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Biology

Discovering the dominance of the non-native European eel in the upper reaches of the Tone River system, Japan

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Abstract To investigate the presence of non-native anguillid eels in Japanese waters, 141 eels were collected from seven sampling sites throughout the Tone River system. Genetic species identification showed an extraordinary dominance of the non-native European eel *Anguilla anguilla* in the uppermost site of the study area. Estimation of age from otoliths suggested that the European eels were introduced into the river in the 1990s, corresponding to previous reports from other Japanese water systems. Comparison of the von Bertalanffy growth curve parameters indicated that the European eels caught in the Tone River system appeared to have a similar or even higher growth rate than the same species in the original habitats in Europe. The long-term inhabitation and the normal development of European eels in Japanese waters suggest that regulations prohibiting the release of non-native eels and safeguards against accidental escape from culture ponds must be strictly maintained in order to ensure the conservation of the native Japanese eel.

Keywords Anguillid eels · Distribution · Endangered species · Growth · Non-native species

Introduction

The Japanese eel *Anguilla japonica* is a commercially important fishery species in Japan. However, shortage of Japanese glass eels for aquaculture since the 1970s has led to the importation of large numbers of foreign eel species with the aim of restoring Japanese aquaculture. With similar looks, texture, and taste as the Japanese eel, the European eel *Anguilla anguilla* was first imported to Japan in 1969, and imports reached a peak in 1973 [1]. However, the high mortality and low growth rate in aquaculture of the European eel compared with the Japanese eel led to a decline in imports after 1973. These non-native eel species have dispersed into the Japanese river systems either by escaping culture ponds

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or by mixing with deliberately released Japanese eels that are intensively stocked by local fisheries cooperatives to enhance fisheries catches in various areas. While only two species, the Japanese eel and the giant mottled eel *Anguilla marmorata*, naturally inhabit the main island of Japan, several non-native eel species, such as the European eel and the American eel *Anguilla rostrata* have been reported in Japanese waters [2–5]. In particular, a relatively high proportion of European eels have been reported in some areas [4]. However, with the recent decline of European glass eel imports for aquaculture, there seems to be a decrease in the population of European eels in Japanese waters [6], and the presence of non-native eels has not been confirmed in the past 10 years. Since all temperate-zone anguillid eels presumably inhabit similar ecological niches, and their functional morphology might be similar in terms of feeding and prey capture, introduced non-native eels carry the risk of competing with native Japanese eels for food resources and space. Moreover, since anguillid eels are top predators, fundamental knowledge of the possible ecological effects of these non-native eels in Japanese waters is essential.

The Tone River system is one of the largest river systems and a major eel fishery area in Japan. Commercial fisheries for glass eels and eels (including yellow and silver eels) have operated in this water system for many years, and at their peak in the 1970s, these fisheries accounted for about 70 and 30% of total catches of glass eels and eels in Japan, respectively [7]. Ecological studies on the growth phase of Japanese eels (yellow eels) have also been conducted recently in the lower part of the Tone River system [8, 9]. In the present study, the existence of non-native anguillid eels was investigated throughout the entire Tone River system. Because the three temperate-zone anguillid eels, particularly the Japanese eel, the European eel and the American eel have similar external morphologies, the detailed distribution of non-native anguillid eels is difficult to assess based on reports from local citizens and fisheries cooperatives. Therefore, genetic analysis is required to investigate the distribution of non-native anguillid eels. After more than a decade since the previous discoveries, this article reports the presence of a high proportion of non-native European eels in the upper reaches of the Tone River system.

Materials and methods

Study area

The Tone River system is one of the largest river systems in Japan, with the second longest stream length (322 km) and the largest basin area (16,840 km^2) in the country. A total of five river-crossing structures such as dams and barrages are located throughout the study area (Fig. 1). At the lower part of the river, freshwater and brackish water are divided by the Tone River mouth tidal barrage (Fig. 1a) located 18.5 km upstream from the river mouth. There are stepped fish passes on both sides of the barrage, as well as a low-gradient fish pass on the right side of the barrage. To the upstream of the Tone River mouth tidal barrage, the Tone diversion weir (Fig. 1b) is located 154 km from the river mouth. The Tone diversion weir is equipped with three fish passes, two of which have switchbacks, allowing each fish pass entrance to be located just beneath the weir. Both the Tone River mouth tidal barrage and the Tone diversion weir have adjustable sluice gates that open frequently during high-water periods. In contrast, the Bando barrage (Fig. 1c), the headrace tunnel (Fig. 1d), and the 15-m-high Ayado hydroelectric dam (Fig. 1e), located between sites F and G, do not have adjustable sluice gates. The Bando barrage, the headrace tunnel, and the Ayado hydroelectric dam are each equipped with a single fish pass.

To investigate the existence of non-native anguillid eels in the Tone River system, seven sampling sites were set throughout the water system. Site A is located in the brackish water area downstream from the tidal barrage, and sites B, C, D, E, F, and G are located in the freshwater areas. Site A is located in the lower Tone River, and the other sites are located in its tributaries. Sites B, C, D, and E are located in Lake Kasumigaura, the Nekona River, the Uzuma River, and the Haya River, respectively. Site F consists of the Karasu, Kabura, and Ayu rivers, and site G consists of the Akaya and Usune rivers.

Collection of eels

At sites A and B, eels were collected from June to August 2015 using refuge traps comprised of two cylinders open at both ends. At sites C, D, and E, eels were collected using an LR-24 electrofisher (Smith-Root, Vancouver, WA, USA) in August 2015 and from August to October 2016. At sites F and G, eels were caught by fishermen from June to August 2015 and in August 2016. Eels collected in 2012 using refuge traps at site A were also provided [9]. Collected eels were stored at −20 °C in the laboratory.

Species identification

Ege's [10] morphological characters are generally used as a method of species identification for the genus *Anguilla*, but they were recently deemed insufficient due to underestimation of intraspecific variation [11]. Thus, DNA nucleotide

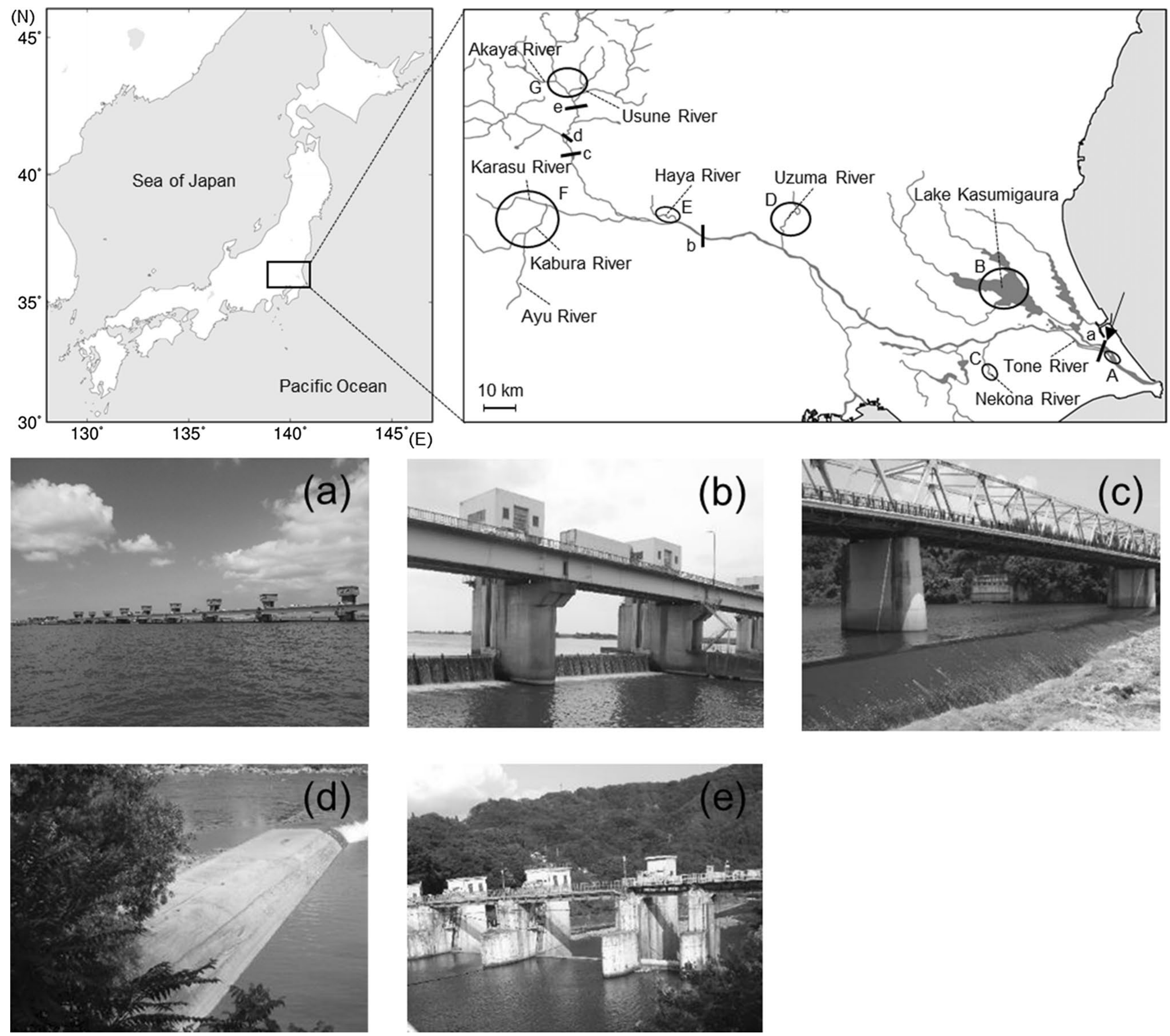

Fig. 1 Map of the study area in the Tone River system. *Circles* (*A* to *G*) indicate sampling sites. *Thick black lines* (*a* to *e*) indicate river-crossing structures. The *black arrow* shows the division between brackish water and freshwater. *Photographs* show the five river-crossing structures located in the study area: the Tone River mouth tidal barrage (**a**), the Tone diversion weir (**b**), the Bando barrage (**c**), the headrace tunnel (**d**), and the Ayado hydroelectric dam (**e**)

sequencing of the partial fragment of the mtDNA 16S rRNA gene was employed, which was previously established as an effective method of species identification in the genus *Anguilla* [4, 11]. Briefly, a DNA fraction was extracted from fin tissues and used for polymerase chain reaction (PCR) amplification of the partial fragment of the 16S rRNA gene (640 bp). Subsequently, DNA nucleotide sequencing and database searching were performed for species identification. The methods of genetic analysis have been described in detail elsewhere [12–14].

Biological characteristics of European eels

The total length of each eel was measured to the nearest 1 mm, and the body weight was measured to the nearest 1 g. The sex of the eels was identified by visual inspection of the gonad morphology. To indicate the degree of sexual maturation, two metrics were used, the eye index, according to Pankhurst [15], and the fin index, according to Durif et al. [16]. European eels with an eye index over 6.5 and a fin index over 4.5 were considered to be at the migratory silver stage.

Age determination and growth history estimation of European eels

The age of the eels based on their otoliths was also determined. For the otolith aging analysis, the sagittal otoliths were removed from the eels and were embedded in epoxy resin (EpoFix Kit, Struers, Westlake, OH, USA). After mounting on slide glasses, the otoliths were grounded on both sides along the longitudinal axis to expose the core. After further polishing with OP-S suspension liquid, the otoliths were etched using 1% HCl for 1 min and stained with 0.05% toluidine blue for 1 h to reveal the annual rings. The age of the eels was determined by counting the number of annual rings under a microscope, following the method of Nagięć and Bawnsawy [17]. The otolith rings were assumed to be generated annually, as discussed by Kotake et al. [18], and assigned the distinct transition check with about 150 mm radius (elver mark) [19] thought to be associated with in-shore recruitment to coastal (brackish water) areas as 0 age. Therefore, the age in this study represents the number of years that an eel lived in freshwater or brackish water.

In order to estimate the individual growth trajectories, the length-at-age back-calculation was applied according to the method of Nagięć and Bawnsawy [17]. The early period of marine life as leptocephalus and the early glass eel stages were excluded from the analysis. Thus, the estimated individual growth trajectories represent the growth phase in rivers after recruitment. The estimated total length (L_t) at age t was calculated from the following equation:

$$L_t = l \times r_t \times R^{-1},$$

where l is the total length of the eel at capture minus the mean length of glass eels (70 mm) [20], r_t is the distance from the first annulus (elver mark) to the tth annulus, and R is the distance from the first annulus to the otolith margin. The annual growth during the growth phase is given by:

$$G_t = L_t - L_{t-1}.$$

In order to compare the growth of European eels found in the Tone River system with the growth of eels that were previously caught in their original habitats in Europe (Germany, Poland, and Ireland), the back-calculated length-at-age data were fitted to the von Bertalanffy growth equation [21]:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right),$$

where L_∞ is the maximum theoretical length, k is the rate at which the length approaches L_∞, and t_0 is the (hypothetical) time at which the fish would have been zero size if it had always grown according to the von Bertalanffy growth equation. The growth curves used for comparison were estimated by using only female eels caught in their original habitats in Europe. This is because growth is known to vary greatly between male and female of European eels [22], and all the European eels caught in the Tone River system were identified as females.

Results

Distribution of anguillid eels in the Tone River system

A total of 141 eels were collected in the Tone River system and were successfully identified by DNA nucleotide sequencing (site A, $n = 31$; site B, $n = 41$; site C, $n = 4$; site D, $n = 26$; site E, $n = 7$; site F, $n = 23$; site G, $n = 9$). The genetic analysis showed that all specimens caught in sampling sites A to F ($n = 132$ in total) were Japanese eels, whereas all specimens from the uppermost site G ($n = 9$) were found to be European eels only.

Biological characteristics of European eels

The biological characteristics of the European eels examined are shown in Table 1. The total length of the European eels caught in the upper river area (site G) ranged from 638 to 1060 mm, with a mean ± SD of 866 ± 122 mm, and body weight ranged from 578 to 2387 g, with a mean ± SD of 1414 ± 544 g. The age ranged from 14 to 22 years, with a mean ± SD of 18.6 ± 2.6 years. The eye index [15] ranged from 5.6 to 17.9, with a mean ± SD of 9.8 ± 3.4, and the fin index [16] ranged from 4.2 to 5.2, with a mean ± SD of 4.8 ± 0.3. Eighty-nine percent ($n = 8$) of the examined eels had an eye index greater than 6.5 and a fin index greater than 4.5, with a strongly melanized blackish dorsal skin from the head to the trunk and a silvery-white belly, which indicated that these eels were sexually maturing silver eels. All eels were determined to be females by visual inspection of the gonads.

Growth history estimation of European eels

The annual length increment estimated by the length-at-age back-calculation varied widely during the first few years, and a gradual decrease in growth was observed thereafter (Fig. 2). The total mean growth rate from ages 0 to 22 years was calculated as 37.4 ± 24.1 mm year^{-1}. Based on the back-calculated length-at-age data, the parameters of the von Bertalanffy growth equation were calculated as $L_\infty = 1070$ mm, $k = 0.088$, and $t_0 = -0.78$; the estimated growth curve is shown in Fig. 3.

Table 1 Total length, body weight, age, eye index, fin index, and sex of European eels collected in the Tone River system

ID	Total length (mm)	Body weight (g)	Age (years)	Eye index	Fin index	Sex
TN15-001	950	1683	16	5.6	4.2	Female
TN15-002	782	957	14	*9.1*	*4.7*	Female
TN15-003	863	1185	19	*8.9*	*5.0*	Female
TN15-004	1060	2387	22	*9.4*	*4.7*	Female
TN16-005	638	578	19	*6.8*	*4.8*	Female
TN16-006	859	1435	18	*11.0*	*4.7*	Female
TN16-007	942	1618	21	*10.2*	*4.8*	Female
TN16-008	915	1856	17	*17.9*	*5.2*	Female
TN16-009	782	1025	21	*9.3*	*5.1*	Female
Mean ± SD	866 ± 122	1414 ± 544	18.6 ± 2.6	9.8 ± 3.4	4.8 ± 0.3	
Max	1060	2387	22	17.9	5.2	
Min	638	578	14	5.6	4.2	

Eye and fin indexes exceeding 6.5 and 4.5, respectively are indicated in italics

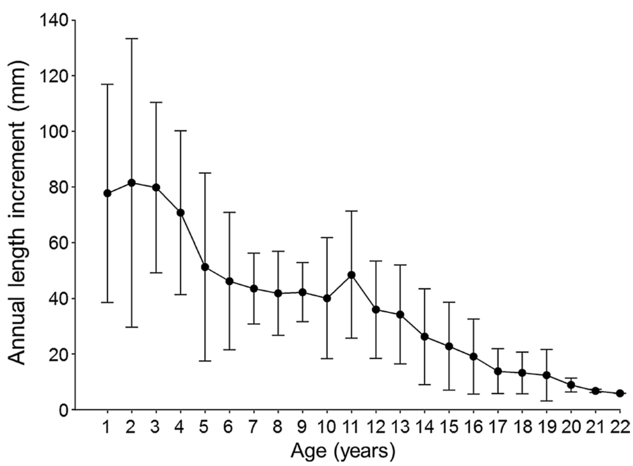

Fig. 2 Annual length increment of European eels ($n = 9$) collected in the Tone River system, estimated by the length-at-age back-calculation based on otoliths. *Markers* and *error bars* indicate means and standard deviations, respectively

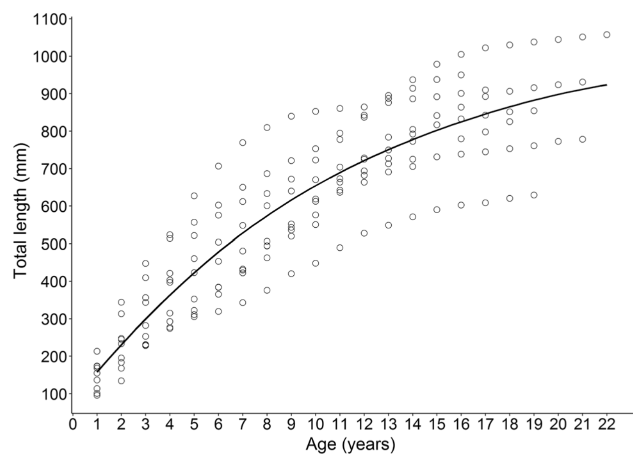

Fig. 3 Back-calculated length-at-age plots of European eels ($n = 9$) caught in the Tone River system. The *solid line* indicates the estimated von Bertalanffy growth curve

Discussion

Genetic species identification revealed that all of the nine eels caught in the upper reach of the Tone River system (site G) were non-native European eels. The presence of European eels in the Tone River system has never been observed in previous surveys. There have been previous reports of the presence of non-native eel species in Japanese waters around the 2000s [2–5], but the present study confirmed that non-native European eels are still distributed in Japan more than a decade after the previous discoveries. Estimates of age from the otoliths suggest that the European eels examined in this study were introduced into the river in the 1990s, which corresponds to previous reports from other water systems [6, 23]. Since the existence of culture ponds was not confirmed around the study area, European eels were likely released deliberately rather than escaping from culture ponds. Comparing the biological characteristics of the silver phase European eels found in Japanese waters in previous studies, the European eels examined in the present study had a larger total length, heavier body weight, and older age than those examined in the Uono River [23] and Mikawa Bay [6] (Table 2). This is likely due to the fact that the age of the total population of European eels in Japanese waters has increased because recruitment of European eels into Japanese waters has drastically decreased recently. Visual inspection of the gonads revealed that all the European eels caught in the Tone River system were females. The dominance of females was also observed in European eels collected in the Uono River [23] and Mikawa Bay [6]. Since males start their downstream

Table 2 Total length, body weight, and age of European eels collected in Japanese water systems in earlier studies

Study area	Total length (mm)	Body weight (g)	Age (years)	References
Tone River	866 ± 122	1414 ± 544	18.6 ± 2.6	The present study
Uono River	694 ± 113	913 ± 31	10.2 ± 2.0	Miyaiet al. [23]
Mikawa Bay	803 ± 104	1029 ± 418	13.2 ± 2.4	Okamura et al. [6]

Total length, body weight, and age are indicated as mean ± SD

migration at an earlier age than females [24], it is possible that the sex ratio bias was due to earlier sexual maturation of males that had already made their downstream migration prior to capture. The present study also suggests that the distribution of European eels is spatially limited; however, European eels were much more abundant than native Japanese eels in the uppermost area of the Tone River system. One possible reason for this limited distribution is that the release of European eels may have been restricted to the upper reaches. The extraordinary dominance of European eels in the upper reaches might also be explained by the absence of competitors. A number of studies in rivers of various sizes suggest that the abundance of eels decreases with distance from the river mouth [25–32]. This tendency also observed for Japanese eels [33], European eels released in the upper areas might have a less chance of competing with the native Japanese eel because of low recruitment of native Japanese eels in the upper reaches of the river. River-crossing structures, such as dams and barrages located intermittently throughout the study area, are considered to limit the upstream movement of eels [34] and may also be a key to understanding the dominance of European eels in the upper reaches of the river system. In order to reach site G (where European eels dominated), naturally recruiting Japanese eels must pass through at least five river-crossing structures, including the 15-m-high Ayado hydroelectric dam (Fig. 1e), that is located in the upper part of the study area, possibly decreasing the number of competing Japanese eels at site G. The Ayado hydroelectric dam might also have been an obstacle for the migrating silver eels. Telemetry studies of the American eel have observed characteristic circling behavior and a movement heading back upstream in front of the structures, possibly delaying the downstream migration of silver eels [35, 36]. The interference of the downstream migration may have resulted in an older age and a larger size at capture compared with European eels observed in other Japanese water systems [6, 23] (Table 2).

Although the von Bertalanffy growth curve estimation was based on otoliths from only nine individuals, comparison of the growth curve parameters showed that the European eels caught in the Tone River system had a similar or even a higher rate at which the length approaches the maximum theoretical length compared with European eels in their original habitats (Table 3). Considering that the European eels caught in the Tone River system presumably experienced warmer culture ponds for a few years in their early life history, their growth does not seem to be poor compared with that of eels in their original habitats. Similar results have been observed for European eels in other Japanese water systems, such as the Uono River in northern Japan [23] and Mikawa Bay in southern Japan [6], showing total mean growth rates of 63 and 58 mm year^{-1}, respectively. These growth rates are high compared with those observed in Europe, ranging widely from 14 to 52 mm year^{-1} [17, 22, 24, 37] (Table 3).

Although the negative impact of these non-native eels on native Japanese eels remains unclear, the possibility of interspecies competition may exist when the eels share the same habitat. A study investigating the development of American eels that were introduced into a European river suggested that American eels were capable of competing for food and space with native European eels [38]. Moreover, predatory non-native species seem to produce severe effects, such as decreasing the population of native species, when they are located at the top of the food chain [39]. As anguillid eels are among the top predators, non-native eels may not only compete with native Japanese eels but also have serious effects on the entire ecosystem.

Table 3 Values of L_∞, k, and t_0 in the von Bertalanffy equation and mean growth rates of European eels caught in the Tone River system and eels previously caught in their original habitats in Europe

References	Study area	L_∞ (mm)	k	t_0	Mean growth rate (mm year^{-1})
The present study	Tone River, Japan	1070	0.088	−0.78	37
Simon [22]	Elbe River, Germany	1009	0.089	−0.96	52
Nagiec and Bahnsawy [17]	Jeziorak Lake, Poland	1086	0.048	−0.17	41
Moriarty [37]	River Barrow, Ireland	1050	0.048	–	33
Poole and Reynolds [24]	Burrishoole system, Ireland	1507	0.013	−4.34	14

As previously pointed out by Okamura et al. [6], another critical concern for native Japanese eels is the dispersal of parasites introduced by non-native eels. Indigenous species are generally less resistant to diseases caused by introduced parasites than are the host species that transport them into new habitats. The non-native nematode *Anguillicola crassus*, which is parasitic in the swim bladder of eels and was originally endemic to East Asia, was mediated by Japanese eels imported for aquaculture from Asia [40]. Infections by this parasite have also occurred in Europe [41] and North America [42]. Infection by the parasite can severely damage the swim bladders of European and American eels and is assumed to be among the factors that initiated the decline of both species [42, 43]. Although such severe invasive diseases have not yet been observed in Japanese eels, the risk remains as long as non-native eels are present in Japanese waters. Because non-native eels tend to persist for long periods in waters where they are introduced, and imports of non-native eels such as *Anguilla bicolor* as the newest "replacement" for the Japanese eel have been increasing recently for aquaculture [44], regulations prohibiting the release of non-native eels and safeguards against accidental escape from culture ponds (e.g., sealing the drain outlet, drying the wall surface) must be strictly maintained. Moreover, since pathogens and parasites introduced by non-native species can also be spread in Japanese waters through the drainage from culture ponds containing non-native eels, pond water must be sterilized and subsequently neutralized before discharge so as not to further increase the pressure on the native Japanese eel and cause further deterioration of its critical stock situation.

The downstream migration of European eels in Japanese waters has been studied, and reports show that they can develop normally until metamorphosis in the silver phase, and probably undergo oceanic spawning migration, even in Japanese waters far from their native habitats [4, 23, 45]. All European eels examined in this study were females, and eight of the nine examined individuals (89%) were in their migratory silver phase. This raises serious concerns about whether the non-native eels might be able to migrate to the spawning area located to the west of the Mariana Islands [46] and interbreed with native Japanese eels. In fact, a sexually maturing European eel was found in the East China Sea migrating to the spawning area together with Japanese eels [4, 47]. If non-native eels can possibly migrate and spawn in the same area as Japanese eels, the possibility of interbreeding and genetic contamination should not be ignored, because interspecific hybrids have been obtained artificially between male European eels and female Japanese eels [48]. Further research on non-native eels in Japanese waters, along with identification of hybrids, is required to ensure the conservation of not only the native Japanese eel, but also the entire ecosystem.

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