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Migration Behavior of *Anguilla celebesensis* Silver Eels within their Tomini Bay Spawning Area

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The tropical Celebes eel, *Anguilla celebesensis*, has a short migration between its spawning and growth habitats. Its spawning areas were hypothesized to be in Tomini Bay and the Celebes Sea after collecting their small leptocephali. However, there is no information about the silver eel oceanic spawning migration behavior of *A. celebesensis*. To better understand their short-distance spawning migration behavior, four large female silver eels (Eel 1–4) were equipped with pop-up satellite archival tags (PSATs) and released near the mouth of the Poso River in Tomini Bay of Sulawesi Island on 22 February (Eel 1–3) and 11 March 2010 (Eel 4). All PSATs ascended in Tomini Bay and transmitted their data. Eel 3 and 4 provided clear records of consistent diel vertical migration (DVM: eight days-Eel 3, 13 days-Eel 4) with daytime dives to mean depths of 444.7 m (Eel 3) and 539.0 m (Eel 4), where mean temperatures were 9.1°C (Eel 3) and 7.7°C (Eel 4), and nighttime ascents to mean depths of 132.8 m (Eel 3) and 112.4 m (Eel 4), where

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mean temperatures were 20.6°C (Eel 3) and 23.4°C (Eel 4). Eel 3 and 4 started to dive to deeper water around nautical dawn and swam up to shallower water around sunset. During nighttime, both eels swam in deeper and colder water during nights with moonlight than during nights without moonlight, and there was a negative linear relationship between experienced water temperatures with the moon in the sky and the lunar age for the eels. The *A. celebesensis* daily rhythm of DVM behaviors was similar to spawningmigration DVM behaviors of other anguillid species. Essential life history characteristics of *A. celebesensis* appear to be a short migration between freshwater growth habitat and ocean spawning habitat, and high GSI values with advanced gonadal development in downstream-migrating silver eels.

Key words: Celebes eel, Diel vertical migration, Lunar cycle, Spawning migration, Migration distance

BACKGROUND

Over the past decade, technological advances in telemetry have transformed the ability to observe aquatic animal behavior and movements (Hussey et al. 2015). The well-known long distance spawning migrations of freshwater eels fascinated biologists and stimulated research (Aoyama 2009), and now they have been studied using new technologies (Béguer-Pon et al. 2017). The early stages of the migration behavior patterns of anguillid silver eels were studied using acoustic tracking methods (see Béguer-Pon et al. 2017), and then more recently the oceanic migration behaviors were studied using pop-up satellite archival transmitting tags (PSATs). The PSATs collect depth, temperature, and light intensity data over long periods up to several months while attached to the silver eels. Many PSATs studies have been conducted on the oceanic migration behaviors of silver eels of the temperate species of Anguilla dieffenbachii (Jellyman and Tsukamoto 2010; Watanabe et al. 2020), A. anguilla (e.g., Aarestrup et al. 2009; Righton et al. 2016; Wright et al. 2022), A. japonica (Manabe et al. 2011; Chen et al. 2018; Higuchi et al. 2018 2021), A. rostrata (e.g., Béguer-Pon et al. 2017), and A. australis (Koster et al. 2021) and also of tropical silver eels of A. marmorata, A. megastoma, A. obscura, and A. bicolor pacifica (e.g., Schabetsberger et al. 2015 2021; Chen et al. 2018). These studies showed that anguillid silver eels, regardless of the species, consistently perform diel vertical migration (DVM) behaviors during their spawning migrations in offshore waters. These DVM behaviors consist of swimming at much deeper depths during daytime (mostly > 800 m) and then coming up to shallower depths at night (mostly < 200 m).

These DVM behaviors of anguillid eels are thought to be for predator avoidance, although thermoregulation to control metabolic rate and gonad maturation may also play a role (Aarestrup et al. 2009; Jellyman and Tsukamoto 2010; Manabe et al. 2011). Higuchi et al. (2021) found three Japanese eels were ingested by predators near dawn at depths when the eels start the decent phase of their DVM, and potential predators were estimated to be tuna and swordfish that have heat conservation ability. European eels and American eels were also documented to be preyed on by several types of fish predators or marine mammals (Righton et al. 2016) and by porbeagle sharks (Lamna nasus) and likely Atlantic bluefin tuna (Thunnus thynnus) in the Gulf of St. Lawrence (Béguer-Pon et al. 2012). Because these DVM behaviors to swim deeper during the day to reduce predation from various predators are performed by both temperate and tropical anguillid silver eels, they may be part of the original characteristics of the genus Anguilla that appears to have originated in tropical regions (see Aoyama 2009). One place where many tropical anguillid species are present and short-distance spawning migrations occur is the Indonesian Seas region. At least five species (A. celebesensis, A. interioris, A. marmorata, A. borneensis, A. bicolor pacifica) of tropical anguillid eels are present in the region around Sulawesi Island of north-central Indonesia (Ege 1939; Sugeha et al. 2001; Aoyama et al. 2003 2018; Kuroki et al. 2006; Sugeha 2012). One of the common species on Sulawesi Island is the Celebes eel (Tsukamoto et al. 2020), A. celebesensis, which has spawning areas in the Celebes Sea and Tomini Bay based on collections of small eel larvae (Aoyama et al. 2003 2018). Because of the small size of Tomini Bay (Fig. 1), the spawning migration of A. celebesensis silver eels is shortest known spawning migration distance among anguillid eels. The spawning migration distance of this species in Tomini Bay was presumed to be only 80-300 km (Aoyama et al. 2003), which contrasts with the much longer migration distances of temperate eels of about 900-8000 km (Aoyama 2009). Moreover, A. celebesensis silver eels migrating out from Lake Poso of central Sulawesi Island have high gonadosomatic index (GSI) values and remarkably welldeveloped oocytes just before downstream migration

Fig. 1. (A) Map of the Indonesian Archipelago region showing Tomini Bay (red rectangle). (B) The release (yellow star) and pop-up locations of the four tagged Celebes eels (red circles), and the location of the CTD hydrographic profile (black circle).



compared to the *A. marmorata* that also migrate out of the lake (Hagihara et al. 2012 2020; Arai 2014), but spawn offshore far to the north in an overlapping area with *A. japonica* (Kuroki et al. 2009).

Because of the possibly unique short-distance spawning migration of *A. celebesensis* in Tomini Bay, studying their migratory behavior could be useful to enhance our understanding of the ecology and evolution of anguillid eels. Therefore, the objective of this study was to examine the spawning migration behavior of *A. celebesensis* in Tomini Bay using PSATs. Furthermore, we also report a possible predation event on a tagged eel detected by analysis of the range of temperature differences between ambient water temperature and tagrecorded temperatures.

MATERIALS AND METHODS

Eel specimens, tag attachment, and release site

Eight migrating Anguilla celebesensis were obtained from commercial fisherman using large weirs in the outlet of Lake Poso (1°45'30"S, 120°38'30"E) on Sulawesi Island, Indonesia during late February and early March 2010. Detailed information about the weirs was described in Hagihara et al. (2018c). Eels captured by the weirs can be regarded as migrating eels that had just started their downstream migration from Lake Poso to Tomini Bay, which is consistent with their silvering-related characteristics, gonadal development, and reproductive hormone levels (Hagihara et al. 2012 2020). These eels were transported in plastic bags (110 cm × 85 cm) in water containing one-third seawater while being cooled with ice until being held in a wooden box (100 cm \times 200 cm \times 100 cm deep) in the seawater along the coast of Tomini Bay for several days before release.

The MiniPAT (Wildlife Computers, USA) used in the study weighed 53 g, were 115 mm in length (excluding antenna) and were pressure tested to a depth of 2000 m. The three tags used on 22 February 2010 (Eel

1–3) were preprogrammed to record water temperature (resolution $\pm 0.05^{\circ}$ C) and depth (resolution ± 0.5 m) every 75 seconds. The tag of Eel 4 used on 10 March 2010 was preprogrammed to record water temperature and depth every five minutes. Moreover, ascents were set at 14 days for Eel 1-3 and at 60 days for Eel 4 after deployment. In case of premature death of the tagged eel or detachment of the tag from its body, the MiniPAT tags were preprogrammed to commence a premature release setup and then transmit data after reaching the surface. The premature release setup initiates compulsorily release of the tag at > 1800 m or after 72 h at a constant depth (\pm 2.5 m). However, this procedure did not work in two of the PSAT tags, because the tag did not surface after 72 h at 1800 m or deeper, but they did eventually detach from the weight that was part of the tag attachment harness.

The four largest A. celebesensis (Eel 1-4) were chosen for attachment with PSAT (Table 1). Before release, they were individually removed from the wooden box, anaesthetized with eugenol (2‰) in a plastic bucket (80 cm \times 80 cm), their lengths and body weights were measured, and the silvering index was determined based on Okamura et al. (2007) and Hagihara et al. (2012). Moreover, dorsal fin tissue was sampled for DNA species identification of each individual. Surgical tagging was carried out according to Manabe et al. (2011). Tagged eels were retained in a plastic bag (110 cm \times 85 cm) with sea water until they recovered from anesthetization. Releases were conducted separately on 22 February and 11 March 2010. Eel 1–3 were released near the mouth of the Poso River in Tomini Bay from a boat at a point where the water depth was more than 200 m deep during daytime from 11:18 to 13:35 on 22 February, and Eel 4 was released at the same point (120°45'E, 1°22'S) at 12:45 on 11 March (Fig. 1B, Table 1). The eels were later genetically confirmed as being A. celebesensis by comparing their mitochondrial DNA 16S ribosome RNA sequences to existing sequences of the species (Aoyama et al. 1999). The eel release points and PSATs surfacing locations in the southern part of the inner/western region

Table 1. Biological data of the four Celebes eels studied with PSAT tagging, and eel release and tracking information.TL: total length; BW: body weight; SI: silvering index

Eel no.	TL (mm)	BW (g)	SI	Release timing -		Release location		Don un timino		Pop-up location		Tracked
						Longitude	Latitude	r op-up tinning		Longitude	Latitude	duration (day)
Eel 1	887	1400	S1	22 February 2010	11:18	120°45'E	1°22'S	14 March 2010	05:29	121°10'E	0°46'S	20
Eel 2	937	2050	S 1	22 February 2010	12:32	120°45'E	1°22'S	09 March 2010	04:10	121°11'E	1°17'S	15
Eel 3	904	1640	S 1	22 February 2010	13:35	120°45'E	1°22'S	09 March 2010	06:43	120°47'E	0°33'S	15
Eel 4	899	1350	S 1	22 March 2010	12:45	120°45'E	1°22'S	17 June 2010	18:24	120°30'E	0°49'S	121

of Tomini Bay were plotted over a bathymetric chart (SRTM_PLUS, Olson et al. 2014; Generic Mapping Tools, Wessel et al. 2013, Figs. 1B, S1).

Definition of behavioral patterns

To analyze the swimming depths and experienced

water temperature of *A. celebesensis* in detail, the tracking records of the whole tracking periods were visually assessed and separated into periods of adaptation (I), DVM (II), predation (III), abnormal vertical behavior (IV), tag drifting or stopped position (V), and tag sinking (VI; Fig. 2). Then, the exact transition points between each status were determined



Fig. 2. Depth and temperature records of the four Celebes eels tagged with PSATs and released into Tomini Bay. The swimming depths (blue lines) and water temperatures (red lines) are shown in each panel. Tracking data were separated into periods of adaptation (I), diel vertical migration (II), predation (III), abnormal vertical behavior (IV), tag drifting or stopped position (V), and tag sinking (VI). The yellow, half yellow, and black circles show days of full moon, first quarter moon, and new moon, respectively. The black inverted triangles show surfaced PSATs. Eel 4 recorded data until 0:00 on 10 April 2010 (D), but the tag remained at the same depth until 20 May, which is not shown.

using R (R Core Team 2015) and the 'changepoint' package (Killick and Eckley 2014), which is explained by Higuchi et al. (2021). The adaptation phase is the period when some eels showed irregular vertical movements before they began performing DVM behaviors. The abnormal vertical behavior phase is the period when the eel ceased showing DVM, possibly because of reduced swimming stamina, or effects of predation. The tag drifting period is when the PSAT drifts on the sea surface after detaching from the eel.

Data analysis of diel vertical migration

To analyze the eels' DVMs (behavior pattern II, Fig. 2C, D) in detail, the daily DVMs were divided into four basic DVM periods of daytime, ascent, nighttime, and descent based on the methods reported in Westerberg et al. (2014), Chow et al. (2015), and Higuchi et al. (2021). In brief, the start and end points were defined as periods that had ≥ 10 consecutive minutes of either ascending or descending depths during each transition period in both shallower nighttime and deeper daytime depths. The swimming depths and water temperatures were compared among the four DVM periods of each of the two eels that showed regular DVM using Kruskal-Wallis tests followed by Steel-Dwass tests. The swimming depths and water temperatures of each of the four DVM periods were compared between the two eels using Brunner-Munzel tests. For nighttime analysis periods, the two tagged eels (Eel 3 and 4) with tracks that covered more than half of a lunar cycle (lunar age: 0-15/15-30) were used to check analysis correlation accuracy between lunar age and the swimming depth and experienced water temperature. Astronomical factors such as lunar age (http://koyomi.vis.ne.jp/) and time of sunrise and sunset (https://keisan.casio.jp/exec/system/1184726771) were estimated at an intermediary point between the release and surfacing locations of each tag (Higuchi et al. 2021). The nighttime swimming depths were separated into when the moon was present in the sky (moon altitude > 0) and absent (moon altitude < 0), and they were compared by Brunner-Munzel tests during each night. The weather conditions such as cloud cover or rainfall were not taken into account in this analysis. The correlations between each astronomical factor and swimming depth and experienced water temperature in each of the four DVM periods were tested by normal/ partial Spearman's rank correlation coefficient.

Estimation of predation

To detect possible predation events for the tagged eels, the recorded depths and water temperature data of

each PSAT were compared to the environmental water temperature structure at the hydrographic observation station using Conductivity Temperature Depth profiler (CTD, Sea-Bird Electronics, USA) in Tomini Bay (120°45'E, 1°2'S, Figs. 1B, S2), which was in the center of the area where the eels were likely swimming. The CTD was made during a R/V *Hakuho Maru* research cruise in the central Indonesian Seas (JAMSTEC, Japan, 9 March 2010, KH-09-5, Leg 7, St. 6) to collect eel larvae (Aoyama et al. 2018) at the time of the eel tagging experiment.

If differences between the tag-recorded temperature and the same-depth CTD profile temperature (Fig. S2) exceeded a standard criterion during tracking, tagged eels were judged to be preved on by an endothermic predator. To establish a criterion of the temperature difference for detecting predation events, the difference between the experienced temperature of Eel 3 and environmental CTD water temperature was used (Higuchi et al. 2021). Large predators such as tunas and swordfish typically have large-scale vertical movement behaviors. The peritoneal cavity temperature of some endothermic fish is higher than the ambient water temperature just after diving from shallower/ warm to deeper/cold layers and lower than ambient water temperature just after rising from deeper/cold to shallower/warm layer (Musyl et al. 2003; Hino et al. 2019). The change point of mean and dispersion data of the temperature difference was used to determine if predation occurred using R (R Core Team 2015) with the 'changepoint' package (Killick and Eckley 2014). After predation occurred (behavior pattern III), the tag-recorded depth and temperature would reflect the swimming depth and peritoneal cavity temperature of the predator. Based on the pattern of the depth variation and temperature characteristics, the general type of the predator was estimated.

RESULTS

Pop-up location and tracking period

All four PSATs that were attached to each eel were eventually released from the eels or egested from a predator and then reached the surface and transmitted their archived data to an ARGOS satellite (Fig. 1B, Table 1). The tags came off of the eels after 15–121 days (Table 1). The pop-up locations for three tags (Eel 1, 3, and 4) were in the southern part of the western region of Tomini Bay and the other tag (Eel 2) ascended near the Tomini Bay coast (Fig. 1B). The tags that surfaced offshore were located over different slope areas of the shallow ridge (< 500 m) that separates two deeper

basins that are > 1500 m deep. The distance from release location to pop-up locations of the four tagged *A*. *celebesensis* ranged from 48.6–91.1 km (Fig. 1B).

Behavioral statuses

The changepoint analyses defined the different status-periods for tracks in four individual eels. There were either three (Eel 1 and 2) or five (Eel 3 and 4) changepoints from the start to the end of the recorded experienced water temperature data of each eel, resulting in the behavioral patterns being divided into two (Eel 1 and 2) or four (Eel 3 and 4) periods (Fig. 2). Pattern I shows irregular vertical movement that occurred until the changepoint when DVM behaviors started, which were defined as behavior pattern II (normal DVM) (Fig. 2C, D). Abnormal vertical behaviors and remaining at almost the same positions were designated as patterns IV and V, respectively (Fig. 2). However, the temperature data during the pattern IV period of Eel 1 showed a DVM pattern was only within a narrow depth range, so it was classified as abnormal. Behavior pattern III was predation (Fig. 2C), which will be described later. Finally, behavior pattern VI consisted of the tag suddenly sinking to the release trigger-depth (recorded maximum depth: 1653 m, Fig. 2C).

Comparisons of diel vertical migration statuses for 2 Celebes eels

The DVM behaviors of Eel 3 and 4 transitioned between deeper/colder layers in daytime (Eel 3: mean depth 444.7 m, Eel 4: 539.0 m, both ranges: 39-611.6 m; Eel 3: mean water temperature 9.1°C, Eel 4: 7.7°C, both ranges: 7-13.1°C; Table S1, including a spike-like ascent by Eel 3 after sunrise: Fig 3A) and shallower/ warmer layers in nighttime (Eel 3: 132.8 m, Eel 4: 112.4 m, both ranges: 10-212 m; Eel 3: 20.6°C, Eel 4: 23.4°C, both ranges: 14.3-29.3°C; Table S1, including several spike-like ascents by Eel 3: Fig 3A), with clear daily rhythms (Fig. 3). The analysis periods of the 2 eels that showed DVMs were performed for 21 days (Eel 3: 8 days around full moon, Eel 4: slightly > 13days from new moon to first quarter moon, Fig. 2C, D). The detailed analysis periods of the DVM of Eel 3 and 4 for correlations between nighttime swimming depth and lunar age had > 15 days. Swimming depths and experienced water temperatures of Eel 3 and 4 each had significant differences among their three phases of daytime, ascent or descent, and nighttime (all p < 0.001; Fig. 4) but were not different between ascent and descent (all p > 0.16; Fig. 4). Furthermore, the swimming depths and experienced water temperatures of Eel 3 and 4 had significant differences between each of their 4 phases of daytime, ascent, nighttime and descent (all p < 0.001, swimming depths: figure 4A vs B, experienced water temperatures: Fig. 4C vs D). The swimming depths and experienced water temperatures of Eel 4 in daytime were deeper and colder than Eel 3 and the swimming depths and experienced water temperatures of Eel 3 in nighttime were shallower and warmer than Eel 4 (Fig. 4).

Nighttime behavior and lunar cycle

Eel 3 and 4 showed several patterns of nighttime swimming depths that were likely related to their locations, the lunar cycle, and whether the moon was present in the sky or absent. Their swimming depths and experienced water temperatures each had significant differences between with-moon and withoutmoon in the sky (all p < 0.001, Fig. 5, Table S2). Eel 3 showed the most distinct changes in swimming depths and experienced different water temperatures at night compared with Eel 4. Eel 3 swam deeper than Eel 4 at night with-moon and swam shallower than Eel 4 at night without-moon (all p < 0.001, Fig. 5A vs B, Table S2). As a result, Eel 3 experienced cooler water temperatures than Eel 4 at night with-moon and experienced warmer water temperatures than Eel 4 at night without-moon (all p < 0.001, Fig. 5C vs D, Table S2). There were significant linear relationships between swimming depths or water temperatures with the moon in the sky and the lunar age for the two eels (rho = 0.28: swimming depths and rho = -0.19: water temperatures, all p < 0.05, Fig. 6A, C). However, there were no significant linear relationships between swimming depths or water temperatures without the moon in the sky and the lunar age for the two eels (rho = 0.21: swimming depths and rho = -0.26: water temperatures, all p > 0.05, Fig. 6B, D). Regardless of moon presence, the eels did not stay at the same depth both during night and day times and were constantly moving up and down in small depth increments (Fig 3A, B).

Predation

The range of temperature differences between ambient water temperature and tag-recorded temperatures of Eel 1, 2, and 4, when there was no evidence of experiencing a predation event, was from -3.6 to +3.5°C (Fig. S3A, B, D). Therefore, if a tagged eel showed a magnitude of temperature difference that exceeded ± 4 °C, it was suggested to be ingested by a predator with heat conservation ability. According to this, Eel 3 was estimated to be ingested by a predator with heat conservation ability, because this tag recorded temperature differences of -9.3 to +15.3°C, Figs. 7,

S3C).

The change point determination analyses of the sudden changes in the vertical distribution behaviors of Eel 3 suggested that it was ingested by a predator when swimming at 197.5 m at 22:59 on the night of 4 March 2010 (Fig. 7). There were clear differences between the ambient and experienced temperatures of Eel 3 before, during and after the predation event (Fig. S3C). Furthermore, the tag-recorded temperatures of Eel 3 before and during predation were distributed within and then out side of the range that was used as the determination criteria for predation events (Fig. 7). Therefore, the PSAT of Eel 3 was apparently recording the peritoneal cavity temperatures of the endothermic predator from ingestion to egestion (Fig. 7). The predator of Eel 3 repeated vertical migrations from near the surface to as deep as 405 m each day for four

days (Fig. 7). Since the depth records of this tagged eel showed that the PSAT fell directly to 1800 m just before tag surfacing, it is presumed that the tag was ejected by the predator and the tag float and weighted harness were separated after the tag sank to that depth (Fig. 7).

DISCUSSION

Diel vertical migration of Celebes eels in their spawning area

The present study released PSAT-tagged *A. celebesensis* silver eels at the edge of their Tomini Bay spawning area of eastern Sulawesi Island, Indonesia. These silver eels were caught at the outlet area of Lake Poso, where they have been found to have more



Fig. 3. The swimming depths (blue lines: A, B) and experienced water temperatures (red lines: C, D) during the diel vertical migrations (stage II) of Eel 3 (left panels: A, C) and Eel 4 (right panels: B, D) with each daily data set plotted together. The swimming depths of each eel are separated into four phases of daytime, ascent, nighttime, and descent.

advanced gonadal development levels than the *A.* marmorata silver eels that also migrate out of the lake (Hagihara et al. 2012; Arai 2014), but spawn in the western North Pacific (Kuroki et al. 2009). Catches of small larvae of *A. celebesensis* indicate that the Celebes eels spawn within Tomini Bay (Aoyama et al. 2003 2018), so the present study is the first study to record the DVM of *A. celebesensis* within their spawning area while having more advanced levels of reproductive development.

Two of the Celebes eels released into Tomini Bay showed continuous patterns of very clear and regular DVM behaviors for more than a week, which were the same type of DVM behaviors seen in previous tagging studies on anguillid eels. The two eels showed some minor differences in their depths occupied during their DVMs, partly due to different release times in relation to the lunar cycle, but they both mostly stayed between about 50–200 m at night. Eel 3 mostly moved down to maximum depths where the temperature was $8-9^{\circ}C$ (~440–520 m) and Eel 4 moved down to a very consistent 7–8°C (~520–610 m) during the day. Both eels gradually swam deeper with sun altitude during the day, indicating that they appeared to be responding to light intensity even at depths of about 400–600 m. These features of DVM behaviors have been observed in some other tropical and temperate anguillid species studied with PSAT tags (Schabetsberger et al. 2015 2021; Higuchi et al. 2021; Watanabe et al. 2020).

Eel 3 Eel 4 0 (A) (B) 100 Swimming depth (m) 200 300 400 500 600 700 30 (C) (D) Experienced water temperature (°C) 25 20 15 10 5 As Nt Ds Dy As Nt Ds Dy Phase

There were significant relationships between

Fig. 4. The swimming depths and experienced water temperatures of each eel during the four phases of daytime (Dy), ascent (As), nighttime (Nt), and descent (Ds). Blue box plots (A, B) show comparisons of the swimming depths and red box plots (C, D) show experienced water temperatures during each of the four phases for Eel 3 (left panels: A, C) and Eel 4 (right panels: B, D).

nighttime behavior of *A. celebesensis* and with the moon in the sky or the lunar age, although the weather was not considered in this study. There were significant differences in nighttime swimming depths between Eel 3 and 4. This is likely because the lunar age in the swimming periods of Eel 3 and 4 was different and was around full moon or from new moon to first quarter moon, respectively. However, the nighttime swimming depths of Eel 3 without the moon was shallower than that of Eel 4. One of the possible reasons for this is that the sun and moon light were hidden by the highelevation mountains (> 1000 m) of North Sulawesi Island around Tomini Bay (Fig. 1B) and there are dark times about two hours after sunset and before sunrise. Another reason is the several spike-like ascents made



Fig. 5. Swimming depths (upper panels: A, B) and experienced water temperatures (lower panels: C, D) with moon (yellow boxes) and without moon (gray boxes) of Eel 3 (left panels: A, C) and Eel 4 (right panels: B, D) that showed DVM behavior in nighttime.

during nighttime by Eel 3.

There were positive significant linear relationships between swimming depths with the moon in the sky and the lunar age for the two analyzed Celebes eels. As a result, the experienced water temperature with the moon present decreased when it was near the full moon and increased when it was near the new moon. There were no significant linear relationships between swimming depths without the moon in the sky and the lunar age for the two eels, which differed in their swimming depths in nighttime without moon as described above.

The swimming depths for the two eels had a similar effect on their experienced water temperatures. For example, there were significant differences in the experienced water temperature between Eel 3 and 4. The swimming depths shallower than the thermocline had a particularly large effect on the experienced water temperatures. The high experienced temperatures of Celebes eels may also contribute to further gonadal development, and the importance of temperature for gonadal development has been hypothesized for other species (Jellyman and Tsukamoto 2010). Because the Celebes eels leave the outlet of Lake Poso before they reach final maturation, the warm waters of Tomini Bay may be important for stimulating the last stages of gonadal maturation after their downstream migration. Tropical eels with short-distance migration such as Celebes eels may experience an unchanging temperature environment in their spawning area compared to temperate eels.

Although data sets of DVM behaviors were obtained, the swimming tracks of Eel 3 and Eel 4 could not be measured directly because of a lack of geolocation data. It appears though, that Eel 1 might have moved relatively directly to its pop-location within five days, while moving up and down through the depths of the thermocline using DVM, but within a narrow range of depths where the temperature changes rapidly. Eel 2 showed similar irregular DVM passing through the thermocline for two nights before the tag detached from the eel, and then the tag drifted at the surface and reached near the shore. In daytime, the swimming depths of Eel 3 were shallower than that of Eel 4. This difference may be due to the differences in sea bottom depth along their migration routes.

The pop-up locations of Eel 3 and 4 that showed longer periods of clear DVM were located on the other side of the shallow ridge that separates the two deep basins of the inner part of Tomini Bay (Fig. S1). However, Eel 3 was ingested by a predator, so its popup location would depend on the predator's swimming pattern. The predator remained < 400 m for the four days it contained the PSAT tag, so it may have crossed the shallow ridge area as the eels' daytime depths seemed to be too deep to cross the ridge.

Similarly, the Eel 4 daytime depths seemed to reach too deep to cross the ridge, so it may have crossed in the last five days during its abnormal DVM period. The continuous up-and-down swimming behavior during those five days seems unique compared to other swimming patterns of eels. The eel performed highly regular DVM for 15 days, then switched to continuously swimming up-and-down mostly through < 150 m depths (Fig. S1), which was within the main thermocline (Fig. S1). It is possible that the eel became weak or was affected by the PSAT tag and stopped performing large scale DVMs, making that abnormal behavior. However, since this eel was released from its native drainage river mouth and was swimming offshore within its general spawning area (a situation not observed in previous studies), it is possible it changed to a different type of natural pre-spawning vertical swimming behavior. For example, Japanese eels seem to spawn somewhere just below the thermocline based on eggs and newly hatched preleptocephali collection depths (see Aoyama et al. 2014), so its behavior might be related to the possible spawning depths. Unfortunately, the present study cannot distinguish between that scenario and abnormal DVM related to tagging effects.

Predation events

Eel 4 was not considered to have experienced predation by a heat-conserving predator, and the unusual DVM just discussed does not seem consistent with known ectothermic fish predators, which usually show diurnal cycles of behavior. However, Eel 3 was clearly ingested by a predator with heat conservation ability as indicated by the sudden changes in the depths of movements and by the comparisons to environmental temperatures. The recorded depths and temperatures appeared to be reflecting the swimming depths and peritoneal cavity temperatures of the predator, because there were repeated unique vertical movements compared to the swimming behaviors of Eel 3, and the peritoneal cavity temperatures also fluctuated between 18-26°C after being 8-29°C during the DVM of the eel (Fig. 7). Wahlberg et al. (2014) reported that marine mammals preyed on three migrating European eels that were tagged with PSATs. However, peritoneal cavity temperatures in the present study were lower than those of a marine mammal (~36°C, Wahlberg et al. 2014). During the ingested period, the tag of Eel 3 recorded relatively higher temperatures than the ambient water temperature just after diving from shallower/warmer



Fig. 6. Swimming depths (upper panels: A, B) and experienced water temperatures (lower panels: C, D) of Eel 3 (orange boxes) and Eel 4 (green boxes) during nighttime in relation to lunar age. The relationship between lunar age and swimming depth and experienced water temperatures with moon presence are shown in left panels (A, C) and without moon presence are shown in right panels (B, D). The two halves of the lunar month (0–30) are superimposed in inverse directions (0–15, new moon to full moon, and 15–30, full moon to new moon).

to deeper/colder layers and lower than ambient water temperature just after rising from deeper/colder to shallower/warmer layers. Higuchi et al. (2021) reported "if a tagged eel showed a magnitude of temperature difference that exceeded \pm 5°C, it was suggested to be ingested by a predator with heat conservation ability". In our study, the criteria range above \pm 4°C was considered evidence of experiencing a predation event.

The peritoneal cavity temperatures of large predators become relatively higher and lower than the ambient temperature when the predator dives to deeper layers and then rises up to shallower layers, respectively (Musyl et al. 2003; Hino et al. 2019). The records of the tag reflect the characteristics of thermal inertia of large predatory fish that make clear vertical movements. Therefore, the predator of Eel 3 was estimated to be a large fish that had high thermal inertia (Béguer-Pon et al. 2012). It is likely that the vertical movements in figure 7 were the W-shaped vertical movement patterns during the day, which are characteristic of bigeye tuna, *Thunnus obesus (i.e.,* descending to 300–500 m and then returning regularly to the surface layer; Musyl et al. 2003; Hino et al. 2019). Therefore, the predator of Eel 3 that repeated DVM in the upper 400 m may likely have been a bigeye tuna that ingested Eel 3 and the tag in the middle of the night and then the PSAT was egested about four days later.



Fig. 7. Predation and PSAT egestion events of Eel 3 that were observed by analyzing the temperatures and depths of the eel/PSAT tag and the predator. Differences between tag-recorded and observed environmental temperatures of Eel 3 (A, gray shaded area: $-4-4^{\circ}$ C). Swimming depths (blue lines) and experienced temperatures (red lines) of Eel 3 (B). The timing of predation and egestion are shown by vertical dotted lines in left and right sides of the predation period, respectively.

Life history of the Celebes eel

The life history of this particular species seems to be the most documented of any tropical anguillid, in part because it is mostly endemic to the central Indonesian Seas region, including the Celebes Sea area and the drainages that flow into Tomini Bay where it has been studied. Catches of small Celebes eel leptocephali indicate that it has at least two spawning populations or spawning areas, which are in the Celebes Sea and in the Tomini Bay (Aoyama et al. 2003 2018), with different seasonal patterns of inshore migration occurring in each area (Sugeha et al. 2001; Sugeha 2012). Two size classes of A. celebesensis leptocephali (13-23, 30-48 mm) were collected in Tomini Bay in May 2001 (Aoyama et al. 2003; Wouthuyzen et al. 2009) and a 17 mm A. celebesensis leptocephalus was also caught in 2010 during the survey associated with the present study (Aoyama et al. 2018) that was very close to the pop-up location of Eel 4. Most of the May 2001 leptocephali including the smallest larvae were caught just north of the Eel 3 pop-up location just northwest of the Eel 2 location. That data and weak surface currents in Tomini Bay and its semi-enclosed structure (Tita et al. 2020), indicate that the leptocephali collected in the bay were likely spawned there.

Larval catches also confirmed Celebes Sea spawning because small Celebes eel leptocephali (12.3-20.0 mm) were collected there in February 2000 (Aoyama et al. 2003; Kuroki et al. 2006; Miller et al. 2009) and a few larger larvae were collected there in May 2001 and September-October 2002 (Kuroki et al. 2006; Wouthuyzen et al. 2009). Otolith microstructure studies on glass eels in Sulawesi Island coastal rivers of the Poigar River and Poso River had ages at metamorphosis and at recruitment that were 90 ± 13.6 days and 112 ± 14.2 days for specimens from the Poigar River and 98 ± 7.2 days and 122 ± 7.2 days for the Poso River (Arai et al. 2003; note that northern Philippines's glass eels in that study, were likely the newly discovered species A. luzonensis of Watanabe et al. 2009, not Celebes eels). A larger sample size of glass eels from the Poigar River in an earlier study had similar ages (Arai et al. 2001; Miller et al. 2009). Sugeha et al. (2001) reported that A. celebesensis was the most abundant species (73-81% of glass eels including A. marmorata and A. bicolor pacifica) returning to the Poigar River in 1997-1999, and it was also the dominant species returning to the Poso River flowing into Tomini Bay from March 2008 to April 2009. The ages of the recruiting A. celebesensis glass eels appear to be the youngest of any species of tropical or temperate anguillid species studied so far (e.g., Miller et al. 2009; Kuroki et al. 2014; Hewavitharane et al. 2020), which is consistent with having a short migration loop.

Other aspects of their life history have been studied to learn about the inland yellow eel growth stage and the migratory silver eels of A. celebesensis. Yellow eels occurred frequently in the inlet rivers of Lake Poso and some were found in Lake Poso (Hagihara et al. 2018b). The age and growth rates of downstream migrating females (n = 63, 58–1083 mm) were 7.5 \pm 1.6 (5–11) years and 100.7 \pm 17.2 (68.1–145.0) mm/ year (Hagihara et al. 2018a). Downstream migrating silver eels in Lake Poso were spawning between late February-early May 2001 (Wouthuyzen et al. 2009) and most silver eels start downstream migration during the early to middle rainy season (Hagihara et al. 2018c). The GSI values (range: 4.6-11.2%) were significantly greater than those of the migrating silver-stage A. marmorata (0.0-6.24%) and A. japonica (1.2-4.0%)(Arai 2014). Hagihara et al. (2020) examined the reproductive physiological characteristics of Celebes eels using downstream-migrating and non-migrating female eels and showed that this species has remarkably well-developed oocytes just before downstream migration.

The results of the present study show that Celebes eels performed DVM behaviors in Tomini Bay where spawning appears to occur based on the previous larval catches. Therefore, the three essential life history characteristics of *A. celebesensis* appear to be 1) a short migration between freshwater growth habitats and local ocean spawning habitats, which 2) begins with the downstream migration of silver eels with high GSI values and well-developed gonads, and 3) the leptocephali then have a short larval duration in retention areas before recruiting to local growth habitats.

CONCLUSIONS

Two of the four Celebes eels released into their Sulawesi Island Tomini Bay spawning area showed regular patterns of DVM behaviors and their swimming depths and timing of movements between shallow nighttime depths and deeper daytime depths were influenced by light levels from both the sun and moon. Their daily rhythm of DVM behavior within the bay where they spawn was the same as has been found in other anguillid species during their spawning migrations. The unique characteristics of the life history of *A. celebesensis* appear to be their short migration between growth habitats and spawning habitats, the high GSI values with advanced gonadal development gonads of downstream migrating silver eels, and the short larval duration. Future studies can continue to contribute to a better understanding of the factors that influence the specific migratory behaviors of swimming depths during DVM and the spawning migration routes of anguillid eels. More research is also needed to understand the migratory and reproductive ecology of the short spawning migrations of the Celebes eel and other anguillid species in the region.

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Authors' contributions: SW, RM, JA, and KT contributed to designing the study, KT provided the popup tags, and TH, SW, RM, and HK analyzed the PSAT data and examined the relationships with astronomical data. SH, RM, TY, and KS collected the silver eels and attached the tags. FYT, HYS, AS, SW, T, and KWAM helped to negotiate and obtain permission for the cruise, eel sampling, and the PSAT tagging experiment in Indonesia from national and local governments. RM, FYT, T, and KS released the tagged eels from the boat in Tomini Bay. SW, FYT, RM, TH, and MJM drafted the manuscript and SW, FYT, HYS, MJM, and other coauthors participated in revising and approving the final manuscript.

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Availability of data and materials: The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Ethics approval consent to participate: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The surgical attachments were done in an anesthetized condition.

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Supplementary materials

Fig. S1. A higher resolution bathymetry map showing release (yellow star) and pop-up locations of the four tagged Celebes eels (red circles) in Tomini Bay. (download)

Fig. S2. The depth changes of water temperature (red dots), salinity (blue dots), sigma-t (orange dots), and chlorophyll-a (green dots) in the upper 1000 m at the CTD hydrographic station in Tomini Bay (black circle in Fig. 1) during KH-09-5. These data of water temperature were used to compare to experienced swimming depth and water temperature from the PSATs data. (download)

Fig. S3. Differences between tag-recorded and observed environmental temperatures in the CTD hydrographic cast for Eel 1 (A), Eel 2 (B), Eel 3 (C), and Eel 4 (D). The gray shaded areas show the same temperatures ranges (-4 to 4° C). (download)

Table S1. The means and standard deviations of swimming depths and experienced water temperatures separated into four phases of daytime, ascent, nighttime, and descent during DVM behavior (II) of Eel 3 and 4. (download)

Table S2. The means and standard deviations of swimming depths and experienced water temperatures with moon and without moon of Eel 3 and 4 that showed DVM behavior (II) in nighttime. (download)