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## Early life history of tropical *Anguilla* leptocephali in the western Pacific Ocean

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**Abstract** In order to examine the early life-history characteristics of tropical eels, otolith microstructure and microchemistry were examined in leptocephali of *Anguilla bicolor pacifica* (27.6–54.1 mm TL,  $n=20$ ) and *A. marmorata* (22.0–47.3 mm TL,  $n=8$ ) collected during a cruise in the western Pacific. *A. bicolor pacifica* occurred between 10°N and 15°N in the west and between 5°S and 10°N farther to the east. *A. marmorata* also occurred in two different latitudinal ranges in the Northern (15–16°N) and Southern Hemispheres (3–15°S) of the western Pacific. The increment widths in the otoliths of these leptocephali increased between the hatch check (0 days) and about an age of 30 days in both species, and then gradually decreased toward the otolith edge. Otolith Sr:Ca ratios showed a gradual increase from the otolith center to the edge. The ages of *A. bicolor pacifica* and *A. marmorata* leptocephali ranged from 40 to 128 days and from 38 to 99 days, respectively. Growth rates of *A. bicolor pacifica* and *A. marmorata* leptocephali ranged from 0.33 to 0.71 mm day<sup>-1</sup> and from 0.45 to 0.63 mm day<sup>-1</sup>, respectively. These leptocephali had estimated growth rates that were spread out throughout most of the reported range of growth rates of the leptocephali of the temperate species, the Japanese

eel and the Atlantic eels. Differences in the spatial distribution in relation to current systems, and the age and size compositions of the leptocephali of *A. bicolor pacifica* and *A. marmorata* suggested different spawning locations for these two species.

### Introduction

Studies on the leptocephali of the catadromous eels of the genus *Anguilla* have almost exclusively been limited to temperate species despite the greater number of tropical species and recent information that suggests the genus originated in the tropics. The temperate anguillid species are well known for their long spawning migrations into the open ocean, but little is known about the spawning migrations of the tropical eels. Two-thirds of the recognized 18 *Anguilla* species/subspecies inhabit tropical regions and, among these, seven species/subspecies occur in the western Pacific around Indonesia (Ege 1939; Castle and Williamson 1974; Arai et al. 1999a). Recent mitochondrial DNA analysis revealed that *A. borneensis* from Borneo Island was closest to the ancestral eel species and that the genus *Anguilla* probably originated near present day Indonesia (Aoyama 1998). Thus, larval dispersal of ancestral tropical species probably played a role in the early global dispersal and consequent speciation within the genus *Anguilla* (Tsukamoto 1994; Tsukamoto and Aoyama 1998). Accordingly, knowledge about the early life-history and oceanic migration patterns of the leptocephali of tropical anguillid species will be important in understanding the ecology and evolutionary history of the genus *Anguilla*.

Recent progress in otolith techniques has resulted in the accumulation of considerable early life-history information on age, growth, and timing of metamorphosis of leptocephali and glass eels of temperate species of *Anguilla* (*A. japonica*: Tabeta et al. 1987; Tsukamoto 1990; Cheng and Tzeng 1996; *A. anguilla*: Castonguay 1987; Lecomte-Finiger 1992; Arai et al. 2000a; *A. rostrata*: Castonguay 1987; Wang and Tzeng 1998; Arai et al.

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2000a; *A. australis*: Arai et al. 1999d; *A. dieffenbachii*: Marui et al. in press). 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 entered freshwater (Arai et al. 1999b, c, in press; Marui et al. in press), but compared with the information gained from otolith studies and from studies of the distribution of the leptocephali of northern temperate species of *Anguilla* (Schmidt 1922; Scoth and Tesch 1982; Kleckner and McCleave 1988; Tsukamoto 1992; McCleave 1993), little is known about the early life history of any tropical species, because there have not been any studies on the leptocephali of tropical anguillid eels since the Dana Expedition during 1928–1930 (Jespersen 1942).

We collected various sizes of tropical eel leptocephali during a cruise of the R.V. "Hakuho-maru", Ocean Research Institute, The University of Tokyo, in the western Pacific, that was conducted from July to September 1995, in both the western North and South Pacific Ocean. The distribution of anguillid leptocephali during this cruise was described by Aoyama et al. (1999), and the otolith microstructure and microchemistry of most of the specimens of *A. bicolor pacifica* and *A. marmorata* that were genetically identified during that study were analyzed during the present study. These samples included medium-sized specimens all the way up to an individual that had reached full grown size, and enabled us to obtain the first information on age and growth of the leptocephali of tropical species of *Anguilla* in relation

to their distribution and the geography of surface current systems in the western Pacific.

The objectives of this study were to describe the ontogenic changes in otolith microstructure and microchemistry and to determine larval ages and growth rates of leptocephali of the tropical eels *A. bicolor pacifica* and *A. marmorata*. We also discuss the implications of these findings in relation to the possible routes of oceanic migration of the leptocephali based on the surface current systems in the western Pacific.

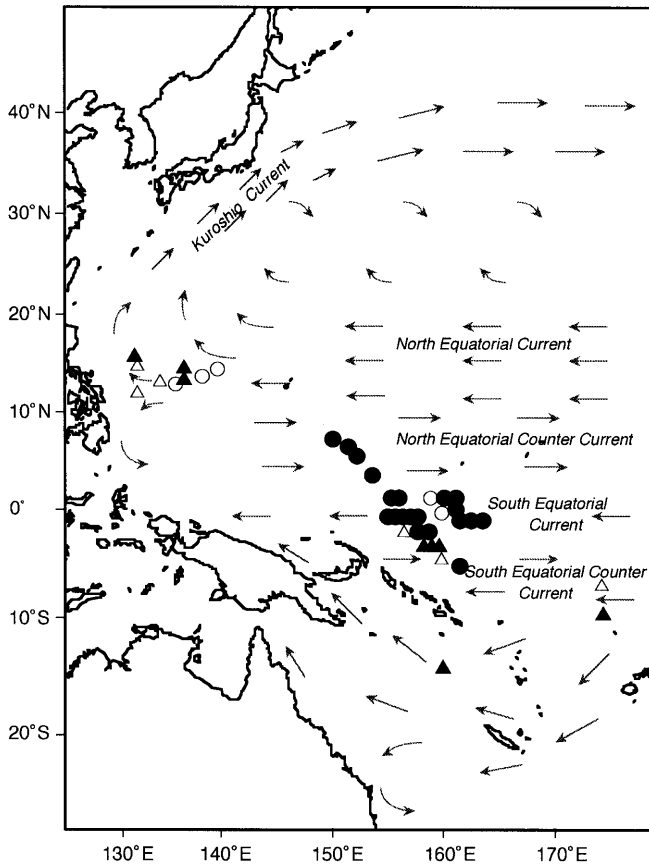
## Materials and methods

A total of 28 leptocephali (20 specimens of *Anguilla bicolor pacifica*, 8 of *A. marmorata*) that were collected during the KH-95-2 cruise of the R.V. "Hakuho-maru" in 1995 were used in this study (Table 1). These specimens were the majority of the leptocephali of these two species from this cruise that were identified using mitochondrial DNA (mtDNA) genotypes by Aoyama et al. (1999). There were a few remaining specimens that were genetically identified but their otoliths were not suitable for analysis. The leptocephali were collected by oblique or horizontal tows of a 3 m Isaacs-Kidd Midwater Trawl (IKMT; mesh aperture: 0.5 mm or 1.0 mm) between the surface and 100–300 m depth in the western Pacific, between 7 July and 27 September 1995 (Fig. 1). Water temperature and salinity within the sampling area ranged from 11.4°C to 18.2°C and from 34.5‰ to 35.9‰, respectively.

*Anguilla* leptocephali were sorted out from plankton samples immediately after each tow. Total length (TL) was measured to the nearest 0.1 mm, and the number of myomeres was counted using a dissecting microscope (Table 1). Specimens were then frozen and stored at –60°C or preserved in 95% ethanol until species identi-

**Table 1** *Anguilla* spp. Total length (TL), total myomeres (TM), preanal myomeres (PAM), otolith radius and age of leptocephali collected in the western Pacific in 1995

Sampling date	Sampling location	TL (mm)	TM	PAM	Otolith radius (µm)	Age (days)
<i>A. bicolor pacifica</i>						
5 Aug	08°56'4N; 147°58'7E	40.0	102	70	74.1	111
7 Aug	01°41'6N; 160°27'5E	27.6	108	75	40.5	40
7 Aug	01°41'6N; 160°27'5E	27.8	105	70	42.1	44
7 Aug	01°25'9N; 160°54'0E	47.9	104	71	71.5	103
8 Aug	01°09'4N; 161°21'5E	48.0	106	69	66.9	95
8 Aug	01°09'4N; 161°21'5E	32.7	104	70	47.7	54
8 Aug	01°09'4N; 161°21'5E	28.1	104	70	38.3	41
7 Sep	02°02'7S; 157°35'9E	48.3	107	72	72.8	96
7 Sep	02°62'7S; 157°35'9E	48.3	106	72	68.5	93
7 Sep	04°59'6S; 160°00'0E	49.0	105	71	72.2	107
8 Sep	01°01'1S; 156°49'0E	54.1	108	70	93.7	122
8 Sep	01°51'4N; 154°32'0E	32.6	107	73	54.4	63
8 Sep	01°01'1S; 156°49'0E	50.9	106	72	78.9	101
8 Sep	01°01'1S; 156°49'0E	49.9	108	69	79.8	115
8 Sep	01°51'4N; 154°32'0E	29.3	104	72	48.3	52
8 Sep	01°01'1S; 156°49'0E	50.9	107	74	77.2	110
8 Sep	01°01'1S; 156°49'0E	51.0	108	73	85.2	128
9 Sep	02°19'6N; 154°09'9E	34.1	104	71	55.5	65
10 Sep	08°18'7N; 149°42'9E	41.9	105	73	70.6	86
10 Sep	06°32'0N; 151°01'1E	41.3	104	74	75.4	101
<i>A. marmorata</i>						
18 Jul	15°59'9N; 130°59'9E	39.6	100	65	62.6	58
23 Jul	14°60'0N; 137°00'1E	22.0	106	–	37.3	38
23 Jul	14°60'0N; 137°00'1E	24.2	104	71	40.3	43
13 Aug	09°58'3S; 174°58'2E	35.8	103	–	67.2	69
3 Sep	14°59'9S; 160°00'3E	47.3	104	69	83.2	99
7 Sep	03°52'7S; 158°59'5E	25.2	105	69	39.9	40
7 Sep	03°52'7S; 158°59'5E	26.3	103	72	43.1	45
7 Sep	03°52'7S; 158°59'5E	36.2	104	71	58.4	63



**Fig. 1** Map showing the distribution of *Anguilla* spp. leptocephali examined in the otolith study (solid symbols), other specimens that were identified but their otoliths were not examined (open symbols) and the prevailing surface oceanic currents in the western Pacific (Pickard and Emery 1990) (circle, *A. bicolor pacifica*; triangle, *A. marmorata*)

fication using mtDNA genotypes (Aoyama et al. 1999). Leptocephali identified as *A. bicolor pacifica* or *A. marmorata* were subsequently used for otolith microstructural and microchemical examinations. *A. bicolor pacifica* leptocephali ranged from 27.6 to 54.1 mm TL and *A. marmorata* leptocephali ranged from 22.0 to 47.3 mm TL (Table 1).

Sagittal otoliths of each fish were extracted and their radii measured; otoliths were then prepared for electron microprobe analyses of the Sr:Ca ratios using a wavelength dispersive X-ray electron microprobe (JEOL JXA-733). The procedures for embedding, grinding and polishing, and the conditions for electron microprobe analyses followed those described by Arai et al. (1997, 1999b,c,d). Microprobe measurement points, seen as burn depressions, were assigned to otolith growth increments, which were examined as described below. The averages of Sr and Ca concentrations pooled for every ten successive growth increments were used for the life-history transect analysis.

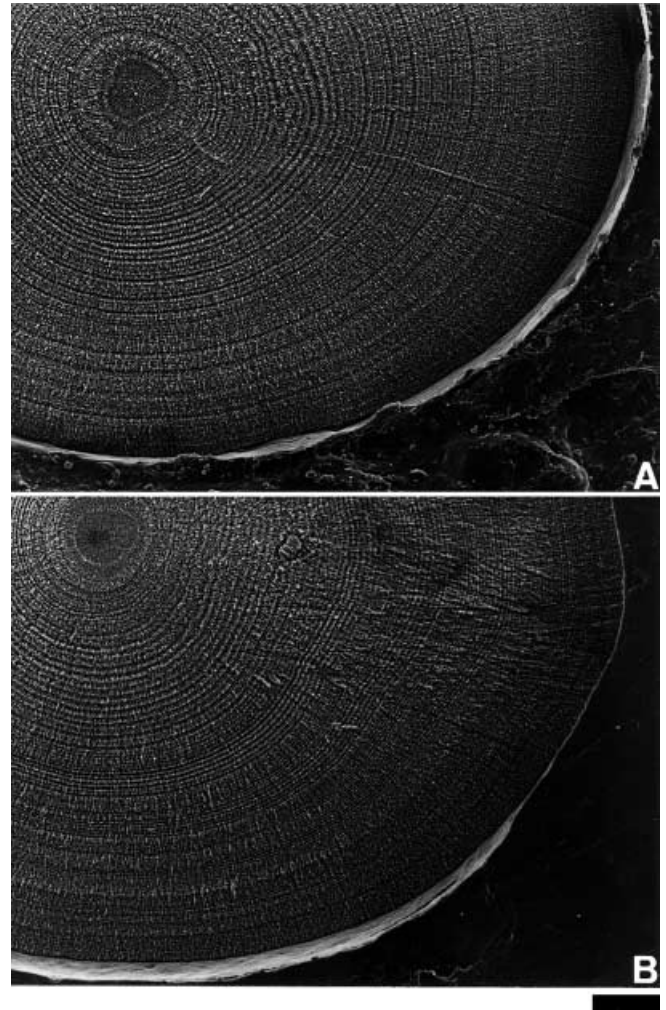
After the electron microprobe analysis, scanning electron microscopic (SEM, Hitachi S-4500) observation was carried out following the procedures described by Arai et al. (1997, 1999b,c,d). The averages of every ten successive increment widths from the hatch check to the edge were used for otolith growth analysis. Because 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 *A. bicolor pacifica* and *A. marmorata* examined in the present study (Table 1).

A mean length of 3 mm TL at hatching was obtained for artificially fertilized *A. japonica*, and this length was deducted from the total length of each leptocephali used in this study (Tsukamoto et al. 1992). Thus, the individual growth rates were calculated as  $(TL-3)/age$ .

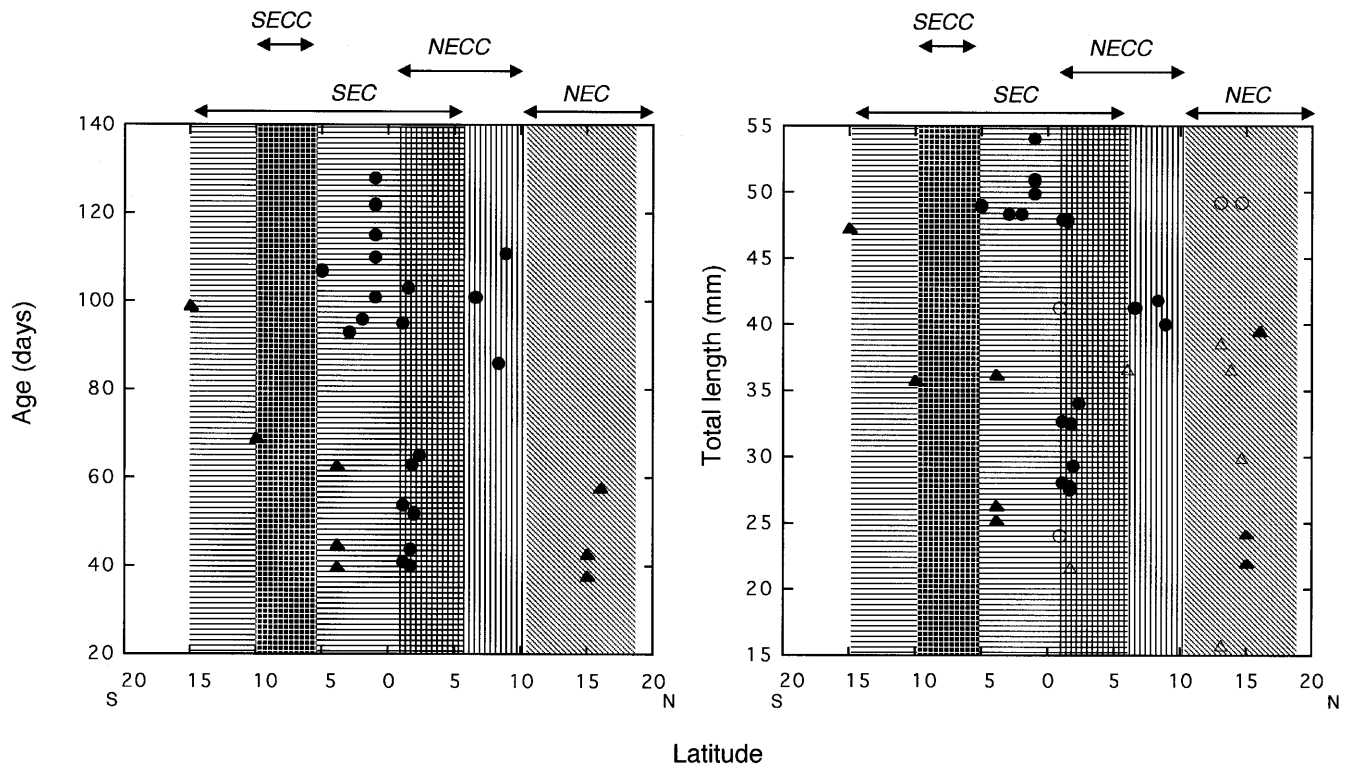
## Results

### Otolith microstructure

The microstructure of otoliths was fundamentally the same between the two species, and was similar to those of the leptocephali of other species of *Anguilla* such as *A. japonica* (Tsukamoto et al. 1989) and *A. anguilla* and *A. rostrata* (Castonguay 1987) (Fig. 2). An otolith core was observed as a deep hole in the etched otolith, and a hatch check (Umezawa et al. 1989) was visible as a deep circular groove surrounding the hole. The diameter of the hatch check was  $9.9 \pm 0.5 \mu\text{m}$  (mean  $\pm$  SD), with a



**Fig. 2A, B** Tropical *Anguilla* spp. SEM photographs showing microstructure of an etched otolith of **A** *A. bicolor pacifica* (47.9 mm TL) and **B** *A. marmorata* leptocephali (47.3 mm TL). Scale bar: 10  $\mu\text{m}$



**Fig. 3** Tropical *Anguilla* spp. Relationship between age distribution and latitude (*left*), and between total length distribution and latitude (*right*) in the western Pacific. The typical latitude ranges of the major surface currents in the western Pacific are indicated with overlapping arrows (NEC North Equatorial Current; NECC North Equatorial Counter Current; SEC South Equatorial Current; SECC South Equatorial Counter Current)

range of 9.2–11.2  $\mu\text{m}$  in *A. bicolor pacifica*, and  $9.8 \pm 0.6 \mu\text{m}$  (mean  $\pm$  SD), with a range of 9.0–10.8  $\mu\text{m}$  in *A. marmorata*. There was no significant difference between the two species (Mann–Whitney *U*-test,  $P > 0.1$ ). Distinct concentric growth increments were observed around the core in both species (Fig. 2). There were no distinct check rings other than the hatch check and the first feeding (yolk absorption) check near the otolith center in the otoliths of *A. bicolor pacifica* and *A. marmorata* leptocephali. This is in contrast to the otoliths of glass eels of the temperate species *A. anguilla* (Lecomte-Finiger 1992) and *A. japonica* (Cheng and Tzeng 1996), in which a metamorphosis check, presumably deposited at the beginning of metamorphosis, has been observed. The radii of otoliths were linearly related to the total lengths of both *A. bicolor pacifica* ( $y = 1.59x - 0.60$ ,  $r = 0.933$ ) and *A. marmorata* leptocephali ( $y = 1.80x - 3.64$ ,  $r = 0.978$ ).

#### Age, growth and hatching date

The age of *A. bicolor pacifica* leptocephali ranged widely from 40 to 128 days (Table 1); that of *A. marmorata* leptocephali was separated into two different latitudinal

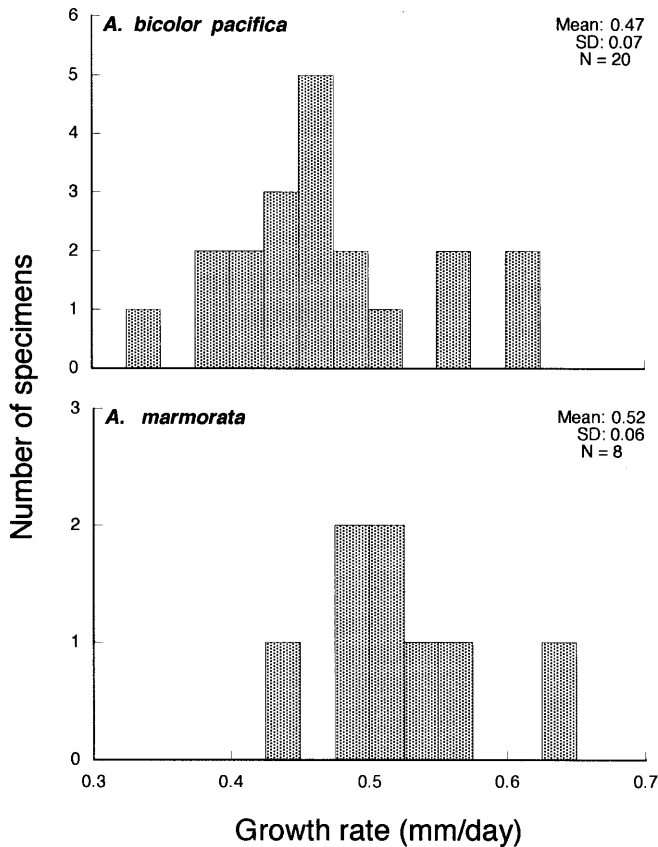
ranges in the Northern and Southern Hemispheres (Fig. 3). In the former age ranged from 38 to 58 days, and in the latter it ranged from 40 to 69 days, plus one specimen collected in the southernmost region that was aged at 99 days. The ages of *A. bicolor pacifica* and *A. marmorata* leptocephali were linearly related to total length in each species (the former:  $y = 0.30x + 15.4$ ,  $r = 0.934$ ; the latter:  $y = 0.41x + 8.73$ ,  $r = 0.936$ ). A similar linear relationship also was found between age and otolith radius in these species (*A. bicolor pacifica*:  $y = 0.54x + 18.9$ ,  $r = 0.975$ ; *A. marmorata*:  $y = 0.78x + 9.44$ ,  $r = 0.973$ ).

The individual growth rates ranged from 0.33 to 0.71  $\text{mm day}^{-1}$  (mean  $\pm$  SD:  $0.47 \pm 0.07 \text{ mm day}^{-1}$ ) in *A. bicolor pacifica* and from 0.45 to 0.63  $\text{mm day}^{-1}$  (mean  $\pm$  SD:  $0.52 \pm 0.06 \text{ mm day}^{-1}$ ) in *A. marmorata* (Fig. 4). The mean growth rates of the two species were significantly different (Mann–Whitney *U*-test,  $P < 0.05$ ).

The estimated hatch dates, back-calculated from their sampling date and ages, were from 15 April to 17 July 1995 in *A. bicolor pacifica*, and from 21 May to 28 July 1995 in *A. marmorata* (21 May to 15 June 1995 in the Northern Hemisphere specimens and 26 May to 28 July 1995 in the Southern Hemisphere specimens) (Fig. 5).

#### Otolith growth and Sr:Ca ratios

The pattern of change in the otolith increment widths along the life-history transects from the core to the otolith edge are shown in Fig. 6. Otolith increment widths increased between the hatch check and age 20–40 days, with a peak at 30 days in both species, and then gradually decreased toward the edge.

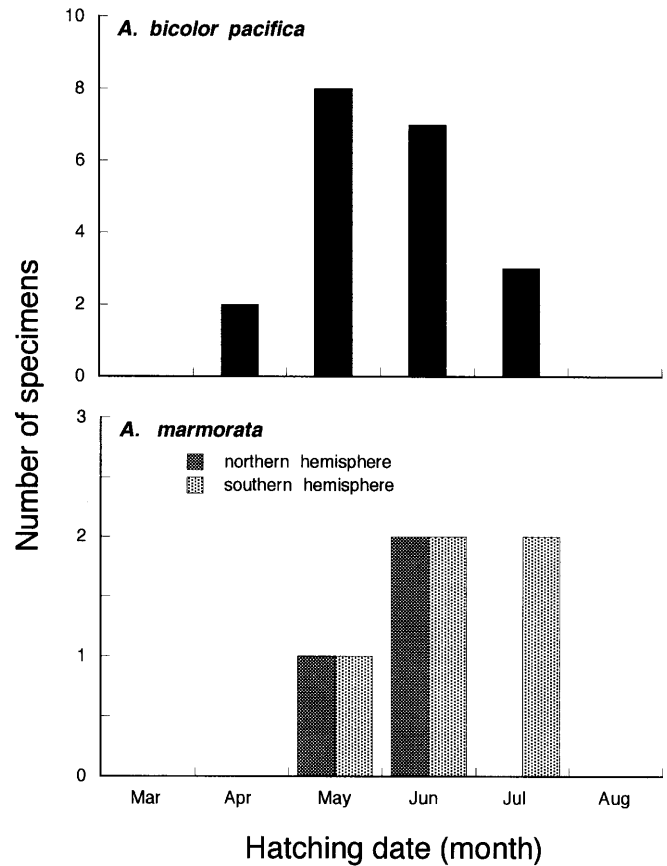


**Fig. 4** Tropical *Anguilla* spp. Growth rates of *A. bicolor pacifica* (upper panel) and *A. marmorata* (lower panel) leptocephali

Otolith Sr:Ca ratios tended to rise from the core toward the edge in both species (Fig. 6). A slight drop in the ratio was found at around 30 days in both species, coinciding with the peak in otolith increment width. The minimum ratio was recorded in the core, with an average of  $8.8 \times 10^{-3}$  in *A. bicolor pacifica* and of  $9.8 \times 10^{-3}$  in *A. marmorata*, and the maximum levels found were in the outermost regions and had average ratios of  $14.8 \times 10^{-3}$  in the former and  $16.2 \times 10^{-3}$  in the latter species. The sharp drop in the Sr:Ca ratio, coinciding with the rapid increase in otolith increment width that has been observed in the otoliths of glass eels of *Anguilla* spp., appears to be correlated to the onset of metamorphosis (Otake et al. 1994; Arai et al. 1997, 1999b,c,d, 2000a), was not observed in any of the leptocephali of *A. bicolor pacifica* or *A. marmorata* examined, including the fully grown leptocephali (> 50 mm in TL, Table 1).

#### Horizontal distribution

The geographic distribution of *A. bicolor pacifica* and *A. marmorata* leptocephali indicated that these two species are widely distributed in the western Pacific and that there appear to be at least two separate spawning areas for each species (Fig. 1). Various sizes (27.6–54.1 mm TL) of *A. bicolor pacifica* leptocephali occurred



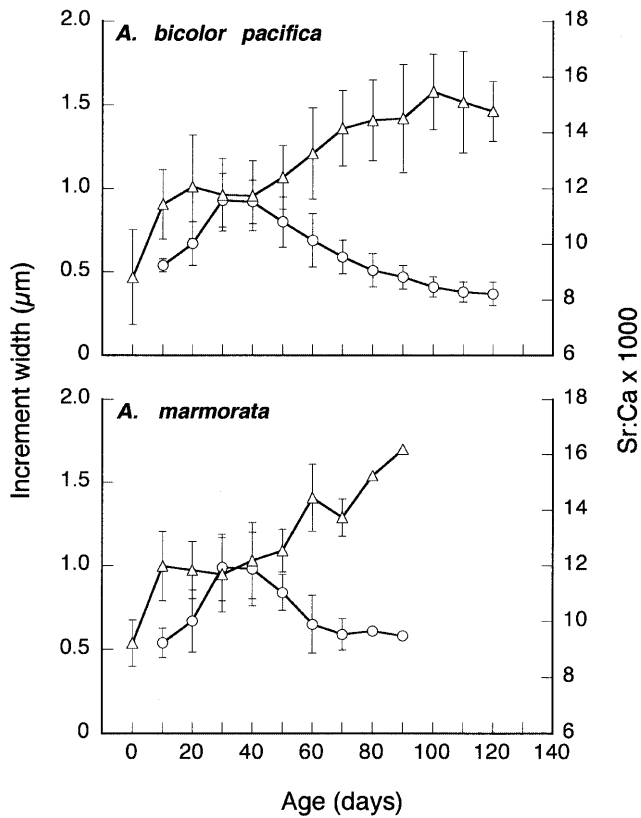
**Fig. 5** Tropical *Anguilla* spp. Hatching months of *A. bicolor pacifica* (upper panel) and *A. marmorata* (lower panel) leptocephali

in the general vicinity of the North Equatorial Current (westward flow, approximately 8–20°N), the North Equatorial Counter Current (eastward flow, approximately 0–8°N) and the South Equatorial Current (westward flow, approximately 15°S–4°N) (Fig. 2). There were three specimens in the North Equatorial Current region, and the remainder were collected between 8°N and 5°S in the region of the North Equatorial Counter Current and the South Equatorial Current. *A. marmorata* leptocephali clearly showed a patchy distribution in both Northern (15–16°N, 22.0–39.6 mm TL) and Southern Hemispheres (3–15°S, 25.2–47.3 mm TL). All northern specimens occurred in the region of the North Equatorial Current, and the southern specimens occurred in the region of the South Equatorial Current or the South Equatorial Counter Current, which is often present from about 5°S to 10°S, close to where a few of the specimens were collected.

#### Discussion

##### Ontogenic changes in otolith growth and Sr:Ca ratios

Changes in otolith Sr:Ca ratios have been considered to relate to environmental factors such as water tempera-



**Fig. 6** Tropical *Anguilla* spp. Profiles of otolith incremental width (circle) and Sr:Ca concentration ratios (triangle) measured with a wavelength dispersive electron microprobe from the core to the otolith edge in leptocephali. Each point represents averaged data ( $\pm$ SD) for every 10 days. Upper panel: *A. bicolor pacifica* ages 10–40 days ( $n=20$ ), 50–90 days ( $n=17-12$ ), 100–110 days ( $n=9-5$ ), 120 days ( $n=2$ ); lower panel: *A. marmorata* ages 10–30 days ( $n=8$ ), 40–60 days ( $n=7-3$ ), 70 days ( $n=2$ ), 80–90 days ( $n=1$ )

ture (Radtke et al. 1990; Townsend et al. 1992, 1995) and salinity or Sr concentration in ambient water (Kalish 1990; Secor et al. 1995; Radtke et al. 1996; Tzeng et al. 1997; Arai and Tsukamoto 1998; Tsukamoto et al. 1998; Tsukamoto and Arai in press). However, in *Anguilla japonica* leptocephali, observed ontogenetic increases in Sr:Ca ratios have been suggested to be affected by endogenous physiological factors rather than exogenous environmental factors (Otake et al. 1994; Arai et al. 1997), because the leptocephali apparently spend their lives in relatively constant environmental conditions in oceanic currents such as the North Equatorial and Kuroshio Currents. As suggested by Otake et al. (1997) for the conger eel *Conger myriaster*, variations in otolith Sr:Ca ratios in leptocephali may reflect the amount of synthesis and accumulation of body glycosaminoglycans (GAG) during ontogeny, because these compounds are thought to have a high affinity for Sr. It is likely that the same phenomenon would occur in the leptocephali of tropical eels.

The otolith growth pattern of the *A. bicolor pacifica* and *A. marmorata* leptocephali was divided into two

phases by the peak in increment width and the period of decrease in the Sr:Ca ratios at about 30 days. The same characteristics were found in the otoliths of *A. japonica* leptocephali (Otake et al. 1994; Arai et al. 1997) and of the glass eels of tropical (Arai et al. 1999b,c, 2000a, in press) and temperate eel species (Arai et al. 1999d, 2000a; Marui et al. in press). Otake et al. (1997) also observed the same phenomenon in otoliths of *Conger myriaster* leptocephali. Such patterns of change in otolith growth and Sr:Ca ratios in the leptocephalus stage appear to be typical of anguillid fishes. The inflection in otolith growth ca. 30 days from hatching might be related to favorable somatic growth after successfully switching their nutritional source from yolk material to exogenous feeding, which probably occurs after 10 days, based on the observation that artificially hatched eel larvae exhausted their yolk material after about 10 days (Yamauchi et al. 1976; Tanaka et al. 1995). In the white grunt, *Haemulon plumieri*, it has been reported that Sr:Ca ratios decreased within the faster growing incremental zone (Sadovy and Severin 1992). The temporal decrease in the Sr:Ca ratios found at about 30 days after hatching in tropical eel otoliths might be due to physiological factors relating to an accelerated rate of growth, but this needs to be tested in the future.

#### Growth rate and maximum size

Although the growth rates of the leptocephali of the tropical species of *Anguilla* examined here were similar to those of temperate species, the maximum size attained by the leptocephali of tropical species appears to be less than that of temperate species. The growth rates of the leptocephali examined during this study ranged from 0.33 to 0.71 mm day<sup>-1</sup>. This was within the range reported for the temperate eels *A. anguilla* and *A. rostrata* (0.33–0.44 mm day<sup>-1</sup>) (Castonguay 1987) and *A. japonica* (0.48–0.90 mm day<sup>-1</sup>) (Tsukamoto et al. 1989, 1992). However, the sizes of fully grown leptocephali of tropical eels have been suggested to be smaller than those of temperate species, with the total lengths of fully grown leptocephali of Indo-Pacific tropical eels reported to average about 50 mm (Jespersen 1942). Arai et al. (1999b,c) analyzed the otoliths of glass eels and estimated that the durations of the leptocephalus stages of *A. bicolor pacifica* and *A. marmorata* were 120 and 135 days, respectively. Accordingly, the linear relationship between age and total length indicated that the maximum sizes of those leptocephali would be 55.9 mm TL for *A. bicolor pacifica* and 57.9 mm TL for *A. marmorata*, respectively. Thus, the largest specimen of this study (54.1 mm TL, *A. bicolor pacifica*) was probably a fully grown leptocephalus. In contrast, the total lengths of fully grown leptocephali of the temperate eels *A. anguilla*, *A. rostrata* and *A. japonica* were 75 mm (Jespersen 1942), 70 mm (Kleckner and McCleave 1985) and 60 mm (Tabeta and Konishi 1986), respectively. The smaller size of the fully grown leptocephalus stage in

tropical eels, with similar growth rates to those of temperate eels, suggests that the duration of the leptocephalus stage is shorter in tropical than in temperate species.

In *A. japonica*, it also has been reported that the predicted total length at hatching (6.56 mm), calculated from the relationship between age and total length of leptocephali (Mochioka 1996), was apparently greater than that observed at hatching in artificially spawned larvae (3.0 mm) (Yamamoto and Yamauchi 1974). Similarly, the predicted total length at hatching, from the linear relationship between age and total length, was 15.4 mm for *A. bicolor pacifica* and 8.73 mm for *A. marmorata*, which were apparently larger than the observed size at hatching. The predicted otolith radius at hatching was 18.9  $\mu\text{m}$  in *A. bicolor pacifica* and 9.44  $\mu\text{m}$  in *A. marmorata*, and was also larger than the values observed in the otoliths of leptocephali, which were 4.95  $\mu\text{m}$  in the former and 4.90  $\mu\text{m}$  in the latter. The pattern of change in otolith increment width suggested that the somatic growth rate was not constant, but had a period of rapid growth from age 20–40 days in the leptocephali of both species (Fig. 6). Therefore, it might be concluded that the accelerated early growth in body size and otolith increments for both species could explain the discrepancy between the predicted values and observed ones. This could be further examined in the future by collecting larvae younger than 40 days.

#### Oceanic migration and recruitment

Leptocephali of both species were present in the far western region of the North Equatorial Current (Fig. 1). The westward flow of the North Equatorial Current has been consistently observed at these latitudes during the late summer and early fall (Reverdin et al. 1994; Kaneko et al. 1998; Kawabe and Taira 1998; Wijffels et al. 1998), suggesting that the leptocephali in this region were being transported westward into the northward-flowing Kuroshio Current or the southward-flowing Mindanao Current (Lukas et al. 1991) and they might have been distributed to various areas such as the southern islands of Japan, Taiwan or the Philippines in a similar fashion as are the leptocephali of the Japanese eel (Tsukamoto 1992). The specimens of *A. bicolor pacifica* in this area were large and probably at least 3 months old, so it is impossible to determine where they were spawned, although this species has been reported from the Mariana Islands to the east and is present in the Philippines, Indonesia and Papua New Guinea (Ege 1939). In contrast, much smaller *A. marmorata* leptocephali, ranging in age from 35 to 58 days, were present in this region, suggesting that this species may spawn within the North Equatorial Current west of the Mariana Islands as does *A. japonica* (Tsukamoto 1992). Similarly, the ages of *A. japonica* leptocephali previously collected in the same area of the North Equatorial Current ranged from 27 to 42 days (Tsukamoto et al. 1992). A recent molecular

study on the population structure of *A. marmorata* demonstrated that this species was clearly divided into North Pacific and South Pacific populations (Ishikawa 1998), so this area is a possible spawning area for the North Pacific population.

Five other specimens of *A. marmorata*, ranging in size from 21.3 to 36.3 mm TL, were collected much farther south and east, to the north of the Solomon Islands, between the equator and 6°S (Figs. 1, 3), which must have originated from a different spawning area of a South Pacific population. Surface currents in this area are usually dominated by the westward flow of the South Equatorial Current (Delcroix et al. 1987, 1992), but there is considerable seasonal and interannual variation in the latitudinal location and the direction of currents in the equatorial region (Kuroda and McPhaden 1993; Reverdin et al. 1994; Yu and McPhaden 1999); some of this variation is associated with the El Niño–Southern Oscillation (Roden 1998; Johnson and McPhaden 2000). If the current just to the south of the equator was westward at the time of an El Niño event, the *A. marmorata* leptocephali were probably in a region that would have enabled eventual recruitment to the northern Solomon Islands or Papua New Guinea (Fig. 1). The isolated specimens further south and east were also in the region of the typical westward flow of the South Equatorial Current (Reverdin et al. 1994), but the easternmost specimen at 10°S was at a latitude where the eastward-flowing South Equatorial Counter Current is often present (Delcroix et al. 1987, 1992) so the transport history of this specimen is uncertain. Other anguillid leptocephali that were not identified genetically were present in these two areas of the South Pacific, so it is possible that additional individuals were present there, but that the large size of the specimens examined in the present study make it difficult to speculate on their spawning location.

In the northern equatorial region, 15 *A. bicolor pacifica* leptocephali, from 24.0 to 54.1 mm TL and with ages ranging from 40 to 128 days, were collected in the region of variable current flow. All but two of the larger specimens (>45 mm TL) were just south of the equator and were most likely within the westward flow of the South Equatorial Current; however, all of the smaller specimens (<35 mm TL) were just north of the equator (Figs. 1, 3), in a region characterized by greater variability of current structure, but usually with eastward flow as part of the North Equatorial Counter Current (Reverdin et al. 1994; Delcroix et al. 1987, 1992; Roden 1998). The core of the North Equatorial Counter Current is usually at or south of 5°N at this longitude, so the intermediate-sized specimens (40–42 mm TL) that were present between 5°N and 10°N (Figs. 1, 3) may have been in a region of slower flow or in an area dominated by eddies associated with the boundary between the North Equatorial Counter Current and the North Equatorial Current. The separation of most of the specimens of the different size classes by latitude suggests that they were within dif-

ferent current systems, and makes it impossible to determine if all these leptocephali were even from the same spawning area.

Additional sampling over a wider area during several different seasons will be required to identify the spawning areas of tropical eels in the western Pacific, because recruitment data on glass eels of several tropical species entering freshwater suggests that they spawn throughout most of the year (Arai et al. *in press*). In addition, the total length and age of their leptocephali are probably not as fixed, within limited areas along their migration routes from the spawning area to their juvenile/adult habitats, as is the case for *A. japonica* leptocephali (Tsukamoto et al. 1989, 1992; Arai et al. 1997). This difference from temperate species of anguillid eels was illustrated by Jespersen (1942), by simultaneous collections of leptocephali, which were probably mostly *A. bicolor bicolor*, of various sizes from preleptocephalus to metamorphosing stages in the waters off Sumatra Island (Jespersen 1942). These observations and the findings of a wide range of sizes and ages of leptocephali of tropical eels during the present study indicate that some species of tropical eels may have fundamentally different reproduction and recruitment mechanisms than temperate eels, but additional research will be required to determine the spawning and recruitment patterns of tropical eels.

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