



Two-way habitat use between reefs and open ocean in adult greater amberjack: evidence from biologging data

Kazuki Tone^{1,*}, Wei-Chuan Chiang², Hsin-Ming Yeh³, Sheng-Tai Hsiao³, Chun-Huei Li³, Kazuyoshi Komeyama⁴, Kensuke Kudo⁵, Takamasa Hasegawa^{5,6}, Takashi Sakamoto⁷, Itsumi Nakamura¹, Yoshitaka Sakakura⁵, Ryo Kawabe^{1,5}

¹Institute for East China Sea Research, Organization for Marine Science and Technology, Nagasaki University, 1551-7 Taira-machi, Nagasaki 851-2213, Japan

²Eastern Marine Biology Research Center, Fisheries Research Institute, Council of Agriculture, 22 Wuchuan Road, Taitung, Chenggong 961, Taiwan

³Fisheries Research Institute, Council of Agriculture, 199 Hou-Ih Road, Keelung 20246, Taiwan

⁴Faculty of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido 041-8611, Japan

⁵Graduate School of Fisheries and Environmental Sciences, Nagasaki University, 1-14 Bunkyo-machi, Nagasaki 852-8521, Japan

⁶Iki Fisheries Extension Center, Nagasaki Prefecture Iki Development Bureau, 1290 Ishida-cho, Iki, Nagasaki 811-5215, Japan

⁷Department of Marine Biosciences, Tokyo University of Marine Science and Technology, 4-5-7 Konan, Minato, Tokyo 108-8477, Japan

ABSTRACT: We investigated the relationships between vertical movements and both oceanographic features and physiological factors in greater amberjack *Seriola dumerili*, which is a reef-associated predator in the East China Sea. *S. dumerili* in the coastal waters of eastern Taiwan were equipped with archival tags or pop-up satellite archival tags that recorded depth and temperature, resulting in a dataset covering a total of 1331 d from 12 individuals. To classify the vertical movement patterns of *S. dumerili*, we performed a hierarchical cluster analysis for the depth profile. We observed multiple vertical movement patterns. Around topographic features, *S. dumerili* showed short-step dives (averaging <35 m) during both the daytime and nighttime. In contrast, *S. dumerili* in offshore areas showed diel vertical movements. *S. dumerili* occasionally performed frequent dives to approximately 150 m throughout the day. These movements may be related to foraging behaviors associated with changes in water depth. We further analyzed the response of the peritoneal cavity temperature to variations in the ambient temperature in 7 *S. dumerili* with archival tags. The peritoneal cavity temperatures fluctuated according to the ambient temperature changes, indicating that the vertical movement of *S. dumerili* is limited by physiological constraints for the maintenance of body temperature. Together, our results indicate that the vertical movement of *S. dumerili* may be affected by the trade-off between foraging and thermoregulation.

KEY WORDS: Greater amberjack · *Seriola dumerili* · Vertical movement pattern · Behavioral thermoregulation · Electronic tagging · East China Sea

1. INTRODUCTION

The ocean has a large vertical variation of physical environments (e.g. temperature, light level, oxygen concentration) and biological environments (e.g. pri-

mary production), and marine fishes can easily experience different environments by moving vertically over distances of several hundred meters. The knowledge of how and why marine fishes perform vertical movements would thus contribute to our understand-

*Corresponding author: kazu.bz.kazu@gmail.com

ing of the ecology of marine fishes (Andrzejaczek et al. 2019). Given that large marine predators exert top-down control on marine ecosystems (Heithaus et al. 2008, Estes et al. 2011), it is especially important to understand the vertical movement patterns of predatory fishes and the factors that contribute to vertical movement patterns; these behaviors and factors have interested researchers for several decades (e.g. Carey & Scharold 1990). Some of the functions that have been suggested to be involved in the vertical movement of marine predatory fishes (and are not mutually exclusive) include foraging, mating, locomotion cost-saving, thermoregulation, and navigation (Weihs 1973, Carey & Scharold 1990, Klimley 1993, Willis et al. 2009). However, despite the great geographic variation of topographic features in oceans, few studies have examined how the vertical movement of marine predatory fishes may differ between coastal and pelagic habitats in relation to topographic features.

Improvements in electronic tagging technology have allowed the recording of the behavior, internal states, and ambient environments of free-living marine predatory fishes (Block et al. 2011, Hussey et al. 2015). However, analyses of vertical movements become more difficult when there is a lack of clear boundaries between each vertical movement, or when different functions overlap in the same vertical movement (Andrzejaczek et al. 2019). For example, several vertical movements of marine predatory fishes can change in frequency and amplitude over time (e.g. Kitagawa et al. 2000, Shepard et al. 2006). The vertical movement patterns of a variety of marine predatory fishes occasionally change dramatically during their migrations, such as reproductive migration (Block et al. 2001, Tone et al. 2022) and coast-to-offshore migration (Stehfest et al. 2014, Coffey et al. 2017). These studies indicated great variability in the vertical movements of marine predatory fishes and thus complexity in the classification of movement patterns. Cluster analyses have been used to objectively classify these vertical movement patterns to determine depth profiles (Jorgensen et al. 2012, Andrzejaczek et al. 2018, Furukawa et al. 2020). Although a cluster analysis for a depth profile is useful for understanding the vertical movement patterns of marine predatory fishes and the driving factors of vertical movements, the use of cluster analyses has been limited to use in some epipelagic fishes (e.g. sharks, Jorgensen et al. 2012, Andrzejaczek et al. 2018; yellowtail *Seriola quinqueradiata*, Furukawa et al. 2020).

Vertical movements of marine predatory fishes are driven by physiological and ecological processes. Since the water in which fish live has high thermal

conductivity, the ability of fish to maintain their body temperature during vertical movement is a factor that can be used to determine their vertical distribution and the duration of vertical movement. For example, in fishes with low physiological thermal tolerance, such as ectothermic dolphinfish *Coryphaena hippurus* (Furukawa et al. 2015), the duration of vertical movement below the thermocline is limited to a short period of time. Bigeye tuna *Thunnus obesus*, an endothermic fish (Holland et al. 1992), and swordfish *Xiphias gladius*, a regional endothermic fish (Stoehr et al. 2018), both have high physiological thermal tolerance and can remain below the thermocline for longer periods of time. Thus, the analysis of thermal responses using continuous data of body temperatures (e.g. peritoneal cavity and muscle temperatures) of marine fishes during the vertical movement of the fish can help us understanding the effects of water temperature changes with depth on the vertical distribution and movement of marine fishes (e.g. Holland et al. 1992). Even in ectothermic fishes, it is suggested that the thermal responses vary by species and body mass (Nakamura et al. 2020, Watanabe et al. 2021). Although most species of fish are ectotherms, reports on the temperature responses of ectotherms have been limited to a few species.

The greater amberjack *Seriola dumerili* is a commercially valuable large reef-associated fish with a circumglobal distribution from tropical to temperate waters (Gold & Richardson 1998, Nakada 2008), and it is the largest carangid with a maximum reported size of 190 cm total length and a maximum recorded body weight of 80.6 kg (Froese & Pauly 2009). Although this species is considered an opportunistic feeder, a difference in prey-species preference in adult greater amberjack was observed among samples collected from different locations in the central Mediterranean Sea; one specimen consumed mostly pelagic organisms (Sley et al. 2016) and another consumed both pelagic and demersal fishes (Andaloro & Pipitone 1997). These reports imply that there may be multiple foraging patterns in the vertical and horizontal movements of greater amberjack.

Several studies using electronic data loggers and transmitters showed that greater amberjack spend the majority of their time below the thermocline and rarely inhabit the surface mixed layer (Murie et al. 2011, Jackson et al. 2018, Tone et al. 2022), but a detailed analysis of the vertical movement patterns of these fish has not yet been conducted. The majority of the research on the behavior of adult greater amberjack in the field has been conducted near a coast (Murie et al. 2011, Jackson et al. 2018), and adult

greater amberjack had been thought to be associated primarily with topographic features and to rarely migrate long distances. However, our recent biologging study in the East China Sea (ECS) revealed that adult greater amberjack inhabit more diversified habitats during the pre- and post-spawning periods than previously thought (Tone et al. 2022). Interestingly, Tone et al. (2022) showed that greater amberjack migrate offshore at bottom depths deeper than 1000 m, far beyond the usual depth range (50–200 m), suggesting that these fish do not always aggregate on bottom structures such as natural reefs. Based on these results, we speculated that adult greater amberjack may have 2 types of vertical movement patterns: one associated with the topographic features in coastal habitats and another that is not associated with topographic features in offshore habitats. Tracking the vertical movements of adult greater amberjack, which has multiple feeding behaviors and migrates between different oceanographic environments, will therefore provide new insights into the relationships between the vertical movements of marine predatory fishes and both oceanographic features and behavioral factors.

We conducted the present study to clarify the relationships between vertical movements and both oceanographic features and physiological factors in greater amberjack, which is one of the top predators in the ECS. To accomplish this, we used published data of free-swimming greater amberjack (Tone et al. 2022) and objectively classified the vertical movement patterns of greater amberjack by performing a cluster analysis for the depth profile. We also analyzed the peritoneal cavity temperature of tagged greater amberjack during their vertical movement to gain a greater understanding of the response of the peritoneal cavity temperature to variations in the ambient temperature. Finally, we examined spatial and temporal variations in the vertical movement patterns of greater amberjack, and we discuss the influence of oceanographic and physiological factors on these variations.

2. MATERIALS AND METHODS

2.1. Field experiments

Greater amberjack were captured by commercial hand-line fishing in coastal waters (22.8–23.1°N, 121.4°E) off Green Island in southeastern Taiwan in November 2016 and November 2017. Of these, 22 fish with fork lengths of 68–101 cm were selected for

tagging, and all tagged fish were assumed to be mature based on the estimated size at maturity (Harris et al. 2007). The tagging deployment and tag specification details are described by Tone et al. (2022).

We used either a temperature–depth recorder (TDR-Mk9; Wildlife Computers) or a pop-up satellite archival tag (MiniPAT; Wildlife Computers). The TDR-Mk9 recorded depth (range: 0–1700 m; resolution: $0.5 \text{ m} \pm 1.0\%$) every 1 s, external and internal temperatures (-40 to $+60^\circ\text{C}$; $0.05 \pm 0.1^\circ\text{C}$) every 5 s, and light measurements (470 nm; logarithmic range: 5×10^{-12} to $5 \times 10^{-2} \text{ W cm}^{-2}$) every 30 s. The MiniPAT recorded depth (0–1700 m; $0.5 \text{ m} \pm 1.0\%$), ambient temperature (-40 to $+60^\circ\text{C}$; $0.05 \pm 0.1^\circ\text{C}$), and light measurements (470 nm; logarithmic range: 5×10^{-12} to $5 \times 10^{-2} \text{ W cm}^{-2}$) at time intervals of 3 or 5 s for each tag (Table 1). Each of the fish was also tagged with 2 conventional plastic dart tags with contact information placed at the base of the second dorsal fin on both the right and left sides. Each tagging procedure never exceeded 5 min.

The MiniPAT detaches following a pre-programmed deployment duration and then transmits its position and a portion of archived data via Argos satellites. However, only low-resolution, summarized data are transmitted to the satellites due to the limited battery capacity and restricted transmission capability. Such summarized data may conceal key behaviors such as foraging and spawning that occur at finer timescales (Fisher et al. 2017). Therefore, a physical recovery of the MiniPAT was required to access the dataset of the entire record and to understand the details of vertical movements of the greater amberjack. The recovery of the detached MiniPATs at sea was attempted by using a CLS RGX-134 digital receiver with an RG-58 direction-finding antenna (CLS America), following the procedure described by Fisher et al. (2017).

2.2. Data management and analysis

Seven of the TDR-Mk9s and 5 of the MiniPATs were physically recovered (Table 1). Of these, 2 tags (GA10A and GA24A) stopped recording due to mechanical problems (on 14 August and 8 March 2018). We thus obtained data in durations from 7 to 273 d (mean: 111 d) (Table 1). We plotted and analyzed the time-series data of depth and temperature using R 4.1.0 software (R Core Team 2021) and IGOR Pro software (ver. 6.1; WaveMetrics). The release and recapture days were removed from the analyses because there were fewer data points for these days compared to the other days, which would have made

Table 1. Tag type, sex, data duration, sampling interval, fork length at tagging/recapture, body weight at tagging/recapture, tagging position, and recapture/pop-off position for all analyzed greater amberjack. BW: body weight, D: depth, F: female, L: light, M: male, NA: not applicable data, P: MiniPAT, T: temperature, TD: TDR-Mk9

Fish ID	Tag type	Sex (M/F)	Analysis period (duration, d)	Sampling interval (s)	Fork length (cm)		BW at recapture (kg)	Tagging position		Recapture position or pop-off position	
					Tagging	Recapture		Lat. °N	Long. °E	Lat. °N	Long. °E
GA01P	P	NA	26 Nov 2016 to 2 Dec 2016 (7)	DTL: 3	80	NA	NA	23.063	121.417	24.558	121.931
GA02P	P	M	26 Nov 2016 to 15 Feb 2017 (82)	DTL: 3	68	70.5	5.2	23.063	121.417	22.896	121.417
GA07A	TD	M	15 Nov 2017 to 8 Feb 2018 (86)	D:1, T:5, L:30	87	88	9	22.781	121.433	22.432	121.448
GA09A	TD	M	15 Nov 2017 to 17 May 2018 (184)	D:1, T:5, L:30	72	76.5	7.4	22.896	121.426	22.897	121.397
GA10A	TD	F	15 Nov 2017 to 14 Aug 2018 (273)	D:1, T:5, L:30	70	81.5	8.3	22.896	121.426	22.897	121.427
GA11A	TD	M	15 Nov 2017 to 21 Dec 2017 (37)	D:1, T:5, L:30	82	82	7	22.896	121.426	22.897	121.427
GA13P	P	F	15 Nov 2017 to 9 Dec 2017 (25)	DTL: 5	96	98	11	22.896	121.418	22.947	121.586
GA14P	P	F	15 Nov 2017 to 13 May 2018 (180)	DTL: 5	97	104.5	18	22.896	121.417	22.937	121.482
GA15P	P	F	15 Nov 2017 to 22 Jan 2018 (69)	DTL: 3	87	88.7	10.1	22.897	121.418	22.678	121.473
GA20A	TD	M	23 Nov 2017 to 19 Apr 2018 (148)	D:1, T:5, L:30	86	88	9.3	22.896	121.418	22.837	121.425
GA23A	TD	F	23 Nov 2017 to 5 Apr 2018 (134)	D:1, T:5, L:30	98	102	13.9	22.886	121.412	22.897	121.415
GA24A	TD	M	23 Nov 2017 to 8 Mar 2018 (106)	D:1, T:5, L:30	101	106	16.9	22.945	121.398	22.983	121.383

it difficult to analyze the dataset on a daily scale. To visualize the vertical temperature structure experienced by the tagged fish, we constructed daily vertical ambient temperature profiles by estimating the mean ambient temperature at 10 m depth intervals.

To objectively define the daily vertical movement patterns, we performed a hierarchical cluster analysis for the depth profile of each individual fish. Hierarchical cluster analyses have been used to distinguish the vertical movement patterns of several marine fishes (e.g. Jorgensen et al. 2012). In the present study, we defined a 'dive' as beginning when a tagged fish descended >10 m from its mean daytime or mean nighttime depth and ending when the fish subsequently ascended >10 m from each mean depth. We defined 'dive step' as the vertical distance from the starting point of the dive to the greatest depth reached during each dive, and we defined 'dive duration' as the time elapsed during each dive.

We calculated the daily behavioral components (i.e. mean depth, standard deviation of depth, maximum depth, minimum depth, mean dive step, and mean dive duration) for each individual, and these components were used in the hierarchical cluster analysis. The daily behavioral components were analyzed for each individual at each of 3 diel time periods: daytime (sun above the horizon), twilight (sun between 0 and 6° below the horizon, corresponding to civil twilight), and nighttime (sun lower than 6° below the horizon). The 3 diel time periods were determined by the altitude of the sun, calculated using the estimated daily location data of each fish.

Hierarchical cluster analysis was performed on the pooled data of all individuals using the 'City block' measure and Ward's method (using the 'hclust' function in R). Although the 'Euclidian' distance measure appears to be the most commonly used distance measure for a hierarchical clustering analysis, since distance is computed in multi-dimensional space, the Euclidian measure is inappropriate if the dimensions are of differing scales, such as in the vertical migration of fish (Jorgensen et al. 2012). We therefore calculated the 'City block' distance, also a very commonly used measure for hierarchical clustering analyses; it is simply the average distance along each dimension, and it is more appropriate for discrete data.

In addition, Ward's method tended to produce compact groups of well-distributed sizes and was the least sensitive to small outlier groups among several methods (Fig. S1 in the Supplement, www.int-res.com/articles/suppl/m699p135_supp.pdf). The number of vertical movement patterns (i.e. clusters) was determined by a visual inspection of the behavioral data

and the dendrogram. The difference value of depth (i.e. the vertical swimming speed) was computed for 5 s time windows.

The daily location data of each fish were established from recorded light data with the use of a hidden Markov model built by the tag manufacturer (WC-GPE3; Wildlife Computers). The details of the horizontal movements of these tagged greater amberjack in the ECS were reported by Tone et al. (2022).

2.3. Analyses of the fish peritoneal cavity temperature

To examine the response of the peritoneal cavity temperature of greater amberjack to variations in the ambient water temperature, we used a heat-budget model (Holland et al. 1992). The change in the peritoneal cavity temperature of the greater amberjack is proportional to the difference between the ambient water temperature and the peritoneal cavity temperature, and can be calculated using the following equation:

$$(dT_b(t))/dt = k(T_a(t) - T_b(t)) + \dot{T}_m + \varepsilon \quad (1)$$

where $T_a(t)$ is the ambient water temperature ($^{\circ}\text{C}$) as a function of time t (min), $T_b(t)$ is the peritoneal cavity temperature of the fish ($^{\circ}\text{C}$) as a function of time t (min), k is the whole-body heat-transfer coefficient ($^{\circ}\text{C min}^{-1} \text{ } ^{\circ}\text{C}^{-1}$), \dot{T}_m is the rate of temperature change due to internal heat production ($^{\circ}\text{C min}^{-1}$), and ε is white Gaussian noise. Since k is known to vary with the ambient temperature (Holland & Sibert 1994, Kitagawa & Kimura 2006), we examined 2 different possibilities for the value of k :

$$(A) \quad k = \text{a constant value,}$$

$$(B) \quad k = \begin{cases} k_1; T_a(t) < T_b(t) \\ k_2; T_a(t) \geq T_b(t) \end{cases},$$

where Model (B) assumes different whole-body heat-transfer coefficients k between an increase and a decrease in the peritoneal cavity temperature; k_1 is at cooling, and k_2 is at warming. We estimated the parameters for each model by using a maximum-likelihood method. The 'optim' function in R was used to maximize the likelihood by adjusting all parameters. To select the best-fit model, we used the Bayesian information criterion (BIC; Schwarz 1978) of models (A) and (B). The model that had the lowest BIC value was regarded as the more parsimonious model. To investigate the contribution of \dot{T}_m to the

changes in T_b , we compared the BIC value between the model with \dot{T}_m and the model without \dot{T}_m .

3. RESULTS

3.1. Vertical movement pattern

The clustering of daily depth profiles (a total of 1331 d) from all pooled individuals (7 to 273 d) (Table 1) allowed us to distinguish 5 clusters representing 5 vertical movement patterns (Fig. 1A). The dendrogram shows the relative distances between the vertical movement patterns, representing differences in the daily depth profiles. To visualize the diurnal changes in the depth profile of each vertical movement pattern, we calculated the characteristics (maximum, median, 25th–75th percentile, and 2.5th–97.5th percentile values) of vertical distribution and diving behavior at 1 h intervals from 00:00 to 24:00 h Taiwan Standard Time (UTC + 8 h) (Fig. 1B–D).

Cluster 1 was characterized by the fish swimming in a shallower zone compared to the other clusters during all periods of the daytime, twilight, and nighttime (Fig. 1B). The mean \pm SD depths of this cluster were 64.2 ± 16.3 m in the daytime, 60.7 ± 10.1 m in the twilight, and 61.2 ± 10.3 m in the nighttime. This cluster was also characterized by having the shortest step dives (daytime: 20.2 ± 27.0 m; twilight: 9.0 ± 7.0 m; nighttime: 8.7 ± 8.1 m) of all clusters. This cluster accounted for only 6.8% of the total period.

Cluster 2 was distinguished by frequent periodic dives to ca. 150 m during all periods of daytime, twilight, and nighttime. The mean \pm SD depth and dive step of this cluster during the daytime (nighttime) were 127.3 ± 24.6 (112.4 ± 24.1) m and 44.9 ± 44.5 (40.8 ± 46.2) m, respectively (Table 2). The mean \pm SD depth and diving distance at twilight for this cluster were 129.8 ± 30.6 and 40.5 ± 40.4 m, respectively. Cluster 2 was also characterized by the deepest dive (up to 521.0 m) of all of the modes (Table 2, Fig. 1B). This cluster accounted for only 4.9% of the total period.

Cluster 3 had common characteristics with diel vertical movements (DVMS, i.e. going to deeper depths during the daytime and to shallower depths during the nighttime). The mean \pm SD dive step in cluster 3 during the daytime was 44.9 ± 44.5 m (Table 2). As a result, tagged fish in cluster 3 reached a depth of approximately 150–250 m during the daytime (Fig. 1B). During the nighttime (and twilight), the mean \pm SD dive step in cluster 3 was 26.0 ± 33.2 (29.0 ± 34.6) m. Cluster 3 accounted for 24.1% of the total period. In clusters 2 and 3, the nighttime vertical swimming

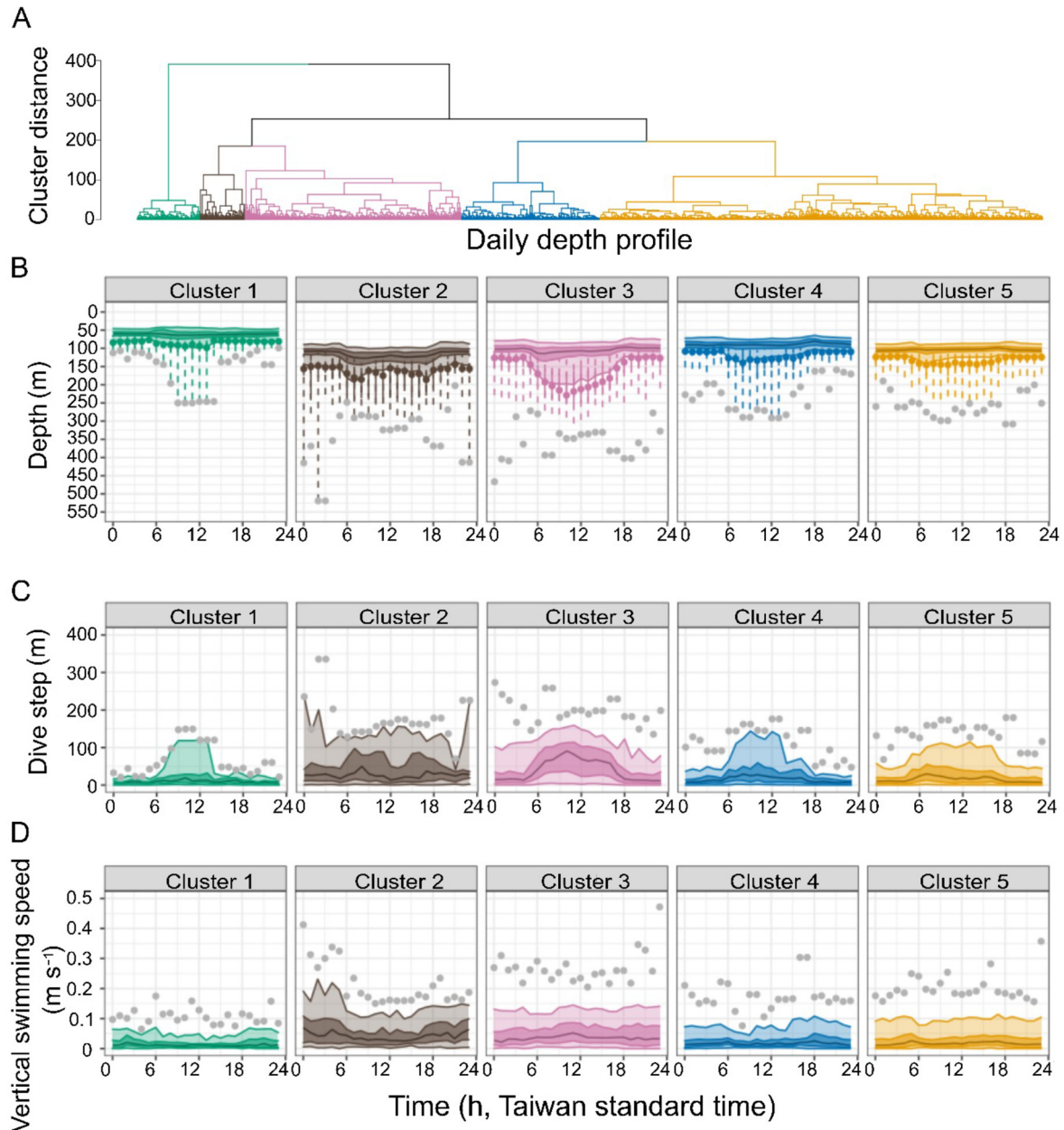


Fig. 1. (A) Dendrogram of greater amberjack vertical behavior, determined from a hierarchical cluster analysis of diving patterns. (B) Hourly changes in the overall swimming depth; the median (solid line), 25th–75th percentile (darker shading) and 2.5th–97.5th percentile (lighter shading), and the dive depths as the median (circle), max. (gray circle), 25th–75th percentile (vertical solid line) and 2.5th–97.5th percentile (vertical dashed line) in each cluster. (C) Hourly changes in dive step; the max. (gray circle), 25th–75th percentile (darker shading), and 2.5th–97.5th percentile (lighter shading). (D) Hourly changes in vertical swimming speed; the max. (gray circle), 25th–75th percentile (darker shading) and 2.5th–97.5th percentile (lighter shading). The data were pooled from all individuals. Taiwan standard time is UTC + 8 h

speeds (cluster 2: 0.064 ± 0.055 m s⁻¹, cluster 3: 0.047 ± 0.039 m s⁻¹) were 2–3 times faster than the vertical swimming speeds of the other clusters.

Cluster 4 showed behavior with characteristics of both cluster 1 and cluster 3 (i.e. short-step dives and DVMS) (Fig. 1B). The total frequency of cluster 4 was 15.0% (Table 2).

Cluster 5 had a vertical movement pattern that was similar to that of cluster 4, but the swimming was at a slightly deeper zone (daytime: 105.1 ± 15.0 m, twilight: 101.6 ± 8.9 m, nighttime: 104.2 ± 11.3 m) and showed slightly longer step dives than cluster 4. The mean \pm SD dive step during the daytime (nighttime) for cluster 5 was 32.8 ± 31.4 (15.2 ± 18.7) m (Table 2).

Table 2. Frequency, overall swimming depth, dive step, vertical swimming speed, and ambient temperature for all greater amberjack behavioral clusters. Data are mean \pm SE

Cluster	Frequency (%)	Swimming depth (m) (range)		Dive step (m) (max.)		Vertical swimming speed (m s ⁻¹) (max.)		Ambient temperature (°C) (range)	
		Daytime	Nighttime	Daytime	Nighttime	Daytime	Nighttime	Daytime	Nighttime
1	6.8	64.2 \pm 16.3 (27.1–250.1)	61.2 \pm 10.3 (32.8–144.9)	20.2 \pm 27.0 (149.4)	8.7 \pm 8.1 (60.3)	0.014 \pm 0.015 (0.17)	0.023 \pm 0.023 (0.13)	22.2 \pm 1.14 (13.8–26.2)	0.020 \pm 0.021 (0.16)
2	4.9	127.3 \pm 24.6 (77.4–324.3)	112.4 \pm 24.1 (36.3–521.0)	44.9 \pm 44.5 (174.9)	40.8 \pm 46.2 (335.6)	0.041 \pm 0.035 (0.32)	0.062 \pm 0.044 (0.32)	20.4 \pm 1.9 (9.5–26.9)	0.064 \pm 0.055 (0.41)
3	24.1	116.1 \pm 31.5 (37.9–390.3)	100.8 \pm 19.1 (28.9–454.2)	65.9 \pm 44.4 (258.4)	26.0 \pm 33.2 (273.4)	0.051 \pm 0.040 (0.29)	0.047 \pm 0.039 (0.29)	20.3 \pm 1.9 (9.5–28.1)	0.047 \pm 0.039 (0.47)
4	15.0	93.3 \pm 18.4 (43.0–291.2)	88.9 \pm 12.9 (33.0–241.5)	32.8 \pm 34.8 (176.2)	13.1 \pm 13.9 (128.4)	0.023 \pm 0.024 (0.30)	0.033 \pm 0.026 (0.15)	21.4 \pm 1.7 (13.0–27.1)	0.024 \pm 0.026 (0.22)
5	49.2	105.1 \pm 15.0 (49.7–298.6)	104.2 \pm 11.3 (42.6–308.1)	32.8 \pm 31.4 (173.4)	15.2 \pm 18.7 (179.8)	0.028 \pm 0.030 (0.28)	0.032 \pm 0.029 (0.17)	20.5 \pm 1.7 (12.7–27.4)	0.027 \pm 0.032 (0.36)

Cluster 5 was the most common of all clusters, accounting for 49.2% of all time periods.

The vertical movement patterns of the fish changed spatiotemporally as shown in Figs. 2 & 3 and Fig. S2. Around the shallow ridge (<500 m) on Green Island, around the southern tip of the ECS, and along the east coast of Taiwan, clusters 1 and 5 were predominantly detected from November through April (Figs. 2 & 3). Tagged fish swam mainly in a mixed layer (20–22°C) in clusters 1 and 5 (Fig. 3C,D; Fig. S2). However, the tagged fish occasionally experienced colder water (17–19°C) without vertical movements in clusters 1 and 5 (e.g. mid-November to mid-December; Fig. 3C,D).

In offshore locations at bottom depths >1000 m, cluster 3 was predominant (Figs. 2 & 3A,B). In addition, the fish made vertical excursions with wide depth ranges in thermally stratified waters in cluster 3 (Fig. 3C,D; Fig. S2). As a result, the tagged fish experienced a wider range of ambient temperatures (9.5–28.1°C) in cluster 3 than in clusters 1 and 5 (12.7–27.4°C) (Table 2). Cluster 3 became dominant after January when clusters 1 and 5 tapered off (Fig. 3C,D; Fig. S2).

In cluster 2, the fish also experienced a wide range of ambient temperatures (9.5–26.9°C) (Table 2), because the fish swam vertically in stratified water similar to cluster 3 (Fig. 3C,D; Fig. S2).

Cluster 4 was observed in both coastal and offshore areas (Figs. 2 & 3A,B; Fig. S2), and this cluster was often observed in the period between cluster 3 and cluster 5 (Fig. 3C,D; Fig. S2). Especially in fish GA20A, cluster 4 was observed continuously from mid-January to mid-April (Fig. S2).

3.2. Ambient temperatures, peritoneal cavity temperatures, and swimming behavior during vertical movements

The tagged fish periodically made vertical movements, and they experienced a wide ambient temperature range (9.6–27.1°C) during their vertical movements (Table 3, Figs. 3 & 4). During the vertical movements, the details of the temperature changes differed between the peritoneal cavity temperature and the ambient temperature; the ambient temperature rapidly decreased with diving, whereas the peritoneal cavity temperature changed slowly (Fig. 4) and rarely dropped below 16°C (Fig. 5). The dive durations ranged from 1 to 317 min (Fig. 6A), with 95% of the dives lasting <21 min (Fig. 6B). Long-duration dives lasting >50 min were rarely confirmed

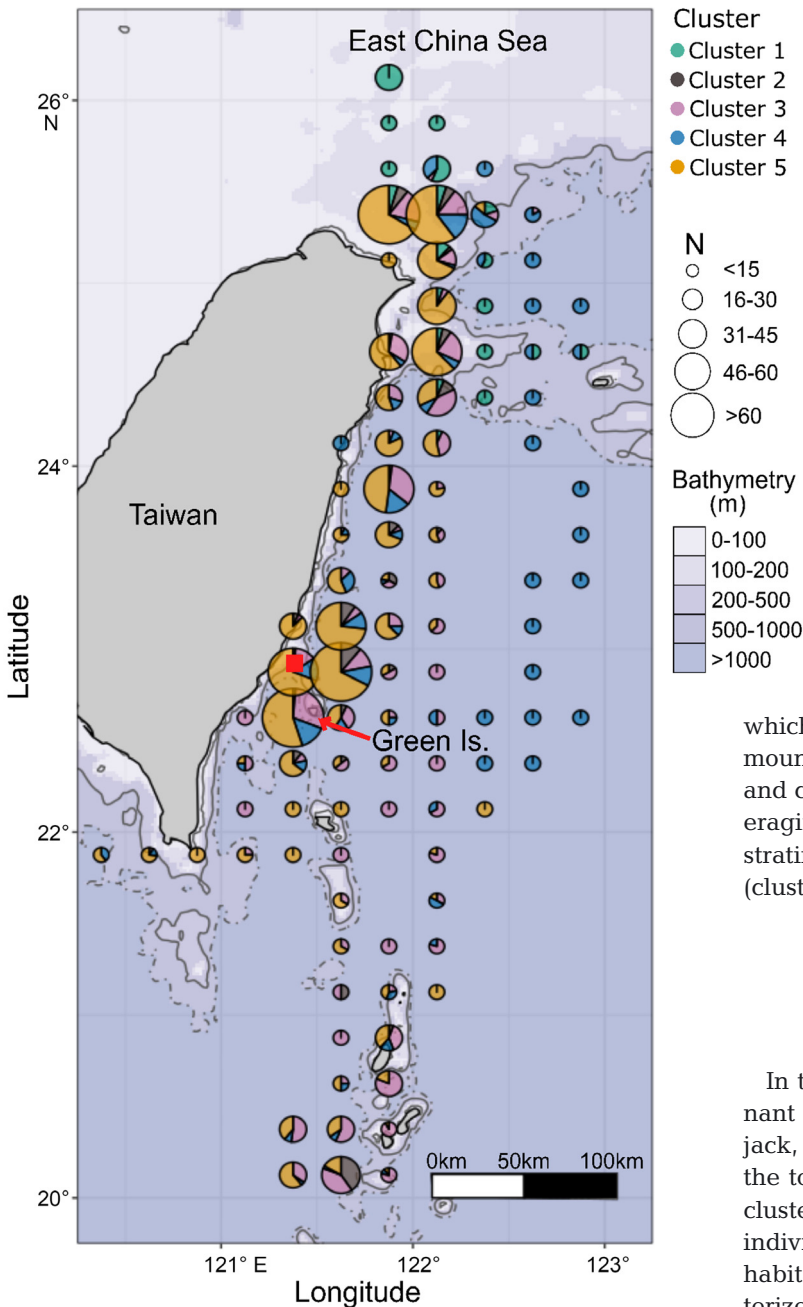


Fig. 2. Distribution of greater amberjack and the fractions of the behavioral clusters. The sizes of the circles indicate the cumulative total number of observed days in each 0.25° × 0.25° grid cell. The red square indicates the release location of the tagged individuals

(<0.05 % of the total; Fig. 6C). The median dive duration was 3 min.

The calculated BIC value of each model showed that the variable-*k* model (B) had a lower BIC than the constant-*k* model (A) in all 7 of the fish tagged with a TDR-Mk9 (Table 3). In the variable-*k* model (B), all analyzed fish showed lower heat-transfer coefficients

during cooling (*k*₁) compared to that during warming (*k*₂). In the variable-*k* model, since the version with \dot{T}_m yielded a lower BIC value than the version without \dot{T}_m in all fish analyzed, we adopted the model with \dot{T}_m (Table 3). The ranges of values of *k* and \dot{T}_m produced by the variable-*k* model (B) with \dot{T}_m for each fish were as follows. *k*₁: 3.65 × 10⁻² to 6.32 × 10⁻² °C min⁻¹ °C⁻¹, *k*₂: 5.22 × 10⁻² to 8.83 × 10⁻² °C min⁻¹ °C⁻¹, and \dot{T}_m : 3.05 × 10⁻³ to 7.31 × 10⁻³ °C min⁻¹ °C⁻¹ (Table 3). The ratio of *k*₂ to *k*₁ in model (B) with \dot{T}_m for each fish ranged from 1.29 to 1.70 (mean: 1.47).

4. DISCUSSION

Our analyses provided new insights into the vertical movements and thermoregulation of greater amberjack *Seriola dumerili*. We observed mainly 2 different vertical movement patterns of greater amberjack, which varied over spatiotemporal scales. Around seamounts, continental slopes with an undulating seabed, and coastal areas, the fish made short-step dives (averaging <35 m; clusters 1 and 5) (Figs. 2 & 3). In well-stratified offshore regions, the fish showed DVMS (cluster 3) (Figs. 2 & 3).

4.1. Vertical movement patterns of greater amberjack

In this study, clusters 3 and 5 were the most dominant vertical movement patterns of greater amberjack, as 73.3 % (cluster 3: 24.1 %, cluster 5: 49.2 %) of the total recording period was classified into these 2 clusters (Table 2). The vertical movement patterns of individual fish varied greatly depending on their habitat (Fig. 2). Eastern Taiwanese waters are characterized by the Kuroshio Current (which flows northward along the coast) and by variable seabed topography, including steep slopes cut by gullies and canyons, linear ridges, and deep basins (Yu & Song 2000). Around the topographic areas (e.g. the shallow ridge and the southern tip of the ECS), the tagged greater amberjack showed short-step dives (clusters 1 and 5) (Figs. 2 & 3). In general, zooplankton, micronekton, and fishes frequently aggregate on these undulating seabed topographies due to upwelling and a topographic blockage mechanism (Genin 2004).

Tagged greater amberjack experienced cold water (17–19°C) without any vertical movements

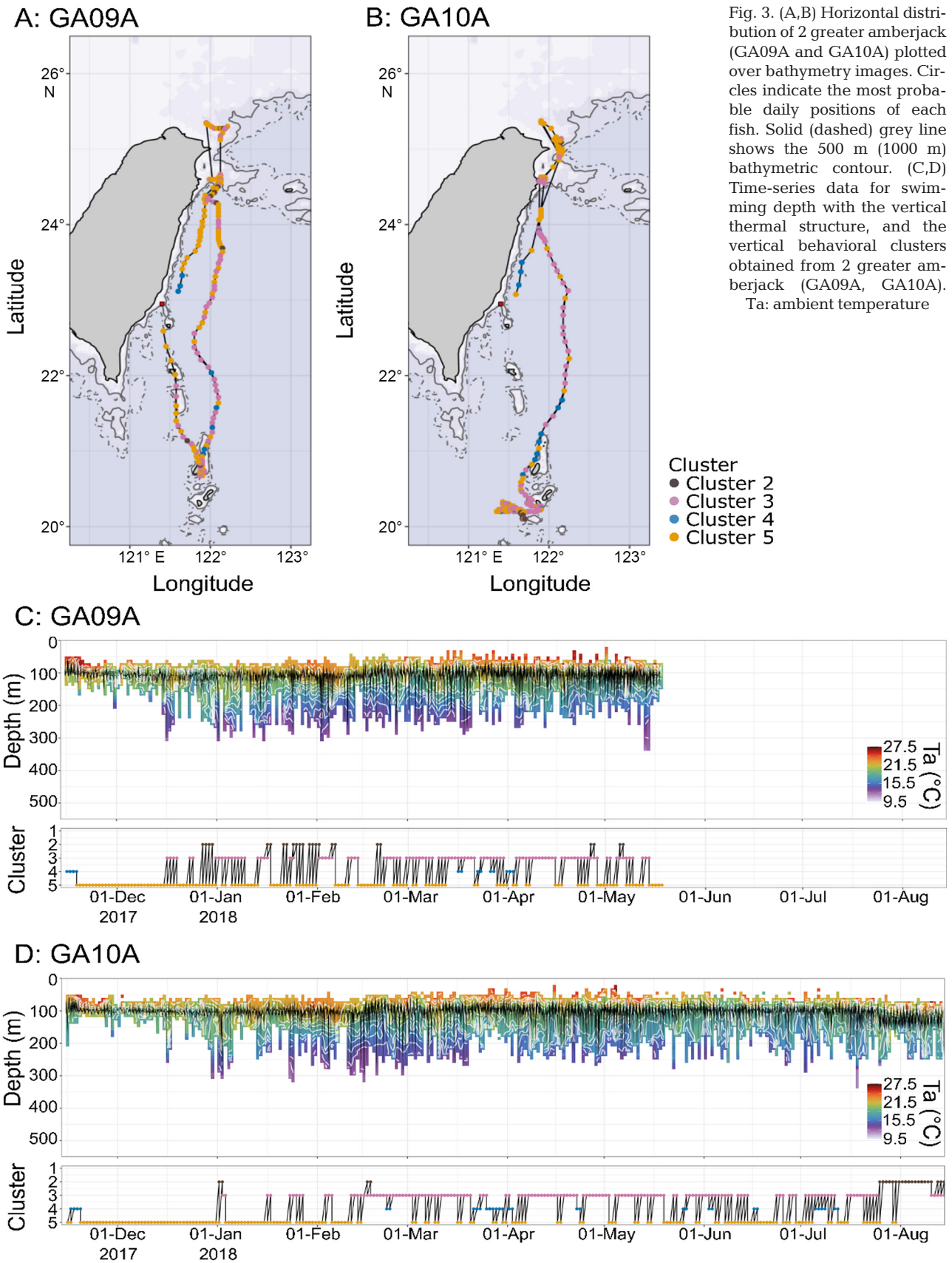


Fig. 3. (A,B) Horizontal distribution of 2 greater amberjack (GA09A and GA10A) plotted over bathymetry images. Circles indicate the most probable daily positions of each fish. Solid (dashed) grey line shows the 500 m (1000 m) bathymetric contour. (C,D) Time-series data for swimming depth with the vertical thermal structure, and the vertical behavioral clusters obtained from 2 greater amberjack (GA09A, GA10A). Ta: ambient temperature

Table 3. Temperature information and result summary of parameters estimated using the heat-budget models for greater amberjack. The column 'Model k ' indicates A: the fixed heat-transfer coefficient (k) model or B: the variable- k model. The column 'Model \dot{T}_m ' indicates +: including or -: not including the rate of temperature change due to internal heat production (\dot{T}_m) in the model. k : in the fixed- k model. k_1 : k at cooling in the variable- k model. k_2 : k at warming in the variable- k model. BIC: Bayesian information criterion; T_a : ambient water temperature, T_b : peritoneal cavity temperature, NA: not applicable

Fish ID	T_a (°C) (range)	T_b (°C) (range)	Model k	\dot{T}_m (°C min ⁻¹ °C ⁻¹)	k (°C min ⁻¹ °C ⁻¹)	k_1 (°C min ⁻¹ °C ⁻¹)	k_2 (°C min ⁻¹ °C ⁻¹)	\dot{T}_m (°C min ⁻¹)	BIC	Δ BIC	$k_2 k_1^{-1}$
GA07A	20.7 ± 2.3 (10.2–27.2)	21.0 ± 1.9 (14.3–27.0)	A	+	5.45 × 10 ⁻²	NA	NA	1.41 × 10 ⁻²	-607734	12049	NA
			A	-	5.25 × 10 ⁻²	NA	NA	NA	-598153	21630	NA
			B	+	NA	4.43 × 10 ⁻²	7.51 × 10 ⁻²	3.05 × 10 ⁻³	-619783	0	1.70
			B	-	NA	4.30 × 10 ⁻²	7.68 × 10 ⁻²	NA	-619457	326	1.79
GA09A	20.6 ± 1.7 (11.9–27.4)	20.8 ± 1.5 (15.5–25.7)	A	+	6.64 × 10 ⁻²	NA	NA	1.25 × 10 ⁻²	-1223072	7497	NA
			A	-	6.33 × 10 ⁻²	NA	NA	NA	-1211827	18742	NA
			B	+	NA	5.69 × 10 ⁻²	8.83 × 10 ⁻²	5.56 × 10 ⁻³	-1230569	0	1.55
			B	-	NA	5.35 × 10 ⁻²	9.31 × 10 ⁻²	NA	-1229003	1566	1.74
GA10A	20.0 ± 1.7 (11.7–28.1)	20.1 ± 1.5 (13.7–25.6)	A	+	7.01 × 10 ⁻²	NA	NA	1.08 × 10 ⁻²	-2094525	6160	NA
			A	-	6.70 × 10 ⁻²	NA	NA	NA	-2069370	31314	NA
			B	+	NA	6.32 × 10 ⁻²	8.15 × 10 ⁻²	7.07 × 10 ⁻³	-2100685	0	1.29
			B	-	NA	5.75 × 10 ⁻²	8.74 × 10 ⁻²	NA	-2093347	7338	1.52
GA11A	20.6 ± 1.8 (12.7–27.2)	20.8 ± 1.6 (16.4–25.4)	A	+	4.50 × 10 ⁻²	NA	NA	7.32 × 10 ⁻³	-298444	788	NA
			A	-	4.28 × 10 ⁻²	NA	NA	NA	-295529	3702	NA
			B	+	NA	3.96 × 10 ⁻²	5.22 × 10 ⁻²	4.63 × 10 ⁻³	-299231	0	1.32
			B	-	NA	3.55 × 10 ⁻²	5.55 × 10 ⁻²	NA	-298436	795	1.56
GA20A	21.4 ± 1.6 (9.5–27.0)	21.6 ± 1.5 (15.25–25.8)	A	+	5.51 × 10 ⁻²	NA	NA	1.00 × 10 ⁻²	-1384634	6822	NA
			A	-	4.97 × 10 ⁻²	NA	NA	NA	-1348798	42657	NA
			B	+	NA	4.88 × 10 ⁻²	6.74 × 10 ⁻²	7.31 × 10 ⁻³	-1391455	0	1.38
			B	-	NA	4.10 × 10 ⁻²	7.45 × 10 ⁻²	NA	-1376956	14499	1.82
GA23A	20.7 ± 1.5 (10.9–26.3)	20.9 ± 1.3 (15.3–25.5)	A	+	4.33 × 10 ⁻²	NA	NA	9.24 × 10 ⁻³	-1216519	11724	NA
			A	-	3.98 × 10 ⁻²	NA	NA	NA	-1192654	35589	NA
			B	+	NA	3.65 × 10 ⁻²	5.91 × 10 ⁻²	5.00 × 10 ⁻³	-1228243	0	1.62
			B	-	NA	3.26 × 10 ⁻²	6.38 × 10 ⁻²	NA	-1222959	5284	1.96
GA24A	22.0 ± 1.4 (12.7–26.2)	22.2 ± 1.2 (15.0–25.8)	A	+	4.92 × 10 ⁻²	NA	NA	8.26 × 10 ⁻³	-1063585	6561	NA
			A	-	4.38 × 10 ⁻²	NA	NA	NA	-1034723	35424	NA
			B	+	NA	4.32 × 10 ⁻²	6.27 × 10 ⁻²	5.93 × 10 ⁻³	-1070147	0	1.45
			B	-	NA	3.61 × 10 ⁻²	6.96 × 10 ⁻²	NA	-1058369	11778	1.93

around the topographic area in clusters 1 and 5 (Fig. 3C,D), which indicates that the fish would have experienced upwelling. This suggests that greater amberjack would be attracted to these topographic features (i.e. the shallow ridge and the southern tip of the ECS) for foraging. The main components of the stomach contents of adult greater amberjack sampled around topographic features are demersal and pelagic prey (Andaloro & Pipitone 1997), suggesting that topographic features could provide preferable feeding grounds for greater amberjack. Although the mean bottom depth in waters of eastern Taiwan is >1000 m, the topographic features where clusters 1 and 5 were observed (i.e. the shallow ridge and the southern tip of the ECS) have a very shallow depth (50–200 m) (Fig. 3). Thus, greater amberjack may reach the topographic features, which are preferable feeding grounds, with short-step dives.

We also observed that as tagged fish moved from coastal to offshore areas, the vertical movement pattern shifted from cluster 5 to cluster 3. For example, the vertical movement pattern of fish GA10A shifted from cluster 5 to cluster 3 in March (Fig. 3D), when it migrated to an offshore region where the Kuroshio Current flows. As the water depth in offshore regions of eastern Taiwan (>1000 m) is more than twice the maximum swimming depth (521.0 m) of the tagged greater amberjack, the fish are not able to reach the seabed. Greater amberjack are thus unable to engage in reef-associated swimming in the offshore region of eastern Taiwan.

The tagged fish showed DVMs, using greater depths during the daytime (116.1 ± 31.5 m) than the nighttime (100.8 ± 19.1 m) in the offshore region (Table 2, Fig. 1B). The deeper-by-daytime and shallower-by-nighttime pattern (i.e. DVM) has been reported in pelagic predatory fishes including blue

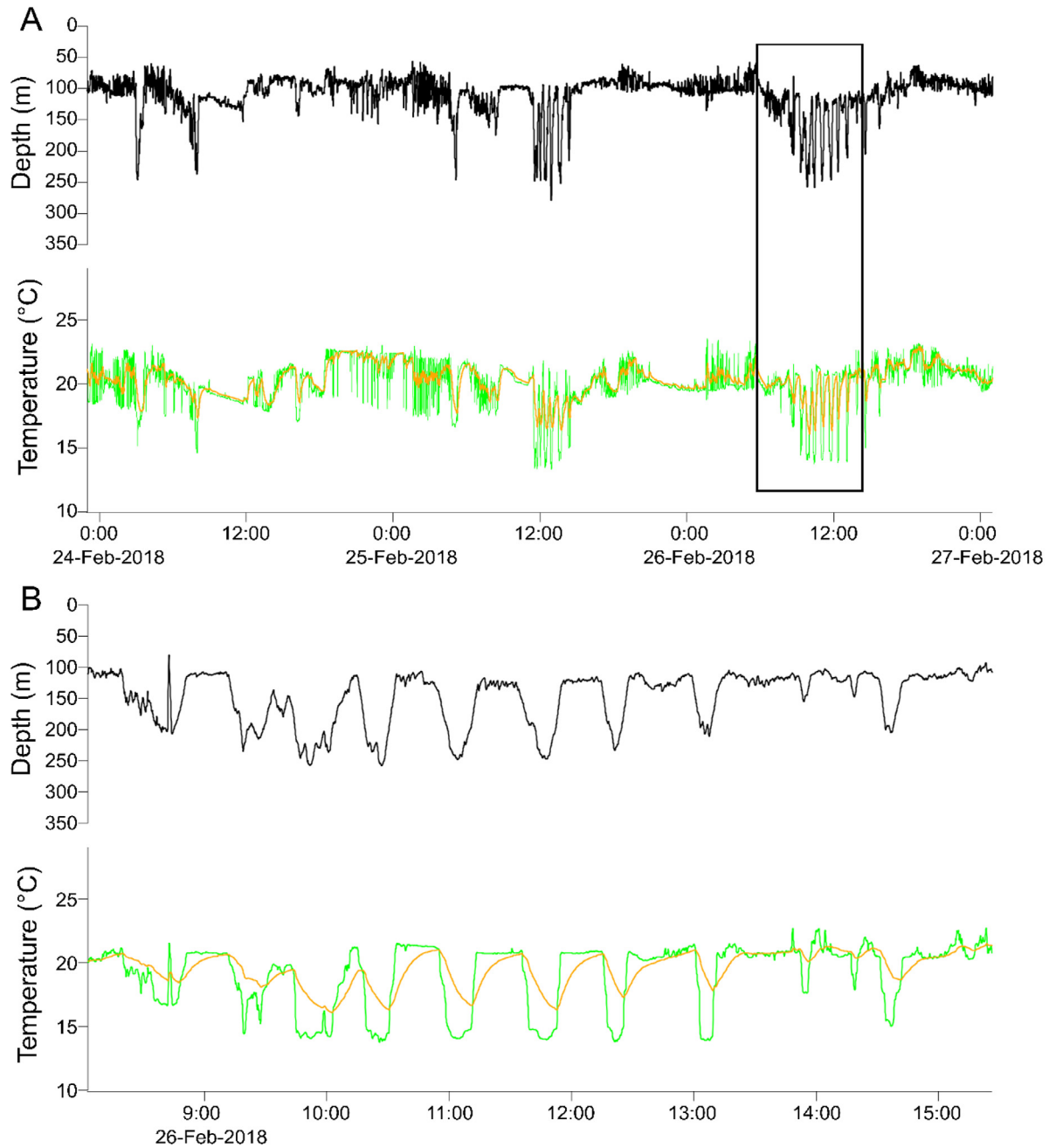


Fig. 4. (A) Example of time-series data of swimming depth (black), ambient temperature (green) and peritoneal cavity temperature (orange) obtained from an individual tagged greater amberjack (GA10A). (B) Expanded view of the boxed portion in panel (A)

shark *Prionace glauca* (Carey & Scharold 1990), swordfish (Carey & Robison 1981), and Atlantic bluefin tuna *Thunnus thynnus* (Block et al. 2001). Those studies suggested that DVMs are associated with foraging in the deep scattering layer (DSL). The DSL off eastern Taiwan during the daytime was generally observed around depths of 180–280 m (Chou et al. 1999). The depths of the daytime vertical movements by tagged fish in the present study (approaching

~150–250 m) (Fig. 1B) are roughly consistent with the depths of the DSL, suggesting that the DVMs of the greater amberjack could be related to the DSL. Cluster 3 would thus represent not reef-associated foraging behavior, but rather a foraging behavior in accordance with the DVMs of prey in offshore regions.

Cluster 3 may be related not only to foraging but also to reproductive behavior. Cluster 3 was observed after January, and it appeared frequently

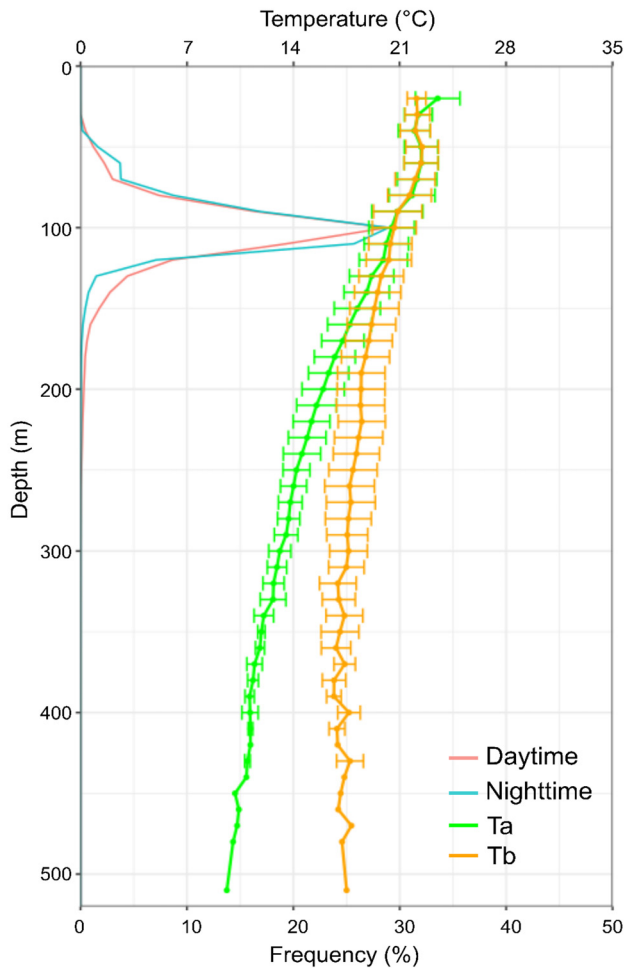


Fig. 5. Frequency distribution of the swimming depth from all individuals during the daytime (red) and nighttime (blue), with the vertical profile of mean temperature and standard deviation in each bin. Green: ambient water temperature (Ta); orange: peritoneal cavity temperature (Tb)

and continually in February–April (Fig. 3). For example, 2 females (GA10A and GA14P) showed the cluster 3 pattern that continued for >1 wk in February–April (Fig. 3D; Fig. S2). The greater amberjack of the ECS spawn in the Kuroshio Current off eastern Taiwan (Tone et al. 2022) from February to April (Hasegawa et al. 2020). An association between DVM and reproductive behavior during the spawning season has been observed in several pelagic fishes, including Atlantic bluefin tuna (Block et al. 2001), European eel *Anguilla anguilla* (Aarestrup et al. 2009), and New Zealand longfin eel *A. dieffenbachii* (Jellyman & Tsukamoto 2010). In addition, several fishes that spawn floating eggs (e.g. greater amberjack, Tachihara et al. 1993; Pacific halibut *Hippoglossus stenolepis*, Seitz et al. 2005; Japanese flounder *Paralichthys olivaceus*,

Yasuda et al. 2013; Atlantic halibut *H. hippoglossus*, Fisher et al. 2017) have been observed performing rapid vertical swimming during spawning, also known as a ‘spawning rise’.

A laboratory study indicated that spawning greater amberjack engaged in spawning rises during the nighttime and early morning (~03:00 to 05:00 h) that were >3× faster than any of their other swimming (Tachihara et al. 1993). In the present study, tagged fish engaged in cluster 3 behavior demonstrated rapid vertical swimming (max.: 0.47 m s⁻¹) in the nighttime (Fig. 1D). This rapid vertical swimming was >10× faster than the average vertical swimming speed of cluster 3 (daytime: 0.051 m s⁻¹, twilight: 0.047 m s⁻¹, nighttime: 0.047 m s⁻¹) (Table 2). Indeed, in our previous study using the same behavioral data of greater amberjack (Tone et al. 2022), we observed rapid vertical swimming during the continuous DVM associated with spawning behavior.

These results suggest that the continual cluster 3 that appeared from February to April in the offshore water may have been comprised of 2 behaviors (foraging and reproductive behavior); however, the present analyses were unable to distinguish between the 2 behaviors. Specific body vibrations have been reported in the greater amberjack during spawning behavior in an aquarium (Sakaji et al. 2018). Because the archival tags that we used (MiniPAT and TDR-Mk9) did not have accelerometers to measure body vibrations, it was not possible to identify spawning events. Further research is needed to identify whether cluster 3 behavior represents foraging and/or reproductive behavior.

Cluster 2 was characterized by frequent dives to ~150 m during the entire day and by the deepest dive (up to ~520 m) of all of the behavior patterns (Table 2, Fig. 1B). The frequent dives might be for navigation, foraging, behavioral thermoregulation, predator avoidance, or a combination of these behaviors (Carey & Scharold 1990, Klimley 1993, Andrzejczek et al. 2019). In some pelagic predatory fishes, deep dives have been postulated to be associated with navigation because geomagnetic and depth cues can be obtained at great depths (Klimley 1993). The greater amberjack in the ECS undertake seasonal north–south migrations that are >1000 km, and they can return to locations with fidelity of <10 km (Tone et al. 2022). The navigation hypothesis thus cannot be ruled out for greater amberjack. The vertical movements for navigation observed in the previous studies occurred mainly during the twilight period, when the intensity of the Earth’s magnetic field reaches its maximum (Willis et al. 2009), whereas the

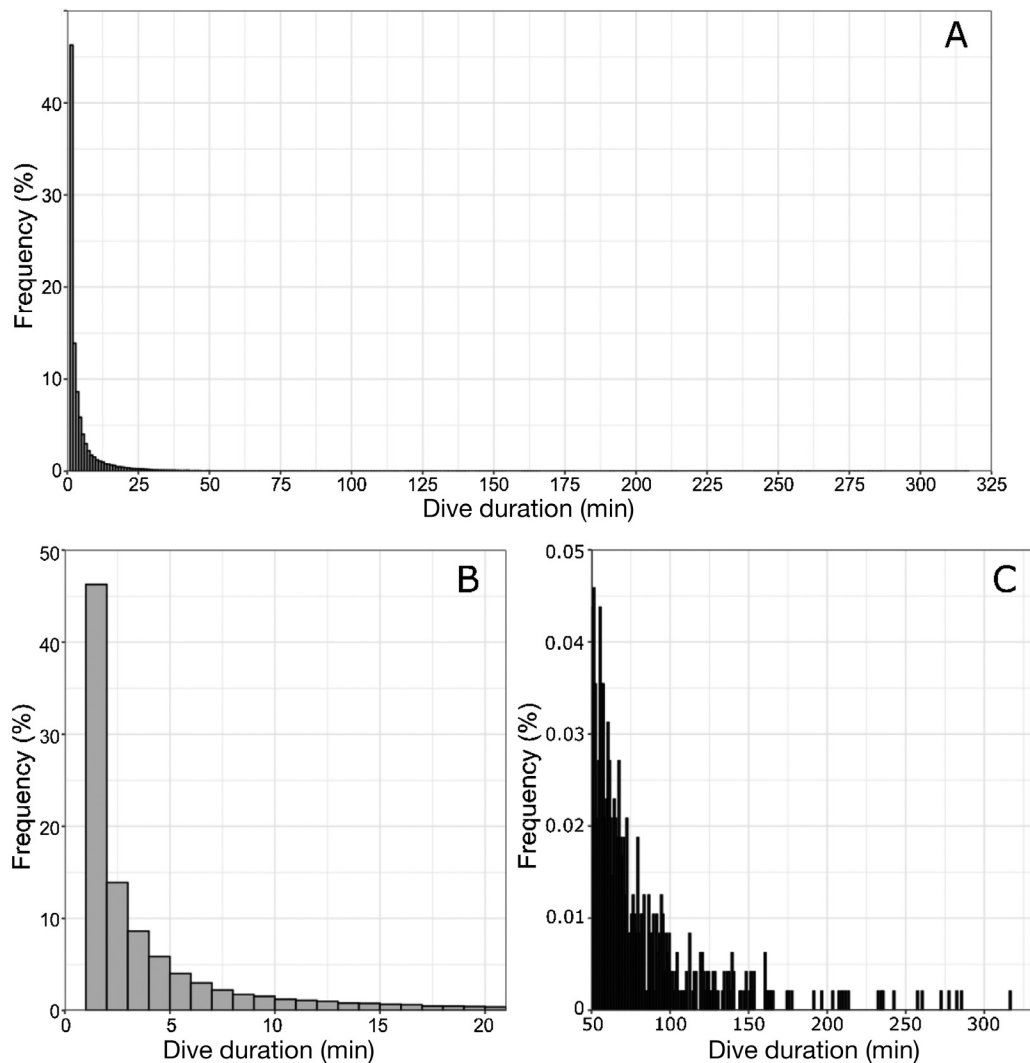


Fig. 6. (A) Duration frequency of each dive obtained from all individual greater amberjack. The maximum dive time was 317 min. (B) Enlarged view of the 0 to 21 min portion of (A). (C) Enlarged view of the 50 to 317 min portion of (A)

frequent dives of the greater amberjack in the present study occurred not only during the twilight period but also during both the daytime and nighttime. The navigation hypothesis is therefore unlikely to be the main function of the frequent dives in cluster 2 in the greater amberjack.

Another possible main function of the frequent dives in cluster 2 is foraging behavior. In cluster 2, tagged fish were observed swimming vertically in well-stratified waters, as in cluster 3 (Fig. 3). Olfactory and gustatory stimuli that are useful for locating prey are distributed more extensively in the horizontal plane than vertically, due to current shear between water layers of different densities (Carey & Scharold 1990). Moving vertically in stratified waters would thus be an effective strategy for detecting cues to prey locations. Interestingly, the tagged fish swam

to similar depths in cluster 2 (127.3 ± 24.6 m) and cluster 3 (116.1 ± 31.5 m) during the daytime (Table 2), but nighttime diving occurred only in cluster 2 (Fig. 1). This difference in diving behavior between the 2 clusters implies that the greater amberjack could switch to a different foraging behavior between cluster 2 and cluster 3.

For example, if greater amberjack cannot find an area with sufficient food resources such as the DSL during the daytime, they will need to continue foraging during the nighttime. Indeed, several pelagic predatory fishes have been reported to shift their vertical movement patterns according to the distribution of their prey (e.g. Queiroz et al. 2012, Stehfest et al. 2014). Because the prey of greater amberjack is diverse (Andaloro & Pipitone 1997, Sley et al. 2016), changes in vertical movement patterns between

cluster 2 and cluster 3 may be a response to shifts in available prey species.

Our results suggest that clusters 3 and 5 reflect the foraging behavior of the greater amberjack when the fish are in areas of high food concentrations, whereas cluster 2 may reflect alternative foraging behavior when the fish are in a resource-poor area. Synthesizing these results, we propose that the abundance of prey would have the greatest influence on vertical movement patterns (i.e. diving depth and the occurrence of DVM) of greater amberjack. Although they are known to be associated primarily with topographic features (Murie et al. 2011, Jackson et al. 2018), greater amberjack in the ECS migrate to offshore regions during the spawning season (Tone et al. 2022). A possible reason for this offshore migration is so that the fish can experience a slowly elevating water temperature regime to induce final oocyte maturation and ovulation (Tone et al. 2022).

The vacuity index values (= percentage of empty stomachs) of mature greater amberjack decrease in the early stage of spawning (Andaloro & Pipitone 1997, Sley et al. 2016), suggesting that greater amberjack may require more energy during the gamete-development phase (i.e. November to January). However, since offshore regions (e.g. the Kuroshio Current) are areas of low productivity, their prey abundance will be lower there than in coastal regions. Greater amberjack may thus have changed their behavior from the reef-associated foraging behavior to the DVM pattern to satisfy their energy requirements for gamete development and subsequent spawning activity. This finding supports the hypothesis that greater amberjack might change their foraging strategy depending on their habitat.

4.2. Behavioral thermoregulation of greater amberjack

The frequent dives observed in clusters 2 and 3 would also be affected by the physiological constraints. As mentioned, deep water (e.g. the DSL) may provide an attractive foraging environment for greater amberjack. However, our data demonstrated that the tagged fish did not stay at the depth of the DSL throughout the daytime: rather, they exhibited frequent vertical movements. The ambient temperature in deep water (approximately $<16^{\circ}\text{C}$) is colder than that at the depth where greater amberjack are usually observed ($20.0^{\circ}\text{--}22.0^{\circ}\text{C}$) (Table 3, Fig. 5). This suggests that deep, cold water would be a physiologically limiting factor for greater amberjack.

Our present study is the first to record the peritoneal cavity temperature of greater amberjack, and we successfully described the behavioral responses of the fish to the surrounding thermal environment. The peritoneal cavity temperature of the tagged fish fluctuated according to the ambient water temperature changes (Fig. 4). The heat budget model showed that all of the individual fish tagged with a TDR-Mk9 had a higher k -value during warming compared to cooling (Table 3). According to Holland et al. (1992), bigeye tuna undergo physiological thermoregulation by changing their k -value by 2 orders of magnitude. In contrast, the ratio of the changes in k of greater amberjack was within 1 order of magnitude, which indicates that these fish do not undergo physiological thermoregulation as do bigeye tuna.

The k and the ratio of k for fishes of various sizes are strongly correlated with body mass (Nakamura et al. 2020, Watanabe et al. 2021). We observed that the k and the ratio of k of greater amberjack were not exceptional among fishes of similar body mass, as shown in these previous studies. In our present analyses, the calculated BIC values were lower in the variable- k model with \dot{T}_m than the version without \dot{T}_m in all tagged fish (Table 3). A temperature elevation $\geq 2.7^{\circ}\text{C}$ above the ambient temperature has been proposed as a benchmark for determining whether fishes are able to retain their body temperature as endothermic (Dickson 1994). In greater amberjack, the mean temperature difference between the ambient water temperature and peritoneal cavity temperature was 0.2°C (Table 3). These results indicate that greater amberjack are ectothermic fish, in which the physiological heat must be relatively small or negligible in thermoregulation.

If a greater amberjack, an ectothermic fish, remains in deep, cold water throughout the daytime, its body temperature will drop to the temperature of the ambient water temperature. Since the fish cannot physiologically maintain its body temperature in cool water below the optimal habitat temperature, it is then necessary to find a way (i.e. behavioral thermoregulation) to stay in cool water to do it. Several fishes with large k -values have been reported to maintain their peritoneal cavity temperature in cool water by performing periodical short-duration dives rather than a single long-duration dive (e.g. chum salmon *Oncorhynchus keta*; Azumaya & Ishida 2005). In the present study, the median duration of periodic dives was <3 min (Fig. 6). Here, we used Eq. (1) to simulate a peritoneal cavity temperature change when a tagged fish showed periodic short-duration dives

(3 min) or a single long-duration dive (50 min), as shown in Fig. 7. During the periodic short-duration dives, the estimated peritoneal cavity temperature almost never dropped below 16°C (Fig. 7A).

In contrast, during the single long-duration dive, the peritoneal cavity temperature dropped below 16°C and then decreased until it became equal to the ambient water temperature (Fig. 7B). The greater amberjack shifted from descents to ascents before their peritoneal cavity temperature became <16°C (Figs. 4 & 5). These results indicate that periodic short-duration dives by this species are likely to be for behavioral thermoregulation, which enables greater amberjack to access deep, cold water while maintaining their peritoneal cavity temperature. We thus postulate that the duration of the vertical movement of greater amberjack would be limited by physiological constraints to maintain their body temperature.

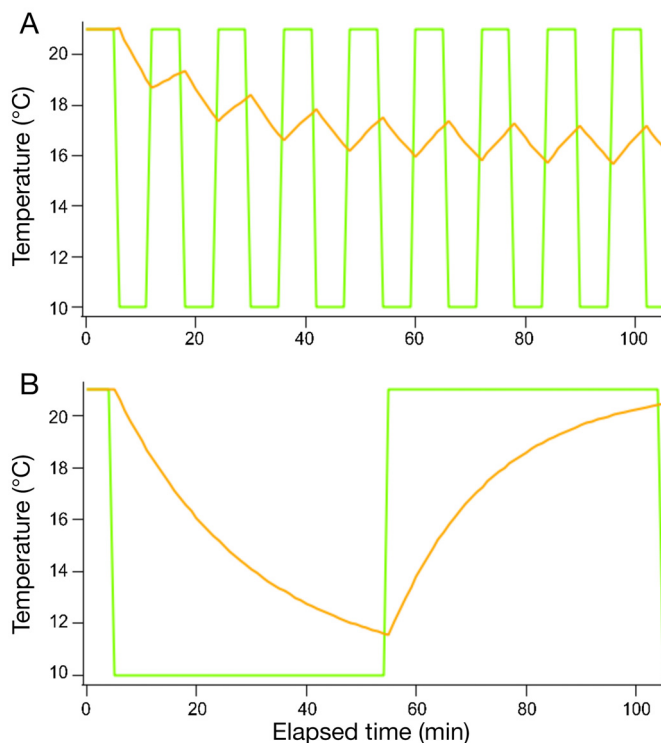


Fig. 7. Estimated peritoneal cavity temperature changes of a single greater amberjack (GA10A) when it showed (A) periodical short-duration (3 min) dives and (B) a single long-duration (60 min) dive. Green: ambient water temperature; orange: estimated peritoneal cavity temperature, which was calculated using values of k_1 (heat-transfer coefficient; cooling) = $6.32 \times 10^{-2} \text{ } ^\circ\text{C min}^{-1} \text{ } ^\circ\text{C}^{-1}$, k_2 (heat-transfer coefficient; warming) = $8.15 \times 10^{-2} \text{ } ^\circ\text{C min}^{-1} \text{ } ^\circ\text{C}^{-1}$, and \dot{T}_m (the rate of temperature change due to internal heat production) = $7.07 \times 10^{-3} \text{ } ^\circ\text{C min}^{-1}$ from the archival tag attached to the fish (GA10A)

4.3. Conclusions

The results of this study demonstrated that the vertical movement pattern of greater amberjack is related mainly to foraging behaviors associated with topographic feature changes and is limited by physiological constraints for the maintenance of body temperature. It is thus likely that greater amberjack make frequent and repeated vertical movements in order to balance the trade-offs between foraging and thermoregulation. We also observed that performing a cluster analysis using depth profiles is effective for classifying vertical movements even in pelagic fish that do not use a specific point (e.g. the sea surface or seabed) as a starting point of the vertical movement.

The functions of the vertical movement pattern with short-step dives similar to cluster 5 (i.e. cluster 4), which was observed in both offshore and coastal areas, remain unclear. In addition to foraging and behavioral thermoregulation, it has been suggested that the purposes of vertical movement include navigation, predator avoidance, and energy conservation (Weihs 1973, Carey & Scharold 1990, Klimley 1993, Andrzejczek et al. 2019). For example, negatively buoyant fishes can conserve locomotion costs by alternating passive gliding during descents and active swimming during ascents compared with continuous horizontal swimming (Weihs 1973, Gleiss et al. 2011). Since there are many large predatory fishes (e.g. sharks) that are potential predators of greater amberjack in eastern Taiwanese waters (Chiang et al. 2014), some of their vertical movements might represent evasion from predators. Further tagging surveys using acceleration data loggers to simultaneously record swimming speeds and tail beat activity (Kawabe et al. 2004, Furukawa et al. 2011) and miniaturized camera tags (Nakamura et al. 2015) will contribute to our understanding of the behavioral factors of the vertical movements.

Acknowledgements. We gratefully acknowledge Captain Zai-Ci Chang and the crew of the FV 'Jian-Fa No. 66' for their help catching fish to be tagged and released, and we thank all of the local fishermen who kindly helped recover our tags. We also thank Prof. Sheng-Ping Wang, Dr. Ching-Ping Lu, Mr. Shian-Jhong Lin (National Taiwan Ocean University), Mr. Yosuke Nakamura (Hokkaido University), and all of the members of the Eastern Marine Biology Research Center, Fisheries Research Institute, Council of Agriculture, Taiwan, for their assistance in this project. This project was funded by Grants-in-Aid for Scientific Research from the Japan Society for the Promotion of Science (nos. 16H05794, 16H05795, 17K07913, 19H00952, 21H02270).

LITERATURE CITED

- Aarestrup K, Økland F, Hansen MM, Righton D and others (2009) Oceanic spawning migration of the European eel (*Anguilla anguilla*). *Science* 325:1660
- Andaloro F, Pipitone C (1997) Food and feeding habits of the amberjack, *Seriola dumerili* in the Central Mediterranean Sea during the spawning season. *Cah Biol Mar* 38:91–96
- Andrzejaczek S, Gleiss AC, Jordan LK, Pattiaratchi CB, Howey LA, Brooks EJ, Meekan MG (2018) Temperature and the vertical movements of oceanic whitetip sharks, *Carcharhinus longimanus*. *Sci Rep* 8:8351
- Andrzejaczek S, Gleiss AC, Pattiaratchi CB, Meekan MG (2019) Patterns and drivers of vertical movements of the large fishes of the epipelagic. *Rev Fish Biol Fish* 29: 335–354
- Azumaya T, Ishida Y (2005) Mechanism of body cavity temperature regulation of chum salmon (*Oncorhynchus keta*) during homing migration in the North Pacific Ocean. *Fish Oceanogr* 14:81–96
- Block BA, Dewar H, Blackwell SB, Williams TD and others (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293: 1310–1314
- Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* 475:86–90
- Carey FG, Robison BH (1981) Daily patterns in the activities of swordfish *Xiphias gladius*, observed by acoustic telemetry. *Fish Bull* 79:277–292
- Carey FG, Scharold JV (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar Biol* 106:329–342
- Chiang WC, Lin PL, Chen DC, Liu DC (2014) Marine fishes in eastern Taiwan. Taiwan Fisheries Research Institute, Keelung (in Chinese with English and scientific nomenclature)
- Chou SC, Lee MA, Lee KT (1999) Diel vertical movement of the deep scattering layer on the continental slope of I-Lan Bay, Taiwan. *Fish Sci* 65:694–699
- Coffey DM, Carlisle AB, Hazen EL, Block BA (2017) Oceanographic drivers of the vertical distribution of a highly migratory, endothermic shark. *Sci Rep* 7:10434
- Dickson K (1994) Tunas as small as 207 mm fork length can elevate muscle temperatures significantly above ambient water temperature. *J Exp Biol* 190:79–93
- Estes JA, Terborgh J, Brashares JS, Power ME and others (2011) Trophic downgrading of planet Earth. *Science* 333:301–306
- Fisher JA, Robert D, Le Bris A, Loher T (2017) Pop-up satellite archival tag (PSAT) temporal data resolution affects interpretations of spawning behaviour of a commercially important teleost. *Anim Biotelem* 5:21
- Froese F, Pauly D (2009) FishBase. www.fishbase.org (accessed 22 February 2022)
- Furukawa S, Kawabe R, Ohshimo S, Fujioka K and others (2011) Vertical movement of dolphinfish *Coryphaena hippurus* as recorded by acceleration data-loggers in the northern East China Sea. *Environ Biol Fishes* 92:89–99
- Furukawa S, Chiang WC, Watanabe S, Hung HM and others (2015) The first record of peritoneal cavity temperature recording in free-swimming dolphinfish *Coryphaena hippurus* by using archival tags, on the east coast of Taiwan. *J Aquacult Mar Biol* 2:00032
- Furukawa S, Kozuka A, Tsuji T, Kubota H (2020) Horizontal and vertical movement of yellowtails *Seriola quinqueradiata* during summer to early winter recorded by archival tags in the northeastern Japan Sea. *Mar Ecol Prog Ser* 636:139–156
- Genin A (2004) Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *J Mar Syst* 50:3–20
- Gleiss AC, Wilson RP, Shepard EL (2011) Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods Ecol Evol* 2:23–33
- Harris PJ, Wyanski DM, White DB, Mikell PP, Eyo PB (2007) Age, growth, and reproduction of greater amberjack off the southeastern US Atlantic coast. *Trans Am Fish Soc* 136:1534–1545
- Hasegawa T, Lu CP, Hsiao ST, Uchino T and others (2020) Distribution and genetic variability of young-of-the-year greater amberjack (*Seriola dumerili*) in the east China sea. *Environ Biol Fishes* 103:833–846
- Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends Ecol Evol* 23:202–210
- Holland KN, Sibert JR (1994) Physiological thermoregulation in bigeye tuna, *Thunnus obesus*. *Environ Biol Fishes* 40:319–327
- Holland KN, Brill RW, Chang RKC, Sibert JR, Fournier DA (1992) Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* 358:410–412
- Hussey NE, Kessel ST, Aarestrup K, Cooke SJ and others (2015) Aquatic animal telemetry: a panoramic window into the underwater world. *Science* 348:1255642
- Jackson LS, Drymon JM, Nelson TR, Powers SP (2018) Biotelemetry based estimates of greater amberjack (*Seriola dumerili*) post-release mortality in the northern Gulf of Mexico. *Fish Res* 208:239–246
- Jellyman D, Tsukamoto K (2010) Vertical migrations may control maturation in migrating female *Anguilla dieffenbachii*. *Mar Ecol Prog Ser* 404:241–247
- Jorgensen SJ, Arnoldi NS, Estess EE, Chapple TK, Rückert M, Anderson SD, Block BA (2012) Eating or meeting? Cluster analysis reveals intricacies of white shark (*Carcharodon carcharias*) migration and offshore behavior. *PLOS ONE* 7:e47819
- Kawabe R, Naito Y, Sato K, Miyashita K, Yamashita N (2004) Direct measurement of the swimming speed, tailbeat, and body angle of Japanese flounder (*Paralichthys olivaceus*). *ICES J Mar Sci* 61:1080–1087
- Kitagawa T, Kimura S (2006) An alternative heat-budget model relevant to heat transfer in fishes and its practical use for detecting their physiological thermoregulation. *Zool Sci* 23:1065–1071
- Kitagawa T, Nakata H, Kimura S, Itoh T, Tsuji S, Nitta A (2000) Effect of ambient temperature on the vertical distribution and movement of Pacific bluefin tuna *Thunnus thynnus orientalis*. *Mar Ecol Prog Ser* 206:251–260
- Klimley AP (1993) Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. *Mar Biol* 117:1–22
- Murie D, Parkyn D, Austin J (2011) Seasonal movement and mixing rates of greater amberjack in the Gulf of Mexico and assessment of exchange with the South Atlantic spawning stock. SEDAR33-DW12. Southeast Data, Assessment, and Review, North Charleston, SC
- Nakada M (2008) Capture-based aquaculture of yellowtail. In: Lovatelli A, Holthuis PF (eds) Capture-based aquacul-

- ture. Global overview. FAO Fish Tech Pap 508, FAO, Rome, p 199–215
- ✦ Nakamura I, Goto Y, Sato K (2015) Ocean sunfish rewarm at the surface after deep excursions to forage for siphonophores. *J Anim Ecol* 84:590–603
- ✦ Nakamura I, Matsumoto R, Sato K (2020) Body temperature stability in the whale shark, the world's largest fish. *J Exp Biol* 223:jeb210286
- ✦ Queiroz N, Humphries NE, Noble LR, Santos AM, Sims DW (2012) Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. *PLOS ONE* 7:e32374
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Sakaji H, Hamada K, Naito Y (2018) Identifying spawning events of greater amberjack using accelerometers. *Mar Biol Res* 14:637–641
- ✦ Schwarz G (1978) Estimating the dimension of a model. *Ann Stat* 6:461–464
- ✦ Seitz AC, Norcross BL, Wilson D, Nielsen JL (2005) Identifying spawning behavior in Pacific halibut, *Hippoglossus stenolepis*, using electronic tags. *Environ Biol Fishes* 73: 445–451
- ✦ Shepard ELC, Ahmed MZ, Southall EJ, Witt MJ, Metcalfe JD, Sims DW (2006) Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Mar Ecol Prog Ser* 328:205–213
- ✦ Sley A, Taieb AH, Jarbouy O, Ghorbel M, Bouain A (2016) Feeding behaviour of greater amberjack *Seriola dumerili* (Risso, 1810) from Central Mediterranean (Gulf of Gabes, Tunisia). *J Mar Biol Assoc UK* 96:1229–1234
- ✦ Stehfest KM, Patterson TA, Barnett A, Semmens JM (2014) Intraspecific differences in movement, dive behavior and vertical habitat preferences of a key marine apex predator. *Mar Ecol Prog Ser* 495:249–262
- ✦ Stoehr A, St. Martin J, Aalbers S, Sepulveda C, Bernal D (2018) Free-swimming swordfish, *Xiphias gladius*, alter the rate of whole body heat transfer: morphological and physiological specializations for thermoregulation. *ICES J Mar Sci* 75:858–870
- ✦ Tachihara K, Ebisu R, Tsukashima Y (1993) Spawning, eggs, larvae and juveniles of the purplish amberjack *Seriola dumerili*. *Bull Jpn Soc Sci Fish* 59:1479–1488 (in Japanese with English abstract)
- ✦ Tone K, Nakamura Y, Chiang WC, Yeh HM and others (2022) Migration and spawning behavior of the greater amberjack *Seriola dumerili* in eastern Taiwan. *Fish Oceanogr* 31: 1–18
- ✦ Watanabe YY, Nakamura I, Chiang WC (2021) Behavioural thermoregulation linked to foraging in blue sharks. *Mar Biol* 168:161
- Weihls D (1973) Mechanically efficient swimming techniques for fish with negative buoyancy. *J Mar Res* 31: 194–209
- ✦ Willis J, Phillips J, Muheim R, Diego-Rasilla FJ, Hobday AJ (2009) Spike dives of juvenile southern bluefin tuna (*Thunnus maccoyii*): a navigational role? *Behav Ecol Sociobiol* 64:57–68
- ✦ Yasuda T, Katsumata H, Kawabe R, Nakatsuka N, Kurita Y (2013) Identifying spawning events in the Japanese flounder *Paralichthys olivaceus* from depth time-series data. *J Sea Res* 75:33–40
- Yu HS, Song GS (2000) Submarine physiographic features in Taiwan region and their geological significance. *J Geol Soc China* 43:267–286

Editorial responsibility: Simon Pittman,
Oxford, UK
Reviewed by: 2 anonymous referees

Submitted: March 1, 2022
Accepted: August 29, 2022
Proofs received from author(s): October 10, 2022