

Seasonal variation in the migratory history of the Japanese eel *Anguilla japonica* in Mikawa Bay, Japan

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ABSTRACT: The seasonal variation in the migratory history and biological characteristics of Japanese eels *Anguilla japonica* was examined using 554 eels collected with set nets that were fished all year in Mikawa Bay from May 2000 to April 2002. The largest catches occurred in November and December of both years and consisted mostly of female silver eels (71.2%) with relatively high gonadosomatic index (GSI) values (0.4 to 4.3) that were beginning their spawning migration. Otolith strontium and calcium concentrations of 176 females and 23 males, measured by X-ray electron microprobe analysis, indicated that 40% of the eels were categorized as 'sea eels', which may never have migrated into freshwater throughout their life history, 43% were 'estuarine eels', which stayed in the estuary or frequently moved between freshwater and marine habitats, and 17% were 'river eels', which showed a typical catadromous migration. River eels occurred only in autumn and early winter during the spawning migration season, but at least a few sea eels or estuarine eels occurred throughout the year, with their numbers increasing dramatically in November and December. There were no major differences in the size or age among the different migratory types of eels, but the growth rates of both sexes appeared to be slightly lower in freshwater. These findings show that river, estuarine, and sea eels begin their migration out of Mikawa Bay toward the open ocean at about the same time, and that the estuarine and brackish water habitats of Mikawa Bay appear to be producing the majority of spawning migrants in this area.

KEY WORDS: *Anguilla japonica* · Migratory history · Otolith Sr:Ca ratio · Age · Growth · Reproductive maturation · Seasonal variation

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INTRODUCTION

The Japanese eel *Anguilla japonica* is widely distributed in East Asia from Taiwan, through China, Korea and in the northern part of Japan (Tesch 1977). This species performs a spectacular migration of thousands of kilometers between its freshwater and estuarine habitats, and its offshore spawning area to the west of the Mariana Islands in the western North Pacific (Tsukamoto 1992). *A. japonica* leptocephali drift from the spawning area toward the coastal waters of East Asia in the North Equatorial and the Kuroshio currents and then metamorphose into glass eels and begin their

inshore migration (Tsukamoto & Umezawa 1990). The glass eels start to become pigmented elvers when they enter estuaries. In general, large numbers of elvers typically migrate up freshwater streams and rivers or enter lakes, where they become yellow eels. After 5 to 15 yr of this yellow eel growth phase, they metamorphose into the silver eel stage, with mature gonads and enlarged eyes, and they move back downstream to the ocean and begin their migration to the spawning area.

The Japanese eel is an important commercial species, and there have been many studies on its early life history characteristics, such as on larval growth, larval duration, metamorphosis, and recruitment, that have

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provided valuable information on the leptocephalus and glass eel stages of this species (see Tsukamoto 1990, 1992, Tsukamoto & Umezawa 1990, Tzeng 1990, Cheng & Tzeng 1996, Arai et al. 1997). However, there is a general lack of knowledge about the age, growth, maturation, and migration of the silver eels that leave their juvenile habitats in East Asia and migrate towards the offshore spawning area. Some recent studies have been done on the environmental triggers of migration, ovarian morphology, and Sr:Ca ratios of silver eels in Mikawa Bay, Japan (Okamura et al. 2002, Tzeng et al. 2003a, Utoh et al. 2004), on the occurrence of silver eels in the East China Sea (Sasai et al. 2001), and the growth rates (Tzeng et al. 2003b) and morphology (Han et al. 2003) of silver eels. However, basic studies on many aspects of the ecology and reproductive migration of the Japanese eel are still lacking compared to other anguillid species such as the Atlantic eels.

Recent studies using otolith strontium (Sr) and calcium (Ca) ratio analysis have provided valuable new information about the apparent habitat use of yellow and silver phase Japanese eels and have revealed a previously unknown complexity in the migratory history of this species. Tsukamoto et al. (1998) used otolith Sr:Ca ratio analysis to show that yellow and silver eels of both the Japanese eel and the European eel *Anguilla anguilla* caught in marine areas adjacent to their typical freshwater habitats had never migrated into freshwater but instead had spent their entire lives in the ocean. Tsukamoto & Arai (2001) used these Sr:Ca ratios to divide the migratory histories of Japanese eels collected in Japanese coastal waters into 3 migratory types: (1) 'sea eels', (2) 'estuarine eels' (stayed in the estuary or frequently moved between freshwater and marine habitats), and (3) 'river eels' (a typical catadromous migration). These same 3 general types have also been detected among Japanese eels in Taiwan (Tzeng et al. 2002), and some differences in the sex ratios of individuals of the different migratory types have been detected in eels in a coastal area of southern Japan (Kotake et al. 2003). Furthermore, other temperate anguillid species, such as the European eel *A. anguilla* (Tsukamoto et al. 1998), and the New Zealand eels *A. australis* and *A. dieffenbachii* (Arai et al. 2004), were found to have some individuals that skipped the freshwater phase after recruitment to coastal waters and remained in the sea or brackish water until the silver eel stage.

While these studies have established that there is considerable variation in the habitat use of northern temperate anguillid eels, they give rise to many questions about what factors affect the decision of glass eels to enter freshwater or to remain in estuarine or coastal waters, or what causes eels to switch from one habitat

to another during their life. Other biological questions relate to how the process of sexual maturation may differ between eels living in freshwater or marine habitats and whether the timing of migration is the same among different habitats. Such questions are of critical importance in understanding the ecological aspects of the growth phase and sexual maturation of temperate anguillid eels, which are experiencing drastic population declines in some areas, thus causing serious concerns among scientists (see Dekker et al. 2003).

The present study was designed to address this lack of knowledge about the life history and migratory behavior of the Japanese eel by comparing the biological and otolith characteristics of a large sample of eels collected over a 2 yr period in Mikawa Bay, Japan. Okamura et al. (2002) reported that the fine-scale timing of migration of the silver eels captured in set nets in Mikawa Bay in the autumn appeared to be related to low pressure systems moving over Japan. The ovarian morphology of these migrating silver eels has also been documented over a 4 yr period (Utoh et al. 2004). However, the age, growth, and migratory history of eels collected at different times of year in Mikawa Bay have not been examined. The primary objectives of this study were: (1) to determine the seasonality of movement or migration of each migratory type in relation to their levels of reproductive maturation throughout the year, and (2) to determine the age and growth rates of each migratory type to gain a greater understanding of the habitat use and migratory behavior of Japanese eels in the Mikawa Bay area.

MATERIALS AND METHODS

Sampling site. The eels examined in this study were collected near the southern shore of Mikawa Bay, which is located in Aichi Prefecture along the east coast of central Japan, (34°N, 137°E, Fig. 1). Mikawa Bay has an area of about 200 km² with a mean depth of about 12 m, and about 20 inflowing streams, including 2 rivers (the Toyo and Yahagi Rivers). Monthly data on seawater temperature in Mikawa Bay and river water temperature in the Toyo River (from 30 km upstream from its mouth) were obtained from the Aichi Fisheries Research Station. The surface seawater temperature in the bay and the river water temperature in the Toyo River were highest in July or August and lowest in January each year (Fig. 2). The salinity in Mikawa Bay ranged from 29.4 to 32.5 psu.

Collection and morphological measurements. Eels were collected with set nets (3 cm mesh) in Mikawa Bay for 2 yr from May 2000 to April 2002. These eels were identified to be Japanese eels on the basis of their morphological characteristics, and a few eels suspected to

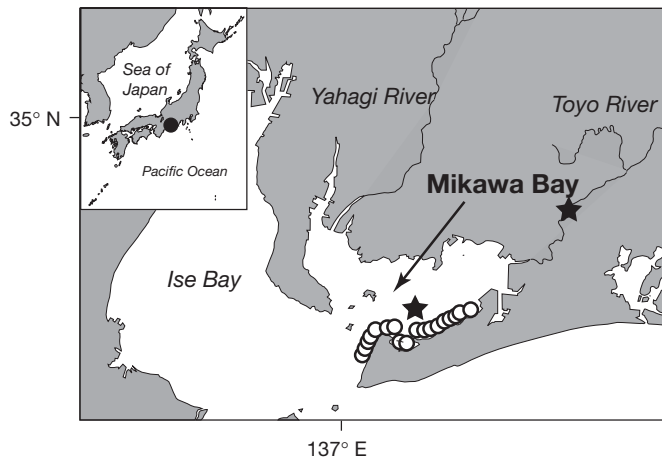


Fig. 1. Map of the sampling area in Mikawa Bay in Aichi Prefecture along the east coast of Japan. Locations of the set nets used to capture eels (O), and the stations for measuring water temperature in the bay and in the Toyo River (★) are shown

be European eels were cross-checked using the molecular genetic technique PCR-RFLP (polymerase chain reaction-restriction fragment length polymorphism) according to the criteria of Zhang et al. (1999), because there were reports that European eels had been collected in this bay (Zhang et al. 1999, Okamura et al. 2002). The fishing gear was set at depths of 2 to 3 m, approximately 50 m from the shoreline, and was set at dawn; the eels were recovered the next morning. A total of 506 Japanese eels (24 males and 482 females) were collected during the duration of the study.

The total length (TL) of each eel was measured to the nearest 1 mm, the skin color was observed to help in categorization as either yellow or silver eels, and sex was determined by examining the gonads. Gonad weight (GW, to 0.01 g) and body weight (BW, to 0.1 g) were measured to determine the gonadosomatic index (GSI), which was calculated as follows: $GSI = \text{gonad weight (g)} / \text{BW (g)} \times 100$. GSI values were not obtained for a few individuals because they were used in other studies that prevented examination of their gonads.

Otolith preparation. A total of 198 eels were used for otolith examination. These included all 54 females collected from May to October and January to April 2000–2002, 121 females collected in November and December 2000–2001 that were randomly selected each month, and all but 1 of the 24 males collected during the study period. The extracted otoliths were embedded in epoxy resin (Struers, Epofix) and ground to expose the core along the anterior-posterior direction in the frontal plane using a grinding machine equipped with a diamond cup-wheel (Struers, Disco-plan-TS). They were further polished with OP-S liquid

(Struers), cleaned using distilled water and ethanol, and dried at 50°C in an oven prior to examination. The 'radius' of the elver mark (the longest distance from the otolith core to the elver mark) was measured on light microscope photographs.

Otolith X-ray microprobe analysis. For electron microscope analysis, otoliths were Pt-Pd-coated by a high vacuum evaporator. These otoliths were used for 'life-history transect' analysis of Sr and Ca concentrations, which were measured in a line along the longest axis of each otolith from the core to the edge using a wavelength-dispersive X-ray electron microprobe (JEOL JXA-8900R) as described in Tsukamoto & Arai (2001). CaSiO_3 and SrTiO_3 were used as standards. The accelerating voltage and beam current were 15 kV and 12 nA, respectively. The electron beam was focused on a point 10 μm in diameter, with measurements spaced at 10 μm intervals.

Tsukamoto & Arai (2001) determined the migratory patterns of Japanese eels using the otolith Sr:Ca ratios outside the 'high Sr core', which corresponded to the period of ocean life during leptocephalus and the early glass eel stages (Otake et al. 1994, Arai et al. 1997, Tsukamoto & Arai 2001). In accordance with the criteria of Tsukamoto & Arai (2001), we omitted the high Sr core (mean: 150 μm radius from otolith core), and only values outside the high Sr core were used to obtain a mean otolith Sr:Ca ratio for each specimen. We then grouped these specimens into the general categories 'sea eels' ($\text{Sr:Ca} \geq 6.0 \times 10^{-3}$), 'estuarine eels' ($2.5 \times 10^{-3} \leq \text{Sr:Ca} < 6.0 \times 10^{-3}$) and 'river eels' ($\text{Sr:Ca} < 2.5 \times 10^{-3}$), using their mean otolith Sr:Ca ratios to enable statistical comparisons to be made between eels with different habitat use histories. We realize that many individuals in the estuarine eel category may have moved between freshwater and marine habitats during their yellow eel phase. The detailed individual variations in

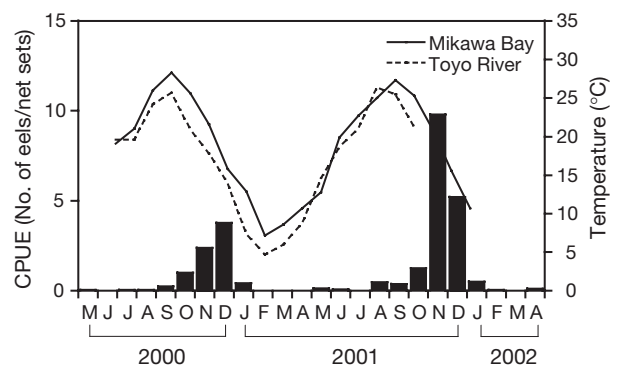


Fig. 2. *Anguilla japonica*. Monthly catch per unit effort (CPUE) of Japanese eels in set nets in Mikawa Bay from May 2000 to April 2002 (bar graph), and the seasonal seawater and freshwater temperature changes in Mikawa Bay and the Toyo River (lines)

Table 1. *Anguilla japonica*. Morphological characteristics of female and male eels collected from Mikawa Bay, Japan

	Mean ± SD	Range	n
Total length (cm)			
Total			
Female	71.7 ± 8.1	(47.2–104.0)	482
Male	54.5 ± 6.0	(41.2–66.3)	24
Sea eel			
Female	70.7 ± 6.9	(54.4–86.1)	77
Male	61.3 ± 3.0	(58.5–64.4)	3
Estuarine eel			
Female	70.4 ± 9.6	(48.8–97.2)	75
Male	55.0 ± 5.5	(44.6–66.3)	10
River eel			
Female	71.3 ± 11.2	(47.2–89.0)	23
Male	51.9 ± 5.9	(41.2–60.0)	10
Body weight (g)			
Total			
Female	587 ± 223	(129–1685)	482
Male	232 ± 81	(100–412)	24
Sea eel			
Female	551 ± 193	(198–1037)	77
Male	324 ± 81	(252–412)	3
Estuarine eel			
Female	565 ± 270	(129–1384)	75
Male	226 ± 65	(100–355)	10
River eel			
Female	597 ± 259	(140–1187)	23
Male	202 ± 65	(100–324)	10
Gonadosomatic index			
Total			
Female	2.1 ± 0.9	(0.2–4.3)	236
Male	0.2 ± 0.2	(0.0–0.4)	12
Sea eel			
Female	1.8 ± 0.9	(0.3–3.1)	48
Male	–	(0.4)	1
Estuarine eel			
Female	1.9 ± 1.0	(0.2–3.5)	47
Male	0.3 ± 0.1	(0.2–0.4)	5
River eel			
Female	2.9 ± 1.0	(0.9–4.3)	17
Male	0.2 ± 0.2	(0.0–0.4)	6
Age (yr)			
Total			
Female	7.8 ± 1.9	(4–17)	171
Male	6.9 ± 1.7	(4–10)	21
Sea eel			
Female	7.8 ± 1.6	(4–12)	73
Male	7.0 ± 1.7	(6–9)	3
Estuarine eel			
Female	7.6 ± 1.9	(4–14)	74
Male	6.7 ± 1.8	(4–10)	10
River eel			
Female	8.3 ± 2.8	(5–17)	24
Male	7.0 ± 1.6	(4–9)	8
Growth rate (cm yr⁻¹)			
Total			
Female	8.7 ± 2.1	(4.1–14.7)	171
Male	7.5 ± 2.1	(4.7–12.3)	21
Sea eel			
Female	8.7 ± 2.1	(4.8–14.7)	73
Male	8.2 ± 1.9	(6.1–9.7)	3
Estuarine eel			
Female	8.9 ± 2.1	(4.1–14.5)	74
Male	7.8 ± 2.1	(4.7–12.1)	10
River eel			
Female	8.1 ± 2.1	(4.8–13.9)	24
Male	7.0 ± 2.4	(5.0–12.3)	8

their otolith Sr:Ca ratios and the apparent habitat use patterns of these eels will be reported elsewhere.

Age and growth. Following the electron microprobe analysis, the otoliths were repolished to remove the coating, etched with 1% HCl, and thereafter stained with 1% toluidine blue. The age of specimens was determined by counting the number of blue-stained transparent zones outside the elver mark, following the method of Nagieć & Bahnsawy (1990). GR was calculated as follows: $GR = (TL - 6.0)/Age$, where 6.0 is the mean length (cm) of glass eels when they recruit to estuaries (Tsukamoto 1990).

RESULTS

Seasonal pattern of occurrence and morphological characteristics

Monthly catches of eels in Mikawa Bay increased from October to December during both years, with peaks in December 2000 and November 2001. Catches decreased greatly in January and there were at least a few eels caught in each month during at least 1 of the years, except for March (Fig. 2). Most eels collected from October to February were silver eels, while those from April to September were apparently yellow eels. Females were predominant and comprised 95% of the catch ($n = 482$), while males comprised only 5% ($n = 24$). A total of 497 females and males (90%) were collected only in 3 months (October, November and December), and males were only collected during this period each year.

Female eels showed typical larger body sizes than male eels (Table 1, Fig. 3). The TL of females ranged from 47.2 to 104.0 cm, with a mean ± SD of $71.7 ± 8.1$ cm. The TL of males ranged from 41.2 to 66.3 cm, with a mean of $54.5 ± 6.0$ cm. The BW of females ranged from 129 to 1685 g, with a mean of $587 ± 222$ g and that of males from 100 to 412 g, with a mean of $232 ± 81$ g. Consistent with other species of anguillid eels (Burnet 1969, Todd 1981, Vøllestad 1992, Poole & Reynolds 1996, Krueger & Oliveira 1997), the females collected during this study were significantly larger in both TL and BW than the male eels (Mann-Whitney *U*-test, $p < 0.001$). Most eels collected from October to February were silver eels, while those of from April to September were apparently yellow eels, and the body size of females collected from October to December ($n = 428$, TL: 47.2 to 104 cm, BW: 129 to 1685 g) was significantly larger than that of females collected from January to September ($n = 54$, TL: 52.9 to 90.0 cm, BW: 202 to 1224 g, Mann-Whitney *U*-test, $p < 0.001$), because most females collected from January to September were less than about 75 cm (Fig. 3).

The GSI values of females changed seasonally and were much higher than in males. For females, the lowest value (0.2) occurred in August 2001 and in both years, the GSI values increased markedly in either October or November, with the highest values occurring in November of each year (mean \pm SD: 2.1 ± 0.9 , Fig. 3). The GSI values of females collected from October to December (0.3 to 4.3) were significantly higher than those of females collected from January to September, when the catches were lower (0.1 to 4.0, Mann-Whitney *U*-test, $p < 0.001$). The GSI of males ranged from 0.0 to 0.4, with a mean of 0.2 ± 0.2 , and their GSI values were significantly lower than those of females (Mann-Whitney *U*-test, $p < 0.001$, Fig. 3).

Age and growth

Examinations of the annuli in the otoliths of the eels caught in Mikawa Bay indicated that the females reached greater ages than the males. The age of females ranged from 4 to 17 yr with a mean \pm SD of 7.8 ± 1.9 yr ($n = 171$, Table 1) and their GR ranged from 4.1 to 14.7 cm yr^{-1} , with a mean of $8.7 \pm 2.1 \text{ cm yr}^{-1}$. The ages of males ranged from 4 to 10 yr with a mean of 6.9 ± 1.7 yr ($n = 21$), and their GR ranged from 4.7 to 12.3 cm yr^{-1} , with a mean of $7.5 \pm 2.1 \text{ yr}$ (Table 1). Females were significantly older than males (Mann-Whitney *U*-test, $p > 0.05$), and the GR of females was significantly higher than that of males (Mann-Whitney *U*-test, $p < 0.001$). Females collected from October to December ($n = 132$, mean = 7.9 yr) were significantly older than females collected from January to September (7.1 yr, Mann-Whitney *U*-test, $p > 0.001$), but there were no significant differences in the GR between females collected from October to December (8.4 cm yr^{-1}) and those collected from January to September (8.5 cm yr^{-1} , Mann-Whitney *U*-test, $p > 0.05$).

Migratory type and differences in biological characteristics

The Sr:Ca ratios of all otoliths had a peak of high values at the center of the otolith inside the elver mark (high Sr core, see Fig. 4). The actual radius of the high Sr core ranged from 121.5 to 169.2 μm with a mean \pm SD of $141.3 \pm 8.5 \mu\text{m}$. The mean Sr:Ca ratio values that were measured starting at 150 μm outside the core ranged from 1.0 to 8.5×10^3 . In some specimens that may have remained in habitats with a relatively constant salinity, the Sr:Ca ratios outside the core remained within similar ranges throughout the otolith, as shown in Fig. 4, but in other specimens there were greater variations, which indicated that those indi-

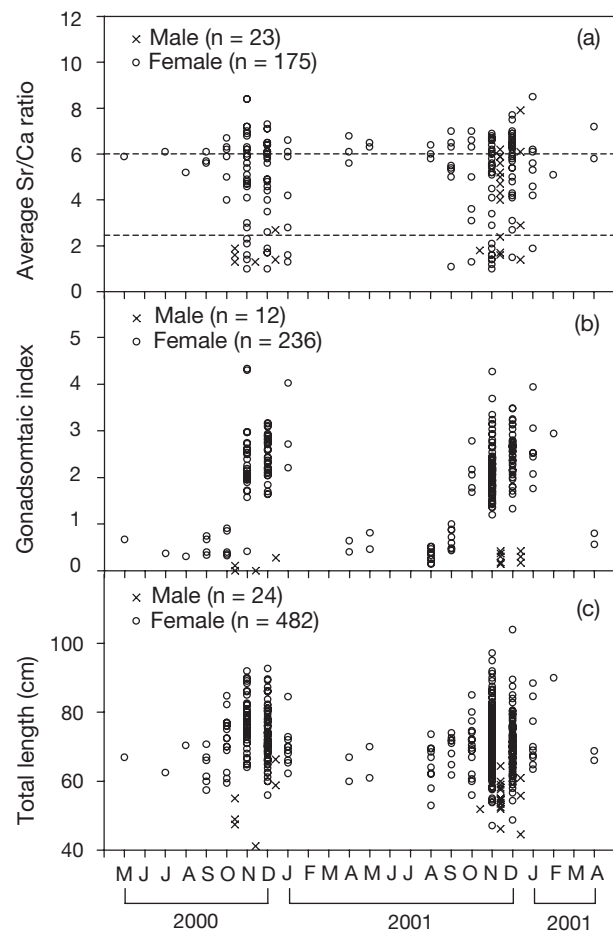


Fig. 3. *Anguilla japonica*. Plots of the (a) average Sr:Ca ratio outside the central core in the otoliths, (b) gonadosomatic index, and (c) total length of the male and female Japanese eels caught each month in set nets in Mikawa Bay from May 2000 to April 2002. Values of the Sr:Ca ratio used to separate each eel into the general categories of river (lowest values), estuarine and sea eels (highest values) are shown by the dotted lines in (a)

viduals had experienced different salinities, probably as a result of moving between different habitats (not shown).

The mean Sr:Ca ratios in the otoliths of 198 eels indicated that estuarine eels were the most abundant (43%, $n = 85$) of the 3 migratory types, sea eels were second most abundant (40%, $n = 80$) and 'river eels' accounted for only 17% ($n = 33$) (Fig. 5). The migratory type of male eel was mainly river eels (43%) and estuarine eels (43%), with only 3 specimens of sea eels (13%). In contrast, the migratory type of females was almost equal between sea eels (44%) and estuarine eels (43%), with a lower percentage of river eels (13%). Of the female eels collected from October to December, sea eels were the most abundant (45%) of the 3 migratory types, estuarine eels were second most abundant (41%) and river eels accounted for only

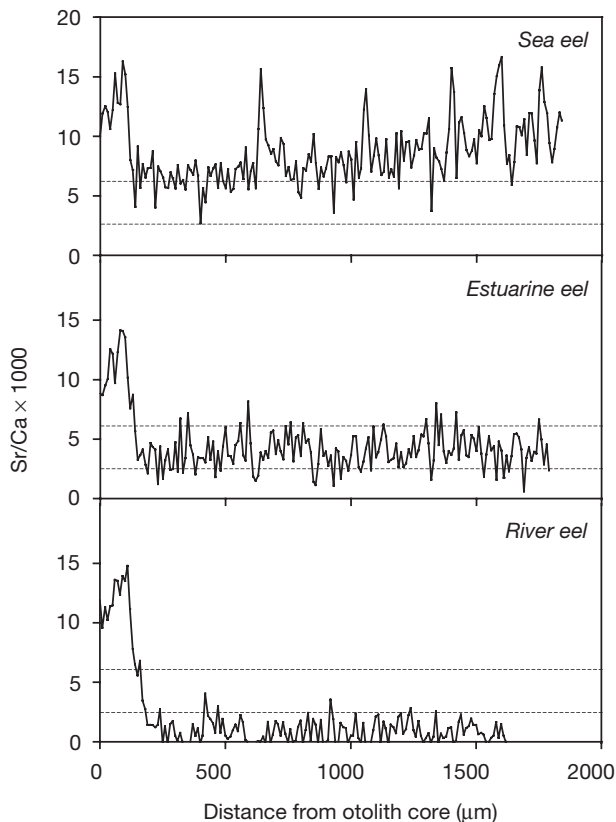


Fig. 4. *Anguilla japonica*. Typical patterns of otolith Sr:Ca ratios along line transects from the core to the edge of sagittal otoliths of 3 eels collected in Mikawa Bay. Each specimen of this study was classified into 1 of these 3 general migratory categories based on the average Sr:Ca outside the central 150 μm in the core of their otolith. Values of the Sr:Ca ratio used to separate each eel into the general categories of river, estuarine and sea eels are given

14%. River eels appeared during late autumn and early winter (October 2000 to January 2001 and September 2001 to January 2002), and most estuarine eels and sea eels appeared at about the same time, with only a few individuals being caught at other times of the year (Fig. 3).

There was no significant difference in the TL among female river eels (mean = 71.3 cm), estuarine eels (70.4 cm) and sea eels (70.7 cm, Kruskal-Wallis test, $p > 0.05$, Table 1). There was also no significant difference in the BW among female river eels (597 g), estuarine eels (565 g) and sea eels (551 g, Kruskal-Wallis test, $p > 0.05$, Table 1). As was the case for female eels, there were no significant differences in TL or BW among male eels from different migratory types (Kruskal-Wallis test, $p > 0.05$, Table 1).

The mean GSI of females was significantly higher in river eels (2.9) than in estuarine eels (1.9) and sea eels (1.8) (Kruskal-Wallis test, $p < 0.01$) during October and

December (Table 1), while no significant difference was detected for male eels among the 3 migratory types (Kruskal-Wallis test, $p > 0.05$, Table 1).

For female eels, average age was 7.8 yr (range: 4 to 12 yr) for sea eels, 7.6 yr (4 to 14 yr) for estuarine eels and 8.3 yr (5 to 17 yr) for river eels (Table 1). The GR of female sea eels ranged from 4.8 to 14.7 cm yr^{-1} (8.7 cm yr^{-1}), that of female estuarine eels from 4.1 to 14.5 cm yr^{-1} (8.9 cm yr^{-1}) and that of female river eels from 4.8 to 13.9 cm yr^{-1} (8.1 cm yr^{-1}). There were no significant differences in age or GR among the females of the 3 migratory types (Kruskal-Wallis test, $p > 0.05$, Table 1). However, if the outlier values of 3 estuarine and 1 sea eel with slow GRs, and 1 river eel with a high GR were removed, the GRs of river eels were significantly lower than both estuarine and sea eels (ANOVA, Tukey-Kramer test, $p < 0.05$). These differences were illustrated by the observation that 70% of female river eels had GRs lower than 8.5 cm yr^{-1} , compared to only 45 and 53% of estuarine and sea eels, respectively, having GRs in that range.

The age of male sea eels ranged from 6 to 9 yr (mean: 7.0 yr), that of male estuarine eels, from 4 to 10 yr (6.7 yr) and that of male river eels from 4 to 9 yr (7.0 yr). The GR of male sea eels ranged from 6.1 to 9.7 cm yr^{-1} (8.2 cm yr^{-1}), that of estuarine eels from 4.7 to 12.1 cm yr^{-1} (7.8 cm yr^{-1}) and that of male river eels from 5.0 to 12.3 cm yr^{-1} (7.0 cm yr^{-1}). There were also no significant differences in both age and GR of males among any of the 3 migratory types (Kruskal-Wallis test, $p > 0.05$, Table 1); however, if the outlier values of 1 low GR estuarine eel and 1 high GR river eel were removed, male river eels had significantly lower GRs than the pooled values of the estuarine and sea eels (Mann-Whitney U -test, $p < 0.05$).

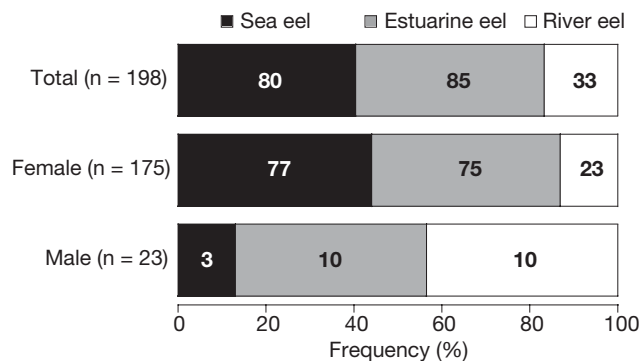


Fig. 5. *Anguilla japonica*. Frequency compositions of eels of the 3 migratory types (sea, estuarine and river eels) collected in set nets in Mikawa Bay from May 2000 to April 2002. Numbers within each bar indicate the number of eels belonging to each type

DISCUSSION

This is the first study to use otolith Sr:Ca ratio analysis to document the migratory history of anguillid eels in conjunction with age and GSI analyses of eels collected continuously at a fixed location throughout the year. Previous studies using the same technique to determine the migratory history of anguillid eels have shown that many Japanese (Tsukamoto & Arai 2001, Tzeng et al. 2002, 2003a, Arai et al. 2003, Kotake et al. 2003), American (Jessop et al. 2002, 2004) and European (Tsukamoto et al. 1998, Tzeng et al. 2000) eels live in marine and estuarine habitats, in addition to those that show the typical catadromous migration pattern of entering freshwater. The analysis of the Sr:Ca ratios in the otoliths of almost 200 eels collected using set nets in the brackish water of Mikawa Bay showed that all 3 of the general migratory types of eels (sea, estuarine and river eels) were present, but that there were some seasonal differences in their occurrences. The majority of eels were caught during the typical spawning migration season in the autumn, but those that were caught in other months were all sea or estuarine eels.

The greatest numbers of eels were caught during autumn and early winter, and especially during November and December, when their GSI values were high in both years. The GSI of the female eels caught primarily from November to January and October to January of the 2 years were markedly higher than during the rest of the year, indicating that these eels were maturing and had likely began their spawning migration. The GSI of these female eels was similar or higher than those of migrating female silver eels reported previously (1.1 to 2.5; Sasai et al. 2001, Okamura et al. 2002). The individuals caught in April and May of both years were medium-sized females, with low GSI values, that may have been caught while foraging, or as they were moving to a new area in the spring season. The remaining females, with low GSI values, were caught from July to September or October. These eels may have been beginning their spawning migrations even though their GSI values were still relatively low.

Male eels were only present during October and November in Mikawa Bay, and this period coincided with the timing of collections of maturing males in other coastal areas of Japan (Sasai et al. 2001, Kotake et al. 2003). The GSI values of the male eels examined in this study (0.0 to 0.4) were similar to those in the studies mentioned above. However, due to the difficulty in collecting migrating eels around the coastal areas of Japan and the highly skewed sex ratio of the specimens collected, information on the maturity of male Japanese eels at the beginning of their spawning migration is more scarce than for female eels (Matsui

1957, Sasai et al. 2001, Okamura et al. 2002, Kotake et al. 2003). All reported GSI values for males have been under 1.0 (0.2 to 0.6) during the spawning migration season (Sasai et al. 2001, Kotake et al. 2003). These results suggest that the male eels collected in Mikawa Bay were also beginning their spawning migration.

All of the river eels were caught during the spawning migration season. The GSI values of some of the female river eels were the highest among the 3 migratory patterns. These river eels were caught from September to January and all but one had relatively high GSI values. These eels must move downstream from rivers to the bay at the onset of maturation, while estuarine and sea eels begin their migration in estuaries and coastal areas. It is possible that most eels begin their spawning migration in the ocean at about the same maturity level, and the catch data from Mikawa Bay suggest that river eels may begin migration earlier than most individuals of the other 2 migratory types. Otherwise, the catches of the river eels would presumably be later than those of the other types because they inhabit freshwater areas further from the sampling location. The earlier start of downstream migration in river eels is probably why some had higher GSI values than the other types. However, the GSI level reaches 30 to 60 at the final stage of maturation in Japanese eels that are artificially matured with hormone treatments (Satoh et al. 1992, Sato 2003), so minor differences in maturity at the beginning of the spawning migration should not be an impediment to reproduction.

The migratory type of female eels included a high percentage of sea eels (45%), while the migratory male eels were mainly river (42%) and estuarine eels (42%). Kotake et al. (2003) also reported that female silver eels caught near the Amakusa Islands of western Japan included many sea eels (44%) and that males were mainly river eels (43%). As sex determination in anguillid eels appears to be controlled by environmental factors (Krueger & Oliveira 1999), these findings suggest that marine habitats may produce more female Japanese eels than males, while the relatively small-sized streams and river habitats adjacent to Mikawa Bay and the Amakusa Islands may produce more males. Alternatively, after sex differentiation, more females may tend to move to marine or brackish habitats, while males may remain in freshwater until they start their spawning migration. However, the sex ratio of eels from freshwater may vary according to the size of the river or the quality of the habitat, and recently Oliveira et al. (2001) reported that the sex ratios of the American eel were different among several rivers. Compared to North America, Japan is a relatively narrow and mountainous landmass, with extensive urban and agricultural development adjacent to most lowland rivers and

streams, so the number and quality of freshwater habitat may be somewhat limited.

Overcrowding and poor feeding conditions are thought to give rise to male eels, and low population densities with rich feeding appears to favor female eels (Tzeng et al. 1995, Krueger & Oliveira 1999). The specific environments in the coastal areas of Japan that have potentially food-rich and low population density might favor the production of female eels, while the potentially food-poor or higher population density of freshwater habitats might favor male eels. In this study and a previous one (Tzeng et al. 2003), the growth rates of Japanese eels were all relatively high compared to those observed in other temperate eels (e.g. Poole & Reynolds 1996, Jellyman 1997, Oliveira 1999, Jessop et al. 2004), possibly due in part to the relatively mild winters in this part of Japan. The males were found to have slower growth rates than females, and the growth rates of river eels of both sexes were slightly slower than eels that primarily used estuarine or marine habitats. Jessop et al. (2004) also found that near the northern edge of their species range, where the winters are much colder than in central Japan, female American eels grew faster than males and eels with a history of primarily estuarine residence had faster growth rates than those that resided in freshwater. In more southern regions of North America, where many of the rivers extend far inland with large drainages, Helfman et al. (1987) noted that female American eels tended to be distributed upstream, while male eels were more restricted to estuarine areas. The likely cause for this may be that many individuals recruit to the estuaries and the number of eels reaching upstream areas decreases with increasing distance. Similarly, in New Zealand, all the male *Anguilla australis* examined by Arai et al. (2004) using Sr:Ca analysis had remained in estuarine habitats until their spawning migration and had slower growth rates than females that had used either freshwater or estuarine habitats. However, in New Zealand, the factors associated with habitat use and growth are more complicated than for other temperate anguillids, because of the presence of another sympatric species *A. dieffenbachii*, which reaches larger sizes (Jellyman 1997). Similar interactions may exist in areas such as Taiwan, where *A. japonica* is found sympatrically with the widely distributed tropical species *A. marmorata*, which is a similarly large-sized species (Shiao et al. 2003). *A. marmorata* also recruits to the islands of southern Japan (Yamamoto et al. 2001), but it is probably extremely rare in areas as far north as the study area in Mikawa Bay.

The results of this study in Mikawa Bay showed a consistent pattern during the 2 years of the investigation. Both river eels and estuarine and sea eels began

their marine spawning migration toward the open ocean at about the same time. This type of synchronization of migration and gonadal maturation, and the apparent predominance of estuarine and marine habitats in the central region of Japan, has important implications for the conservation of this species. It implies that eels from both freshwater and marine habitats can mix together during the spawning migration and potentially contribute to the next generation, and that estuarine and marine habitats may be very important for eels around Japan. Further studies are needed to examine the factors affecting the apparently flexible pattern of habitat use by the Japanese eel to assist in developing a new management strategy for preventing a further decline of this important species.

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