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RESEARCH ARTICLE

Fine-scale Vertical Movements and Behavior of Immature Skipjack Tuna (*Katsuwonus pelamis*) off Eastern Taiwan

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Abstract

Skipjack tuna are globally distributed in tropical and temperate seas but little is known about their fine-scale diving patterns and how fish size and (or) maturity influences patterns off eastern Taiwan. A total of 211 immature skipjack (36 − 47 FL cm) in the study were caught by trolling near subsurface fish aggregating devices (FADs) near Green Island (southeastern Taiwan) and were tagged with Lotek LAT-2910 archival tags. The low rate of recovery (2.4%) suggests a high post-release mortality but this low rate could also be consistent with large population sizes, dispersal, tag loss or uncooperative fishers. Five individuals were recovered near the release locations and tags provided data archiving 11-31 days-at-liberty. Tagged skipjack tuna dove deeper during daytime than at nighttime ($p < 0.001$) and displayed repetitive bounce-diving behavior to depths between 50 - 310 m during daytime. During the deepest dives, ambient temperatures reached a low of 13.1°C with peritoneal temperatures at 17.0°C. The vertical movements and habitat preferences reported herein this study are the first fishery-independent observations on immature skipjack and provide evidence of the degree of ecological niche and fisheries interactions of skipjack tuna in eastern Taiwan.

Keywords: Archival tag, Diel oscillation, Ecological niche, Fish aggregating devices, Habitat preference

1. Introduction

Skipjack tuna is a highly migratory pelagic species with a global distribution from equatorial to temperate zones of the world's oceans [19]. The distribution of skipjack is influenced by the 29°C sea surface temperature (SST) isotherm and by strength of the El Niño-Southern Oscillation [14]. Biotic and abiotic factors also shape the habitat utilization of skipjack. Physiological tolerances of temperature [9,1] and oxygen [9] have indicated that skipjack inhabit predominantly the mixed-layer but make occasional brief dives below the thermocline. In turn, temperature and dissolved oxygen tolerances have been used in numerical modelling approaches as an accessibility coefficient to estimate skipjack foraging habitat [15,26].

Archival tagging studies in the western Pacific Ocean indicated that skipjack thermal habitat was defined by temperatures ranging from 18.8 °C to 28.2 °C with the 18 °C isotherm as an approximate boundary for the lowest limit [13]. Advances in electronic tagging have provided fishery-

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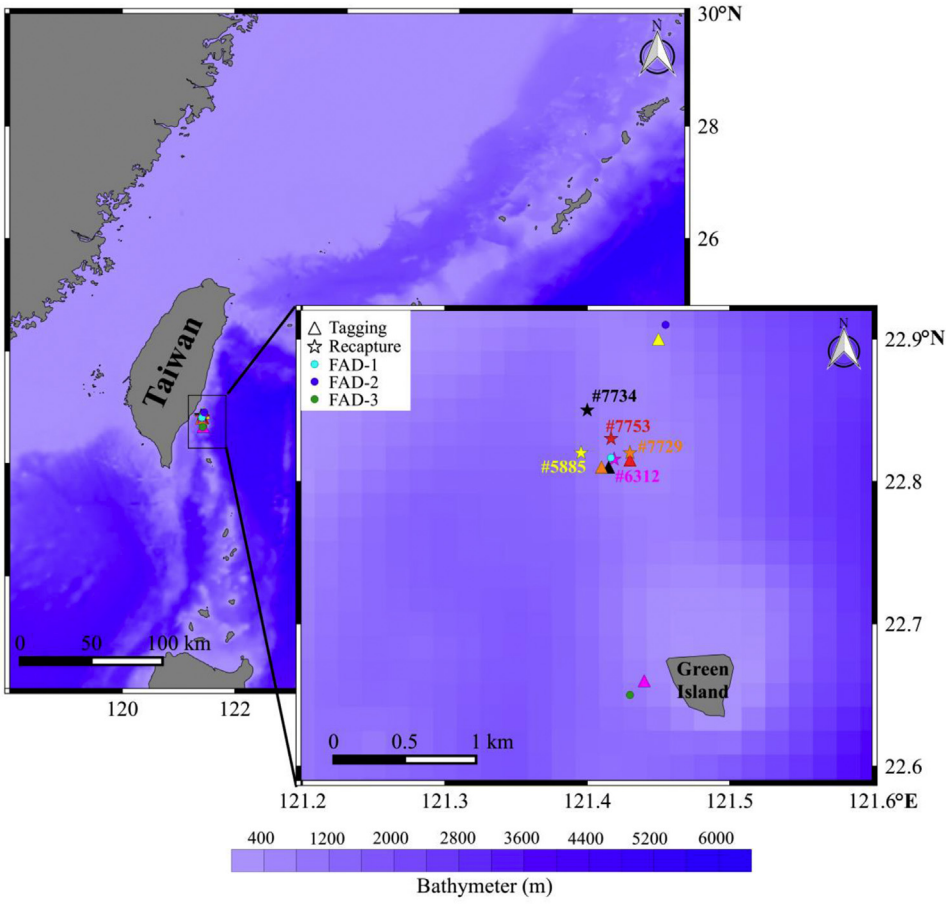

Fig. 1. Location of FADs off eastern Taiwan (near Green Island) and 5 skipjack tuna (#5885, 6312, 7753, 7734 and 7729) tagged (triangle shape) and recaptured area (star shape).

independent investigations on potential foraging and spawning habitats of similar tuna species [22,25,17,2,3] as well as new insights into the ecology and migration of skipjack [24]. Studies have been conducted on the behavior of skipjack using ultrasonic telemetry [9,11,18,30].

Fish aggregating devices (FADs) have been used by fisheries to attract and aggregate many marine species, including tuna and non-tuna species, because of the natural tendency of species to follow drifting objects [16,9,21]. Using ultrasonic tags, [30] reported that juvenile yellowfin tuna and skipjack tuna were the main species occupying FADs in southwestern Taiwan. Other studies have reported on the behavior of adult skipjack associated with anchored or drifting FADs [24]. The objectives of this study were to elucidate the vertical movement patterns and behavior of immature skipjack associated with subsurface FADs in eastern Taiwan.

2. Material and Methods

2.1. Archival tag deployments

Skipjack tuna were captured by trolling methods (pink feathers and swimming ballyhoo) around three anchored FADs during the early morning in

Table 1. Tagging details for skipjack tuna implanted with archival tags that were recovered.

Survey year	Archival tag #ID	Deployment date	Deployment location		Fork length at release (cm)	Recapture date	Recapture location		Recapture fork length (cm)	Days-at liberty
			Lat (N)	Lon (E)			Lat (N)	Lon (E)		
2018	5885	16 December 2018	22.90	121.45	44	15 January 2019	22.82	121.40	45	31
2019	6312	14 March 2019	22.66	121.44	44	8 April 2019	22.82	121.42	47	26
2019	7753	16 December 2019	22.82	121.28	41	26 December 2019	22.83	121.41	45	11
2019	7734	11 December 2019	22.81	121.42	41	23 December 2019	22.85	121.40	45	13
2019	7729	10 December 2019	22.81	121.41	43	2 January 2020	22.82	121.43	44	23

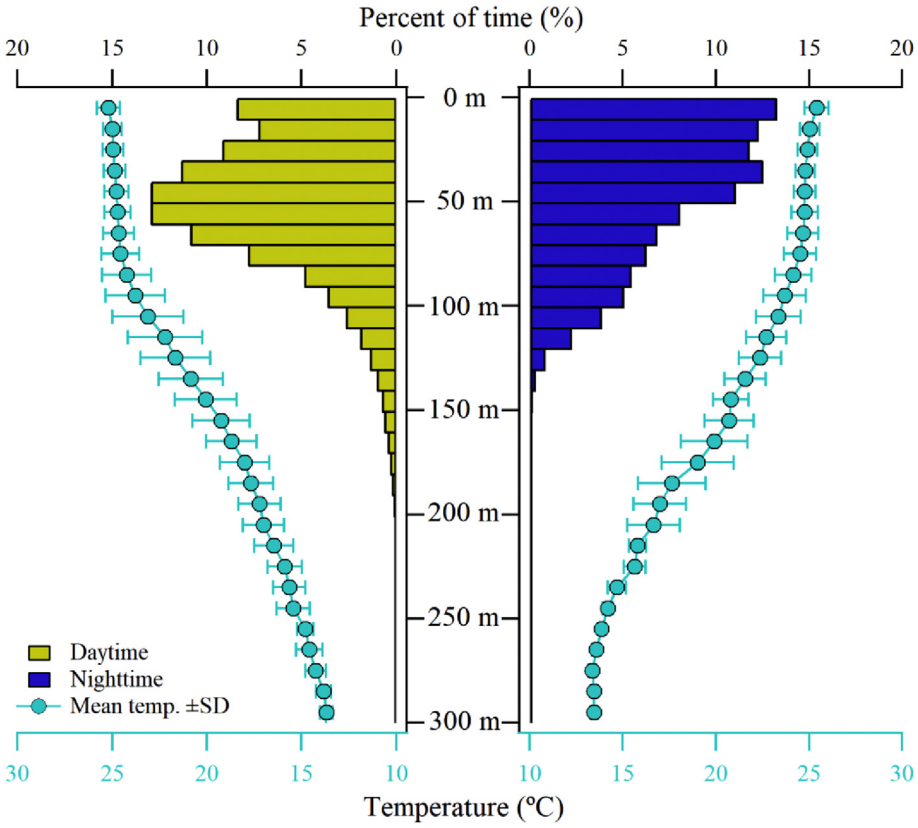

Fig. 2. Frequency distribution of the swimming depth (bar) and vertical profile of mean ambient water temperature (solid line and circle markers) and standard deviation (error bar) for five tagged skipjacks in the daytime (yellow bar) and nighttime (blue bar).

southeastern Taiwan (Table 1, Fig. 1). Each captured skipjack was lifted onto a padded wooden cradle and placed ventral side up to remove the hook. Fish in excellent condition (vigorous with no bleeding or serious injury) were selected for tag deployment. Archival tags (24 × 8.2 mm, weight 2.9 g) used in this study were model LAT-2910 (Lotek Wireless, Newmarket, ON, Canada). Tags were programmed to record time-series of external and internal temperatures, depth and light intensity acquired every 30 s with an 8 MB of onboard memory. The maximum depth rating was 2,000 m (resolution of 0.05%, accuracy of ±1%) and the temperature range was from −5° to 45°C (resolution of 0.2°C, accuracy of 0.05°C)

The tag was inserted into the abdominal cavity by making a small incision (~1.5 cm) by scalpel and the wound was sutured closed with leukoclips® (Leukoclip Stapler SD Handle, AMA PRODUCTS, Australia). Conventional plastic dart tags (PDA tag: length 14 cm, diameter 1.7 mm; Hallprint Pty Ltd., Hindmarsh Valley, South Australia, Australia) were attached near the base of the second dorsal fin to aid in tag recovery or if the archival tag was expelled. Tagging procedures were completed within ~60 s and tagged fish were immediately released near the FADs (Fig. 1, Table 1). A total of 724 individuals [fork length (FL) 36−47 cm] were released (211 conducted with archival tags) between December 2017 and March 2020 (Table S1 in Supplementary Material). Information posters were displayed at fish markets on how to report tag recoveries and receive rewards.

2.2. Data analysis

Time-series of depth and temperature were downloaded using proprietary software provided by Lotek Wireless. Archived time series for pressure (depth) and temperature were categorized into daytime and nighttime periods by calculating times of local sunrise and sunset time (http://aa.usno.navy.mil/). The behavior for each day at-liberty was classified as associated or unassociated with floating objects, on the basis of behavioral characteristics from ultrasonic telemetry observations of skipjack tuna associated with floating objects [23]. Moreover, W-shaped vertical movement patterns during the day were characterized as non-

associative behavior with floating objects where deep descents were followed by upward excursions into the uniform-temperature surface layer [20]. Ambient light data from recaptured tags were downloaded and the daily position of each skipjack tuna was estimated using the Lat Viewer Studio software, version 2.9.36 (Lotek Wireless. Inc.).

To further explore daytime and nighttime differences, we used one-sample Kolmogorov−Smirnov tests to compare distributions of ambient temperature and depth data to that of a normal distribution and all were non-normally distributed. As a result, we used non-parametric two-sample Kolmogorov−Smirnov and Mann−Whitney W-tests to compare differences in medians between daytime and nighttime data for depth and temperature distributions and Kruskal-Wallis non-parametric ANOVAs to compare across tags [33]. Time-at-depth and time-at-temperature data were aggregated into 20-m and 1 °C bins, respectively. These data were subsequently expressed as a fraction of the total time of observation for skipjack tuna. The $P < 0.05$ level was taken to indicate statistical significance.

3. Results

Five skipjack (41-44 cm FL at release) were recovered near FADs and provided data archiving 11-31 days-at-liberty for a total of 104 days of data in aggregate (Fig. 1, Table 1). The release and recapture locations around FADs were within 0.5 to 1.5 km (Fig. 1). Two skipjack tuna were recaptured after only 11 (#7753) and 13 days (#7734) after release (Table 1) by trolling with lures and indicated the released skipjack resumed normal feeding activities after surgical implantation of the archival tags.

3.1. Vertical distribution

For all recovered tags, the mean daytime depth was 55.2 m (±36.9 SD, range 0 to 310.6 m), ambient temperature was 24.1 °C (±1.6 SD, range 13.2 to 28.3°C) and peritoneal cavity temperature was 24.9 °C (±1.0 SD, range 17.0 to 28.2 °C). At nighttime, mean depth was 46.1 m (±32.6 SD, range 0 to 301.0 m), ambient temperature was 24.7 °C (±1.1 SD, range 13.1 to 27.0 °C), and peritoneal cavity temperature was 25.0 °C (±0.9 SD, range 18.5 to 27.3 °C) (Table 2). The recovered data show that skipjack spend the majority of their time in the uniform surface-temperature layer between 24 to 28 °C (Fig. S1) but skipjack #6312 occupied significant deeper depths than the other tagged skipjack (Kruskal-Wallis non-parametric ANOVA, $P < 0.005$). Skipjack #7734 and #7729 were released on consecutive days showed similar vertical movement patterns (Fig. S1) and might be travelling in the same schools around FADs.

3.2. Diel oscillation

Daytime and nighttime depths indicated significantly different diel patterns (Fig. 2, S2) with all possible pairwise Kolmogorov−Smirnov and Mann−Whitney W-tests tests significantly different at $P < 0.001$. In daytime, tagged skipjack stayed mostly from the surface to 80 m and at nighttime from the surface to 60 m at ambient temperatures from 24.5 to 26.5 °C (Fig. 3).

3.3. Diving behavior

All skipjack displayed characteristic W-shaped vertical movement patterns and exhibited repetitive bounce diving more pronounced during daytime (Fig. S3). A 2-day portion of the time series is presented for #5585 where the fish displayed dissimilar diel movement patterns (Fig. 4) presumably when unassociated with the FAD (Fig. 4, panel A) and primarily surface activity when associated with the FAD (Fig. 4 panel B).

Table 2 shows daily maximum temperature (SST), minimum temperature and maximum depth experienced by tagged skipjack. The ΔSST analysis

Table 2. Summary of depth, ambient temperature and peritoneal cavity temperature obtained for archival tags deployments on skipjack tuna. Minimum, maximum and mean are provided where SD is the standard deviation.

Archival tag #ID	Depth (m) Min.-max. (mean ± SD)		Ambient temp. (°C) Min.-max. (mean ± SD)		Peritoneal cavity temp. (°C) Min.-max. (mean ± SD)	
	Daytime	Nighttime	Day	Night	Day	Night
#5885	0-223.9 44.4 ± 31.2	0-271.4 29.4 ± 26.9	14.8-26.9 24.5 ± 1.7	13.1-27.0 25 ± 0.8	16.9-28.8 25.2 ± 1.0	19.0-27.3 25.4 ± 0.6
#6312	0-310.6 86.7 ± 43.2	0-301.0 73.2 ± 35.3	13.2-28.3 24.0 ± 2.5	13.3-26.8 24.4 ± 1.6	18.8-27.6 24.7 ± 1.5	18.5-27.1 24.8 ± 1.4
#7753	0-205.8 40.3 ± 21.8	0-105.8 31.4 ± 13.2	14.2-26.1 24.5 ± 0.8	20.9-26.1 24.6 ± 0.4	19.9-26.4 24.7 ± 0.7	23.5-26.4 24.8 ± 0.4
#7734	0-167.4 45.8 ± 19.0	0-136.4 38.5 ± 23.8	17.6-25.5 24.4 ± 0.4	21.3-25.4 24.5 ± 0.4	21.4-26.1 24.7 ± 0.3	23.2-25.4 24.7 ± 0.3
#7729	0-199.4 48.2 ± 25.2	0-181.4 50 ± 25.6	14.4-26.1 24.5 ± 0.8	21.3-25.4 24.5 ± 0.4	20.1-27.0 25.0 ± 0.6	22.5-26.4 24.8 ± 0.6
Total	0-310.6 55.2 ± 36.9	0-301.0 46.1 ± 32.6	13.2-28.3 24.4 ± 1.6	13.1-27.0 24.7 ± 1.1	17.0-28.2 24.9 ± 1	18.5-27.3 25.0 ± 0.9

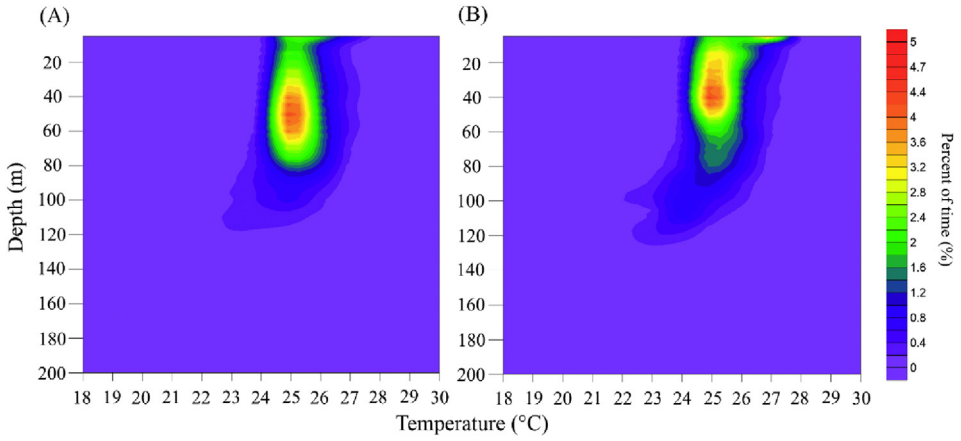

Fig. 3. Aggregated temperature-depth profiles of skipjack showing thermal preferences in daytime (A) and nighttime (B).

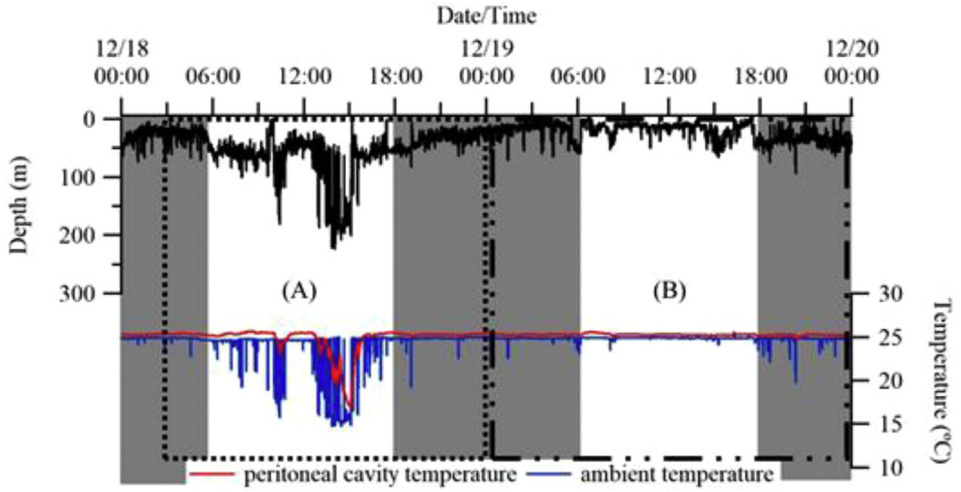

Fig. 4. Depth, peritoneal cavity and ambient temperature records for skipjack tuna (#5885) recorded on 18-19 December 2018. (A) Skipjack showing unassociated repetitive bounce diving behavior; (B) skipjack showing associated repetitive bounce diving behavior.

showed that skipjack spent ~90% of their time at temperatures with 6 °C of the warmest water available (Table 3). Three skipjack (#7753, #7734 and #7729) displayed similar diving patterns with occasional deep forays whereas skipjack #5885 and #6312 exhibited much deeper diving patterns (Fig. 5). Skipjack #6312 descended to 310.6 m (14.2 °C) on 30 March for 30 s with a peritoneal cavity

Table 3. Cumulative percentage of temperature readings from archival tags inserted to skipjack tuna in eastern Taiwan expressed as differences from daily calculated sea surface temperature △SST (°C) by daytime and nighttime.

Archival tag #ID	△SST													
	Time	0	1	2	3	4	5	6	7	8	9	10	11	12	13
#5885	Day	0.2	73.3	87.2	92.1	93.5	94.5	95.5	96.5	97.2	98.3	99.6	100		
	Night	0.8	86.4	93.5	96.5	98.9	99.6	99.7	99.8	99.9	99.9	100			
#6312	Day	0.2	37.9	59.4	71.8	78.8	84.7	89.0	92.7	95.1	96.9	98.4	99.2	99.8	100
	Night	0.6	38.0	58.6	73.8	87.7	92.8	97.2	98.6	99.5	99.6	100			
#7753	Day	0.1	74.2	95.8	97.6	99.0	99.5	99.6	99.7	99.8	99.9	100			
	Night	0.1	72.0	99.6	100										
#7734	Day	0.1	85.9	98.5	99.5	99.7	99.8	99.9	100						
	Night	0.8	84.4	98.6	100										
#7729	Day	0.4	79.7	94.2	97.2	98.5	99.2	99.6	99.7	99.9	100				
	Night	0.5	71.7	95.5	98.8	99.9	100								
Summary	Day	0.2	70.2	87.0	91.6	93.9	95.5	96.7	97.7	98.0	98.8	99.3	99.6	99.8	100
	Night	0.6	70.5	89.2	93.8	95.5	97.4	98.5	99.2	99.7	99.8	99.9	100		
	Total	0.4	70.3	88.1	92.7	94.5	96.2	97.2	98.2	98.6	99.1	99.6	99.7	99.9	100

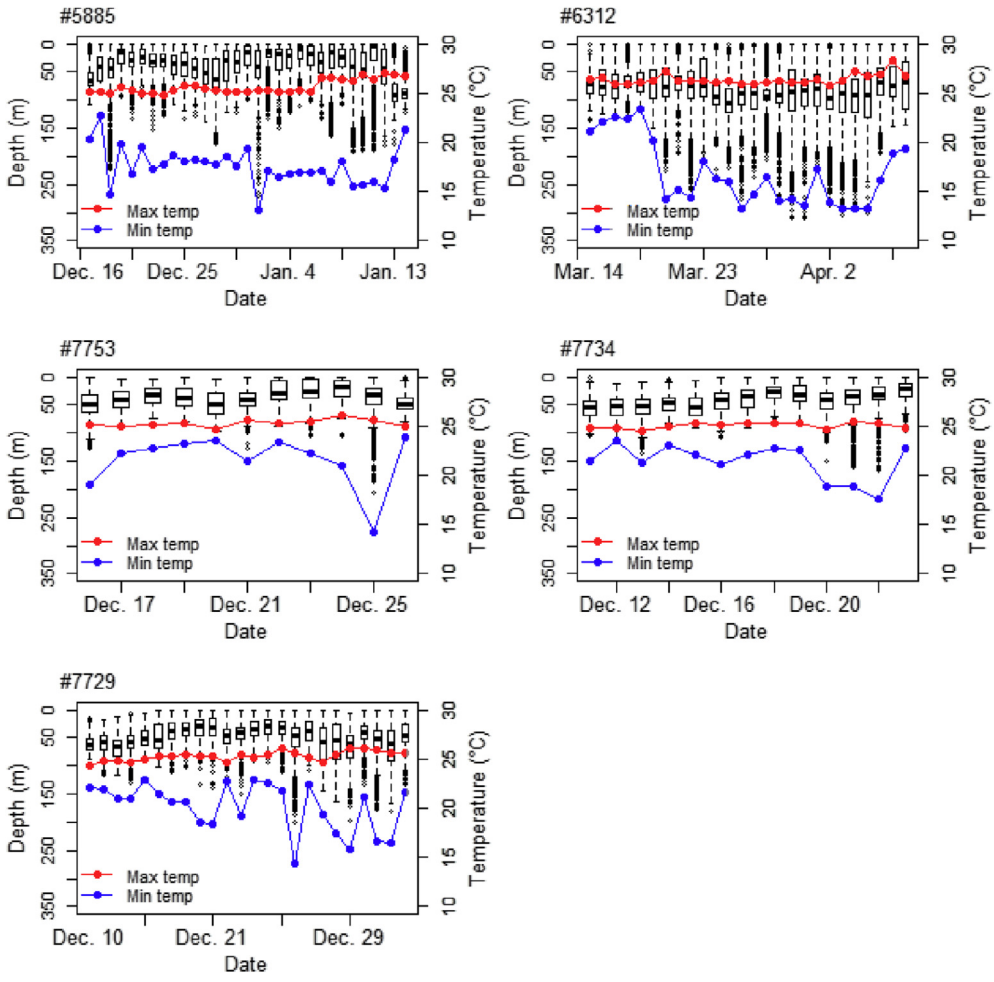

Fig. 5. Minimum and maximum daily temperature (SST) and depths experienced by tagged skipjack where boxplots represent depth. Boxes represent 95%CI, the centerline represents the median and the bars represents maximum and minimum (dots represent outliers).

temperature of 22.3 °C. Before this deep excursion, the fish was at 100 m, then made the deep descent and returned to 100 m in ~6 minutes (Fig. S4). Temperature, salinity and dissolved oxygen near the study site indicated the mixed-layer was at ~100 m at 19° to 21 °C. The salinities from the surface to 200 m were 34.3 to 34.7‰, and dissolved oxygen from the surface to 150 m was 5.5 to 6.7 mg/L, with an extended thermocline to ~500 m at temperatures <10°C with oxygen concentrations of 5.5 to 3.6 mg/L (Fig. 6).

4. Discussion

We recovered five immature skipjack ranging in sizes from 41-44 cm FL at release which indicated that the released skipjack probably resumed normal feeding activities after surgical implantation of the archival tag and may have exhibited schooling behavior. These fish are all about one year old [29] and are called “Hatsu Gatsuwo” which means “first and fresh bonito of the year” [13]. This is the first study to archival tag juvenile skipjack in the eastern Taiwan area to gain information on thermal habitat and behaviors around FADs. Our low tag recovery rate (2.4%) suggests a high post-release mortality but this low rate could also be consistent with large population sizes, dispersal, tag loss or uncooperative fishers.

4.1. Resident time around FADs

Schaefer and Fuller [24] and Matsumoto et al. [18] indicated skipjack tuna tagged around surface FADs stayed around for only a few days and then left. However, in our study, the days at-liberty near FADs for tagged skipjack were ~11-31 days, although the details about fine-scale horizontal movements were not able to be resolved with light and (or) SST based geolocations. Weng et al. [30]

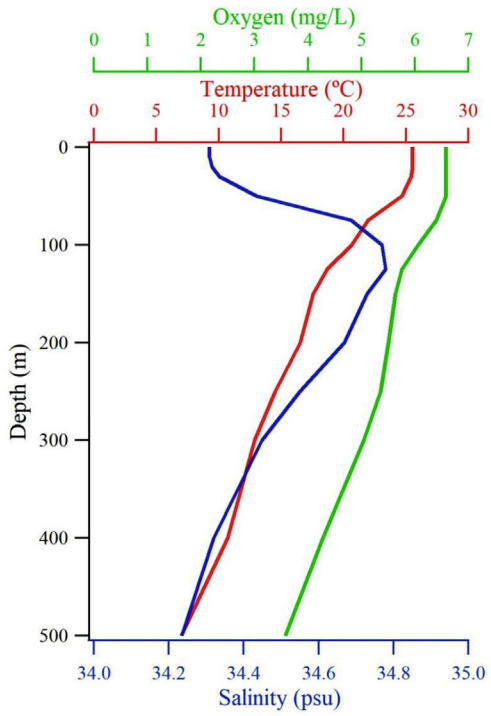

Fig. 6. Temperature, salinity and dissolve oxygen around Green Island. Data source: NOAA National Oceanographic Data Center (http://www.nodc.noaa.gov) (2018/12).

indicated juvenile yellowfin tuna stayed at subsurface FADs for ~31 days. For skipjack #6312, the fish tagged at FAD2 and was recaptured at FAD1 (Fig. 1) after 26 days and indicated skipjack may use the FAD network for orientation and/or socialization purposes [20]. Subsurface FADs have been used to aggregate tunas off southwestern Taiwan [30,31] and fishes may stay at the FADs until the conditions are unsuitable [8].

4.2. Vertical movements

Schaefer and Fuller [24] defined four behavioral types for skipjack: (1) associated, (2) unassociated with floating objects, (3) deep diving behavior and (4) surface-oriented behavior. When skipjack are near floating objects, they make frequent deep dives primarily during daytime and occasionally at nighttime. Unassociated with floating objects, skipjack make significantly deeper dives diving during daytime than nighttime. Matsumoto et al. [18] also reported skipjack diving correlated with proximity to FADs with shallow diving associated near FADs and increasingly deeper dives the further away from FADs. Skipjack tuna do not possess a swim bladder [4] and during rapid directional changes whilst diving, not having to adjust for accompanying pressure changes could provide advantages to increase prey encounter rates without extensively increasing linear travel distance and expending energy [12]. As previous studies have reported, the W-shaped movement patterns during daytime are an optimal search strategy to increase prey encounters [27] and these behaviors and physiological adaptations confer a foraging strategy for tunas [20,31,32].

4.3. Thermal habitat

Kiyofuji [13] discussed northward migration of skipjack tuna (size range: 38 to 51 cm FL) in the western Pacific Ocean. The results indicated that skipjack tuna in the Kuroshio current did not enter water cooler than 18°C. Our results, however, indicated that immature skipjack tuna in eastern Taiwan can visit temperatures of as low of 13.1°C on an ephemeral basis. The temperature preference of tagged immature skipjack (Fig. 4) were mostly between 18-28°C in daytime (90% of time above 24°C) and 22-27°C at nighttime (94% of time above 24°C). These findings are similar with [18] who indicated skipjack mostly stayed at 16-27°C in daytime and at 24-30°C in nighttime and [7] provided a range of 22-30°C. Schaefer and Fuller [24] reported adult skipjack (53-73 cm FL) stayed at temperatures from 20-26°C (mostly at 25°C) and the deepest dive recorded was 596 m where the ambient temperature was 7.7°C. Dizon et al. [9] reported temperature tolerances of 15-33°C based on tank experiments. The length at maturity of skipjack tuna was estimated to be about 46 cm FL [28] and collectively based on previous tagging studies, suggests that deeper diving is probably correlated with body size and lack of structure. The skipjack tuna in our research were young of year (YOY).

Gooding et al. [10] used captive skipjack to estimate threshold oxygen concentrations of 4.0 mg/L whereas [9] recorded skipjack swimming behavior under high (4.1 mg/L) to low oxygen (2.1 mg/L) environments that correlated with reduced swim speeds for fish 44-45 cm FL. Cayré et al. [7] monitored skipjack (41-52 cm FL) near the Comoros Archipelago and reported oxygen concentrations at 150-200 m were 3.2-3.5 mg/L. Matsumoto et al. [18] reported skipjack (36-65 cm FL) usually occupied depths less than 100 m with oxygen concentrations at 2.7-3.2 mg/L. Therefore, it does not appear oxygen concentrations were limiting dive behavior in this study (Fig. 6).

Oxygen concentration is one of four principal factors (prey availability, temperature, hydrostatic pressure, dissolved oxygen) that restrict the

distribution of pelagic fishes [5]. By examining the behavioral and thermal niche that define immature skipjack vertical habitat, this study provides important information to improve ecological understanding of thermal niche and provide useful data for inclusion into stock assessments.

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Appendix.

Table S1. Tagging numbers for skipjack tuna implanted with conventional tags and archival tags during 2017 to 2020.

Survey year	Conventional tag conducted number	Archival tag implanted number	Conventional tag recaptured number (%)	Archival tag recaptured number (%)
2017	33	20	0	0
2018	138	78	3	1
2019	419	78	16	4
2020	134	35	2	0
Total	724	211	21 (3%)	5 (2%)

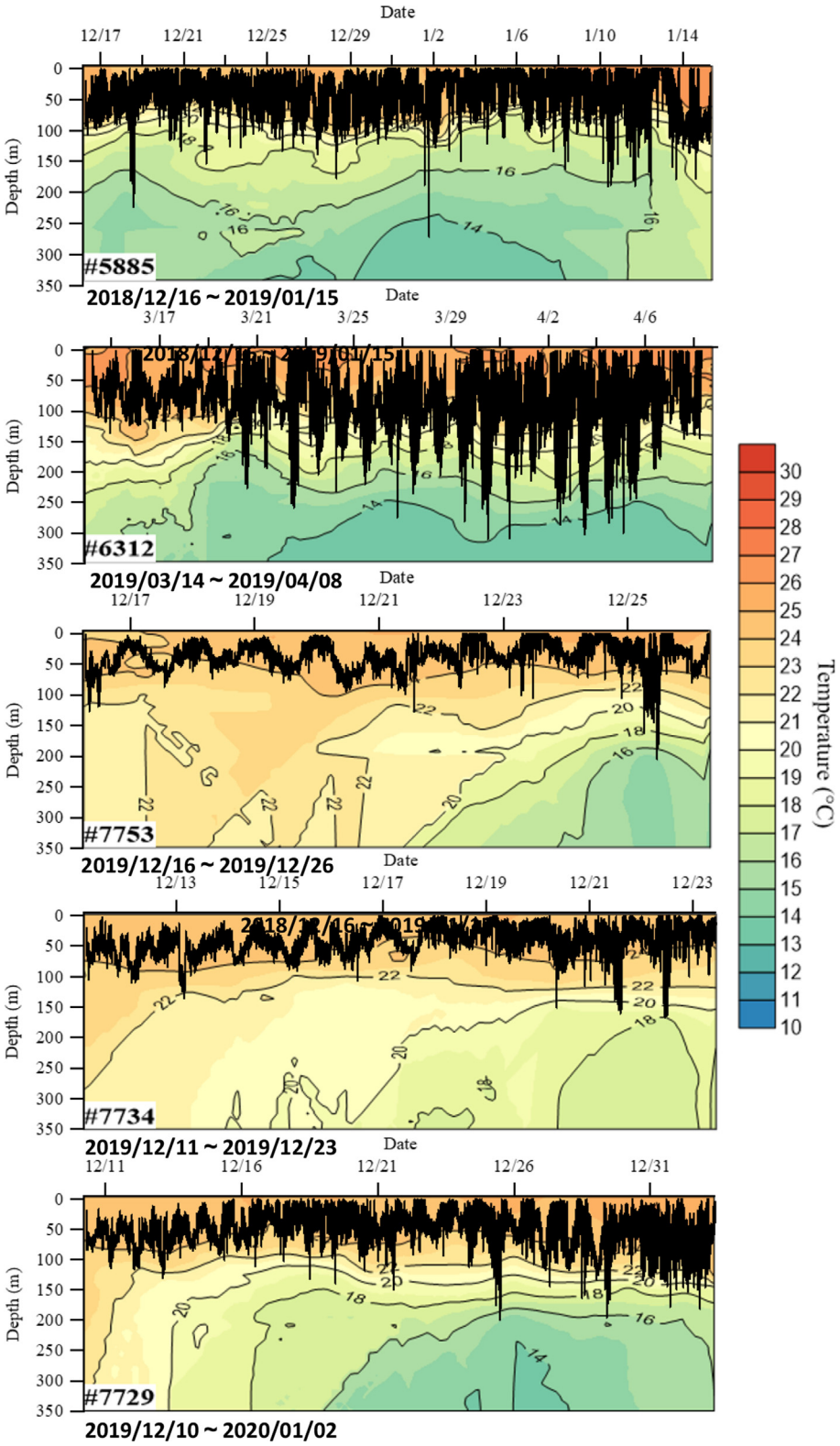

Fig. S1. Time series of depth and temperature diving patterns for tagged skipjack.

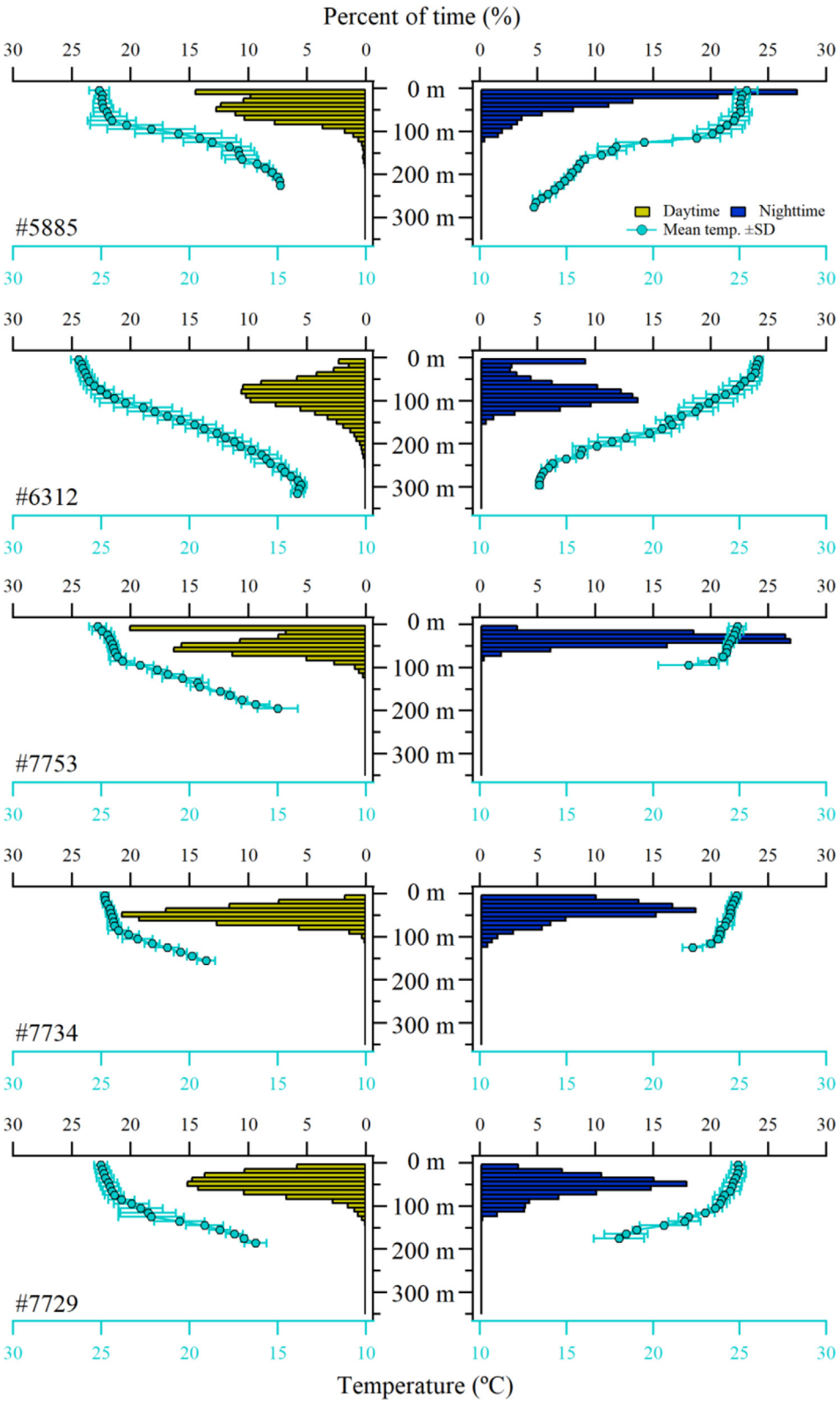

Fig. S2. Depth distribution of skipjack for daytime (yellow bar) and nighttime (blue bar) with ambient water temperature profiles.

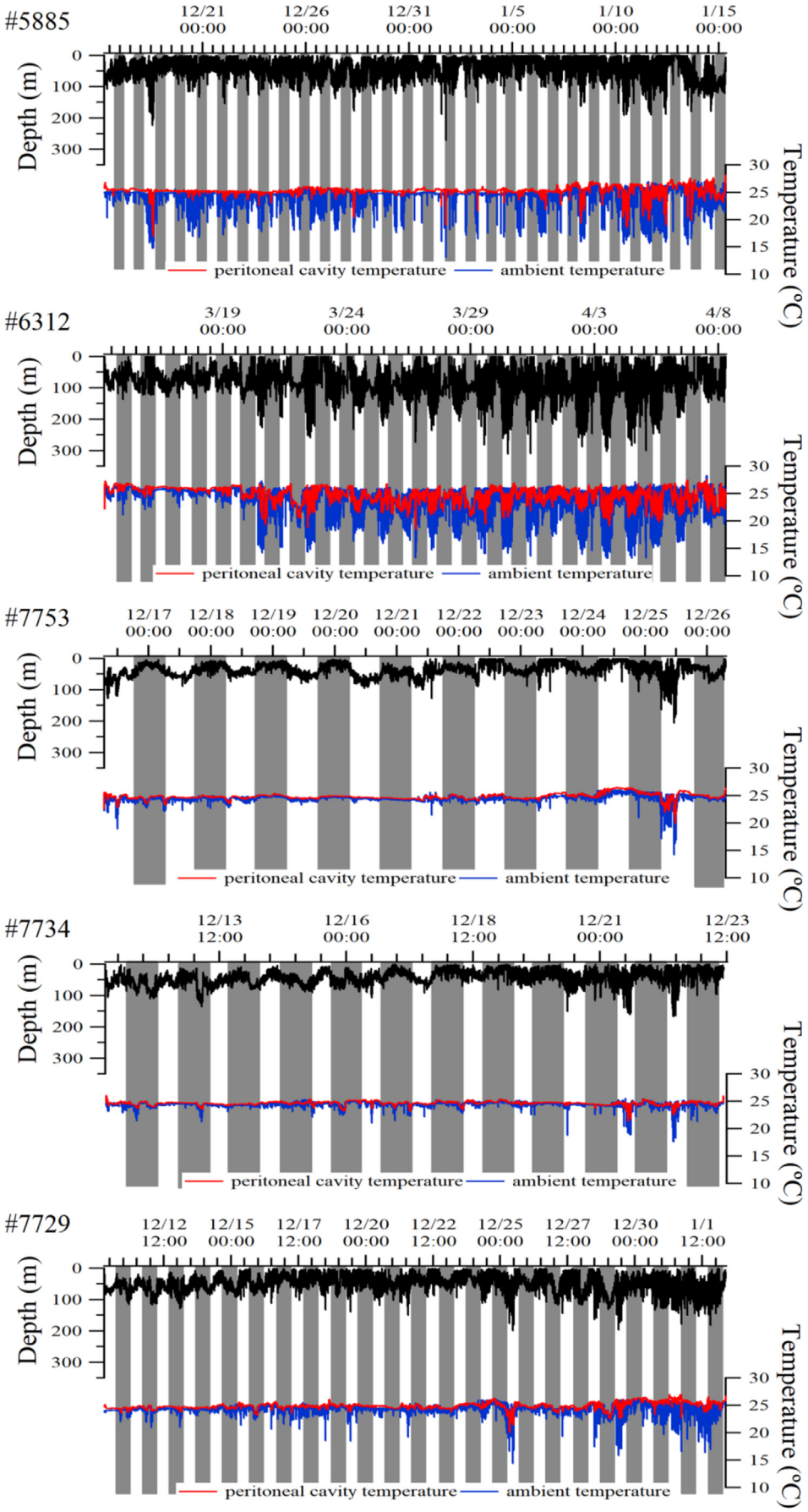

Fig. S3. Time series of depth (black), peritoneal cavity temperature (red) and ambient temperature (blue) for skipjack during daytime and nighttime (grey shading indicates nighttime).

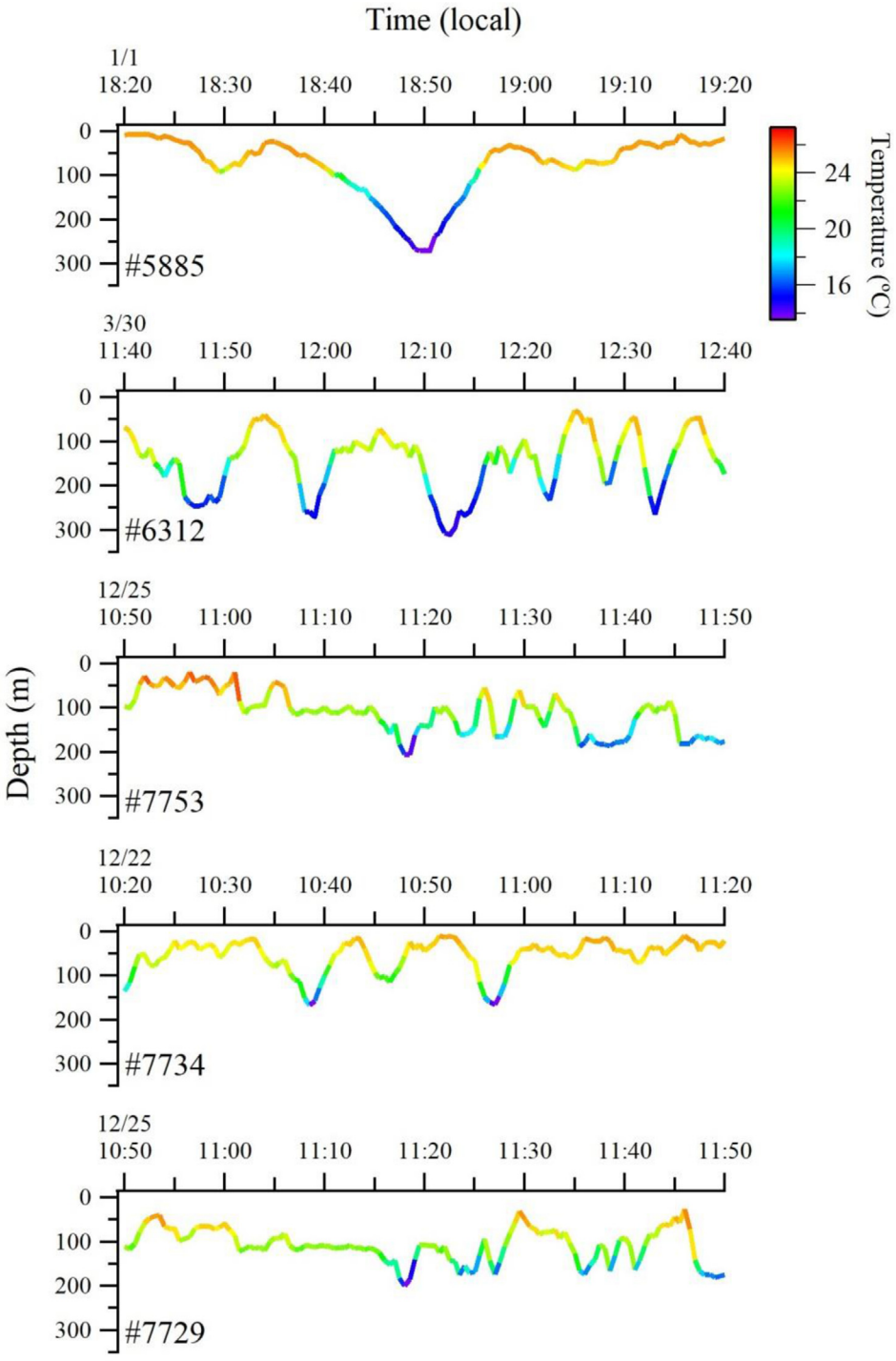

Fig. S4. Depth and temperature data by skipjack exhibiting occasional episodes of deep excursions.

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