

Growth and Habitat Residence History of Migrating Silver American Eels Transplanted to Taiwan

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Abstract.—In Taiwan, there has been a shortage of local Japanese eel *Anguilla japonica* elvers for culture, so culturists have imported American eel *Anguilla rostrata* (Le Sueur) elvers from North America to meet their needs. From 1999 to 2001, six exotic adult American eels were found in the estuary of the Kaoping River of Taiwan that had escaped from aquaculture ponds as young eels and stayed in the river until silvering. This study compares growth performance and migratory behavior, using otolith strontium (Sr)/calcium (Ca) ratios of those six American eels with cohabitating Japanese eels and American eels in North America. Regardless of sex, mean age at maturity of the exotic American eels was greater and mean annual growth rate was less than that of Japanese eels in Taiwan and similar to that of American eels in the southern United States. Sr/Ca ratios at the otolith edge of the six exotic American eels, which recorded their salinity history, increased significantly. Furthermore, four of the six exotic American eels spent more than one year in the high-salinity estuary. Their extended residence in the estuary may be due to a delayed spawning migration resulting from a failure to orientate and migrate properly to their native spawning site.

Introduction

Anguillid eels are catadromous fish that spawn in the ocean and grow in freshwater (Tesch 1977). Of the 15 described species and 3 subspecies of anguillid eels in the world (Ege 1939; Castle and Williamson 1974), all are distributed in the Indo-Pacific region except for the European eel *Anguilla anguilla* (L.) and the American eel *A. rostrata* (Le Sueur), which occur in the North Atlantic Ocean. In Taiwan, four native anguillid eels exist: Japanese eel *A.*

japonica Temminck and Schlegel, marbled eel *A. marmorata* Quoy and Gaimard, *A. bicolor pacifica* Schmidt, and Celebes longfin eel *A. celebesensis* Kaup (Tzeng 1982; Tzeng and Tabeta 1983; Han et al. 2001). Of these species, the Japanese eel is most abundant and is commercially important for aquaculture in Taiwan (Tzeng et al. 1995). The catch of Japanese eel elvers is insufficient to meet the aquaculture demand (Tzeng 1996a), and elvers of exotic eel species, mainly American and European eels, have been imported since 1969 and 1977, respectively (Li 1997).

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Six exotic American eels—four females (AR1 to AR4) and two males (AR5 and AR6)—were caught in the estuary of the Kaoping River of Taiwan; these were distinguished from Japanese eels (Han et al. 2002) by their different morphology. These eels had thick snouts, round heads, abundant mesenteric fat, and unusually large eyes. Vertebral counts, quantified gonadal histology, and phylogenetic analysis of the mitochondrial cytochrome b gene validated them as American eels in the silver stage (Han et al. 2002). These eels had escaped from culture ponds early in life and had lived in the Kaoping River for years.

Otolith Sr/Ca ratios, in combination with age data, were used to reconstruct the environmental history of these exotic American eels and assist interpretation of their life history. The concentration of strontium (Sr) is approximately 100-fold greater in seawater than in freshwater, and the Sr/Ca ratio in otoliths is positively correlated to ambient salinity (Tzeng 1996b; Campana 1999), making the Sr/Ca ratio a valuable tool for analyzing migration behavior of eels (Tzeng et al. 1997, 2002, 2003). In this study, we (1) compared annual growth rate of the exotic American eels with that of Japanese eels collected at the same time in the Kaoping River and with that of American eels in North America and (2) examined their life history traits (e.g., age at maturity and migration).

Materials and Methods

Specimen Collection

A total of 61 silver Japanese eels and six exotic American eels were collected by plastic eel pots in the Kaoping River estuary of southern Taiwan from 1999 to 2001 (Figure 1) (Han et al. 2002, 2003). The pots were fixed on the bottom along the riverbank. After collection, eels were immobilized with ice and immediately transferred to the labora-

tory for detailed analysis. Total length ($TL \pm 0.1$ cm) and body weight ($BW \pm 0.1$ g) were measured. Sex of each eel was determined by histological examination of the gonads. Maturation stages were determined, following Han et al. (2002, 2003), by coloration of the pectoral fins and the dorsal region, as well as by silver color on the belly and gonadal development. Growth and age at maturity of the exotic American eels were compared with those of American eels in North America reported in the scientific literature.

Otolith Preparation for Age Determination and Sr/Ca Ratio Analysis

Sagittal otoliths, the largest of the three pairs of otoliths in the inner ear, were used for determining Sr/Ca ratios and ages of the 61 silver Japanese eels and six exotic American eels. An electron probe microanalyzer (EPMA, JEOL JXA-8900R) was used to measure otolith strontium (Sr) and calcium (Ca) concentrations. The procedure for preparing the otoliths for Sr/Ca ratio analysis followed that of previous studies (Tzeng et al. 1997). Sr and Ca concentrations in the otolith were measured from the primordium to the otolith edge at an interval of 20 μm with an electron beam diameter of 5 μm . The accelerating voltage of EPMA was set at 15 kV and probe current at 5 nA. After microchemistry analysis, the otolith was polished to remove the carbon coating and etched 1–2 min with 5% EDTA to reveal the annular marks for age determination (Tzeng et al. 1994, 1997).

Back Calculation of Total Length at Annulus Formation and Growth Rate Measurement

The radii from the primordium to the glass eel mark (r_o), annuli (r_n) and otolith edge (R) were measured to estimate total length at annulus formation (l_n) by the Dahl-Lea formula (Francis 1990):

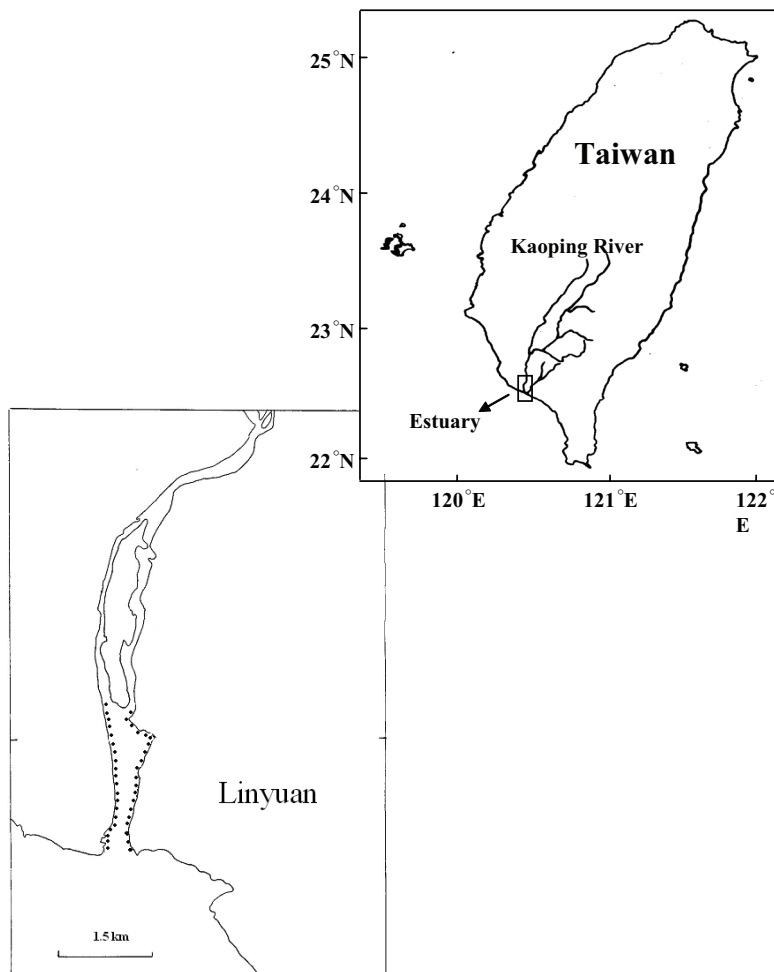


Figure 1. Sampling site of Japanese and exotic American eels in the estuary of the Kaoping River of southern Taiwan. Dots along the shore indicate where eel pots were set.

$$l_n = l_o + (r_n - r_o) (R - r_o)^{-1} (L - l_o)$$

where L is total length of the silver eel at capture. Total length at the glass eel stage (l_o) was defined as 54 mm, based on Tzeng and Tabeta (1983). Mean absolute annual growth rate (G) for individual silver eels was calculated according to the formula:

$$G = (l_n - l_{n-1})$$

where l_n is total length at year n and l_{n-1} is total length at year $n-1$. Mean annual growth rates (G_a) for each geographic and sex group

were estimated as $G_a = \text{mean TL (mm)}/\text{mean age (yr)}$ to enable comparison of data from other sites.

Statistical Analysis

Differences in morphometric indexes among exotic American eels in Taiwan, native American eels in Nova Scotia, Canada, and native Japanese eels in Taiwan were examined by using analysis of variance (ANOVA) followed by Tukey's multiple comparison test, as appropriate. The variable data for each ANOVA were logarithmically (base 10)

Table 1. Morphological characters of the six exotic silver American eels (AR1-AR6) collected in the Kaoping River estuary from 1999 to 2001.

Specimen Characters	AR-1	AR-2	AR-3	AR-4	AR-5	AR-6
Date of collection	Jul. 1999	Jul. 1999	Oct. 2000	Sep. 2000	Feb. 2001	Feb. 2001
Total length (mm)	700	612	635	515	425	415
Body weight (g)	454.6	519.2	591.2	236.3	129.4	125.1
Sex	F	F	F	F	M	M
Age (yr)	10+	9+	10+	8+	8+	9+
G_a (mm/yr)	66.7	64.4	58.8	58.5	52.5	45.6

transformed to reduce their heterogeneity of variance and nonnormality of distribution (differences were considered significant at $\alpha \leq 0.05$).

Results

Comparison of Morphological Indices Among Eel Species and Locations

Length of the female exotic American eels ranged from 515 to 700 mm and the males from 415 to 425 mm, while ages ranged from 8 to 10 years (Table 1). Females were significantly longer ($F = 15.26$, $df = 1,4$, $P = 0.017$) and heavier ($F = 15.63$, $P = 0.017$) than males and grew faster ($F = 31.18$, $P = 0.005$) but were similar in age at maturity ($F = 0.88$, $P = 0.40$). Mean total length and body weight of the male exotic American eels in the silver stage were larger than those of American eels in Nova Scotia and smaller than those of Japanese eels (male TL: $F = 163.3$, $df = 2,53$, $P < 0.001$; male BW: $F = 158.1$, $df = 2,53$, $P < 0.001$) (Table 2a, 2b). Mean TL of the female exotic American eels was similar to that of Japanese eels and larger than that of American eels from Nova Scotia, while body weight was greater than that of American eels from Nova Scotia and less than Japanese eels (female TL: $F = 51.1$, $df = 2,69$, $P < 0.001$; female BW: $F = 30.6$, $df = 2,69$, $P < 0.001$). Mean ages of Amer-

ican eels of both sexes in Taiwan were lower than those of eels from Nova Scotia but higher than those of Japanese eels (male: $F = 126.5$, $df = 2,53$, $P < 0.001$; female: $F = 127.1$, $df = 2,69$, $P < 0.001$) (Table 2c).

Comparison of Mean Annual Growth Rate Among Exotic American Eels

Back-calculated annual growth rate (G) of the six exotic American eels varied greatly (Figure 2). Growth in the first year was not rapid, as is usually observed in cultured eels due to nutrition (Tzeng, personal observation). Alternatively, if these eels grew slowly in the culture ponds for some reason, their life span in the ponds would not exceed two years because farmers commonly drain the ponds every two years. Because of their older ages at capture, it is obvious that these exotic American eels escaped from the culture ponds very early in life.

Comparison of Growth Rate Among Eel Species and Locations

For each sex, mean annual growth rate (G_a) of exotic American eels from Taiwan was much lower than that of Japanese eels from Taiwan but much higher than eels from Nova Scotia (male: $F = 361.7$, $df = 2,53$, $P < 0.001$, $CA < TA < TJ$; female: $F = 330.3$, $df = 2,69$, $P < 0.001$, $CA <$

Table 2. Comparison of total length (cm), body weight (g), and age at maturity (yr) of American eels from Taiwan (TA) and Nova Scotia, Canada (CA), and Japanese eels from Taiwan (TJ).

	Canada (American eel)				Taiwan (American eel)				Taiwan (Japanese eel)				Comparison
	<i>n</i>	mean	range	SD	<i>n</i>	mean	range	SD	<i>n</i>	mean	range	SD	
Total length													
Female	26	47.0	37.8–74.0	8.7	4	61.6	61.2–70.0	7.7	42	64.1	49.8–78.5	6.3	CA<TA=TJ
Male	35	35.5	32.6–41.2	1.8	2	42.0	41.5–42.5	0.7	19	55.6	44.1–67.5	7.1	CA<TA<TJ
Weight													
Female	26	211.4	92.6–882.2	179.1	4	450.3	454.6–591.2	153.2	42	452.7	163.6–829.3	169.9	CA<TA=TJ
Male	35	78.9	62.7–115.2	10.0	2	127.3	125.1–129.4	3.0	19	269.4	148.0–461.5	98.8	CA<TA<TJ
Age													
Female	26	17.1	10–29	4.1	4	9.9	8–10	0.9	42	6.9	4–10	1.5	CA>TA>TJ
Male	35	15.4	10.22	3.0	2	8.6	8–9	0.7	19	5.3	4–7	1.5	CA>TA>TJ

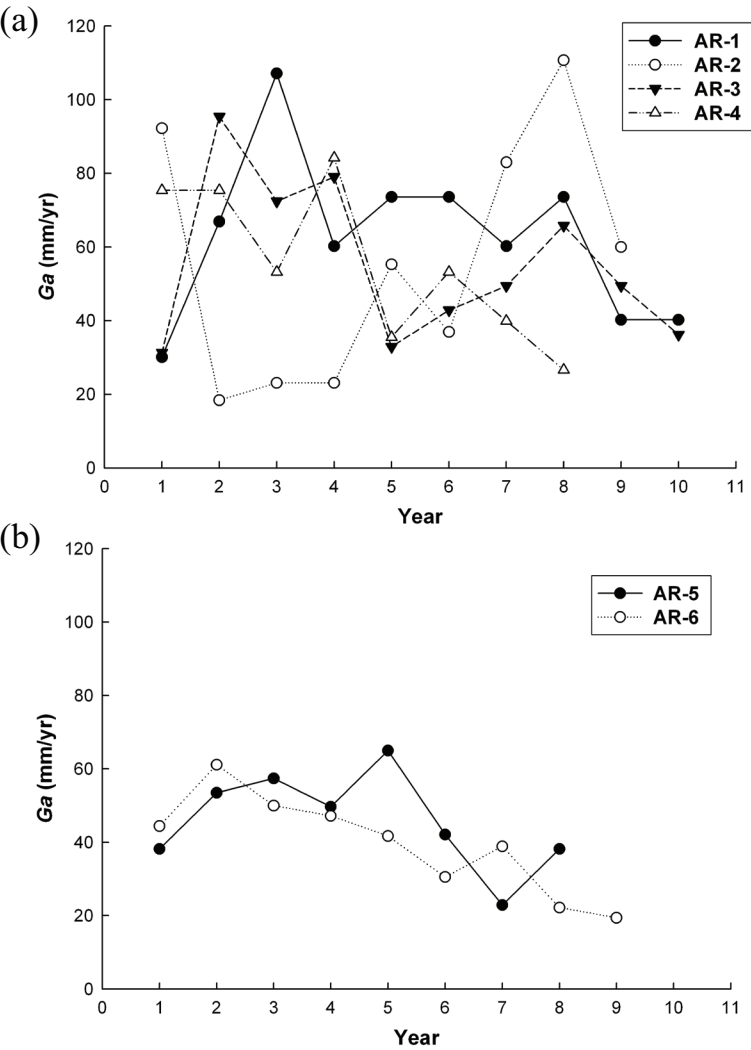


Figure 2. Comparisons of back-calculated annual growth rate for (a) four female and (b) two male exotic American eels in Taiwan.

TA < TJ) and slightly lower than that of eels from the southern United States (Table 3). Although no statistical comparison can be made, the mean G_a values are sufficiently similar that no significant difference likely exists between American eels in Taiwan and those in the southern United States. The Nova Scotia habitat has low pH and low productivity and would be expected to have eels with a lower growth rate than those from a more productive site at that latitude.

Mean annual growth rate of native male (r

= -0.94, 95% CI = -1.0 to -0.80, $n = 5$, $P < 0.001$, estimated by the bootstrap method) and female ($r = -0.69$, 95% CI = -0.87 to -0.37, $n = 12$, $P = 0.016$) American eels declines significantly with increasing latitude (Oliveira 1999; Jessop, unpublished data). American eels from a wide range of latitudes also showed a better significant negative correlation between G_a and age at maturity for each sex (male: $r = -0.95$, 95% CI = -1.0 to -0.88, $n = 5$, $P < 0.001$; female: $r = -0.86$, 95% CI = -0.96 to -0.71, $n = 12$, $P < 0.001$), while no significant correla-

Table 3. Comparison of latitude, total length (TL), age, and annual growth rates (G_a) by sex for silver American eels (AR) from North America and Taiwan and silver Japanese eels (AJ) from Taiwan

Site	Latitude		TL		Age		G_a		TL		Age		G_a		References
	(°N)	Sex	n	(mm)	(yr)	(mm•yr ⁻¹)	Sex	n	(mm)	(yr)	(mm•yr ⁻¹)	Sex	n	(mm)	
East R., NS (AR)	44.6	F	27	468	17.1	23.8	M	35	354	15.4	19.1				Jessop et al. 2002
Cooper R., SC (AR)	33.2	F	19	563	7.9	64.8									Hansen and Eversole 1984
Charleston Hbr., SC (AR)	32.8	F	38	550	5.8	85.9									Michener and Eversole 1985
Ogeechee R., GA (AR)	32.1	F	7	584	8.6	61.9	M	73	329	5.5	50.4				Facey and Helfman 1987
Altamaha R., GA (AR)	31.4						M	8	387	4.1	81.7				Helfman et al. 1984
Kaoping R., Taiwan (AR)	22.4	F	4	616	9.9	62.2	M	2	420	8.6	48.8				This study
Kaoping R., Taiwan (AJ)	22.4	F	42	628	6.8	92.9	M	19	556	6.3	88.8				This study

tion was found between G_a and TL at the silver stage for either male ($r = 0.32$, $n = 5$, $P = 0.60$) or female ($r = -0.06$, $n = 12$, $P = 0.86$) eels (Jes-sop, unpublished data).

Sr/Ca Ratios in Otoliths of Exotic American Eels

Otolith Sr/Ca ratios of the six exotic silver American eels increased from the primordium with a peak at the distance 60–100 μm from the primordium, which corresponded to the timing of metamorphosis from leptocephalus to glass eel (Figure 3). Beyond the check associated with metamorphosis, the otolith Sr/Ca ratios decreased rapidly up to the elver check (EC), which is deposited when glass eels enter freshwater in the estuary. Otolith Sr/Ca ratios were greater than 4.0‰ in the early life of five of the six eels. The 4.0‰ Sr/Ca ratio distinguishes between freshwater and seawater habitats (Tzeng et al. 2002, 2003). Sr/Ca ratios increased, exceeding 4.0‰ only at the very edge of the otolith for two eels (AR-1 and AR-3, Figure 3); this was coincident with silvering. However, Sr/Ca ratios at the edge of the otoliths of the other four eels were greater than 4.0‰ for several years (Figure 3). This indicated that these four eels had migrated into and resided in the high-salinity water of the estuary a number of years earlier.

Discussion

In the wild, juvenile eels from northern latitudes grow for a much shorter period of the year than do those from southern latitudes because annual temperatures are lower in the north and above the growth threshold for a shorter period of time. Thus, northern eels are expected to have a lower annual growth rate than more southerly eels. This decreased growth rate may also be reflected in the age of maturity (Vøllestad 1992). Exotic male American eels in Taiwan silvered and migrated to the sea within the range of lengths and

growth rates of emigrants in North America. This was consistent with the observation that size of male American eels is not correlated with latitude (Oliveira 1999). As expected, female silver American eels in Taiwan also migrated at sizes more comparable to those in the southern United States, confirming the negative correlations between latitude, length at migration, and growth rate. These results are consistent with Oliveira's (1999) conclusion that the panmictic life cycle of the American eel prevents long-term selection of growth rates in different habitats and that growth rates result from environmental conditions in a habitat. American eels in Taiwan were older at migration and grew much more slowly than did native Japanese eels, suggesting between-species differences in biological characteristics or reduced adaptability to environmental conditions substantially different from those of streams, even in the southern United States.

Sr/Ca ratios at the otolith edges of Japanese eels increased significantly from the yellow to the silver stages, confirming that eels migrate from freshwater to high-salinity waters during silvering (Han et al. 2003). For the six exotic American eels, the Sr/Ca ratio had increased at the otolith edge (<4‰) only very recently for two individuals (AR-1 and AR-3) but was elevated for two to three years for the other four eels (Figure 3). If the rise of Sr/Ca ratios at the otolith edges coincided with silvering, then the spawning migration of these exotic American eels must have been interrupted, causing them to remain in the estuary.

Silver eels are generally thought not to feed because the digestive tract resorbs (Sinha and Jones 1975; Pankhurst and Sorensen 1984; Han et al. 2003). However, Beulleus et al. (1997) observed that cultured male eels may continue to eat and grow in the silver stage but not feed well. Dollerup and Graver (1985) fed male silver eels in which they had repeatedly induced testes matura-

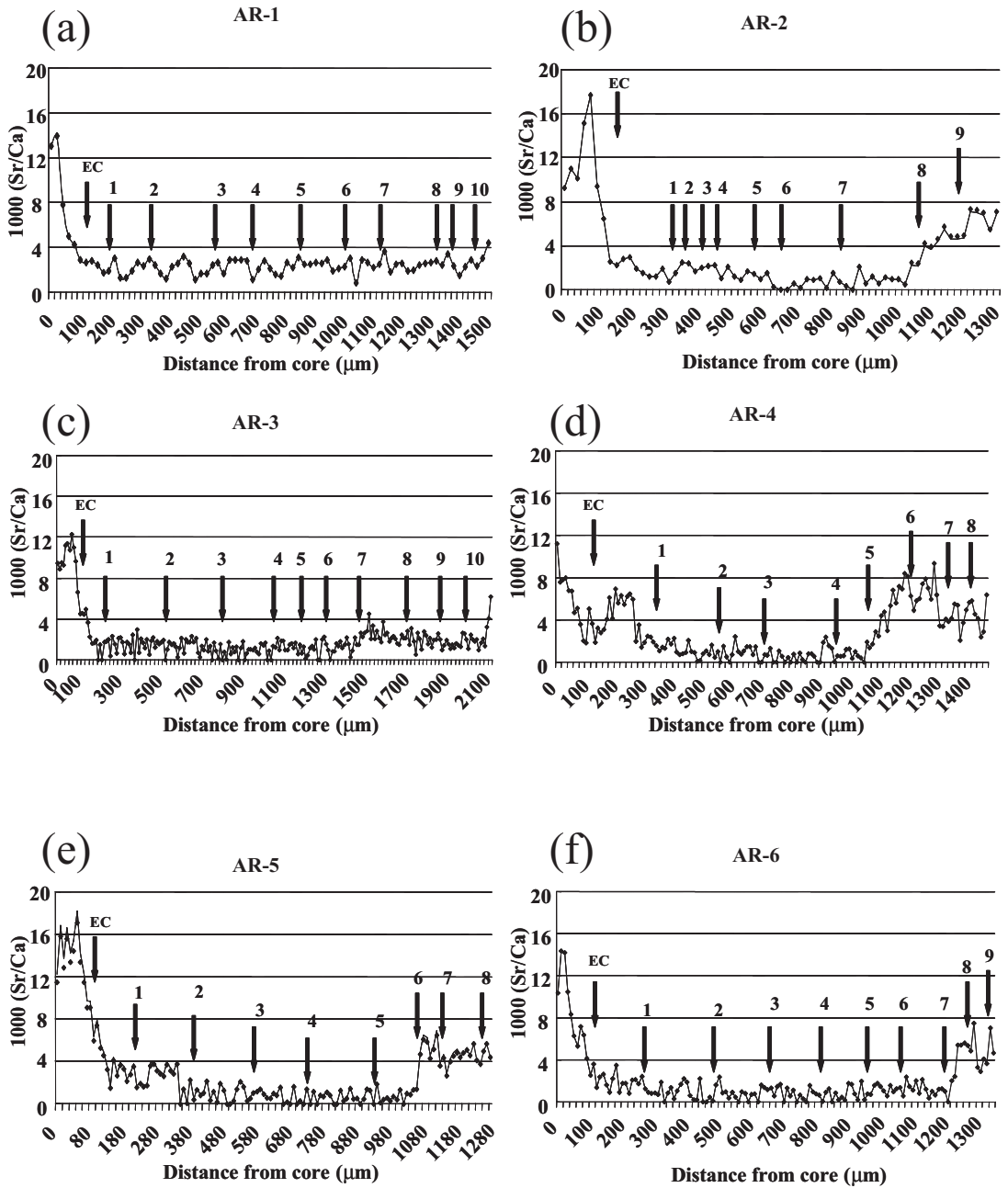


Figure 3. Otolith Sr/Ca ratio analysis for the six exotic American eels from (a) AR-1 to (f) AR-6, respectively. EC indicates the elver check; arrows and numbers (1–10) indicate annuli.

tion with hCG to stimulate sperm development. They found that food intake gradually increased and that the eels grew both in size and weight and their atrophied alimentary tracts regenerated. Thus, silver eels might continue growing, but at a slower rate, if their natural spawning emigration was interrupted. When compared with growth in freshwater, the growth rate of exotic American eels AR-2, 4, and 6 decreased after the fish entered high-salinity water (presumably in the silver stage) (Figure 2). By contrast, Jessop et al. (2004) found that American eel growth was usually higher in estuarine waters than in freshwater. Furthermore, if increased Sr/Ca ratios at the otolith edges represented the silvering stage of the exotic American eels, true mean age and total length at maturity would decrease and mean annual growth rate would increase, becoming more similar to that of American eels in the southern USA (Table 2). We believe that exotic American eels AR-2, 4, 5, and 6 had been in the silver stage for more than one year.

In Japan, exotic European eels have been found in Shinjiko Lake, Mikawa Bay (Zhang et al. 1999), and the Uono River (Aoyama et al. 2000). A migrating silver-phase European eel has also been captured in the East China Sea (Aoyama et al. 2000), indicating that spawning migration of introduced eels might be possible. Since the life cycle and larval transport routes of American eels and Japanese eels are, in general, quite similar (i.e., North Equatorial Current and Kuroshio Current in the north Pacific for Japanese eels; North Equatorial Current and Gulf Stream in the North Atlantic for American eels) (Cheng and Tzeng 1996; Wang and Tzeng 1998, 2000), interspecific hybridization could occur (Han et al. 2002). However, the silver exotic American eels found in the estuary of the Kaoping River in Taiwan seemed to encounter some difficulty orienting properly to a potential spawning site. Thus, the threat of hybridization by exotic American eels with

Japanese eels seems unlikely. Further study is needed to assess the ecological importance of in-stream and migratory behaviors of exotic anguillid eels.

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