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Present Status of the Japanese Eel: Resources and Recent Research

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Abstract.—The Japanese eel, *Anguilla japonica*, is an important food fish in East Asia, and catches of glass eels and of eels in freshwater appear to have declined dramatically in recent decades, causing increasing concern for the health of wild stocks. During that time, research efforts to understand its biology have progressed considerably. The spawning area was successfully outlined to the west of the Mariana Islands in 1991, and other research suggests that their recruitment success may be related to El Niño events, which appear to affect the transfer of leptocephali from the north equatorial current into the Kuroshio Current. Otolith microstructure and microchemistry studies have revealed various aspects of their early life history that relate to their oceanic larval migration. The discovery of sea eels that live in marine habitats without entering freshwater may change the common understanding of freshwater eel ecology and affect management plans. Most genetic studies suggest that the Japanese eel is composed of a single panmictic population throughout East Asia. Therefore, international management is needed among the countries of China, Taiwan, Korea, and Japan, where glass eels recruit from a common stock and are used extensively for aquaculture.

Introduction

In recent years, there has been growing concern about declining stocks of various species of anguillid eels around the world, including the commercially important Japanese eel, *Anguilla japonica* (Dekker et al. 2003). The Japanese eel is an extremely important food fish in Japan and is also eaten in other East Asian countries. This species is reared extensively from wild-caught glass eels by an aquaculture industry in four different countries, and after some bad recruitment seasons in recent years, such as in 1997 and 2005, concern for the health of the species' resources has increased considerably. Although recruitment has been better in subsequent years, the extent of the decline is not well known, because there are relatively few reports on this subject (Tatsukawa 2003).

One problem with quantifying the health of stocks of this species is that there has been little research on its freshwater phase even though it is extensively harvested as a food fish and as stock for aquaculture when it enters freshwater rivers upon recruitment. To help address this problem, some recent research projects have been carried out in Japan to provide basic knowledge about sex ratio, size, age, and growth. These studies have found that growth rates of eels using both freshwater and estuarine or coastal habitats are higher than those observed in other

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temperate anguillid species (Tzeng et al. 2003; Anonymous 2004; Kotake et al. 2005, in press; Yokouchi 2005). Other studies on Japanese eels have examined their homing behavior (Aoyama et al. 2002), morphology of their burrows in soft mud sediments (Aoyama et al. 2005) and habitat use (Shiao et al. 2003), and various aspects of silver eel ecology including their gonadal morphology (Han et al. 2003a; Utoh et al. 2004), silvering stages (Okamura et al. 2007), salinity preference (Han et al. 2003a), and spawning behavior in captivity (Dou et al. 2007).

However, until recently most researchers have worked on ecological or physiological subjects instead of focusing on the freshwater ecology of the Japanese eel, with many studies related to artificial spawning and production of glass eels (see Aida et al. 2003), which has recently succeeded (Tanaka 2003; Kagawa et al. 2005). Ecological researchers have focused more on other subjects, such as understanding the various aspects of migration and marine life history.

As a result, knowledge of the ecology of the Japanese eel has increased remarkably in the past 15 years because of a considerable number of studies, including some on the much less studied species of tropical eels. Studies have dealt with anguillid taxonomy (Watanabe 2003, 2004, 2005), phylogeny (e.g., Tsukamoto and Aoyama 1998; Aoyama et al. 2001; Lin et al. 2001), and population structure (e.g., Sang et al. 1994; Chan et al. 1997; Ishikawa 1998; Ishikawa et al. 2001a; Tseng et al. 2006). Other studies have focused on early life history (e.g., Tsukamoto 1990; Tsukamoto and Umezawa 1990; Otake et al. 1994; Cheng and Tzeng 1996; Arai et al. 1997, 2001a, 2001b, 2002; Sugeha et al. 2001; Dou et al. 2003; Kuroki et al. 2005, 2006a,b, 2007; Sasai et al. 2007), adult migration (Kuo et al. 1996; Aoyama et al. 1999a, 2002; Sasai et al. 2001; Okamura et al. 2002), larval distribution (e.g., Tsukamoto 1992; Aoyama et al. 1999b, 2003, In press; Ishikawa et al. 2001b; Miller et al. 2002), larval transportation (Kimura et al. 1994, 1999), and oceanic glass eels (Otake et al. 2006).

Much recent research is reviewed in the book *Eel Biology*, which covers all major areas of basic eel biology but focuses on the biology of the Japanese eel and other anguillid species rather than resource management (Aida et al. 2003).

However, despite all the ecologically related research, compared with the two Atlantic species—the European eel *A. anguilla*, and the American eel *A. rostrata*—basic knowledge of the resources and the freshwater phase of the Japanese eel is still lacking. Furthermore, wild freshwater eel fisheries for this species provide less than 1% of total eel consumption, with the remainder coming from aquaculture (Tatsukawa 2003). However, to restore healthy wild populations of the Japanese eel and to maintain stable use of the eel resource, ecological research on the freshwater phase, as well as the marine phase, will be indispensable.

In this paper, we describe the general status of research on the Japanese eel and its resources in east Asia and review the research on some of the factors affecting population fluctuations in order to help build a better understanding of the causes of the declines of this important commercial species.

Resources of the Japanese eel

Eel Industry in East Asia

One of the unique characteristics of the Japanese eel resource is that glass eels recruit to the four widely separated East Asian countries of Taiwan, Japan, China, and Korea, where they are used for aquaculture. These glass eels are extensively fished and reared in aquaculture facilities in each country, but in recent years, a much greater proportion of annual aquaculture production is occurring in China (Figure 1). China still imports Euro-

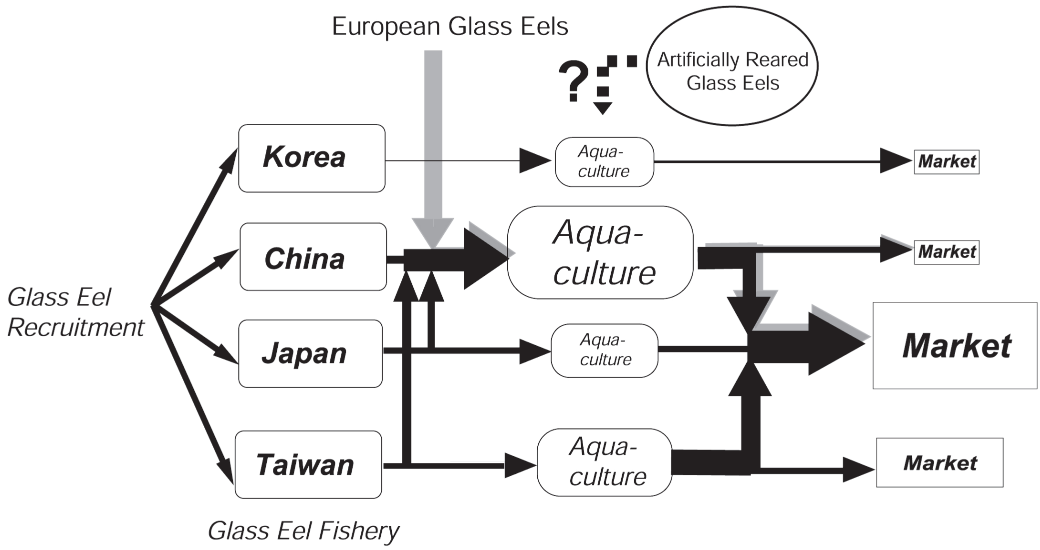

Figure 1. A diagrammatic representation of the use and international trade of the Japanese eel, *A. japonica*, in East Asia, showing the countries where glass eels recruit, their various general pathways into the aquaculture industry, and the pathways of the products to the market. Import and use of the European eel, *A. anguilla*, in some countries is shown with shaded arrows. Relative thickness of the arrows and sizes of the components reflect the general proportions of the quantity of glass eels or eel products in the industry.

pean glass eels to supplement their eel production, most of which is sold in Japan. However, American glass eels have been found to be less successful for aquaculture production than the Japanese and European eels, and are not used to any great extent in recent years in China or Japan.

Once eels reach marketable size, they are sold to eel traders and distributed to commercial outlets. Although production of eels in Japan has been decreasing, Japan is still the biggest consumer of cultured eels, now up to about 130,000 metric tons (mt) per year. Grilled eel, or *kabayaki*, is popular in restaurants and is also sold in supermarkets year-round in Japan. However, the less expensive *kabayaki* is imported from other East Asian countries, and mtDNA analysis has shown that about 70% of this is European eel (T. Wakao, unpublished data). Introduced European eels also have been found living in the wild in Japan after they escaped or were released (Miyai et al. 2004; Okamura et al., In press).

Research efforts have been underway for years to artificially spawn and rear eel larvae so that the aquaculture industry will not have to rely on wild-caught glass eels. Because of the unusual physiology and feeding biology of leptocephalus larvae, progress has been quite slow and difficult. However, leptocephali have recently been reared through metamorphosis into glass eels and even into yellow eels in small numbers (Tanaka 2003; Kagawa et al. 2005), so there is still hope for revolutionizing the eel industry through artificial production.

Decline in Catches

Statistics about the resources of the Japanese eel are not widely available for many parts of its range, but catches appear to be decreasing in Japan. Catches of yellow and silver

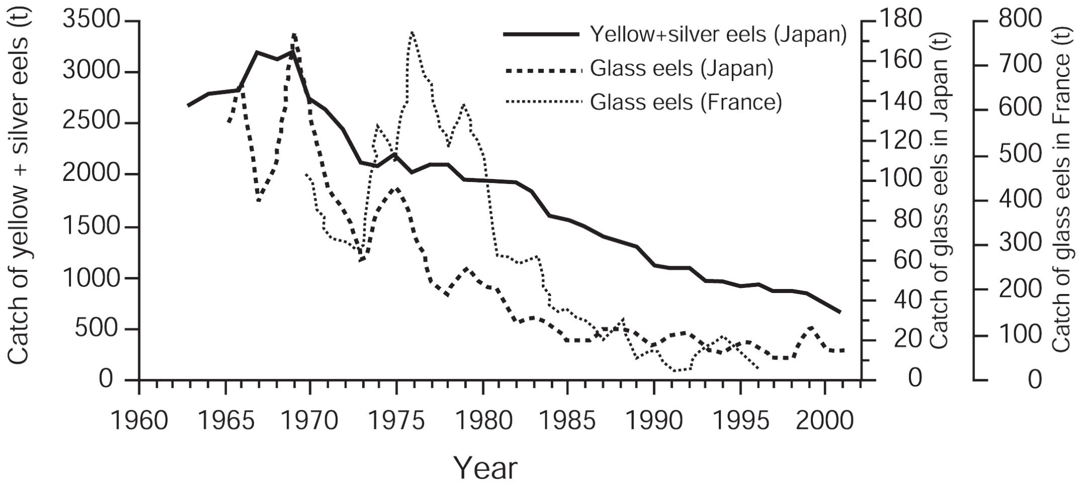

Figure 2. Historical eel catches in Japan and France, showing the catches of yellow and silver eels and glass eels of the Japanese eel in Japan, and catches of glass eels of the European eel at the estuary of the Loire River in France. Data for the Japanese eel were obtained from the Japan Fisheries Agency (Anonymous 2004).

eels in Japanese freshwater habitats decreased continuously from 1969 (3,194 mt) through 2001 (ca 677 mt) (Figure 2). Catches of glass eels in Japanese estuaries also decreased from a peak of 174 mt in 1969 to 14 mt in 2001. Other evidence, such as microsatellite analysis of temporal genetic variation of the Japanese eel, suggests that effective population size appears to be declining (Tseng et al. 2003a).

A similar decreasing trend has been seen for the glass eel fishery in France, which peaked in 1976 (770 mt) and then decreased to only 1% of that at present (Figure 2). This appears to reflect a general decrease in recruitment of the European eel since about 1976 (Dekker 2003), and similar declines have been observed for the American eel (Casselman 2003). The exact timing of the decrease of the Japanese eel in the Pacific seems to have been different from that of the European eel in the Atlantic. In addition, the magnitude of the resources was different: catches of European glass eels in France were approximately six times larger than those of Japanese eels. This suggests that mechanisms for population fluctuation between these species may be different or may be the same but over different time periods; thus, we need to determine the fluctuation mechanisms for each species.

Population Estimates

An important aspect to better understanding the population fluctuations of a heavily exploited species such as the Japanese eel is to begin to build a model for estimating overall population size. This is very difficult to do for the Japanese eel because there is relatively little quantitative data on regional stocks or on mortality of the various life history stages. However, to illustrate the types of data needed to build such a model, the tentative population model of Tsukamoto and Otake (1994) can be useful. This model shows the connectivity of the different stages of the total life history of the species, so if changes at one stage are thought to occur, the effects on the other stages can be predicted.

Based on an estimated 72 mt of glass eel catches by all East Asian countries in the 1994 fishing season, we roughly estimated the number of silver eels that successfully leave

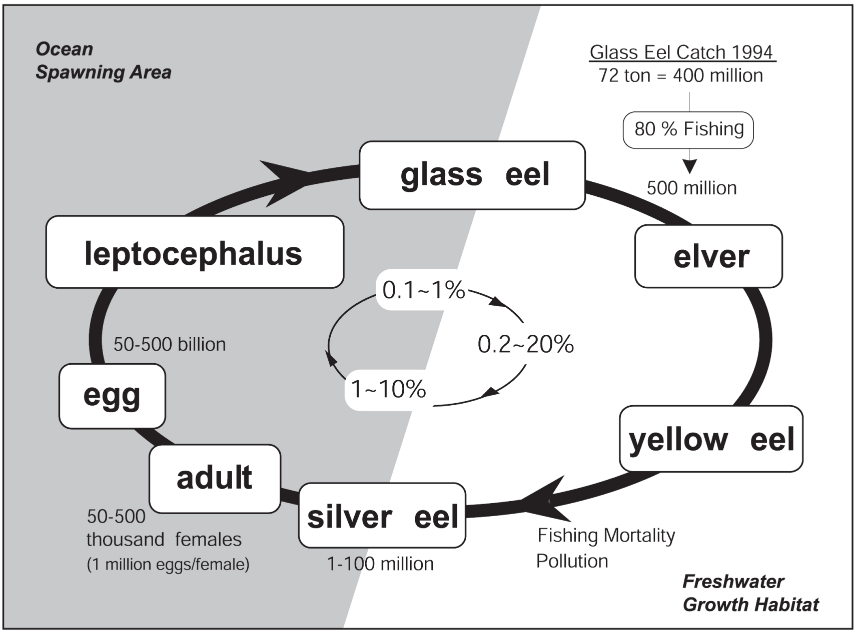

Figure 3. Population estimates for some developmental stages in the catadromous life history of the Japanese eel and estimates of mortality rates. Values in the center of the plot are possible survival rates during larval migration and the yellow and silver eel stages.

their growth habitats in East Asia (spawner escapement) and begin their migration to the spawning area (Figure 3, Tsukamoto and Otake 1994). Seventy-two mt is equivalent to about 400 million glass eels (5,500 fish/kg), so at least 500 million glass eels should have recruited to the estuaries of East Asia because of heavy exploitation of glass eels at estuaries. More than 80% of glass eel recruitment may be caught at estuaries in Japan (Tsukamoto and Otake 1994), and a similar estimate of 85% has been made for exploitation of glass eels in Europe (Dekker 2003). Assuming a 0.1% to 1.0% survival rate during larval migration from the spawning area to estuaries, 50 to 500 billion eggs should have been spawned; this number is equivalent to about 50,000 to 500,000 females (at 1 million eggs per female). Thus, silver eels that escape from growth habitats in East Asia were estimated to be 1 million to 100 million by assuming a roughly 1:1 sex ratio and a 1% to 10% survival rate during the spawning migration. This estimation may be useful as a starting point for further detailed population estimates and a quantitative ecological approach to mortality rates during each developmental stage, which have so far only been hypothesized.

Possible Reasons for Decline

When discussing population fluctuations, it is helpful to separate resource trends into three different time scales: short-, mid-, and long-term. Short-term changes are annual to several-year variations in recruitment caused by changes of climate or ocean-atmosphere events such as El Niño, while mid-term changes occur over 10 to hundreds of years and include events such as regime shifts or global warming. Long-term changes refer to an extremely long fluctuation, including extinction caused by long geological events such as glacial cycles or continental drift.

Fluctuations shown in most data sets (Figure 2) are likely a mixture of the first two time-scale changes due to the relatively short time periods for which data are available.

Three major factors are possible causes for the population decrease of the Japanese eel: (1) overfishing, (2) environmental destruction in freshwater habitats, and (3) environmental fluctuations in oceanic habitats. The first and second factors are derived from anthropogenic effects. Overfishing is obviously a major factor for population decrease, since most of the glass eels each year that have recruited to estuaries in East Asia (60–80% or more) have been caught before growing into yellow eels (e.g., Tzeng 1984). Human impacts such as pollution and construction of river channelization structures and dams have drastically decreased freshwater habitat for eels (Tatsukawa 2003), as well as reducing prey in the affected river communities. These human impacts may cause short- or mid-term fluctuations in eel resources. The third type of possible causes are short- or mid-term environmental fluctuations in the ocean, which could include changes in food available to the leptocephali or changes in oceanographic conditions affecting the transport of leptocephali to their recruitment areas (Kimura et al. 2001; Knights 2003; Friedland 2007), as is discussed later.

Factors Affecting Population Fluctuation

Spawning Area

The offshore spawning area of freshwater eels is both the end and the beginning of their life cycle, and thus the location and number of spawning areas of a species has a significant influence on their recruitment success, population fluctuations, and population structure. Recently, the spawning area of the Japanese eel has been identified as a relatively small area in the North Equatorial Current to the west of Guam (Figure 4; Tsukamoto 1992, 2006; Tsukamoto et al. 2003; Ishikawa et al. 2001b). This is in contrast to the vast region previously estimated for the spawning area of Atlantic eels in the Sargasso Sea, which spreads over more than one million square km (about 20 to 30°N, 48 to 79°W; McCleave et al. 1987), and is also in contrast to the local spawning areas of some tropical anguillids in the Indonesian Seas region (Aoyama et al. 2003).

The spawning area of the Japanese eel in the North Equatorial Current appears to be south of a salinity front in the region, but it is also near three seamounts in the West Mariana Ridge (15°N, 142 to 143°E), which, based on the distribution of leptocephali, have been hypothesized to be associated with the spawning area (Figure 4, seamount hypothesis; Tsukamoto et al. 2003). These seamounts are located about 200 km northwest of the Mariana Islands (Guam) along the northern margin of the unbroken westward flow of the north equatorial current and may serve as landmarks by providing olfactory or geomagnetic cues to migrating eels that help define the spawning area.

Although tiny preleptocephali 4–6 mm TL have been collected recently (Tsukamoto 2006), for a more precise determination of the spawning site, we need to collect eggs or observe adults spawning. This challenge will be helped by the new moon hypothesis, which resulted from otolith analyses of leptocephali (Tsukamoto 1996; Tsukamoto et al. 2003). These data indicate that the Japanese eel does not spawn continuously throughout the long spawning season from April to November (Tsukamoto 1990), but may spawn periodically once a month during the new moon. This knowledge will allow sampling for eggs and spawning eels to be more concentrated during new moon periods.

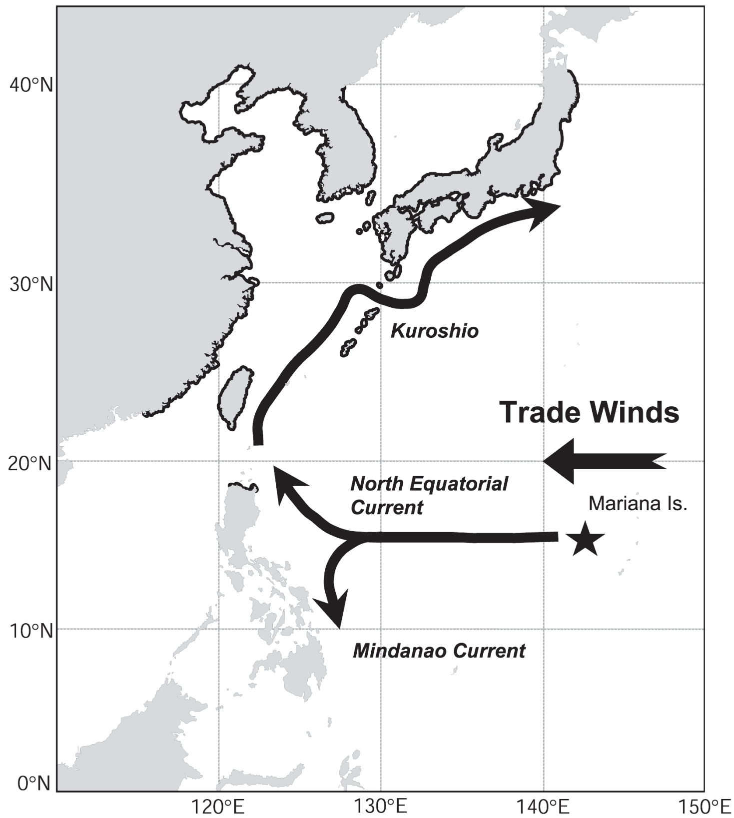

Figure 4. Estimated spawning area of the Japanese eel (closed star), and the major current systems affecting larval transport. Thick black lines on the coastlines of East Asia show the range of the Japanese eel.

Oceanographic Conditions

The success of the larval migration of Japanese eel leptocephali from their offshore spawning area to their growth habitats in East Asia may be one of the key factors affecting yearly recruitment. They must move westward and metamorphose into glass eels in the Kuroshio Current system before recruiting to coastal waters and estuaries (Figure 4). In typical years, many leptocephali may be found within a strong current zone on the southern side of an east-to-west salinity front (34.6 psu) that is normally present at the northern margin of the North Equatorial Current at about 16°N (Kimura et al. 1994, 2001), because in 1991, the largest catches of leptocephali were made just south of this front (Tsukamoto 1992).

This transport of leptocephali along the northern margin of the North Equatorial Current may be important in the recruitment success of leptocephali, because they must avoid southward transport into the Mindanao Current, which would cause recruitment failure (Kimura et al. 1994). At the end of their larval migration, the leptocephali must become entrained into the northward-flowing branch that flows into the Kuroshio Current in the bifurcation zone of the North Equatorial Current (Figure 4), around 127°E (Toole et al. 1990). This is particularly important because the North Equatorial Current also has a southward-flowing branch that becomes the Mindanao Current (Lukas et al. 1991).

One mechanism that has been proposed to help ensure that leptocephali entrain into the northward flow is that when they reach a certain large size as they approach the bifurcation zone, they develop a diel vertical migration into the Ekman layer. This increased northward Ekman transport is driven by the trade winds and has been proposed to be a key factor facilitating the transfer of leptocephali from the North Equatorial Current into the Kuroshio for successful recruitment to East Asia (Kimura et al. 1994). Therefore, disruptions in the trade winds could result in southward transport, or excessive northward Ekman transport might result in entrainment into the eddy of the Kuroshio countercurrent at about 20 to 24°N, which could also result in unsuccessful transport to East Asia.

Other environmental factors such as ENSO events (El Niño) have also been proposed as affecting the transport of Japanese eel leptocephali. The latitude of the westward flow south of the salinity front appears to shift among years and be influenced by El Niño, which may also affect recruitment of glass eels to East Asia (Kimura et al. 2001; Kimura 2003; Kimura and Tsukamoto 2006). This type of disruption would be caused by a southward shift of the salinity front, which could cause a greater proportion of leptocephali to be entrained into the southward flow of the Mindanao Current. This hypothesis has been supported by a correlation between years with poor glass eel recruitment and El Niño years as expressed by the Southern Oscillation Index (Kimura et al. 2001). Recently the first direct evidence that some leptocephali are transported southward by the Mindanao Current has been obtained as a result of the collection of a 42.8 mm Japanese eel leptocephalus in the Celebes Sea, which has an inflow of water from the Mindanao current (Miller et al., unpublished manuscript).

Sea Eels

New information about habitat use by species such as the Japanese eel has indicated that the freshwater environment may not be the only growth habitat that is important for the health of eel populations. Although freshwater eels have been generally believed to migrate upstream after recruitment to estuaries, recent studies based on otolith strontium and calcium ratios have shown that in some areas, many individuals remain in estuaries or even in marine coastal areas. This discovery of non-catadromous individuals (residents), termed "sea eels," which spend all their life in marine habitat without entering freshwater (Tsukamoto et al. 1998; Tsukamoto and Arai 2001), in addition to the normal catadromous individuals ("river eels"), has shown that there is considerable plasticity in the migratory behavior of freshwater eels (Daverat et al. 2006). An intermediate type of migratory pattern used by eels that inhabit estuaries or move between estuarine and freshwater habitats also has been found, and individuals exhibiting this pattern were termed "estuarine eels" (Tsukamoto and Arai 2001).

Factors affecting the occurrence of eels that don't move into freshwater are not known, but the phenomenon appears to be quite widespread among temperate eels in some areas. The occurrence of sea eels and estuarine eels in temperate areas has been reported in the Japanese eel (Tsukamoto et al. 1998; Tsukamoto and Arai 2001; Tzeng et al. 2002, 2003; Kotake et al. 2003, 2005), European eel (Tsukamoto et al. 1998; Tzeng et al. 2000; Daverat et al. 2006), the American eel (Jessop et al. 2002, 2004), and New Zealand eels (Arai et al. 2004). However, the distribution of the three types of migratory patterns may vary among localities and species, because a latitudinal cline has been suggested in the occurrence of sea eels along the Japanese coast (Figure 5, Kotake 2003). Tsukamoto and Arai (2001) hypothesized that more sea eels would occur in species that are distributed at higher latitudes, where food is more available in the marine environment than in the nutrient-poor stream and small river freshwater habitats, and proposed that sea eels may be an eco-phenotype that uses an ancient type of behavior of anguillid eels. As a mirror image to sea eels of the catadromous freshwater eels, anadromous salmonids have river residents or land-locked populations (Tsukamoto et al. 2002).

These new findings on the presence of sea eels may be important enough for species such as the Japanese eel that the common understanding of their life histories may change and stock management plans would be affected. Some indication of this was found recently when the proportion of river eels among 500 silver eels collected around the Japanese coast as they were migrating back to their spawning area was estimated as only 16% (Kotake 2003). This proportion was unexpectedly small, suggesting that the contribution to the next generation by river eels may be smaller than by other migratory types in some areas of Japan. It is unclear whether this is a typical historical proportion for some areas of Japan or if recent human impacts in

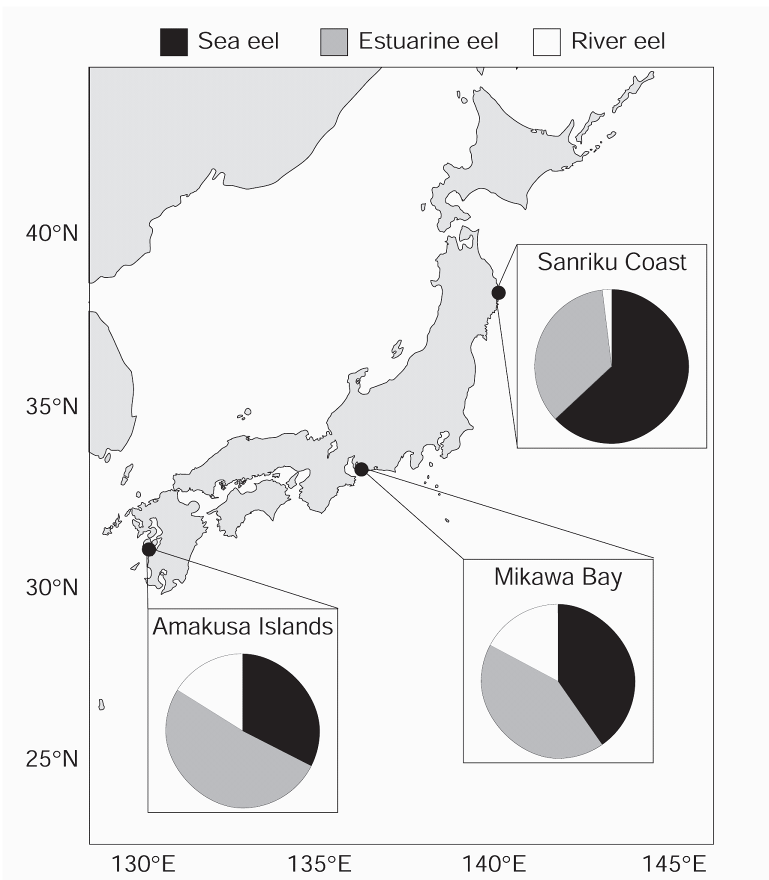

Figure 5. Proportion of the three different migratory types of the Japanese eel at three sampling sites along the Japanese coast. Each type of eel was categorized as being either a sea eel, an estuarine eel, or a river eel, based on otolith Sr:Ca ratios (sample sizes: Amakusa Islands, 37; Mikawa Bay, 199; and Sanriku Coast, 47).

freshwater and estuarine habitats have caused the low number of river eels in these samples. Similar detailed studies are urgently needed in other East Asian coastal waters around Taiwan, China, and Korea to estimate the overall proportion of migratory types in the Japanese eel.

Population Structure

Knowledge about the population structure of anguillid eels is also important for better management of eel resources. The exact nature of the population structure of temperate species such as Japanese and Atlantic eels has been the subject of considerable debate because of their long-distance spawning migrations and unique catadromous life histories (see Avise 2003). For the Japanese eel, mtDNA analysis showed no geographic difference in genetic composition of individuals from all over their range in East Asia, suggesting that it has a panmictic population structure (Sang et al. 1994; Ishikawa et al. 2001a). However, Chan et al. (1997) reported that an allozyme analysis indicated a geographic cline in allele frequency at some loci in glass eels and suggested some genetic heterogeneity among populations. A similar discrepancy was observed in the American eel when an mtDNA analysis suggested a single population (Avise et al. 1986), while a geographic cline was found at a few allozyme loci (Williams et al. 1973; Koehn and Williams 1978). It was assumed that these geographic clines detected by allozyme analysis might be derived from natural selection within the single generation after hatching (Nishida 2001).

New techniques using nuclear DNA markers of microsatellite loci have also found variable results in population studies of anguillid eels. For example, the Wirth and Bernatchez (2001) study on the European eel and a study using microsatellite loci suggested the presence of genetic heterogeneity over the range of the Japanese eel (Tseng et al. 2003b, 2006, 2009, this volume). However, a more extensive study of the European eel that used the same techniques found no evidence of population structure (Dannewitz et al. 2005), and no evidence of population structure was found recently using microsatellite loci in the American eel (Wirth and Bernatchez 2003). These recent microsatellite studies may need to be interpreted with caution, however, because other research on Atlantic eels has suggested that the molecular evolutionary nature of these microsatellite loci may not always be easy to interpret (Mank and Avise 2003).

Regardless of the significance of various studies on population structure of anguillid eels, all found remarkably low levels of genetic variation compared with studies of other marine species (Avise 2003). This may be due in part to the influence of other factors such as single spawning areas, ocean current variability, or the effect of variable growth rates during the leptocephalus stage on regulating the timing of metamorphosis (Kuroki et al. 2006a), which, in the case of the Japanese eel, could determine the timing of detrainment from the Kuroshio and therefore the region of recruitment in East Asia (Tsukamoto and Umezawa 1990).

Future Perspectives

It is likely that overfishing and habitat loss have had a major role in the overall decline of stocks of the Japanese eel, but recent research is beginning to suggest that the important factors that affect short-term population fluctuations may be hidden in the ocean. In fact, this may be more so for the Japanese eel than for most other anguillid species because of the precarious position of its spawning area, which is within a current that bifurcates into two completely different directions. Of course, we cannot manipulate events that occur far offshore or longer-term ocean-atmosphere changes, but building a greater understanding of the mechanisms of population fluctuation is important for the conservation of this species even if they are beyond our control. In contrast, human impacts such as overfishing of glass and silver eels and destruction of river environments can be reduced to conserve eel resources, and the potential influence of these factors urgently needs to be evaluated in East Asia.

For conservation of Japanese eels, attention also must be focused on international trade of the species (Figure 1), and international management plans need to be developed in cooperation with all four East Asian countries. Five years ago, we established a nongovernmental organization called the East Asia Eel Consortium (EASEC), in which scientists and eel traders of the four East Asian countries discuss issues related to the Japanese eel and work toward the conservation and sustainable use of this shared resource. These and other recent efforts indicate the beginning of what we hope will be a new era of research on the resources of the Japanese eel that can bring together knowledge from both science and industry to ensure the survival of this remarkable fish.

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