is strikingly little evidence to confirm that they rely on mesopelagic prey resources (Braun et al. 2022). Deep crepuscular diving aligns with theoretical expectations for maximizing foraging opportunities during these times by intercepting migrating DSLs (Thygesen and Patterson 2019), some of our observed very deep dives to 800-900m (e.g., >1,500 m; (Abecassis et al. 2012)) are well beyond the depth of the primary DSL, which is typically found between approximately 400 and 650 m (Proud et al. 2017).

Lin et al. (2021) showed deep diving correlated with body size in bigeye tuna. This finding was similar to the meta-analysis, suggesting thermal inertia may allow larger tuna to undertake longer and deeper excursions than smaller bigeye tuna. Several studies on vertical movements in bigeye tuna in the Pacific and Atlantic reported significant differences in vertical diving behaviour that correlated with fish size (Musyl et al. 2003, Arrizabalaga et al. 2008, Williams et al. 2018, Braun et al. 2019, Hino et al. 2020, Andrzejaczek et al. 2023). Moreover, contemporaneously collected data on environmental factors would better define the temporal and spatial scales of swordfish distribution and habitat. Lastly, spatially explicit, fisheries-independent information (e.g., tagging experiments) in the high-catch areas will be required to understand fishery interactions better.

Conclusions and management implications

Black marlin spent the majority of daytime in the surface mixed-layer to ~50 m and exhibited basking behaviour, and at nighttime they were confined exclusively to the surface. Swordfish demonstrated pronounced diel vertical movement patterns reaching daytime of depths >400 m and occupying the surface mixed layer <100 m at nighttime. Like other istiophorid billfish, black marlins are vulnerable to surface fishing gears due to their dive behavior and preference for surface water. The swordfish spends considerable time in the mesopelagic zone during the day, and their duration increases with their size. Due to its unique physiological and morphological adaptations, swordfish are able to search for food more effectively at cooler temperatures and exploit a wider range of resources in the water column than other fish. The largest threat to billfish taxa, is bycatch from drifting commercial longlines that are set in epipelagic waters, primarily targeting tunas, and swordfish (Cramer 2003). Most of what we know about billfish biology and life history has been revealed by electronic tag technology (Braun et al. 2015). A particular benefit of electronic tags has been the ability to fill gaps in species-specific behavior relevant to population modeling and reducing bycatch in data-poor regions and species (Lam et al. 2022). We predict that black marlin may be more vulnerable to baited hooks during the day, as they will likely forage during this time. Seasonal distribution data could be paired with knowledge of diel vertical distributions to understand the hours of the day and times of year that a marlin may be most vulnerable to a baited hook at a given depth and region. Integrate existing and future tag data with chemical and physical oceanographic datasets to better understand billfishes' relevant biophysical interactions, thereby enhancing management capabilities for these economically and ecologically important fish species. Further understanding of black marlin and swordfish capture vulnerabilities will be facilitated by larger sample sizes and longer tracking durations, especially for under-sampled seasons.

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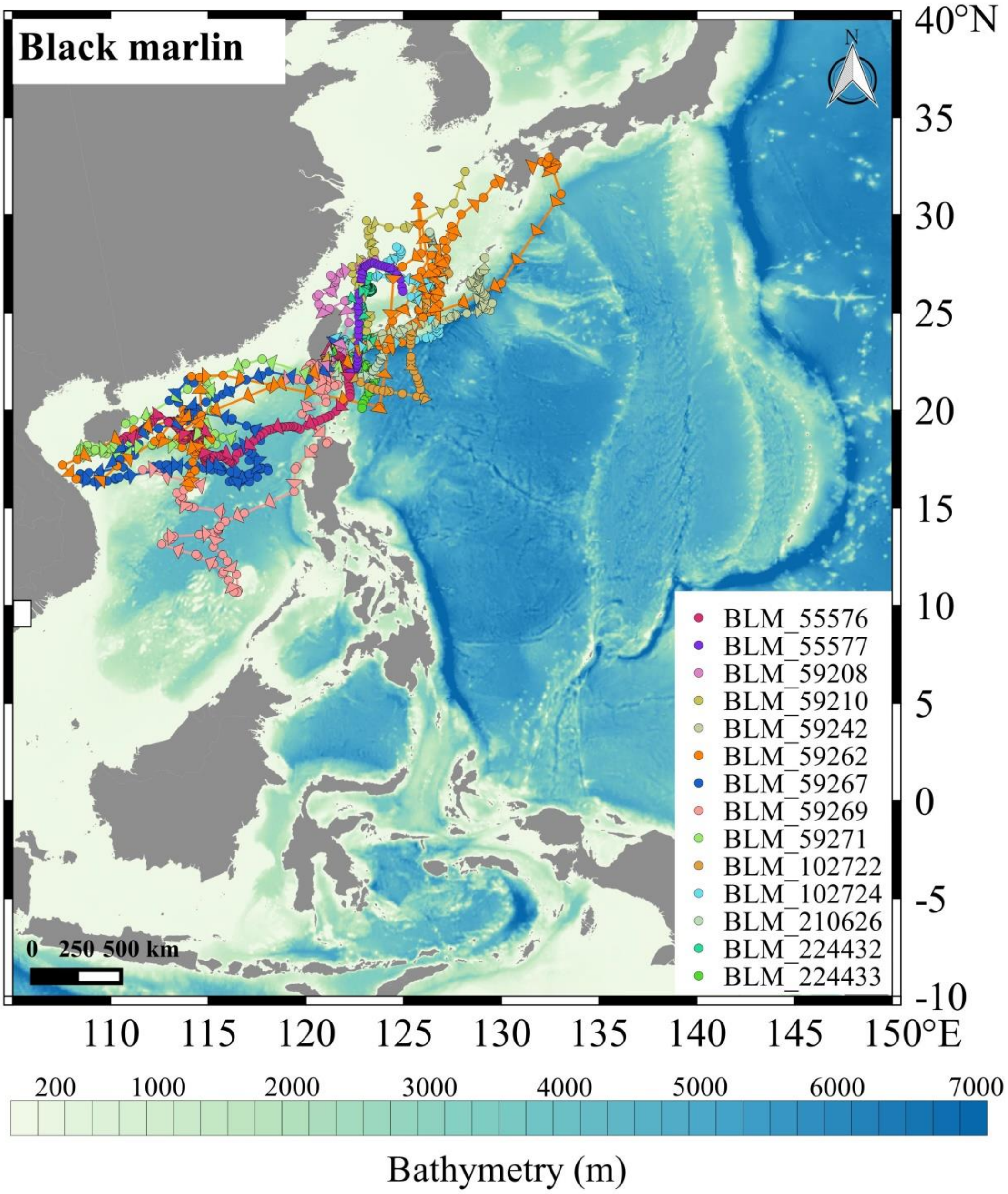

Fig. 1. Map of most probable track (MPTs) of 14 black marlin deployed with PSATs during the period from December 2008 to November 2021.

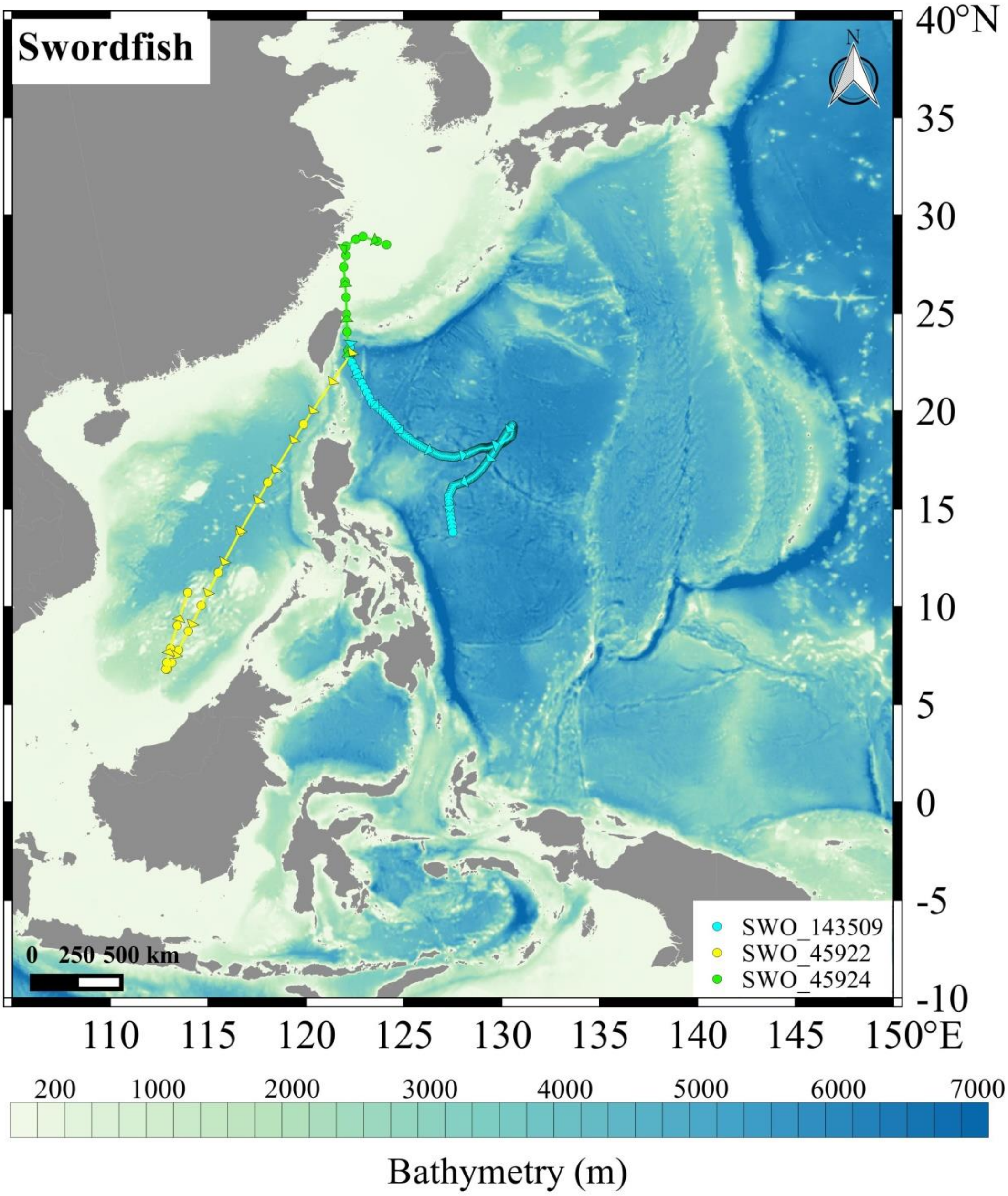

Fig. 2. Map of most probable track (MPTs) of 3 swordfish deployed with PSATs during the period from March 2016 to January 2018.

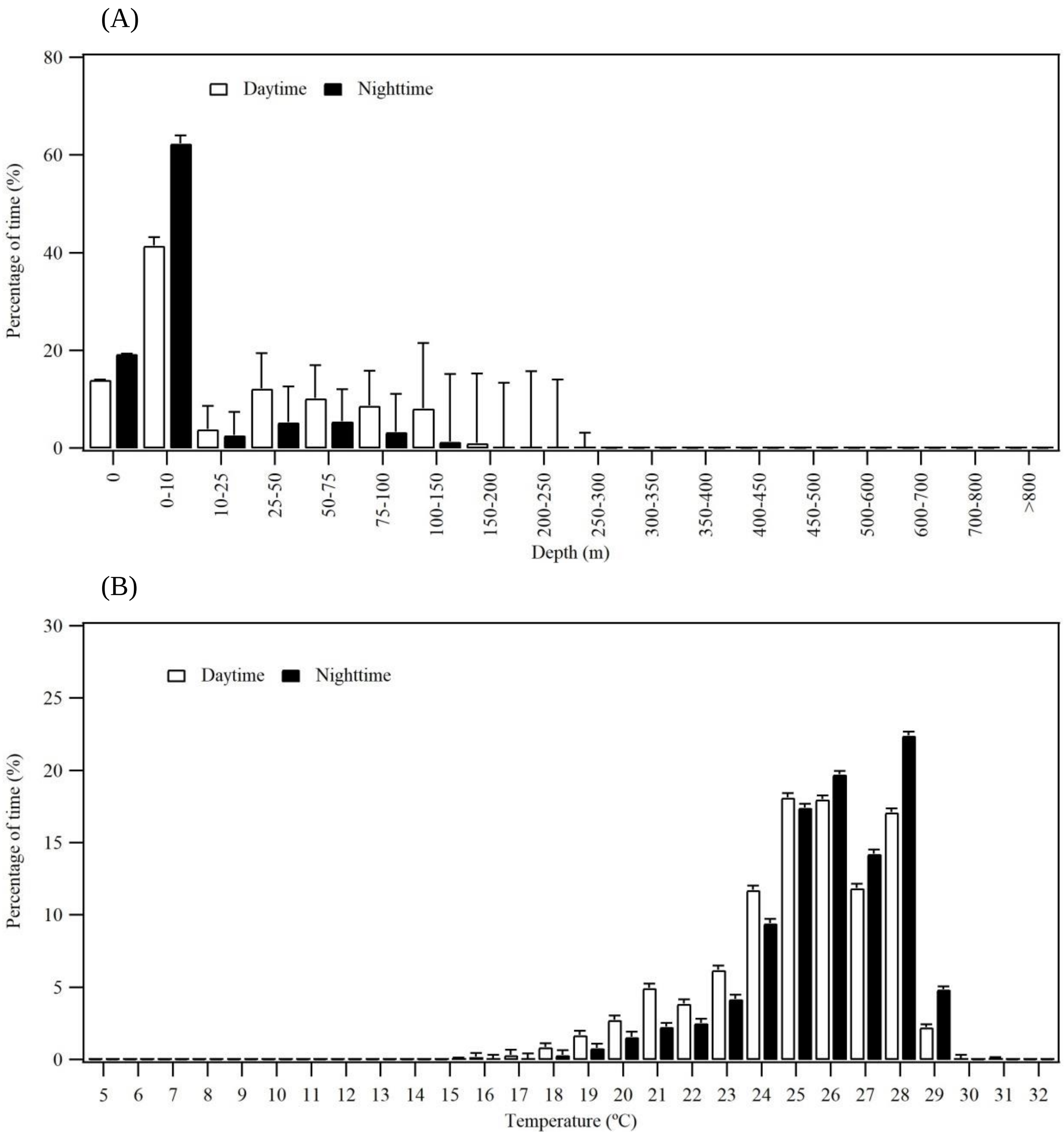

Fig. 3. Combined depth and temperatures occupied for all black marlin in the study. Fraction of time during daytime (white bars) and nighttime (black bars) spent in (A) individual depth strata, and (B) temperature strata.

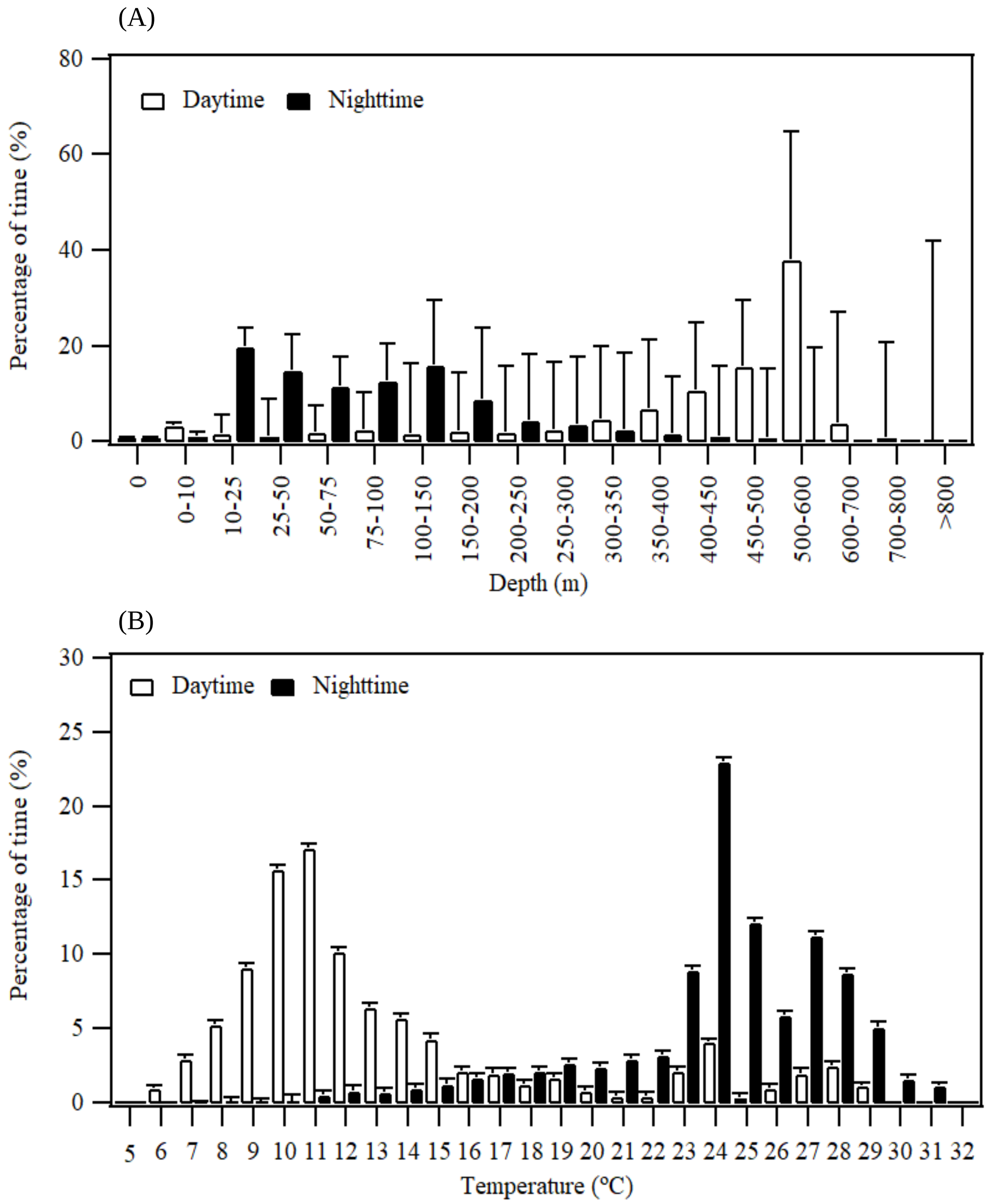

Fig. 4. Combined depth and temperatures occupied for all swordfish in the study. F Fraction of time during daytime (white bars) and nighttime (black bars) spent in (A) individual depth strata, and (B) temperature strata.

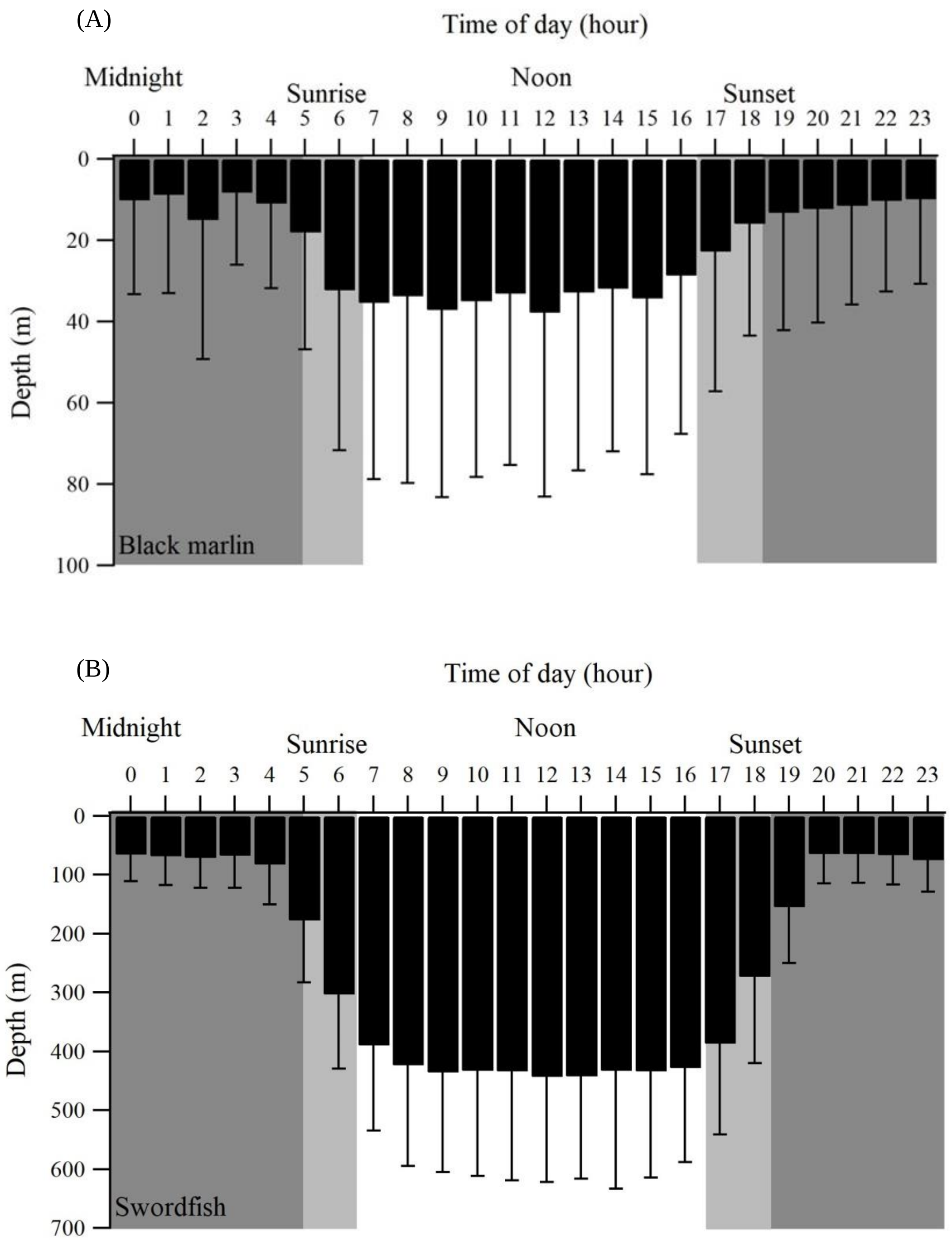

Fig. 5. Average depth by time for (A) black marlin and (B) swordfish (error bar is the standard deviation). Tag numbers are provided.

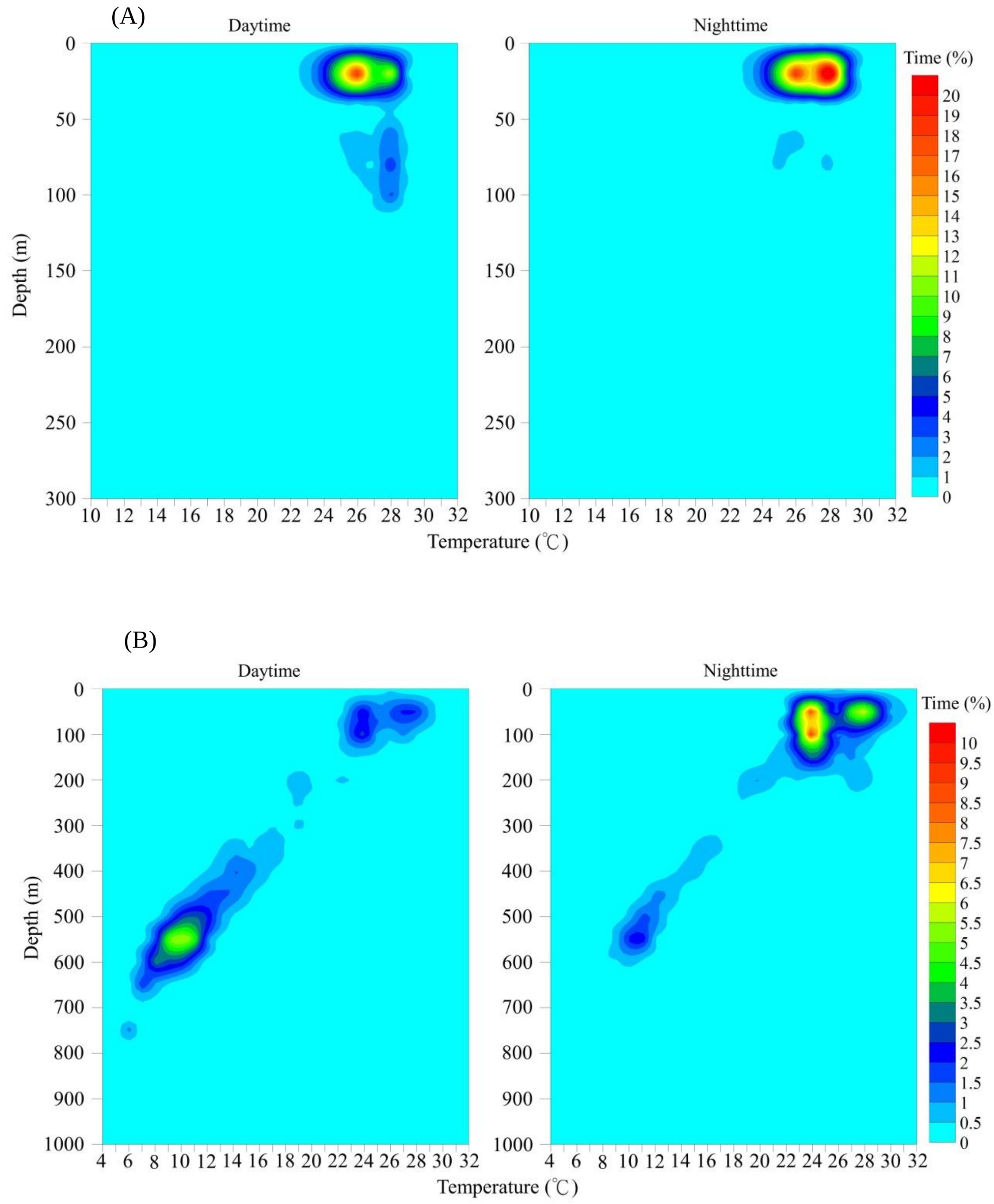

Fig. 6. Aggregated daytime and nighttime temperature at-depth profile showing the overall vertical habitat utilization for (A) black marlin and (B) swordfish tagged with PSATs.

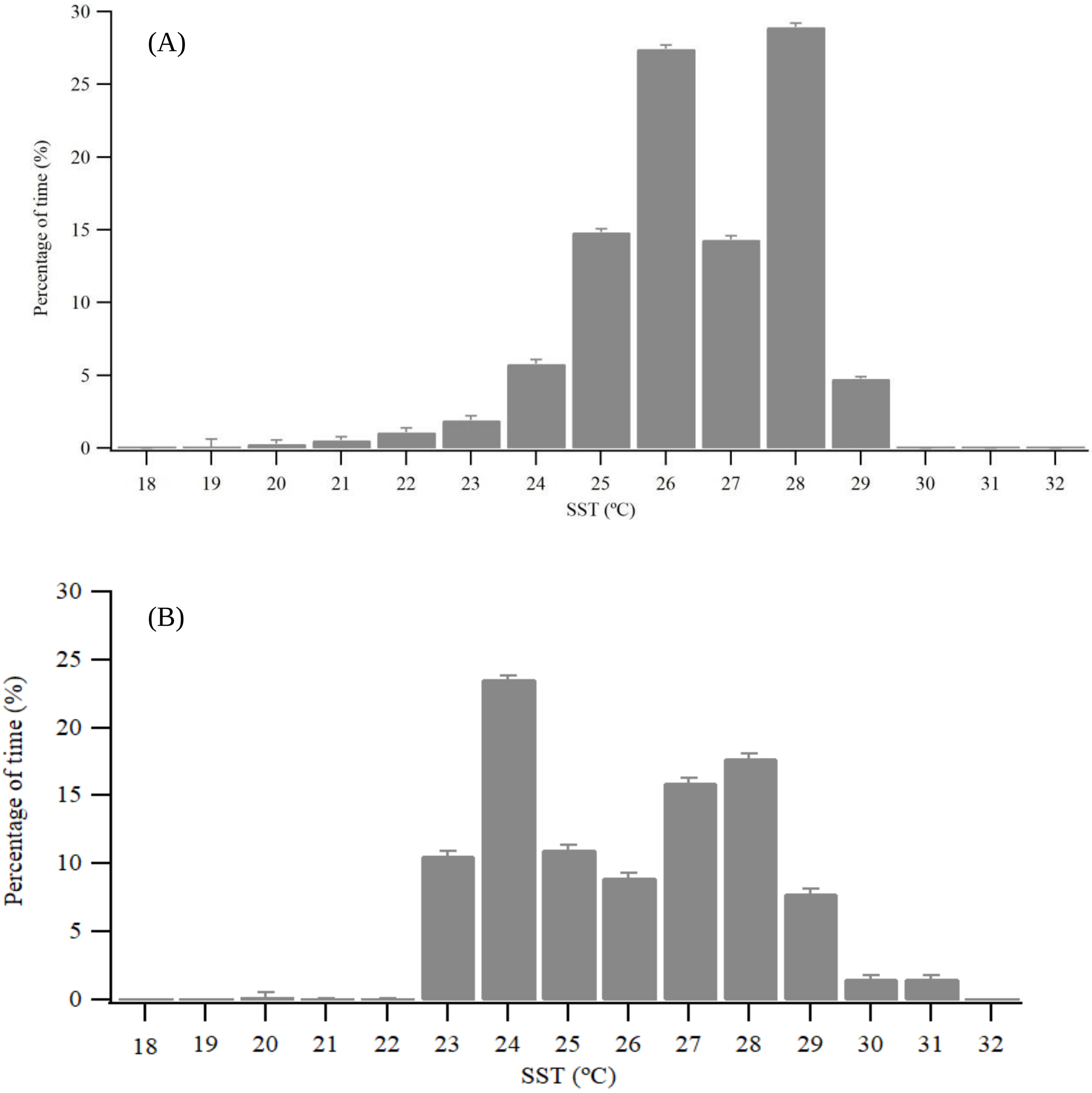

Fig. 7. Histogram of aggregated sea surface temperature experienced by tagged (A) black marlin and (B) swordfish in the Northwestern Pacific Ocean.

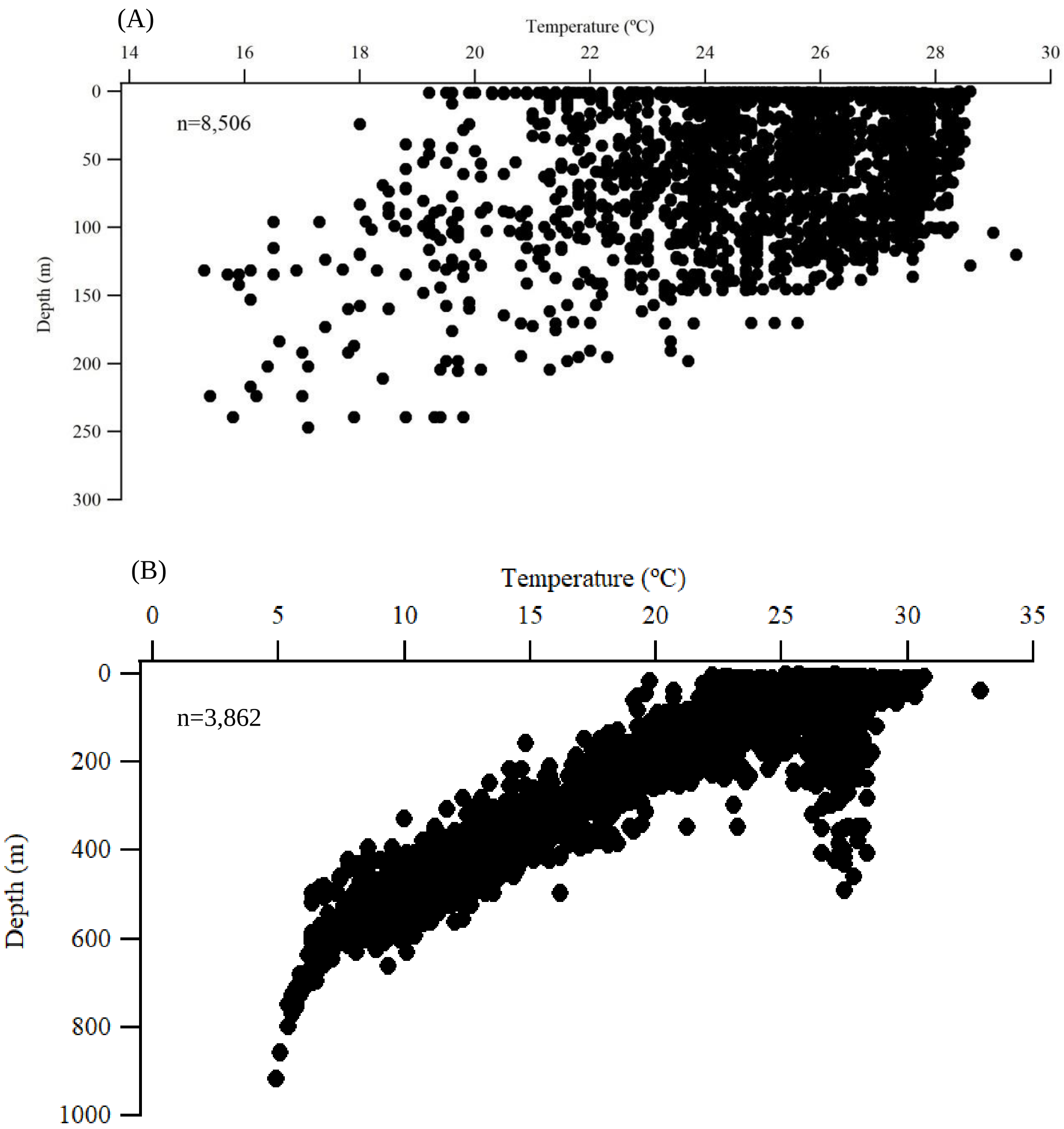

Fig. 8. Temperature-depth profiles obtained from the aggregated data from (A) black marlin and (B) swordfish tagged in the Northwestern Pacific Ocean.

Table 1. Details for pop-up satellite archival tags (PSATs) deployed on black marlin and swordfish 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. Weights were estimated by the captain of the fishing boat. (*: Chiang et al. (2015) reported data for 9 black marlin BLA_03-11)

Species	Species_#	PTT ID	PAST version	Tagging date	Fishing method	Estimated weight (kg)	Deployment location	Days at liberty	Reporting location	Straight-line distance (km)	Linear speed (km/day)
Black marlin	BLA_01	55576	MK-10	17-Dec-08	Harpoon	90	22°98’N 121°37’E	155	18°43'N 110°57'E	1,231	7.9
Black marlin	BLA_02	55577	MK-10	18-Jan-10	Harpoon	80	22°15’N 122°24’E	50	26°08'N 124°97'E	517	10.3
Black marlin	BLA_03*	59208	PTT-100	23-Feb-10	Harpoon	80	22°57’N 121°23’E	35	27°40’N 123°32’E	567	16.2
Black marlin	BLA_04*	59210	PTT-100	25-Feb-10	Harpoon	90	22°55’N 121°26’E	18	27°37’N 122°93’E	563	31.3
Black marlin	BLA_05*	59242	PTT-100	31-Mar-10	Harpoon	190	22°53’N 121°27’E	95	27°09’N 129°06’E	820	8.6
Black marlin	BLA_06*	59262	PTT-100	4-May-11	Harpoon	180	22°53’N 121°26’E	360	30°38’N 128°21’E	1,101	3.1
Black marlin	BLA_07*	59269	PTT-100	5-Oct-11	Harpoon	110	22°54’N 121°26’E	262	17°02’N 112°33’E	1,133	4.3
Black marlin	BLA_08*	59267	PTT-100	7-Nov-11	Harpoon	150	22°27’N 121°33’E	130	21°50’N 114°50’E	695	5.3

Black marlin	BLA_09*	59271	PTT-100	15-Nov-11	Harpoon	160	23°11’N 121°28’E	157	21°44’N 115°21’E	648	4.1
Black marlin	BLA_10*	102722	PTT-100	27-Mar-12	Harpoon	100	22°56’N 121°24’E	57	27°00’N 127°18’E	746	13.1
Black marlin	BLA_11*	102724	PTT-100	27-Mar-12	Harpoon	140	22°57’N 121°23’E	84	28°21'N 124°38'E	683	8.1
Black marlin	BLA_12	210626	miniPAT	23-Mar-21	Harpoon	70	22°56’N 121°23’E	36	28°21'N 124°39'E	820	22.8
Black marlin	BLA_13	224432	miniPAT	11-Nov-21	Harpoon	130	22°58’N 121°24’E	41	26°85'N 123°28'E	457	11.1
Black marlin	BLA_14	224433	miniPAT	11-Nov-21	Harpoon	80	22°57’N 121°23’E	13	20°13'N 122°88'E	279	21.5
Swordfish	SWO_01	143509	PTT-100	23-Mar-16	Longline	180	23°15’N 122°15’E	229	13°48’N 127°30’E	1,204	5.3
Swordfish	SWO_02	45922	X-tag	27-Dec-17	Longline	150	22°44’N 122°08’E	15	23°07’N 123°20’E	1,605	107.0
Swordfish	SWO_03	45924	X-tag	15-Jan-18	Longline	60	23°15’N 122°15’E	20	23°07’N 123°21’E	392	19.6

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

PSAT ID	Day depth (m) Min.-max. (mean ± SD)	Night depth (m) Min.-max. (mean ± SD)	Day temp. (°C) Min.-max. (mean ± SD)	Night temp. (°C) Min.-max. (mean ± SD)
#55576	0-136 88.4±29.5	0-128 84.0±50.8	18.0-29.4 23.9±2.9	20.8-26.2 23.8±2.7
#59208	0-59 7.1±12.8	0-59 14.7±20.2	17.6-28.8 22.2±2.1	17.6-28.8 22.6±2.9
#59210	0-118 17.3±21.7	0-65 5.2±13.2	22.9-25.1 23.9±0.8	23.1-24.9 24.1±0.5
#59242	0-258 34.8±40.8	0-113 7.8±16.3	17.7-26.0 23.3±1.9	18.4-25.7 23.8±1.5
#59262	0-199 24.1±31.4	0-140 7.3±16.0	15.1-28.9 24.9±2.7	16.9-28.8 25.7±2.2
#59267	0-118 33.7±43.4	0-102 15.7±24.1	14.8-28.8 24.6±2.0	21.7-28.2 25.2±1.5
#59269	0-210 74.7±50.9	0-102 10.5±18.8	15.3-30.2 23.8±2.9	14.5-28.9 25.6±2.2
#59271	0-183 33.2±39.4	0-97 5.9±15.8	20.4-27.5 24.7±1.5	19.4-27.7 25.3±1.8
#102722	0-167 26.9±40.6	0-167 12.1±28.5	16.7-25.7 23.9±1.5	23.1-26.0 24.5±0.8
#102724	0-258 18.3±30.5	0-183 7.9±19.2	16.9-27.3 22.6±2.9	18.6-27.2 24.6±1.0
#210626	0-224 14.2±33.9	0-224 14.3±29.1	15.4-27.8 24.0±2.3	16.1-27.5 24.1±2.3
#224432	0-240 44.9±45.2	0-131 10.2±20.5	4.9-25.1 25.9±2.1	5.8-27.1 26.5±1.0
#224433	0-198 70.3±44.7	0-176 17.2±30.8	19.5-28.5 26.9±1.2	21.4-28.5 27.6±0.6
Grand Average	0-258 27.9±38.9	0-247 12.6±27.4	14.8-30.2 24.9±2.4	14.5-28.9 25.0±2.3

Table 3. Summary of the depth and temperatures obtained for pop-up satellite archival tags (PSATs) deployments on swordfish.

PSAT ID	Day depth (m) Min.-max. (mean±SD)	Night depth (m) Min.-max. (mean±SD)	Day temp. (°C) Min.-max. (mean±SD)	Night temp. (°C) Min.-max. (mean±SD)
#143509	5.4-737	5.4-521	6.3-30.7	7-32.9
	477.7±92.9	114.5±105.6	11.3±2.7	23.5±4.4
#45922	0-914.5	0-677.8	4.9-25.1	5.8-27.1
	508.8±157.1	127.2±117.2	9.4±3.9	22.3±3.8
#45924	2.7-559.4	5.4-295.9	7.9-28.6	13.5-28.6
	156.5±177.8	65.1±57	19±6.6	24.1±2.4
Grand Average	0-914.5	0-677.8	4.9-30.7	5.8-32.9
	419.4±173.4	105.5±101.4	12.9±5.5	23.4±3.9

Table 4. Cumulative percentage of temperature readings from pop-up satellite archival tags (PSATs) attached to black marlin expressed as differences from daily mean sea surface temperature (ΔSST). SST was calculated as per Nielsen et al. (2006) and is analogous to Brill et al.'s (1993) surface layer. Fish PTT ID number is provided.

Fish	Time	△SST(℃)								
		0	-1	-2	-3	-4	-5	-6	-7	<-8
59208	Day	22.31	81.54	95.38	98.46	99.23	99.23	100	100	100
	Night	15.45	78.18	88.18	95.45	100	100	100	100	100
59210	Day	26.37	68.13	89.01	100	100	100	100	100	100
	Night	2.60	70.78	99.35	100	100	100	100	100	100
59242	Day	11.95	76.60	88.71	92.14	95.09	97.87	99.67	99.67	99.67
	Night	16.63	94.20	97.87	99.81	99.81	100	100	100	100
59262	Day	12.31	53.55	74.49	80.71	86.29	91.62	95.18	98.22	99.37
	Night	19.03	83.91	95.44	97.32	98.12	99.06	99.60	99.87	99.87
59267	Day	19.32	65.46	86.71	94.20	94.93	96.86	98.79	99.52	99.76
	Night	32.95	91.19	97.73	98.86	99.15	99.72	100	100	100
59269	Day	16.89	39.86	60.81	66.89	74.32	80.41	86.49	94.59	97.97
	Night	29.49	92.31	95.51	98.08	99.36	99.36	100	100	100
59271	Day	15.60	68.81	86.24	93.58	95.41	98.17	98.17	100	100
	Night	27.43	88.50	98.23	99.12	99.12	99.12	100	100	100
102722	Day	20.77	70.00	86.92	90.77	90.77	93.85	97.69	99.23	100
	Night	20.91	85.45	100	100	100	100	100	100	100
102724	Day	17.06	66.36	82.24	87.73	92.87	95.44	98.25	99.77	100
	Night	15.07	88.45	97.89	99.30	99.58	99.86	100	100	100
210626	Day	16.60	80.00	91.17	94.79	96.63	97.48	97.91	98.29	98.46
	Night	19.67	79.32	90.30	94.58	96.73	98.35	99.51	99.70	99.85
224432	Day	34.32	78.17	84.06	88.99	91.97	94.17	96.97	98.33	99.05
	Night	60.21	97.85	99.14	99.45	99.82	99.88	99.88	99.94	100
224433	Day	7.72	70.09	84.16	91.50	96.09	98.63	99.61	99.90	99.90
	Night	20.71	91.12	96.63	98.67	99.80	99.90	99.90	100	100
Total	Day	18.44	68.21	84.16	89.98	92.80	95.31	97.39	98.96	99.52
	Night	23.35	86.77	96.36	98.39	99.29	99.60	99.91	99.96	99.98

Supplementary Material

Movements and vertical habitat of black marlin (*Istiompax indica*) and swordfish (*Xiphias gladius*) in the northwestern Pacific Ocean

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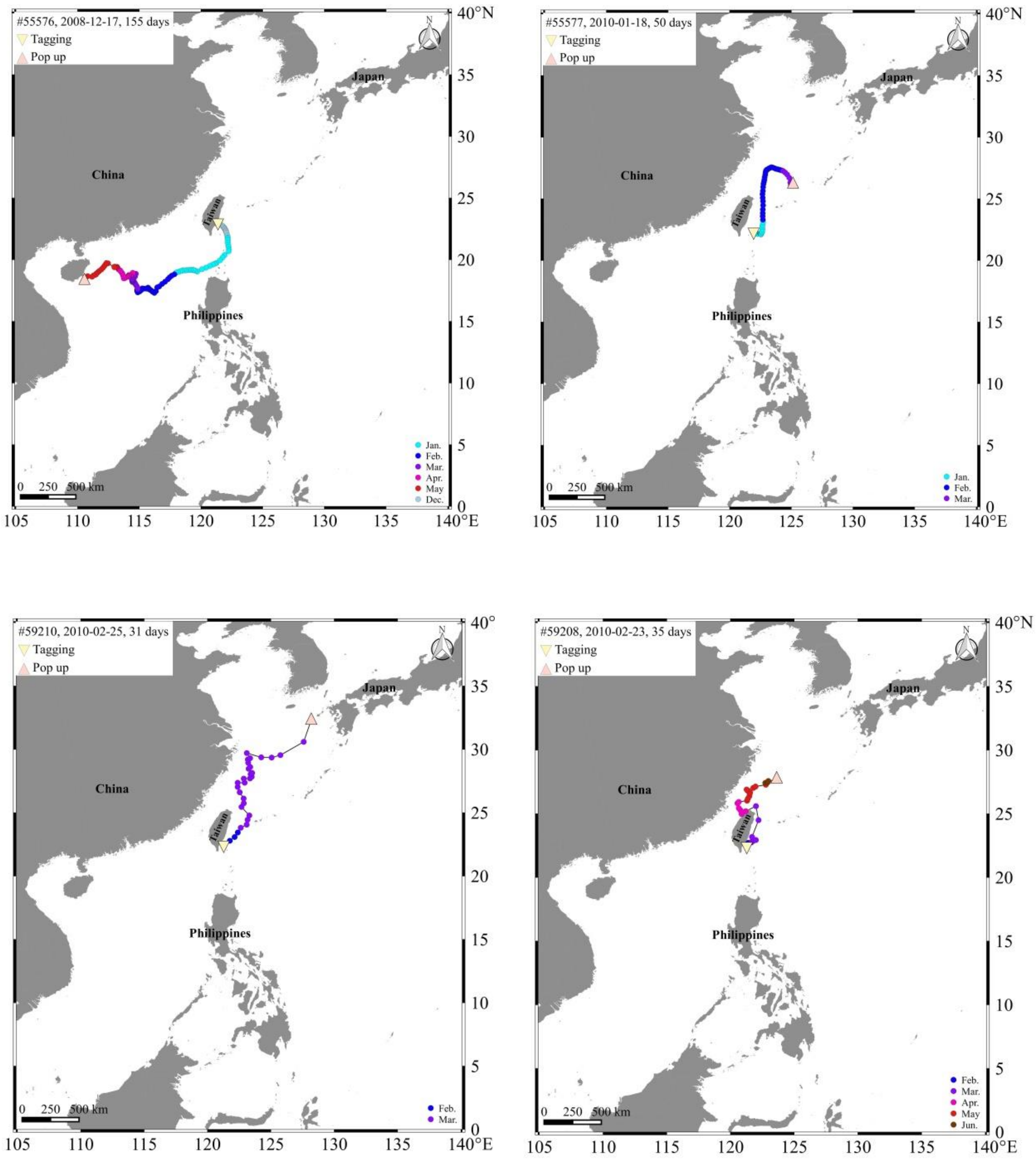

Figure S1-1. Map of PSAT deployments on black marlin (yellow inverted triangles). Most probable track (circles and line) where colour indicates month and pop-up location (pink triangles).

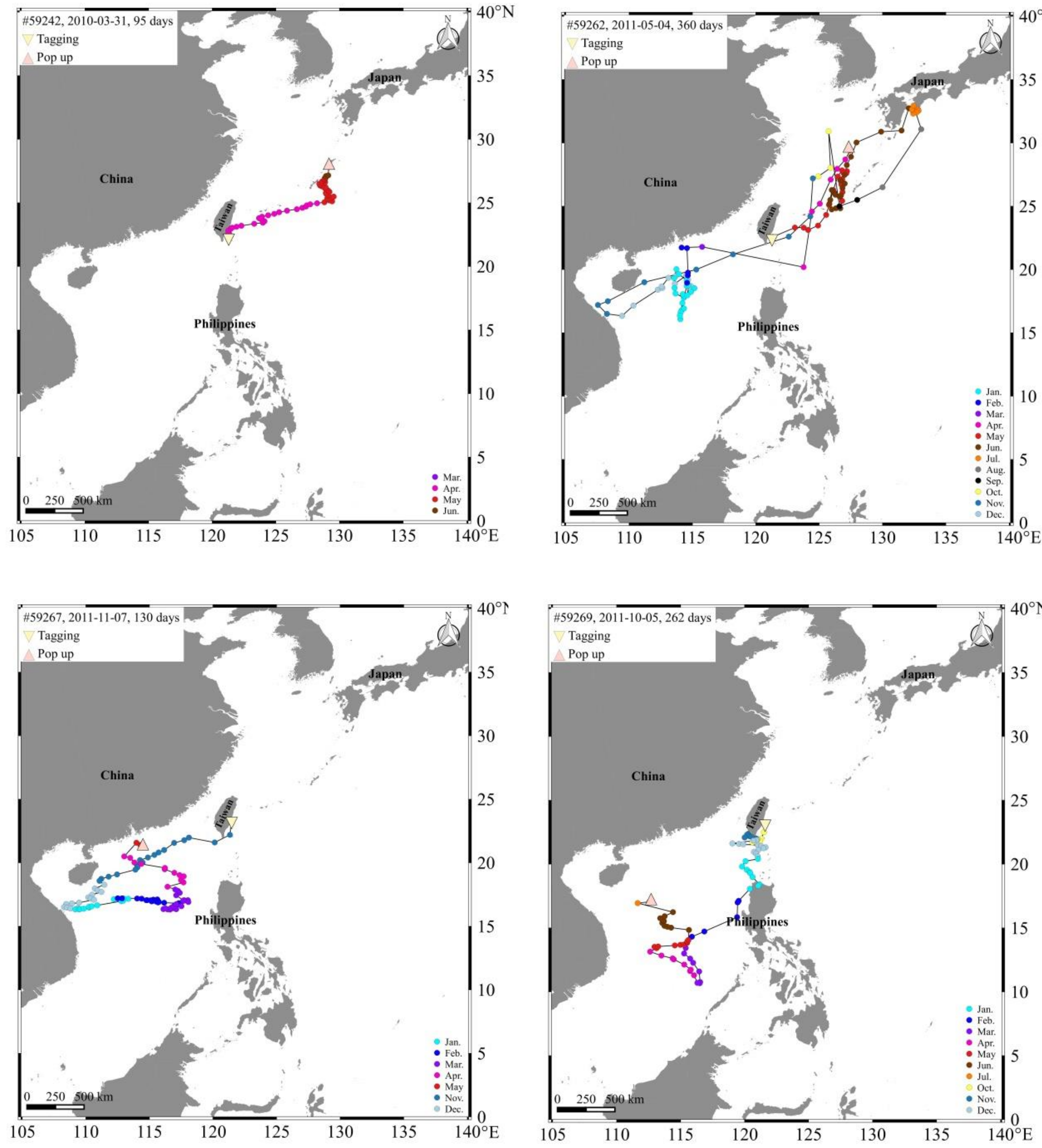

Figure S1-2. Map of PSAT deployments on black marlin (yellow inverted triangles). Most probable track (circles and line) where colour indicates month and pop-up location (pink triangles).

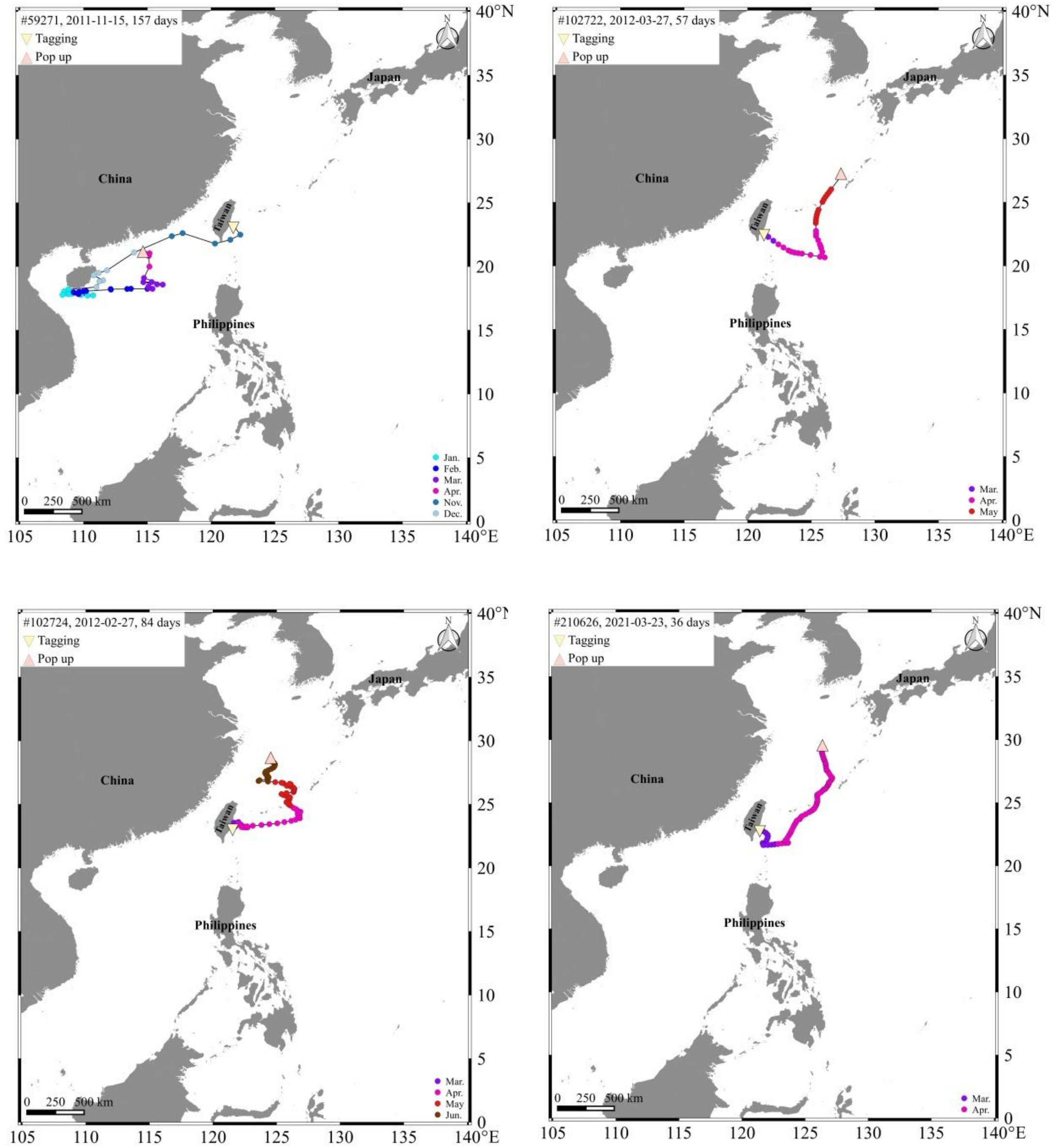

Figure S1-4. Map of PSAT deployments on black marlin (yellow inverted triangles). Most probable track (circles and line) where colour indicates month and pop-up location (pink triangles).

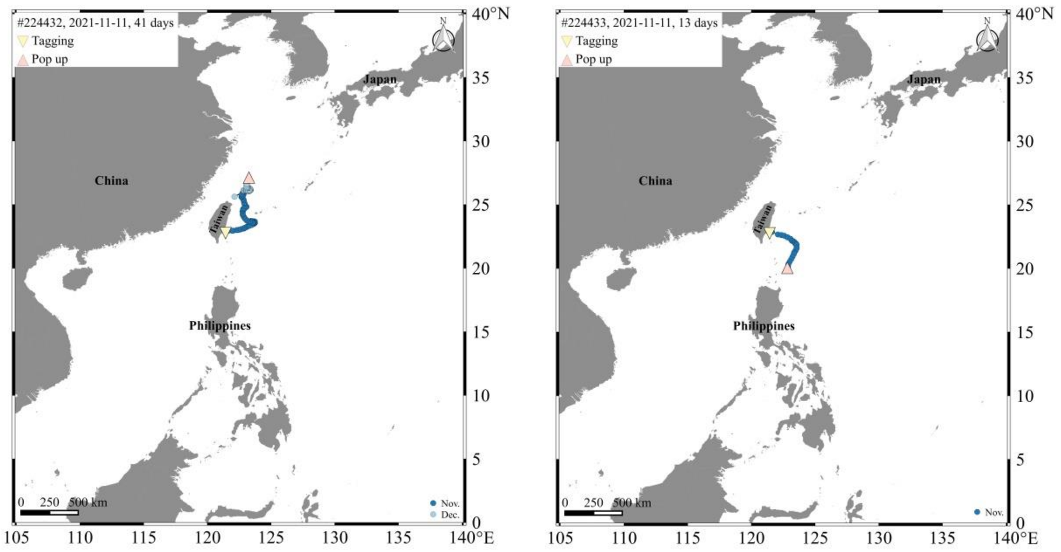

Figure S1-5 Map of PSAT deployments on black marlin (yellow inverted triangles). Most probable track (circles and line) where colour indicates month and pop-up location (pink triangles).

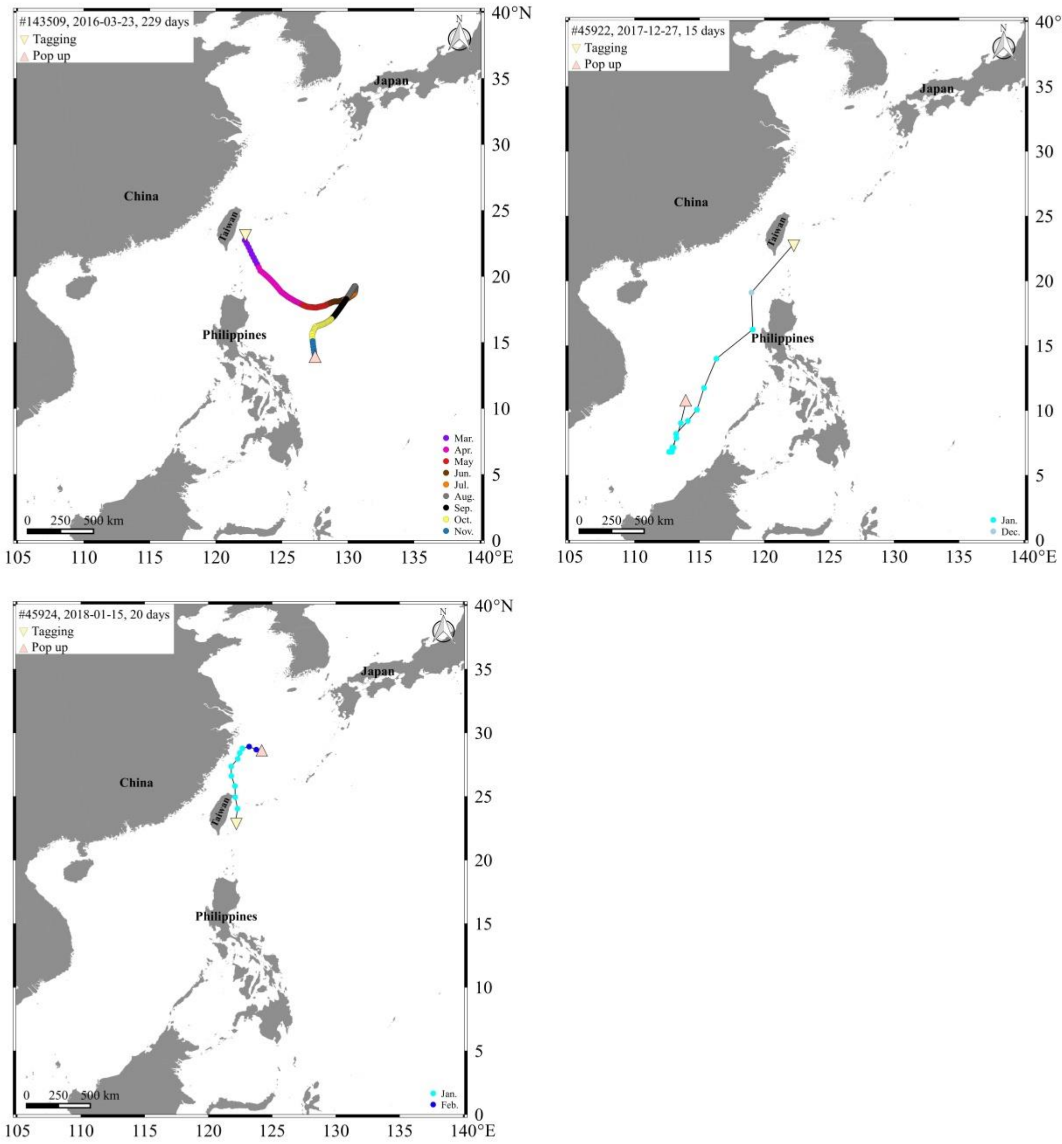

Figure S2. Map of PSAT deployments on swordfish (yellow inverted triangles). Most probable track (circles and line) where colour indicates month and pop-up location (pink triangles).

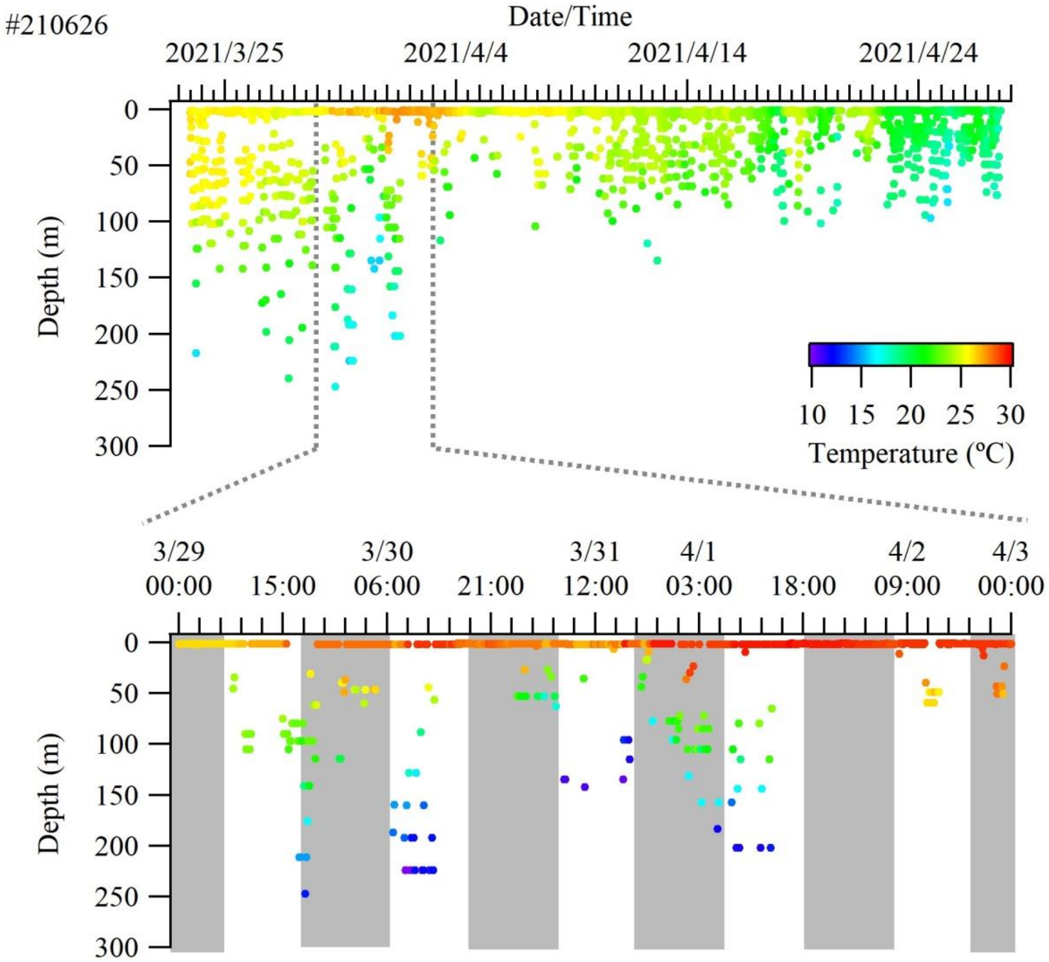

Figure S3. Swimming depth and temperature obtained from black marlin #210626. The upper panel shows the entire record covering 36 days-at-liberty, while the lower forum covers 5 days. Horizontal black bars indicate nighttime

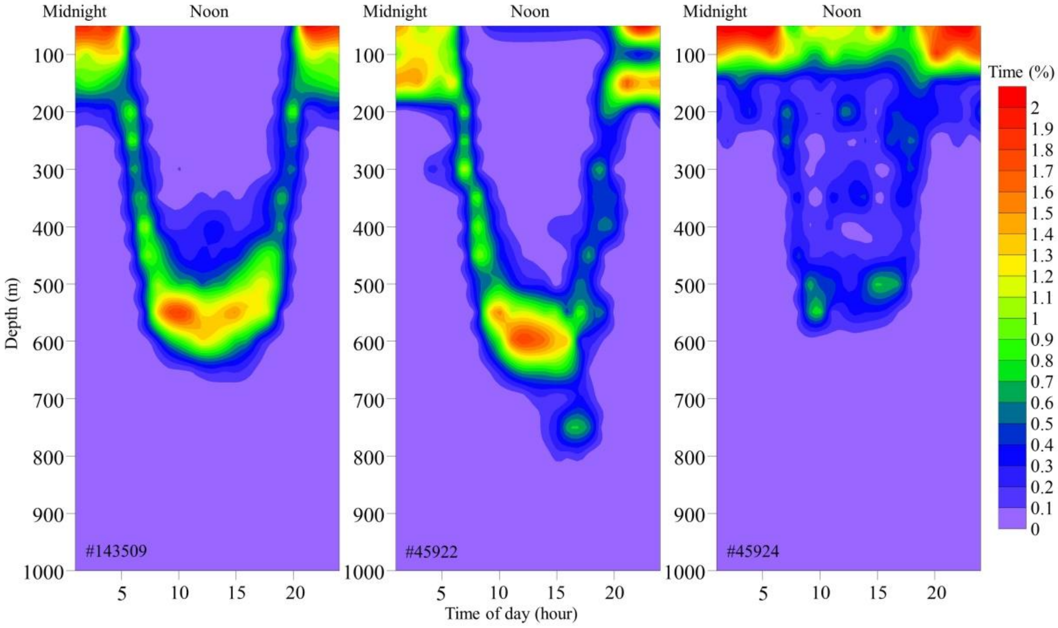

Figure S4. Depth records within an hour interval aggregated by time of 3 tagged swordfish.

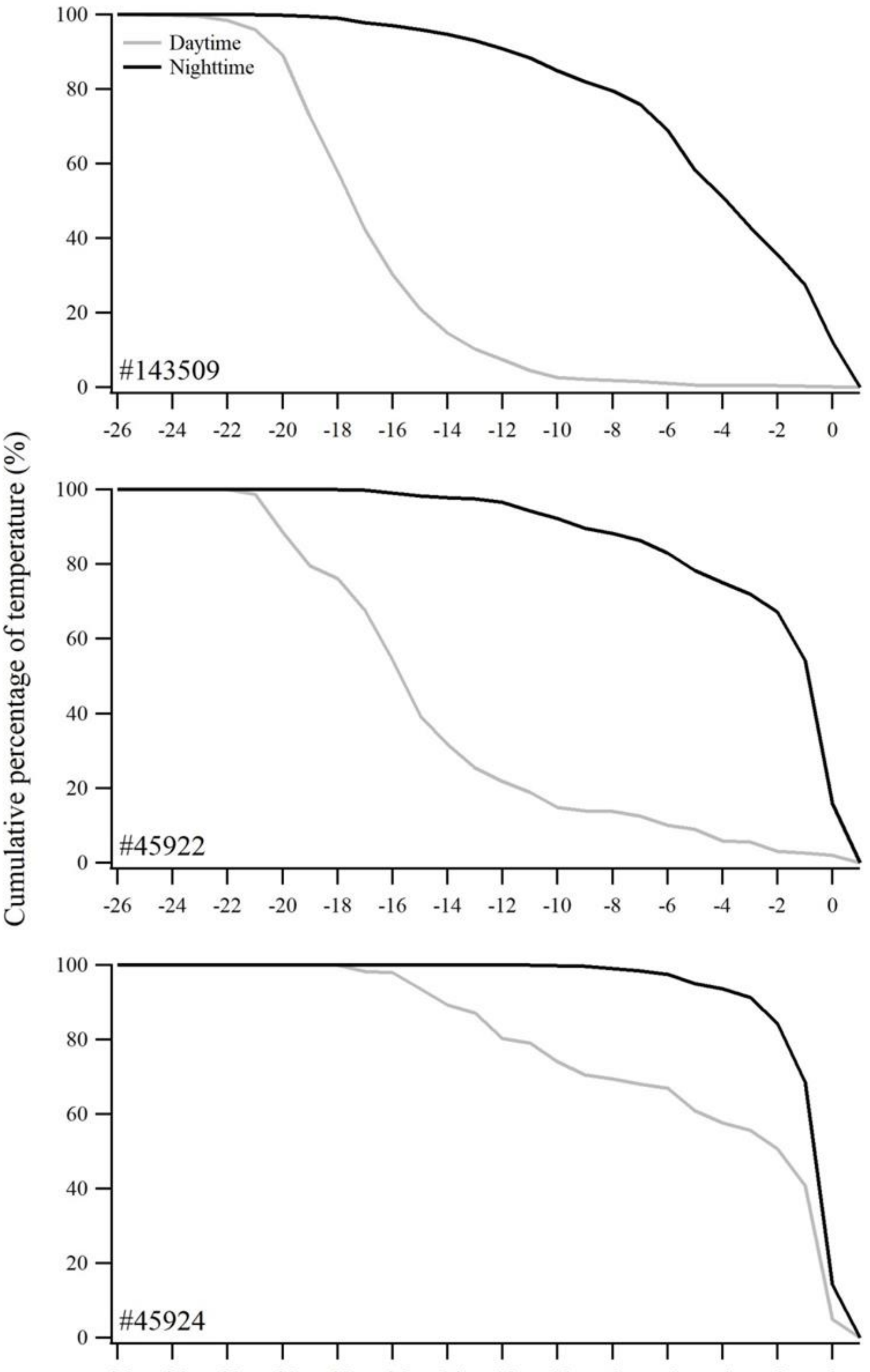

Figure S5. Cumulative percentage of temperature readings from pop-up satellite archival tags (PSATs) attached to 3 swordfish expressed as differences from daily mean sea surface temperature (ΔSST). SST was calculated as per Nielsen et al. (2006) and is analogous to Brill et al's (1993) surface layer.