Japanese Eel, Anguilla japonica

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Related Organaizations

The organizations responsible for the management of Japanese eels include the Food and Agriculture Organization of the United Nations (FAO), the International Union for Conservation of Nature (IUCN), and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In addition, cooperation among Japan, China, Korea, and Chinese Taipei is promoted through the Informal Consultation on International Cooperation for Conservation and Management of Japanese Eel Stock and Other Relevant Eel Species (hereafter referred to as Informal Consultation), which began in September 2012 at the invitation of Japan.

Recent Trends

Japanese eel is traded internationally in its various life stages. Adult eels are consumed directly as food, whereas glass eels and eel fries are used as seedlings for aquaculture. The decline of the Japanese eel population continues to be of concern to fisheries and conservation managers. Promoting population management through both domestic measures and international cooperation is crucially important for ensuring the sustainable use of the species. In 2014, Japan, China, the Republic of Korea, and Chinese Taipei released a Joint Statement at the 7th Informal Consultation, restricting input of eel seeds into aquaculture ponds: the amount of input of eel seeds for the 2014–2015 input season was to be no more than 80% of that of the 2013–2014 input season (hereafter referred to as Joint Statement).

The conservation of eel species, including Japanese eel, has also been discussed at CITES. According to the Decisions of the Conference of the Parties at the 18th meeting held in August 2019, range states of non-CITES eel species in international trade are encouraged to collaborate and cooperate with other range states to develop shared objectives, establish monitoring programs, and enhance knowledge of the biology of the species. As a follow up from this, the 14th Informal Consultation, held between May and July 2021, agreed that there was a need for scientific advice, and the first Scientific Meeting on Japanese eel and other relevant eels (hereafter referred to Scientific Meeting) was held online in April 2022. The second scientific meeting was held in person in Ueda (Nagano), Japan in May 2023. At this meeting, scientists exchanged opinions and shared information on scientific findings related to eels, particularly Japanese eel. The scientists also agreed on a roadmap for joint research to strengthen cooperation in research activities related to Japanese eel, including the collection and compilation of long-term time-series and eDNA data to understand stock trends, and the exchange of information on techniques to clarify migration routes to spawning grounds and the analysis and evaluation of migration route data. In addition, opinions were exchanged on the proposed standard working format for statistics on the catch, input into aquaculture ponds, aquaculture, and trade of glass eel, juvenile eel, and adult eel.

The 16th Informal Consultation, held in Tokyo in July 2023, discussed and confirmed the status of compliance with the Joint Statement, reviewed the management measures taken by each country/region since the Joint Statement, set the maximum input into aquaculture ponds volume for the next fishing seasons (November 2023 to October 2024), discussed the preparation and maintenance of statistics on the harvest, input into aquaculture ponds volume, and trade of glass eels in each country/region, and discussed the results of the second Scientific Meeting.

Usage

One typical eel dish in Japan is grilled eel or *Kabayaki*, often served as *Unaju* or *Unadon*. There are also some local eel dishes in Japan such as *Hitsumabushi* and *Seiromushi*. Japanese eel serum contains poison; it should never be eaten raw (Yoshida et al., 2008). In China, Japanese eel consumption has seen a recent increase following the development of products suitable for Chinese consumers, including dried shredded snack eel, eel hot-pot, and eel zongzi. Japanese eel is not only used as a food source but also as an ingredient for traditional medicine in China and on the Korean peninsula (Kuroki, 2019).

Overview of the Fishery

Farmed eels account for most of the domestic supply in Japan. However, wild yellow eels (developmental stage) are still caught by longlines or traps set in freshwater and brackish waters (Mochioka, 2019). The history of eel fisheries in Japan extends back to the Edo era (1603–1868). In fact, official data of eel catches have been available since 1894 (Hakoyama et al., 2016). The domestic eel catch was stable at 3,000 to 4,000 tons in the early 19th century, but it decreased during World War II. Although it recovered temporarily to the 3,000-ton range in the 1960s, the catch has been declining since 1970(Fig.1). The domestic catch in 2022 was 59 tons, the lowest ever. The number of inland fishers (the number of fishery management entities in lakes that mainly targeted yellow/silver eels) during this period also decreased remarkably (Hakoyama et al., 2016). Eel farming developed in the 19th century, with domestic eel farming using elver eels (juvenile stage) having begun in 1879. The eel farming industry became viable in the 1920s, as the methods for raising glass eels advanced. Aquaculture production exceeded the wild catch in the 1930s(Tanaka, 2019): its peak amounted to 39,704 tons in 1988, but it has been stable at around 20,000 tons since 1997; production was 19,155 tons in 2022 (Fig.2).

Glass eels, which serve as seeds for eel farming, are harvested in four regions: Japan, China, Korea, and Chinese Taipei. In Japan, the harvest period is generally December–April. Harvesters catch eels by scooping or using set nets in coastal estuaries and river mouths. Glass eel fisheries are managed by prefectural governments under a licensing system. Prefectural governors issue permits typically restricting the harvesting period, fishing gear, and fishing area. Domestic catch of seeds exceeded 100 tons before 1966, but they fell drastically from 1971 to less than 20 tons in 1990 (Fig.3). Figure 3 shows the total seed catch in the sea and inland waters. Seeds caught in the sea had "glass eel" labels as their item name or had footnotes that denote they are glass eels. The eels caught in inland waters had no clear description or labels on them, but the quantities collected in rivers and lakes were recorded. According to the Minister's Secretariat Statistics Department, most seeds were assumed to be glass eels, but some elvers might have been included in the data (Personal communication from the Statistics Department of the Minister's Secretariat, January 14, 2011). Around 1960, the developing eel farming industries of Shizuoka, Aichi, and Mie prefectures introduced large amounts of elvers from the Tone River system in Ibaraki and Chiba. During the fishing season, from the middle of March to late October, the seeds collected from the lower Tone River included elver eels: they were 5-20 g and 15–25 cm long. Of these, 60% were supplied to Shizuoka, Aichi, and Mie prefectures as seeds for eel farming (Matsui, 1972a, pp. 333–335). Since at least 1978, the fishing season for seeds in the nine major aquaculture prefectures has been limited to glass eels during winter (Eel Culture Research Council, 1980). This information suggests that eels caught around 1960 included more elver eels than recent catches. If this is the case, the rate of decrease in glass eel catch is likely to be smaller than that shown in Figure 3.

The global catch of Japanese eel (not including the catch in China) decreased from 3,619 tons in 1969 to 100 tons in 2021, reflecting the trend seen in wild adult eel catches in Japan, which account for approximately 63% of the global catch (Fig.4). Regarding recent glass eel catches from 2009 to 2023, China had the highest annual catch, followed by Japan. The catches of these two countries accounted for most of the total. During the last several decades, the total amount of glass eels caught in the four regions has fluctuated from year to year, ranging from 20 to 90 tons. In the 2019 fishing season, the catches were 3.7 tons in Japan, 14.5 tons in China, 0.6 tons in Korea, and 2.75 tons in Chinese Taipei, but the catches in the 2020 fishing season increased significantly to 17.1 tons in Japan, 50 tons in China, 4.5 tons in Korea, and 5.2 tons in Chinese Taipei. In the 2023 fishing season, the catches were 5.6 tons in Japan, 40.5 tons in China, 2.2 tons in Korea, and 1.9 tons in Chinese Taipei (Fig.5).

Biological Properties

Life History

Japanese eel is a migratory species (catadromous fish) that breeds in the ocean and grows in freshwater, brackish waters, and coastal habitats. The estimated age of silver eels (eels during spawning migration when their body color is silver) based on otoliths ranges from 4 to 17 years, with a mean age of 8 years for females (Kotake et al., 2005, 2007; Han et al., 2009; Yokouchi et al., 2009), and the spawning migration is estimated to take 6 months (Han et al., 2009; Chang et al., 2016). Thus, the generation time of Japanese eels is estimated to be 8.5 years. The species spawning area is regarded as the West Mariana Ridge (Tsukamoto, 1992; Tsukamoto et al., 2011). The Kuroshio current transports hatched larvae for thousands of kilometers to freshwater and brackish water habitats on the coasts of eastern Asian countries. The spawning season is estimated as extending from April through August. It is likely to take place concurrently with a new moon (Tsukamoto et al., 2003; Shinoda et al., 2011). No direct observations of spawning behavior in the wild have been made. However, indirect evidence from genetic analyses of preleptocephali larvae collected near the West Mariana Ridge indicates that eels may mate more than once over several days and with different partners (Takeuchi et al., 2022). Laboratory studies also suggest the formation of spawning aggregations (Dou et al., 2007). The eggs, each having a diameter of approximately 1.6 mm, are laid at a depth of 150–200 m (Tsukamoto et al., 2011) in waters of 25°C.

The transparent, willow-like Japanese eel larva is called a leptocephalus. Leptocephali are transported westward via the North Equatorial Current (NEC) and mesoscale vortex. They drift northward at the boundary of the Kuroshio Current as they transform into glass eels (Fig.6). Arriving in coastal areas, the glass eels (already about 0.2 g) will then disperse to freshwater, brackish, and coastal habitats. Upon settling in their respective habitats, glass eels shift into a benthic sheltering behavior. Their body surface gradually turns black. Eels with sufficient pigmentation on their bodies are called elver eels. Their ventral side becomes yellowish as they grow into the yellow eel stage: the longest eel life stage. After living in rivers, matured yellow eels show morphological changes (e.g. enlargement of the eyes) and transform into silver eels before migrating (Matsui, 1972b).

The recruitment season of glass eels varies by country or region, but in Japan it mainly occurs during winter, from December through April (Han, 2011). Figure 7 presents the monthly glass eel catch from 2002 (2002–2003) to 2018 (2018–2019). The peak of recruitment can occur anytime during winter or spring and varies every year. These fluctuations in migration patterns are not yet fully understood. In 2019 in the Saigo River, Fukutsu City, Fukuoka Prefecture, a survey conducted by Kyushu University during the new moon revealed that the largest recruitment (1,086 individuals) occurred on April 4, followed by February 2 (240 individuals) and May 3 (106 individuals). Only three individuals were collected during June–August; none were collected in September (Fig.8). Nevertheless, quantitative evaluation of the amount of migration is difficult using such a small survey.

A ten-year survey of glass eels in the Pearl River, China showed that glass eel CPUE decreased from 2011 to 2022 and was generally higher during the full moon (and corresponding large tidal range) and when water temperature dropped below 8°C (Shuai et al., 2023). Evidence for the influence of lunar cycle and water temperature on glass eel recruitment is mixed and may be confounded by other environmental factors(Guo et al., 2017; Hwang et al., 2014; Tzeng, 1985; Yamamoto et al., 2001). Modelling by Shuai et al. (2023) suggested that the Pearl River glass eel CPUE for 2023–2026 will remain low but stable, but the authors warn that climate change, dams and overfishing continue to threaten the overall spawning stock.

An analysis of glass eel recruitment in Lake Hamana, Japan from 1971 to 2014 showed that water temperature difference (an indicator of warm water intrusions from the Kuroshio current) may be a good indicator of glass eel catch in non-meander periods of the Kuroshio (Miyake et al., 2023).

A study of glass eel body length in Chinese Taipei showed that environmental condition in the spawning area influenced the TL of glass eels (Hsiung et al., 2022). Specifically, total length was larger during El Niño years (possibly because of delayed recruitment due to changes in circulation etc.). These findings suggest that eel development may be affected by climate change.

Population Genetics, Phylogeny, and Demographic History

Elucidating the population genetic structure of organisms is indispensable, not only for defining the management units of natural resources but also for accurately estimating the effective size of

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populations (Ne), which can be used to evaluate population viability and perenniality. In recent years, the population genetic structure of the Japanese eel has been a subject of intense debate. Earlier population genetic studies that used limited numbers of genetic markers supported panmixia in Japanese eel (e.g., Ishikawa et al., 2001; Sang et al., 1994), although Tseng et al. (2006) revealed the presence of two genetically different groups (northern and southern groups). More recently, a genome-wide analysis of single nucleotide polymorphisms (SNPs) using the whole-genome resequencing technique (Igarashi et al., 2018) suggested that an estuary population from the Kuma River (Kumamoto Prefecture) is genetically divergent from other populations. On the other hand, another study based on SNPs detected using restriction site-associated DNA sequencing found limited temporal and spatial genetic differentiation among populations along the coasts of Japan and China (Gong et al., 2019). Thus, although the population genetic structure of Japanese eel has been the subject of intense debate, most studies now clearly indicate that Japanese eel exists as a single panmictic population (Yu et al., 2020; Gong et al., 2019; Han et al., 2010; Ishikawa et al., 2001) and should be managed accordingly. Current research now focuses on estimating the long-term and current Ne of Japanese eel.

The Ne is different from a standard measure of population size. It makes an estimate of the number of individuals that are effectively contributing to the next generation (thus it is generally smaller than the actual population size). Ne estimated from genomic data is a population index independent of fisheries catch statistics, and estimation over year provides information other than catch data on recent stock trends. Assessing historical changes in the Ne also can provide an evolutionary perspective on current population dynamics. Whole genome level analyses using pairwise and multiple sequentially Markovian coalescent (PSMC and MSMC) methods (Mather et al., 2020) indicate that between 4 and 1 million years ago (Ma) Ne of Japanese eel decreased, then from approximately 1 Ma up until around 22,000–30,000 years ago Japanese eel underwent a steady increase in Ne, peaking at approximately 80,000 individuals (Faulks et al., 2022). During the Last Glacial Maximum (LGM: 19,000-33,000 years ago) the Ne decreased to around 60,000 individuals. Due to the restricted power of the PSMC and MSMC methods to detect changes within the last 20,000 years, changes in the population size of Japanese eel following the LGM are still unknown. However, several studies have used alternative methods (microsatellite markers) to assess contemporary Ne and found values ranging from approximately 400–600 to 4000–6000 (Han et al., 2008; Takeuchi et al., 2022; Tseng et al., 2003). In addition, ongoing studies using single nucleotide polymorphism data and linkage disequilibrium analyses (Waples and Do, 2010) indicate that the current Ne is around 20,000 individuals (M. Sekino, personal communication, January 26, 2022). Overall, these results indicate that Japanese eel has experienced several population bottlenecks which could mean that Japanese eel may be sensitive to further declines in population size.

The time to the most recent common ancestor of the anguillid eels traces back to approximately 20 million years ago (Minegishi et al., 2005). The Japanese eel is a component of a monophyletic clade that contains the Indo-Pacific species. The divergence of Japanese eel from the other species is thought to have occurred at the foremost stage of the speciation process within this clade (Minegishi et al., 2005; Zhu et al., 2018).

Growth and Maturation

The growth rate of Japanese eel varies widely among individuals, ranging from 5–20 cm per year (Yokouchi et al., 2008, 2012). Individuals usually mature at the yellow eel stage of 5–10 years, but

some have matured at age 22, which is the estimated maximum lifespan (Chino and Arai, 2009; Kotake et al., 2007; Lin and Tzeng, 2009; Sudo et al., 2013; Yokouchi et al., 2009). Sex is determined by the environment an individual experiences from the glass eel to the elver phase. The effect of sex on the growth rate is poorly understood, but females mature at a larger size and at an older age than males (Chino and Arai, 2009; Kotake et al., 2007; Lin and Tzeng, 2009; Sudo et al., 2013; Yokouchi et al., 2009). Water temperatures and food availability affect the growth and maturity rate of eels (Yokouchi et al., 2008) . Faster and higher growth rates are observed at low latitudes with high water temperatures (Hagihara et al., 2018) and in brackish waters (Kaifu et al., 2013; Kotake et al., 2005; Yokouchi et al., 2008, 2012).

Distribution

Japanese eel is distributed in east Asian freshwater and coastal areas such as the Japanese coast, the Korean peninsula, mainland China, and the Philippines (Han et al., 2012; Tsukamoto et al., 2003) (Fig.9). The spawning grounds are located near the Mariana Trench. The larvae are dispersed by the NEC and the Kuroshio Current (Shinoda et al., 2011).

Habitat

Yellow eels that do not settle in rivers might stay in bays or estuaries or even migrate back and forth many times between the sea and river, displaying migratory polymorphisms and habitat shifts (Arai et al., 2003). Yellow eels tend to hide in refuges such as holes, crevices, and mud burrows (Aoyama et al., 2005; Tesch, 2003).

Freshwater

Yellow eels are distributed over a wide area from downstream to upstream rivers or lakes. Eels are found mainly near the shore and tend to avoid the center of rivers (Aoyama et al., 2002; Itakura et al., 2018). Movement between both shores of the river is uncommon, suggesting short home ranges (Itakura et al., 2018). Eels prefer a deep environment and they are often concentrated in areas with a gentle river slope with many stones in the riverbed (Matsushige et al., 2020). Eels that are less than 25 cm long tend to use lentic habitats with smaller substrates like sand/silt to cobbles, whereas mid-sized fish (25–55 cm) use habitats with larger substrates like pebbles and cobbles(Kumai et al., 2023).

A stable isotope analysis of eels from the Pearl River, China indicated that eels in this system spend most of their lifetime (post elver stage) in freshwater and the authors suggested that high human population density at the river mouth could be a contributing factor (Shuai et al., 2023). The authors also highlighted the importance of understanding habitat use to aid conservation management as strictly freshwater populations may experience different threats (easier to catch, dam construction) than flexible polymorphic populations.

Brackish Water

Japanese eel resides in coastal habitats and occupies shallow estuaries where tidal effects are present (Matsushige et al., 2020). It also resides in tidal flats, where it burrows in sandy mud areas (Aoyama et al., 2005).

Spawning Migration

Silver eels begin their spawning migration from autumn to winter (September–February) (Kotake et al., 2007). Japanese eel spawns in the western waters of the Mariana Islands ($14^{\circ} - 16^{\circ}N$, $142^{\circ}E$), about 3,000 km away from the coast of Japan (Tsukamoto, 1992, 2006). Although the evolutionary process of the spawning migration in eel species remains unclear, the ancestral eel species presumably undertook a short-distance migration in tropical coastal waters then eventually adopted a long-distance migration, similar to that of the extant temperate eels (Arai, 2014). Results of satellite and acoustic tracking have provided only fragmentary information related to Japanese eel migration routes (Abe et al., 2023; Fukuda et al., 2022; Manabe et al., 2011), and the comprehensive picture remains unclear. Japanese eel performs daily vertical movement during their spawning migration (Higuchi et al., 2018; Manabe et al., 2011). It dives into deep waters (500–800 m) to which light does not penetrate during the day. Then it moves to shallower depths of less than 300 m during the nighttime (Chow et al., 2015; Manabe et al., 2011). The swimming depth is affected by the light intensity of the environment (Higuchi et al., 2018; Watanabe et al., 2020). The higher the lunar light intensity becomes, the deeper the nighttime swimming depth becomes (Chow et al., 2015; Higuchi et al., 2018). Anguillid adult eels do not feed after starting the spawning migration (Chow et al., 2010). Their vertical movement is mainly undertaken to avoid visually oriented predators such as tuna and sharks (Chow et al., 2015; Manabe et al., 2011; Watanabe et al., 2020).

Regional differences in migratory pathway and vertical movements were observed in eels tagged on the Sea of Japan coastline and Pacific Ocean coastline of Japan (Abe et al., 2023). One tagged eel in the Sea of Japan did not display typical diel vertical migrations, perhaps due to the different vertical structure of water temperature of this region (Abe et al., 2023). Abe et al. 2023 also observed that eels did not enter deep waters where the water temperature was below 4°C. Acoustic tracking of eels released into the Kuroshio Current near Japan indicated that the movement of eels was largely due to the current, but there was also some active southward swimming (Fukuda et al., 2022). In contrast, the same study showed that active swimming was the main component of movement for eels released near the spawning grounds. The authors suggest that solar cues may be important for eel navigation and movement, but that further studies are required.

Transport of Leptocephalus

After hatching in the West Mariana Ridge, the larval eels, or leptocephali, are transported by the NEC to the east coast of the Philippines and are carried by the Kuroshio Current to habitat areas in east Asia such as Japan and Chinese Taipei. They must enter the north-flowing Kuroshio and not the south-flowing Mindanao Current to reach the habitat areas successfully. In a simulation conducted by Zenimoto et al. (2009), more leptocephali enter the Mindanao Current during El Niño years, thereby decreasing the probability of northward transportation by the Kuroshio. Another simulation conducted by Chang et al. (2018b) implied that weakening of the NEC is a cause of glass eel recruitment decline over the past 20 years.

These analyses were conducted on the assumption that the northward Ekman transport caused by trade winds, as well as the leptocephalus' floating depth, determine the migratory patterns of Japanese eels (Kimura et al., 1994). Leptocephali show diel vertical migration, floating in deep waters during the daytime and in shallow waters during the nighttime. Otake et al. (1998) reported that the nighttime

depth gets shallower as leptocephali grow: 40 mm long eels were found at around 50 m depth. Because the Ekman layer is shallower than 70 m, leptocephali are affected by Ekman transport after they grow to a certain length, probably more than 20 mm. Weakened trade winds during El Niño seasons, which entail a northward shift of the bifurcation point of the NEC into the Kuroshio current and Mindanao current, might account for the decreased rate of northward larval transportation by the Kuroshio current during this event. Another mechanism that may contribute to lower recruitment during El Niño events is the southward shift of the salinity front. The spawning location is estimated as being in the southwest area of the salinity front and the seamount chain cross (Tsukamoto et al., 2011). Therefore, the latitude of the salinity front also influences leptocephalus transport. The salinity front is usually located at about 15° north latitude, but it occasionally moves south beyond 5° north latitude. Because the NEC south of 10° north latitude connects to the Mindanao Current, the southward shift of the salinity front can prevent leptocephali from migrating northward (Kimura et al., 2001).

These models, which assume that the ocean environment prescribes the recruitment of the Japanese eel into the habitat area, are supported by buoy tracking (Kimura and Tsukamoto, 2006) and correlations with catch per unit effort (CPUE) data from Tanegashima Island (Zenimoto et al., 2009). However, statistical analyses using long-term glass eel catch data obtained during 1967–2008 in Chinese Taipei did not provide statistically significant support for a correlation between catch and the bifurcation point of the NEC, or the occurrence of El Niño events (Tzeng et al., 2012). Mature eels are expected to spawn more or less concurrently with new moon periods during April–August (Shinoda et al., 2011). Han et al. (2016) reported that recruitment in Chinese Taipei exhibits batch-like arrival waves of different cohorts at intervals of one month, which are presumably derived from different spawning dates. In addition, leptocephali trapped in mesoscale eddies might have some influence on recruitment patterns (Chang et al., 2018a). The large meander of the Kuroshio might not prohibit recruitment to Japan (Chang et al., 2019).

Recent studies using eDNA, modelling and simulations have provided new insights into leptocephalus and glass eel transport(Kasai et al., 2021; Karaki et al., 2023). Kasai et al. (2021) showed that Japanese eel eDNA concentrations in rivers all along the coastline of Japan were closely associated with oceanic current forecast models. In those simulations the depth of the glass eel migration was important. Karaki et al. (2023) sought to further refine the simulations and to explain the relatively higher concentration/biomass of eels in areas like the Seto Inland Sea and the northern Pacific coastline. They showed that to explain patterns in regional recruitment of glass eels it is important to include behavioral changes such as active horizontal swimming towards areas of lower salinity and a preference for shallower depths when approaching the coast.

There remains much to be uncovered about leptocephalus and glass eel transport patterns. An understanding of these patterns might be useful for improving Japanese eel resource management in the future.

Prey

Japanese eel starts feeding after becoming leptocephali. Although leptocephalus food preferences have not been clarified, their hypothesized consumption of marine snow has become widely supported (Miller et al., 2013; Mochioka and Iwamizu, 1996; Otake et al., 1993). The feeding ecology of glass eels and elver eels is also remains uncertain. Yellow eels in coastal areas and rivers feed on small fish, crustaceans, polychaetes, shellfishes, aquatic insects, etc. (Itakura et al., 2015; Kaifu et al., 2013; Kan et al., 2016). However, diet preferences vary depending on the growth stage, environment, and season (Kaifu et al., 2013) as well as individual differences.

Predators

Knowledge about Japanese eel predators remains limited, although eels are presumed to be preyed upon by various animals throughout their life history. A recent study conducted at the Tone River revealed that channel catfish and blackfin sea bass prey on glass eels (Miyake et al., 2018). During the yellow eel phase, some reports have described predation of New Zealand long-fin eel by catfish, brown trout, cormorants, ducks, kingfishers, and water rats (Jellyman, 1977), and have even revealed predation of American eel by larger conspecifics (Barker, 1997). Results suggest that Japanese eel at the yellow eel stage is caught by carnivorous fish, birds, and mammals. In a satellite tracking study using pop-up tags, tunas and sharks were observed to prey on silver eels during the spawning migration (Béguer-Pon et al., 2012; Manabe et al., 2011).

Population Status

The Ministry of the Environment and IUCN listed Japanese eel as an endangered species (categorized respectively as endangered IB in 2013 and 2014). Although it is difficult to identify the causes of the population decrease of this species, changes in the marine environment, overfishing, and deterioration of habitats have been regarded as important factors. Particularly, reinforcing riverbanks with concrete, in which eels cannot hide, constructing barriers impeding eel migration in rivers, and interrupting connections between rivers and rice paddies might strongly exacerbate damage to eel habitats. To understand the population trends, data of glass eel and yellow eel catches in Japanese habitats are important. Japan's yellow eel catch exceeded 600 tons in the early 2000s, 500 tons after 2005, but less than 100 tons after 2015. The figure plummeted to 59 tons in 2022: the lowest figure ever (Fig.1). The remarkable decrease in inland fishermen during this period must also have contributed to this trend, but the degree of such contribution cannot be estimated due to the lack of necessary data. A survey conducted in Okayama Prefecture revealed that the CPUE of vellow eel decreased by one-third in both longline fisheries and small set net fisheries during 2003–2016 (Kaifu et al., 2018). Glass eel catch data show a decrease to less than 10 tons in 2010–2013, a slight increase to 15 tons in 2014–2017, a reversion to less 10 tons during the 2018–2019 fishing season, and then just 3.7 tons in the 2019 fishing season (Fig.5). However, the catch increased significantly in the 2020 fishing season to 17.1 tons. The catch for the 2023 fishing season was 5.6 tons. Although the catch of glass eels shows fluctuations, these data for Japan indicate that the population has been experiencing a long-term decrease and now remains low. The population assessment of the species is challenging mainly because of its complex life cycle and numerous uncertainties related to its ecology. No assessment exists except for Tanaka (2014). In 2019, the Fisheries Agency of Japan launched a research project with the goal of developing a comprehensive assessment of Japanese eel populations.

Fisheries Management

As described above, the Japanese eel population size has been decreasing. A lack of progress has occurred in developing mathematical methods to predict population dynamics and management strategies because it is difficult to understand the species' biology completely and to identify causes of the population decline. Overfishing, pollution and changes in the marine environment, habitat degradation due to shore protection works and river fragmentation, parasitic diseases, and increased predators have been cited as factors contributing to the decline, but understanding of each factor and their interactions is still in its infancy (Knights, 2003; Friedland et al., 2007; Bonhommeau et al., 2008; Arai, 2014). It is necessary to mitigate risks leading to severe and irreversible effects (precautionary approach) (Gardiner, 2006). Consequently, Japan has taken comprehensive measures including population management and habitat restoration.

For example, Japan called upon the People's Republic of China and Chinese Taipei to engage in an international discussion, the Informal Consultation, in September 2012. The Republic of Korea joined from the fourth meeting in September 2013. In 2014, Japan, China, Korea, and Chinese Taipei released a Joint Statement at the seventh meeting, restricting the input of eel seeds into aquaculture ponds: the amount of input of eel seeds for the 2014–2015 input season will be no more than 80% of that of the 2013–2014 input season. It follows that the upper limit of input into aquaculture ponds in Japan was set at 21.7 tons. Thereafter, the upper limit of input in the next fishing season has been discussed every year through Informal Consultation. The upper limit has remained the same because no scientific evidence has been provided to change it. In addition, based on the Joint Statement, the Alliance for Sustainable Eel Aquaculture (ASEA) was established as an international group of eel management organizations from each country and region to discuss eel resource management on a private sector basis. As of October 2019 three meetings have been held under ASEA.

To implement the upper limit, Japan introduced a licensing system for eel aquaculture under the Inland Water Fishery Promotion Act in June 2015. The amount of initial input of eel seeds is restricted by eel species and is allocated for each farmer under this Act. Farmers are required to report their input amount and production amount to the central government every month. The catch of glass eels is subject to licenses issued by prefectural governments. The fishing season duration is limited. Catches of adult eels using certain fishing gear are also subject to licenses issued by prefectural governments. Each prefecture is implementing various additional measures such as gear restriction, upper limits of harvest for individuals, and time closure for catches of both glass and adult eels, considering the unique situation in each prefecture. Recently, the prohibition of catching silver eels descending to spawn has been introduced in almost all prefectures where wild adult eels are distributed. To prevent poaching of glass eels, glass eels were designated as "specified aquatic animals and plants" from December 2023, and penalties were strengthened. As a result, the former special catch permit for glass eels was transferred to the governor-licensed fishery in December 2023. In addition, the Act on Ensuring the Proper Domestic Distribution and Importation of Specified Aquatic Animals and Plants was enacted in December 2020 and came into effect in December 2022. The purpose of this Act is to prevent the illegal trade of harvested aquatic animals and plants, to ensure the proper domestic distribution and proper import and export of specified aquatic animals and plants, prevent illegal fishing, and contribute to the sustainable use of fishery resources. This will regulate exports and make it obligatory for businesses that harvest and handle glass eel to report their business information, communicate their catch numbers, and create transaction records and maintain them. In April 2022, juvenile eels (i.e., eels less than 13 centimeters in length) were designated as Specified Class I aquatic animals and plants subject to regulation under the Act, and the regulation will apply to juvenile eels from December 2025.

In addition to fisheries management, continuous efforts have been made towards the creation and conservation of favorable riverine environments. The concept of "nature-oriented river works" has been adopted in river management to conserve and create the habitat that rivers intrinsically have. A study from Lake Shinji suggests that the use of neonicotinoid pesticides since 1993 has caused declines in Japanese eel and Wakasagi populations by altering food web structure and dynamics (Yamamuro et al., 2019), hence the management of pesticides and other chemicals is also an important issue in inland habitats of Japanese eel.

For future work, it will be important to ascertain population trends and to work towards the sustainable harvest of Japanese eel. To achieve this, it will be necessary to improve the accuracy and timeliness of temporal and spatial data, expand our knowledge regarding the population genetic structure of the species, and use the best available data for the development of a mathematical model for population management. Also, enhancing scientific cooperation and communication with other range states and areas will be important, for example holding regular scientific meetings.

Summary Table

World catch 1 (in the past 5 years)	100-126 tons, 100 ton in 2021 (recent),
	and 117 ton average (2017–2021)
Japanese catch *2 (in the past 5 years)	59-78 tons, 59 ton in 2022 (recent),
	and 66.2 ton average (2018–2022)
Resource assessment methods	Yellow and glass eel catches from annual coastal
	and freshwater fishery statistics and the trend
	of yellow eel CPUE in Okayama Prefecture were
	used for evaluation.
Resource status	Yellow eel catch (59 tons, 2022)
	Glass eel catch (4 tons, 2018)
	Japanese eel abundance is low and the trend is
	stationary (the long-term trend of the above in-
	dices since the 1960s is decreasing, but the in-
	dices are flat over a 5-year period).
Management goals	Under review
Control measures	Management of cultured seedlings in ponds
	Prohibition of catching larvae (length restric-
	tions based on fishery regulation)
	From December 2025, juvenile fish will be reg-
	ulated as "Regulations on Class I Specified
	Aquatic Animals and Plants" under the "Act on
	Ensuring the Proper Domestic Distribution and
	Importation of Specified Aquatic Animals and
	Plants".
	Prohibition of catching parental eels descending
	to spawn (Setting of non-fishing periods based on
	inland fishery management committee instruc-
	tions, etc.)
Management organizations	FAO,IUCN,CITES
Up-to-date year of the resource evaluation	Under review
Next year of the resource evaluation	Under review
*1 EAO (2022): not including the estab in Chine	1

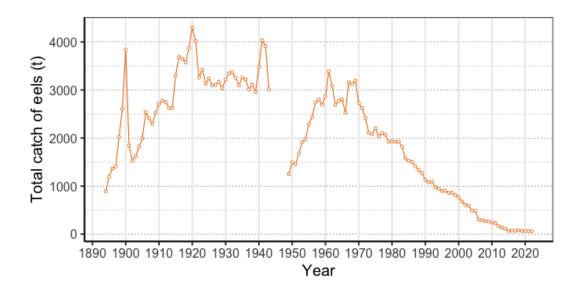
*1 FAO (2023): not including the catch in China

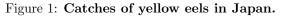
 $\ast 2$ Fisheries statistics of the Government of Japan: The Annual Report of Catch Statistics on Fishery and Aquaculture

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The Japanese Eel





Data are based on the fisheries statistics of the Government of Japan (Hakoyama et al., 2016, The Annual Report of Catch Statistics on Fishery and Aquaculture in 2022).

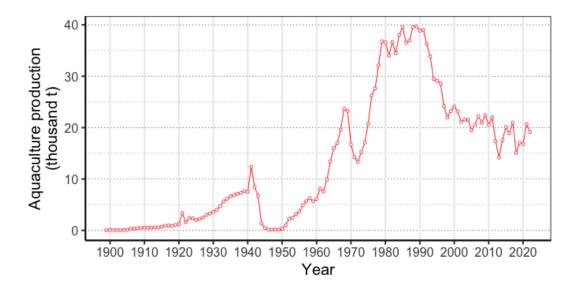


Figure 2: Aquacultural production of eels in Japan.

Data are based on the fisheries statistics of the Government of Japan: The Statistical Yearbook of Ministry of Agriculture and Forestry and the Annual Report of Catch Statistics on Fishery and Aquaculture.

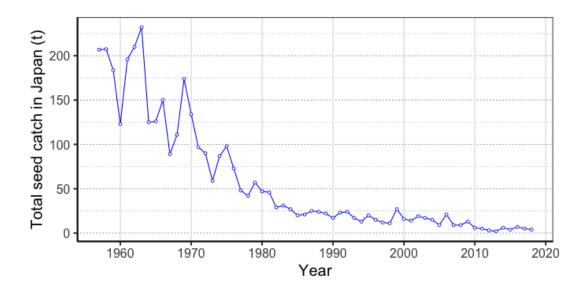


Figure 3: Total seed catch (including glass eels and elver eels) in the sea and inland waters in Japan.

Data from fisheries statistics of the Government of Japan: The Annual Report of Catch Statistics on Fishery and Aquaculture (Hakoyama et al., 2016, The Annual Report of Catch Statistics on Fishery and Aquaculture in 2018).

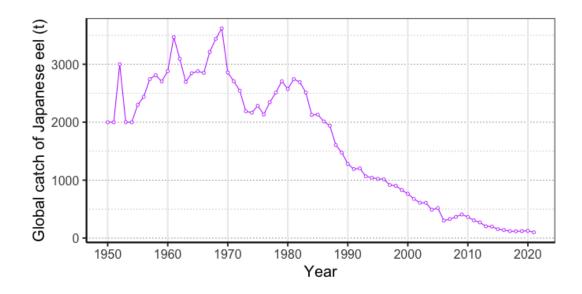


Figure 4: Global catches of wild Japanese eel (including all stages). These data are based on FAO statistics (FAO, 2023) (not including the catch in China).

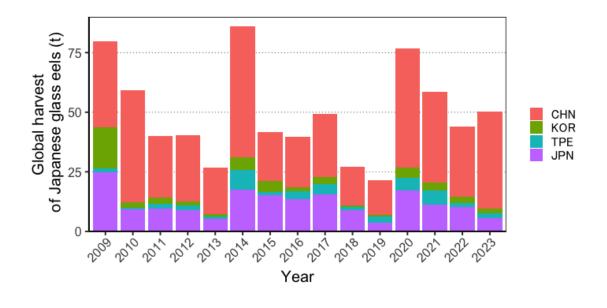


Figure 5: Global harvest of Japanese glass eels. These data are based on the Joint Press Release of the Informal Consultation (Fisheries Agency, 2017, 2023).

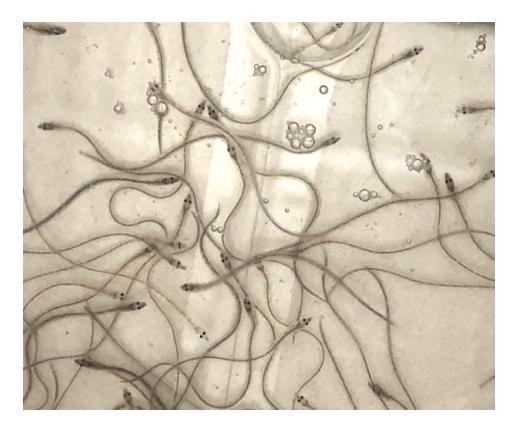


Figure 6: Glass eels. Photo by Chiaki Okamoto.

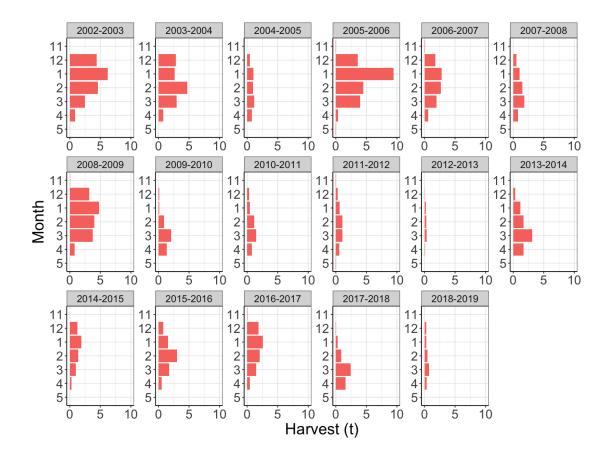


Figure 7: Monthly glass eel harvest in Japan from the 2002–2003 fishery season through to the 2018–2019 season.

These data are based on the harvest reports subject to the special catch permission of the eel seedlings (glass eels) contingent on the prefectural fishery regulations.

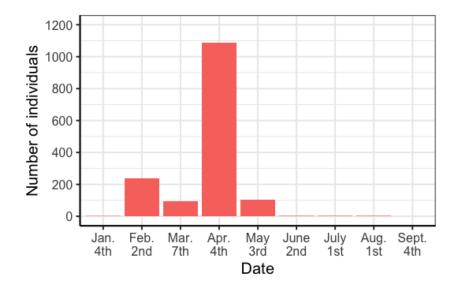


Figure 8: Numbers of individuals by survey date obtained from Saigo River, Fukutsu City, and Fukuoka Prefecture (2019).

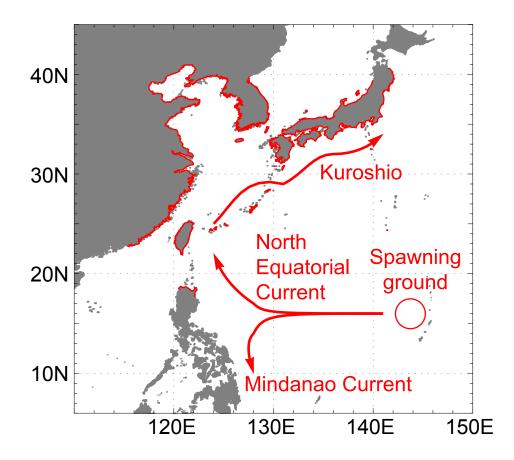


Figure 9: Distribution map of the Japanese eels (modified from Han et al., 2012; Tsukamoto et al., 2003).

References

- Abe, T. K., Galang, I., Daryani, A., Minamikawa, S., Mochioka, N. and Hakoyama, H. (2023). Regional differences in oceanic migratory behavior of Japanese silver eel in waters with different vertical temperature gradients, *Animal Biotelemetry*.
- Aoyama, J., Sasai, S., Miller, M. J., Shinoda, A., Nakamura, A., Kawazu, K. and Tsukamoto, K. (2002). A preliminary study of the movements of yellow and silver eels, *Anguilla japonica*, in the estuary of the Fukui River, Japan, as revealed by acoustic tracking, *Hydrobiologia* 470(1-3): 31–36.
- Aoyama, J., Shinoda, A., Sasai, S., Miller, M. J. and Tsukamoto, K. (2005). First observations of the burrows of Anguilla japonica, Journal of Fish Biology 67(6): 1534–1543.
- Arai, T. (2014). Do we protect freshwater eels or do we drive them to extinction?, *SpringerPlus* **3**(1): 534.
- Arai, T., Kotake, A., Ohji, M., Miyazaki, N. and Tsukamoto, K. (2003). Migratory history and habitat use of Japanese eel Anguilla japonica in the Sanriku Coast of Japan, Fisheries Science 69(4): 813– 818.
- Barker, D. E. (1997). Development of metazoan parasite communities in the American eel, Anguilla rostrata: patterns, processes and applicability as biological tags, PhD thesis, Dalhousie University, Halifax, Nova Scotia.
- Béguer-Pon, M., Benchetrit, J., Castonguay, M., Aarestrup, K., Campana, S. E., Stokesbury, M. J. and Dodson, J. J. (2012). Shark predation on migrating adult American eels (*Anguilla rostrata*) in the Gulf of St. Lawrence, *PLoS ONE* 7(10): e46830.
- Bonhommeau, S., Chassot, E. and Rivot, E. (2008). Fluctuations in European eel (Anguilla anguilla) recruitment resulting from environmental changes in the Sargasso Sea, Fisheries Oceanography 17(1): 32–44.
- Chang, Y.-L. K., Miyazawa, Y., Béguer-Pon, M., Han, Y.-S., Ohashi, K. and Sheng, J. (2018a). Physical and biological roles of mesoscale eddies in Japanese eel larvae dispersal in the western North Pacific Ocean, *Scientific reports* 8(1): 5013.
- Chang, Y.-L. K., Miyazawa, Y., Miller, M. J. and Tsukamoto, K. (2018b). Potential impact of ocean circulation on the declining Japanese eel catches, *Scientific reports* 8(1): 5496.
- Chang, Y.-L. K., Miyazawa, Y., Miller, M. J. and Tsukamoto, K. (2019). Influence of ocean circulation and the Kuroshio large meander on the 2018 Japanese eel recruitment season, *PLoS ONE* 14(9): e0223262.
- Chang, Y. L., Miyazawa, Y. and Béguer-Pon, M. (2016). Simulating the Oceanic Migration of Silver Japanese Eels, *PLoS ONE* 11(3): e0150187.
- Chino, N. and Arai, T. (2009). Relative contribution of migratory type on the reproduction of migrating silver eels, *Anguilla japonica*, collected off Shikoku Island, Japan, *Marine Biology* **156**(4): 661–668.

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- Chow, S., Kurogi, H., Katayama, S., Ambe, D., Okazaki, M. and Watanabe, T. (2010). Japanese eel *Anguilla japonica* do not assimilate nutrition during the oceanic spawning migration: evidence from stable isotope analysis, *Marine Ecology Progress Series* **402**: 233–238.
- Chow, S., Okazaki, M., Watanabe, T., Segawa, K., Yamamoto, T., Kurogi, H., Tanaka, H., Ai, K.-i., Kawai, M., Yamamoto, S.-i., Mochioka, N., Manabe, R. and Miyake, Y. (2015). Light-sensitive vertical migration of the Japanese eel *Anguilla japonica* revealed by real-time tracking and Its utilization for geolocation, *PLoS ONE* 10(4): e0121801.
- Dou, S., Yamada, Y., Okamura, A., Tanaka, S., Shinoda, A. and Tsukamoto, K. (2007). Observations on the spawning behavior of artificially matured Japanese eels Anguilla japonica in captivity, Aquaculture 266(1-4): 117–129.
- Eel Culture Research Council (1980). The 9th report of the eel culture research council.
- FAO (2023). Global capture production Quantity 1950 2021.
 URL: https://www.fao.org/fishery/statistics-query/en/capture/capture_quantity
- Faulks, L., Kaushik, P., Taniguchi, S., Sekino, M., Nakamichi, R., Yamamoto, Y., Fujimori, H., Okamoto, C., Kodama, S., Daryani, A. et al. (2022). Inferring the demographic history of Japanese eel (Anguilla japonica) from genomic data: Insights for conservation and fisheries management, Aquatic Conservation: Marine and Freshwater Ecosystems 32(6): 1092–1098.
- Fisheries Agency (2017). Data from Joint Press Release of the Tenth Meeting of the Informal Consultation on International Cooperation for Conservation and Management of Japanese Eel Stock and Other Relevant Eel Species.

URL: http://www.jfa.maff.go.jp/j/press/sigen/attach/pdf/170711-2.pdf

- Fisheries Agency (2023). Data from Joint Press Release of the Tenth Meeting of the Informal Consultation on International Cooperation for Conservation and Management of Japanese Eel Stock and Other Relevant Eel Species.
- Friedland, K. D., Miller, M. J. and Knights, B. (2007). Oceanic changes in the Sargasso Sea and declines in recruitment of the European eel, *ICES Journal of Marine Science* 64(3): 519–530.
- Fukuda, N., Yamamoto, T., Yokouchi, K., Kurogi, H., Okazaki, M., Miyake, Y., Watanabe, T. and Chow, S. (2022). Active swimming and transport by currents observed in Japanese eels (*Anguilla japonica*) acoustically tracked in the western North Pacific, *Scientific Reports* 12(1): 3490.
- Gardiner, S. M. (2006). A core precautionary principle, Journal of Political Philosophy 14(1): 33–60.
- Gong, X., Davenport, E., Wang, D. and G. Clark, A. (2019). Lack of spatial and temporal genetic structure of Japanese eel (*Anguilla japonica*) populations, *Conservation Genetics* **20**(3): 467–475.
- Guo, H., Zhang, X., Zhang, Y., Tang, W. and Wu, J. (2017). Effects of environmental variables on recruitment of Anguilla anguilla glass eels in the Yangtze Estuary, China, Fisheries science 83: 333– 341.

- Hagihara, S., Aoyama, J., Limbong, D. and Tsukamoto, K. (2018). Age and growth of migrating tropical eels, Anguilla celebesensis and Anguilla marmorata, Journal of Fish Biology 92(5): 1526– 1544.
- Hakoyama, H., Fujimori, H., Okamoto, C. and Kodama, S. (2016). Compilation of Japanese fisheries statistics for the Japanese eel, *Anguilla japonica*, since 1894: a historical dataset for stock assessment, *Ecological research* **31**(2): 153.
- Han, Y.-S. (2011). Temperature-dependent recruitment delay of the Japanese glass eel Anguilla japonica in East Asia, Marine biology 158(10): 2349–2358.
- Han, Y.-S., Hung, C.-L., Liao, Y.-F. and Tzeng, W.-N. (2010). Population genetic structure of the Japanese eel Anguilla japonica: panmixia at spatial and temporal scales, 401: 221–232.
- Han, Y.-S., Sun, Y.-L., Liao, Y.-F., Liao, I., Shen, K.-N., Tzeng, W.-N. et al. (2008). Temporal analysis of population genetic composition in the overexploited Japanese eel Anguilla japonica, Marine Biology 155(6).
- Han, Y.-S., Tzeng, W.-N., Liao, I.-C. et al. (2009). Time series analysis of taiwanese catch data of Japanese glass eels Anguilla japonica: possible effects of the reproductive cycle and el niño events, Zool Stud 48(5): 632–639.
- Han, Y.-S., Wu, C.-R. and Iizuka, Y. (2016). Batch-like arrival waves of glass eels of *Anguilla japonica* in offshore waters of Taiwan, *Zoological Studies* **55**(36).
- Han, Y.-S., Zhang, H., Tseng, Y.-H. and Shen, M.-L. (2012). Larval Japanese eel (Anguilla japonica) as sub-surface current bio-tracers on the East Asia continental shelf, Fisheries Oceanography 21(4): 281–290.
- Higuchi, T., Watanabe, S., Manabe, R., Kaku, T., Okamura, A., Yamada, Y., Miller, M. J. and Tsukamoto, K. (2018). Tracking *Anguilla japonica* silver eels along the West Marina Ridge using pop-up archival transmitting tags, *Zoological Studies* 57(24): 2018–57.
- Hsiung, K.-M., Kuo, Y.-C., Lin, Y.-T., Tseng, Y.-H. and Han, Y.-S. (2022). North Equatorial Current and Kuroshio velocity variations affect body length and distribution of the Japanese eel *Anguilla japonica* in Taiwan and Japan, *Scientific Reports* **12**(1): 2888.
- Hwang, S. D., Lee, T. W., Choi, I. S. and Hwang, S. W. (2014). Environmental factors affecting the daily catch levels of *Anguilla japonica* glass eels in the Geum River estuary, South Korea, *Journal* of Coastal Research **30**(5): 954–960.
- Igarashi, Y., Zhang, H., Tan, E., Sekino, M., Yoshitake, K., Kinoshita, S., Mitsuyama, S., Yoshinaga, T., Chow, S., Kurogi, H., Shinoda, A., Han, Y.-S., Wakiya, R., Mochioka, N., Yamamoto, T., Kuwada, H., Kaji, Y., Suzuki, Y., Gojobori, T., Kobayashi, T., Saitoh, K., Watabe, S. and Asakawa, S. (2018). Whole-genome sequencing of 84 Japanese eels reveals evidence against panmixia and support for sympatric speciation, *Genes* 9(10): 474.
- Ishikawa, S., Aoyama, J., Tsukamoto, K. and Nishida, M. (2001). Population structure of the Japanese eel *Anguilla japonica* as examined by mitochondrial DNA sequencing, *Fisheries Science* **67**(2): 246–253.

- Itakura, H., Kaino, T., Miyake, Y., Kitagawa, T. and Kimura, S. (2015). Feeding, condition, and abundance of Japanese eels from natural and revetment habitats in the Tone River, Japan, *Environmental Biology of Fishes* 98(8): 1871–1888.
- Itakura, H., Miyake, Y., Kitagawa, T. and Kimura, S. (2018). Site fidelity, diel and seasonal activities of yellow-phase Japanese eels (*Anguilla japonica*) in a freshwater habitat as inferred from acoustic telemetry, *Ecology of Freshwater Fish* 27(3): 737–751.
- Jellyman, D. J. (1977). Summer upstream migration of juvenile freshwater eels in New Zealand, New Zealand Journal of Marine and Freshwater Research 11(1): 61–71.
- Kaifu, K., Miyazaki, S., Aoyama, J., Kimura, S. and Tsukamoto, K. (2013). Diet of Japanese eels Anguilla japonica in the Kojima Bay-Asahi river system, Japan, Environmental Biology of Fishes 96(4): 439–446.
- Kaifu, K., Yokouchi, K., Higuchi, T., Itakura, H. and Shirai, K. (2018). Depletion of naturally recruited wild Japanese eels in Okayama, Japan, revealed by otolith stable isotope ratios and abundance indices, *Fisheries science* 84(5): 757–763.
- Kan, K., Sato, M. and Nagasawa, K. (2016). Tidal-flat macrobenthos as diets of the Japanese eel Anguilla japonica in western Japan, with a note on the occurrence of a parasitic nematode Heliconema anguillae in eel stomachs, Zoological Science 33(1): 50–62.
- Karaki, T., Sakamoto, K., Yamanaka, G., Kimura, S. and Kasai, A. (2023). Inshore migration of Japanese eel Anguilla japonica encouraged by active horizontal swimming during the glass eel stage, Fisheries Oceanography.
- Kasai, A., Yamazaki, A., Ahn, H., Yamanaka, H., Kameyama, S., Masuda, R., Azuma, N., Kimura, S., Karaki, T., Kurokawa, Y. et al. (2021). Distribution of Japanese eel Anguilla japonica revealed by environmental DNA, Frontiers in Ecology and Evolution 9: 621461.
- Kimura, S., Inoue, T. and Sugimoto, T. (2001). Fluctuation in the distribution of low-salinity water in the North Equatorial Current and its effect on the larval transport of the Japanese eel, *Fisheries Oceanography* **10**(1): 51–60.
- Kimura, S. and Tsukamoto, K. (2006). The salinity front in the north equatorial current: a landmark for the spawning migration of the Japanese eel (Anguilla japonica) related to the stock recruitment, Deep Sea Research Part II: Topical Studies in Oceanography 53(3-4): 315–325.
- Kimura, S., Tsukamoto, K. and Sugimoto, T. (1994). A model for the larval migration of the Japanese eel: roles of the trade winds and salinity front, *Marine Biology* **119**(2): 185–190.
- Knights, B. (2003). A review of the possible impacts of long-term oceanic and climate changes and fishing mortality on recruitment of anguillid eels of the Northern Hemisphere, *Science of the total Environment* **310**(1-3): 237–244.
- Kotake, A., Arai, T., Okamura, A., Yamada, Y., Utoh, T., Oka, H., Miller, M. and Tsukamoto, K. (2007). Ecological aspects of the Japanese eel, *Anguilla japonica*, collected from coastal areas of Japan, *Zoological Science* 24(12): 1213–1221.

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- Kotake, A., Okamura, A., Yamada, Y., Utoh, T., Arai, T., Miller, M., Oka, H. and Tsukamoto, K. (2005). Seasonal variation in the migratory history of the Japanese eel Anguilla japonica in Mikawa Bay, Japan, Marine Ecology Progress Series 293: 213–221.
- Kumai, Y., Kuroki, M., Goto, A., Takai, K., Muramatsu, K. and Yamakawa, T. (2023). Ontogenetic habitat shift of *Anguilla marmorata* and *A. japonica* in the rivers of southern Japan: Implications for habitat use evaluation and conservation, *Aquatic Conservation: Marine and Freshwater Ecosystems* 33(11): 1295–1308.
- Kuroki, M. (2019). 1.3 Food culture (in Japanese), Science of eels, Asakura Publishing, pp. 10–16.
- Lin, Y. J. and Tzeng, W. N. (2009). Validation of annulus in otolith and estimation of growth rate for Japanese eel Anguilla japonica in tropical southern Taiwan, Environmental Biology of Fishes 84(1): 79–87.
- Manabe, R., Aoyama, J., Watanabe, K., Kawai, M., Miller, M. and Tsukamoto, K. (2011). First observations of the oceanic migration of Japanese eel, from pop-up archival transmitting tags, *Marine Ecology Progress Series* 437: 229–240.
- Mather, N., Traves, S. M. and Ho, S. Y. (2020). A practical introduction to sequentially markovian coalescent methods for estimating demographic history from genomic data, *Ecology and evolution* **10**(10).
- Matsui, I. (1972a). The Study of Eels (Aquacultural Stury) (in Japanese), Kouseisha Kouseikaku.
- Matsui, I. (1972b). The Study of Eels (Biological Study) (in Japanese), Kouseisha Kouseikaku.
- Matsushige, K., Yasutake, Y. and Mochioka, N. (2020). Spatial distribution and habitat preferences of the Japanese eel, *Anguilla japonica*, at the reach and channel-unit scales in four rivers of Kagoshima Prefecture, Japan, *Ichthyological Research* pp. 67: 68–80.
- Miller, M. J., Chikaraishi, Y., Ogawa, N. O., Yamada, Y., Tsukamoto, K. and Ohkouchi, N. (2013). A low trophic position of Japanese eel larvae indicates feeding on marine snow, *Biology Letters* 9(1): 20120826.
- Minegishi, Y., Aoyama, J., Inoue, J. G., Miya, M., Nishida, M. and Tsukamoto, K. (2005). Molecular phylogeny and evolution of the freshwater eels genus *Anguilla* based on the whole mitochondrial genome sequences, *Molecular Phylogenetics and Evolution* 34(1): 134–146.
- Miyake, Y., Takeshige, A., Itakura, H., Itoh, H., Onda, H., Yamaguchi, A., Yoneta, A., Arai, K., Hane, Y. V. and Kimura, S. (2018). Predation on glass eels of Japanese eel Anguilla japonica in the Tone River estuary, Japan, Fisheries Science 84(6): 1009–1014.
- Miyake, Y., Tellier, M.-A., Takeshige, A., Itakura, H., Yoshida, A., Yokouchi, K., Shiozaki, M. and Kimura, S. (2023). Coastal water temperature difference, a potential predictor of glass eel recruitment in *Anguilla japonica* during non-meander periods of the Kuroshio, *Journal of Oceanography* pp. 1–9.
- Mochioka, N. (2019). 4.1 fishing gear and fishing method (in Japanese), *Science of eels*, Asakura Publishing, pp. 120 125.

- Mochioka, N. and Iwamizu, M. (1996). Diet of anguilloid larvae: Leptocephali feed selectively on larvacean houses and fecal pellets, *Marine Biology* **125**(3): 447–452.
- Otake, T., Inagaki, T., Hasumoto, H., Mochioka, N. and Tsukamoto, K. (1998). Diel vertical distribution of Anguilla japonica leptocephali, Ichthyological Research 45(2): 208–211.
- Otake, T., Nogami, K. and Maruyama, K. (1993). Dissolved and particulate organic matter as possible food sources for eel leptocephali, *Marine Ecology Progress Series* 92: 27–34.
- Sang, T.-K., Chang, H.-Y., Chen, C.-T. and Hui, C.-F. (1994). Population structure of the Japanese eel, Anguilla japonica, Molecular Biology and Evolution 11(2): 250–260.
- Shinoda, A., Aoyama, J., Miller, M. J., Otake, T., Mochioka, N., Watanabe, S., Minegishi, Y., Kuroki, M., Yoshinaga, T., Yokouchi, K., Fukuda, N., Sudo, R., Hagihara, S., Zenimoto, K., Suzuki, Y., Oya, M., Inagaki, T., Kimura, S., Fukui, A., Lee, T. W. and Tsukamoto, K. (2011). Evaluation of the larval distribution and migration of the Japanese eel in the western North Pacific, *Reviews in Fish Biology and Fisheries* 21(3): 591–611.
- Shuai, F., Li, J., Yu, S. and Yang, J. (2023). Temporal Pattern of the Occurrence of Japanese Glass Eels (*Anguilla japonica*) in the Pearl River Estuary, *Fishes* 8(5): 256.
- Sudo, R., Fukuda, N., Aoyama, J. and Tsukamoto, K. (2013). Age and body size of Japanese eels, Anguilla japonica, at the silver-stage in the Hamana Lake system, Japan, Coastal marine science 36(1): 13–18.
- Takeuchi, A., Sawayama, E., Kuroki, M., Miller, M. J., Watanabe, S. and Tsukamoto, K. (2022). Preliminary insight into parental contributions to japanese eel (*Anguilla japonica*) preleptocephali spawned on different nights, *Journal of Fish Biology* 101(6): 1601–1605.
- Tanaka, E. (2014). Stock assessment of Japanese eels using Japanese abundance indices, Fisheries Science 80(6): 1129–1144.
- Tanaka, H. (2019). 5.1 History and current status of eel aquaculture (in Japanese), *Science of eels*, Asakura Publishing, pp. 157 161.
- Tesch, F.-W. (2003). The eel, 5th edn, Blackwell Publishing.
- Tseng, M.-C., Tzeng, W.-N. and Lee, S.-C. (2003). Historical decline in the japanese eel Anguilla japonica in northern taiwan inferred from temporal genetic variations., Zoological studies **42**(4): 556–563.
- Tseng, M.-C., Tzeng, W.-N. and Lee, S.-C. (2006). Population genetic structure of the Japanese eel Anguilla japonica in the northwest Pacific Ocean: evidence of non-panmictic populations, Marine Ecology Progress Series 308: 221–230.
- Tsukamoto, K. (1992). Discovery of the spawning area for Japanese eel, Nature 356(6372): 789.
- Tsukamoto, K. (2006). Oceanic biology: spawning of eels near a seamount, Nature 439(7079): 929.

- Tsukamoto, K., Chow, S., Otake, T., Kurogi, H., Mochioka, N., Miller, M. J., Aoyama, J., Kimura, S., Watanabe, S., Yoshinaga, T. et al. (2011). Oceanic spawning ecology of freshwater eels in the western North Pacific, *Nature communications* 2: 179.
- Tsukamoto, K., Otake, T., Mochioka, N., Lee, T.-W., Fricke, H., Inagaki, T., Aoyama, J., Ishikawa, S., Kimura, S., Miller, M. J., Hasumoto, H., Oya, M. and Suzuki, Y. (2003). Seamounts, new moon and eel spawning: the search for the spawning site of the Japanese eel, *Environmental Biology of Fishes* 66(3): 221–229.
- Tzeng, W.-N. (1985). Immigration timing and activity rhythms of the eel, Anguilla japonica, elvers in the estuary of northern Taiwan, with emphasis on environmental influences, Bull Jpn Soc Fish Oceanogr 48: 11–28.
- Tzeng, W.-N., Tseng, Y.-H., Han, Y.-S., Hsu, C.-C., Chang, C.-W., Di Lorenzo, E. and Hsieh, C.-H. (2012). Evaluation of multi-scale climate effects on annual recruitment levels of the Japanese eel, *Anguilla japonica*, to Taiwan, *PLoS ONE* 7(2): e30805.
- Waples, R. S. and Do, C. (2010). Linkage disequilibrium estimates of contemporary ne using highly variable genetic markers: a largely untapped resource for applied conservation and evolution, *Evolutionary applications* **3**(3): 244–262.
- Watanabe, S., Higuchi, T., Noshiro, M., Manabe, R., Miller, M., Jellyman, D. and Tsukamoto, K. (2020). Reexamination of the spawning migration of Anguilla dieffenbachii in relation to water temperature and the lunar cycle, New Zealand Journal of Marine and Freshwater Research 54(1): 131– 147.

URL: https://doi.org/10.1080/00288330.2019.1614075

- Yamamoto, T., Mochioka, N. and Nakazono, A. (2001). Seasonal occurrence of anguillid glass eels at Yakushima Island, Japan, *Fisheries science* 67(3): 530–532.
- Yamamuro, M., Komuro, T., Kamiya, H., Kato, T., Hasegawa, H. and Kameda, Y. (2019). Neonicotinoids disrupt aquatic food webs and decrease fishery yields, *Science* 366: 620–623.
- Yokouchi, K., Aoyama, J., Oka, H. and Tsukamoto, K. (2008). Variation in the demographic characteristics of yellow-phase Japanese eels in different habitats of the Hamana Lake system, Japan, *Ecology of Freshwater Fish* 17(4): 639–652.
- Yokouchi, K., Fukuda, N., Miller, M., Aoyama, J., Daverat, F. and Tsukamoto, K. (2012). Influence of early habitat use on the migratory plasticity and demography of Japanese eels in central Japan, *Estuarine, Coastal and Shelf Science* 107: 132–140.
- Yokouchi, K., Sudo, R., Kaifu, K., Aoyama, J. and Tsukamoto, K. (2009). Biological characteristics of silver-phase Japanese eel, Anguilla japonica, collected from Hamana Lake Japan, Coastal marine science 33(1): 54–63.
- Yoshida, M., Sone, S. and Shiomi, K. (2008). Purification and characterization of a proteinaceous toxin from the serum of Japanese eel Anguilla japonica, The protein journal 27(7-8): 450–454.

- Yu, L., Liu, Y. and Liu, J. (2020). Gene-associated microsatellite markers confirm panmixia and indicate a different pattern of spatially varying selection in the endangered Japanese eel Anguilla japonica, Journal of Oceanology and Limnology 38(5): 1572–1583.
- Zenimoto, K., Kitagawa, T., Miyazaki, S., Sasai, Y., Sasaki, H. and Kimura, S. (2009). The effects of seasonal and interannual variability of oceanic structure in the western Pacific North Equatorial Current on larval transport of the Japanese eel Anguilla japonica, Journal of Fish Biology 74(9): 1878–1890.
- Zhu, K., Gong, L., Jiang, L., Liu, L., Lü, Z. and Liu, B.-j. (2018). Phylogenetic analysis of the complete mitochondrial genome of Anguilla japonica (Anguilliformes, Anguillidae), Mitochondrial DNA Part B 3(2): 536–537.