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Growth history and inshore migration of the tropical eel, *Anguilla marmorata*, in the Pacific

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Abstract A comparative study of the otolith microstructure and microchemistry of *Anguilla marmorata* glass eels in the western North Pacific (Japan, Taiwan, the Philippines, Indonesia) determined the timing of metamorphosis and age at recruitment to freshwater habitats with a view to learning about the early life history and recruitment of this species of tropical anguillid eel, which has a wide range throughout much of the western Pacific and parts of the Indian Ocean. Three new samples (from Japan, Taiwan, Indonesia) were analyzed and statistically compared along with two other previously published samples that were analyzed using the same techniques. Ages at metamorphosis and recruitment, respectively, were 123 ± 13.4 days (mean $\pm$ SD) and 154 ± 17.0 days in specimens from Japan, 116 ± 14.6 days and 145 ± 15.6 days in those from Taiwan, 120 ± 13.0 days and 154 ± 13.5 days in the Philippines stock and 132 ± 9.7 days and 159 ± 11.7 days, and 120 ± 15.6 days and 152 ± 15.2 days in the Indonesian stock. The average duration of the period of metamorphosis estimated from otolith microstructure was very similar (15–17 days) in the specimens from all locations. A close linear relationship was found between the ages at metamorphosis and recruitment at all locations, suggesting that individuals that metamorphosed earlier were recruited to freshwater habitats at a younger age. Back-calculated hatching dates ranged over about 6 months of the year, suggesting that this species may spawn throughout much of the year. It is hypothesized that specimens from all four sites are from the same spawning population originating in a spawning area in the North Equatorial Current of the western North Pacific.

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Introduction

The catadromous tropical eel *Anguilla marmorata* is one of the most common anguillid species in the Indo-Pacific (Ege 1939; Jespersen 1942). The adults of this species reach greater sizes than most temperate species, and range over a much more oceanographically diverse region than any temperate species, since *A. marmorata* is found around the southern half of Japan, throughout the Indo-Pacific, Polynesia, and in several areas in the Indian ocean. Like all anguillid species, *A. marmorata* spawns in the ocean and has a leptocephalus larva that undergoes a remarkable metamorphosis into the glass eel stage before recruitment to fresh water. The lengthy duration of the leptocephalus stage and the timing of metamorphosis is probably an important biological determinant of the geographical distribution of anguillid eels (Tsukamoto and Umezawa 1994). This potential for long-term larval migration in the ocean may have been a key factor in the worldwide distribution and speciation of anguillid eels (Tsukamoto and Aoyama 1998).

Recent progress in otolith analytical techniques has revealed considerable details of the early life history, including the timing and duration of metamorphosis of temperate species of *Anguilla*, such as *A. japonica* (Tsukamoto 1990; Otake et al. 1994; Cheng and Tzeng 1996; Arai et al. 1997), *A. anguilla* (Lecomte-Finiger 1992; Arai et al. 2000a), *A. rostrata* (Wang and Tzeng 1998; Arai et al. 2000a), *A. australis* (Arai et al. 1999a) and *A. dieffenbachii* (Marui et al. 2001). In addition, there have been a few recent studies on the otoliths of the glass eels of several tropical species that were

collected as they recruited to coastal areas (Arai et al. 1999b, c, 2001a), but compared with the information gained from otolith studies in the temperate species of *Anguilla*, relatively little is known about the early life history of any tropical species.

The wide distribution of *A. marmorata* throughout the subtropical and tropical western Pacific, the tropical western South Pacific, and Indian Ocean indicates that it differs from temperate species of anguillid eels and has many spawning areas. Recent studies on the genetic species identification, distribution and otolith microstructure of *A. marmorata* leptocephali in the North and South Pacific indicate that it must have several spawning areas, even within the western Pacific (Aoyama et al. 1999; Arai et al. 2001b). In addition, a genetic study of specimens from a variety of locations throughout the range of this species found genetic differentiation that suggested the presence of several regional populations (Ishikawa 1998).

In the present study, we examined the otolith microstructure and microchemistry of *A. marmorata* glass eels collected as they recruited to coastal areas in temperate, subtropical and tropical regions of the western North Pacific. We determined the timing and duration of metamorphosis, age at recruitment and hatching date of specimens collected from sites in southern Japan, Taiwan, and Sulawesi Island, Indonesia, ranging over about 30 degrees of latitude. For comparison, we include the data from our previously published analyses of the otolith microstructure and microchemistry of specimens collected at the northern edge of the Philippines and from another nearby river on Sulawesi Island (Arai et al. 1999c). These data form the basis of a discussion of the spawning location and the larval-migration mechanisms of *A. marmorata* in relation to the major surface currents in the region.

Materials and methods

Fish and otolith preparation

Glass eels of *A. marmorata* were collected at night during new moon with dip and scoop nets along the beach of Tanegasima Island, Japan, on 16 February 1999, at the mouth of the Tung-Kang River, Taiwan, on 15 February 1999, and near the mouth of the Poigar River, on Sulawesi Island, Indonesia, on 7 July 1997 (Fig. 1). The glass eels sampled were preserved in 99% ethanol immediately after collection. Total lengths were measured to the nearest 0.1 mm and pigmentation stages determined according to Bertin (1956). Sagittal otoliths were extracted from each fish, embedded in epoxy resin (Struers, Epofix) and mounted on glass slides. The otoliths were ground to expose the core in the sagittal plane, using a grinding machine equipped with a diamond cup-wheel (Struers, Discoplan–TS), and further polished with 6-μm and 1-μm diamond paste on an automated polishing wheel (Struers, Planopol–V). They were then cleaned in an ultrasonic bath and rinsed with deionized water pending subsequent examination.

The previously reported otolith data (Arai et al. 1999c), which are included for comparison, were from specimens collected with scoop nets at the mouth of the Cagayan River, Philippines, on 24 September 1994, and from the mouth of the Dumoga River, on Sulawesi Island, on 5 June 1996. Thus, a total of 88 specimens (19 specimens from Japan, 19 specimens from Taiwan, 10 specimens from Philippines, 20 from the Poigar River and 20 from the Dumoga River, Indonesia) were included in the present study (Table 1).

Otolith X-ray microprobe analysis

For electron microprobe analyses, five glass eel otoliths from each site were carbon coated by a high-vacuum evaporator. Otolith Sr and Ca concentrations were measured along the longest axis using a wavelength dispersive X-ray electron microprobe (JEOL JXA–8900R), with calcite ($CaCO_3$) and strontianite ($SrCO_3$) as standards. The procedures for embedding, grinding and polishing, and the conditions for electron-microprobe analyses, followed those described by Arai et al. (1997, 1999a, b, c). Microprobe measurement points, which were seen as burn depressions, were assigned to otolith growth increments that were examined as described below. The averages of successive data of Sr and Ca concentrations pooled for every ten successive growth increments were used for the life history transect analysis. "X-ray intensity maps" of both elements were made for six glass eel samples. The beam current was 0.01 μA, counting time was 0.1 s, and the other analytical conditions followed those for the life-history transect analyses.

Otolith-increment analysis

Following the electron-microprobe analysis, the otoliths were repolished to remove the coating, etched with 0.05-M HCl and vacuum-coated with Pt–Pd in an ion-sputterer for scanning electron

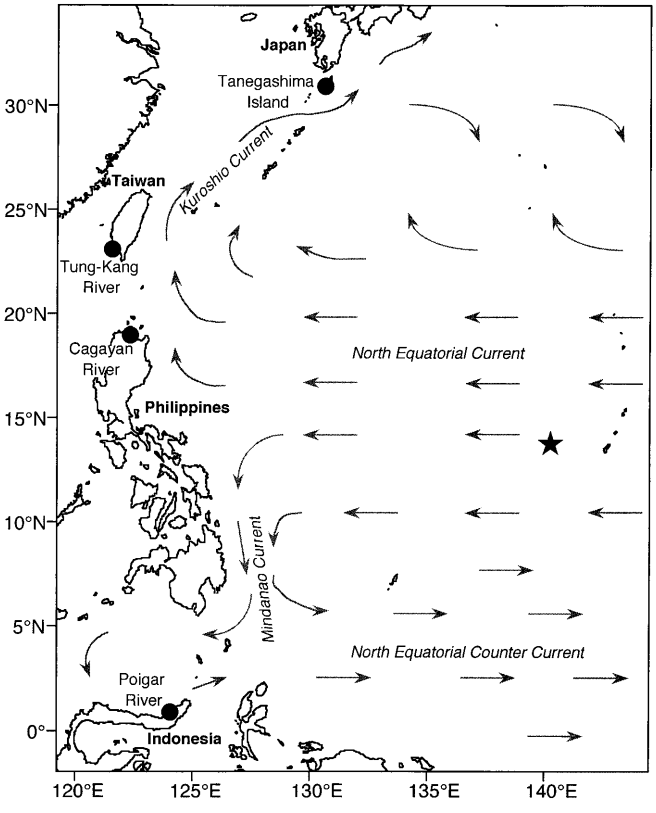

Fig. 1 Map showing sampling locations (●), the prevailing surface currents in the region (after Pickard and Emery 1990; Godfrey 1996) and the estimated spawning area (★) (Arai et al. 2001b) of *Anguilla marmorata* in the Pacific Ocean

Table 1 *Anguilla marmorata*. Total length, otolith radius, age at metamorphosis, duration of metamorphosis stage, age at recruitment, total age and hatching date

Sampling location	Tanegasima Island beach, Japan	Tung-Kang River, Taiwan	Cagayan River, Philippines	Poigar River, Indonesia	Dumoga River, Indonesia
Number of specimens age-determined	19	19	10	20	20
Total length (mm)	49.2 ± 1.9, 45.1–54.2	50.3 ± 1.6, 48.0–53.4	49.9 ± 1.4, 47.2–51.6	51.2 ± 1.5, 48.2–53.8	50.9 ± 2.0, 47.9–54.8
Otolith radius (μm)	152 ± 6.6, 139–163	149 ± 7.3, 134–159	160 ± 10.2, 143–174	147 ± 8.9, 129–165	146 ± 5.3, 134–156
Age at metamorphosis (days)	123 ± 13.4, 100–155	116 ± 14.6, 92–145	120 ± 13.0, 105–140	132 ± 9.7, 117–155	120 ± 15.6, 96–147
Duration of metamorphosis stage (days)	17 ± 4.0, 12–24	15 ± 3.0, 10–20	17 ± 4.3, 12–26	17 ± 3.8, 9–23	17 ± 3.3, 13–24
Age at recruitment (days)	154 ± 17.0, 133–189	145 ± 15.6, 116–166	154 ± 13.5, 136–178	159 ± 11.7, 141–182	152 ± 15.2, 129–177
Total age (days)	155 ± 16.8, 137–189	146 ± 15.5, 116–167	166 ± 13.6, 151–190	159 ± 11.5, 141–182	153 ± 11.7, 141–182
Hatching date	13 September 1998 ± 16.8	21 September 1998 ± 15.5	11 April 1994 ± 13.6	28 January 1997 ± 11.5	3 January 1996 ± 11.7
	11 August–2 October 1998	1 September–22 October1998	21 March–26 April 1994	6 January–16 April 1997	11 December1995–28 January1996

microscope observations (SEM, Hitachi S–4500) as described by Arai et al. (1997, 1999a, b, c). Otoliths of 43 glass eels (14 from Japan, 14 from Taiwan, 15 from Indonesia), which had not been used for electron-microprobe analysis, were also etched and coated by the same procedure as that for SEM observation. The averages of every ten successive ring widths between the hatch check and the edge were used for otolith-growth analysis. Since otolith increments in *Anguilla* species, such as *A. japonica* (Tsukamoto 1989; Umezawa et al. 1989; Umezawa and Tsukamoto 1991), *A. rostrata* (Martin 1995) and *A. celebesensis* (Arai et al. 2000b), were confirmed to be deposited daily, we considered the increment number as the age in days for the *A. marmorata* specimens examined in the present study (Table 1).

Interpretation of early life history

Based on previous data for otolith-increment width and Sr:Ca ratios in *A. japonica* (Otake et al. 1994; Arai et al. 1997), *A. rostrata* (Arai et al. 2000a), *A. australis* (Arai et al. 1999a), *A. bicolor pacifica* (Arai et al. 1999b), *A. celebesensis*, *A. marmorata* and *A. bicolor bicolor* (Arai et al. 1999c), *A. anguilla* (Arai et al. 2000a), and *A. dieffenbachii* (Marui et al. 2001), the age at a marked increase in otolith-increment width, which was coincident with a drop in Sr:Ca ratios (Figs. 2, 3), was regarded as the onset of metamorphosis in each specimen examined here. X-ray intensity maps of Sr content in the glass eel otoliths also revealed one distinct and often additional concentric rings showing areas of relatively high Sr content (Fig. 4). The duration of the metamorphosis stage was regarded as the period between the onset of a marked increase in otolith-increment width and the maximum width recorded. The innermost check on the otolith edge was regarded as a freshwater check, which was formed when the glass eel entered fresh water (Arai et al. 1999a, c, 2000a; Marui et al. 2001). We used the number of increments between the hatch check (Umezawa et al. 1989) and the freshwater check as the age at recruitment. In the case of there being no check at the otolith edge, we considered increments from hatch check to the edge as the age at recruitment. Total age was the number of increments between the hatch check and otolith edge (Table 1).

Statistical analyses

Differences among data were tested by an analysis of variance (ANOVA) and, afterwards, Scheffe's multiple-range tests for the combination of two data sets. Significance of the correlation coefficient and regression slope was tested by Fisher's Z transformation and an analysis of covariance (ANCOVA) (Sokal and Rohlf 1969).

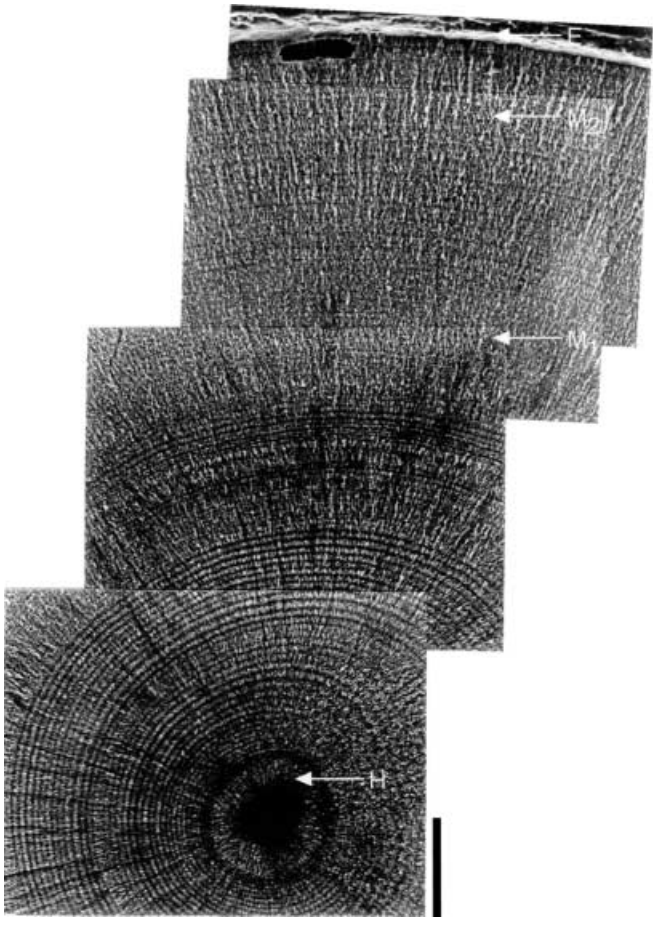

Fig. 2 *Anguilla marmorata*. SEM photographs showing the otolith microstructure of a glass eel (TL: 48.3 mm) collected in the Tung-Kang River, Taiwan on 15 February 1999. The *arrowheads* indicate the interpretation of the early life history of *A. marmorata*. *H* Hatching check; M_1 onset of metamorphosis; M_2 termination of metamorphosis; *E* edge of otolith. Scale bar 50 μm

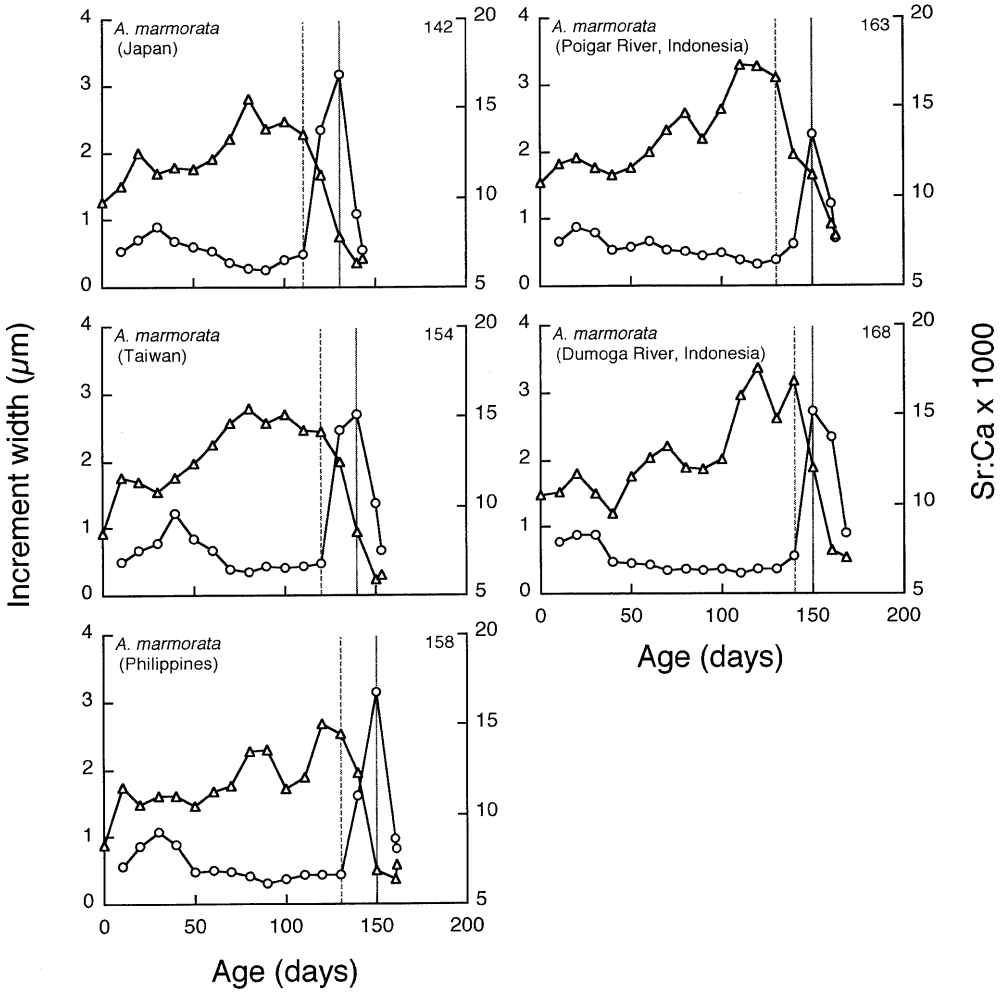

Fig. 3 *Anguilla marmorata*. Profiles of otolith incremental widths from the core to the edge (*circles*) and otolith Sr:Ca concentration ratios measured with a wavelength-dispersive electron microprobe from the core to the edge (*triangles*). Each point represents the average of data for every 10 days. Numbers at the upper right indicate age (days). The *dotted* and *straight lines* indicate age at metamorphosis and age at termination of metamorphosis, respectively

Results

Size and stage at recruitment

The total lengths (mean ± SD) of the specimens of *A. marmorata* from Japan, Taiwan, the Philippines, and the Poigar and Dumoga Rivers in Indonesia were 49.2 ± 1.9 mm (range: 45.1–54.2 mm), 50.3 ± 1.6 mm (range: 48.0–53.4 mm), 49.9 ± 1.4 mm (range: 47.2–51.6 mm), and 51.2 ± 1.5 mm (range: 48.2–53.8 mm) and 50.9 ± 2.0 mm (range: 47.9–54.8 mm), respectively (Table 1). A significant difference in total length was found between the specimens from Japan and those from Poigar River in Indonesia (ANOVA, $P < 0.05$), but no significant difference was apparent in other combinations (ANOVA, $P > 0.05$).

The mean (± SD) radii of otoliths of specimens of *A. marmorata* from Japan, Taiwan, the Philippines, and the Poigar and Dumoga Rivers in Indonesia were 152 ± 6.6 μm (range: 139–163 μm), 149 ± 7.3 μm (range: 134–159 μm), 160 ± 10.2 μm (range: 143–174 μm), and 147 ± 8.9 μm (range: 129–165 μm) and 146 ± 5.3 μm (range: 134–156 μm), respectively (Table 1). A significant difference in otolith radius was found between the samples from Taiwan and the Philippines, and between those from the Philippines and both samples from Indonesia (ANOVA, $P < 0.005$–0.05), but no significant difference was apparent in other combinations (ANOVA, $P > 0.1$).

Pigmentation in all of the specimens except those from the Philippines was poorly developed and was limited to the caudal, cranial, or rostral regions of the body (VA or VB). The pigmentation in specimens from the Philippines was advanced along the entire dorsal region of the body, resulting in classification as stage VIA_{II} or VIA_{IV} and thus had begun the transition to the elver stage.

Timing and duration of metamorphosis

Ages at metamorphosis (mean ± SD) of *A. marmorata* from Japan, Taiwan, the Philippines, and the Poigar and Dumoga Rivers in Indonesia were 123 ± 13.4 days (range: 100–155 days), 116 ± 14.6 days (range: 92–145 days), 120 ± 13.0 days (range: 105–140 days) and 132 ± 9.7 days (range: 117–155 days) and 120 ± 15.6 days (range: 96–147 days), respectively (Table 1). A significant difference was found between the specimens from

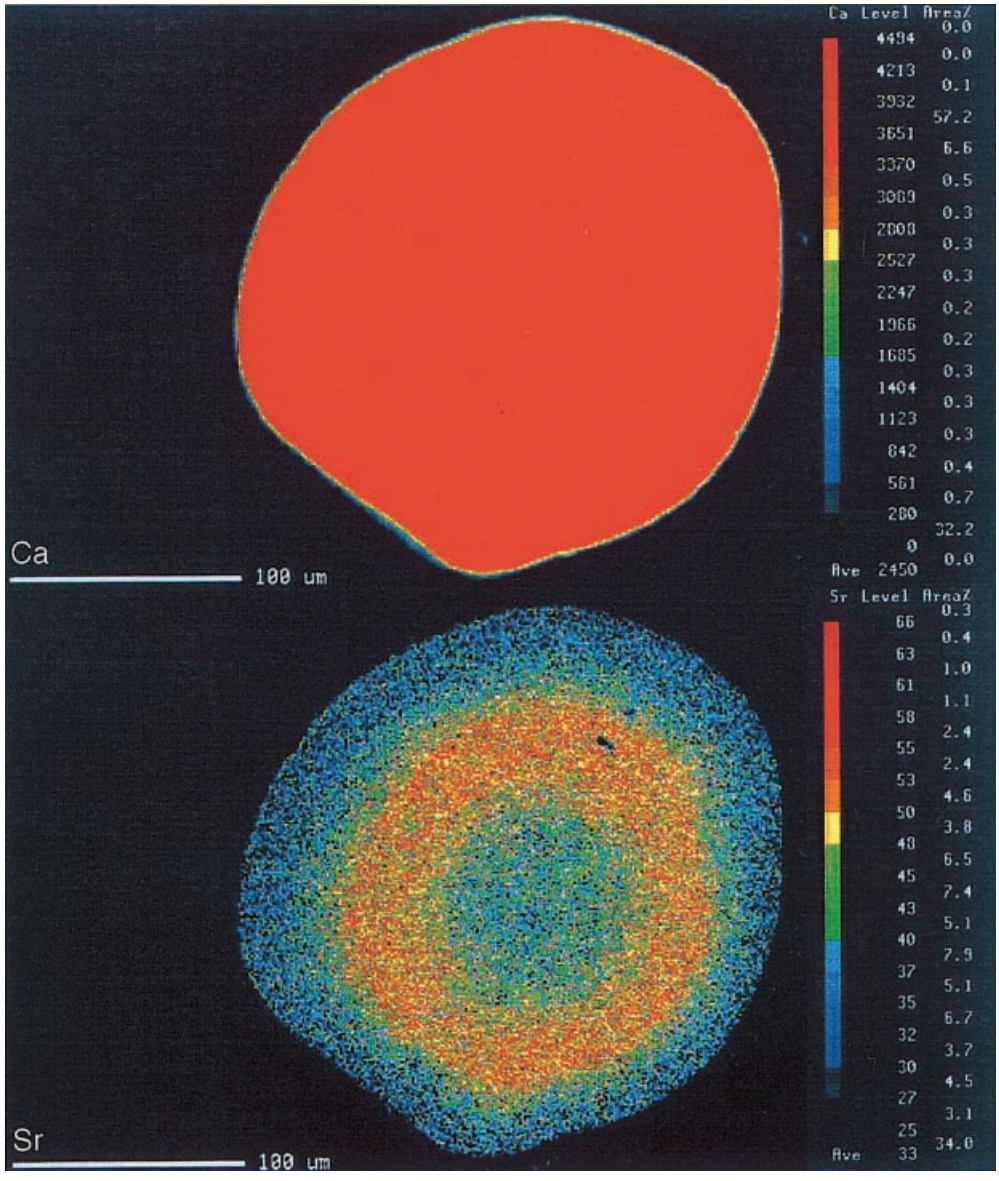

Fig. 4 *Anguilla marmorata*. X-ray-intensity maps of Ca (top) and Sr (bottom) contents in an otolith of a glass eel (TL: 47.8 mm) collected at the Tanegasima Island beach, Japan on 16 February 1999

Taiwan and those from Poigar River in Indonesia (ANOVA, $P < 0.05$), but no significant difference was apparent in other combinations (ANOVA, $P > 0.1$).

Duration of the metamorphosis stage (mean ± SD) of *A. marmorata* from Japan, Taiwan, the Philippines and the Poigar and Dumoga Rivers in Indonesia was 17 ± 4.0 days (range: 12–24 days), 15 ± 3.0 days (range: 10–20 days), 17 ± 4.3 days (range: 12–26 days), and 17 ± 3.8 days (range: 9–23 days) and 17 ± 3.3 days (range: 13–24 days), respectively (Table 1). The mean duration of metamorphosis did not differ among the different samples (ANOVA, $P > 0.1$).

Age at recruitment

Age at recruitment (mean ± SD) of *A. marmorata* from Japan, Taiwan, the Philippines, and the Poigar and Dumoga Rivers in Indonesia was 154 ± 17.0 days (range: 133–189 days), 145 ± 15.6 days (range: 116–166 days), 154 ± 13.5 days (range: 136–178 days), 159 ± 11.5 days (range: 141–182 days), and 152 ± 15.2 days (range: 129–177 days), respectively (Table 1). The age at recruitment did not differ among the different samples (ANOVA, $P > 0.5$).

Close linear relationships were apparent between the ages at metamorphosis and ages at recruitment in all samples (Fisher's Z transformation, $P < 0.0001$; Fig. 4), and these relationships (Fig. 5) were similar to those observed in *A. japonica* (Tsukamoto and Umezawa 1994), *A. australis* (Arai et al. 1999a), *A. bicolor pacifica* (Arai et al. 1999b), *A. celebesensis*, *A. marmorata* and *A. bicolor bicolor* (Arai et al. 1999c), *A. anguilla* and *A. rostrata* (Arai et al. 2000a) and *A. dieffenbachii* (Marui et al. 2001). No significant differences in regression slopes were found among the five samples (ANCOVA, $P > 0.1$).

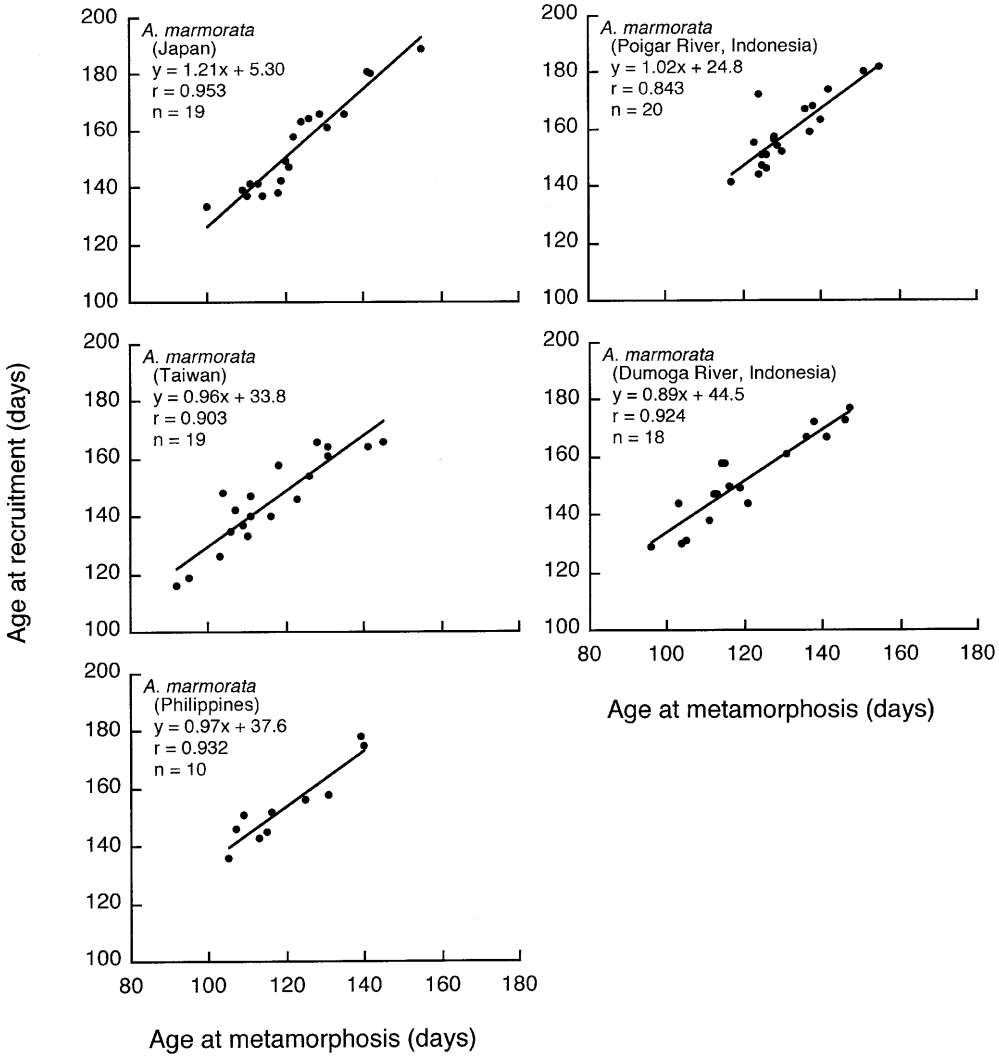

Fig. 5 *Anguilla marmorata*. Relationship between age at metamorphosis (days) and age at recruitment (days) of glass eels collected from the coasts of Japan, Taiwan, the Philippines and Indonesia

Hatching date

The estimated hatching dates, back-calculated from sampling dates and ages of the specimens from the different sampling areas, varied widely and ranged over about six different months of the year (Table 1). The hatching dates of the specimens from Japan, Taiwan, the Philippines, and the Poigar and Dumoga Rivers in Indonesia were from 11 August 1998 to 2 October 1998, from 1 September 1998 to 22 October 1998, from 21 March 1994 to 26 April 1994, and from 6 January 1997 to 16 April 1997 and from 11 December 1995 to 28 January 1996, respectively.

Discussion

Inshore migration

The relationship between the age at metamorphosis and age at recruitment clearly showed that glass eels that metamorphosed at an earlier age also tended to migrate to coastal regions at younger ages, indicating that early-metamorphosing larvae recruited earlier (Fig. 4). Metamorphosis seems to be a key factor during the larval migration that is related to the timing of the inshore migration of glass eels. Tsukamoto and Umezawa (1994), Arai et al. (1997, 1999a, 2000a) and Marui et al. (2001) found the same phenomenon in the temperate eels, *A. japonica*, *A. australis*, *A. anguilla* and *A. rostrata*, and *A. dieffenbachi*, respectively. This relationship between the timing of metamorphosis and the inshore migration of glass eels seems to be typical for anguillid eels.

The early-life-history parameters were almost the same among the five samples of *A. marmorata*, with the average durations of the leptocephalus stage ranging between 116 days (Taiwan) and 132 days (Indonesia) and the ages at recruitment ranging between 145 days (Taiwan) and 159 days (Indonesia). Although not all of the recruitment period was covered by the present study, the ages at metamorphosis and recruitment of *A. marmorata* glass eels were found, in previous work, to be constant throughout the year in the Poigar Estuary,

Sulawesi Island, Indonesia (Arai et al. 2001a). If this phenomenon is applicable to other sites, these results suggest that early-life-history parameters, such as age at metamorphosis (duration of the leptocephalus stage) and age at recruitment, are similar in *A. marmorata* in the western North Pacific, in spite of their different geographic locations, ocean migration routes, and growth histories.

Early growth

The average total lengths of *A. marmorata* at recruitment (49.2–51.2 mm) were 10–20 mm less than those of temperate *Anguilla* species, such as *A. anguilla* (68 mm; Lecomte-Finiger 1992) and *A. japonica* (57 mm; Cheng and Tzeng 1996; Arai et al. 1997), even though all three species were at the same pigmentation stage; i.e. stage VA or VB. Arai et al. (1999b, c, 2001a) also reported small sizes in tropical glass eels (44.7–52.6 mm in *A. celebesensis*, 49.4 mm in *A. bicolor bicolor*, and 48.6–51.5 mm in *A. bicolor pacifica*) that were similar to the sizes of *A. marmorata*, when they arrived at river mouths in tropical areas. Furthermore, differences in the total lengths of fully grown leptocephali have also been found between tropical and temperate species. The total lengths of fully grown leptocephali of the temperate eels, *A. anguilla*, *A. rostrata* and *A. japonica*, were estimated as 75 mm (Jespersen 1942; Tesch 1977), 70 mm (Kleckner and McCleave 1985) and 60 mm (Tabeta and Konishi 1986), respectively, while those of tropical species collected in the Indo-Pacific region, including *A. marmorata*, have been reported as being around 50 mm (Jespersen 1942; Arai et al. 2001b).

According to our age determinations, the growth rate of *A. marmorata* leptocephali was estimated to range from 0.38 to 0.43 mm/day (Arai et al. 2001b), which is less than those reported for the temperate eel, *A. japonica* (0.56–0.59 mm/day; Umezawa and Tsukamoto 1990; Tsukamoto et al. 1992), which has a similar duration of the leptocephalus stage (116–138 days; Cheng and Tzeng 1996). The lower growth rate during the leptocephalus stage of tropical eels, including *A. marmorata*, seems to result in a smaller size of the fully grown leptocephalus and smaller size at recruitment in the species.

Oceanic migration

Despite being a geographically widespread species, there is relatively little known about the life history of *A. marmorata* in the wide range of areas the juveniles and adults inhabit. There is very little information available about the reproductive ecology and migratory behavior of *A. marmorata*, and only the general area of one of their spawning areas in the Pacific has been identified, based on the genetic identification of leptocephali in the North Equatorial Current west of the Mariana Islands (Aoyama et al. 1999). Based on the age of these leptocephali and the predominant westward flow in the region (Reverdin et al. 1994; Kaneko et al. 1998; Kawabe and Taira 1998; Wijffels et al. 1998), Arai et al. (2001b) suggested that this species spawns within the North Equatorial Current, as does *A. japonica* (Tsukamoto 1992), and is transported westward in a similar fashion (Fig. 1). However, the North Equatorial Current divides into northward and southward flows that become the Kuroshio and Mindanao Currents, respectively (Fine et al. 1994). Therefore, *A. marmorata* leptocephali in the northern half of the North Equatorial Current probably drift westward towards the Philippines and then north toward Taiwan or then to the northeast toward southern Japan in the flow of the Kuroshio Current. In contrast, the leptocephali in the southern half of the North Equatorial Current probably get transported southward by the Mindanao Current (Lukas et al. 1991) along the east coast of the southern Philippines. Some leptocephali may subsequently get transported westward by water that flows from the Mindanao Eddy region, southeast of the southern Philippines, into the Celebes Sea (Miyama et al. 1995; Godfrey 1996) and then recruit to Sulawesi Island and other areas adjacent to the Celebes Sea.

This hypothesis for the spawning location and subsequent transport of *A. marmorata* leptocephali westward and then both to the north and south, even as far as into the Celebes Sea, is supported by the genetic study of the population structure of *A. marmorata* by Ishikawa (1998). Specimens from all four of these areas were found to be part of the same northern population of *A. marmorata*, which was genetically differentiated from five other apparent populations spread out across the range of the species. This suggests that eels from throughout the northwest part of the range of *A. marmorata* in the Pacific may migrate to the western North Equatorial Current region to spawn and then their leptocephali are transported back to a wide range of areas spread over 30 degrees of latitude as proposed above. The slight differences observed in the duration of the leptocephalus stage and the ages at recruitment observed in this study may be due to the different distances from the North Equatorial Current spawning area, seasonal differences in the speed of the North Equatorial, Kuroshio and Mindanao Currents (Qui and Lukas 1996), or the dynamics of the coastal currents in the various areas.

However, in contrast to the two Atlantic anguillid species and *A. japonica*, only relatively few leptocephali of *A. marmorata* have been caught in the Pacific (Jespersen 1942; Aoyama et al. 1999). More information on the geographic distribution, age and growth of leptocephali is needed to verify the spawning location and recruitment mechanisms of the northern population of *A. marmorata* and to determine other spawning locations and recruitment patterns of this species.

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