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Environmental history of Japanese eel, *Anguilla japonica* collected in Miyako Bay, northeastern Japan

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The environmental history in combination with age of the Japanese eel, *Anguilla japonica*, collected in Miyako Bay along the Sanriku Coast of Japan, was examined using the otolith microstructure and analysis of strontium (Sr) and calcium (Ca) concentrations with wavelength dispersive X-ray spectrometry by an electron microprobe. The line analysis of Sr:Ca ratios along the life history transect of each otolith showed a peak (ca $12-17 \times 10^{-3}$) between the core and elver mark, which corresponded to the period of their leptocephalus and early glass eel stages in the ocean. The mean Sr:Ca ratios from the elver mark to the otolith edge indicated that there were eels with several general categories of migratory history, that included sea eels that never entered freshwater (average Sr:Ca ratios, $>6.0 \times 10^{-3}$) and others that had entered freshwater for brief periods, but returned to the estuary or bay. This evidence of the occurrence of sea eels indicates that Japanese eels in this northern area do not necessarily migrate into freshwater rivers during recruitment as glass eels at the beginning of their growth phase, and even those that do enter freshwater may later return to the marine environment.

Key words: Japanese eel, *Anguilla japonica*, otolith, Sr:Ca ratios, migration, sea eel

INTRODUCTION

The Japanese eel, *Anguilla japonica* Temminck & Schlegel is a catadromous fish (McDowall 1988). The eel is widely distributed in East Asia, from Taiwan in the south, through eastern China, in Korea, and up to the Sanriku Coast of northern Honshu Island, Japan (Tesch 1977). The Japanese eel spawns in waters west of the Mariana Islands (Tsukamoto 1992) and their leptocephali drift within the North Equatorial and Kuroshio Currents (Kimura et al. 1994). As they approach the continental shelf, leptocephali metamorphose into glass eels and leave the Kuroshio for coastal waters. The glass eels become elvers in the estuaries (Bertin 1956). After upstream migration, the elvers become yellow eels and live in the freshwater habitats such as rivers and lakes for 5–20 years. Then during the silver eel stage in autumn and winter, their gonads begin maturing and they start their downstream migration into the ocean and back out to the spawning area where they spawn and die.

However, Tsukamoto et al. (1998) used otolith strontium (Sr) and calcium (Ca) analysis, and recently found yellow and silver eels of *Anguilla japonica* in marine areas adjacent to their typical freshwater habitats that have never migrated into freshwater and have spent their entire life history in the ocean. Furthermore, Tsukamoto and Arai (2001) also used Sr:Ca ratios and found an intermediate type between marine and freshwater residents of *A. japonica*, which appear to frequently move between different environments during their growth phase. Such a migratory behaviour was also found in other anguillid eels *A. anguilla*

(Tsukamoto et al. 1998; Tzeng et al. 2000) and *A. rostrata* (Jessop et al. 2002). This discovery of marine (“sea eels”) and estuarine (“estuarine eels”) residents of *A. anguilla*, *A. japonica* and *A. rostrata* suggests that anguillid eels do not all have to be catadromous and calls into question the generalized classification of diadromous fishes.

Patterns in the strontium (Sr) to calcium (Ca) ratio of otoliths, in combination with age, have been used to elucidate the migratory history of fish such as the habitat use and seasonal migration for diadromous fishes, including the anguillid eels, *Anguilla japonica* (Tsukamoto et al. 1998, Tsukamoto and Arai, 2001, Arai et al. 2003), *A. anguilla* (Tsukamoto et al. 1998; Tzeng et al. 2000) and *A. rostrata* (Jessop et al. 2002). The Sr:Ca ratios in the otoliths of *A. japonica* are positively correlated to ambient salinity (Tzeng 1996) as they appear to be in a variety of teleost fishes (Secor and Rooker 2000, Arai 2002). Accordingly, the Sr:Ca ratios in the otoliths of eels are useful to reconstruct their migratory environmental history.

In this study we examined the age and the fluctuation patterns of Sr:Ca ratios along the life history transect in the otoliths of the Japanese eel *Anguilla japonica* collected from marine habitats at the northernmost edge of the species range, the Sanriku Coast of Japan, where there is little information available about the migration and habitat use by *A. japonica*. Thus, the objective of this study was to reconstruct the environmental history of *A. japonica* caught in a bay of northeastern Japan where there are apparently low densities of eels and to compare the findings to the patterns of migratory history of eels sampled farther south in

Japan where densities may be higher.

MATERIALS AND METHODS

Specimens of *Anguilla japonica*, were collected by eel pots and set nets in Miyako Bay of the Sanriku Coast of Japan, from May to August 2002 (Table 1, Fig. 1). A total of 20 specimens in yellow stage were used in the present study. Total length, body weight and gonad-somatic index (GSI) were measured (Table 1). Species identification of each eel was carried out using polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) analysis of the mitochondrial 16 rRNA gene as described by Aoyama et al. (2000), and all eels were confirmed to be *A. japonica*.

Sagittal otoliths were extracted from each fish, embedded in epoxy resin (Struers, Epofix) and mounted on glass slides. The otoliths were then ground to expose the core, using a grinding machine equipped with a diamond cup-wheel (Struers, Discoplan-TS), and polished further with 6 μm and 1 μm diamond paste on an automated polishing wheel (Struers, Planopol-V). Finally, they were cleaned in an ultrasonic bath and rinsed with deionized water prior to being examined.

For electron microprobe analyses, all otoliths were Pt-Pd coated by a high vacuum evaporator. 'Life-history transect' analysis of Sr and Ca concentrations, were measured along a line down 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 Arai and

Table 1. Specimens of *Anguilla japonica* used for otolith microchemistry analyses.

GSI: gonad-somatic index

Fish number	Total length (mm)	Body weight (g)	Sex	Age (years)	GSI (%)
OZ08	789	715	♀	8+	0.70
OZ09	796	980	♀	10+	1.00
OZ10	778	622	♀	7+	0.73
OZ11	624	360	♀	7+	0.62
OZ12	724	596	♀	6+	0.54
OZ13	613	390	♀	7+	0.51
OZ14	722	618	♀	7+	0.59
OZ15	557	225	♀	3+	0.34
OZ16	643	438	♀	7+	0.71
OZ17	690	502	♀	7+	0.55
OZ26	716	560	♀	8+	0.53
OZ27	631	364	♀	8+	0.96
OZ28	538	232	♀	6+	0.34
OZ29	518	179	♀	5+	0.45
OZ30	464	125	♀	9+	0.57
OZ31	564	238	♀	3+	0.44
OZ32	530	189	♀	8+	0.34
OZ33	610	365	♀	7+	0.44
OZ34	479	165	♀	4+	0.25
OZ35	526	206	♀	5+	0.28

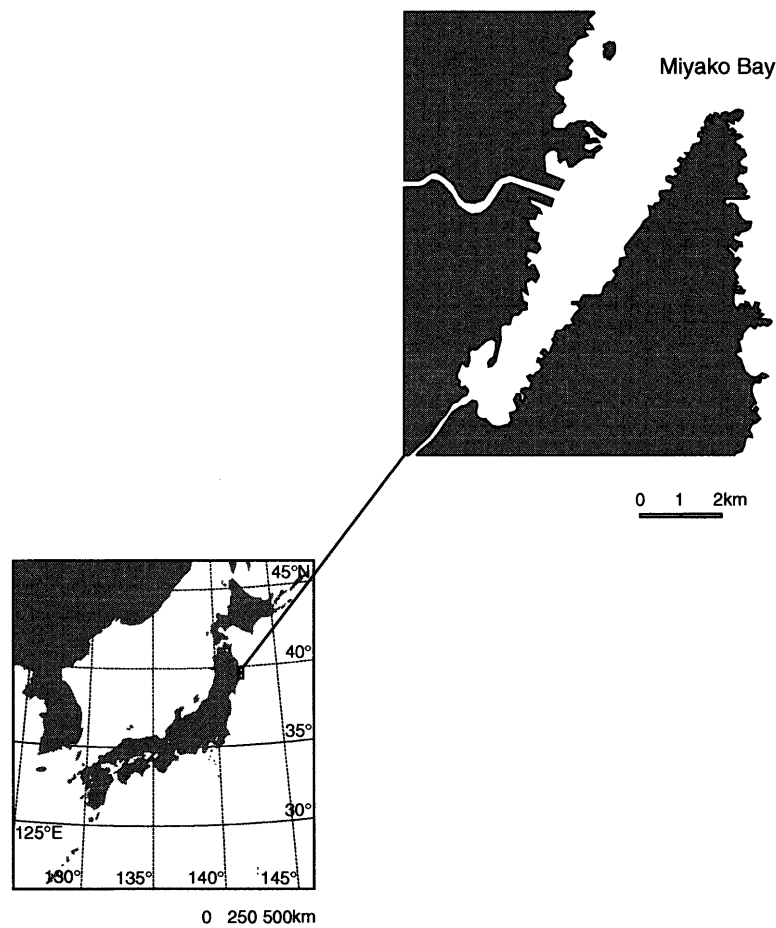


Fig. 1. Sampling sites for the Japanese eel, *Anguilla japonica*, in the Miyako Bay along the Sanriku Coast of Japan.

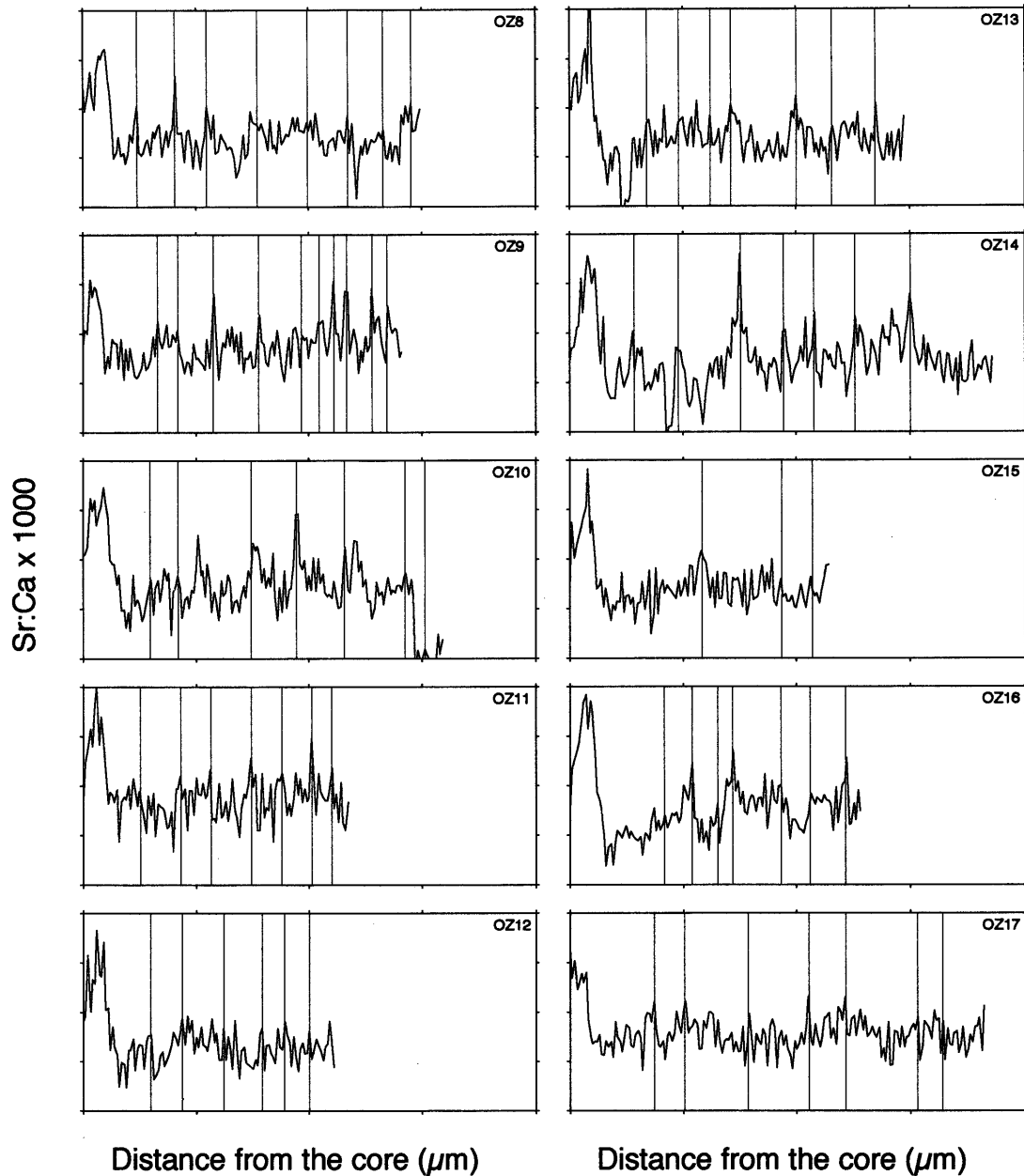


Fig. 2

Tsukamoto (1998) and Arai et al. (1997, 2001, 2003). Calcite (CaCO_3) and strontianite (SrCO_3) were used as standards, and the accelerating voltage and beam current were 15 kV and 1.2×10^{-8} A, respectively. The electron beam was focused on a point 10 μm in diameter, with measurements spaced at 10 μm intervals.

Following the electron microprobe analysis, the otoliths were repolished to remove the coating, etched with 1% HCl and thereafter stained with 1% toluidine blue (Arai et al., 2003). The age of the specimens was determined by counting the number of blue-stained transparent zones following Arai et al. (2003). The positions of the transparent zones were then correlated to elemental analysis points. The relative ages at particular elemental analysis points could then be assigned.

We calculated the average Sr:Ca ratios for the values outside the elver mark, and according to the criteria of Tsukamoto and Arai (2001), we categorized the specimens

into “sea eels” (Sr:Ca ratios, $\geq 6.0 \times 10^{-3}$), “estuarine eels” (Sr:Ca ratios, $2.5\text{--}6.0 \times 10^{-3}$) or “river eels” (Sr:Ca ratios, $< 2.5 \times 10^{-3}$).

RESULTS

The line analysis (Fig. 2) showed that otolith Sr:Ca ratios were remarkably variable among the specimens examined. All otoliths had a central region with high Sr:Ca ratios (ca 12×10^{-3} – 17×10^{-3}). This high Sr:Ca ratios was considered to correspond to the oceanic leptocephalus stage up to the early glass eel stage just after metamorphosis, which would be the part of the life history from the spawning grounds to coastal waters (Arai et al. 1997). The high Sr:Ca ratios in the central core region during the leptocephalus stage may be derived from the large amounts of gelatinous extracellular matrix that fill their bodies until metamorphosis. This material is composed of sulfated glycosaminoglycans (GAG), which is converted into other

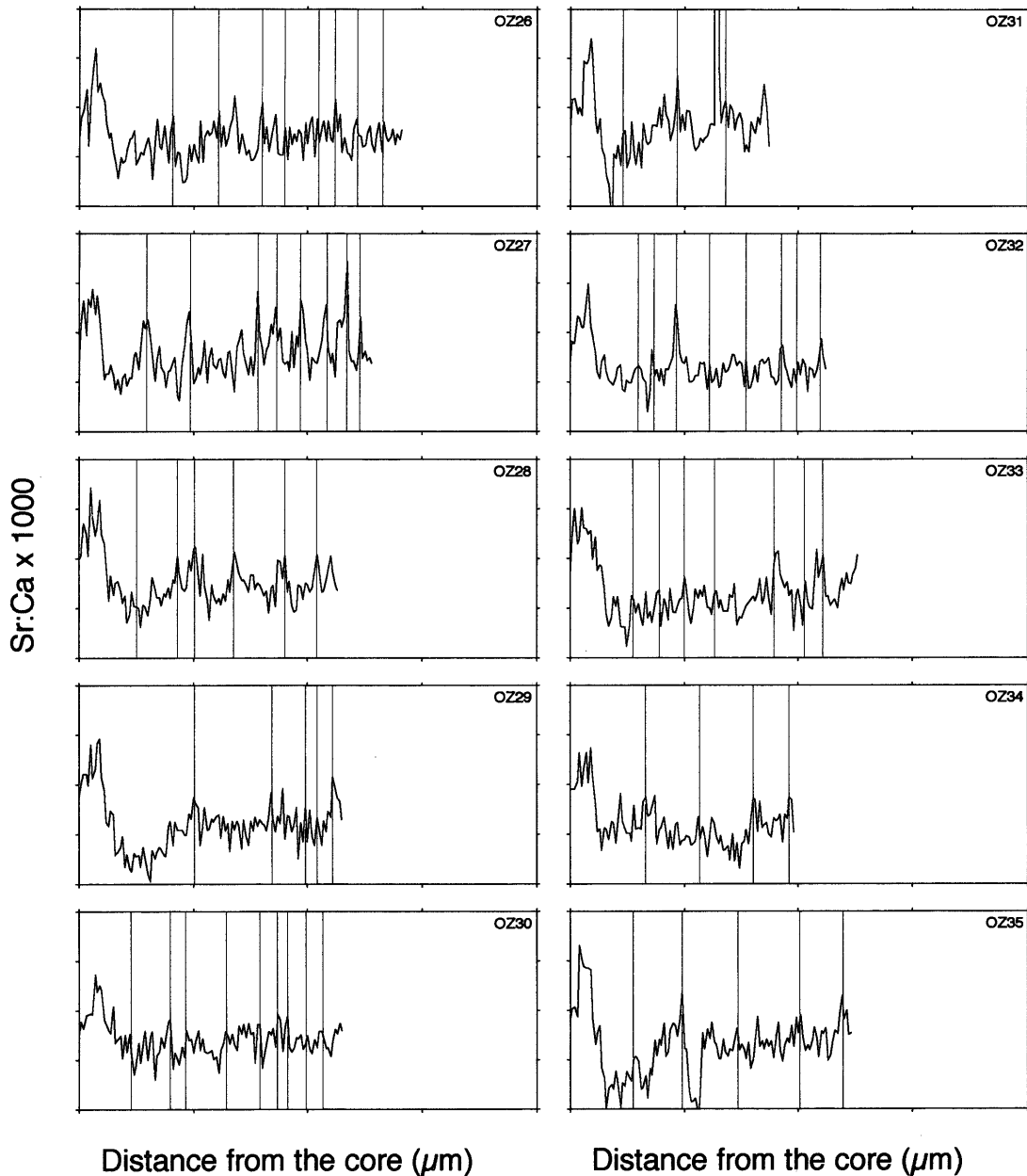


Fig. 2. *Anguilla japonica*. Plots of the otolith Sr:Ca ratios along line transects from the core ($0\ \mu\text{m}$) to the edge of all otoliths collected in the Miyako Bay, along the Sanriku Coast of Japan. The vertical lines correspond the annual rings in the frontal plane of the sagittal otoliths. The number at the upper right indicates fish number.

compounds during metamorphosis (Pfeiler 1984). The drastic decrease in Sr at the outer region in all samples after metamorphosis to glass eels, may occur because these sulfated polysaccharides have an affinity to alkali earth elements, and are particularly high in Sr, suggesting that a high Sr content in the body has a significant influence on otolith Sr content through saccular epithelium in the inner ear, and the sudden loss of Sr-rich GAG during metamorphosis probably results in the lower Sr concentration in otoliths after metamorphosis (Arai et al. 1997).

Outside of the high Sr:Ca ratios around the core of otolith, 16 of 20 specimens had consistently high ranges of Sr:Ca values (Fig. 2) that were higher than 6×10^{-3} (6.2×10^{-3} – 8.8×10^{-3}) (Fig. 3), suggesting a long-term residence in the sea with little, or more likely, no movement into freshwater. In contrast, the four other specimens appeared

to recruit to freshwater, or to a low salinity estuarine habitat, for the first year of its growth phase, and then it apparently returned to the bay, and accumulated high levels of Sr:Ca in its otolith (Fig. 2).

In the present study, there were no specimens with the typical pattern of low Sr:Ca ratios observed in eels sampled in freshwater as reported previously (Tsukamoto and Arai, 2001) (Fig. 3), which showed uniformly low Sr:Ca ratios all over their otoliths, except for the high Sr:Ca ratios around core.

DISCUSSION

The Sr:Ca ratios in fish otoliths are positively correlated to ambient salinities (Tzeng 1996, Secor and Rooker 2000, Arai 2002). Thus, the temporal changes of Sr:Ca ratios in otoliths have been used to discriminate the environmental

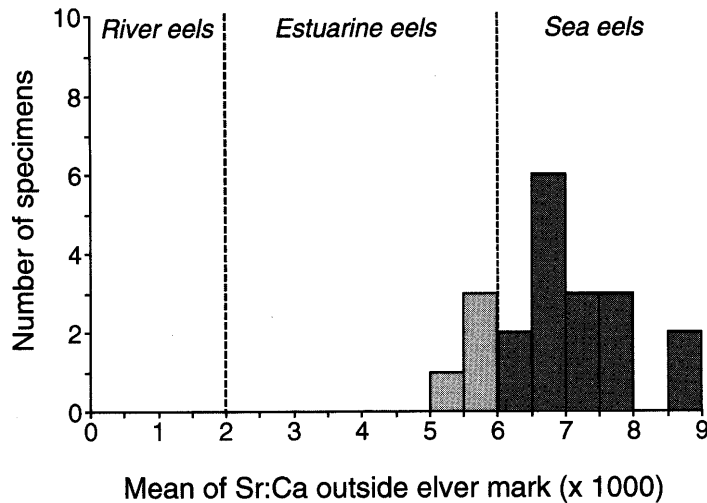


Fig. 3. *Anguilla japonica*. Frequency distribution of the mean values of Sr:Ca ratio outside the elver mark ($150\ \mu\text{m}$ in radius) in each otolith of specimens of the Japanese eel.

history of a variety of anadromous, catadromous and amphidromous fishes (Arai and Tsukamoto 1998, Tsukamoto et al. 1998, Secor and Rooker 2000, Tzeng et al. 2000, Tsukamoto and Arai 2001, Arai 2002, Jessop et al. 2002, Arai et al. 2003). In this study, the life history analysis using otolith Sr:Ca ratios revealed that the Japanese eels caught in Miyako Bay along the Sanriku Coast near the northern edge of the range of this species were mostly sea eels had either lived in the bay during their entire growth phase until capture, or had entered freshwater only for relatively short periods. This finding suggests that *A. japonica* which recruit to this northern area have a flexible migration strategy with a high degree of behavioral plasticity to decide whether or not to enter freshwater or to return to the bay. The occurrence of sea eels was indicated in the otoliths of yellow and silver eels of *A. japonica* at other localities in the southern part of Japanese coastal waters (Tsukamoto et al. 1998, Tsukamoto and Arai 2001). Otolith analyses of the yellow and silver eels of the European eel have also been found to show evidence of marine residency in the North and Baltic Seas (Tsukamoto et al. 1998, Tzeng et al. 2000). Jessop et al. (2002) also found that American eels in the growth phase yellow stage irregularly migrated between freshwater and estuary. Therefore, migration into freshwater in anguillid eels is not an obligate pathway but a facultative catadromy with seawater residents as an ecophenotype.

It is not clear why during the growth phase some eels migrate to freshwater and others do not. The occurrence of fish migration is generally explained by the existence of a difference in food abundance between marine and freshwater habitats. Gross (1987) proposed that diadromy occurs when the gain in fitness from using a second habitat minus the migration costs of moving between habitats exceeds the fitness from staying in only one habitat. Juvenile anadromous salmon utilize freshwater habitats at high latitudes with low productivity, and they migrate to higher productivity habitats in the ocean for growth before returning to freshwater for breeding. In contrast, catadromous freshwater eels that recruit at low latitudes might migrate upstream into freshwater habitats of higher productivity for growth

before returning to the ocean for breeding.

In the present study, the eels residing in the bay along the Sanriku Coast appeared to be resident sea eels that in some cases had entered freshwater for relatively short periods of time. The observation that these individuals had entered freshwater, but returned to the bay suggests the possibility that the bay has better conditions for feeding and growth than the freshwater habitats in this temperate region which is near the northern limit of the species range. Recently, Arai et al. (2003) found that *A. japonica* in the silver stage caught in Miyako Bay was also sea eel had entire lived in the bay just before the spawning migration to open sea. At high latitudes *A. japonica* might show a reduced tendency to migrate upstream into, or stay in, these northern freshwater habitats of lower productivity for growth. If this is true there may be latitudinal cline in marine habitat use by *A. japonica* throughout its range. Eels that have entered freshwater and remained there have been found using Sr:Ca ratio analysis of eels in more southern parts of Japan (Tsukamoto and Arai 2001), but more research is needed on the proportion of freshwater and marine habitat use by the Japanese eel to determine the importance of each habitat for eels in this northern part of Japan. Further study using analysis of otolith Sr:Ca ratio can be used to evaluate the potential for latitudinal variation in the distribution of sea eels and to begin to estimate their relative contributions to the spawning stock.

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