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Disparities in habitat use and migratory behavior between tropical eel *Anguilla marmorata* and temperate eel *A. japonica* in four Taiwanese rivers

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ABSTRACT: Strontium (Sr):calcium (Ca) ratios in otoliths of the eels *Anguilla japonica* and *A. marmorata* caught in 4 Taiwanese rivers were examined to reconstruct their migratory environmental history. In all sampling locations, each eel species preferred a different environment and all were differently distributed in the river. *A. japonica* was more abundant than *A. marmorata* in the lower reach, accounting for 76 to 86% of the eel population. In contrast, *A. marmorata* was more abundant than *A. japonica* in the upper reach, accounting for 76 to 100% of the eel population. *A. japonica* consisted of diversified migratory contingents, including freshwater, brackish-water and seawater eels, but *A. marmorata* tended to reside in freshwater and seemed to avoid seawater during the yellow eel stage. This disparity in migratory behaviors and habitat use between species may reflect interspecific competition and adaptive radiation. The flexible migratory behavior and adaptation to different salinities of *A. japonica* may be an advantageous evolutional fitness when facing competition, heavy fishing pressure and environmental stress. The freshwater-restricted *A. marmorata* is more easily threatened by both fishing pressure and continuous habitat degradation than *A. japonica*.

KEY WORDS: *Anguilla japonica* · *Anguilla marmorata* · Otolith microchemistry · Environmental history · Migratory behaviors · Adaptive radiation

INTRODUCTION

There are 4 species of *Anguilla* eels in Taiwan. *A. japonica* is the most abundant, followed by *A. marmorata*. The other 2 tropical species, *A. bicolor pacifica* and *A. celebesensis*, are rare and only occasionally found in the estuaries of Taiwan (Tzeng 1982, 1983, Tzeng & Tabeta 1983, Tzeng et al. 1994, Han et al. 2001). *A. japonica* is a temperate species, occurring from Taiwan through to Japan in NE Asia (Ege 1939, Tesch 1977). The eels spawn west of the Mariana Islands (Tsukamoto 1992). Their leaf-like leptocephalus larvae take ca. 4 to 5 mo to migrate with the North Equatorial and Kuroshio Currents, and metamorphose into transparent glass eels on the edge of the NE Asian continental shelf (Tzeng 1990, 2003, Tzeng & Tsai 1994, Cheng & Tzeng 1996). The glass eels become pigmented elvers in the estuaries and live in the river for approximately 5 to 8 yr, during which they develop from elvers to the yellow and silver eel stages. The sexually maturing silver eels migrate to the spawning ground, where they die after spawning.

Anguilla marmorata is widely distributed in NE Asia and the Indo-Pacific Ocean. It is an endangered species in Taiwan. Budimawan (1997) and Arai et al. (2002a,b) have reported its age at recruitment and seasonal occurrence in the estuaries of Japan, Taiwan and other Pacific countries. They may spawn west of the Mariana Islands, like *A. japonica* (Miller & Tsukamoto

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2001). The species is relatively long-lived; a 17 yr old female *A. marmorata* was found in the Pearl River of south China (Williamson 1993). Knowledge of this eel's life history is very limited.

Anguilla japonica and *A. marmorata* coexist in Taiwanese rivers, and may share the same niches, use the same demersal habitats and forage for the same prey (Tzeng et al. 1995). Thus, interspecific competition might play an important role in regulating their habitat use and population size. Mechanisms may exist to avoid interspecific competition and attain maximum benefit for each eel species in the river. Habitat segregation and behavior differentiation might be the effective means. Fishermen's experience has indicated that *A. japonica* is dominant in the lower reach of the river and estuary, while *A. marmorata* dominates in the middle to upper reaches of the river. However, in many small brooks of Taiwan, ecological niches are seriously compressed, so that there is no apparent boundary to distinguish lower reach from middle reach, or middle reach from upper reach. Consequently, the presumed segregative distribution of the 2 eel species in the rivers needs evaluation. Tzeng et al. (2002) found that *A. japonica* tended to stay in brackish waters in the rivers of Taiwan. The other temperate eels, *A. anguilla* in Europe, and *A. rostrata* in North America, also have a flexible migratory life cycle, i.e. a portion of the eel population might skip freshwater residence and live in estuarine and coastal waters until maturation (Tzeng et al. 1997, 2000a, Tsukamoto et al. 1998, Tsukamoto & Arai 2001, Jessop et al. 2002). Whether the tropical eel *A. marmorata* has a similarly flexible migratory behavior or merely resides in freshwater, is still unclear and intriguing.

Fish otoliths are metabolically inert and grow by seasonal accretion throughout the life of the fish (Pannella 1971). Strontium (Sr) can substitute for calcium (Ca) in the process of otolith deposition, because it has a similar ionic charge and radius to Ca (Payan et al. 1999). The concentration of Sr is approximately 100-fold greater in seawater (8.7×10^{-5} M) than freshwater (9×10^{-7} M) (Campana 1999) and the Sr:Ca ratios in fish otoliths are higher in marine and brackish waters than in freshwater (Tzeng 1996a). Thus, otolith Sr:Ca ratios are extensively used to study the migratory environmental history of diadromous fishes (Radtke et al. 1988, 1990), including freshwater eels (Otake et al. 1994, Tzeng & Tsai 1994, Arai et al. 1997, 1999, Tzeng et al. 1997, 2000a, Kawakami et al. 1998, Jessop et al. 2002).

The aim of this study is to (1) reconstruct the migratory environmental history of *Anguilla marmorata* and *A. japonica* in Taiwanese rivers by examining otolith Sr:Ca ratios using an electron probe microanalyzer (EPMA) and to determine their age by examining otolith annuli, (2) examine the adaptive distribution of *A. japonica* and *A. marmorata* in the rivers, and (3) compare the distribution and migratory environment of these 2 species, to improve understanding of the species-specific habitat use and migratory behavior of anguillid eels.

MATERIALS AND METHODS

Fish collection and sampling area. *Anguilla japonica* and *A. marmorata* of yellow and silver eel stages were collected with a bamboo eel pot (Fig. 1). The pot was approx. 100 cm long and 10 to 15 cm in diameter, and an earthworm was placed inside as bait. The eel pot was set on the river bottom, with the entrance facing downstream, and was retrieved the following morning to check the catch. Each eel collected was measured to the nearest 5 mm in total length and dissected to determine its sex by gonadal histology (Han et al. 2001). The developmental stage of each eel was determined by its morphological characteristics, e.g. size, color, diameter of eyes and degree of sexual maturation. The specimens used for otolith Sr:Ca ratio analysis and age determination from each location and species are listed in Table 1.

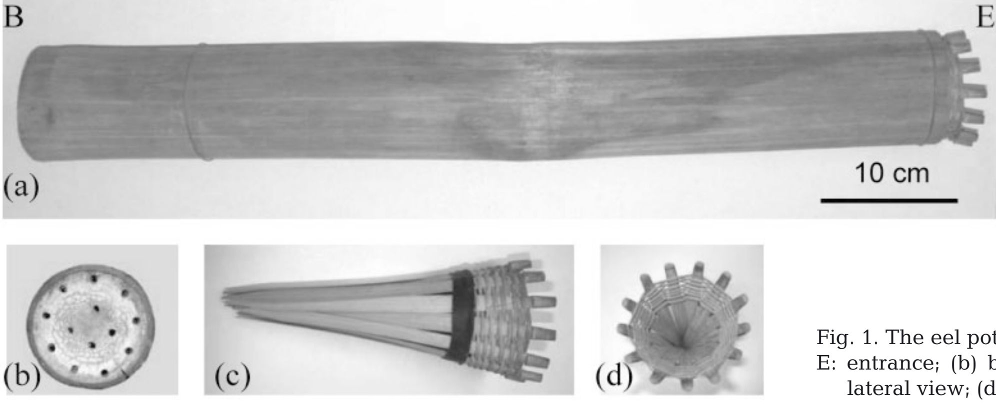

Fig. 1. The eel pot. (a) Lateral view, B: bottom, E: entrance; (b) bottom view; (c) funnel cap, lateral view; (d) funnel cap, bottom view

Table 1. *Anguilla japonica* and *A. marmorata*. Mean (±SD) total length and body weight, by developmental stages and sex, from the middle (M) and lower reaches (L) of 4 rivers in Taiwan. Numerals in parentheses under 'Sample size' are the numbers of specimens aged

Sampling site Date	Species	Sex	Sample size	Total length (mm) Mean ± SD (range)	Weight (g) Mean ± SD (range)	Age (yr) Mean ± SD (range)
Touchien River Jun 1998	*A. japonica*	Female	12(7)	529.0 ± 102.2 (347–687)	279.8 ± 199.1 (62.9–711.4)	5.4 ± 1.3 (3–7)
		Male	2(2)	603.0 ± 22.6 (578.7–619)	435.7 ± 125.8 (346.7–524.6)	7.0 ± 0.0 (7)
		Undetermined	5(5)	410.1 ± 71.7 (306–484)	106.9 ± 54.3 (48.8–172.4)	4.4 ± 1.1 (3–6)
	A. marmorata	Undetermined	6(6)	443.2 ± 92.0 (338–580)	247.2 ± 215.4 (80.0–663.0)	5.5 ± 1.2 (4–7)
Kaoping River	*A. japonica*	Female (M)	5(4)	495.0 ± 51.6 (433–562)	179.2 ± 59.2 (121.1–259.8)	6.3 ± 2.3 (5–9)
May, Nov 1998		Female (L)	33(12)	513.4 ± 95.6 (397–696)	254.7 ± 220.3 (56.5–869.3)	5.2 ± 0.9 (4–6)
May 1999		Male (M)	2(1)	417.0 ± 77.8 (362–472)	133.8 ± 83.5 (54.7–113.8)	4
Apr, May 2000		Male (L)	4(3)	514.6 ± 118.1 (357.5–631)	271.1 ± 181.0 (50.9–461.5)	5.0 ± 0.0 (5)
Oct 2001		Undetermined (M)	1(1)	361	53.2	4
		Undetermined (L)	19(19)	336.7 ± 97.2 (222–539)	71.1 ± 72.1 (12.9–246.4)	3.8 ± 1.0 (2–5)
	A. marmorata	Female (M)	2(2)	498.5 ± 30.4(477–520)	348.9 ± 90.2 (285.1–412.6)	6.5 ± 0.7 (6–7)
		Female (L)	2(2)	501.5 ± 75.7 (448–555)	347.0 ± 180.1 (219.6–474.3)	5.5 ± 0.7 (5–6)
		Male (M)	3(3)	477.3 ± 31.2 (455–513)	281.4 ± 67.5 (220.2–353.8)	5 (5)
		Male (L)	1(1)	534	354.2	7
		Undetermined (M)	20(20)	411.9 ± 86.3 (272–572)	215.1 ± 160.8 (41.2–543.4)	4.9 ± 1.1 (3–7)
		Undetermined (L)	5(5)	469.3 ± 87.2 (378–612.5)	296.1 ± 253.1 (111.2–736.3)	5.4 ± 2.1 (4–9)
Linpien River May 1999	*A. marmorata*	Female	1(1)	513	356.3	7
		Male	1	343	86.6	–
		Undetermined	63(52)	271.6 ± 71.3 (166–504)	54.3 ± 57.2 (9.6–344)	3.1 ± 1.3 (2–6)
Hsiukuluan River Aug 1998	*A. marmorata*	Male	1(1)	339	125.3	4

Eels were collected between 1998 and 2001 from the Touchien River, northern Taiwan, the Kaoping and Linpien Rivers in southern Taiwan, and the Hsiukuluan River in eastern Taiwan. A single survey, duration approx. 3 to 5 d, was conducted in each of the Touchien, Linpien, and Hsiukuluan Rivers. In the Kaoping River, 6 surveys were carried out. The eels in the Touchien River were sampled at the head of tidal influence, just downstream of a small dam, and upstream in the middle reach of the river (Fig. 2).

The Kaoping River is the largest river in Taiwan, approx. 171 km long with a drainage area of 3256 km^2. The lower reach (Lin-yuan) of the river is an estuary containing environments from freshwater to brackish water and a salinity range from 0 to 32 ppt. The middle reach (Chi-san) of the river is a freshwater environment about 40 km from the coast.

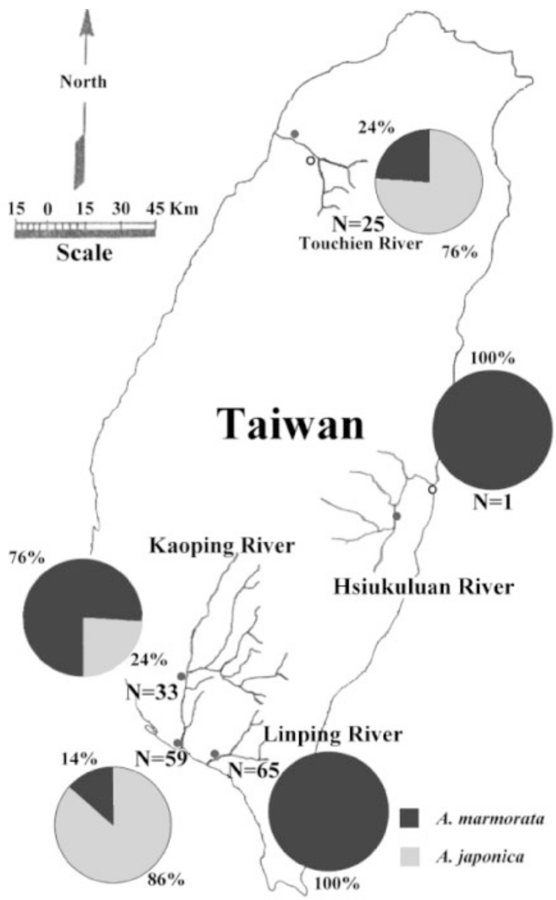

Fig. 2. *Anguilla japonica* and *A. marmorata*. Species composition of eels collected in the lower and middle reaches of the 4 rivers. ●: Sampling site; ○: no eel was collected

Two small agricultural irrigation dams occur in the middle and upper reaches of the river. The annual river discharge of the river was approx. 8455 million m^3, with 761 million m^3 flowing during the dry season (October to March) and 7694 m^3 during the rainy season (April to September).

The Linpien River, 42 km long, has a drainage area of 344 km^2. No water reservoirs or dams occur in this small river except in the upper reach. The sampling site was in freshwater about 6 km from the coast. The water level at the sampling site was about 50 cm deep but became almost dry about 5 km further upstream. The sampling site, although not far from the coast, should be regarded as a middle-reach environment in this short river.

The sampling sites in the middle and lower reach of the Hsiukuluan River are also freshwater environment. The river, 81 km long, is the largest river in eastern Taiwan and has a drainage area of 1790 km^2 that drains into the Pacific Ocean.

Otolith preparation and Sr:Ca analysis. Otoliths were embedded in epofix resin, ground and polished until their primordium was exposed. For electron probe microanalysis, the polished otolith was carbon-coated under a high vacuum evaporator. Sr and Ca concentrations from the primordium to the otolith edge were quantified using an EPMA. A JEOL JXA-8900R system, equipped with wavelength dispersive X-ray spectrometers, was used. Quantitative analyses were conducted using beam conditions of 15 kV for the acceleration voltage, 3 nA for the current, and a 5 × 4 µm rectangular scanning beam. The quantitative data were corrected by the ZAF method to calculate oxide compositions (Goldstein et al. 1984), using the standard calibration of calcite ($CaCO_3$, NMNH 136321) and strontiantite ($SrCO_3$, NMNH R10065). Sr concentration was measured for 80 s at Sr *L*α peak positions and 20 s at both the lower and upper sides of the baseline. Ca was measured for 20 s at the Ca *K*α peak and for 10 s at both sides of the baseline. After Sr:Ca ratio analysis, the otolith was polished again to remove the carbon layer and etched for 1 to 2 min with 5% EDTA to reveal annular marks for age determination. Then, the time spent by the eel in different habitats was determined by examining the temporal trend in the Sr:Ca ratio, relative to their observed value ranges in freshwater, estuarine and marine conditions.

RESULTS

Species composition of the eels

The species composition of the eels differed among sampling sites (Fig. 2). In the lower reach of the Touchien River, 76% (n = 25) of eels were *Anguilla japonica* and 24% were *A. marmorata*, while no eels were found in the middle reach of the river. In the lower reach of the Kaoping River, 86% (n = 59) of eels were *A. japonica* and 14% were *A. marmorata*. In the middle reach of the Kaoping River, 24% (n = 33) of eels were *A. japonica* and 76% were *A. marmorata*. All eels in the lower reach of the Linpien River (n = 65) and the middle reach of the Hsiukuluan River (n = 1) were *A. marmorata* (100%). No eels were caught in the lower reach of the Hsiukuluan River.

Size and relative growth

Mean (±SD) total lengths of the eels from the 4 Taiwanese rivers ranged from 271.6 to 501.5 mm, and weights ranged from 54.3 to 348.9 g for *Anguilla marmorata*, and from 336.7 to 603.0 mm and 71.1 to 435.7 g for *A. japonica* (Table 1). The size ranges overlapped between species and rivers. The sexes of 2 to 4 yr old *A. marmorata* from the middle reach of the Kaoping River and lower reach of the Linpien River were mostly undetermined because of gonadal immaturity. The length (X)–weight (Y) relationship was $Y = 5.6 \times 10^{-8} X^{3.5}$ for *A. japonica* and $Y = 5.7 \times 10^{-7} X^{3.2}$ for *A. marmorata* (Fig. 3). The relative growth of length and weight was significantly different between these 2 eel species (analysis of covariance, $F = 12.2$, $p < 0.001$, $t = 3.5$, $p < 0.001$ for slope, $t = 12.5$, $p < 0.001$ for intercept). *A. marmorata* was heavier than *A. japonica* at similar lengths.

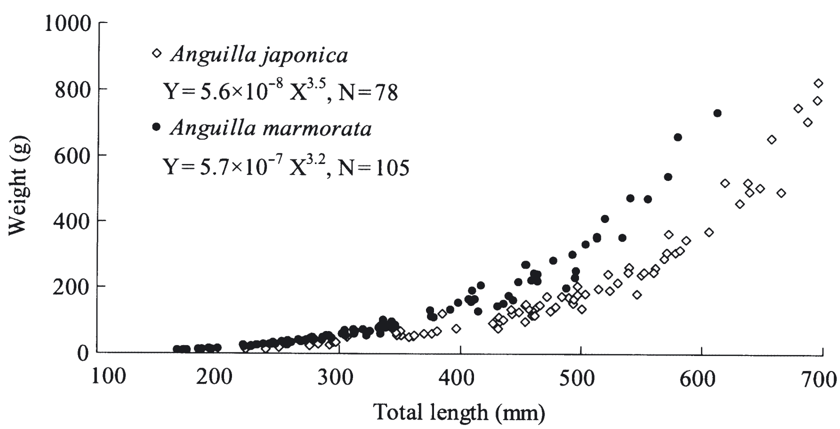

Fig. 3. *Anguilla japonica* and *A. marmorata*. Length–weight relationships

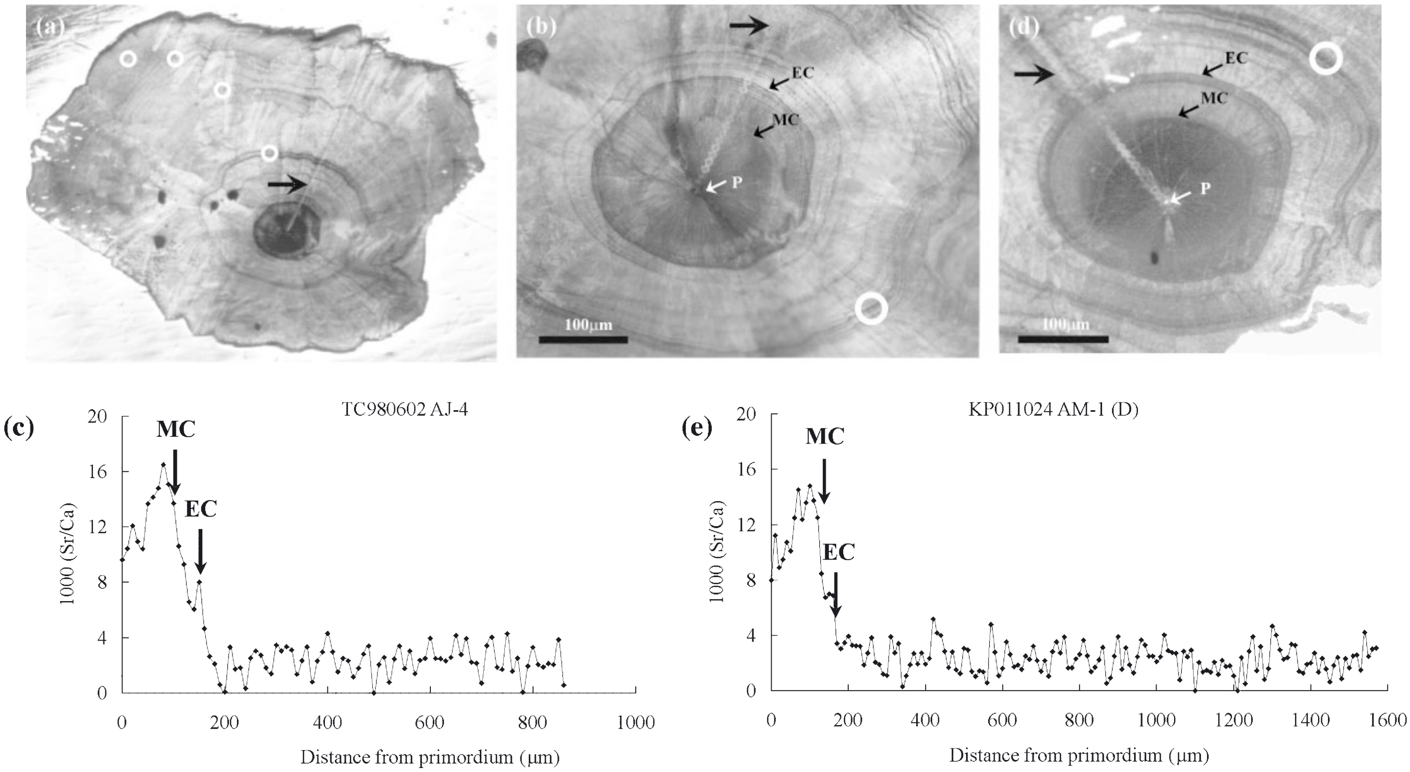

Fig. 4. *Anguilla japonica* and *A. marmorata*. (a,b,d) Growth checks and (c,e) corresponding changes of Sr:Ca ratios in otoliths of *A. japonica* (a–c) and *A. marmorata* (d,e). Panel (b) was magnified from (a). Thick arrows in (a), (b) and (d): spots of Sr:Ca ratio measurements; open circles: annuli; P: primordium; MC: metamorphosis check; EC: elver check

Growth check and corresponding Sr:Ca ratios in otolith before elver stage

The electron probe created an approx. 1 µm deep hole in the sectioned surface of the otolith during the measurement of Sr:Ca ratios. The position of the hole in combination with the growth check could be used as a time marker to understand the chronological change of the Sr:Ca ratios in otoliths, such as the check of metamorphosis from leptocephalus to glass eel, the check for the elver at estuarine arrival, and the annulus of the adult eel (Fig. 4a,b,d).

The Sr:Ca ratios in the otolith of a selected *Anguilla japonica* increased from approx. 10×10^{-3} in the primordium to a peak of approx. 16×10^{-3} at a distance of 110 µm from the primordium, which corresponded to the timing between metamorphosis from the leptocephalus to the glass eel stage. The Sr:Ca ratios decreased to approx. 7×10^{-3} when the glass eel became an elver at estuarine arrival (Fig. 4c). Similar changes in both otolith growth check and Sr:Ca ratios were also found in *A. marmorata* (Fig. 4d,e). This indicates that the environmental history of these 2 eels was similar during the marine leptocephalus stage. However, the patterns of the Sr:Ca ratios beyond the elver stage were greatly different between these 2 species (Figs. 5 & 6).

Sr:Ca ratios in *Anguilla japonica* otolith

For the 6 eels collected from the middle reach of the Kaoping River, the otolith Sr:Ca ratios beyond the elver check were all lower than 4×10^{-3}, with a highest value of 3.7×10^{-3} (Fig. 5a, Table 2). The sampling site of these eels was a purely freshwater environment about 40 km from the coast and completely free from tidal influence. Thus, eels with otolith Sr:Ca ratios lower than 4×10^{-3} can be considered to be freshwater residents and eels with Sr:Ca ratios larger than 4×10^{-3} can be regarded as estuarine or marine residents. Based on these criteria, the environmental history of *Anguilla japonica* beyond the elver stage was classified into 3 different migratory contingents:

Type 1 (freshwater contingent): all Sr:Ca ratios from elver mark to the edge of otolith were less than 4×10^{-3}. All eels from the middle reach of the river were Type 1, as were 14% of the eels from the lower reach of the Kaoping River (Table 2). The mean (±SD) Sr:Ca ratios in otoliths of Type 1 eels in the middle reach

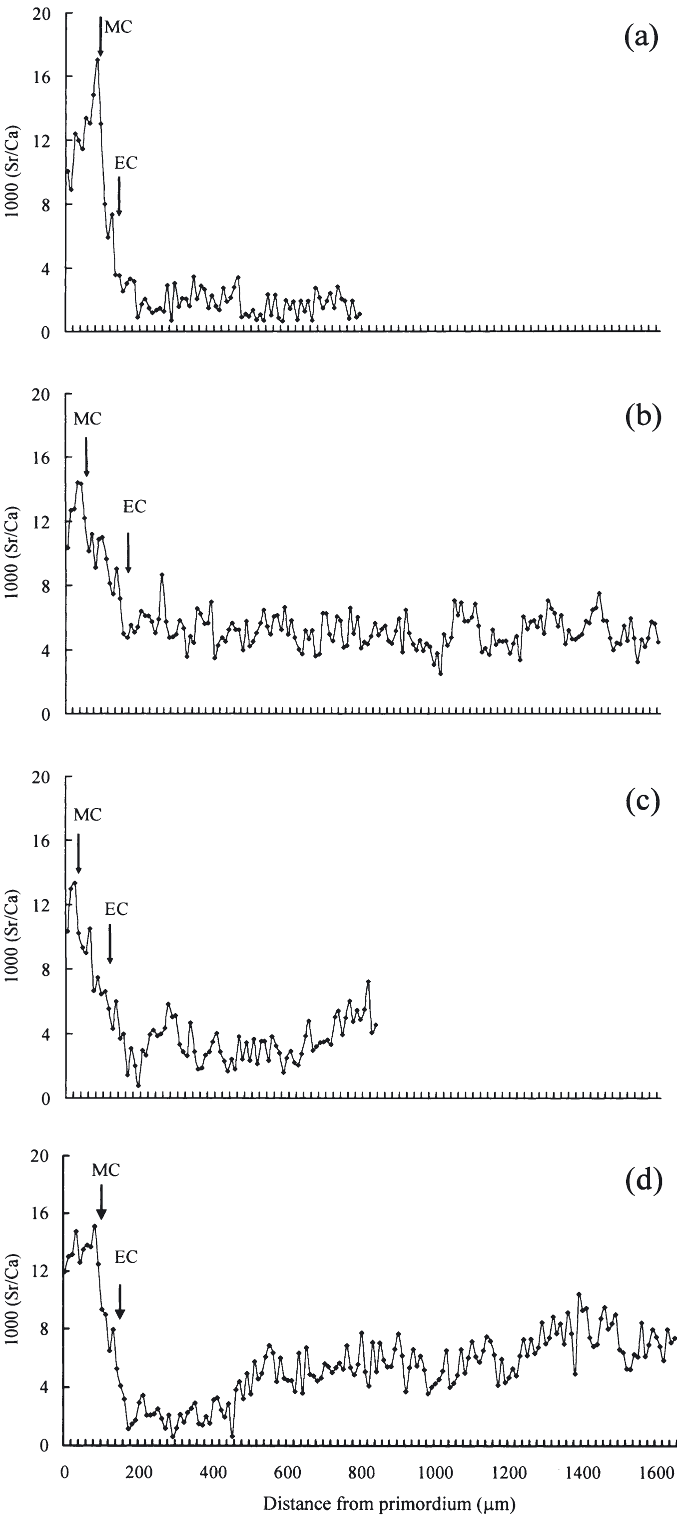

Fig. 5. *Anguilla japonica.* Temporal changes in the Sr:Ca ratios of otoliths of different migratory contingents, collected from the middle and lower reaches of the Kaoping River. (a) Type 1 (freshwater), (b) Type 2 (seawater), (c,d) Types 3a and 3b (estuarine). EC: elver check, MC: metamorphosis check. Panel (a): 41.8 cm yellow eel, (b): 63.5 cm silver eel, (c): 45.1 cm silver eel, (d): 59.3 cm silver eel

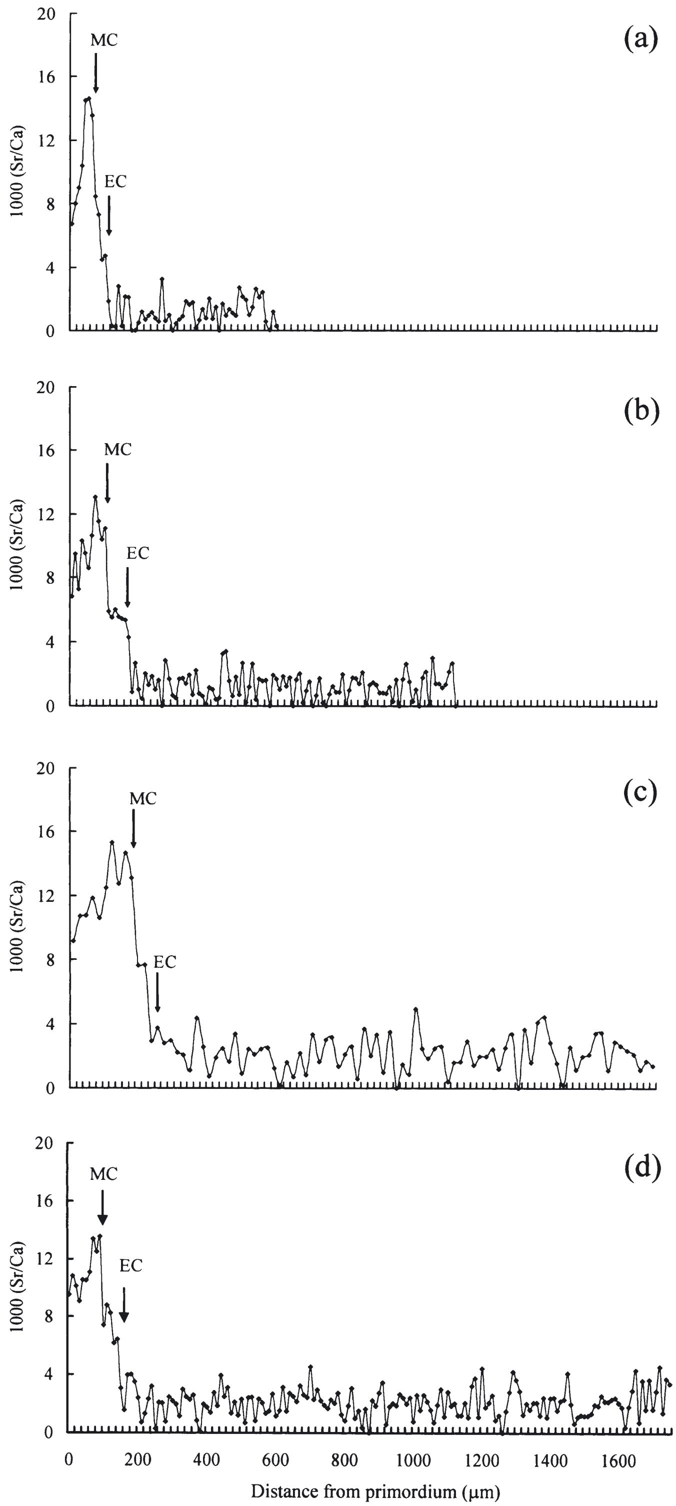

Fig. 6. *Anguilla marmorata.* Temporal changes in the Sr:Ca ratios of otoliths of different migratory contingents collected from the lower reach of the Linpien River. (a,b) Type 1 (freshwater), (c,d) Type 3a (estuarine). Panel (a): 22.1 cm yellow eel; (b): 32.5 cm yellow eel; (c): 43.1 cm yellow eel; (d): 62.3 cm silver eel

Table 2. *Anguilla japonica* and *A. marmorata*. Mean (±SD) Sr:Ca ratios in otoliths, classified by their life history patterns. Type 1: freshwater, Type 2: seawater, Type 3a: estuarine with freshwater predominant, where more than half of the otolith Sr:Ca ratio measurements were less than 4×10^{-3}, Type 3b: estuarine with seawater predominant, where more than half of the otolith Sr:Ca ratio measurements were greater than 4×10^{-3}. Mean Sr:Ca ratios were calculated from elver check to otolith edge. n: sample size, LP: Linpien River, Mid-KP: middle reach of Kaoping River, Low-KP: lower reach of Kaoping River, TC: Touchien River, HKL: Hsiukuluan River

Life history pattern	Mean Sr:Ca ratio × 10^{-3}																	
	A. marmorata											*A. japonica*						
	n	LP	n	Mid-KP	n	Low-KP	n	TC	n	HKL	Total	n	Mid-KP	n	Low-KP	n	TC	Total
Type 1	46	1.6 ± 0.9	8	2.0 ± 0.9	1	2.1 ± 0.2	4	2.0 ± 1.0	1	1.8 ± 0.9	60	6	1.8 ± 0.2	8	2.2 ± 0.8	3	2.0 ± 0.9	17
Type 2											0			3	5.5 ± 1.1			3
Type 3a	6	1.7 ± 1.0	12	2.0 ± 1.0	6	2.0 ± 1.0	2	2.2 ± 0.9			26			35	3.1 ± 1.5	9	2.2 ± 1.1	44
Type 3b														12	4.6 ± 1.5			12
Total	52		20		7		6		1		86	6		58		12		76

($1.8 \pm 0.2 \times 10^{-3}$, range: 0.0 to 3.7×10^{-3}) were very close to those in the lower reach of the Kaoping River ($2.2 \pm 0.8 \times 10^{-3}$, range: 0.0 to 4.5×10^{-3}) (Table 2). Three *Anguilla japonica* (25%) from the Touchien River were also Type 1, with a mean Sr:Ca ratio of $1.98 \pm 0.9 \times 10^{-3}$, which was also very close to that of the Type 1 eels from the Kaoping River (Table 2).

Type 2 (seawater contingent): of the 58 eels collected in the lower reach of the Kaoping River, 3 (5%) were Type 2. The mean Sr:Ca ratio in the otoliths of Type 2 eels beyond the elver stage was $5.5 \pm 1.1 \times 10^{-3}$ (range 2.5 to 8.8×10^{-3}) (Table 2). The higher and varied Sr:Ca ratios in the otoliths of Type 2 eels indicated that they seasonally migrated to high-salinity seawater during their stay in the lower reach (Fig. 5b).

Type 3 (estuarine contingent): of the 58 eels collected from the lower reach of the Kaoping River, 47 (81%) were Type 3 (Table 2). After the elver stage, the mean Sr:Ca ratios in the otoliths of Type 3 eels varied considerably among individuals. Type 3 eels did not have consistently low or high Sr:Ca ratios as did those of Types 1 and 2. Type 3 eels illustrated a variety of temporal patterns in the Sr:Ca ratios of their otoliths (Fig. 5c,d). Type 3 eels were further divided into 2 subtypes, according to the duration of their estuarine residence, which varied from several months to years. Type 3a (freshwater-favoring contingent) had Sr:Ca ratios less than 4×10^{-3} over more than half of their life span, while Type 3b (seawater-favoring contingent) had Sr:Ca ratios greater than 4×10^{-3} over more than half of their life span. Type 3a eels were approx. 3 times more abundant than Type 3b, indicating that this species preferred freshwater when they migrated into the estuary (Table 2). In the Touchien River, 75% of *Anguilla japonica* (9 eels) were Type 3a, with a mean Sr:Ca ratio of $2.2 \pm 1.1 \times 10^{-3}$.

Sr:Ca ratios in *Anguilla marmorata* otolith

The mean Sr:Ca ratios in Type 1 *Anguilla marmorata* otoliths were similar to those of Type 1 *A. japonica* (Table 2). No Type 2 or 3b eels were found for *A. marmorata*. The pattern of Sr:Ca ratios in otoliths of *A. marmorata* of Type 3a (Fig. 6c,d) was more similar to that for Type 1 (Fig. 6a,b) than for Type 3a of *A. japonica* (Fig. 5c). The *A. marmorata* of Type 3a had few spots with Sr:Ca ratios higher than 4×10^{-3}, indicating that *A. marmorata* did not frequently inhabit a highly saline environment.

In the Linpien River, 46 *Anguilla marmorata* were Type 1 (88%) and 6 were Type 3a (12%). The mean otolith Sr:Ca ratios of Type 1 ($1.6 \pm 0.9 \times 10^{-3}$) and Type 3a ($1.7 \pm 1.0 \times 10^{-3}$) eels were similar (Table 2). In the middle reach of the Kaoping River, of 20 eels, 8 (40%) were Type 1 and 12 (60%) were Type 3a, with mean

Sr:Ca ratios of $2.0 \pm 0.9 \times 10^{-3}$ and $2.0 \pm 1.0 \times 10^{-3}$, respectively (Table 2). In the lower reach of the Kaoping River, of 7 eels, 1 was Type 1 (14%) and 6 (86%) were Type 3a, with mean Sr:Ca ratios of $2.1 \pm 0.2 \times 10^{-3}$ and $2.0 \pm 1.0 \times 10^{-3}$, respectively (Table 2). The mean otolith Sr:Ca ratios were not significantly different between Types 1 and 3a eels, whether they were from the middle or lower reach of the Kaoping River (2-way ANOVA, $p = 0.83$ for Types 1 and 3a, $p = 0.38$ for middle and lower reaches, and $p = 0.19$ for interaction). In the Touchien River, 4 eels were Type 1 (67%) and 2 eels (33%) were Type 3a, with mean Sr:Ca ratios of $2.0 \pm 1.0 \times 10^{-3}$ and $2.2 \pm 0.9 \times 10^{-3}$, respectively (Table 2). The only *A. marmorata* caught in the Hsiukuluan River was also Type 1, with a mean otolith Sr:Ca ratio of $1.8 \pm 0.9 \times 10^{-3}$. Of the total 86 eels, 60 individuals (70%) were of the completely freshwater contingent (Type 1) and 26 individuals (30%) resided in brackish water for a short period (Type 3a, Table 2). This indicates that *A. marmorata* is a freshwater-oriented species in the growth phase (yellow eel stage).

DISCUSSION

Habitat segregation

The difference in percentage composition of *Anguilla japonica* and *A. marmorata* between middle and lower reaches of the Kaoping River (Fig. 2) indicated that *A. marmorata* tended to reside in the upper reach while *A. japonica* tended to reside in the lower reach of the river. In contrast, all of the 65 eels caught in the lower reach of the Linpien River approx. 6 km from the river mouth were *A. marmorata*, and no *A. japonica* were found. Although the lower reach of the Linpien River was not far from the coast, it was free from the influence of tidal flux. The sampling site in the Linpien River, which consisted of shallow water and fast current, was more similar to a middle reach than to a lower reach. Thus, this environment was not attractive to *A. japonica* but was attractive to *A. marmorata*, which became dominant in the lower reach of the Linpien River. Most (88%) of the 65 eels from the Linpien River were of the freshwater type (Table 2). This also supported the hypothesis of a geographic separation in the distribution of these 2 species within the river.

Anguilla marmorata and *A. japonica* also differed in microhabitat preferences. *A. marmorata* preferred deep pools in the river, whereas *A. japonica* preferred sandy and muddy substrates with shelters. Eels of different size also differed in habitat preference. The larger eels tended to reside in deep pools in the upper reach, but small eels chose shallow waters in the lower reach of the river. The deep pool in the middle reach of the Kaoping River was approximately 2 m deep, which was suitable for adult *A. marmorata*. The upper reach of the Linpien River was not suitable, however, because it became too shallow during the dry winter season. The drought conditions commonly found in the steep and short rivers of Taiwan may negatively influence the migratory behavior and habitat use of the eel by confining it to isolated, deep pools and interrupting their movement between pools.

Different migratory behavior

Anguilla japonica has a more phenotypic plasticity than *A. marmorata*, and can be classified into freshwater, seawater and estuarine contingents (Table 2, Fig. 5). Approx. 80% of *A. japonica* in the lower reach of the Kaoping River were estuarine-oriented, as was noted by Tzeng et al. (2002, 2003). In contrast, *A. marmorata* was mainly freshwater-oriented and apparently avoided residence in a brackish water environment, as inferred from the few Sr:Ca ratios higher than 4×10^{-3} in the otoliths of the Type 3 eels (Table 2, Fig 6c,d). One possible explanation for this difference in migratory behavior and habitat use between species is that the brackish water habitat was overwhelmingly dominated by *A. japonica*. Consequently, no surplus estuarine habitats were available for *A. marmorata*. Therefore, *A. marmorata* was expelled to the upper reaches, where the habitats were less productive and unstable. In contrast, if *A. marmorata* occupies fresh water habitats in the middle and upper reaches of rivers, *A. japonica* would be expelled to the lower reach.

These 2 eel species may have coped with interspecific resource competition by allopatric rather than sympatric distribution (Fig. 2). Interspecific competition possibly plays an important role in the distribution of the 2 eel species in the river. Migrating to the upper river takes greater risk and costs more energy than residing in estuary and the lower river. If no interspecific interaction exists, it seems difficult to explain the geographic separation of the 2 eel species in the river. Environmental factors as well as the interspecific interactions might influence the habitat choice of fish. The specific differences in habitat choice should be carefully interpreted because the difference might not be a simple interaction among competitors (Helfman et al. 1997). A species occurs where it does because the fish functions best there, i.e. the choice of habitat reflects the use of physiologically optimal environments rather than being the result of interactions with other species over limiting resources. If this is what governs the habitat choice of *Anguilla japonica* and *A. marmorata*, brackish waters may be the optimal environment for *A. japonica* and freshwater for *A. marmorata*. Chloride cells in the gill epithelium of

A. japonica markedly increased during their first week after transfer from freshwater to seawater (Shirai & Utida 1970). When the seawater adapted eel was transferred to freshwater, their chloride cells degenerated slowly over the following 10 wk. The ability of chloride cells to develop quickly is essential for euryhaline fish such as *A. japonica*, to maintain a constant osmolality under variable salinity environments such as the estuary. No study on the salinity tolerance of *A. marmorata* has yet been conducted, and we do not know if it can adapt to large changes in salinity during the yellow stage. If it can, it should have evolved a phenotypic behavior similar to that of *A. japonica*, and may then be expected to compete for the same resources. However, *A. marmorata* does not have as many migratory contingent types as *A. japonica*.

A hypothesis of adaptive radiation

To date, 3 temperate eels, *Anguilla anguilla*, *A. rostrata* and *A. japonica*, have been found to have flexible migratory patterns, including freshwater, seawater and estuarine contingents (Tzeng et al. 2000b, 2002, 2003, Tsukamoto & Arai 2001, Jessop et al. 2002). Whether the other 2 temperate eels *A. australis* and *A. dieffenbachii* have similar behavior is not clear. *A. dieffenhachii* and *A. australis* are usually found in the brackish estuaries of New Zealand (Jellyman et al. 1997) and numerous *A. australis* reside in a salty inland lake in South Australia (L. McKinnon pers. comm.). *A. australis* and *A. dieffenbachii* yellow eels are evidently able to regulate the plasma osmolality in hyper-saline environments. Thus, they are likely to have different migratory contingents.

Temperate eels are believed to have evolved from tropical eels (Ege 1939, Aoyama et al. 1996, Aoyama et al. 2001, Lin et al. 2001). If the tropical species, such as *A. marmorata*, conserved the freshwater preference in the growth phase, the temperate species have to adapt to seawater to find vacant niches, and this may have led them to develop diversified migratory contingents. The salinity choice by the congeners of the eel may be regarded as 'character displacement' similar to that for other species for adaptive radiation (Brown & Wilson 1956, Schluter 1994, 2000). Estuarine and coastal waters have higher productivity than freshwater rivers in the temperate zone, while freshwater rivers have higher productivity than seawater in the tropical zone (Gross 1987). Occupation of the lower reach of rivers and coastal waters in the temperate area could have optimal evolutionary fitness for temperate eels such as *A. japonica*. The tropical eel *A. marmorata* is an ancient species of the freshwater eel that seems to have a more conservative, freshwater-oriented migratory life cycle in which they migrate upstream to expand their habitat. But in subtropical Taiwan, where the temperate and tropical species coexist, the most productive lower reach of the river would be best for both species groups. Since these 2 eel species are apparently geographically segregated in distribution, productivity of the river seems not to be the only or determinant factor in eel distribution, especially when similar species coexist in the same river. Otherwise, *A. marmorata* would be as abundant as *A. japonica* in the estuary and lower reach, where the productivity is generally higher than in the upper reach of the river. A disparity in habitat preferences reflects the biological differences between the species, such as growth, feeding preferences, and preferences for water temperature, depth and bottom type. *A. marmorata* may simply out-compete *A. japonica* in the habitat typical of the upper reaches of freshwater streams, and conversely *A. japonica* may out-compete *A. marmorata* in the lower reaches and estuary, forcing them upstream. Competition combined with 'evolutionarily developed preferences' seems a more plausible explanation for the geographic segregation in *A. japonica* and *A. marmorata* distribution.

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