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REVIEWS

# How have spawning ground investigations of the Japanese eel *Anguilla japonica* contributed to the stock enhancement?

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**Abstract** After Schmidt's discovery of the spawning area of the Atlantic eels *Anguilla anguilla* and *A. rostrata*, the search for the Japanese eel *A. japonica* began in the Pacific Ocean. In 1991, the spawning area of the Japanese eel was determined to be the western North Pacific. Because of enthusiastic research, eggs and maturing eels have been collected in the Japanese eel. These findings are the first for one of the 19 freshwater eels. The population sizes of the Japanese and Atlantic eels are linearly decreasing. Thus, these eel population sizes are considered outside of safe biological limits, and the current fisheries are not sustainable. Artificial propagation has not yet succeeded for the freshwater eels. Stock assessment and management of the European eel have received increasing attention; however, such assessments and management of the Japanese eel have not yet been seriously considered. This paper is an overview of the results of intensive spawning ground investigations of the Japanese eel and describes how the outcomes of these studies have contributed not only to biological interests but also to stock enhancement. During the past 20 years of expeditions, noticeable findings have only been collected for wild eggs and mature adult specimens in spite of the expenditure of large research grants and the large amounts of time invested. The outcomes throughout an expedition do not necessarily contribute to the development and improvement of artificial breeding techniques and stock enhancement. Thus, eel research should be more focused on the studies related to eel stock management.

**Keywords** Artificial breeding · Enhancement efficiency · Japanese eel · Spawning ground · Stock management

## Introduction

At the beginning of the twentieth-century, Schmidt (1922) conducted numerous expeditions and discovered that the spawning areas for both the European eel (*Anguilla anguilla*, Anguillidae) and American eel (*A. rostrata*, Anguillidae) were located far offshore in the Sargasso Sea of the Atlantic Ocean. Approximately 70 years after Schmidt's (1922) discovery, the spawning area of the Japanese eel (*A. japonica*, Anguillidae) was found in the North Equatorial Current to the west of the Mariana Islands and approximately 3,000 km from their growth habitats in east Asia in 1991 (Tsukamoto 1992). Since this discovery, intensive investigations have been conducted almost every year for approximately the last 20 years. Of further note the preleptocephali have been collected just after hatching (Tsukamoto 2006), and the eggs and the maturing eels

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have been collected in the spawning area (Tsukamoto et al. 2011). These findings have not yet been reported for 18 of 19 anguillid eel species and such findings and studies would further contribute to understanding the life history, migration route and behaviour and ecological involvement with other species for the other 18 eel species.

Freshwater eels are the most significant of the eel families because they have a unique catadromous life history and are used as food resources, especially in Asia and Europe. The life cycle of the freshwater eel has five principal stages: the leptocephalus, glass eel, elver, yellow eel and silver eel stages. The larvae, or leptocephali, drift on ocean currents and are transported by these currents. The leptocephali leave oceanic currents after metamorphosing into glass eels and then typically migrate upstream as elvers 4–8 months after hatching (Arai et al. 2001) to grow in freshwater habitats during the yellow stage (immature stage). After upstream migration, the elvers develop into yellow eels and live in freshwater habitats such as rivers and lakes. Then during the silver eel stage (early maturing stage) in autumn and winter, their gonads begin to mature and they start their downstream migration into the ocean and back out to the spawning area, where they spawn and die. During their five life stages, almost every life stage, from glass eel to silver eel, is targeted by eel fishery industries. Consumers in Asia and Europe value the nutritional properties of the eel, making it a high-value aquaculture commodity. Of the 19 anguillid eel species, four are commonly cultured: the Japanese eel, the European eel, the American eel, and the Australian eel (*A. australis*, Anguillidae). All young eels for used in cultivation are wild glass eels (elvers), which are captured in estuaries. Unstable supplies and prices of glass eels are serious problems in the eel culture industry. Almost all (90 %) of the total world eel supply in 2000 came from aquaculture (FAO 2010). Therefore, the supply of eel resources for human consumption is completely dependent on wild catch.

However, the population size of wild glass eels has linearly decreased from over 200 tonnes in the early 1960s to 20 tonnes at present, and with regards to the Japanese eel, a shortage of fry has become a very serious problem for fish cultures in recent years in the Japanese eel. Eel stocks in whole Europe are also declining (Dekker 2003a), and eel fishery yields have decreased in most European countries. The population of the European eel is considered outside of safe biological limits, and current fisheries are not sustainable (Dekker 2003b). The European eel was even recently categorised as critically endangered by the European Union (EU) and the United Nations (UN) (CITES 2007). Since the early 1980s, glass eel recruitment has decreased and dropped to 1 % of the levels encountered in the 1970s. The causes of decline in stock and recruitment are not well understood. Overfishing, habitat loss and migration barriers, increased natural predation, parasitism, ocean climate variation, and pollution might have an impact (Knights 2003; Marcogliese and Casselman 2009; Bonhommeau et al. 2008; Friedland et al. 2007).

To address the rapid decline in eel resources, artificially induced breeding techniques for the eel have been intensively studied in Japan. A challenging research project for the artificial production of glass eels commenced in the late 1960s. Since then, through a continuing process of trial and error, the production of second-generation larvae was finally achieved in 2010 (Ijiri et al. 2011). However, the techniques for producing glass eels in captivity are not yet firmly established. The quality of eggs obtained through controlled maturation is still highly variable, and the survival rates of the larvae are usually extremely low. In addition, the growth of the larvae is slower in captivity than in the wild (Tanaka et al. 2003). Therefore, further studies will be required to improve the culture condition and environment for enhancing the eel stock in the future.

In this paper, I discuss and evaluate the evidence from intensive investigations of the spawning ground of the Japanese eel, which has been accruing for the past 20 years since its discovery in 1991, and discuss how these efforts have contributed to eel stock enhancement rather than to biological interests. Based on this discussion, future perspectives on eel research are also discussed with regards to eel stock enhancement.

## History of the spawning ground discovery

The search for the spawning area of the Japanese eel began in the 1930s, approximately 10 years after Schmidt (1922, 1925) discovered the spawning area of the Atlantic eels (Tsukamoto et al. 2003). At the beginning of the search, information on the life history and ecology of the Japanese eel was scant. Thus, Matsui (1957) hypothesised that the Japanese eel spawned in an area east of Taiwan and south of Okinawa because the adult Japanese eel reaches the southernmost limit of its continental distribution near Taiwan (Fig. 1). The first collection of Japanese eel leptocephalus was a fully grown at a total length (TL) of 57 mm, which was just before metamorphosis at the Bashi Strait just off the southern tip of Taiwan in 1967 (Matsui et al. 1968) (Fig. 1). Kuo (1971) suggested that the Japanese eel of Taiwan would spawn locally in the waters off southwestern Taiwan because the elver catches were higher on the west coast of Taiwan than on the east coast. Thus, the spawning ground proposed by Matsui (1957) was plausible only if the east coast of Taiwan was supplied with eel larvae that have been transported by the Kuroshio Current from south to north. In the 1970s, a total of 55 leptocephali (approximately 50–50 mm TL) were collected predominantly in the waters east of Taiwan (Tanaka 1975; Takai and Tabeta 1976). However, in the 1980s, smaller leptocephali (approximately 40–50 mm TL) were collected in more southern waters east of Luzon Island off of the Philippines (Kajihara 1988; Tsukamoto et al. 1989). Subsequent research efforts collected a total of 28 smaller Japanese eel larvae (approximately 20–31 mm TL) in a more eastern area (Ozawa et al. 1989, 1991). Based on these collected data and the current patterns in this area, the spawning ground of the Japanese eel was estimated to occur somewhere around the Mariana Islands (Fig. 1). In 1991, a large collection of 958 leptocephali (approximately 10–20 mm TL), including the smallest leptocephalus (7.7 mm TL) ever collected, revealed that the spawning ground of the Japanese eel is located at approximately 15°N, 140°E in the North Equatorial Current to the west of the Mariana Islands (Tsukamoto 1992) (Fig. 1). These research efforts suggest that the estimated spawning ground of the Japanese eel has historically moved from north (off Taiwan) to south (off the Philippines) and then from west to east to the west of the Mariana Islands in the western North Pacific (Fig. 1).

After the discovery of the spawning ground of the Japanese eel in 1991, further intensive investigations have been conducted almost every year since for more than 20 years to determine the precise location where the actual spawning occurs. In 2005, a total of 130 preleptocephali (4.2–6.5 mm TL just after hatching) and 60 leptocephali (11.7–18.4 mm TL) were

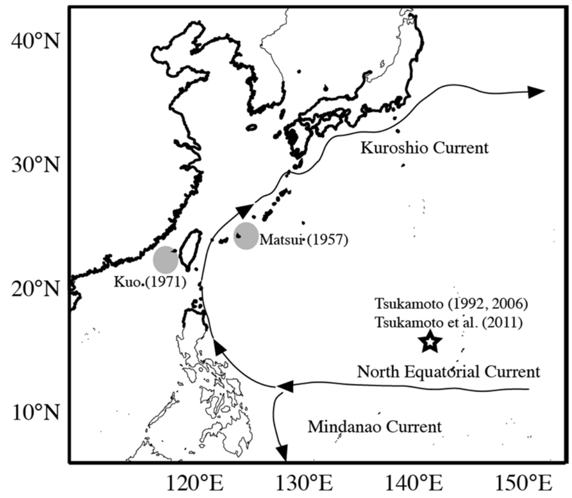


**Fig. 1** Spawning area of the Japanese eel showing the spawning locations speculated by Matsui (1957) and Kuo (1971) (*grey circle*) and estimated by Tsukamoto (1992, 2006) and Tsukamoto et al. (2011) (*star*) along with the major current systems in the western North Pacific. Areas covered by *thick lines* indicate the geographic range of the Japanese eel

collected at 14°N, 142°E in the region of the North Equatorial Current (Tsukamoto 2006). Back-calculated hatching dates using the daily incremental growth rate of the otolith, which was observed for these preleptocephali and other leptocephali specimens, demonstrated that the Japanese eel had hatched at approximately the time of the new moon in those years (Tsukamoto 2006). In 2009, thirty-one Japanese eel eggs and three female eels with functional ovaries were collected in the spawning ground (Tsukamoto et al. 2011).

The spawning area was determined to be just south of a weak salinity front that is typically present in the region as a result of tropical rainfall (Kimura et al. 1994, 2001, Kimura and Tsukamoto 2006). The salinity front was hypothesised to act as a cue for the eels to help them find the spawning area. Although Tsukamoto et al. (2003) and Tsukamoto (2006) proposed the Japanese eel might spawn near seamounts as a landmark for forming spawning aggregations, spawning adult males and a large number of the Japanese eel preleptocephali were collected further from the seamounts (Chow et al. 2009). If the Japanese eel spawns around seamounts, it should be possible to constantly collect eggs and small larvae without any annual variation. However, only 31 eggs have been collected during 20 years of intensive surveys in spite of the fact that the fecundity (number of eggs) of anguilld eels, including the Japanese eel is reported to be higher than a million per eel (MacNamara and McCarthy 2012). Therefore, these findings suggest that Japanese eel spawning can occur in the open water of the spawning ground with no relation to seamounts.

## History of aquaculture

Global demand for eels is met largely through the aquacultural production of essentially two species, the Japanese eel and the European eel (Fig. 2). Consumers in East Asia and Europe value the nutritional properties of these eels, making it a high-value aquaculture commodity. Almost all (90 %) of the world's eel supply comes from aquaculture (FAO 2010).

The culturing of eels was pioneered by countries where eels are a delicacy. Eel culturing began in 1879 in Japan (Matsui 1952) and at approximately the same time in Italy and France (Gousset 1990; Heinsbroek 1991; Ciccotti and Fontenelle 2001). Initially, eel was raised in polyculture systems (Gousset 1992). Large-scale commercial production started in the early 1960s when formulated feeds became available (Liao et al. 2002).

Eel farming depends completely on the collection of juvenile stages such as the glass eel and elver from the wild. Therefore, the annual recruitment of the glass eel is very important to the eel culturing industry. However, recent recruitments of the glass eel stage of the Japanese eel have fallen to 10 % of the early 1960s rate (Ijiri et al. 2011). For the European eel, recruitment has also fallen, on average to <5 % of the peak levels of the late 1970s and early 1980s (Dekker et al. 2007) (Fig. 2), and the ICES continues to advise that the stock is outside of safe biological limits and that current fisheries are not sustainable (ICES 2006).

Unstable supplies and prices for glass eels are serious problems for the eel culturing industry. Therefore, the development of artificial breeding techniques for the eel is eagerly desired. In Japan, attempts to induce the artificial maturation of the Japanese eel started in the 1960s (Tanaka et al. 2003). Yamamoto and Yamauchi (1974) were the first to successfully obtain fertilised eggs and larvae from the Japanese eel using hormone treatments, and after a 2-week rearing period the preleptocephalus larvae reached 7 mm TL (Yamauchi et al. 1976). However, the larvae did not feed, and the transition into leptocephalus larvae did not occur. Since this study, although many researchers have succeeded in obtaining eel preleptocephali (Satoh 1979; Wang et al. 1980), larval feeding and the production of leptocephali were not successful until 2001 (Tanaka et al. 2001). For other eel species, such as the European eel (Prokhorchik 1986) and the New Zealand short- and long-finned eels (*A. australis* and *A. dieffenbachii,* Anguillidae) (Lokman and Young 2000), experimentally produced larvae have only survived for a few days and, as with the Japanese eel, did not develop into leptocephali. After much trial and error, Tanaka et al.

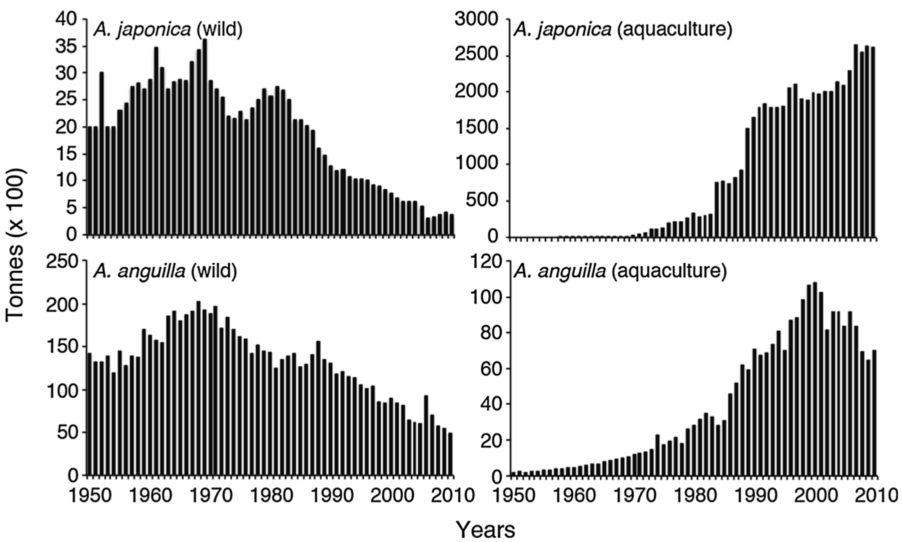


**Fig. 2** Global capture (*left*) and aquaculture (*right*) production in 1950–2010 for the Japanese eel (*top*) and the European eel (*bottom*). *Sources* FAO. ©2010–2012. FAO FishFinder—Web Site. FAO FishFinder Contacts. In: FAO Fisheries and Aquaculture Department (online). http://www.fao.org/fishery/fishfinder/contacts/en

(2001) found that preleptocephali were strongly attracted to and actively fed on shark egg powder. Thereafter, leptocephali have been successfully reared using this diet in aquaria for 100 days and have been raised to 22.8 mm TL, and the morphological characteristics and age of the reared leptocephali overlap with those of wild leptocephali (Tanaka et al. 2001). Soon after this study was performed, Tanaka et al. (2003) reported further progress in rearing larvae to the glass eel stage and even further to the yellow eel stage in 2003 (Ijiri et al. 2011). After succeeding in rearing the eels to the leptocephalus stage (Tanaka et al. 2001), their diet was improved by supplementation with krill hydrolysate, soybean peptide, vitamins and minerals (Tanaka et al. 2003). The leptocephali that fed on this new diet grew to 50–60 mm TL and had begun to metamorphosis into glass eels approximately 250 days after hatching (Tanaka et al. 2003). The artificially produced glass eels could be grown and were artificially matured (Ijiri et al. 2011). Thereafter, a second generation of larvae was produced in 2010 (Ijiri et al. 2011). However, the techniques for producing glass eels are not yet firmly established (Tanaka et al. 2003). The egg quality is unstable, and the survival rates of the larvae are usually extremely low. In addition, the growth of the larvae is slower in captivity than in the wild, approximately 100 days (Arai et al. 1997). Under such conditions, the mass production of glass eels for use in aquaculture has not succeeded until recently.

## Differences between freshwater eel and salmon in ecology and artificial propagation

The freshwater eels are distributed throughout the world (Tesch 2003). The Japanese eel is widely distributed from the northern Philippines in the south, through Taiwan eastern China, Korea, and up to the Sanriku Coast of northern Honshu Island, Japan (Tesch 2003) (Fig. 1). The Japanese eel and other eel species are generally considered catadromous fish species (McDowall 1988) and spawn in the North Equatorial Current to the west of the Mariana Islands. Their transparent leaf–like larvae (leptocephali) are transported from the spawning area toward the coastal waters of East Asia by the North Equatorial and Kuroshio currents, where they metamorphose into glass eels. In general, the glass eels migrate upstream to grow into the elver and yellow eel stages in freshwater. At maturation, the yellow eels metamorphose into silver eels, which migrate downstream to the ocean to begin their spawning migration (Tesch 2003).

However, otolith microchemistry studies have recently revealed that some yellow and silver eels of the anguillid eels never migrate into freshwater and spend their entire life history in the ocean (Arai and Chino 2012). The application of otolith Sr:Ca ratios to tracing the migratory history of eels has also revealed otolith signatures intermediate to those of the marine and freshwater residents of several anguillid species: the Japanese eel (Tsukamoto and Arai 2001; Arai et al. 2003a, b, 2008, 2009; Kotake et al. 2003, 2005; Chino and Arai 2009), the European eel (Arai et al. 2006; Daverat et al. 2006), the American eel (Lamson et al. 2006), the New Zealand short- and long-finned eels (Arai et al. 2004), the giant mottled eel (*A. marmorata*, Anguillidae) (Chino and Arai 2010a; Arai et al. 2013) and a tropical short-finned eels (*A. bicolor bicolor* and *A. bicolor pacifica*, Anguillidae) (Chino and Arai 2010b, c; Arai et al. 2013), all of which appear to reflect an estuarine residence or demonstrate clear evidence for switching between different salinity environments. Thus it appears that a proportion of eels frequently move between different environments during their growth phases. Therefore, because individuals of several anguillid species have been found to remain in estuarine or marine habitats, it appears that anguillid eels do not all enter into freshwater environments and that these species display more of a facultative catadromy (Arai and Chino 2012).

Based on recent findings regarding the anguillid eel life histories, eel migration can be simply summarised as: the eel spawns in the open ocean and grows in coastal and fresh waters. Therefore, the life history of anguillid eels makes it difficult to conduct artificial propagation. Although nobody has yet attained for the artificial propagation using wild eggs (and sperm), the propagation must require the open ocean spawning ground or the transport of the wild eggs to coastal or fresh water nurseries over long distances of more than thousands of kilometres. Due to such catadromous life histories and the unsuccessful application of artificial breeding to anguillid eels, all juveniles used in eel culturing must be wild glass eels and/or elvers with no or significantly less fishery management, especially for the Japanese eel.

Salmon are considered important marine and freshwater resources in many countries. Anadromous salmon spawns in fresh water and grown in the coastal and open ocean, and the life histories and spawning ecology are just diametrically opposed with those of catadromous anguilld eels.

Hatchery programmes involving the mass release of cultured fish have been implemented worldwide to supplement wild populations and to increase fishery harvests. The chum salmon (*Oncorhynchus keta,* Salmonidae) has the widest natural geographic distribution among all Pacific salmon and is found in streams of the North Pacific and the Arctic Ocean with Japan being the southernmost limit of its distribution on the Asian continent (Salo 1991). In Japan, almost all chum salmon stock has been sustained by artificial propagation (Kobayashi 1980; Kaeriyama 1989; Mayama and Ishida 2003). Hatchery-reared chum fry are released annually into rivers for coastal fisheries that target adult returning salmon along the Sea of Japan coast and along the Pacific Ocean coast. Although the use of hatchery programmes has long been debated (Hilborn 1992; Waples 1999; Brannon et al. 2004), and the negative effect on wild fish productivity is one of the most frequent criticisms (Levin et al. 2001; Chilcote 2003; Nickelson 2003), the mass releases of cultured salmons such as chum salmon, pink salmon (*Oncorhynchus gorbuscha,* Salmonidae) and sockeye salmon (*O. nerka,* Salmonidae) have been implemented worldwide to supplement wild populations and to increase harvests (Fig. 3).

Due to the anadromous life history of salmon, its artificial propagation is much easier than that of the anguillid eels, and there are currently established hatchery programmes for a number of salmons. To obtain eggs (and sperm) from the natural brood stock for hatchery production, the returning adults are only captured in weirs at the bottom of rivers in their tributaries. Therefore, the efforts required for wild egg collection and farming are much less than those required for anguillid eels.

Further, the number of chum and pink salmons returning to Hokkaido Island (Japan) have increased dramatically during the last quarter of the twentieth-century (Morita et al. 2006) (Fig. 3). It has been suggested that advances in hatchery technology have been a major contributor to the recent increase in coastal catches (Kobayashi 1980; Hiroi 1998; Kaeriyama 1998, 1999; Nagata and Kaeriyama 2003). In particular, the apparent return rate for the chum and pink salmon increase has been attributed to increases in the body weights of the fry released and to the appropriate timing of their release from hatcheries (Kobayashi 1980; Mayama 1985; Kaeriyama 1998, 1999; Nagata and Kaeriyama 2003). These results suggest that the substantial efforts of hatchery programmes and fishery management in some salmon species are well organised and established (Fig. 3).

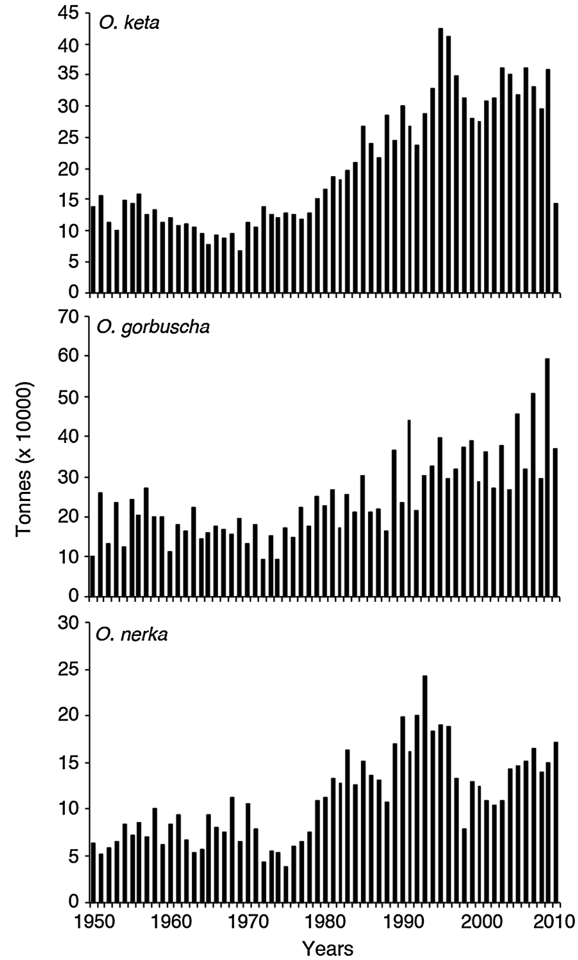


**Fig. 3** Global capture in 1950–2010 for chum salmon (*top*), pink salmon (*middle*) and sockeye salmon (*bottom*). *Sources* FAO. ©2010–2012. FAO FishFinder—Web Site. FAO Fish-Finder Contacts. In: FAO Fisheries and Aquaculture Department (online). http://www.fao.org/fishery/fishfinder/contacts/en

## Missing link between field investigations and stock enhancement and propagation

Although the intensive spawning ground investigations of the Japanese eel for approximately the last

20 years since the discovery of the spawning ground have provided some updated biological information for the eel, the eel stock is decreasing linearly with the increasing of aquaculture demand for human consumption (Fig. 2). The reasons for investigating the eel's spawning ground other than the biological interests are to facilitate efforts to prevent further declines in its populations (Tsukamoto et al. 2011) and to provide some clues to help advance the establishment of commercial glass eel production, i.e., to understand the environmental conditions of the spawning ground for implementation in commercial production (Ijiri et al. 2011).

The fluctuation of the Japanese eel, population has garnered particular attention (Miller et al. 2009) because of its high economic value (FAO 2010), complex life history (Arai and Chino 2012), and its declining recruitment since the 1970s (Tatsukawa 2003). A similar declining trend has also been reported for the European and American eels (Dekker et al. 2003). The reasons for the recruitment declines of these temperate anguillid eels are not clear but have possibly been caused by overfishing, habitat degradation, pollution, parasites, virus, and global climate change (Knights 2003; Marcogliese and Casselman 2009; Bonhommeau et al. 2008; Friedland et al. 2007). In addition, their impacts would be different depending on the eel life histories.

During the oceanic life stage, it has been suggested that the recruitment variability of the Japanese eel is affected by ocean–atmospheric forcing (Miller et al. 2009). In particular, the latitudinal shifts of spawning locations in relation to larval transport by the North Equatorial Current (NEC) are considered an important determinant of recruitment success (Kimura et al. 2001). If the eels can travel westward using the NEC and enter the Kuroshio Current, they have a significantly enhanced probability of recruitment success. In contrast, if the eels are entrained into the south-flowing Mindanao Current or mesoscale eddies east of Taiwan, recruitment is reduced (Kim et al. 2007). Specifically, when precipitation is low during some ENSO years, the salinity front (and thus the spawning location) may move considerably southward, thereby increasing the possibility that the eel larvae will enter the Mindanao Current (Kimura et al. 2001, Kimura and Tsukamoto 2006). In addition, the bifurcation latitude of the NEC varies both seasonally and interannually (Qiu and Lukas 1996), which potentially also affects the recruitment variability of the Japanese eel (Zenimoto et al. 2009). In particular, ENSO events shift the bifurcation latitude of the NEC northward, which results in more NEC water flowing into the Mindanao Current and hampers eel recruitment (Zenimoto et al. 2009). Another possible climatic effect is the change in ocean productivity, which may be critical for feeding success and for larval survival during their migration route (Miller et al. 2009, Bonhommeau et al. 2008).

Spawning ground investigations can provide exact locations and this information might be useful for estimations of the possible transportation route of the leptocephali. This information might provide further data to predict the possible recruitment mechanism for glass eels. However, the spawning ground has been reported to shift in association with ocean climate change (Kimura and Tsukamoto 2006). Although the NEC region is the only spawning area of the Japanese eel, the 2002 expedition indicated that the larval distribution of the species is likely related to a salinity front generated by two distinct waster masses in the NEC. This investigation was conducted during an El Nino event, and the salinity front had moved. Smaller larvae (less than 10 mm TL) were collected just south of the salinity fronts, where these larvae have never been collected during typical years (Kimura and Tsukamoto 2006). Because the latitudinal location of the Japanese eel spawning events was found to shift by months or years (Tsukamoto 2009), the determination of the exact spawning ground might be difficult. Further, the examined spawning locations were not so different from the first spawning ground discovery in 1991 (Tsukamoto 1992) even though these investigations have been conducted almost annually during this period over the past 20 years (Tsukamoto et al. 2011) through snapshot findings (Tsukamoto 2006). Such ocean climate effects leading to fluctuations of the Japanese eel population during the oceanic life stage could be estimated using ocean climate data, satellite tracked buoy data and a coupled ocean–atmosphere circulation model using the data from the first discovery.

Information about the environmental conditions in the spawning ground may help advance the establishment of artificial breeding techniques for the production of commercial glass eels in captivity. Water temperature, spawning depth and diet during hatching and the early developmental stages of the larvae in the spawning ground are accessible and fundamental information for improving and developing eel culture techniques.

Knowing the optimal temperature range will lead to the efficient production of healthy Japanese eel larvae and healthy larvae are essential for producing glass eels. Tanaka (1996) reported a higher hatching rate (60–70 %) at a relatively high temperature (25–28 °C); however the survival rate for prefeeding larvae was low (0 %, 8 days after hatching). Chang et al. (2004) indicated that the Japanese eel eggs and yolk sac (prefeeding) larvae could adapt to a wide range of temperatures (3–32 °C) and suggested that the optimal temperature range might be 24–26 °C for incubating eggs and 26–28 °C for prefeeding larvae. Recently, Okamura et al. (2007) provided an answer for producing healthy larvae. Their results demonstrated that many larvae become deformed at 19–22 °C, whereas much fewer become deformed at 25–28 °C. Assuming that the occurrence rate of deformed fish is a more effective index for determining the optimum temperature for eel larvae, the optimal temperature range is approximately 25–28 °C (Okamura et al. 2007). This result is in good agreement with the environmental conditions likely experienced by wild larvae, a temperature range of 25–28 °C corresponds to depths of 150–200 m in the spawning ground (Tsukamoto et al. 2011). At these depths in this area, the specific gravity of the sea water ranges from 1.022 to 1.023, which is almost the same for artificially fertilised eggs (Okamura et al. 2007). These results suggest that the optimal water temperatures for the Japanese eel eggs and prefeeding larvae in the wild and in captivity are approximately 25–28 °C. As a result, the experimental studies in captivity reveal the optimal water temperature for incubating eggs and rearing larvae of the Japanese eel, and this information might be more useful for predicting where to find wild eggs and larvae, which would better help to determine the spawning layer in the spawning ground than extracting information from the spawning ground investigation field data for the eel.

Despite intensive research on wild and captive eels, no resource has provided access to all life cycle stages of the Japanese eel since the production of preleptocephali 25 years ago (Tanaka et al. 2001). Therefore, the transition from the preleptocephalus (newly hatched larva) to the leptocephalus stage (typical leaf-like eel larva) has remained the missing link in the eel life cycle. Yamamoto and Yamauchi (1974) first succeeded in obtaining fertilised eggs and larvae of the Japanese eel, and preleptocephalus larvae were reared for 2 weeks, reaching 7 mm TL (Yamauchi et al. 1976). Thereafter, eel larvae could be successfully obtained; however suitable larval feeds were not identified. As a result, the preleptocephalus larvae could not survive beyond the depletion of their yolk and oil droplet stores. In other eel species, for example, the European eel (Prokhorchik 1986) and the New Zealand eels *A. dieffenbachii* and *A. australis* (Lokman and Young 2000), experimentally produced larvae survived only for a few days and, like the Japanese eel, did not develop into leptocephali. Tanaka et al. (2001) finally found that a slurry-type diet made from shark egg powder is a suitable feed for captive-bred eel larvae. The larvae were successfully reared with this diet in aquaria for 100 days and raised to 22.8 mm TL. The age, TL and body proportions of the reared specimens overlapped with those of wild leptocephali (Tanaka et al. 2001). Although preleptocephalus larvae can be reared using this diet, it remains inadequate because the leptocephali reared in this manner cannot be raised to the subsequent stage. Soon after the findings on this diet by Tanaka et al. (2001), the diet was improved by supplementation with krill hydrolysate, soybean peptide, vitamins and minerals. Leptocephali fed on this new diet had grown to 50–60 mm in TL and begin to metamorphose into glass eels (Tanaka et al. 2003). The artificially produced glass eels can then be grown and artificially matured (Ijiri et al. 2011). Thereafter, a second generation of larvae was produced in 2010 (Ijiri et al. 2011).

Although there have been a few studies, the feeding ecology of leptocephali, including the anguillid eel is still not well understood. On the basis of analyses of gut contents, gut pigment content and nitrogen stable isotopes, the most likely food source of congrid leptocephali (*Conger myriaster* and *C. japonicus*, Congridae) has been inferred to be particulate organic matter (POM) (Otake et al. 1993). Mochioka and Iwamizu (1996) examined the gut contents from five families of eels (Congridae, Muraenidae, Muraenesocidae, Nettastomatidae and Ophichthidae) and reported larvacean houses, and their faecal pellets were commonly found in their guts. These studies indicate that the trophic level of leptocephali should be low considering their gut contents, e.g., larvacean houses and POM. Kimura and Tsukamoto (2006) reported that the carbon isotope ratios of the Japanese eel leptocephali corresponded to the carbon stable isotope ratios of POM, which confirms that POM is the likely food source of leptocephali. A likely reflection of this complex composition of POM was observed in a recent study using DNA barcoding for the qualitative analysis of the diet of small European eel leptocephali, which suggested that gelatinous zooplankton such as Hydrozoa, Thaliacea and Ctenophora may somehow contribute to the diet of the early larvae of that species (Riemann et al. 2010). However, the comparisons of POM stable isotope ratios and those of the Japanese eel leptocephali indicated that leptocephali appear to feed more on POM rather than directly feeding on zooplankton or secondary consumers (Miyazaki et al. 2011) even if their DNA sequences were detected in the gut contents of the European eel leptocephali by Riemann et al. (2010). More recently, the nitrogen isotope enrichment values of reared larvae have suggested that the primary food source of wild larvae is also consistent with only POM such as marine snow and discarded appendicularian houses (Miller et al. 2012). These results all lead to the conclusion that leptocephali appear to feed on POM and do not directly feed on zooplankton or secondary consumers.

Although the findings using shark egg powder, krill hydrolysate, soybean peptide, vitamins and minerals as optimal diets for larvae in captivity (Tanaka et al. 2001, 2003) have provided a significant breakthrough for cultivating eel larvae, these diets could not be found in the NEC in the spawning ground and are highly different from those of wild larvae (POM; Kimura and Tsukamoto 2006, Miyazaki et al. 2011, Miller et al. 2012). Judging from these results and the present state of eel farming for the Japanese eel, the eels can be reared throughout their lives from eggs to adults in captivity.

Other environmental conditions such as salinity, light intensity (wavelength), water circulation and water quality might also be important factors affecting the survival rate in captivity and these factors may directly determine the location of the spawning ground. In addition to water temperature and diet, other factors at optimal conditions must be considered in determining rearing conditions (Tanaka et al. 2001, 2003; Tanaka 2003; Kagawa et al. 2005; Okamura et al. 2009a, b). Therefore, to determine the optimal conditions for the various ambient factors involved in artificial eel culturing, field investigations of the spawning ground of the Japanese eel might be less relevant and not as important a link to eel propagation in captivity.

## Future perspectives for research: factors involved in improving artificial breeding techniques and the conservation of wild stocks for their enhancement

The intensive spawning ground investigations of the Japanese eel after the first discovery of its spawning ground in 1991 have provided valuable biological information such as on wild egg collection and the wild spawning conditions adult specimens collected in the spawning ground. These findings are the first for a member of the 19 species of the freshwater eel. However, this exertion and long-term (20 years) expedition might be less influential for improving and developing artificial breeding and culturing techniques and stock enhancement for the Japanese eel than previously thought, as mentioned above.

Although the glass eel has been successfully artificially produced grown and matured in captivity, the quality of eggs obtained through this type of controlled maturation is still highly variable, and the survival rates of the larvae are usually extremely low for the Japanese eel (Tanaka et al. 2003; Ijiri et al. 2011). Therefore, further studies should be focused on developing better maturation induction procedures and rearing regimes for the larvae to establish techniques for the consistent mass production of glass eels. Unlike anadromous salmon, the spawning grounds of all catadromous eels are located in open ocean, generally more than thousands of kilometres away from coastal and inland farming facilities. It is almost impossible to establish eel propagation facilities and eel farming industries in the open ocean, but even consistent mass collections of wild eggs will succeed in the future. However, the spawning ground is possibly shifted by oceanic climate conditions on a monthly and yearly basis, which might prove to be a challenge to the collection of wild eggs for propagation. Furthermore, the wild eggs and spawning condition adult eels in the open ocean might be considered a common property. Thus, international fishery management for the usage of precious resources must be considered because the Japanese eel is distributed widely in the east Asian countries of Japan, China, Korea and Taiwan and in the Philippines in southeast Asia countries as a panmictic population (Sang et al. 1994). These facts suggest that further studies will be specifically required to improve and develop techniques for the consistent mass production of glass eels in captivity to improve Japanese eel propagation and stock enhancement, which is in contrast to further intensive spawning ground investigations.

The world-wide decline of the anguillid eels is one of the major concerns for fishery management. Similar to the American eel and the European eel, the Japanese eel has experienced a sharp decline across its range over the last 30–40 years (ICES 2006; Aprahamian et al. 2007; Castonguay et al. 1994; Dekker et al. 2007; Tatsukawa 2003) (Fig. 2). There have been dramatic declines in the populations of these eels which have plummeted to approximately 1–10 % of their levels from the 1970–1980s (Dekker et al. 2007; Casselman 2003; Tatsukawa 2003), and the effective population size of the Japanese eel has also decreased (Tzeng 2004). Current populations are far below the biologically safe limit, and extinctions in the near future are a distinct possibility. The reasons for the population declines are still uncertain but may relate to changes in oceanic currents and global climate, degradation of habitat, pollution, exotic parasite infection, and overfishing. Population levels of the American, European and Japanese eels are on the verge of collapse, and the need for management and conservation is urgent because eel fishing is performed on almost every life stage, from glass eel to silver eel.

For the European eel, as a consequence, the European Commission has agreed to an eel recovery plan (ERP), the aim of which is to return the European eel stock to sustainable levels of adult abundance and glass eel recruitment (Svedang and Gipperth 2012). In October 2003, the European Commission presented the Council and the European Parliament with a recovery plan for the European eel. The European Council then asked the Commission to come forward with proposals for the long-term management of the eel in Europe. The Parliament adopted a solution in November 2005 calling on the Commission to propose legislation regarding eel recovery measures (Svedang and Gipperth 2012). In June 2007, the European eel was listed in Appendix II of the CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora), and Appendix II "includes species not necessarily threatened with extinction, but in which trade must be controlled to avoid utilisation incompatible with their survival" (CITES 2007). The EU passed Council Regulation (EC) number 1100/2007 for the purpose of establishing measures for the recovery of the stock of the European eel in 2007 (Svedang and Gipperth 2012). According to this EU regulation, national recovery plans should be developed to meet the stipulated objectives. Regulation EC1100/2007 recognises several possible measures to reduce eel mortality: reducing/closing fisheries (both commercial and recreational), facilitating migration and improving river habitats, and transporting silver eels from inland waters to waters from which they can escape freely to the Sargasso Sea (Svedang and Gipperth 2012). A critical feature of these plans is to permit the escapement to sea of at least 40 % of the virgin silver eel biomass, which would have occurred prior to anthropogenic influences. The principle behind this conservation measure is that escape is one of the key stages of the European eel's catadromous life cycle that can be controlled, and it is hypothesised that positive alterations to this will in turn have a proportionally positive effect on recruitment (the number of juveniles migrating to the freshwater habitat for maturation) (Bilotta et al. 2011). Although stock assessment and management of the European eel have received increasing attention from both the scientific community and the fisheries agencies in recent years (ICES 2006), such assessment and management of the Japanese eel have not yet been well studied with a concrete policy and destination for stock enhancement. Please note that the despite the high demand for the product, the peak capture of Japanese eels is less than the lowest captures of European eels (Halpin 2007). This fact indicates the relatively low virgin biomass of Japanese eels. Landings of Japanese eels have declined since the 1970s, with a brief increase in the 1980s from an increased effort in South Korea. Though landings have decreased, the consumption of eels has climbed (Fig. 2), most markedly in Japan where more than 50 % of the world production of eels is consumed (Ringuet et al. 2002). More than 90 % of the world production of eels is cultured in East Asian countries, in particular Japan, Taiwan and China (Ringuet et al. 2002). In November 2007, Taiwan banned the exports of glass eels; however further strict regulations for the

Japanese eel trade and fishery, especially in the glass and silver eel stages, and for the conservation of wild eel stocks, which have all been discussed at length by EU countries, are indispensable for eel stock enhancement in Asian countries. There is a need to define a joint assessment of wild eel stocks. This step includes quantitative parameters of the world populations (distribution, structure and abundance) for each biological stage and qualitative parameters (e.g., the fecundity of spawners) to define appropriate stock enhancement targets. It is also necessary to improve the monitoring of eel stocks to better appreciate the efficiency of stock enhancement programmes.

## Conclusion

The intensive spawning ground investigation of the Japanese eel has played an important role in accumulating our basic knowledge of freshwater eel biology. During the past 20 years expeditions, however, a significant amount of human power, research funding, cruise costs and plenty of time have also been expended almost every year on the research cruises that span thousands kilometres. After the first discovery of the spawning ground in 1991, important findings have been collected for wild eggs and mature adults in the spawning ground only. The outcomes of these expeditions do not necessarily contribute to the development and improvement of artificial breeding techniques for the complete propagation and stock enhancement of the Japanese eel. In addition to the Japanese eel, other anguillid eels, such as the American and European eels, are threatened. Because recruitment remains in decline and stock recovery will be a long-term process for biological reasons, studies aimed at eel stock management in coastal and inland waters should be the current focus. Furthermore, the present eel aquaculture completely (100 %) depends on wild glass eels or elvers as fry. More than 90 % of the world production of eels is cultured in East Asia, in particular Japan, Taiwan and China (Ringuet et al. 2002). Rearing eel larvae to the glass eel stage has never been successfully completed commercially. Therefore, to enhance eel stocks and their commercial use for human consumption, studies related to the establishment of commercial glass eel production are urgently required and should be more focused on this goal. Because eels are not protected under local or international law, the Japanese eel and European eels are currently seriously threatened with extinction.

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