

RESEARCH

Open Access



Regional differences in oceanic migratory behavior of Japanese silver eel in waters with different vertical temperature gradients

Takaaki K. Abe¹, Ishmerai Galang¹, Ayu Daryani¹, Shingo Minamikawa², Noritaka Mochioka³ and Hiroshi Hakoyama^{1*}

Abstract

Background The Japanese eel *Anguilla japonica* has a single spawning area on the west coast of the Mariana Islands, and the larvae disperse widely via the North Equatorial Current and the Kuroshio Current to freshwater and coastal areas of East Asia for nursery and growth habitats. Spawning adults reared in their respective habitats begin their migration to spawn from September to February, but little is known about regional differences in migration routes, their contribution to spawning populations, or their migratory behavior. To better understand the spawning migrations of Japanese eels, we tracked adult migratory stage eels (silver eels) captured in coastal areas of three regions (Tokai region, Sea of Japan coastline, and Tohoku region) from October 2019 to February 2020 using pop-up satellite archival tags.

Results Twenty-three tagged eels were released in each coastal area, and data were collected on 15 eels for a maximum of 59 days. Eels released in the Tokai region migrated southeast along the Kuroshio Current. On the other hand, eels on the Sea of Japan coastline and in the Tohoku region tended to migrate westward and southward against the ocean current, respectively, but no eels from either region reached waters near the Kuroshio Current. In addition, the present study found region-specific vertical movement patterns among the eels. Eels from the Tokai region showed typical diurnal vertical movements, while an eel from the Sea of Japan coastline repeated non-diurnal vertical movements, which was attributed to regional differences in bathymetry and water mass structure. Except for one eel suspected of being preyed upon, all other eels did not venture into depth zones with temperatures below 4 °C, thus suggesting that the maximum depth of vertical movement is limited by water temperature.

Conclusions This study provided new insights into the migratory behavior of Japanese silver eel from the Sea of Japan coastline and the Tohoku region, but further long-term tracking is required to reveal the fate of the spawning adults from the coast of Japan.

Keywords Pop-up satellite archival tags, Japanese eel, Spawning migration, Diel vertical migration

*Correspondence:

Hiroshi Hakoyama

hiroshi-hakoyama@nagano.ac.jp

¹ Institute of Freshwater Biology, Nagano University, 1088 Komaki,

Nagano 386-0031, Japan

² Fisheries Resources Institute, Japan Fisheries Research and Education

Agency, 2-12-4 Fukuura, Yokohama 236-8948, Japan

³ Laboratory of Fisheries Biology, Faculty of Agriculture, Kyushu University,

744 Motooka, Nishi-ku, Fukuoka 819-0395, Japan

Background

The Japanese eel *Anguilla japonica* is a catadromous species native to the temperate zone of East Asia and is an important target of commercial fisheries. However, the abundance of the Japanese eel, associated with a decline in glass eel recruitment, has declined severely throughout its range in recent decades [1–3], similar to other temperate Northern Hemisphere eel species,



© The Author(s) 2023. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

including the European eel *A. anguilla* and the American eel *A. rostrata* [4]. The Japanese eel is widely distributed in freshwater and coastal areas of East Asia, including the Japanese coast, the Korean peninsula, mainland China, and the Philippines [5], and has a single spawning ground in the waters to the west of the Mariana Ridge [6–8] (Fig. 1A). Therefore, management measures need to be implemented throughout the distribution area based on an understanding of the species population structure and life history.

Larvae (leptocephali) hatched on the spawning ground are transported westward by the North Equatorial Current [6, 7]. The North Equatorial Current bifurcates along the east coast of the Philippines, becoming the northward flowing Kuroshio Current and the southward flowing Mindanao Current, and the larvae transported by the Kuroshio Current are distributed to the coastal areas of East Asia [9]. In the process of transport to the coastal zone, leptocephali metamorphose into glass eels. After reaching the coastal zone, they enter estuaries and rivers for further growth, beginning the yellow eel phase. After 5 to 15 years of the yellow eel growth phase, Japanese eels transform into migratory silver eels, and during their migration, their gonads mature and their eyes enlarge [10–12]. Japanese silver eels from each region of East Asia begin their spawning migrations in the autumn and winter period, specifically from October to February [13–15], and migrate to the spawning grounds thousands of kilometers away.

Recent studies using pop-up satellite archival tags (PSATs) on migrating stage individuals have provided useful information on the oceanic migration of anguillid eels [16–20]. Seven species of anguillid eels have been tagged with PSATs, and European eels have been tracked for up to 273 days [21]. American eels were tracked throughout their migration from the Scotian Shelf to the spawning area, the northern boundary of the Sargasso Sea, suggesting that rivers and estuaries around the Scotian Shelf are growth areas for juvenile American eels that contribute individuals to the spawning population [21]. Moreover, a previous study of European eels from throughout the species distribution showed that the migration routes of the spawning adults leaving from different locations corresponded to the ocean current that transports larvae, implying that European eels are able to return to their spawning grounds regardless of the growth area [21]. A series of satellite tracking studies have shown that all species of silver eels tagged by PSAT exhibit diel vertical migration (DVM) in pelagic waters. Silver eels have been shown to descend to deep waters (500–800 m) during the day and ascend to shallow waters (100–400 m) at night. Swimming depth appears to vary within species [22] and is thought to be affected by the ambient light conditions (lunar and sun altitude) [23]. DVM behavior has been reported to be absent in shallow waters [24] and to be interrupted in areas where strong currents are present [25]. Therefore, DVM behavior during oceanic migration is also considered to be affected by water structure, bathymetry, and currents [23, 25].

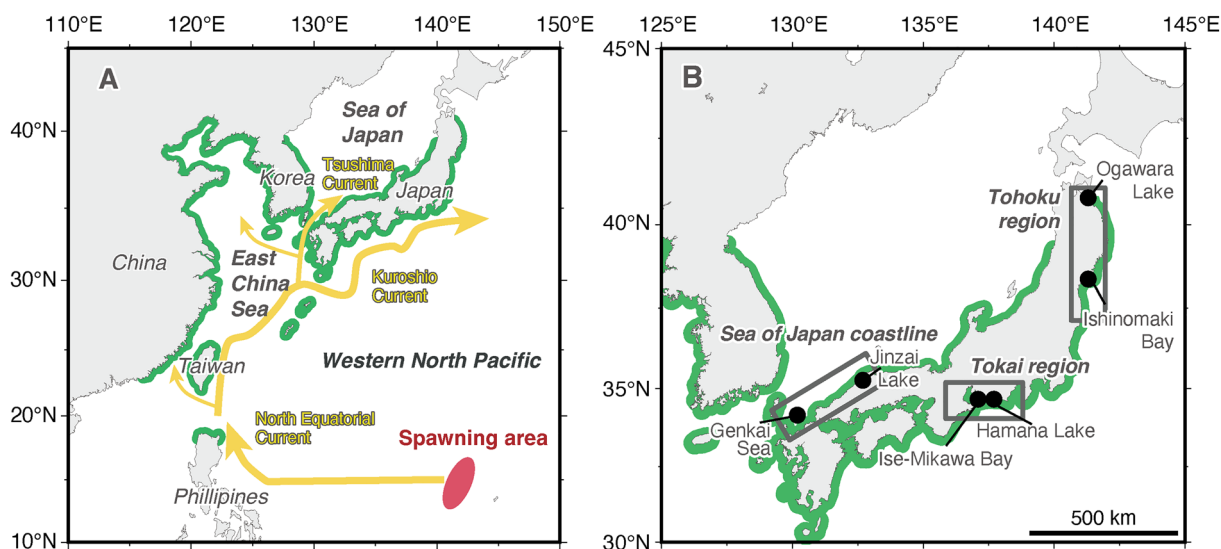


Fig. 1 The distribution area of the Japanese eel and the research sites of the present study. **A** The range of the Japanese eel (green). Japanese eel spawns in the waters around the Mariana Islands (red-shaded area). The larvae are transported by the North Equatorial Current and dispersed to East Asia by the Kuroshio Current and the branches (yellow arrows). **B** The Japanese eel is widely distributed along the coast of Japan. Eels for satellite tracking were collected from a total of six sites located in the Tohoku, Tokai, and Sea of Japan regions

Attempts have been made to track the oceanic migration of Japanese silver eels to their spawning grounds, and these studies have provided information on their behavior and migration routes in the open ocean [18, 23, 26, 27]. However, due to their relatively small body size (0.8–1.2 kg) compared to other Atlantic and South Pacific species (> 2 kg), long-term tracking has not been successful, and the tracking trajectories are fragmented. Satellite tracking of Japanese eel has been limited to areas near the Kuroshio Current. Migrating silver eels have also been found in the East China Sea [14] and the Tohoku region of Japan [28], but the migratory behavior of eels leaving their respective growth habitats is poorly understood. In the present study, we released PSAT-tagged Japanese silver eels from six sites in three regions along the coast of Japan to study the spawning migration of Japanese eels and to provide information on the early phase of oceanic migration of Japanese eels (Fig. 1B).

Results

Tag fate and tracking profiles

A total of 23 eels were tagged and released in the coastal area near their capture site (Table 1), and 15 PSATs successfully transmitted data (6 of 10 X-tags, 60%; 9 of 13 mrPATs, 74%) (Fig. 2). All PSATs popped-up prematurely, and the actual duration of PSAT attachment ranged from 1 to 59 days (Table 2). The maximum geographic tracking range in great circle distance (GCD) was 382 km (Table 1). The movement speed calculated from the GCD ranged from 0.9 to 37.5 km day⁻¹, excluding one preyed eel (HM1902 in Table 1). Two eels were considered dead

shortly after their release (JZ1906 and GK1901 in Table 1) because they sank to the bottom and remained there for three days. All eels released in the Tokai region migrated to the southeast or east, and two eels reached nearby Hachijojima Island (Fig. 2A). Three out of five eels released from the Sea of Japan coastline showed a westward movement pattern, but one eel (JZ1903) was observed to move in a northeasterly direction (Fig. 2B). Only two of seven tags attached to eels released in the Tohoku region transmitted pop-up positions from south of the release site (Fig. 2C), but for unknown reasons one tag, attached to IS1901, did not transmit temperature data.

Vertical movement and ambient water temperature

Time series of depth and water temperature were obtained from the X-tagged individuals, and daily maximum and minimum water temperatures were obtained from the mrPAT-tagged individuals (Figs. 3 and 4). Among the individuals released in the Tokai region, X-tagged individuals exhibited a pattern of DVM, diving to depths of 500–800 m during the day and ascending to 100–500 m at night (HM1905, HM2001, and HM2006 in Fig. 3A, C, and E). Although one eel (HM2006) released in December 2020 showed a similar pattern of DVM to the other two eels (Fig. 3A, C, and E), it tended to stay at a deeper depth (250–600 m) during the night compared to the two (100–400 m) (Figs. 3 and 5). Two of the three X-tagged eels (HM1905 and HM2001) exhibited similar depth and water temperature profiles, experiencing water temperatures of 4–10 °C during the day and 14–22 °C at night (Figs. 3 and

Table 1 Information on the capture, release and tag type of the 15 eels for which data transmission was confirmed

ID	Capture point	Region	TL (cm)	BW (g)	Tag type	Release date	Predation	Duration (days)	GCD (km)	Azimuth (deg.)
HM1902	Hamana Lake	Tokai	77	790	mrPAT	2019/12/11	Endothermic fish	2	123	85
HM1905	Hamana Lake	Tokai	81	790	X-tag	2019/12/11		55	322	136
MK1902	Ise-Mikawa Bay	Tokai	89	1140	mrPAT	2020/02/07		47	243	131
HM2001	Hamana Lake	Tokai	81	960	X-tag	2020/11/27		9	218	100
HM2006	Hamana Lake	Tokai	85	900	X-tag	2020/12/24		12	181	88
HM2007	Hamana Lake	Tokai	79	850	mrPAT	2020/12/24		47	42	103
HM2008	Hamana Lake	Tokai	81	850	mrPAT	2020/12/24		12	166	92
JZ1901	Jinzai Lake	Sea of Japan	74	800	mrPAT	2019/11/12	Suspected	59	87	247
JZ1902	Jinzai Lake	Sea of Japan	83	1200	mrPAT	2019/11/12		21	287	264
JZ1903	Jinzai Lake	Sea of Japan	78.5	1000	X-tag	2019/11/12		18	382	19
JZ1905	Jinzai Lake	Sea of Japan	76.5	960	mrPAT	2019/11/12		7	61	309
JZ1906	Jinzai Lake	Sea of Japan	78.5	900	X-tag	2019/11/12		3	12	69
GK1901	Genkai Sea	Sea of Japan	79.6	810	X-tag	2020/02/04		3	8	63
IS1901	Ishinomaki Bay	Tohoku	86.5	980	mrPAT	2019/11/07		6	225	194
IS1902	Ishinomaki Bay	Tohoku	87.5	1120	mrPAT	2019/11/07		7	60	250

TL: total length; BW: body weight; GCD: great circle distance

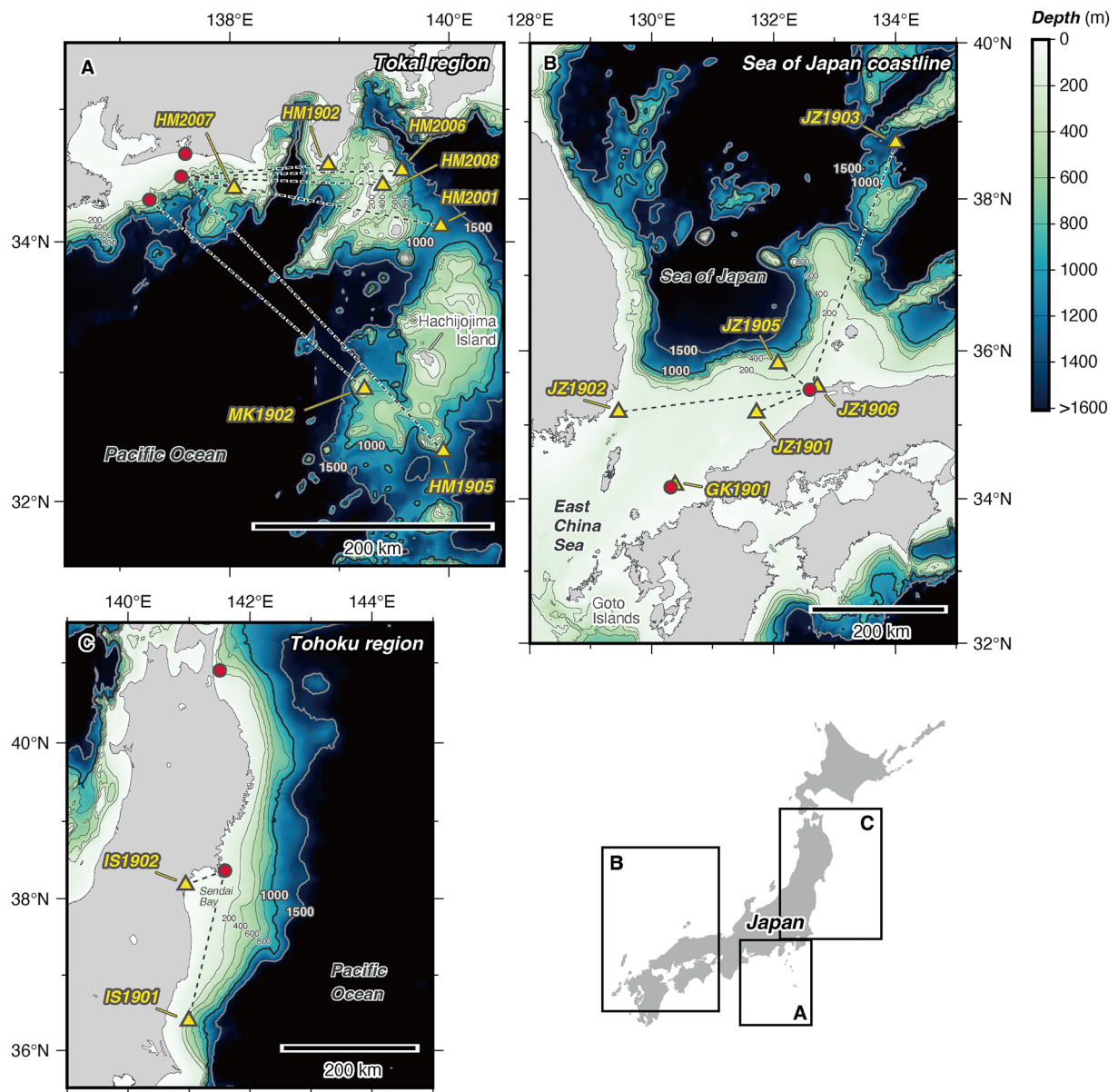


Fig. 2 Eel release points and pop-up satellite archival tags (PSATs) pop-up points. Silver eels were released from three regions: **A** the Tokai region, **B** the Sea of Japan coastline, and **C** the Tohoku region. Red circles represent the release points of tagged eels and yellow triangles represent the pop-up points of PSATs. The labels on the contour lines indicate the water depth in meters (m)

Table 2 The summary of the fate of tags attached to eels in each catchment

Region	Total	Transmit	Duration (days)	GCD (km)	Azimuth (deg.)	Movement speed (km day ⁻¹)
Tokai	10	7	26 (2–55)	185 (42–322)	105 (85–136)	18.1 (0.9–61.5)
Sea of Japan	6	6	18 (2–59)	134 (8–382)	162 (19–309)	8.8 (1.5–21.2)
Tohoku	7	2	6.5 (6–7)	143 (60–225)	222 (194–250)	23.0 (8.6–37.5)
Total	23	15	21 (2–59)	161 (8–382)	143 (19–309)	15.0 (0.9–61.5)

GCD: great circle distance. Duration, GCD, Azimuth, and moving speed are represented as means. The minimum and maximum range is given in parentheses

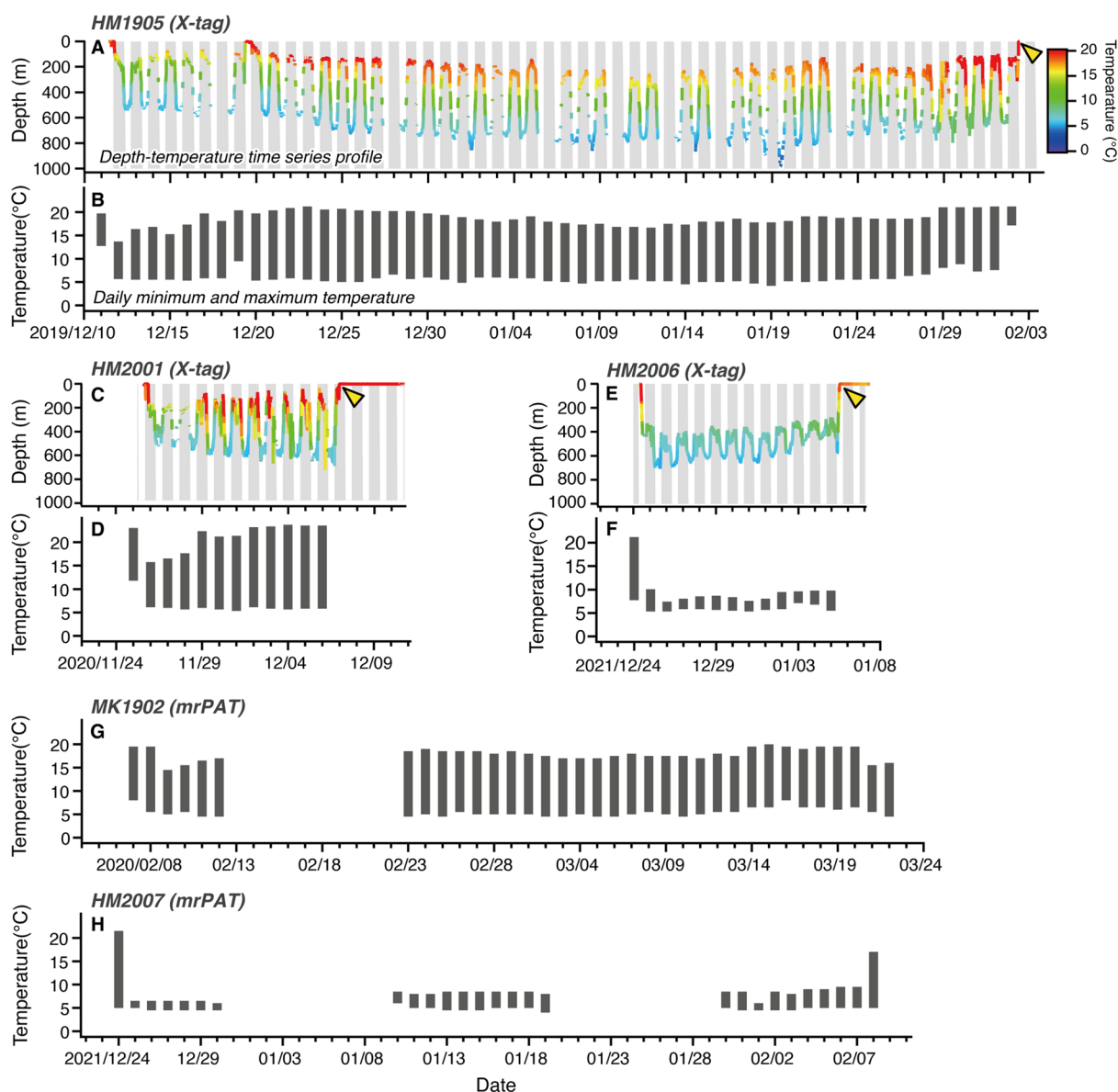


Fig. 3 The temperature and depth profiles of tagged eels released from the Tokai region. The time series data retrieved from pop-up satellite archival tags are shown: **A, B** HM1905, **C, D** HM 2001, **E, F** HM2006, **G** MK1902, and **H** HM2007. The tag type is represented in the parenthesis after each eel ID. **A, C, E** The time series data of depth and temperature retrieved from the X-tags are shown as colored lines. The gray shaded area denotes nighttime and yellow triangles indicate the surfacing time of the X-tag. **B, D, F–H** The daily minimum and maximum temperatures recorded for each individual eel are represented by the gray bar lines

5). An eel released from Ise-Mikawa Bay in February 2020 (MK1902) also showed a similar pattern of daily temperature range (Fig. 3G). Eel HM2006, which stayed at deeper depths during the night, also experienced a lower temperature range throughout the entire tracking period compared to other eels released in the Tokai region (Fig. 3E and F). A similar pattern of temperature range was also found in another eel, HM2007, released on the same day (Fig. 3H).

In contrast to the eels departing from the Tokai region, which showed a clear DVM, an eel released in the Sea of Japan (JZ1903) did not show a DVM, but instead repeated vertical movements at irregular intervals (Figs. 4A and 5M–P). This eel never dived deeper than 200 m and sometimes stayed near the surface (Fig. 5N). Ambient temperatures detected by the tag of this eel did not differ between day and night and ranged from 5 to 20°C (Fig. 5N, and P). Daily maximum water

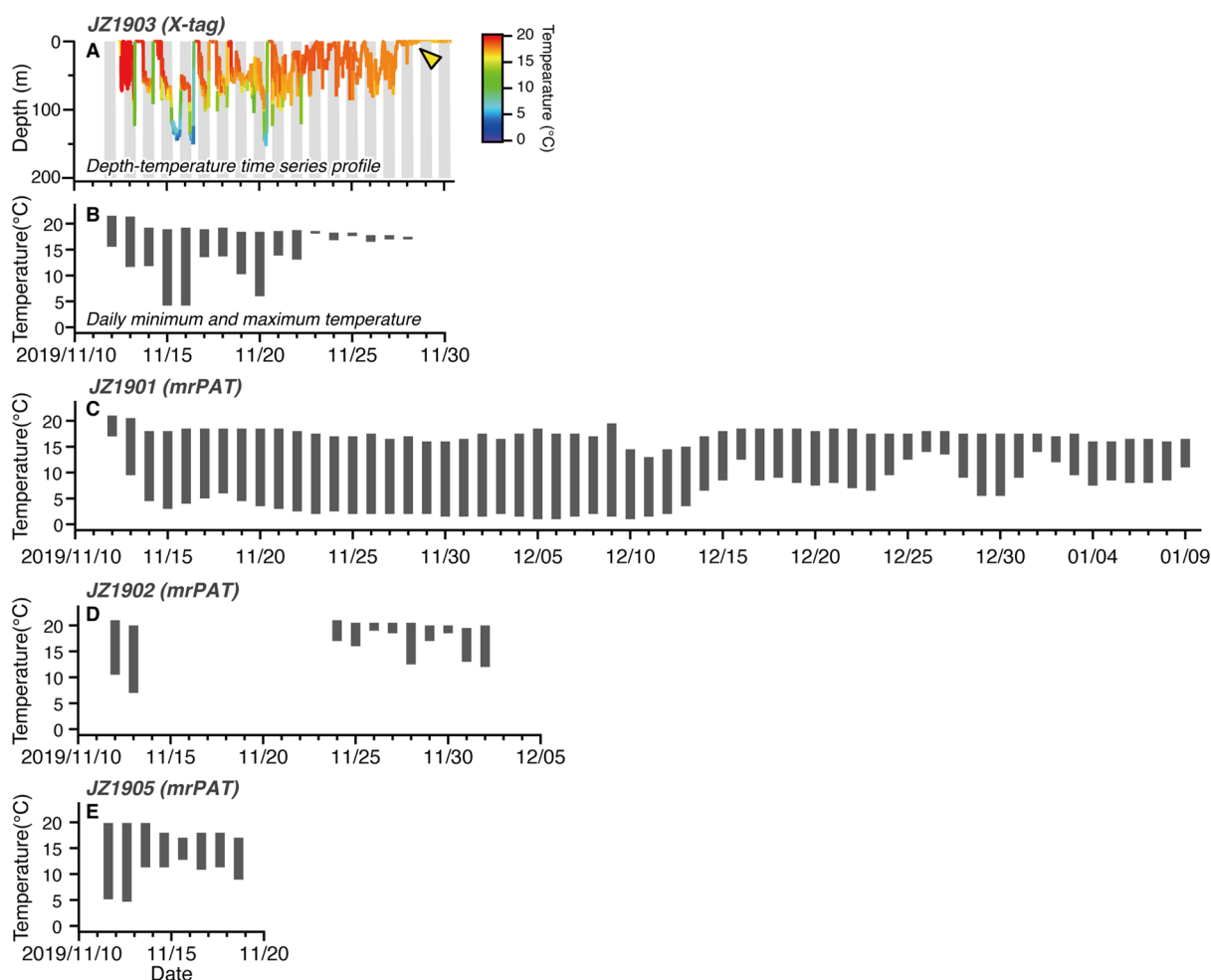


Fig. 4 The temperature and depth profiles of four tagged eels released from the Sea of Japan coastline. The time series data retrieved from pop-up satellite archival tags are shown: **A, B** JZ1903, **C** JZ1901, **D** JZ1902, and **E** JZ1905. The tag type is represented in the parenthesis after each eel ID. **A** The depth–temperature time series profile retrieved from the X-tag are shown as the colored line. The gray shaded area denote nighttime and yellow triangle indicate the surfacing time of the X-tag. **B–E** The daily minimum and maximum temperatures recorded for each individual eel are represented by the gray bar lines

temperatures experienced by all eels released on the Sea of Japan coastline were in close proximity to the sea surface temperature (SST) range of 18–20°C (Fig. 6). Daily minimum water temperature showed daily variation, even within the same individual, and ranged from 1 to 18 °C (Figs. 4B–E and 6).

Comparing the water mass structure in the areas where the eels migrated, the temperature in the Tokai region gradually decreased with depth, reaching 4 °C around 500–1000 m (Fig. 5B, F, and J), while in the Sea of Japan, the thermocline was at a shallow depth and the water temperature reached 4 °C around 150 m (Fig. 5N). Except for one eel (JZ1901), the lowest recorded water temperature for all eels never dropped below 4 °C (Figs. 4C and 6).

Predation

Among the 15 tags that transmitted data, one tag (HM1902) recorded temperatures 4 °C higher than the surrounding sea surface temperature (Fig. 7), indicating predation by an endothermic animal. In particular, since the maximum temperature was 25.5 °C, an endothermic fish, such as tuna, or an endothermic shark, is thought to have preyed on the eel. An eel released in the Sea of Japan was suspected to be predated based on the pop-up location and its recorded data. The tag, which took 59 days for its first transmission, popped-up 87 km from its release site (Fig. 2B and Table 1). In addition, this was the only tag to record water temperatures lower than 4°C, down to 1 °C (Fig. 6). Because the mrPAT used in this study did not provide fine-scale time series data on depth

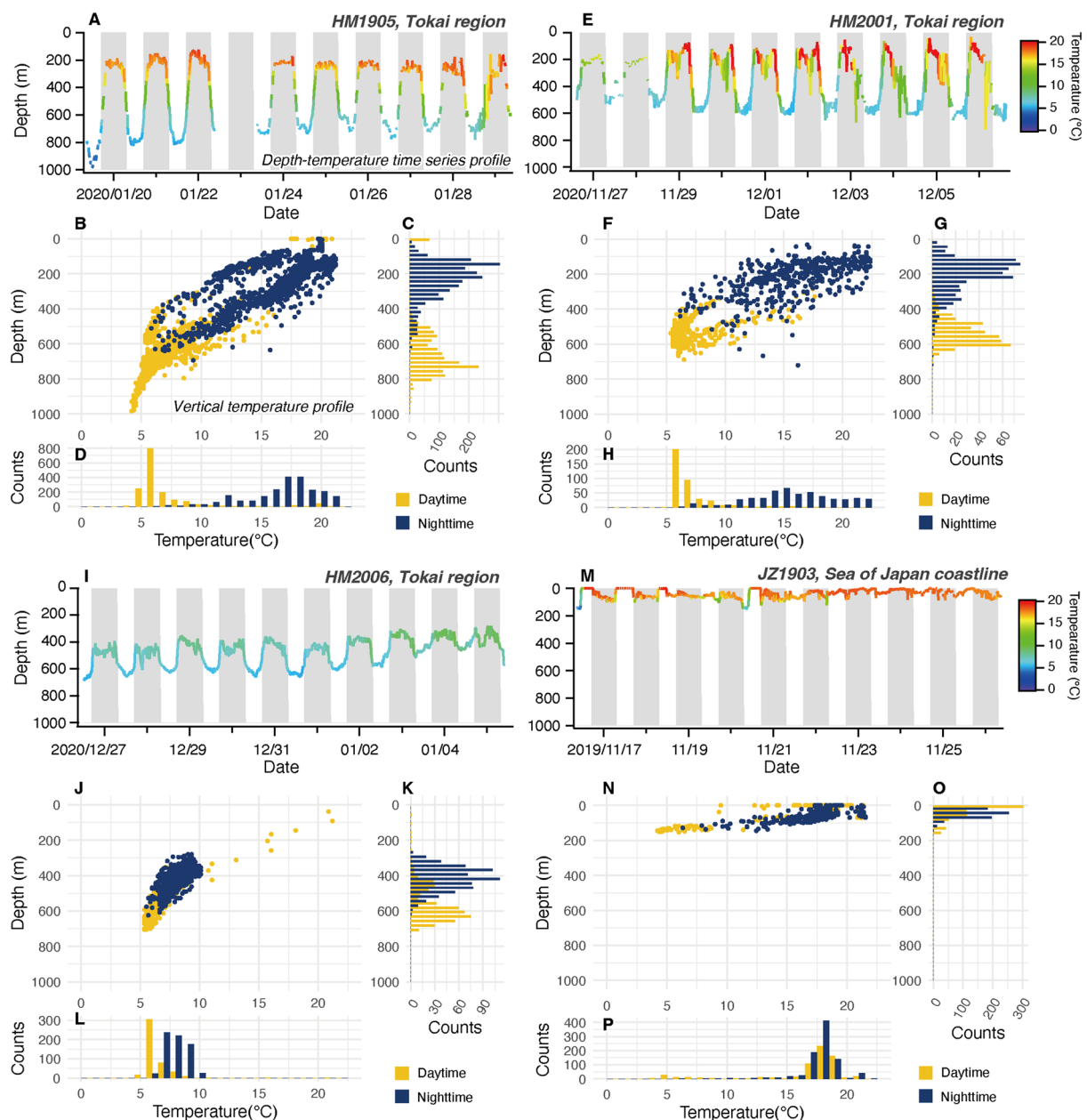


Fig. 5 Vertical movement patterns of four X-tagged eels: **A–D** HM1905, **E–H** HM2001, **I–L** HM2006, and **M–P** JZ1903. HM1905, HM2001, and HM2006 were released from the Tokai region and JZ1903 was released from the Sea of Japan coastline. **A, E, I, M** Part of the time series data of the vertical movement of X-tagged eels. The colors of the lines in the time series data indicate water temperature and the shaded area indicate nighttime. **B–D, F–H, J–L, N–P** The vertical temperature profile (**B, F, J, N**), the frequency of swimming depth (**C, G, K, O**) and temperature (**D, H, L, P**) of the eels through the tracking period. The colors in the scatterplot and histogram indicate daytime (yellow) and nighttime (blue) data

and temperature, it was difficult to definitively determine if the eel was predated.

Discussion

The PSAT has been widely used to track the large-scale movements of animals, making it a valuable tool for monitoring the oceanic migrations of silver eels. In

particular, many PSATs have been attached to both European and American eels [21, 29], and studies have shown that the PSAT is capable of tracking the migrations of these eels over long periods [21], with the European eel being tracked for up to 273 days. Although attempts have been made to track the spawning migrations of Japanese eels, long-distance tracking has not yet been achieved to

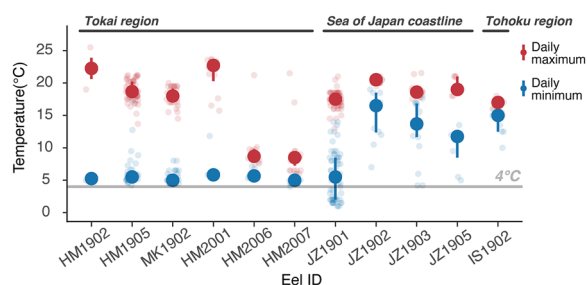


Fig. 6 The daily maximum and minimum temperatures recorded by the pop-up satellite archival tags. Jitter plots show the daily maximum (red) and minimum (blue) temperatures for each eel. Solid color circles and scale bars show the median values and the interquartile range, respectively. The gray horizontal line represents 4 °C

the same extent as for American and European eels due to the comparatively small size of the species. In the present study, we used the relatively small PSATs to track the oceanic migration of Japanese eels. However, the PSATs detached from the eels prematurely, and the eels were not followed throughout their entire oceanic migration to the spawning ground, which is about 3000 km away from the Japanese coast. The maximum attachment duration of

PSATs was 55 days, except for the eels suspected of predation, which was an intermediate value compared with other studies of Japanese eels (21 days, Chen et al., 2018 [27]; 39 days, Manabe et al., 2011 [18]; 43 days, Higuchi et al., 2018 [26]; 69 days, Higuchi et al., 2021 [23]). The migration speed estimated from the great circle distance ranged from 0.9–37.5 km day⁻¹, and the speeds were not much different from the previous studies of Japanese eel [18, 23, 26].

Migration behavior

Three possible migratory routes to the spawning ground have been proposed for the Japanese eel, although the actual route remains unknown. The first hypothesis is that Japanese silver eels move eastward with the Kuroshio Current and then, when they reach the south coast of Japan, they start to migrate southward to the spawning area [30]; the second is that they migrate directly from each growth habitat to the spawning area via the great-circle route (shortest route) [31]; and the third hypothesis is that they swim to the spawning ground following the Kuroshio and North Equatorial Current, i.e., in the reverse direction of larval drift [32]. According to migration simulations of

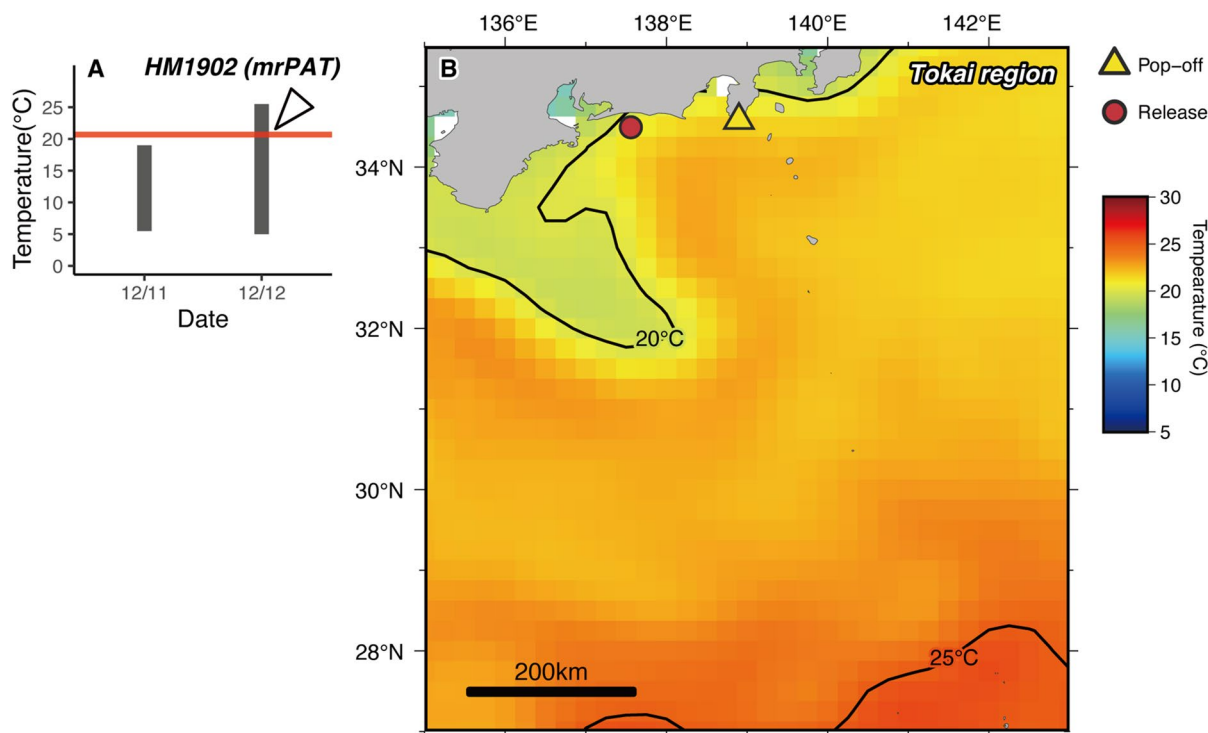


Fig. 7 Temperature ranges recorded by the mrPAT of a predated eel. **A** Temperature ranges of HM1902 released from the Tokai region. The horizontal red line represents the sea surface temperature (SST) near the tag’s pop-up location and the yellow triangle indicates when the maximum value recorded by the tag exceeded the SST. **B** The release (red filled circle) and pop-up location (yellow filled triangle). The colored grid and black lines on the map represent the SST and isotherm, respectively

Japanese silver eels, oceanic currents have a large influence on migration cost and duration, and eels are able to take advantage of the Kuroshio Current, recirculation, and subtropical gyre to save energy and time [33]. The eels released on the south coast of Japan and Taiwan, the areas facing the Kuroshio Current, have been shown to migrate along the Kuroshio Current, supporting the first hypothesis [18, 23, 27]. In the present study, we released Japanese eels in the Tokai region, located on the south coast of Japan, and all eels tracked moved towards the east or southeast (Fig. 2A and Table 2). The results of the present study partially support the notion that silver eels, at least those departing from areas facing the Kuroshio Current, might utilize the Kuroshio current in the early phase of the spawning migration. It should be noted, however, that we cannot rule out the possibility that the tags were still too large for the Japanese eels and that the silver eels were carried away easier than usual by the Kuroshio Current.

In contrast to the eels released in the Tokai region, which followed the ocean current, those released from the Sea of Japan coastline tended to migrate westward against the ocean current, in the opposite direction of the larval transport route (Fig. 2B and Table 2). The longest tracked eel reached as far as the boundary between the Sea of Japan and the East China Sea (JZ1902 in Fig. 2B). In the East China Sea, migrating silver eels are reported to be caught on the sea surface from autumn to winter [14]. As the fishery area shifts southward in winter compared to autumn, it is thought that silver eels might migrate southward through the East China Sea to the Pacific Ocean. The oceanic migration of eels leaving from the Tohoku region is poorly understood, and to date, only one case of silver eel caught in bottom trawls off the coast of Sendai Bay has been reported [28]. In this study, eels released in the Tohoku region also moved southward against the ocean currents and larval transport route (Fig. 2C). The migration directions of the eels from the Tohoku region and the Sea of Japan coastline were roughly consistent with the direction to the spawning ground. Although it is not completely clear how Japanese eels can move to the spawning ground, it has been reported that Japanese eels released in the Kuroshio Current and subtropical regions can migrate toward the spawning grounds while compensating for the effects of ocean currents suggesting that they have sufficient navigational ability [34] as shown in other temperate eels [19, 21]. However, whether in the Sea of Japan or the Tohoku region, the number of tracked fish is still small, and the tracking period is not long enough. Therefore, further tracking studies are needed to gain a better understanding of the spawning migration of Japanese eels from these regions.

Migratory behavior that appears to be straying or a deviation has been observed in European eels [21]. It is not clear what causes this migratory behavior, but it has been attributed to entrapment within eddies or navigational responses to hydrographic or bathymetric features [21]. Among the eels released in the Sea of Japan, JZ1903 migrated in a direction unrelated to the spawning grounds, and this aberrant migratory behavior may be due to the same reasons (Fig. 2B).

Vertical movement and water mass structure

Anguillid eels have been reported to exhibit DVM during their spawning migrations, diving into deep waters during the day and ascending into shallow waters at night. In the present study, the individuals released in the Tokai region also showed regular DVM (Fig. 5A, I, and M). The ecological reasons for the DVM of silver eels during spawning migration are considered to be predator avoidance behavior or behavioral thermoregulation [29].

Recently, in the context of behavioral thermoregulation, it has been proposed that the empirical day–night temperature difference in spawning migratory eels may be a consequence of DVM rather than a driver [25]. European eels released in the Mediterranean Sea showed DVM in the region, although there was no day–night temperature difference (about 13 °C) despite DVM (daytime 450–650 m; nighttime 250–450 m). In the present study, the eels released in the Tokai region stayed in different depth and temperature environments during the daytime and nighttime, and the nighttime water temperatures recorded by tagged eels released in late December 2020 were lower than those of individuals released in late November 2020 or early December 2019. It has been suggested that lunar age, water clarity, and temperature should also affect nighttime depth in DVM [23, 26], but in our study nighttime depth does not appear to be largely affected by temperature. Previous studies have also shown that water temperature should have a significant effect on the maximum daytime depth in the DVM [23, 27]. In our study, the eels exhibiting DVM experienced a narrow temperature range and showed a tendency to swim along the depth of the 5 °C isotherm in the daytime (Fig. 3A, C, and E). Furthermore, the other eels also seemed to avoid water temperatures below 5 °C (Fig. 6). This trend is consistent with previous studies that show Japanese silver eels rarely stay in water temperatures below 5 °C during oceanic migration [18, 23, 27].

An eel released in the Sea of Japan showed repeated vertical movements, not regular DVM, unlike the eels released in the Tokai region (Fig. 5M). In addition, the maximum depth experienced by this eel in the Sea of Japan was about 150 m, while the eels released in the Tokai region ranged from 750 to 1000 m (Fig. 5). It is

known that American and European eels do not show regular DVM, similar to the eel released in the Sea of Japan, and American eels have shown similar vertical movement behavior in the early stages of migration, such as on the continental shelf [24]. The difference in vertical movement behavior of eels in the Sea of Japan and on the Pacific coast can be attributed to the bathymetry and water mass structure of the Sea of Japan. In the Sea of Japan, the shallow depth zone continues for a while near the coast, which is very different from the Pacific Ocean, where the depth zone deepens rapidly offshore. As for the water mass structure, the surface layer in the Sea of Japan is warm, but the water temperature drops sharply after 100 m depth (Fig. 5N), in contrast to the gradual decrease in water temperature observed off the southern coast of Japan (Fig. 5B, F, and J). It is likely that the eels released in the Sea of Japan did not use the deep waters, but instead made repeated vertical movements in the shallow depth zone due to the low water temperature in the middle layer. Although we cannot directly know the vertical movement of the eels with mrPATs (tags without depth sensors), the daily maximum and minimum water temperatures suggest that these eels also used a limited shallow depth zone near the surface, as the daily minimum water temperatures were never below 4 °C (except for one eel) and the maximum values were close to the SST (18–20 °C) (Figs. 4 and 6). There have been cases of migrating silver eels captured at the surface in both the Sea of Japan and the East China Sea, but no eels have ever been captured at the surface near the southern coast of Japan, where the Kuroshio Current flows. The cases of surface-captured migrating silver eels in both the Sea of Japan and the East China Sea may reflect regional differences in vertical migration behavior.

Predation

Migratory European and American silver eels are known to be predated by endothermic fishes (tunas or endothermic sharks) [20, 27], ectothermic fishes [21], and marine mammals [21, 25, 35], suggesting that these animals are also potential predators for Japanese eels. In fact, predation by tunas and swordfish has been reported in Japanese eel [18, 23, 27], and in the present study, an eel released from the Tokai region is thought to have been predated. The predated PSAT (HM1902) recorded a maximum temperature of 25.5 °C on the second day after release, 4°C higher than the SST near the tag surfacing location (Fig. 7). Body temperatures several degrees above water temperature have been reported for mako and salmon sharks and tuna species, with stomach temperatures of 25–28 °C [36, 37]. In other endothermic animals (cetaceans and birds),

the body temperature is about 35 °C or higher. Thus, we infer that this eel was predated by an endothermic fish (e.g., tuna or endothermic shark).

One eel, JZ1901, which was released on the Sea of Japan coastline, was also probably predated because its mrPAT recorded a water temperature of 1 °C (Fig. 6) and its surfacing point did not differ greatly from its release point 59 days earlier (Fig. 2). Alternatively, it is also possible that Japanese eels can tolerate water temperatures below 1 °C, as has been shown for European eels, which can experience water temperatures of 1 °C in the Norwegian Sea [21]. However, European eels in other parts of the species distribution do not experience such temperatures, and Japanese eels released on the Sea of Japan coastline appeared to actively avoid such temperatures, suggesting that this one eel (JZ1901) was preyed upon. In contrast to HM1902, the highest water temperature recorded by JZ1901 was not higher than the SST at the release location and time, so if it was preyed upon, the predator was likely an ectothermic fish.

The predation rate of migrating silver eels clearly differs between seasons or sea areas in European and American eels [21, 38], but in the present study, we did not release enough individuals to observe a trend in predation rates. Thus, further long-term and regional studies may reveal regional differences in the predation of Japanese eels.

Conclusions

In the present study, a total of 23 silver Japanese eels with PSATs were released from three regions of Japan. The migratory direction of the Japanese eels varied among the release regions, and in all cases, it was consistent with movement toward the spawning grounds. All three X-tagged Japanese eels released in the Tokai region showed regular patterns of DVM. During the day, the tracked eels appeared to move along 5 °C isotherms, while at night, one of them moved to a deeper depth than the other two. The X-tagged eel released on the Sea of Japan coastline exhibited repeated vertical movements, in contrast to the DVM observed in eels from the Tokai region. Japanese eels also seemed to avoid water depths with a temperature lower than 4 °C during their spawning migrations, with the exception of one eel. The region-specific differences in migration behavior suggest that bathymetric and water-mass structure affect migratory behavior, especially DVM. In the present study, we described the early phase of the oceanic migration of Japanese eels and the region-specific migratory behavior of this species. However, the route from each growth habitat to the spawning area is still unknown, so further studies are needed to unravel the mysteries of the Japanese eel spawning migration.

Materials and methods

Study sites and animals

Fieldwork was conducted at six sites (Hamana Lake, Ise-Mikawa Bay, Jinzai Lake, Genkai Sea, Ogawara Lake, and Ishinomaki Bay,) from November 2019 to February 2020 and at Hamana Lake from November 2020 to December 2020. Hamana Lake and Ise-Mikawa Bay are located in the Tokai region, central Honshu, Japan, adjacent to the Kuroshio Current (Fig. 1B). Jinzai Lake and Genkai Sea are adjacent to the Sea of Japan in southwestern Honshu, Japan. Ishinomaki Bay and Ogawara Lake are located in the Tohoku region, northern Honshu, Japan, the northernmost distribution area of the species, and are adjacent to the western Pacific Ocean. Hamana Lake, Jinzai Lake, and Ogawara Lake are brackish lakes.

All of the silver eels used in this study were caught by local fishermen at each study site. The eels collected in Hamana Lake, Ise-Mikawa Bay, Jinzai Lake, and Ogawara Lake were captured by set nets. The eels collected in the Genkai Sea were captured with dip nets while migrating on the surface, and those collected in Ishinomaki Bay were captured by tubular pots. Eels were held for two days to one month before release. The silvering stages of eels were determined as S1 and S2 stages, according to the morphological index reported in a previous study [39], and eels in the S2 stage were selected for tagging. To avoid the negative effects of drag caused by the external tags, small eels (≤ 750 g) were not selected. Three to six hours after tagging, the fish were transported by chartered vessel to coastal release sites at each study site. The release sites were located 1–53 km offshore, where the water depths ranged from 10–700 m.

PSATs and tagging

A total of 23 silver eels were tagged with two different types of pop-up satellite tags: 10 tags were X-tags from Microwave Telemetry, and 13 were Mark Report PATs (mrPATs) from Wildlife Computers. The X-tag is 122 mm long, has a maximum diameter of 33 mm, and weighs 45 g in air. The X-tags recorded depth, temperature, and light intensity. The release mechanism of the X-tags was triggered by a programmed period of time or constant pressure for 3 consecutive days; they were actually drifting on the surface for 3 days before the first transmission location was calculated by the Argos system. The mrPAT is 127 mm long, has a maximum diameter of 28 mm, and weighs 40 g in air. mrPATs are equipped with temperature, tilt, and wet/dry sensors. mrPATs begin transmitting daily max/min temperature after they float to the surface. The release mechanism of mrPATs was triggered by a programmed date or detecting water surface for a certain duration. The duration of surface detection

was two consecutive hours between November 2019 and February 2020, but the duration was changed to 15 consecutive hours from November 2020. The maximum tracking period of the PSATs was programmed to be 4 to 8 months from the start of each tag operation, but all PSATs were released by different triggers (constant pressure or water surface detection) before this maximum period was reached (Additional file 1: Table S1).

In order to attach PSATs, all fish were anesthetized with FA100 (eugenol, 107 mg ml^{-1} ; DS Pharma Animal Health Co. Ltd, Osaka, Japan) at a concentration of 2.0–3.0 mg ml^{-1} . Body size and mass were measured prior to surgical tagging. Surgical tagging was then performed by using the Westerberg method, described in a previous study [40], with three attachment points. A wire with a loop at each end was made by twisting a 0.8-mm-diameter stainless steel wire. The angle between the two loops at each end was perpendicular. A leader was then threaded through the tag and through one loop, and an eye was made at the end. Three 0.8-mm-diameter stainless steel wires were threaded through needles and placed under the skin of the fish. The wire closest to the head of the fish was passed through the eye in the leader, the second wire was passed through the loop threaded with the leader and closed, and the third wire was passed through the other loop and closed. Between November 2019 and February 2020, fluorocarbon monofilament thread (ϕ 1.5 mm, 215 lb.) was used as the leader for the PSATs, after which Zylon braid thread (ϕ 0.8 mm, 325 lb.) was utilized.

Data analysis

Previous studies of PSAT-tagged European and American eels have used a geolocation method based on daily sunrise and sunset data [41], and geolocation estimation has been applied to the tropical eels [42]. These methods were tested on the time-series depth data derived from the X-tags in our study, but they did not work. For this study, the pop-up point for each PSAT was defined as the point where the PSAT first transmitted its signal to the satellite and the great circle distance (GCD) and the azimuth between the release and pop-up points of each eel were calculated using the 'geosphere' package in R. Tracking durations of PSATs were calculated from the actual duration that eels were tagged. For all tags, the beginning of the actual duration was defined as the release date of the tagged eel. However, the determination of the end date varied by tag type due to differences in tag release mechanisms. In the case of X-tags, the end of actual duration was determined by the time of tag surfacing, which was recorded in each tag as time-series depth data. mrPATs begin transmitting within at least 1 day of surfacing, as their programmed release mechanism is triggered by surface

detection for 2 or 15 consecutive hours. Therefore, the end of the actual attachment duration of mrPATs was determined by the start date of transmission (Additional file 1: Table S1).

Since the depth and temperature data obtained from the X-tag were a time-series of 15-min intervals, Igor Pro V8.1 and its application of Ethographer were used for data analysis [43]. The solar altitude at a point was used to divide the data into daytime and nighttime. Since the difference in longitude and latitude between the eel release point and the PSAT pop-up point was within 5 degrees, the coordinates for each eel were calculated using the midpoint between the release point and the pop-up point. Daytime and nighttime were divided by the solar altitude of -6° , the boundary altitude between civil and nautical twilight.

After predation, tags are assumed to record the depth and/or temperature that reflects the swimming behavior and body cavity temperature of the predator [18, 25]. To confirm predation by endothermic animals (e.g., tuna or whales), the surface temperature recorded by PSAT was compared with the physical model, OISST (optimal interpolation sea surface temperature), provided by NOAA (National Oceanic and Atmospheric Administration, <https://www.noaa.gov/>).

Abbreviations

DVM	Diel vertical migration
GCD	Great circle distance
PSATs	Pop-up satellite archival tags
SST	Sea surface temperature

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-023-00338-x>.

Additional file 1: Table S1. Tag type, programmed pop-off date, actual transmission start date, and transmission trigger information for the 15 eels with confirmed data transmission.

Acknowledgements

We are very grateful to the eel fishermen who helped us catch eels for tagging. We thank colleagues from the Institute of Freshwater Biology, Nagano University, for helpful comments.

Author contributions

Research plan: HH, SM, TKA. Data curation: TKA, IG, AD, NM. Data analysis: TKA. Methodology: TKA, IG, AD, HH, SM, NM. Project administration: HH, SM. Visualization: TKA. Writing: TKA, HH. All authors read and approved the final manuscript.

Funding

The research was funded by a grant from the Japan Fisheries Agency.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

This study was conducted according to the Guidelines for Animal Experimentation of Fisheries Research Institute, Fisheries Research Agency, Japan.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Received: 24 April 2023 Accepted: 23 June 2023

Published online: 07 July 2023

References

- Hakoyama H, Fujimori H, Okamoto C, Kodama S. Compilation of Japanese fisheries statistics for the Japanese eel, *Anguilla japonica*, since 1894: a historical dataset for stock assessment. *Ecol Res.* 2016;31(2):153–153. <https://doi.org/10.1007/s11284-015-1332-9>.
- Hakoyama H, Rousseau Y, Faulks L, Kodama S, Okamoto C, Fujimori H, Sekino M. Japanese eel (*Anguilla japonica*). In: Fisheries Agency of Japan, and Japan Fisheries Research and Education Agency (ed.) Current Status of International Fishery Stocks in 2022;2022. https://kokushi.fr.go.jp/R04/R04_82_EIJ_English.pdf.
- Kaifu K, Yokouchi K, Higuchi T, Itakura H, Shirai K. Depletion of naturally recruited wild Japanese eels in Okayama, Japan, revealed by otolith stable isotope ratios and abundance indices. *Fish Sci.* 2018;84(5):757–63. <https://doi.org/10.1007/s12562-018-1225-2>.
- Jacoby DMP, Casselman JM, Crook V, DeLucia M-B, Ahn H, Kaifu K, Kurwie T, Sasal P, Silfvergrip AMC, Smith KG, Uchida K, Walker AM, Gollock MJ. Synergistic patterns of threat and the challenges facing global anguillid eel conservation. *Glob Ecol Conserv.* 2015;4:321–33. <https://doi.org/10.1016/j.gecco.2015.07.009>.
- Kasai A, Yamazaki A, Ahn H, Yamanaka H, Kameyama S, Masuda R, Azuma N, Kimura S, Karaki T, Kurokawa Y, et al. Distribution of Japanese eel *Anguilla japonica* revealed by environmental DNA. *Front Ecol Evol.* 2021;9:83. <https://doi.org/10.3389/fevo.2021.621461>.
- Tsukamoto K. Discovery of the spawning area for Japanese eel. *Nature.* 1992;356(6372):789. <https://doi.org/10.1038/356789a0>.
- Tsukamoto K. Oceanic biology: spawning of eels near a seamount. *Nature.* 2006;439(7079):929. <https://doi.org/10.1038/439929a>.
- Aoyama J, Watanabe S, Miller MJ, Mochioka N, Otake T, Yoshinaga T, Tsukamoto K. Spawning sites of the Japanese eel in relation to oceanographic structure and the West Mariana Ridge. *PLoS ONE.* 2014;9(2):88759. <https://doi.org/10.1371/journal.pone.0088759>.
- Han Y-S, Zhang H, Tseng Y-H, Shen M-L. Larval Japanese eel (*Anguilla japonica*) as sub-surface current bio-tracers on the East Asia continental shelf. *Fish Oceanogr.* 2012;21(4):281–90. <https://doi.org/10.3390/su11092572>.
- Chino N, Arai T. Relative contribution of migratory type on the reproduction of migrating silver eels, *Anguilla japonica*, collected off Shikoku Island, Japan. *Mar Biol.* 2009;156(4):661–8. <https://doi.org/10.1007/s00227-008-1116-7>.
- Lin Y-J, Tzeng W-N. Validation of annulus in otolith and estimation of growth rate for Japanese eel *Anguilla japonica* in tropical southern Taiwan. *Envir Biol Fishes.* 2009;84(1):79–87. <https://doi.org/10.1007/s10641-008-9391-1>.
- Yokouchi K, Sudo R, Kaifu K, Aoyama J, Tsukamoto K. Biological characteristics of silver-phase Japanese eels. *Coast Mar Sci.* 2009. <https://doi.org/10.15083/00040704>
- Kotake A, Arai T, Ozawa T, Nojima S, Miller M, Tsukamoto K. Variation in migratory history of Japanese eels, *Anguilla japonica*, collected in coastal waters of the Amakusa Islands, Japan, inferred from otolith Sr/Ca ratios. *Mar Biol.* 2003;142(5):849–54. <https://doi.org/10.1007/s00227-003-1136-2>.

14. Sasai S, Aoyama J, Watanabe S, Kaneko T, Miller MJ, Tsukamoto K. Occurrence of migrating silver eels *Anguilla japonica* in the East China Sea. *Mar Ecol Prog Ser.* 2001;212:305–10. <https://doi.org/10.3354/meps212305>.
15. Sudo R, Okamura A, Fukuda N, Miller MJ, Tsukamoto K. Environmental factors affecting the onset of spawning migrations of Japanese eels (*Anguilla japonica*) in Mikawa Bay Japan. *Environ Biol Fishes.* 2017;100(3):237–49. <https://doi.org/10.1007/s10641-017-0575-4>.
16. Jellyman D, Tsukamoto K. The first use of archival transmitters to track migrating freshwater eels *Anguilla dieffenbachii* at sea. *Mar Ecol Prog Ser.* 2002. <https://doi.org/10.3354/meps233207>.
17. Jellyman D, Tsukamoto K. Vertical migrations may control maturation in migrating female *Anguilla dieffenbachii*. *Mar Ecol Prog Ser.* 2010. <https://doi.org/10.3354/meps08468>.
18. Manabe R, Aoyama J, Watanabe K, Kawai M, Miller M, Tsukamoto K. First observations of the oceanic migration of Japanese eel, from pop-up archival transmitting tags. *Mar Ecol Prog Ser.* 2011;437:229–40. <https://doi.org/10.3354/meps09266>.
19. Béguer-Pon M, Castonguay M, Shan S, Benchetrit J, Dodson JJ. Direct observations of American eels migrating across the continental shelf to the Sargasso Sea. *Nat Commun.* 2015;6(1):1–9. <https://doi.org/10.1038/ncomms9705>.
20. Aarestrup K, Okland F, Hansen MM, Righton D, Gargan P, Castonguay M, Bernatchez L, Howey P, Sparholt H, Pedersen MI, McKinley RS. Oceanic spawning migration of the European eel (*Anguilla anguilla*). *Science.* 2009;325(5948):1660. <https://doi.org/10.1126/science.1178120>.
21. Righton D, Westerberg H, Feunteun E, Økland F, Gargan P, Amilhat E, Metcalfe J, Lobon-Cervia J, Sjöberg N, Simon J, et al. Empirical observations of the spawning migration of European eels: the long and dangerous road to the Sargasso Sea. *Sci Adv.* 2016;2(10):1501694. <https://doi.org/10.1126/sciadv.1501694>.
22. Schabetsberger R, Miller MJ, Olmo GD, Kaiser R, Økland F, Watanabe S, Aarestrup K, Tsukamoto K. Hydrographic features of anguillid spawning areas: potential signposts for migrating eels. *Mar Ecol Prog Ser.* 2016;554:141–55. <https://doi.org/10.3354/meps11824>.
23. Higuchi T, Watanabe S, Manabe R, Tanimoto A, Miller MJ, Kojima T, Tsukamoto K. Horizontal and vertical migration behavior of silver-phase Japanese eels in coastal, pelagic and spawning areas observed by pop-up satellite archival tags. *J Exp Mar Biol Ecol.* 2021;542: 151587. <https://doi.org/10.1016/j.jembe.2021.151587>.
24. Béguer-Pon M, Shan S, Castonguay M, Dodson JJ. Behavioural variability in the vertical and horizontal oceanic migrations of silver American eels. *Mar Ecol Prog Ser.* 2017;585:123–42. <https://doi.org/10.3354/meps12380>.
25. Amilhat E, Aarestrup K, Faliex E, Simon G, Westerberg H, Righton D. First evidence of European eels exiting the Mediterranean Sea during their spawning migration. *Sci Rep.* 2016;6:21817. <https://doi.org/10.1038/srep21817>.
26. Higuchi T, Watanabe S, Manabe R, Kaku T, Okamura A, Yamada Y, Miller MJ, Tsukamoto K. Tracking *Anguilla japonica* silver eels along the West Mariana Ridge using pop-up archival transmitting tags. *Zool Stud.* 2018;57:24. <https://doi.org/10.6620/ZS.2018.57-24>.
27. Chen S-C, Chang C-R, Han Y-S. Seaward migration routes of Indigenous Eels, *Anguilla japonica*, *A. marmorata*, and *A. bicolor pacifica*, via satellite tags. *Zool Stud.* 2018. <https://doi.org/10.6620/ZS.2018.57-21>.
28. Matsuya N, Hagihara S, Wada T, Ijiri S, Adachi S. Morphological and physiological characteristics of an oceanic-migrating Japanese eel *Anguilla japonica* off Fukushima, Japan. *Coast Mar Sci.* 2015;38(1):8–11. <https://doi.org/10.15083/00040615>.
29. Béguer-Pon M, Dodson JJ, Castonguay M, Jellyman D, Aarestrup K, Tsukamoto K. Tracking anguillid eels: five decades of telemetry-based research. *Mar Freshw Res.* 2018;69(2):199–219. <https://doi.org/10.1071/MF17137>.
30. Tsukamoto K. Origin of diadromous fishes and mechanism of migration. In: Goto A, Tsukamoto K, Maekawa K, editors. *Freshwater fishes migrating between River and the Sea*. Tokyo: Tokai University Press; 1994. p. 42–58. **(in Japanese)**
31. Matsui I. *Eel Biology-biological Study* (in Japanese). Tokyo: Kouseisha-Kouseikaku; 1972. **(in Japanese)**
32. Yokose H. Geological approach to the spawning sites of the Japanese eel. *Kaiyo Monthly.* 2008;48:45–58. **(in Japanese)**
33. Chang Y-L, Miyazawa Y, Béguer-Pon M. Simulating the oceanic migration of silver Japanese eels. *PLoS ONE.* 2016;11(3):0150187. <https://doi.org/10.1371/journal.pone.0150187>.
34. Fukuda N, Yamamoto T, Yokouchi K, Kurogi H, Okazaki M, Miyake Y, Watanabe T, Chow S. Active swimming and transport by currents observed in Japanese eels (*Anguilla japonica*) acoustically tracked in the western North Pacific. *Sci Rep.* 2022;12(1):3490. <https://doi.org/10.1038/s41598-022-05880-x>.
35. Wahlberg M, Westerberg H, Aarestrup K, Feunteun E, Gargan P, Righton D. Evidence of marine mammal predation of the European eel (*Anguilla anguilla* L.) on its marine migration. *Deep Sea Res Part I: Oceanogr Res Papers* 2014;86:32–38. <https://doi.org/10.1016/j.dsr.2014.01.003>.
36. Carey FG, Teal JM. Mako and porbeagle: warm-bodied sharks. *Comp Biochem Physiol.* 1969;28(1):199–204. [https://doi.org/10.1016/0010-406X\(69\)91335-8](https://doi.org/10.1016/0010-406X(69)91335-8).
37. Sepulveda C, Kohin S, Chan C, Vetter R, Graham J. Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. *Mar Biol.* 2004;145(1):191–9. <https://doi.org/10.1007/s00227-004-1356-0>.
38. Béguer-Pon M, Benchetrit J, Castonguay M, Aarestrup K, Campana SE, Stokesbury MJ, Dodson JJ. Shark predation on migrating adult American eels (*Anguilla rostrata*) in the Gulf of St. Lawrence. *PLoS ONE.* 2012. <https://doi.org/10.1371/journal.pone.0046830>.
39. Okamura A, Yamada Y, Yokouchi K, Horie N, Mikawa N, Utoh T, Tanaka S, Tsukamoto K. A silvering index for the Japanese eel *Anguilla japonica*. *Environ Biol Fishes.* 2007;80(1):77–89. <https://doi.org/10.1007/s10641-006-9121-5>.
40. Økland F, Thorstad EB, Westerberg H, Aarestrup K, Metcalfe JD. Development and testing of attachment methods for pop-up satellite archival transmitters in European eel. *Anim Biotelemetry.* 2013;1(1):3. <https://doi.org/10.1186/2050-3385-1-3>.
41. Westerberg H, Sjöberg N, Lagenfelt I, Aarestrup K, Righton D. Behaviour of stocked and naturally recruited European eels during migration. *Mar Ecol Prog Ser.* 2014;496:145–57. <https://doi.org/10.3354/meps10646>.
42. Chang Y-LK, Olmo GD, Schabetsberger R. Tracking the marine migration routes of South Pacific silver eels. *Mar Ecol Prog Ser.* 2020;646:1–12. <https://doi.org/10.3354/meps13398>.
43. Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S. Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE.* 2009;4(4):5379. <https://doi.org/10.1371/journal.pone.0005379>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

