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Life History Patterns of Japanese Eel *Anguilla japonica* in Mikawa Bay, Japan

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Abstract.—The otolith microchemistry of female Japanese eels *Anguilla japonica* collected in Mikawa Bay, Japan, in June 1998 to June 1999 was examined with an electron probe microanalyzer. Total length ranged between 62.0 and 96.0 cm, and body weight between 291 and 2057 g. Gonadosomatic index (GSI) increased from less than 0.2 in August to greater than 4.0 in January. Temperature of the sampling site ranged between 6.6°C and 28.8°C, and salinity between 24.6‰ and 32.7‰. Otolith Sr:Ca indicated that the life history patterns of eels could be classified into three types: Type 1, Sr:Ca from approximately 150 μm from primordium to edge of the otolith maintained at the level of approximately 0–4 × 10^{-3}, indicating that eels after the elver stage stayed in fresh water until the silver eel stage; Type 2, the ratios were 4–10 × 10^{-3}, indicating that eels stayed in seawater from elver stage to the silver eel stage; Type 3, the ratios fluctuated between those of Types 1 and 2, indicating that eel migrated between freshwater and seawater before the silver stage. Results suggest that the growth phase of yellow stage Japanese eel does not have definite habitat selection and that the population is predominately estuarine.

Introduction

The Japanese eel *Anguilla japonica* is widely distributed in the northwestern Pacific, south from Taiwan, through China, Korea, and north to Japan (Tesch 1977). The eel's life cycle has five principal phases, i.e., leptocephalus, glass eel, elver, yellow eel, and silver eel (Bertin 1956). Japanese eel is presumed to be a panmictic population (Sang et al. 1994), spawning in the waters west of the Marian Islands, 15°N 140°E (Tsukamoto 1992). Leptocephali drift on the North Equatorial Current for approximately five to six months before arriving to the continental shelves (Tzeng 1990; Tzeng and Tsai 1992; Cheng and Tzeng 1996). Upon arriving to coastal waters they metamorphose to glass eels and become pigmented elvers in the estuary. Elvers are over-exploited for restocking and thus the eel population has decreased (Tzeng 1985, 1986, 1996a). The yellow eels spend approximately five to eight years growing in rivers before they metamorphose into silver eels (Tzeng et al. 2000a), which migrate downstream in the autumn to return to their spawning grounds.

In recent years, trace elemental strontium (Sr) in otoliths has been used to study the salinity history and, therefore, migratory movements of eels. The absolute concentration of Sr ranges from 9 × 10^{-7}M in freshwater to 8.7 × 10^{-5}M in seawater, an almost 100-fold difference (Campana 1999). The molar ratio of Sr to calcium (Sr:Ca) in seawater (8.6 × 10^{-3}) is about 4.8 times greater than that of freshwater (1.8 × 10^{-3}). Otolith Sr:Ca is positively correlated to ambient salinity (Secor et al. 1995; Tzeng 1996b; Kawakami et al. 1998). Because the eel is diadromous, otolith Sr:Ca has been used to investigate their migratory environmental history (Casselman 1982; Otake et al. 1994; Tzeng and Tsai 1994; Arai et al. 1997; Tzeng et al. 1997, 1999, 2000b; Tsukamoto et al. 1998).

In general, freshwater eels are presumed to grow in fresh water and spawn at sea. However,

recent otolith Sr:Ca studies indicate that some of the eels skip freshwater growth entirely to complete their life cycle in the ocean or in brackish water (Tsukamoto et al. 1998; Tzeng et al. 2000b; Limburg et al., this volume). These recent observations indicate the life history pattern of the yellow stage eel is diversified. To understand the migratory movements of yellow stage Japanese eel between fresh and saline waters, otolith Sr:Ca of silver eels collected in the Mikawa Bay, middle Japan, were examined.

Methods

Japanese eels were collected in Mikawa Bay on the east coast of mid Japan, 137°E 34°45'N (Figure 1). The three rivers connected with the bay allow fish to migrate freely upstream into fresh water. Thus, the bay is an ideal area to test if they migrate opportunistically. Specimens for otolith microchemistry analysis were randomly selected from silver eels collected from the bay for artificial propagation by the Irago Institute in Japan. Eels were collected monthly using both set net and eel tubes during the period from June 1998 through June 1999. The fishing gear was set at 2–3 m depth, approximately 50 m from shoreline. The gear was set at dawn and captured eels were recovered the following morning. Water temperature and salinity at the sampling site were recorded.

Total length (TL) and body weight (BW) were measured after anesthetizing in a solution of 800 ppm 2-phenoxythanol for about five minutes.

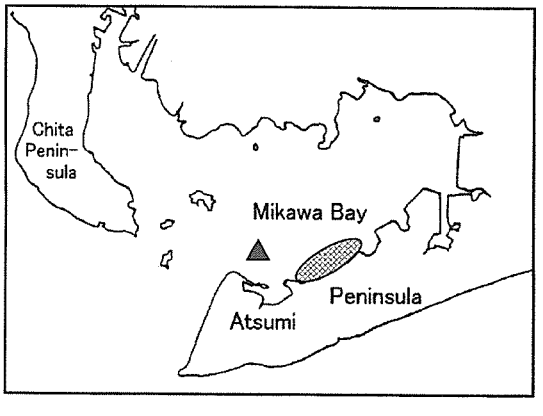

Figure 1. Sampling site of the eel ( ) and location of temperature, and salinity measurements (▲) in Mikawa Bay, Japan.

Maturity status was analyzed based on gonadosomatic index (GSI, ovary weight/body weight × 100%) and ovum diameter (OD). Otoliths were removed and preserved in a dry chamber for Sr:Ca analysis. A total of 45 otoliths of female silver eels were examined.

EPMA (Electron Probe Micro-analyzer, JEOL, JXA-8800M) was used to analyze Sr:Ca. $SrTiO_3$ and $CaMnO_4$ were used as standards for Sr and Ca measurements. Sr and Ca concentrations were measured along a transect from the primordium to the edge of otolith with a beam current of 3nA and 15 KeV accelerating voltage. At intervals of approximately 10 μm, the electron beam was focused on an area approximately 1 μm in diameter. The energy dispersive strength of Ca and Sr was evaluated using 10 seconds scanning periods. After ZAF (Z = atomic number effect; A = absorption factor; F = fluorescence effects) correction, Sr:Ca was calculated. In addition, a subsample of otoliths was selected for mapping Sr and Ca concentration to examine the temporal change of Sr:Ca. Otolith growth annuli were identified as described in Tzeng et al. (1994, 1999).

Results

Water Temperature and Salinity

Surface water temperature in the Mikawa Bay was highest in July (about 28.8°C) and lowest in January (about 6.6°C). Salinity was approximately 32‰ in the winter but fluctuated considerably during the summer (range 24.6‰–32.7‰). The lower salinity in the summer was probably due to high river discharge (Figure 2).

Seasonal Variation of Maturity

Gonadosomatic index (GSI) was lowest in August (approximately 0.2), but increased thereafter and reached a maximum in January (approximately 4.0) (Figure 3). This indicates that maturity was inversely related to water temperature. In addition, the maximum ovum diameter (OD) at the highest GSI was approximately 200 μm (Figure 4), indicating that silver eels collected from the bay were immature.

Otolith Sr:Ca

Sr:Ca increased from approximately 8×10^{-3} at the primordium to a peak of $16 \sim 18 \times 10^{-3}$ at

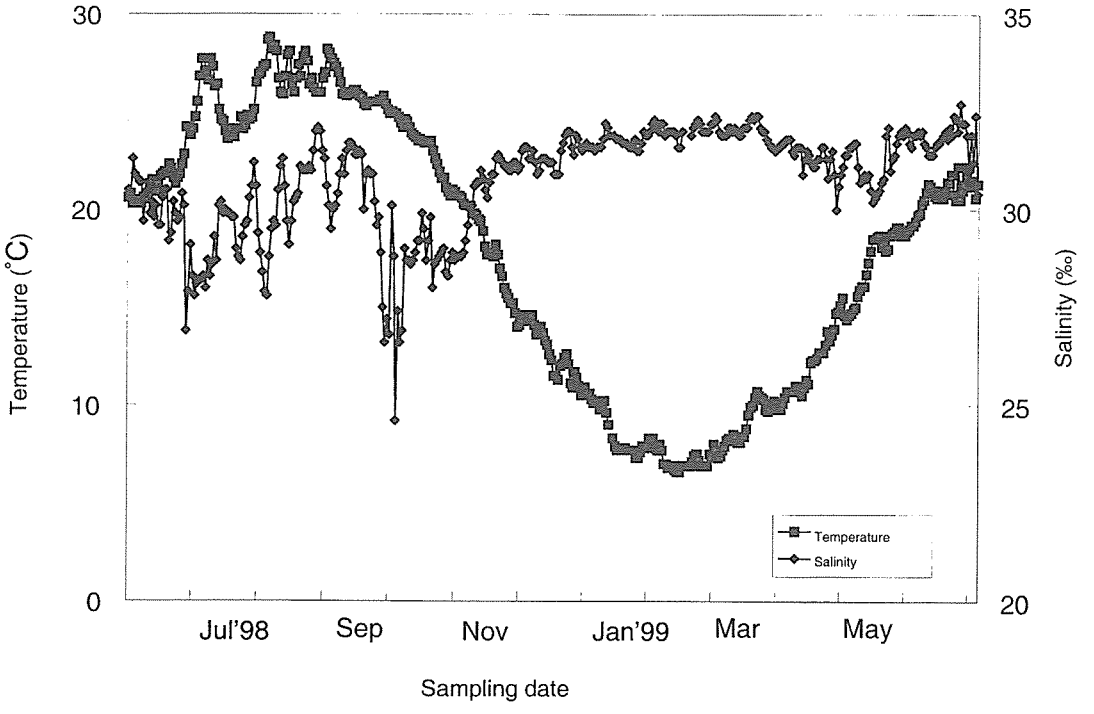

Figure 2. Seasonal variations of water temperature, and salinity in Mikawa Bay, Japan.

approximately 150 μm from the primordium. This pattern of Sr:Ca was similar among individuals, because the migratory environment at the marine leptocephalus stage was similar for all. However, from the elver stage, the Sr:Ca profiles divided the eels into three types (Figure 5), each of which are subsequently described.

Type 1 (freshwater resident): Sr:Ca in the layer approximately 150 μm from the primordium to the edge of the otolith fluctuated between 0 and 4×10^{-3}, indicating that the eels after the elver stage had migrated into fresh water to grow and later metamorphose to silver eel (Figure 5a). Otolith microchemistry mapping indicated that Ca was

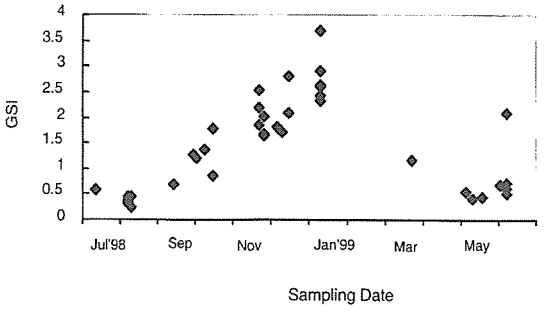

Figure 3. Seasonal variation of gonadosomatic index (GSI).

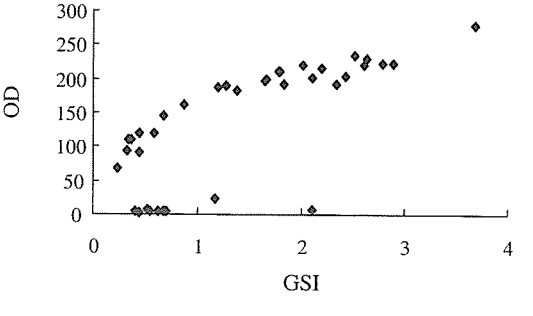

Figure 4. The relationship between ovum diameter (OD) and gonadosomatic index (GSI).

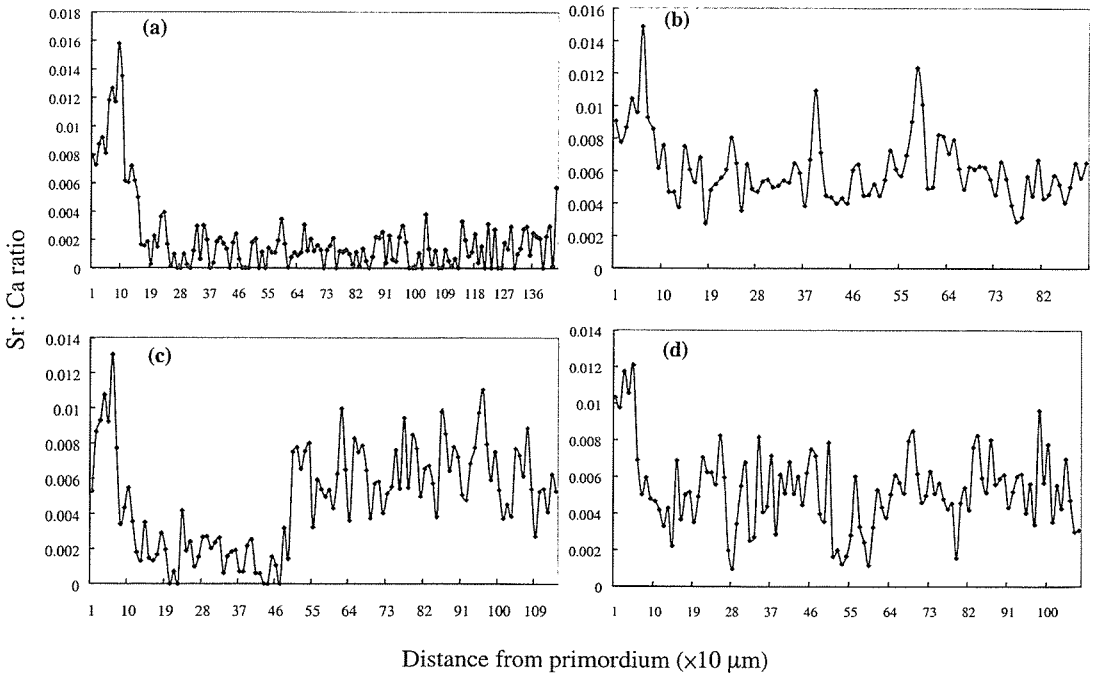

Figure 5. Classification of migratory environments of the eel based on the otolith Sr:Ca at yellow eel stage: (a) 66.8 cm TL, Type 1 (freshwater); (b) 76.6 cm TL, Type 2 (seawater); (c) 80.0 cm TL, Type 3a (freshwater then seawater); and (d) 76.0 cm TL, Type 3b (between fresh water, and seawater).

homogenous throughout the otolith (Figure 6a, b, and c). Sr concentration, however, markedly changed across the life history transect. Sr was highest in the core, which corresponds to the marine leptocephalus stage. It then decreased slightly which indicates a brackish water elver stage, with further decrease that indicates freshwater residency during the yellow eel stage. Sr concentration increased again in the edge of the otolith when the eel migrated from fresh to brackish water of the bay. The level of Sr was similar in the layer approximately 150 μm from primordium and in the edge of the otolith, indicating that the eel at elver stage and silver stage stayed in a similar saline environment (Figure 6a).

Type 2 (seawater resident): Sr:Ca 150 μm from the primordium to the edge of the otolith ranged from 4 to 10 × 10^{-3} and averaged approximately 6 × 10^{-3}, indicating that the elvers had remained in brackish water to grow and later metamorphose to the silver stage (Figure 5b). The transect concentration of Ca was also similar to that of Type 1 otoliths (Figure 6b). The concentration of Sr, however, was different from that of Type 1 except at the core. Sr concentration from the elver stage to silver stage were higher than those of Type 1 and four growth annuli of higher Sr concentration were identified during the yellow stage growth phase (Figure 6b). Accordingly, eels grew in the seawater for approximately four to five years with the Sr band being formed in the winter when water temperature was lowest and salinity was highest (Figure 2).

Type 3 (estuarine resident): an intermediate type between Types 1 and 2. Postelver Sr:Ca were lower than 4 × 10^{-3} in the early yellow stage, but thereafter increased to higher than 6 × 10^{-3} until the edge of otolith. This pattern indicates that the elvers had been migrating to freshwater and later returned to seawater at the yellow stage where they remained until metamorphosing to silver stage (Figure 5c). An alternative type, Sr:Ca changed between 2 × 10^{-3} and 8 × 10^{-3}, approximately a fourfold difference (Figure 5d). This indicates that the eel irregularly

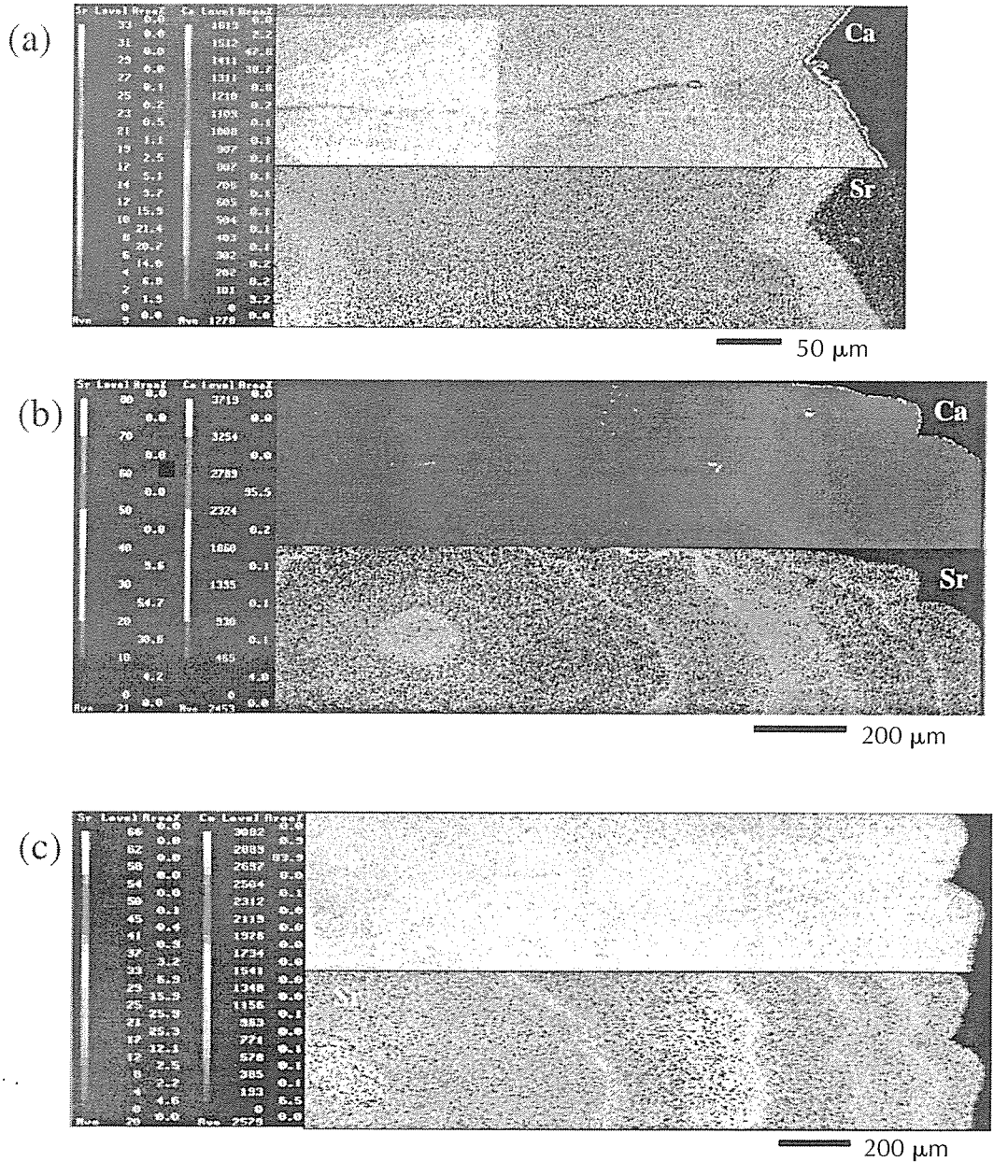

Figure 6. Ca, and Sr concentration maps of otoliths: (a) Type 1 or Type 3a; (b) Type 2: and (c) Type 3b. The eel (a) measured 73.0 cm TL, while the eels (b) and (c) are the same as (b) and (d) in Figure 5.

migrated between fresh and seawater throughout the yellow stage growth phase. There were also four growth annuli with higher Sr concentration, indicating that growth phase of the eel lasted for approximately four to five years (Figure 6c).

Composition of Life History Types

Based on Sr:Ca, the migratory environments during the growth phase of yellow stage eels was divided into three types, i.e., Type 1 (freshwater), Type 2 (seawater), Type 3a (freshwater

then seawater) and Type 3b (between freshwater and seawater). Types 3a and 3b constituted nearly 58% of the total eels examined (Table 1), indicating that approximately half of the eels in the Mikawa Bay migrated between fresh water and seawater during the yellow stage. The remainder of the population was almost equally distributed among freshwater eel (20%) and seawater eel (22%).

Comparison of Length, Weight, and GSI Among Different Life History Types

Mean length, weight and GSI of female eels did not vary significantly among life history types (Kruskal-Wallis one way analysis of variance (ANOVA) on ranks, $P = 0.162 - 0.843$). This indicated that size distribution and maturation were independent of migratory environments (Figure 7).

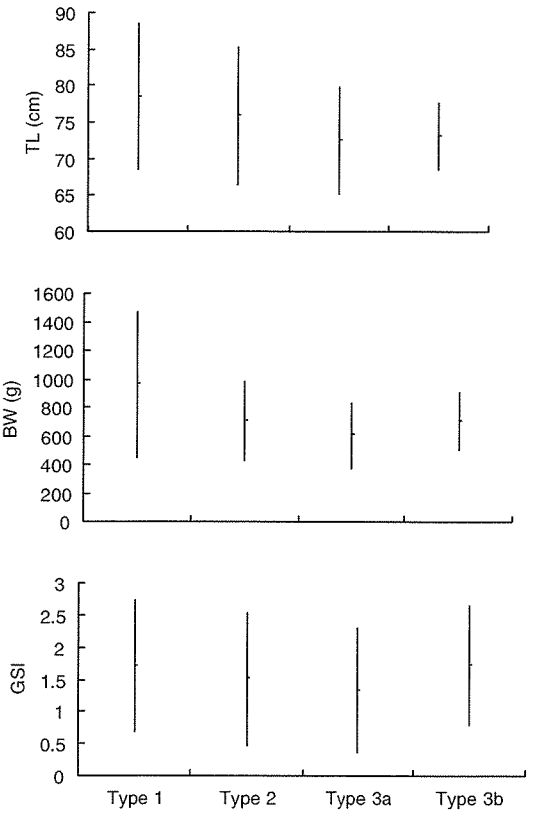

Figure 7. Comparison of mean (± SD) total length, body weight, and gonadosomatic index (GSI) of the eels among the four different life history types.

Discussion

Our measure of otolith Sr:Ca beyond the elver stage was approximately 0–4 × 10^{-3} in freshwater eel (Type 1) and approximately 4–10 × 10^{-3} with a mean of 6 × 10^{-3} in seawater eel (Type 2). Campana (1999) reported that Sr:Ca is approximately 1.8 × 10^{-3} in fresh water and 8.6 × 10^{-3} in seawater. The difference in Sr:Ca between the eels of Types 1 and 2 was similar to those of fresh water and seawater. Accordingly, our classification of eels into freshwater and seawater types in this study is believed to be reliable. In addition, regular spaced bands of higher Sr concentration were found in otolith of the seawater eels (e.g., Figure 6b and c). This indicated that the seasonal change in salinity of Mikawa Bay likely influences the variable levels of otolith Sr:Ca of the seawater eel. Similar observations have also been reported for the European eel, *A. anguilla* (Tzeng et al. 1999).

The relationship between otolith Sr:Ca of Japanese eel and ambient salinity was established using rearing experiments (Tzeng 1996b; Kawakami et al. 1998). The otolith Sr:Ca in relation to salinity was used to reconstruct the past salinity history of the striped bass *Morone saxatillis* in Chesapeake Bay (Secor et al. 1995; Secor and Rooker 2000). We did not, however, attempt to do a similar back-calculation of absolute salinity history as performed by these researchers for young-of-year striped bass, because we found that the mean otolith Sr:Ca of the eel reared in fresh water was 4.2 × 10^{-3} at the temperature of 22–28°C (Tzeng 1996b), and between 4.5 (± 0.91) and 5.0 (± 0.68) × 10^{-3} at the temperature of 12–27°C (Kawakami et al. 1998),

Table 1. Composition of life history types of female silver stage eels in Mikawa Bay, Japan.

Life history type	Number of eels	Percent of total
Type 1: freshwater	9	20.0
Type 2: seawater	10	22.2
Type 3a: freshwater then seawater	20	44.5
Type 3b: between freshwater and seawater	6	13.3
Total	45	100.0

which was significantly higher than those of the freshwater eel of Type 1 in this study ($0–4 \times 10^{-3}$) and fresh water (1.8×10^{-3}) (Campana 1999). This Sr:Ca discrepancy between freshwater-reared eels and the natural freshwater eel of Type 1 was probably due to the effect of Sr uptake from food. The Sr content of the food organism, tubifex worm *tubificid oligochaetes* was close to seawater and higher than fresh water (Kawakami et al. 1998). Enriched otolith Sr:Ca resulting from food uptake was also found in American shad *Alosa sapidissima* (Limburg 1995). On the contrary, the otolith Sr:Ca of the eel reared in the 35‰ seawater with the tubifex worm averaged 9.27×10^{-3} (Tzeng 1996b) and $8.5 (\pm 0.64)$ to $9.1 (\pm 1.27) \times 10^{-3}$ (Kawakami et al. 1998), which was close to that of seawater (8.6×10^{-3}) (Campana 1999). This indicated that the effect of Sr from food uptake was not simply additive. Thus, the use of a standard curve of otolith Sr:Ca versus salinity established by rearing experiment to back-calculate the absolute salinity history of the eel should be made cautiously.

In addition, otolith Sr:Ca was not only influenced by ambient salinity, but also influenced by ontogenetic developmental stage (Tzeng and Tsai 1994; Otake et al. 1994; Tzeng 1996b). Sr:Ca was significantly higher in leptocephali than in elvers, particularly around metamorphosis from leptocephalus to glass eel (Figure 6). This indicated that the relationship between otolith Sr:Ca and salinity was different among development stage of the fish. Incorporation of Sr into the otolith is a complicated biochemical process influenced by physical factors such as temperature, salinity and water chemistry, as well as by biological factors such as genetics, developmental stage, growth rate, food and physiological condition of the fish (Campana 1999; Dodd 1967; Gallahar and Kingsford 1992; Kalish 1989; Radtke and Shafer 1992; Sadovy and Severin 1992).

The Japanese eel *A. japonica*, similar to other *Anguilla* species, is considered to be a catadromous fish; i.e., it spawns in the ocean and grows in freshwater environments. Otolith Sr:Ca measured in this study indicates that individual eels were widely distributed from freshwater to seawater during growth-phase yellow stage. Migration to freshwater for the yellow eel is not an obligate pathway, but rather is a facultative diadromy with seawater residents as an ecophenotype (Tsukamoto et al. 1998). The migration of diadromous fishes may be a direct response to the environment, especially temperature, water level, and food availability (Baker 1978; Northcote 1978; McDowall 1987; Tzeng et al. 2000b), and influenced by the actions of conspecific competitors (e.g., Gross 1985). Diadromy may, therefore, be a complex collection of life history traits, some of which are strategies and others simple in random distribution. The Mikawa Bay estuary, like other estuaries around the world, is among the most productive areas on earth with productivity comparable to that of coastal upwelling areas (Haedrich and Hall 1976). The food availability in the bay may lead to the eel of Type 3 to be dominant. On the contrary, if the freshwater migration of the eel is an obligate pathway, the freshwater eel in the population should be dominant; however, the freshwater eel constituted only 20% of the population. Most of the eel in the Mikawa Bay were brackish-water residents. Thus, the distribution of the eel population probably depends on the carrying capacity of the environment. The brackish-water eel likely dominated the study area because the Bay's carrying capacity far exceeded the capacity of habitat found in the Bay's adjacent rivers.

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