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Effects of metamorphosis timing and the larval growth rate on the latitudinal distribution of sympatric freshwater eels, *Anguilla japonica* and *A. marmorata*, in the western North Pacific

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Abstract

Background: Early life history traits of the temperate eel *Anguilla japonica* and tropical eel *Anguilla marmorata* were examined to determine the possible reason why these two species have similar spawning areas and oceanic larval transport in the North Equatorial Current and yet are recruited to different but partly overlapping continental growth habitats in northern East Asia. To understand the segregative migration of these two sympatric eel species, their glass eels were collected from nine estuaries in the Philippines, Taiwan, Japan, and China. The age at metamorphosis from leptocephalus to glass eel (T_m), the age at estuarine arrival (T_t), the time between metamorphosis and estuarine arrival (T_{t-m}), and the growth rate (G_t) of glass eels were calculated from daily growth increments in their otoliths.

Results: Results indicated that the G_t was faster and the T_m was younger in *A. marmorata* than in *A. japonica*. On the other hand, fish length and the T_t at estuarine arrival were larger in *A. japonica* than in *A. marmorata*, indicating that elvers of *A. japonica* experience a longer oceanic drift than those of *A. marmorata*. In addition, the T_{t-m} also indicated that *A. japonica* experienced a longer coastal migration than *A. marmorata*.

Conclusion: This study validated that the T_m and G_t seem to play important roles in the segregative migration and latitudinal distribution of these two sympatric freshwater eel species in the northwestern Pacific.

Keywords: Otolith; Daily growth increment; Japanese eel; Giant mottled eel; Larval migration

Background

Due to their mysterious life history and economic importance, freshwater eels (*Anguilla* spp.) have been the focus of much scientific research for decades. However, despite these efforts, most of the aspects of their early life history are still not completely understood. In the past three decades, dramatic declines in glass eel recruitment of temperate species like the American (*Anguilla rostrata*), European (*Anguilla anguilla*), Japanese (*Anguil la japonica*), and Australian (*Anguilla australis*) eels have raised concerns (Jellyman et al. 2000; Hoyle and Jellyman 2002; Tatsukawa 2003; Dekker 2008; Richkus and Whalen 2000). The reasons for the declines are unclear but are probably due to reductions in spawning stocks (Jansen et al. 2007; Winter et al. 2007; Clevestam et al. 2011), overfishing (Tzeng et al. 1995; Moriarty and Dekker 1997; Jellyman et al. 2000; Hoyle and Jellyman 2002; Briand et al. 2003; Chisnall et al. 2003; Dekker 2003; Lin et al. 2010), growth habitat and access reductions (Busch et al. 1998; Haro et al. 2000; McCleave 2001; McCleave and Jellyman 2004; Verreault et al. 2004; Graynoth et al. 2008), pollution (Amiard-Triquet et al. 1988; Robinet and Feunteun 2002; Palstra et al. 2006; van Ginneken et al. 2009), swim bladder and gill parasites and viral infections (Haenen et al. 2002; Szekely et al. 2002; Kirk 2003; Sures and Knopf 2004; van Ginniken et al. 2005; Han et al. 2008, 2009a; Sasal et al. 2008; Parker et al. 2011), global climate change

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(Castonguay et al. 1994; Kimura et al. 2001; Casselman 2002; Knights 2003; Han et al. 2006, 2009b; Friedland et al. 2007; August and Hicks 2008; Bonhommeau et al. 2008; Miller et al. 2009), and the solar cycle (Tzeng et al. 2012). To understand the declines, it is necessary to study the early life history of anguillid eels. The life history of eels during the continental growth phase is well documented, but knowledge of the marine larval life stage from the spawning ground to the estuary is still fragmented (McCleave 1993; Cheng and Tzeng 1996; Wang and Tzeng 2000; Tzeng 2003; Edeline et al. 2009; Miller 2009). Early life history information is very important because it is a key factor in understanding possible reasons for recruitment success or failure of anguillid eels and also for their artificial propagation.

The temperate eel *A. japonica* and tropical eel *Anguil la marmorata* are just two dominant species of anguillid eels in Taiwan, the distribution and recruitment season of which differ (Tzeng 1982; Tzeng and Tabeta 1983; Kuroki et al. 2009; Leander et al. 2012). Both species spawn in waters west of the Mariana Islands in the Pacific Ocean (Kuroki et al. 2009; Tsukamoto et al. 2011), and their marine larvae or leptocephali are transported westward by the North Equatorial Current (NEC) from their spawning grounds to the continental shelf of the northwestern Pacific. Furthermore, *A. marmorata* larvae drift in both the northwardly flowing Kuroshio Current (KC) and the southwardly flowing Mindanao Current, while *A. japonica* larvae only enters the northwardly flowing KC that transports them to East Asia, particularly Taiwan, China, Japan, and Korea. Why *A. japonica* larvae only enter the KC region, while *A. marmorata*, after being transported by the NEC, can enter both the northwardly flowing KC (which carries them to eastern China, southern Japan, and Korea) and the southwardly flowing Mindanao Current (that carries them to recruitment areas in northern Indonesia, the Philippines, and Taiwan), is still unclear (Kuroki et al. ×2009). Recently, Han et al. (2012) pointed out that recruitment temperature preferences and oceanic current systems control the distinct biogeography of *A. japonica* and *A. marmorata*. Aside from these abiotic parameters, biological factors should also be taken into consideration in explaining this ecological discrepancy, but the early life histories of these two species particularly during the oceanic phase are not yet fully understood, especially that of *A. marmorata*. Upon reaching continental waters, it was also found that their distributions in estuaries also geographically differed. For example, *A. japonica* is abundant along the northern and western coasts of Taiwan, while *A. marmorata* is abundant along the southern and eastern coasts (Leander et al. 2012; Han et al. 2012). In addition, it was also observed that in the same river system, *A. marmorata* occupied the upper reaches while *A. japonica* occupied the lower reaches (Shiao et al. 2003). These observations indicated that microhabitats of these species evolved differently to avoid interspecific competition for food and space, although their distribution areas overlap. Also, genetic (mitochondrial DNA and microsatellites) and morphological (total number of vertebrae) studies suggested that *A. marmorata* has at least four or five different spawning populations in the entire Indo-Pacific region: the North Pacific (Sulawesi/northern Indonesia, the Philippines, Taiwan, China, Korea, and Japan), South Pacific (Fiji, New Caledonia, and Papua New Guinea), Indian Ocean (Madagascar, Reunion, and Sumatra), Micronesia (Guam, Palau, and the Caroline Islands), and Tahiti (Ishikawa 1998; Ishikawa et al. 2004; Minegishi et al. 2008; Watanabe et al. 2008, 2009).

Recent studies specifically on *A. japonica* (Tzeng 2003) indicated that the otolith microstructure and microchemistry can provide some clues to understanding the early life history of fish during their migration from spawning grounds until recruitment, but little is known about the early life history of most tropical species, particularly *A. marmorata* (Sugeha et al. 2001a; Arai et al. 2002a, b; Miller et al. 2002; Shiao et al. 2003). Also, it was found that the age at metamorphosis from the leptocephalus to glass eel can be determined by changes in otolith microstructures and in strontium/calcium (Sr/Ca) ratios in daily growth increments (DGIs) of otoliths (Tzeng and Tsai 1992, 1994; Tzeng 1995). The Sr concentration in the otolith decreases dramatically during metamorphosis, and a visible metamorphosis check (MC) is also deposited during this period. Since the growth increments of otoliths of anguillid eels are deposited on a daily basis (Martin 1995; Arai et al. 2000; Cieri and McCleave 2001; Sugeha et al. 2001b), the age of the leptocephalus at metamorphosis can be determined from the number of DGIs from the primordium and the MC where the increment pattern and Sr/Ca ratios dramatically change (Tzeng and Tsai 1994; Tzeng 1996; Arai et al. 1999a). In other words, since the structure of growth increments in the anguillid eel's otoliths change with growth and growth checks appear in every life history stage transition, the duration of each life history stage can be determined by counting the DGIs in each section of an otolith.

In the present study, we reviewed the early life history of the temperate eel *A. japonica* which was studied by Cheng and Tzeng (1996). Meanwhile, the early life history of the tropical eel *A. marmorata* collected from three estuaries in the Philippines, Taiwan, and Japan was also studied following the techniques used for *A. japonica* in a previous study (Cheng and Tzeng 1996). Only the North Pacific population of *A. marmorata* was considered in the present study. Based on information such

as the timing of metamorphosis from leptocephalus to glass eel, the inshore migration period of the glass eel, the age and size at estuarine arrival, and growth rates of leptocephali and glass eels, we attempted to understand the evolution and adaptation of these two sympatric species in their distribution areas. Segregative migration and the recruitment mechanism of these two species in the northwestern Pacific were also addressed.

Methods

Fish sample collection

In total, 168 *A. marmorata* glass eels were collected from the estuaries of the Hsiukuluan River, eastern Taiwan (n = 86) on 20 May 2008; the Cagayan River, northern Philippines (n = 45) on 19 May 2008; and the Kurio River, southern Japan (n = 37) on 6 June 1996 (Table 1, Figure 1). Procedures of fish handling were carried out in accordance with the ethical standards and guidelines for animal experiments of National Taiwan University. All specimens were immediately preserved in 95% ethanol after measuring the total lengths (TLs) to the nearest millimeter (mm). On the other hand, *A. japonica* specimens examined from a previous study (Cheng and Tzeng 1996) were collected from the estuaries of the Tungkang River, southern Taiwan (n = 60) on 30 December 1992 and 24 March 1993; the Shuangshi River, northern Taiwan (n = 60) on 20 December 1992 and 17 February 1993; the Mingchiang River, eastern China (n = 30) on 1 March 1993; the Chyantarng River, eastern China (n = 30) on 17 February 1993; the Yalu River, northern China (n = 30) on 3 May 1993; and the Ichinomiya River, eastern Japan (n = 30) on 10 January 1994 (Table 1, Figure 1).

Determination of the developmental stages of the fish samples

Developmental stages of eel samples from the glass eel to the elver stages were determined according to the extent (or absence) of skin pigmentation over the head, tail, and other body regions following the methods described by Strubberg (1913), Bertin (1956), and Tesch (1977, 2003). Postmetamorphic juveniles were subclassified into stages V_A, V_B, VI_{A1}, VI_{A2}, VI_{A3}, VI_{A4}, VI_B, and VII. Juveniles up to stage VI_{A2} were classified as glass eels, while those in stages VI_{A3} and VI_{A4} were in the transition stage to elvers, which become fully pigmented

Table 1 Sampling and age information of *Anguilla japonica* and *Anguilla marmorata* specimens analyzed in this study

Species	Sampling site	Sampling date	Number	Total length (mm)	Age (days)		
					T_m	T_t	T_{t-m}
A. japonica[a]	Tungkang River, Taiwan	30 December 1992	30 (16)	57.0 ± 2.0	138.7 ± 14.3	177.7 ± 17.8	39.0 ± 11.2
		24 March 93	30 (14)	56.1 ± 2.4	134.0 ± 14.1	174.4 ± 17.9	40.4 ± 11.0
	Shuangshi River, Taiwan	20 December 92	30 (12)	56.8 ± 2.3	135.7 ± 16.6	175.0 ± 20.9	39.5 ± 9.2
		17 February 93	30 (13)	55.9 ± 2.2	128.9 ± 14.6	174.4 ± 17.7	45.5 ± 13.4
	Mingchiang River, China	1 March 93	30 (20)	55.1 ± 1.9	139.6 ± 10.1	172.1 ± 14.1	32.5 ± 7.7
	Chyantarng River, China	17 February 93	30 (23)	55.6 ± 1.9	148.1 ± 14.7	194.9 ± 18.6	46.8 ± 8.9
	Yalu River, China	3 May 93	30 (23)	58.3 ± 1.8	157.4 ± 16.1	199.3 ± 15.6	41.9 ± 3.9
	Ichinomiya River, Japan	10 January 94	30 (10)	57.4 ± 2.3	143.3 ± 7.9	186.6 ± 7.0	43.3 ± 5.2
Overall (μ_1)			240 (131)	56.5 ± 2.1	140.7 ± 13.6	181.8 ± 16.2	41.1 ± 8.8
A. marmorata	Cagayan River, the Philippines	19 May 08	45 (13)	49.5 ± 1.5	110.4 ± 12.8	144.8 ± 14.2	34.3 ± 7.9
	Hsiukuluan River, Taiwan	20 May 08	86 (13)	51.6 ± 1.6	112.4 ± 12.3	134.0 ± 15.4	22.6 ± 6.6
	Kurio River, Japan	6 June 96	37 (15)	46.7 ± 1.7	117.7 ± 16.8	145.0 ± 17.8	27.3 ± 8.9
Overall (μ_2)			168 (41)	49.3 ± 1.6	113.5 ± 13.0	141.6 ± 15.8	28.1 ± 7.8
Difference ($\mu_1 - \mu_2$)				7.2	27.2	40.2	13.0
Significance				*A. japonica* > *A. marmorata*	*A. japonica* > *A. marmorata*	*A. japonica* > *A. marmorata*	*A. japonica* > *A. marmorata*

[a]Cheng and Tzeng (1996). Values inside parentheses indicate the number of individuals used for aging. Daily age of glass eels at the estuary (T_t), daily age at metamorphosis from leptocephalus to glass eel (T_m) and the time between the metamorphosis check and estuarine arrival (T_{t-m}).

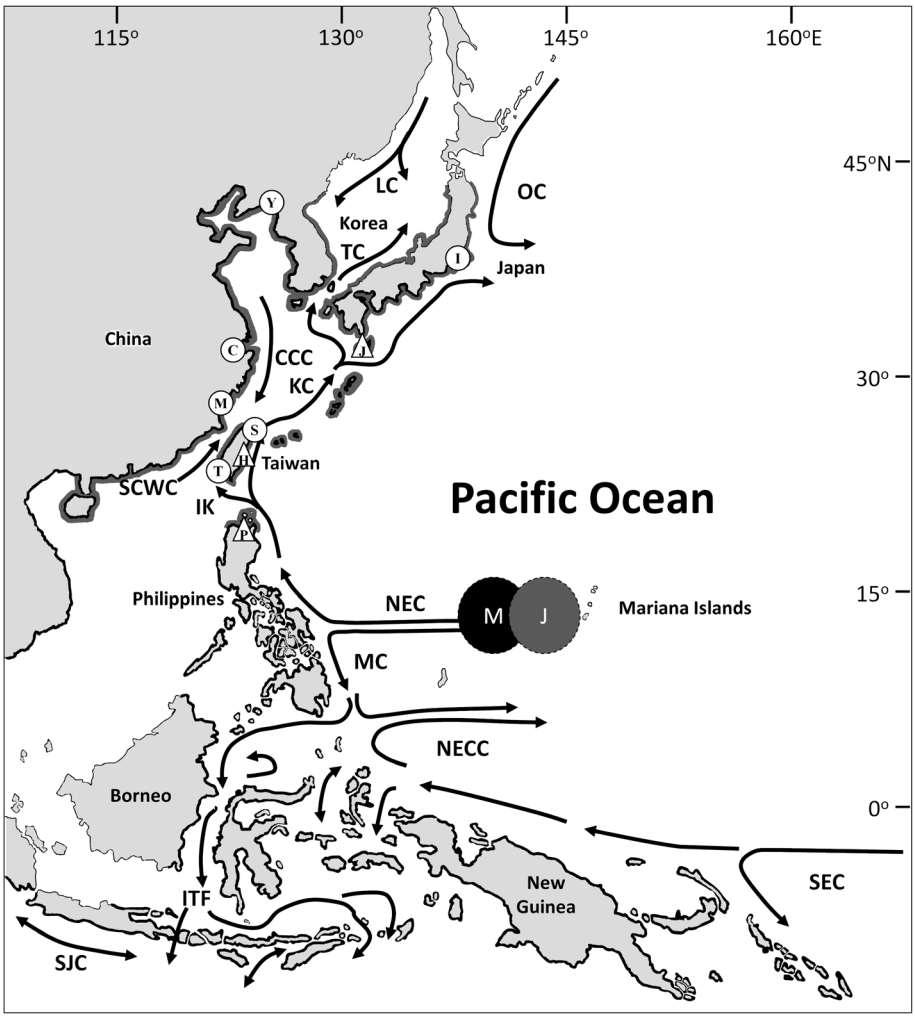

Figure 1 Map showing the geographic distributions of *Anguilla japonica* and *A. marmorata*. Map showing the geographic distributions of *Anguilla japonica* (thick gray lines on the coastlines) and *A. marmorata* (thick black lines on the coastlines) in East Asia and collection sites of samples analyzed in this study (white triangle, *A. marmorata*; white circle, *A. japonica*; Cheng and Tzeng 1996). General patterns of current systems in the western North Pacific and central Indonesian seas (adapted from Nitani 1972 and Lukas et al. 1991) and spawning grounds of *A. japonica* (gray circle with the letter J) and *A. marmorata* (black circle with the letter M) (Kuroki et al. 2009; Tsukamoto et al. 2011) are also shown. Sampling locations: Tungkang River (T) and Shuangshi River (S), Taiwan; Mingchiang River (M), Chyantarng River (C), and Yalu River (Y), China; Ichinomiya River (I), Japan; Cagayan River (P), the Philippines; Hsiukuluan River (H), Taiwan; and Kurio River (J), Japan. NEC, North Equatorial Current; KC, Kuroshio Current; OC, Oyashio Current; TS, Tsushima Current; CCC, China Coastal Current; SCSWC, South China Sea Warm Current; IK, Intruded Kuroshio; MC, Mindanao Current; NECC, North Equatorial Counter Current; SEC, South Equatorial Current.

at stage VI_B stage (Fukuda 2010). Stage VI_B indicates the end of pigmentation, while stage VII represents the fully pigmented, benthic elver (Tabeta and Mochioka 2003).

Otolith preparation for microchemical analyses

Sagittal otoliths, the largest of the three pairs of otoliths in the inner ear, were extracted and embedded in epofix resin. The embedded otolith was ground and polished with a grinding machine until the primordium was exposed. Sr and Ca concentrations were measured from the primordium to the otolith edge at 10-μm intervals with an electron beam of 5 μm in diameter, using an electron probe microanalyzer equipped with a wavelength-dispersive spectrometer (WDS-EPMA, JEOL JX A-8900R, Tokyo, Japan). The accelerating voltage was set to 15 kV and the probe current to 3 nA. The peak concentration of Sr was counted for 80 s with background measurements for 20 s on each side. On the other hand, the peak concentration of Ca was counted for 20 s and each background for 10 s. Strontianite ($SrCO_3$, USNM-R10065) and calcite ($CaCo_3$, USNM-36321) from the Department of Mineral Sciences, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA, were used as standards

to calibrate the Sr and Ca concentration in eel otoliths. After the microchemical analysis, the otolith was polished to remove the carbon layer and etched for 1 to 2 min with 5% ethylenediaminetetraacetic acid (EDTA) to reveal the DGIs. Procedures for embedding, sectioning, polishing, and etching otoliths to reveal the DGIs and measuring the otolith Sr/Ca ratios followed those described in previous studies by Tzeng (1990, 1996), while the procedure for measuring the otolith Sr/Ca ratios followed that of Tzeng and Tsai (1994).

Otolith microstructural analyses

The DGIs in the otoliths were examined from scanning electron microscopic (SEM) photographs at various magnifications (×200, ×1,000, and ×1,500). Both the DGIs and Sr/Ca ratios were measured along the longest otolith axis. Growth checks of each early life history event or transition recorded in the otoliths were identified using both otolith microstructures (the DGI width) and microchemistry (Sr/Ca ratios). DGIs in each of the developmental stages and otolith radius were counted and measured from these landmarks as shown in Figure 2. Because otolith increments in *A. marmorata* and *A. japonica* were confirmed to be deposited on a daily basis (Tabeta et al. 1987; Umezawa et al. 1989; Sugeha et al. 2001b), the increment number was considered as the daily age in each individual examined in the present study. The drastic change in otolith Sr/Ca from the primordium to the otolith edge coincided with major life history events in the life of the young eels, like first feeding, metamorphosis, etc., as reported in previous studies for both temperate and tropical anguillid species (Tzeng and Tsai 1992, 1994; Otake et al. 1994; Tzeng 1996; Arai et al. 1997, 1999a, b, c; Cieri and McCleave 2001; Marui et al. 2001). The age of the leptocephalus at the onset of metamorphosis (T_m) was determined from the number of DGIs between the primordium (P) and MC where the increment pattern and Sr/Ca ratios dramatically changed (Otake et al. 1994, 1997; Tzeng and Tsai 1994; Tzeng 1995; Kuroki et al. 2005; Arai et al. 2002a). To estimate the T_m, 13 days (adjustment factor, N_0) was added to the number of DGIs because a previous study found that no increment was deposited in the core of the otolith during the yolk-sac stage, and otolith growth increment deposition only commences once a larva begins feeding 13 days after hatching (Tanaka et al. 1995). The duration of the metamorphosis stage was determined by counting the number of DGIs between the onset of a marked increase in the otolith increment width and its maximum peak. The amount of time between metamorphosis and estuarine arrival (T_{t-m}) was calculated by counting the number of DGIs between the MC and the edge of the otolith, while the age at recruitment (T_t) was determined as the number of DGIs between the hatch check and otolith edge. On the other hand, radii from the primordium to the first feeding check (R_f), to the MC (R_m), and to the otolith edge (R_t) and the distance from the MC to the otolith edge (R_{t-m}) were measured along the longest sagittal axis of the otolith (Figure 2). Otolith growth rates at different developmental stages were calculated by dividing the otolith radius by the DGI (Equations 1 to 3). Because increments near the metamorphosis zone in the otolith of some samples were often diffusive and obscure, the daily age of samples without counting DGIs was calculated from both the otolith growth rate and otolith radius (Equations 4 to 6):

$$\text{Overall growth rate of otolith,}\quad G_t = \frac{R_t}{T_t} \tag{1}$$

$$\text{Early growth rate of otolith,}\quad G_m = \frac{R_m}{T_m} \tag{2}$$

$$\text{Estuarine growth rate of otolith,}\quad G_{t\text{-}m} = \frac{R_{t\text{-}m}}{T_{t\text{-}m}} \tag{3}$$

$$T_m = \frac{R_m - R_f}{G_m} + N_0 \tag{4}$$

$$T_{t\text{-}m} = \frac{T_{t\text{-}m}}{G_{t\text{-}m}} \tag{5}$$

$$T_t = T_m + T_{t\text{-}m} \tag{6}$$

where G_m and G_{t-m} were obtained from Equations 2 and 3, and N_0 is the adjustment factor (13 days) for the yolk-sac stage duration. Differences in the total length (TL), daily age, and growth rate between *A. japonica* and *A. marmorata* were tested by an analysis of variance (ANOVA) as implemented in SigmaStat vers. 3.1 (Systat Software, San Jose, CA, USA).

DGIs and growth checks in the otoliths

Otolith microstructures between the temperate *A. japonica* and tropical *A. marmorata* were fundamentally the same (Arai et al. 2001a). DGIs in otoliths of glass eels are composed of two layers called the incremental (L) and discontinuous (D) zones, which respectively appeared to be light and dark as revealed by the SEM photo in Figure 2a. The L-zone is rich in calcium carbonate ($CaCO_3$), while the D-zone is very rich in protein but poor in calcium. When etched with hydrochloric acid (HCl) or EDTA and viewed under an SEM, the L-zone appeared elevated while the D-zone appeared as a ridge. A single DGI is usually composed of an L-zone and a D-zone and is generally deposited on a daily basis. Near the otolith edge, a distinct growth check called the elver check was found (Figure 2b). The elver check was deposited in the elver stage during its migration from seawater to freshwater. It also marks the transition from

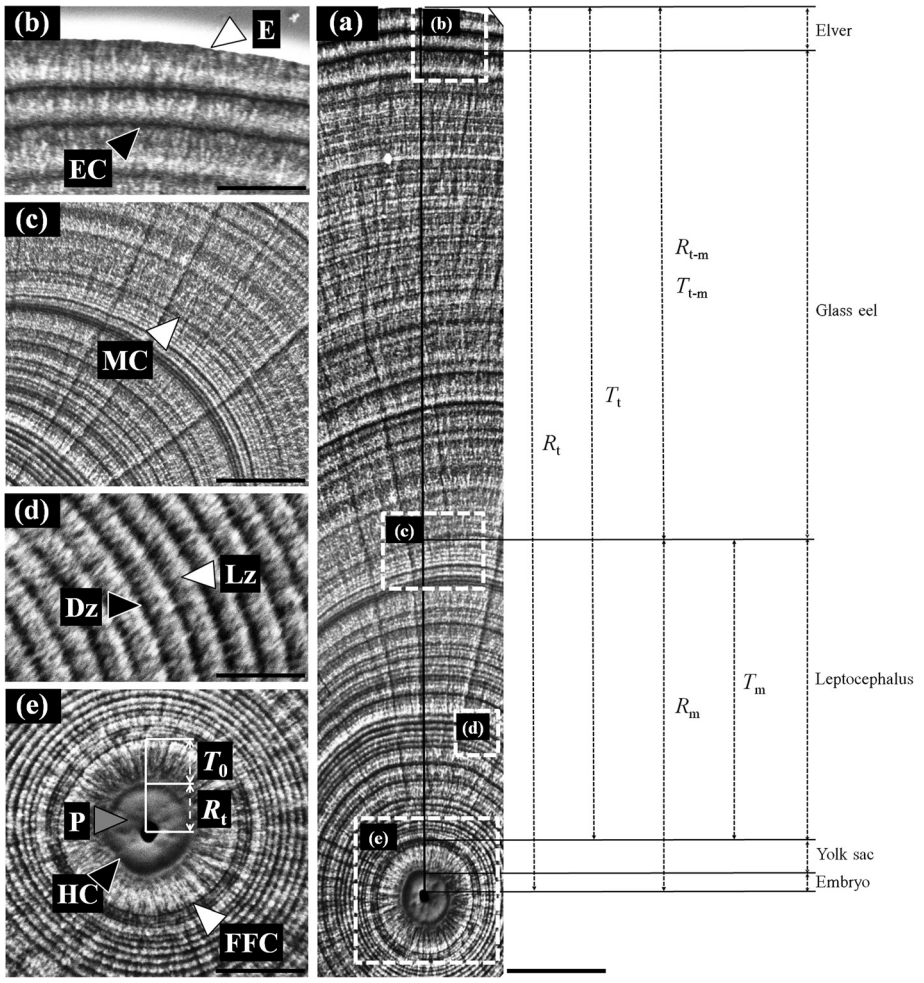

Figure 2 SEM photographs showing daily growth increments (DGIs) and growth checks in an *Anguilla marmorata* otolith. (a) SEM photographs showing daily growth increments (DGIs) and growth checks in an otolith of an *Anguilla marmorata* elver and measurements of otolith radii (*R*) and counts of DGIs (*T*) according to the developmental stage. Scale bar = 20 μm. **(b** to **e)** Magnified portions of **(a)** showing **(b)** estuarine check (EC) and the otolith edge **(e)**, **(c)** metamorphosis check (MC), **(d)** discontinuous (dark band, Dz) and increment (light band, Lz) zones, and **(e)** the primordium (P), hatching check (HC), and first feeding check (FFC). R_f, R_m, R_t, radii from the primordium to the FFC, MC, and OE, respectively; R_{t-m}, distance from the MC to the OE; OL, otolith length; T_m, T_t, T_{t-m}, counts of DGIs on radii of R_m and R_t and the section R_{t-m} between the MC and OE, respectively.

the glass eel to the elver stage. On the other hand, DGIs at the beginning of the leptocephalus stage were wide and clear but became very diffuse and obscure and almost uncountable near the metamorphosis area (Figure 2c). This indicated that the leptocephalus grew fast during the early developmental stage, then gradually slowed down and reached an asymptotic length before metamorphosis. Thus, an MC was deposited at the transition from the leptocephalus to glass eel stage. After the MC to the otolith edge, the DGIs became wider, indicating that growth speeded up after metamorphosis. The P in the otolith of the elver was an amorphous structure which appeared as a deep hole after etching with HCl or EDTA (Figure 2d). Distinct concentric growth increments and check rings were observed around the P that marked hatching (HC) and first feeding (FFC). The HC appeared as a deep circular grove surrounding the P. between the HC and FFC, no distinct DGI was discernible (Figure 2d). From the P to the otolith edge, the change in DGI widths revealed the growth history of the eel as it migrated from the oceanic spawning ground until it was recruited to the estuary (Figure 2e). Also, the DGIs recorded different life history and developmental stage transitions.

Larval dispersal distance and age at metamorphosis

To determine the effect of metamorphosis from leptocephalus to glass eel on the larval dispersal distance, the age at metamorphosis of glass eels from each of the sampling locations in East Asia were compared in

relation to their distances from the spawning grounds of both species in waters west of the Mariana Islands (12 to 17°N, 131 to 143°E; Kuroki et al. 2009).

Results

Differences in size and age at estuarine arrival between species and among locations

TLs of *A. japonica* glass eels at estuarine arrival ranged from 55.1 ± 1.9 mm in the Mingchiang River, southeastern China to 58.3 ± 11.3 mm in the Yalu River near the border of China and North Korea (Table 1), while those of *A. marmorata* ranged from 46.7 ± 1.7 mm in the Kurio River, southern Japan to 51.6 ± 1.6 mm in the Hsiukuluan River, eastern Taiwan. Within the same species, *A. japonica* glass eels from the Yalu River were significantly longer than those from the other estuaries (*t* test, $p < 0.01$), but those from other rivers showed no significant difference (*t* test, $p > 0.05$). On the other hand, no significant difference (*t* test, $p > 0.05$) in TL was observed among *A. marmorata* samples. The length-frequency distribution of recruiting *A. marmorata* and *A. japonica* glass eels in the Philippines, Taiwan, China, and Japan are shown in Figure 3. *Anguilla japonica* glass eels at estuarine arrival were significantly longer than *A. marmorata* ($p < 0.001$). The T_t was observed to be significantly older ($p < 0.001$) in *A. japonica* (181.8 ± 16.2 d) than that in *A. marmorata* (141.6 ± 15.8 days), indicating that the latter were recruited to the estuary earlier than the former. On the other hand, the duration of migration from the time of metamorphosis to the time of estuarine arrival (T_{t-m}) was significantly longer in *A. japonica* (41.1 ± 8.8 days) than that in *A. marmorata* (28.1 ± 7.9 days) ($p < 0.001$). This indicated that after metamorphosing, *A. japonica* experienced a longer drifting time by coastal currents before being recruited to estuaries than did *A. marmorata*.

Developmental stages

The majority of *A. marmorata* collected and examined ($n = 168$) from various estuaries and rivers in East Asia were at stage V_A (55.4%) followed by stage V_B (44.6%) (Table 2). No *A. marmorata* in a more advanced developmental stage (i.e., stages VI or VII) was observed, suggesting that individuals had recently arrived at the river mouth when they were collected. On the other hand, the majority of *A. japonica* examined ($n = 240$) were at stage V_A (51.7%) followed by stages V_B (32.1%), VI_{A1} (12.5%), VI_{A2} (3.3%), and VI_{A3} (0.4%). Also, the occurrence of larger *A. japonica* individuals in the Yalu

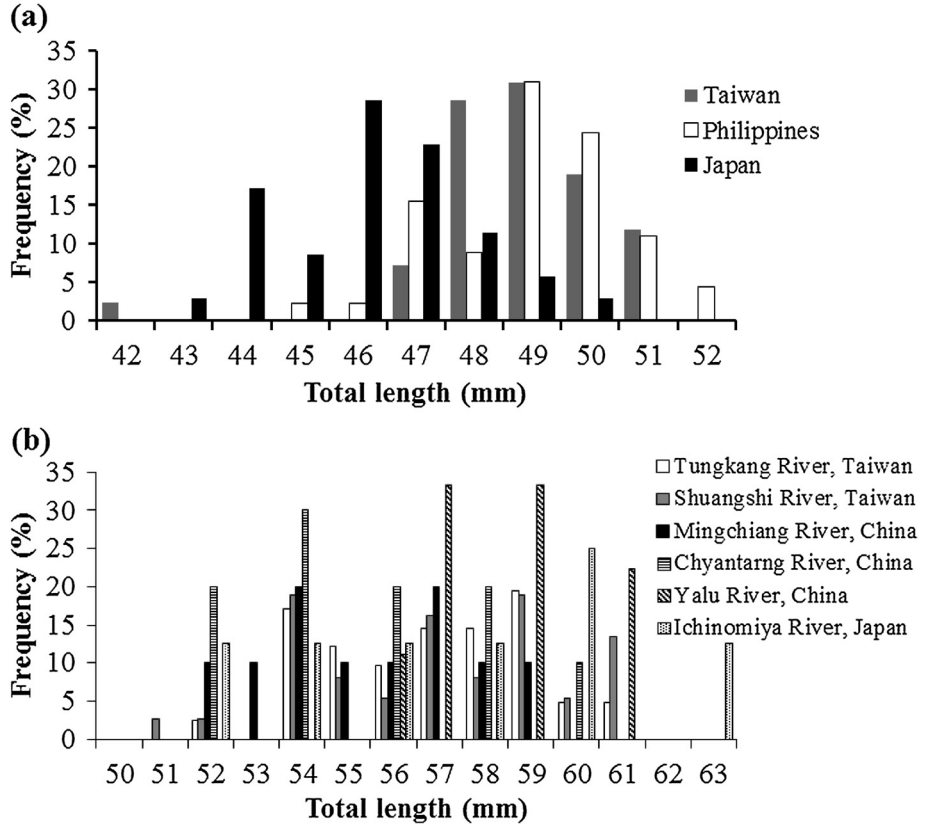

Figure 3 Length-frequency distribution of recruiting *Anguilla marmorata* (a) and *A. japonica* (b) glass eels from the Philippines, Taiwan, China, and Japan.

Table 2 Pigmentation stages of glass eels of *Anguilla japonica* and *Anguilla marmorata* collected from various rivers and estuaries in East Asia

Species	Sampling site	Number	Pigmentation stage						
			V_A	V_B	VI_{A1}	VI_{A2}	VI_{A3}	VI_{A4}	VI_B
A. japonica[a]	Tungkang River, Taiwan	30	28	2	0	0	0	0	0
		30	24	6	0	0	0	0	0
	Shuangshi River, Taiwan	30	13	17	0	0	0	0	0
		30	9	16	5	0	0	0	0
	Mingchiang River, China	30	24	6	0	0	0	0	0
	Chyantarng River, China	30	21	9	0	0	0	0	0
	Yalu River, China	30	0	1	21	7	1	0	0
	Ichinomiya River, Japan	30	5	20	4	1	0	0	0
Total		240	124	77	30	8	1	0	0
% composition			51.7	32.1	12.5	3.3	0.4	0	0
A. marmorata	Cagayan River, the Philippines	45	15	30	0	0	0	0	0
	Hsiukuluan River, Taiwan	86	65	21	0	0	0	0	0
	Kurio River, Japan	37	13	24	0	0	0	0	0
Total		168	93	75	0	0	0	0	0
% composition			55.4	44.6	0	0	0	0	0

[a]Cheng and Tzeng (1996).

River (Table 1) corresponded with their more advanced pigmentation states (VI_{A2} and VI_{A3}) (Table 2).

Ontogenetic changes in daily growth rate of otoliths

The overall mean otolith DGI widths of glass eels at different phases of their early life history are shown in Table 3. The mean DGI width before metamorphosis (R_m/T_m) was 0.8 ± 0.07 μm/days in *A. japonica* and 0.9 ± 0.14 μm/days in *A. marmorata*, which was narrower compared to that of the mean otolith DGI width from the metamorphosis check to the otolith edge (R_{t-m}) which was 1.3 ± 0.28 μm/days in *A. japonica* and 2.1 ± 0.60 μm/days in *A. marmorata*. These results indicated that otolith growth was slower during the leptocephalus stage and faster after metamorphosis in both species. From the primordium to the otolith edge, different otolith growth rates were observed to correspond to different ontogenetic development stages (Figure 2). The first pattern was observed in the region between the primordium and the FFC and was deposited during the yolk-sac stage. In this region, no discernible DGIs were observed, and the Sr/Ca ratio was lower because the yolk sac was of freshwater maternal origin (Figure 2). The second pattern was observed in the region between the FFC and MC and was deposited during the leptocephalus stage. Otolith DGIs, on the other hand, became wider beyond the MC. The third pattern was observed in the region between the MC and otolith edge and was deposited during the glass eel stage. These growth and Sr/Ca ratio patterns in otoliths of *A. marmorata* glass eels were similar to those observed in *A. japonica*. This indicated that both species have similar life histories from the spawning ground to the estuary in their early life stage.

Age at metamorphosis in relation to the growth rate and distance from the spawning grounds and to differences in ages between species

The overall mean (± standard deviation) T_m was significantly older in *A. japonica* (140.7 ± 13.6 days) than that in *A. marmorata* (113.5 ± 13.0 days) ($p < 0.001$, Table 1). It was also found that the T_m increased from south to north in both species (Figure 4). In addition, the T_m was negatively correlated with the growth rate before metamorphosis (G_m) (Figure 5). On the other hand, T_m values of *A. marmorata* and *A. japonica* were positively related to the larval dispersal distance from the spawning grounds (Figure 6).

Discussion

The difference in T_m values between *A. japonica* and *A. marmorata* and its biological significance

In the present study, it was found that at an age of 110 days (Table 1), *A. marmorata* had already metamorphosed and commenced migration to coastal waters of the northern Philippines, while *A. japonica* remained at the pelagic leptocephalus stage and continued to drift with currents in the open ocean until it reached

Table 3 Mean increment widths of radii of R_m, R_t, and R_{t-m} in otoliths of *Anguilla japonica* and *A. marmorata* glass eels

Species	Sampling site	Sampling date	Increment width in μm (*n*)		
			R_m	R_t	R_{t-m}
A. japonica[a]	Tungkang River, Taiwan	30 December 92	0.8 ± 0.07 (5)	0.9 ± 0.09 (5)	1.2 ± 0.31 (5)
		24 March 93	0.8 ± 0.07 (7)	0.8 ± 0.03 (5)	1.4 ± 0.19 (5)
	Shuangshi River, Taiwan	20 December 92	0.8 ± 0.07 (7)	0.9 ± 0.03 (6)	1.5 ± 0.48 (6)
		17 February 93	0.9 ± 0.09 (3)	1.0 ± 0.04 (2)	1.4 ± 0.03 (2)
	Mingchiang River, China	1 March 93	0.7 ± 0.02 (5)	0.9 ± 0.06 (5)	1.4 ± 0.38 (5)
	Chyantarng River, China	17 February 93	0.7 ± 0.08 (7)	0.8 ± 0.03 (4)	1.3 ± 0.17 (4)
	Yalu River, China	3 May 93	0.8 ± 0.09 (8)	0.9 ± 0.05 (8)	1.3 ± 0.45 (8)
	Ichinomiya River, Japan	10 January 94	0.7 ± 0.06 (5)	0.8 ± 0.05 (5)	1.2 ± 0.26 (5)
Overall (μ_1)			0.78 ± 0.07 (47)	0.88 ± 0.05 (40)	1.34 ± 0.28 (40)
A. marmorata	Cagayan River, the Philippines	19 May 08	1.0 ± 0.18 (13)	1.1 ± 0.14 (13)	1.84 ± 0.46 (13)
	Hsiukuluan River, Taiwan	20 May 08	0.9 ± 0.10 (13)	1.2 ± 0.18 (13)	2.29 ± 0.72 (13)
	Kurio River, Japan	6 June 96	0.9 ± 0.14 (15)	1.1 ± 0.17 (15)	2.18 ± 0.61 (15)
Overall (μ_2)			0.93 ± 0.14 (41)	1.13 ± 0.16 (41)	2.10 ± 0.60 (41)
Difference ($\mu_{2-}\mu_1$)			0.15	0.25	0.76
Significance			*A. marmorata* > *A. japonica*	*A. marmorata* > *A. japonica*	*A. marmorata* > *A. japonica*

[a]Cheng and Tzeng (1996). Mean increment widths (±SD) of radii of R_m, R_t, and R_{t-m} in otoliths of *A. japonica* and *A. marmorata* glass eels. *n*, number of individuals used for increment width measurements.

northern Taiwan where it began to metamorphose approximately 24 days later. This must be the reason why the geographic distribution of *A. japonica* is more northerly than that of *A. marmorata*. The metamorphosis of leptocephalus to glass eels transforms the laterally compressed, willow leaf-like shape of the former to a more rounded, streamlined shape of the latter. This transformation reportedly causes drastic reductions in the length and weight of the leptocephalus and an estimated 80% drop in whole body water (Bertin 1951; Otake 2003). Previous studies found that the body shape of the leptocephalus is suitable for drifting with oceanic currents (Miller 2009; Tsukamoto et al. 2009; Tsukamoto et al. 2011). Also, the laterally compressed willow leaf-like body shape of the anguillid leptocephalus and the high body water content greatly contribute to its buoyancy and is favorable for passive planktonic drift and transport by ocean currents, while the body of the glass eel is more adapted for bottom dwelling. Once the leptocephalus metamorphose into a glass eel, it loses buoyancy and leaves the strong ocean currents. In other words, metamorphosis from a leptocephalus to a glass eel in anguillid species terminates the passive drift of eel larvae and initiates migration to coastal waters, and it also determines the ultimate destination of larval dispersal. The completion of eel larval metamorphosis and the onset of the juvenile stage initiate a behavioral shift from pelagic migration to bottom settlement (Moran 1994). Earlier metamorphosing leptocephali are recruited earlier, while delayed metamorphosis leptocephali are bound for longer oceanic dispersal and later estuarine recruitment. Metamorphosis occurs during migration from their offshore marine spawning grounds to their continental freshwater growth habitats, and it marks an adaptive shift from oceanic drifting to river colonization and the beginning of the continental dispersal phase (Edeline et al. 2009). DGIs in otoliths can conveniently provide the timing for metamorphosis (T_m), and the radius from the P to the MC can provide information on the 'metamorphosing size' of anguillid eels. These allowed us to gain insights into the mechanism of metamorphosis of anguillid eels in the wild and provided clues to understanding the biological significance of differences in the T_m, size at metamorphosis, and in growth rate of leptocephali between *A. japonica* and *A. marmorata*. Tsukamoto (1990) suggested that *A. japonica* begins to metamorphose when leptocephali reach 60 mm TL. On the other hand, metamorphosis of leptocephali of *A. marmorata* and other tropical eel species like *Anguilla bicolor pacifica*, *Anguilla borneensis*, and *Anguilla celebesensis* was found to commence at around 50 mm TL (Kuroki et al. 2005, 2006), which is considerably smaller than the metamorphosing size of the temperate *A. japonica*.

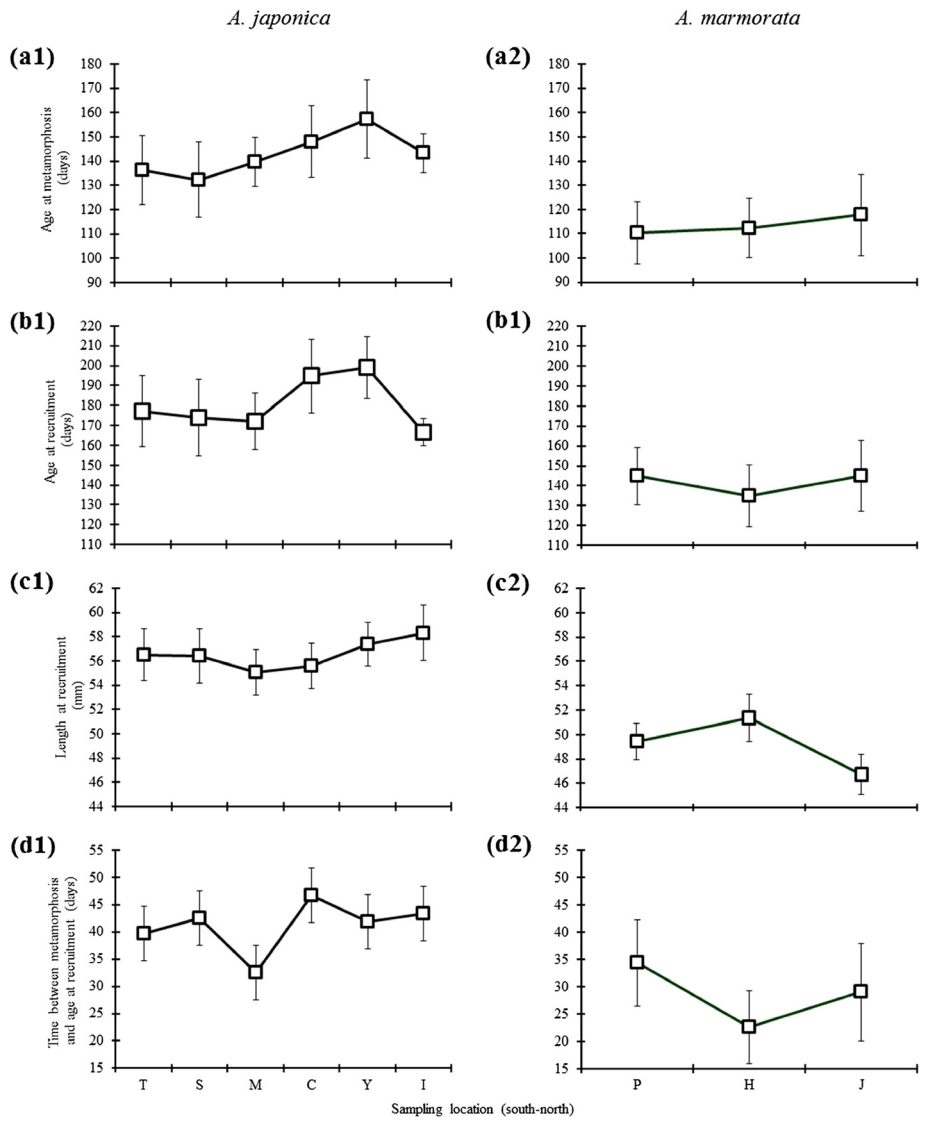

Figure 4 Spatial changes of *Anguilla japonica* and *A. marmorata*. Spatial changes in age at metamorphosis **(a_1 to a_2)**, age **(b_1 to b_2)**, and length **(c_1 to c_2)** at recruitment, and time between metamorphosis and age at recruitment **(d_1 to d_2)** of *Anguilla japonica* and *A. marmorata*. Abbreviations of sampling locations are given in Figure 1.

Differences in the timing and duration of metamorphosis between *A. japonica* and *A. marmorata*

Previous studies indicated that the timing and duration of metamorphosis from leptocephali to glass eels differed between temperate and tropical anguillid eels around the world, with a tendency for tropical species like *A. marmorata* to begin metamorphosis at a much younger age and complete it in a shorter time than temperate species (Chang and Tzeng 1996; Wang and Tzeng 1998, 2000; Arai et al. 1999a; Shiao et al. 2001). In this study, we found that the temperate eel *A. japonica* exhibited older metamorphosis timing and experienced a longer leptocephalus stage than the tropical *A. marmorata*. Arai et al. (2001b) noted that this tendency was brought about by differences in the temperature experienced by leptocephali of temperate and tropical eels during their migration to coastal waters from their spawning areas. However, this might not be true for *A. japonica* and *A. marmorata* since they begin migration from the same general spawning area (Kuroki et al. 2009) and drift with the same current system (NEC and KC). In addition, *A. rostrata* and *A. anguilla* also experience similar temperature and current systems during their inshore migration from their spawning grounds, but their ages at metamorphosis differ from each other (Wang and Tzeng 1998). These facts suggest that genetic modifications and evolutionary strategies (e.g., low growth rate/metabolism during the larval stage and a long larval duration)

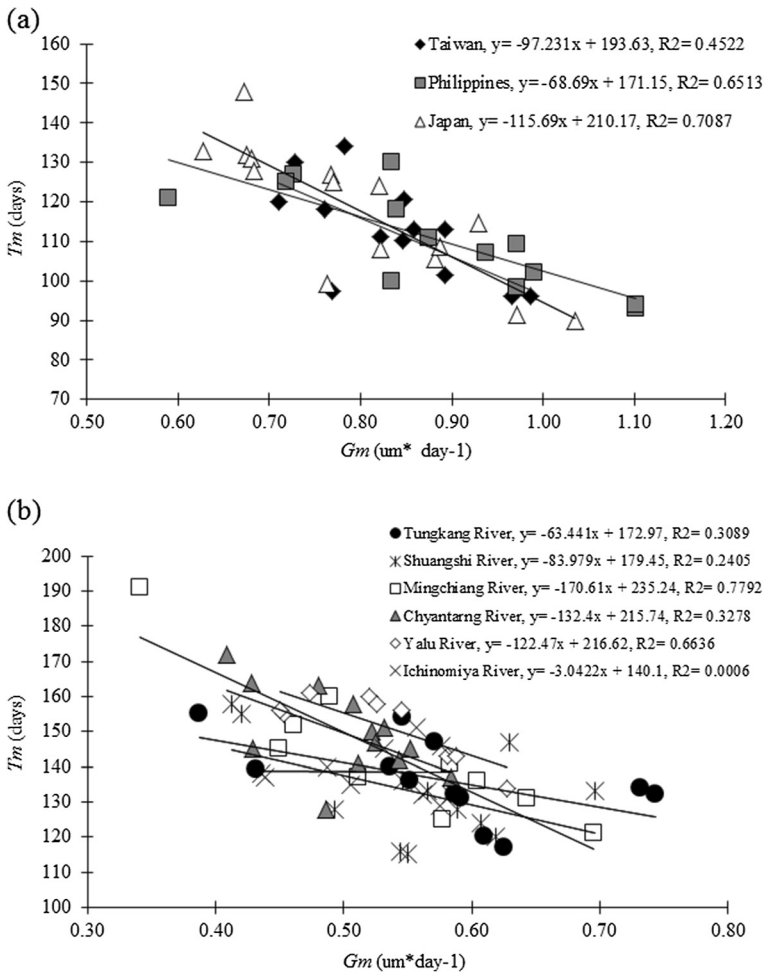

Figure 5 Relationship between the age at metamorphosis and growth rate before metamorphosis. Relationship between the age at metamorphosis (T_m) and growth rate (G_m) before metamorphosis in *Anguilla marmorata* **(a)** and *A. japonica* **(b)**.

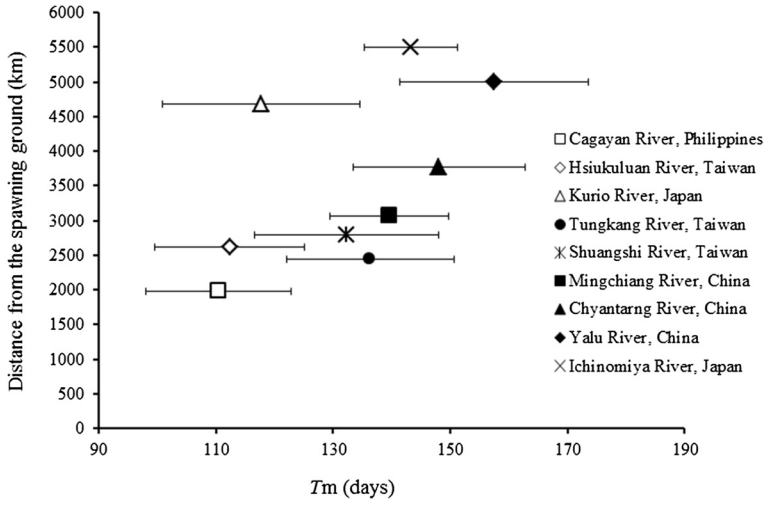

Figure 6 Relationship between the larval dispersal distance and age at metamorphosis. Relationship between the larval dispersal distance and age at metamorphosis (T_m) in *Anguilla marmorata* (open symbols) and *A. japonica* (solid symbols).

of eel species are more important than the influence of temperature on differences in the timing and duration of metamorphosis between *A. japonica* and *A. marmorata*.

Delayed metamorphosis as a means of long-distance dispersal of the eel

At the end of their long transoceanic migration, *A. japonica* and *A. marmorata* leptocephali metamorphose into glass eels and invade coastal and inland habitats. Otolith microchemical studies revealed that after reaching coastal waters, glass eels may either migrate further inland and colonize freshwater habitats or stop their upstream migration and settle in seawater or estuaries (Tzeng et al. 2002; Arai et al. 2004; Daverat et al. 2006). The timing of metamorphosis by a leptocephalus into a glass eel and transport by oceanic currents are considered key determinants of the ultimate destination of eels (Cheng and Tzeng 1996; Tzeng 2003). In the present study, we found that the age of *A. marmorata* at metamorphosis from leptocephalus to glass eel (113.5 ± 13.0 days) was younger than in *A. japonica* (140.7 ± 13.6 days). Because metamorphosis triggers a behavioral switch from pelagic migration to bottom settlement, *A. japonica* leptocephali which arrive in Philippine waters are apparently too young to metamorphose and migrate towards estuaries so they continue drifting northwards or southwards. This must be the reason why Japanese eels are seldom found in the Philippines, while *A. marmorata* occurs in abundance (Tabeta et al. 1975, 1976). A similar scenario was also observed in American and European eels, for which differences in the duration of the leptocephalus stage and growth rates were the principal factors triggering segregative migration of these two species in the Atlantic Ocean (Wang and Tzeng 2000). The delay in metamorphosis of about 12 to 15 months in *A. anguilla* (McCleave 1993; Wang and Tzeng 2000) is necessary for its long-distance dispersal that includes a trans-Atlantic crossing. Similarly, it seems that *A. japonica* has developed a strategy to delay its metamorphosis from leptocephali to glass eels by reducing its growth rate, which enables it to migrate segregatively with *A. marmorata* and experience long-distance dispersal in East Asia. Its faster growing and earlier metamorphosing leptocephali are recruited in Taiwan, while those that do not continue to drift towards eastern China and Japan. On the other hand, the faster growing and earlier metamorphosing leptocephali of *A. marmorata* are recruited earlier in the Philippines, while its slower growing, delayed metamorphosing leptocephali disperse southward (via the Mindanao Current) and northward (via the KC). The difference in age at metamorphosis between *A. japonica* and *A. marmorata* ranged 18.5 to 39.9 days, and the delay in metamorphosis of 18.5 to 39.9 days is enough to allow *A. japonica* to be transported from North Luzon, the Philippines to further north in continental East Asia by the KC. Aside from these considerations, anomalies in the hydrology of the region should also be taken into account because they might also influence the duration of larval drift and subsequently delay metamorphosis and affect recruitment. Anomalies such as El Niño and El Niño Southern Oscillation were found to affect current systems in the region. During El Niño years, the salinity front in the NEC region retreats southward, leading to a southward shift in the spawning grounds, causing poor recruitment (Kimura et al. 2001; Sugimoto et al. 2001; Kim et al. 2007; Han et al. 2009b). During this period, leptocephali experience longer drift, slower growth rates, delayed metamorphosis, and ultimately delayed recruitment. But during non-El Niño years, the hydrology of the region changes with the season, and these changes are more or less regular. Specimens examined in the present study were collected from different years during their peak recruitment seasons during non-El Niño years. Accordingly, the effects of environmental factors, such as El Niño events, on larval transportation and subsequently delayed metamorphosis from leptocephali to glass eels were not examined in this study and would be a good topic for future research and long-term studies.

Early growth of *Anguilla* leptocephali

The migratory segregation between *A. japonica* and *A. marmorata* in the northwestern Pacific can be further understood by examining their larval growth rates. Patterns of ontogenetic changes in otolith DGIs from the P to the otolith edge were found to be similar between *A. japonica* (Cheng and Tzeng 1996; Tzeng 2003) and *A. marmorata* (Table 1, Figure 2); however, otolith DGI widths were greater and increment numbers were fewer in *A. marmorata* than *A. japonica* (Tables 1 and 3). This indicates that during the early stage of development, *A. marmorata* has faster otolith growth rates than *A. japonica*. Faster growing leptocephali are able to metamorphose and are recruited earlier to estuaries in the Philippines, while slower growing ones metamorphose and are recruited later to estuaries in Taiwan, eastern China, Korea, and Japan. In addition to this, a close linear relationship between ages at metamorphosis and recruitment in temperate and tropical eel species was observed (Marui et al. 2001), further suggesting that early-metamorphosing glass eels are recruited at younger ages. A similar phenomenon was also observed in other anguillid species like *A. celebesensis*, *Anguilla bicolor bicolor*, *A. bicolor pacifica*, *A. australis*, *A. anguilla*, *A. rostrata*, and *Anguilla dieffenbachi*. A reduced growth rate in *A. japonica* larvae prevents metamorphosis in synchrony with *A. marmorata* despite their overlapping spawning sites and the same oceanic transport and

migratory routes. Also, the slower growth rate of *A. japonica* during the leptocephalus stage and its longer duration compared to *A. marmorata* seem to be due to the longer transportation distance.

Conclusions

In conclusion, the larval growth rate and metamorphosis timing (T_m) may play important roles in the geographical distribution of the sympatric anguillid eel species *A. japonica* and *A. marmorata* in the northwestern Pacific during their drift from their overlapping spawning grounds in waters west of the Mariana Islands via the NEC and KC to their continental freshwater growth habitats. *A. marmorata* grows faster and metamorphoses earlier than *A. japonica*; thus, it can be abundantly found in the tropical Philippines and subtropical Taiwan, but few are seen in temperate China, Korea, and Japan. On the contrary, the temperate eel *A. japonica* is abundant beyond Taiwan, and few or none are found in the tropical Philippines. This indicates that differences in growth rates and the timing of metamorphosis from leptocephali to glass eels are key factors determining the continental distribution of these two sympatric anguillid eel species. Delayed metamorphosis with a reduced growth rate in *A. japonica* leptocephali may be an evolutionary strategy for temperate species to extend their distribution area from a tropical to a temperate region, farther north than the distribution range of *A. marmorata*.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

NJL participated in the design of the study, carried out otolith analyses, analyzed and interpreted the data and drafted the manuscript. WNT conceived the study and participated in its design and coordination and in the interpretation of data. KNS participated in otolith analyses and interpretation of data. NTY participated in otolith analyses. YSH provided technical and material support and participated in the interpretation and analyses of data. All authors read and approved the final manuscript.

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