

Seaward Migration Routes of Indigenous Eels, *Anguilla japonica*, *A. marmorata*, and *A. bicolor pacifica*, via Satellite Tags

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Shih-Chong Chen, Ching-Rong Chang, and Yu-San Han (2018) The spawning migration of the Japanese eel, *Anguilla japonica*, along the western Mariana Ridge is considered one of the longest animal migrations. To establish an appropriate conservation policy for this species, a complete life cycle study is required, but the migratory routes of anguillid eels remain poorly documented. *Anguilla japonica*, *A. marmorata*, and *A. bicolor pacifica* are three common eel species in Taiwan. The present study used pop-up archival transmitting tags to track their movements during the oceanic phase of their migration. Twenty silver eels (farmed and wild) were tagged and released near the Gueishan and Liuchiu Islands. All three species in the Gueishan Island group were entrained in the Kuroshio Current, and pop-up tag data showed that, after 23 days, the farthest distance travelled was approximately 1,500 km, to the southern waters of Yakushima, Japan. In comparison, eels released near Liuchiu Island moved in the opposite direction, which suggests that they were influenced by the recirculation in the southwestern waters of Taiwan. The migration speed of eels was estimated to be between 12.9 km/d and 65.2 km/d. Several eels exhibited diel vertical migration behavior, moving into deeper water during the daytime and ascending into shallower waters at night. The farmed eels exhibited similar patterns of diel vertical migration to wild eels. The results of this study suggest that eels from Taiwan travel through the Kuroshio Current during their early migration, irrespective of species and source. Of importance, farmed eels appeared to behave similar to wild ones following artificial release. This information provides important rationale for releasing cultivated eels for resource enrichment programs.

Key words: Eel, Spawning migration, Pop-up archival transmitting tag, Diel vertical migration, Kuroshio Current.

BACKGROUND

There are 19 species and subspecies of eel (family Anguillidae, genus *Anguilla*) worldwide. Most species are distributed in the Indo-Pacific Ocean area. Four species of *Anguilla* eel have been found in Taiwan: *A. japonica* (Japanese eel), *A. marmorata* (Giant mottled eel), *A. bicolor pacifica* (Shortfin eel), and *A. luzonensis* (Luzon mottled eel) (Tzeng 1982 1983; Tzeng and Tabeta 1983; Teng et al. 2009; Watanabe et al. 2009). *A.*

japonica and *A. marmorata* are the most common eel species in Taiwan (Han 2010).

The anguillid eel is a catadromous species. *A. japonica* is a temperate eel species that was listed in the IUCN Red List of Threatened Species as an endangered species in 2014. It is characterized by long-distance oceanic migration from continental freshwater habitats to its spawning areas along the western Mariana Ridge, near 14-16°N, 141-142°E (Tsukamoto 2006 2009), which is over 2,000 km away from the Asian continent. *A. marmorata* and *A.*

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bicolor pacifica are tropical eel species, and their spawning areas are assumed to be in the North Equatorial Current (NEC) region, near the Mariana Ridge. Leptocephali of *A. marmorata* have been collected throughout the NEC region to the west of 142°E, but not to the east of it. The latitudinal range (12–18°N) of the leptocephali is wider than the determined spawning area of *A. japonica* (Miller et al. 2002). *A. bicolor pacifica* is distributed throughout the western Pacific Ocean region. The spawning site of *A. bicolor pacifica* has not been determined; however, one study suggested that the spawning area is located in the NEC region. The leptocephali of *A. bicolor pacifica* have been caught in the waters of western New Guinea and to the west of the Mariana Ridge (Aoyama 2009). Thus, establishing the seaward migration of silver eels would provide information on the final stages of their life cycle.

Anguillid eels transform from yellow to silver once they have sufficiently matured for their seawater migration; however, the mechanism triggering this stage remains unclear. When the eels initiate the long oceanic migration, various morphological and physiological changes occur. Various adaptations include the silvering of the skin (Pankhurst and Lythgoe 1982; Han et al. 2003), the enlargement of eyes and pectoral fins (Pankhurst 1982; Han et al. 2003), the degeneration of the alimentary tract (Pankhurst and Sorensen 1984; Han et al. 2003), a shift in retinal sensitivity (Andjus et al. 1998; Zhang et al. 2000), changes to musculature (Egginton 1986) and fat content (Larsson et al. 1990), modifications to the swim bladder (Kleckner 1980; Yamada et al. 2001), and an increase in the chloride cells of the gills (Fontaine et al. 1995; Sasai et al. 1998). These changes appear to improve the swimming ability of eels and reduce the likelihood of predation in the ocean, which, in turn, provide them with a greater chance of reaching the spawning areas.

Previous studies have shown that restocked eels might be an effective way to recover natural eel resources in Europe. In 2006, tagged restocked and wild eels were documented migrating toward the outlets of the Baltic Sea, which included both restocked and wild eels (Sjöberg et al. 2008). One study estimated that 26.7% of all coastal eels at the outlet of the Baltic Sea came from restocked sources (Limburg et al. 2003), while another study estimated 21.3% (Clevestam and Wickström 2008). In Taiwan, the Fisheries Research Institute has been releasing cultured Japanese eels since 1976 (Liao et al. 1994). The eels are released

into rivers or estuaries after being injected with microchips. However, the efficiency of releasing cultured eels has been questioned because the eels are moved from aquafarms, where they have been maintained in an artificial environment for years. It is also questionable whether there are significant differences in the migratory behaviors of wild and cultured eels, including their choices of seaward migration routes. Several tracking studies have used acoustic tags to examine the migratory behavior of silver eels in the ocean (Tesch 1978 1989; Aoyama et al. 1999, 2002; McCleave and Arnold 1999; Chow et al. 2015). However, the tracking duration was too short to cover the entire migratory period and the ocean depth studied was limited.

The development of pop-up satellite archival transmitters has allowed data to be collected for longer periods. Studies of released tagged European eels in the Mediterranean and Baltic Seas have been undertaken for years. In general, released European eels tend to travel to subtropical areas, and then to the Sargasso Sea (Wysujack et al. 2015; Amilhat et al. 2016; Righton et al. 2016). American eels were successfully tracked from the continental shelf and shown to cross the Gulf Stream and swim toward their spawning area in the Sargasso Sea (Béguet-Pon et al. 2015). One tagged *A. marmorata* eel traveled 843 km toward the South Equatorial Current from Vanuatu (Schabetsberger et al. 2013). Only a few tracking studies of Japanese eels have been carried out, and these studies have been designed differently in terms of eel-release positions, methods of tag attachment, and eel life stage (Tsukamoto 2009; Manabe et al. 2011; Chow et al. 2015). Tagged Japanese eels have been recorded swimming in the Kuroshio Current (Manabe et al. 2011). All anguillid eels exhibit diel vertical migration (DVM) behavior during their oceanic migration, with migrating eels preferring shallower water (100–300 m) at night and deeper water (500–700 m) during the daytime.

Eels released in Taiwan have not been previously evaluated. Thus, this study aimed to: (1) determine the seaward migration route of *A. japonica*, *A. marmorata*, and *A. bicolor pacifica* from Taiwan and (2) compare the seaward migration behaviors of wild and farmed eels. Our results provide information on the similarities and differences between farmed and wild eels during migration and suggest the value of release programs using farmed eels.

MATERIALS AND METHODS

Eels

Eels were obtained from the fish market in Ilan and Pingtung Counties, Taiwan. Four farmed eels (two *A. marmorata* and two *A. japonica*) and six wild eels (one *A. marmorata* and five *A. bicolor pacifica*) were selected for tagging and release in 2015, while 10 farmed *A. japonica* were selected for tagging and release in 2016. Eels were selected based on morphological characters that distinguished them as having completed their yellow life stage: black dorsal color, bigger eyes, larger pectoral fins, and more melanin (Han et al. 2003).

The eels were maintained at an ambient temperature (approximately 25°C) in a tank, and the salinity of the water was stepwise increased to 30‰ by adding salt over 10 days. The water was replaced with seawater after the tank reached seawater conditions. The temperature was then controlled using an electric system at a constant 23°C. To assess the condition and stage of the eels, measurements of total length, body weight, eye diameter, and pectoral fin length were made. The ocular index and pectoral fin index was also calculated (Pankhurst 1982; Han et al. 2003) (Table 1).

Release sites

In total, 20 eels were released between 2015 and 2016 at 10 eels per year. In 2015, tagged eels were released in three batches from three different locations around Gueishan Island, Ilan County. One eel was released on August 11, 2015 at 24°51'8.00"N, 121°53'40.00"E (R1, Fig. 1), four on September 18, 2015 at 24°51'50.90"N, 121°59'59.11"E (R2, Fig. 1), and five on November 3, 2015 at 24°51'38.24"N, 121°59'35.10"E (R3, Fig. 1). In 2016, 10 eels were separated into two groups and released around Gueishan Island, Ilan County and Liuchiu Island, Pingtung County. Four eels were released on October 11, 2016 at 24°52'3.00"N, 121°58'7.00"E (R4, Fig. 1) and on November 1, 2016 at 22°23'39.92"N, 120°24'12.77"E (R5, Fig. 1). Release locations ranged from 300 to 400 m in depth.

Types of tags

Two different types of pop-up archival transmitting tags were attached to the eels: the

MiniPAT in 2015 and the mark report PAT (mrPAT) in 2016 (purchased from Wildlife Computers Inc.).

MiniPAT: The MiniPAT tag is 124 mm in length, has a maximal diameter of 38 mm, and weighs 60 g in air. Its range of depth is 0 to 1700 m and range of temperature sensor is -40 to 60°C. The MiniPAT is equipped with depth, temperature, and light sensors. A mortality detection mechanism is set so that the depth variance is recorded within 3 m for 10 days. Once the mortality event is determined, the release pin burns through, which separates the tag from its tether. The tag then floats to the surface and begins transmitting data to Argos satellites.

Mark report PAT: The mrPAT is 121 mm in length, has a maximal diameter of 23 mm, and weighs 26 g in air. It is equipped with only temperature and light sensors, and has no mortality detection mechanism. Sensor data are collected during deployment and archived in its internal memory. Then, on a pre-set interval, the tag is released from its host animal and a summary of the archived data is uploaded to Argos satellites.

Both pop-up tags can obtain light-dependent geolocation data via the Argos satellite system. The tags were programmed to pop-up from 1 to 4 months at each release site (Table 1). The sampling intervals were programmed with 75, 150, 300, and 450 s according to different scheduled days (31, 61, 91, 121).

Tag attachment

To attach the pop-up archival transmitting tags to the eels, nylon wire (105 lb.), PVC pads, polyethylene foam pads, and oval sleeves were used to construct an intrusive strap in front of the dorsal fin by surgery. Eels were anesthetized with 0.2‰ eugenol before surgery. A needle (3.5 in) holding one end of the monofilament nylon wire was inserted from the lateral musculature through the body dorsally. A loop was made for the insertion of the tag. Then, one strap was inserted from the dorsal musculature beside the previous wound for 1.5 cm on the same side. Another strap was constructed the same way, and the pads were used to prevent the wound from worsening at the insertion points (Fig. 2). Povidone-iodine solution was applied to prevent infection at the wound sites. All surgery was scheduled 3 days before release to ensure the eels were in good enough condition for release after tag straps were attached.

Data treatment

The pop-up locations were recorded to map out the approximate seaward migration route of anguillid eels from Taiwan. To increase the accuracy of the migration route, the swimming

depths and temperature data received from the Argos system were also documented. The first pop-up location transmitted from the MiniPAT was related to the location where the tag was released. Data from the MiniPATs were subject to three procedures in order to reconstruct the migration

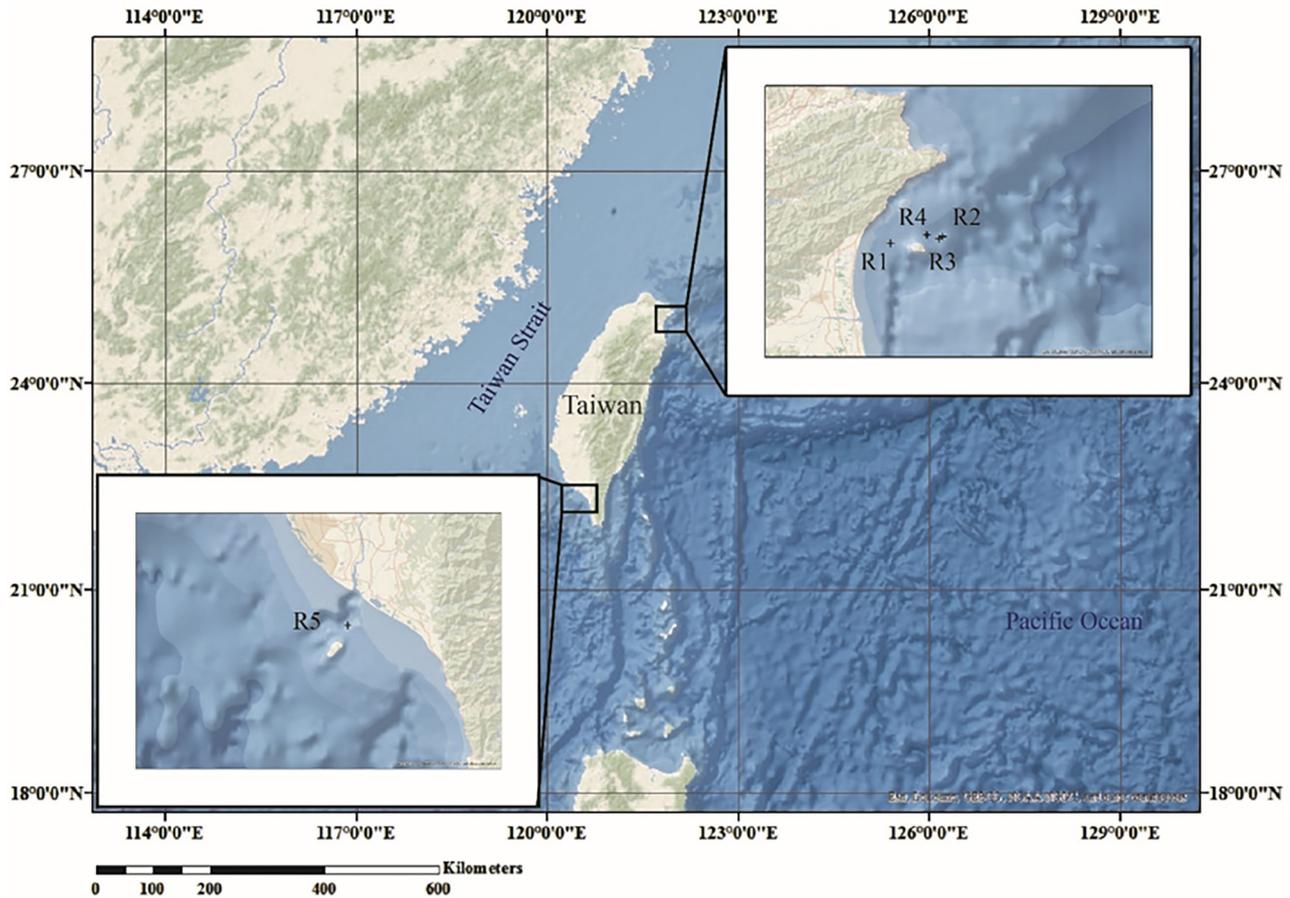


Fig. 1. Release position of tagged eels. R1 (24°51'8.00"N, 121°53'40.00"E), R2 (24°51'50.90"N, 121°59'59.11"E), and R3 (24°51'38.24"N, 121°59'35.10"E) are the positions at which the tagged eels were released in 2015 and R4 (24°52'3.00"N, 121°58'7.00"E) and R5 (22°23'39.92"N, 120°24'12.77"E) are the 2016 release positions. The scale bar can be used in the largest map only. (The original figure was obtained from Google Earth)

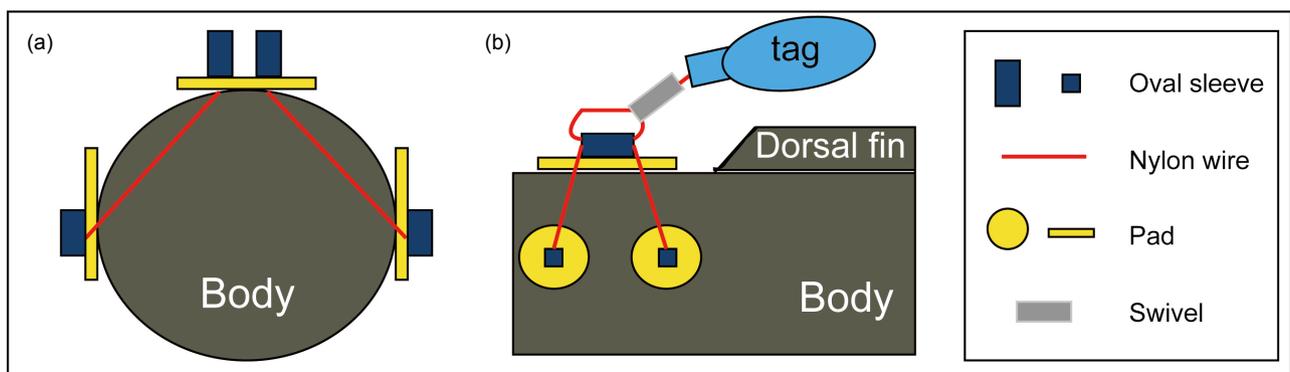


Fig. 2. Schematic diagram of tag attachment with (a) cross-section and (b) lateral views.

routes: (1) confirm the longitudinal position, (2) compare the position with the seabed depth, and (3) compare the temperatures of (1) and (2) at different depths.

The depths the eels migrate at (> 200 m) were too high for the internal daylight geolocation system of the tags to provide meaningful data for light-based estimate locations. The punctual DVM behavior, whereby eels descended through the water column at dawn and ascended at sunset, was used to determine sunrise and sunset times, with this type of migration utilized to study the horizontal movement as well. A previous study showed that migrating Japanese eels rapidly dive to deeper water 50 min before the sun rises (Chow et al. 2015). The data from the sunrisesunsetmap website (<http://sunrisesunsetmap.com/>) was used to cross-reference the real time data obtained from the released eels.

The migration route analysis also used environmental oceanic data obtained from the Mercator Ocean website (<http://www.mercator-ocean.fr/>) Daily Global Physical Bulletin at 1/12°. The maximum depths of migrating eels were restricted by water depth; therefore, the seafloor depth was used to eliminate any locations that were shallower than the recorded maximum depths.

The temperature data were used to eliminate locations that did not match the records of migrating eels, and were obtained from the Mercator Ocean website (<http://www.mercator-ocean.fr/>). The oceanic temperatures at 100 and 300 m were applied to check the possible locations of migrating eels. The warm Kuroshio Current flows from the low latitudinal areas of Taiwan to Japan. The annual average temperature of the Kuroshio Current is 24-26°C, 18-24°C in winter and 22-30°C in summer. Cooler water was measured around the continental shelf, at approximately 15-18°C. These differences in temperature were used to speculate as to whether the migrating eels left the warm Kuroshio Current.

Time-related depth data were not collected from the mrPATs because they did not have the premature pop-up detection mechanism. If the pop-up function of the tag occurred earlier due to shedding, the recorded location at the set time would be further away from the real location of the tagged eel. The released tag would float and keep recording the temperature in the Kuroshio Current. Data on the speed of the current were obtained from the Mercator Ocean website (<http://www.mercator-ocean.fr/>). These data were used

to estimate the approximate location where the tag was shed. However, the migration routes from the release site to the shedding location could only be determined by process of elimination based on temperature records.

RESULTS

Migration duration and distance

In total, 20 eels were tagged and released in two locations (Table 1). A total of 14 tag signals were successfully transmitted (10 MiniPATs and 4 mrPATs). The 10 reporting MiniPATs transmitted on average 54% (range: 30-71%) of their archival data, with recording days from 8 to 132 days and the real active duration from 2 to 32 days. However, 3 of the 10 MiniPAT tag data were defective, due to a high overall loss rate (above 65%), and were excluded from the analysis (Table 2). The mrPATs popped-up at the scheduled times due to no mortality being detected. The duration of the real active time ranged from 10 to 21 days.

Seven pieces of reporting data in 2015 were used to reconstruct possible migration routes, with distances from 81 to 1,500 km (Fig. 3a). In the 2016 reporting data, because the tags lacked several environmental factor detectors, we could only calculate the migration distance by assuming that all of the eels swam along the Kuroshio axis. #164778 and #164780 tags produced raw distances of 1,769 and 1,949 km from the released site, respectively (R4). After elimination and reconstruction, the distances of possible routes were 409 and 667 km, respectively. Tags #164782 and #164785 showed distances of 197 and 466 km from release at site R5, respectively (Table 2).

Migratory speed and pop-up sites

The pop-up locations showed that the eels released in 2015 migrated north-eastward in the Kuroshio Current (Fig. 3a). Five tags popped up in the Okinawa Trough, which is located on the edge of the continental shelf. Two released eels migrated further. Tag #150539 popped up in the southern waters of Yakushima, Japan and tag #150540, which had the longest migratory distance, was geolocated to the eastern waters of Miyazaki. The eels' migration speeds were reported to be 12.9 to 65.2 km/d (minimum and maximum, respectively) (Table 2).

For the mrPATs released in 2016, tags

#164778 and #164780 (Fig. 3b) showed similar routes as those in 2015, with mean migratory speeds of 37.2 and 44.5 km/d, respectively (Table 2). Tags #164782 and #164785 popped up in the eastern waters of Lan Island and the more westward waters near Guangdong Province,

China, respectively (Fig. 3b). These two tags might have been influenced by the recirculation of the southwestern waters of Taiwan, which made it difficult to estimate the migrating speed of the tagged eels.

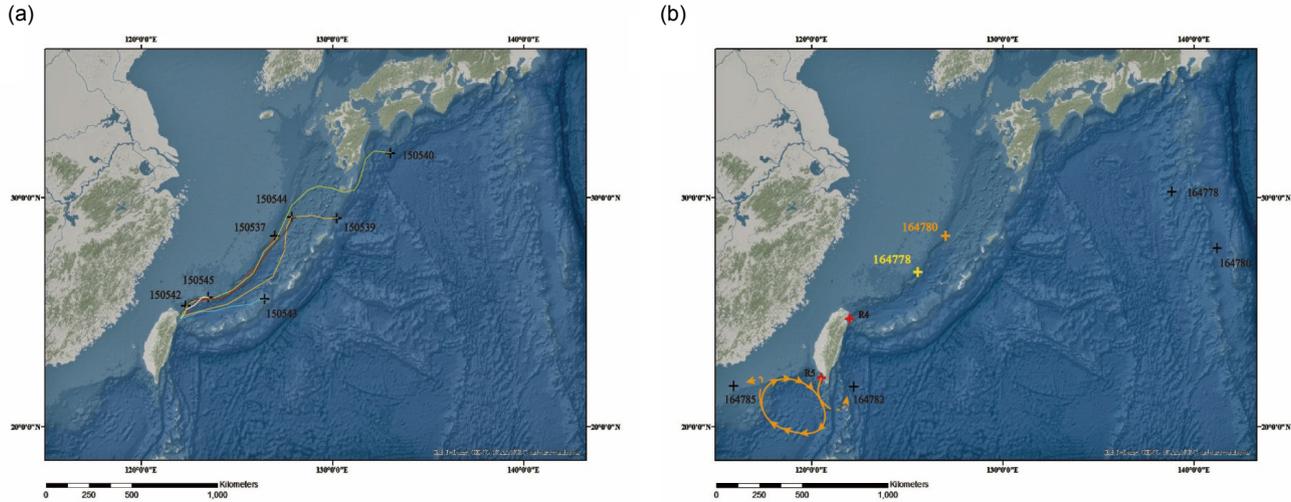


Fig. 3. Pop-up locations and the estimated migratory routes of the released tags in (a) 2015 and (b) 2016. All estimated routes were cross-checked with the timing of dawn and sunset and the timing of decent and ascent. Maximum seafloor depths were used on the route corrections as well.

Because of the recirculation located at the southwestern water of Taiwan, the eels or shedding tags probably recirculated in this region for days. Two individuals left the recirculation: #164782 entrained in *Kuroshio* and #164785 pop-upped at more western waters.

Table 1. Profile of all eels included in the study

No.	Species	TL (mm)	BW (g)	OI	FI	Release site	Scheduled Days	Type of ending	Type
150536	AJ	725	657	3.9	6.1	R3, IL	61	Premature	Farmed
150537	ABP	779	1133	7.3	5.0	R2, IL	61	Premature	Wild
150538	ABP	771	1096	3.7	5.2	R3, IL	61	Premature	Wild
150539	AM	998	4000	7.9	5.3	R2, IL	61	Premature	Farmed
150540	ABP	714	861	7.9	5.7	R2, IL	31	Premature	Wild
150541	ABP	725	1061	5.3	4.8	R3, IL	121	Premature	Wild
150542	AM	1000	5000	-	-	R1, IL	31	Premature	Farmed
150543	ABP	765	960	6.2	4.2	R2, IL	91	Premature	Wild
150544	AM	1162	4000	9.3	4.9	R3, IL	91	Premature	Wild
150545	AJ	755	717	3.7	5.3	R3, IL	31	Premature	Farmed
164777	AJ	683	532	6.0	5.8	R4, IL	31	Lost	Farmed
164778	AJ	667	583	6.7	6.7	R4, IL	61	Premature	Farmed
164779	AJ	725	777	4.6	5.0	R5, PT	91	Lost	Farmed
164780	AJ	672	502	6.3	5.1	R4, IL	91	Premature	Farmed
164781	AJ	646	455	4.7	5.0	R5, PT	31	Lost	Farmed
164782	AJ	682	818	5.2	5.1	R5, PT	61	Premature	Farmed
164783	AJ	801	889	4.5	4.7	R5, PT	121	Lost	Farmed
164784	AJ	710	598	7.9	5.8	R4, IL	121	Lost	Farmed
164785	AJ	672	518	6.3	5.7	R5, PT	91	Premature	Farmed
164786	AJ	761	1120	5.1	5.4	R5, PT	121	Lost	Farmed

AJ: *A. japonica*; ABP: *A. bicolor pacifica*; AM: *A. marmorata*; TL: total length; BW: body weight; OI: ocular index; FI: pectoral fin index.

Migration behaviors

Twelve *A. japonica* eels were released in the present study (two in 2015 with MiniPAT tags and 10 in 2016 with mrPAT tags). Six mrPAT tags in 2016 did not transmit, and only tag (#150545) exhibited DVM behavior. Data recorded from 11:00 to 13:00 (daytime) and 23:00 to 01:00 (nighttime) were selected to calculate the mean depth and temperature during day and night. Five tags exhibited typical DVM behavior (Fig. 4) and their average temperatures and depths are recorded in table 3.

Three *A. marmorata* were released during 2015 in the present study with MiniPAT tags (Table

4).

Five *A. bicolor pacifica* were equipped with the MiniPAT tags in 2015 (Table 5). Their average temperatures are recorded in table 5.

Behavior during migration of released eels

The released eels tended to swim in water that was greater than 200 m deep if there were no limitations to seafloor topography. They exhibited more DVM behavior in deeper water (> 200 m) than in shallower water. #150537, #150539, #150543, #150544 and #150545, according to their occupied depth and temperature between day and night, are thought to have exhibited DVM

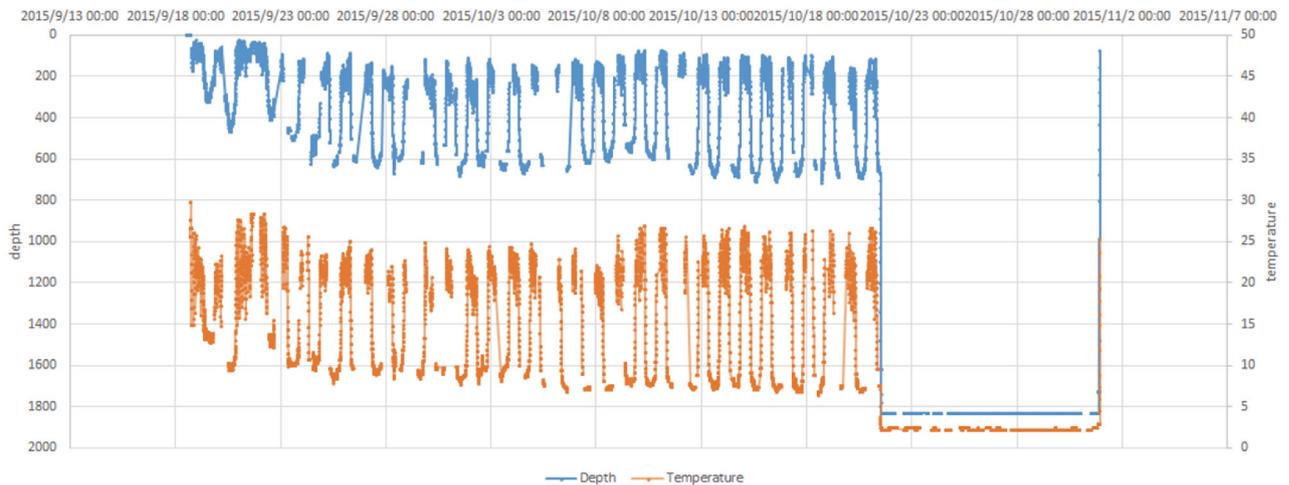


Fig. 4. Typical DVM behavior. Eels ascended to shallow water at night and descended to deeper water in daytime. Blue line is depth; orange line is temperature.

Table 2. Migratory data on all released eels

PTT No.	Recording days	Duration of activity	Distance (km)	Migration speed (km*day ⁻¹)
150536-f	95	uncertain	-	-
150537	62	27	666	24.7
150538	63	uncertain	-	-
150539-f	43	32	1089	34.0
150540	36	23	1500	65.2
150541	132	uncertain	-	-
150542-f	8	2	81.2	40.6
150543	94	25	461	18.4
150544	25	17	816	48.0
150545-f	24	15	194	12.9
164778-f	61	11	409	37.2
164780-f	91	15	667	44.5
164782-f	61	21	197	-
164785-f	91	10	466	-

“-f”: farmed eels.

behavior.

Predation

Typical DVM behavior was interrupted for tags #150540 and #150545 by a sudden change in the records of both temperature and depth, which suggests that predation events had occurred. During these times, the two individuals spent a great amount of time at the surface (depth of 0 m), and the typical DVM curve in the depth data also disappeared. The temperature recorded by the tags rose from 10-24°C to greater than 25°C (Fig. 5).

Light sensitive response

Based on the Chinese lunar calendar, September 27, 2015 was a full moon day and

October 13, 2015 was a new moon day. On these days, eels presented a light sensitive response, *i.e.*, they occupied deeper water depths (approximately 200 m) when the moonlight was strong and the shallower ones (approximately 50-100 m) during the new moon (no moonlight) (Fig. 6).

DISCUSSION

The spawning site of the Japanese eel was previously identified as west of Mariana Ridge, over 2,000 km from Taiwan (141-142°E, 12-16°N) (Tsukamoto 1992). The spawning sites of the *A. marmorata* and *A. bicolor pacific* might overlap with those of the Japanese eel or be nearby (Miller et al. 2002; Aoyama 2009). Therefore, the three species of eel might have similar seawater migration routes from Taiwan. Although the numbers of tagged eels

Table 3. Habitat occupation of *A. japonica*. (*n* = 6) (average ± standard deviation)

Tag	Temperature (°C)		Depth (m)	
	Day	Night	Day	Night
150536	-	-	-	75 ± 12.7
150545	10.2 ± 0.8	20.8 ± 3.2	438 ± 36.1	75 ± 53.9
164778	9.8 ± 4.0	23.6 ± 2.7	-	-
164780	8.2 ± 3.2	21.3 ± 2.7	-	-
164782	6.8 ± 3.2	23.1 ± 3.2	-	-
164785	8.3 ± 4.0	24.7 ± 3.0	-	-

“-”: data deficient. The mrPATs used in 2016 did not provide depth records during the oceanic migration.

Table 4. Habitat occupation of *A. marmorata*. (*n* = 3) (average ± standard deviation)

Tag	Temperature (°C)		Depth (m)	
	Day	Night	Day	Night
150539	8.1 ± 1.6	25.2 ± 2.7	573 ± 64.8	189 ± 80.6
150542	23.0 ± 2.3	25.3 ± 2.2	23 ± 15.7	23 ± 17.5
150544	7.1 ± 1.1	22.1 ± 2.4	597 ± 57.8	84 ± 72.5

Table 5. Habitat occupation of *A. bicolor pacifica*. (*n* = 5) (average ± standard deviation)

Tag	Temperature (°C)		Depth (m)	
	Day	Night	Day	Night
150537	7.5 ± 1.1	20.0 ± 3.8	602 ± 77.3	165 ± 75.6
150538	12.8 ± 2.0	18.7 ± 4.1	-	101 ± 31.1
150540	14.3 ± 6.7	19.5 ± 4.1	295 ± 155.8	109 ± 84.5
150541	9.8 ± 3.9	18.4 ± 4.4	-	136 ± 84.8
150543	8.3 ± 1.1	23.5 ± 4.3	603 ± 88.0	130 ± 73.8

were low in the present study, the results clearly showed that all three species migrate in a similar direction along the Kuroshio Current.

Several theories have been proposed regarding the migratory routes of silver Japanese eels. One study suggested an “anti-Kuroshio route,” whereby Japanese eels migrate upstream of the Kuroshio Current, and then eastward in the NEC (Yokose 2008). Another theory is an “along-Kuroshio route,” which states that the silver Japanese eels swim with the Kuroshio Current during their east-northward migration, and then swim southward in recirculation branches of the subtropical gyre along the Izu-Bonin Arc and down to the west of the Mariana Ridge where they spawn (Tsukamoto 2009; Chang et al. 2016).

Another possibility is that silver Japanese eels migrate along the most direct and shortest route of the estuary to the spawning site. Results from the present study support the “along-Kuroshio route” theory for silver Japanese eels. However, these long migration distances require energy-consuming swimming behavior, and the silver eels have to store most of their energy for gonadal development. Therefore, this migration route appears to be too far for the silver eels. In 2015, a tracking study of American eels recorded one migration route to the spawning area in the Sargasso Sea (Béguer-Pon et al. 2015). In this study, the released eels migrated along the current during the early phase of migration, and then changed direction to reach the spawning area.

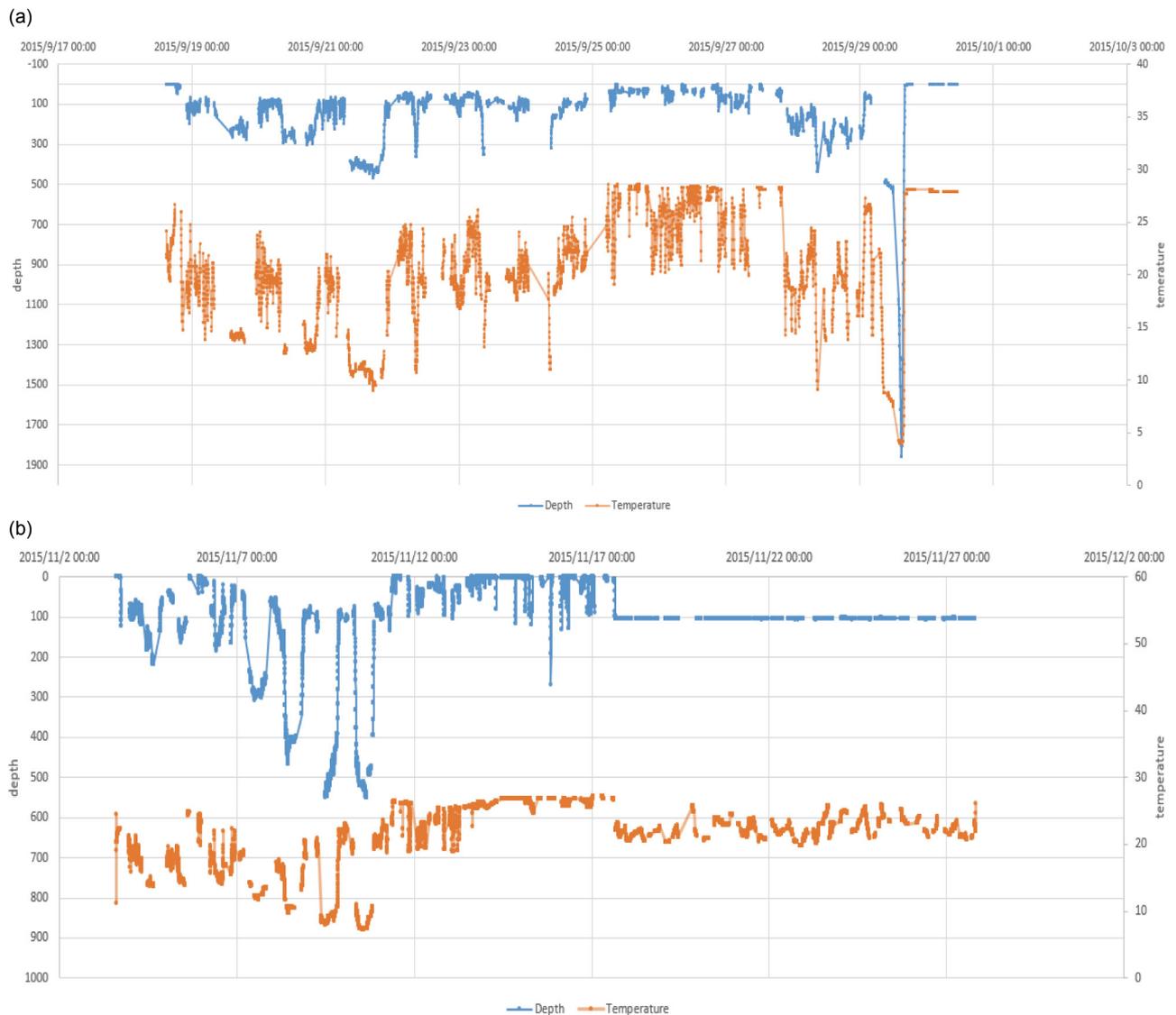


Fig. 5. Predation event on (a) #150540 and (b) #150545. Two types of pattern were displayed in the transmitted data.

Even though the study provided information on changes in temperature and salinity to explain the sudden change in migrating direction, it is possible that the homing abilities of eels rely on magnetic induction and their navigation abilities (Durif et al. 2013). Salmon have similar locating abilities; however, salmon migrate from the ocean to rivers, rather than the other way around (Béguer-Pon et al. 2015). It is likely that migrating silver Japanese eels swim along the Kuroshio Current during the early phase of migration and, once they geolocate their positions, change direction and migrate to the spawning site in the western part of the Mariana Ridge.

The horizontal swimming speed of Japanese silver eels has been estimated to be approximately 2.5-14 km/d based on pop-up satellite archival tags (Manabe et al. 2011). The optimum swimming speed of Japanese eels is unknown. In European

eels, the range of migration speed was shown as 3-47 km/d, and the maximum swimming speed was 55 km/d in laboratory experiments (Righton et al. 2016). The migration speed in the present study was 12.9-65.2 km/d; however, when removing the data from the predation events, the migration speed was 18.4-40.6 km/d. Therefore, the average migration speed observed in the present study was faster than that in previous studies. This may be due to differences in environmental factors that affected the route and made the total migrating distance farther. Furthermore, recovery after the surgery may also influence the body condition of eels, leading to uncertain results.

Several pieces of transmitted data showed typical DVM patterns during eel migration once they were adjusted to the oceanic environment. This study demonstrated that light influences the habitat occupied by migrating eels. Migrating eels

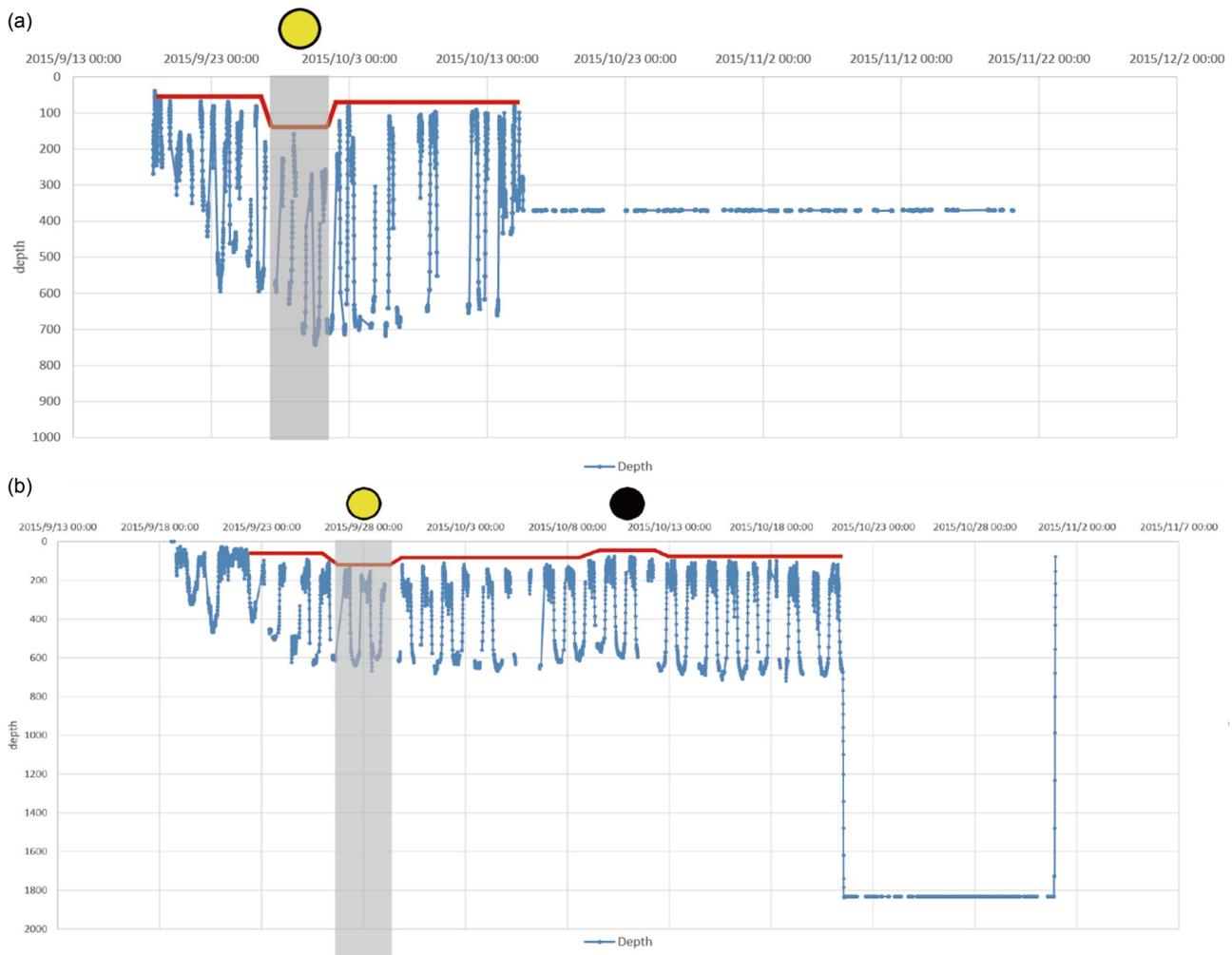


Fig. 6. Light-sensitive vertical migration of (a) #150537 and (b) #150539 (September 18-October 21) and lunar cycle at night. Moon phases are shown above the date; full moon (yellow) and new moon (black).

rapidly ascended to shallower water after sunset; however, they showed different depth records based on the lunar cycle. Three eels showed changes in ascending depth with different moon phases. During the full moon, eels ascended to depths of 50 to 150 m. The eels remained in shallower waters at night when a new moon appeared and there was little light. A similar phenomenon was observed in a previous study by Chow et al. (2015).

Only one of the two farmed Japanese eels released in 2015 (#150545) displayed DVM behavior (Fig. 5b), while the other showed a discontinuous horizontal line (data not shown). This latter movement pattern might be attributed to an error in data transmission. After the individual with tag #150545 had been released for several days, it began to show typical DVM behavior. i.e., it descended to deeper depths of approximately 500-600 m during the daytime and moved to depths of less than 200 m at night. Thus, farmed eels in our study exhibited similar DVM behavior to wild eels; however, further study is required to determine whether farm eels behave like wild eels under all conditions.

The vertical swimming behavior was similar for farmed and wild eels in the present study. Anguillid eels exhibit DVM behavior during their spawning migration; this behavior is related to sunlight and shown through differences in the temperature records. The movement from shallow to deep water is considered predation avoidance behavior (Iwasa 1982). Several predators of eels have been discovered in previous studies, including whales (Schorr et al. 2014; Amilhat et al. 2016), sharks (Béguet-Pon et al. 2012), and tuna (Blank et al. 2007; Béguet-Pon et al. 2012). Each marine animal has distinguished swimming behavior, which can be determined from depth and temperature records. The night ascent into shallower warm water might serve to maintain sufficiently high metabolism and swimming activity (Tesch 2003), whereas the descent to deeper waters during the daytime might maintain their temperature below 11°C to delay gonadal development (Boëtius and Boëtius 1967; Jellyman and Tsukamoto 2010).

There were two clear changes in the DVM patterns that were identified as predation events. A sudden change appeared in the depth occupation and ambient temperature patterns of #150540 and #150545 on the seventh and eighth day after release. The recorded depths suggest possible predation by marine mammals,

but the temperature records from the tags after ingestion by the predator suggested otherwise. The recorded temperatures ranged from 20-28°C and the possibility of being preyed on by whales being ruled out due to the homeothermic nature of this predator. The temperature profiles of predators were recorded to range from 20-28°C, and the temperature profiles inside the guts of porbeagle sharks range from 14-26°C, depending on the ambient temperature (Carey et al. 1969; Sepulveda et al. 2004); therefore, the possibility that these sharks preyed on the migrating eels is low. The vertical migration of possible predators, including tuna and sharks, was also compared. Both tuna and porbeagle sharks occupy water near the surface; however, porbeagle sharks show clear diel vertical patterns, swimming in deeper waters during the daytime and surface waters at night (Béguet-Pon et al. 2012). The rapid ascending and descending movements of tuna did not accurately match the times of sunset and sunrise. The ascents of tuna to the surface occurred more gradually than those of sharks (Béguet-Pon et al. 2012). Eels have not been previously detected in the stomachs of tuna, but tuna could still prey on them. Comparison of the behavior of known predators indicated that tuna represented potential predators in the current study. However, we also cannot exclude other unknown predators.

The early pop-up events meant that researchers received less data for analysis. These events were the result of various factors including predation, the eels being struck by rocks, fishery activities, and defects in the tagging method. The potential impact of the tags on the behavior of fish of relatively small body mass has been observed, causing extra drag force in the water (Burgerhout et al. 2011). However, this tagging technology has been used to track migrating eels for a long time; that is, the disruption of tags to the eels was considered acceptable. Many attachments are available with different materials and fixture methods (Manabe et al. 2011; Økland et al. 2013); however, losing tags is inevitable. Therefore, it is necessary to perform more tests to optimize the attachment of tags to eels.

CONCLUSIONS

The eels in the present study exhibited migrating speeds of 18.4-40.6 km/d. The average depth of *A. marmorata* and *A. bicolor pacifica* that exhibited typical DVM behavior exceeded 500 m

during the day and was shallower than 300 m at night. The average temperature of *A. japonica* during day and at night, also fitted the typical DVM behavioral mode. The farmed eels exhibited DVM behavior, the pattern of which was similar to that of wild eels. Thus, farmed eels might have the same migratory behavior as wild ones, but further investigation is required. Even though none of the migrating eels approached the possible spawning site along the western Mariana Ridge, our results suggest that both farmed and wild eels released to waters near Gueishan Island followed similar migratory routes, swimming through Kuroshio Current during the initial phase of their oceanic movement. These findings provide important rationale for the continued rearing and release of cultivated eels to help recover natural eel resources.

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Consent for publication: Not applicable.

Ethics approval consent to participate: We applied for an "Approval of Animal Use Protocol" from the Animal Research Committee of the National Taiwan University, and it was reviewed by the Institutional Animal Care and Use Committee (IACUC). Our IUCAC approval number is "NTU-101-EL-100".

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