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## Early life history and recruitment of the tropical eel *Anguilla bicolor pacifica*, as revealed by otolith microstructure and microchemistry

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**Abstract** Otolith microstructure and microchemistry of the tropical eel *Anguilla bicolor pacifica* Schmidt were examined in glass eels collected at the mouth of the Dumoga River, North Sulawesi Island, Indonesia. Ages of the glass eels examined (age at recruitment) ranged from 124 to 202 d ( $167 \pm 19.3$  d; mean  $\pm$  SD), hatching being estimated as having occurred between November 1995 and March 1996. Otolith increment widths markedly increased from age 101 to 172 d ( $135 \pm 18.2$  d; mean  $\pm$  SD), coincident with a drastic decrease in otolith Sr:Ca ratios, suggesting that metamorphosis began during that period. The duration of metamorphosis was estimated as 20 to 40 d, on the basis of otolith microstructural characteristics. The fluctuation patterns in otolith increment widths and Sr:Ca ratios were similar to those of the temperate Japanese eel *A. japonica*.

### Introduction

Recent progress in otolith techniques has revealed many important aspects of the early life histories of temperate *Anguilla* species, including *A. japonica* and *A. anguilla*. Numerous reports have demonstrated relationships between otolith characteristics, such as growth patterns (Tabeta et al. 1987; Tsukamoto 1990; Tsukamoto and Umezawa 1990; Tzeng 1990; Umezawa and Tsukamoto 1990; Lecomte-Finiger 1992; Tzeng and Tsai 1992; Cheng and Tzeng 1996) and Sr:Ca ratios (Otake et al.

1994; Tzeng 1994, 1996; Tzeng and Tsai 1994), and metamorphosis in these *Anguilla* species. Arai et al. (1997) proposed that a marked increase in otolith increment width, coincident with a drop in Sr:Ca ratios, heralded the onset of metamorphosis, the latter apparently being completed before the occurrence of maximum otolith increment width.

Compared with temperate *Anguilla* species, little is known about the early life history of tropical species, including aspects such as spawning area and season, larval growth and metamorphosis, and migration and recruitment. Twelve of eighteen *Anguilla* species are known to be distributed in tropical waters, seven occurring in the western Pacific around Indonesia (Ege 1939; Matsui 1972; Castle and Williamson 1974), where freshwater eels are thought to have originated (Aoyama and Tsukamoto 1997). According to Tsukamoto (1994), long-term larval migration in the sea might be the reason for the world-wide distribution and consequent speciation of *Anguilla* species. The early life history, including migration and metamorphosis, of tropical eels, i.e. old-type eels, may provide a key for understanding how *Anguilla* species achieved their world-wide distribution.

The final goals of our study are an understanding of the evolution and distribution of *Anguilla* species from examination of their early life histories, including larval migration and metamorphosis. In the present study otolith microstructure and microchemistry of a tropical species, *A. bicolor pacifica*, from North Sulawesi Island, Indonesia, were examined, and the timing and duration of metamorphosis, in addition to age at recruitment (age at estuarine arrival) and hatching date, determined.

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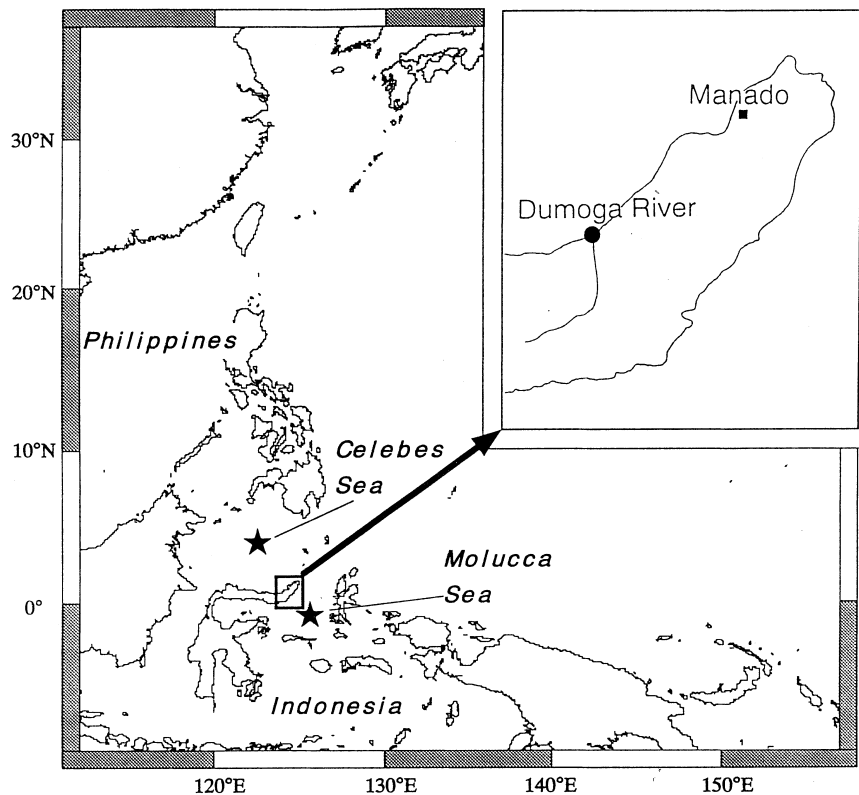
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### Materials and methods

#### Specimens, and otolith preparation

*Anguilla bicolor pacifica* Schmidt glass eels were collected by night (20:00 to 23:00 hrs) with a dip net at the mouth of the Dumoga River, North Sulawesi Island, Indonesia, on 5 June and 22 July 1996 (Fig. 1). The glass eels sampled were preserved in 99% ethanol

**Fig. 1** Map showing sampling location (●) and supposed spawning areas of tropical *Anguilla* species in the vicinity (★) (Jespersen 1942; Tesch 1977)



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. A total of 25 otoliths (15 specimens from the 5 June sample, 10 from the 22 July sample) was used for the present study (Table 1). Those 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  $\mu\text{m}$  and 1  $\mu\text{m}$  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 examinations.

#### Otolith X-ray microprobe analysis

For electron microprobe analyses, ten otoliths from glass eels (5 June sample) ranging from 46.2 to 51.1 mm in total length (mean  $\pm$  SD: 49.1  $\pm$  1.6 mm) 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-733), with calcite ( $\text{CaCO}_3$ ) and strontianite ( $\text{SrCO}_3$ ) as standards. Accelerating voltage and beam current were 15 kV and 7 nA, respectively. The electron beam was focused on a point about 1  $\mu\text{m}$  in diameter, measurements being spaced at 1  $\mu\text{m}$  intervals. Each datum represents the average of three measurements (each counting time: 4.0 s). Microprobe measurement points, which were seen as burn depressions (Fig. 2), were assigned to otolith growth increments which 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.

#### Otolith increment analysis

Following the electron microprobe analysis, the otoliths were re-polished to remove the coating, etched with 0.05 M HCl and vacuum coated with Pt-Pd in an ion-sputterer for scanning electron microscope (SEM, Hitachi S-4500) observations. Otoliths of 15 glass

eels (5 from the 5 June sample, 10 from the 22 July sample), which had not been used for electron microprobe analysis, were also etched and coated by the same procedure for SEM observation. SEM photographs at various magnifications (180 $\times$ , 1000 $\times$ , 1500 $\times$ , 2000 $\times$ ) were used for measuring otolith radii, counting the number of growth increments and measuring their widths. The longest axis of the ground otolith surface was regarded as the otolith radius along which increment widths were measured. The averages of every ten succeeding ring widths between the hatch check and the edge were used for otolith growth analysis. Following the suggestions of Lecomte-Finiger and Yahyaoui (1989), Tsukamoto (1989) and Umezawa et al. (1989), the increment number in *Anguilla bicolor pacifica* was taken to represent the age in days, although the daily deposition was not validated in this species.

## Results

### Size and stage at recruitment

The total lengths of the glass eels collected on 5 June and 22 July 1996 were 48.9  $\pm$  1.4 mm and 48.9  $\pm$  1.7 mm (mean  $\pm$  SD), respectively (Table 1); there was no significant difference between the two sample groups (Mann-Whitney *U*-test,  $p > 0.05$ ).

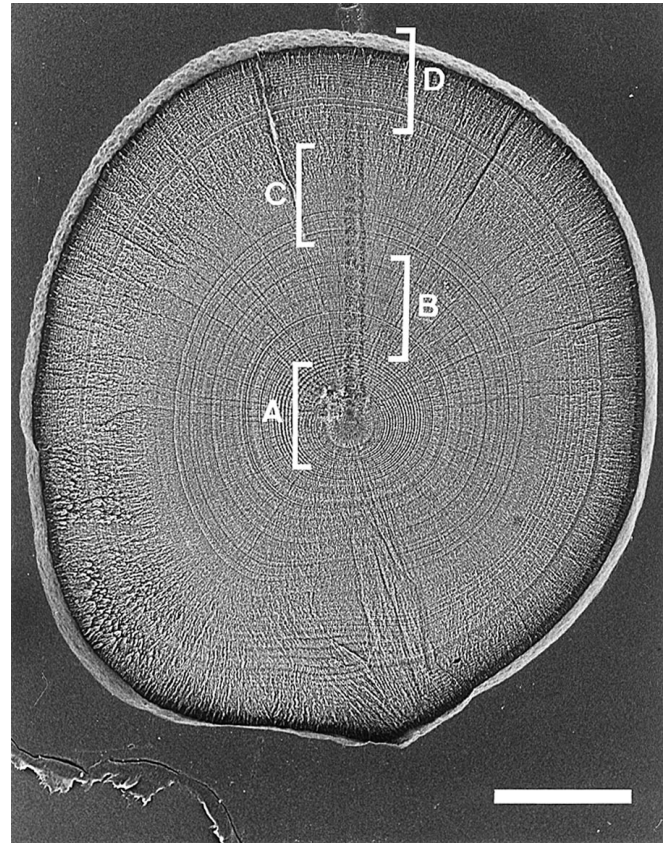
Pigmentation in all of the glass eels conformed to Stage VA, i.e. pigmentation advanced only in the caudal fin region, with no pigmentation on any other portion of the body.

### Otolith microstructure

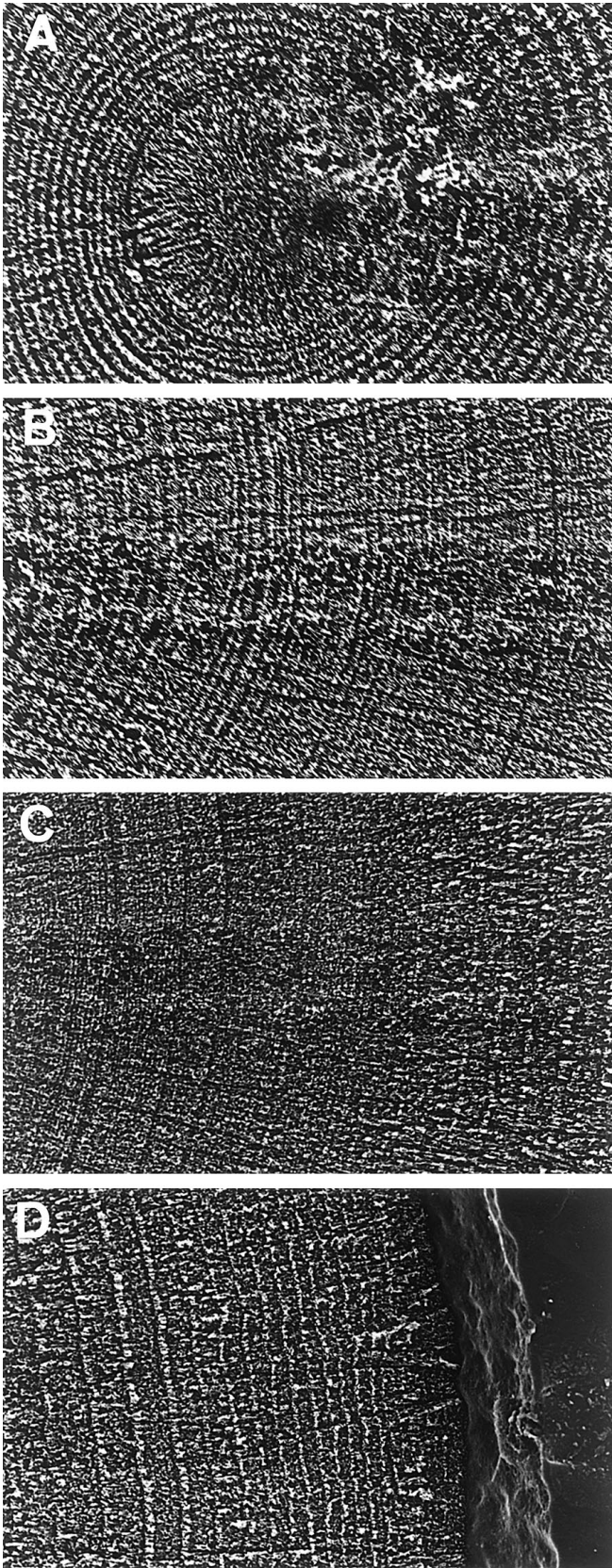
The otoliths of *Anguilla bicolor pacifica* glass eels were oval (Fig. 2), such shape was similar to those observed

**Table 1** *Anguilla bicolor pacifica*. Total length, otolith radius, age and hatching date of glass eels collected in the Dumoga River in 1996

| Sampling date | Specimens of determined age | Total length (mm) |           | Otolith radius ( $\mu\text{m}$ ) |         | Age (d)        |         | Hatching date (d)      |                        |
|---------------|-----------------------------|-------------------|-----------|----------------------------------|---------|----------------|---------|------------------------|------------------------|
|               |                             | Mean $\pm$ SD     | Range     | Mean $\pm$ SD                    | Range   | Mean $\pm$ SD  | Range   | Mean $\pm$ SD          | Range                  |
| 5 June        | 15                          | 48.9 $\pm$ 1.4    | 46.2–51.1 | 150 $\pm$ 4.5                    | 139–157 | 173 $\pm$ 13.3 | 151–195 | 14 Dec 1995 $\pm$ 13.3 | 22 Nov 1995–5 Jan 1996 |
| 22 July       | 10                          | 48.9 $\pm$ 1.7    | 45.7–51.2 | 144 $\pm$ 6.1                    | 135–156 | 159 $\pm$ 24.5 | 124–202 | 12 Feb 1996 $\pm$ 24.5 | 1 Jan 1996–19 Mar 1996 |

**Fig. 2** *Anguilla bicolor pacifica*. SEM photographs showing otolith microstructure of a glass eel (total length: 49.9 mm) collected at the mouth of the Dumoga River on 5 June 1996 [A otolith core and surrounding zone (first phase); B leptocephalus growth zone (first and second phases); C boundary zone between leptocephalus growth and metamorphic zones (second and third phases); D boundary zone between late metamorphic and glass eel growth zones (fourth phase)]. Letters correspond to the parts of Fig. 3. Scale bar: 50  $\mu\text{m}$ 

in *A. japonica* (Cheng and Tzeng 1996) and *A. marmorata* (Budimawan 1997). Mean radii ( $\pm$ SD) of otoliths of the June and July samples were 150  $\pm$  4.5  $\mu\text{m}$  (range: 139 to 157  $\mu\text{m}$ ) and 144  $\pm$  6.1  $\mu\text{m}$  (range: 135 to 156  $\mu\text{m}$ ), respectively (Table 1). An otolith core was observed as a deep hole in the center of the etched otolith, with a hatch check being visible as a deep circular groove surrounding the hole (Figs. 2, 3A). The diameter of the hatch check ranged from 9.6 to 13.3  $\mu\text{m}$  (mean  $\pm$  SD; 11.7  $\pm$  1.1  $\mu\text{m}$ ). A series of distinct concentric growth increments was observed around the core, such structures being similar to those observed in *A. anguilla* (Lecomte-Finiger 1992), *A. japonica* (Tabeta et al. 1987; Tsukamoto 1990; Tzeng 1990; Umezawa and Tsukamoto 1990; Tzeng and Tsai 1992) and *A. marmorata* (Budimawan 1997). No distinct check rings other than the hatch check were observed in otoliths of the *A. bicolor pacifica* glass eels (Fig. 3A to D), unlike the conditions reported in *A. anguilla* (Lecomte-Finiger 1992) and *A. japonica* (Cheng and Tzeng 1996), in which a metamorphosis check, presumably deposited at the beginning of metamorphosis, was visible.



◀  
**Fig. 3** *Anguilla bicolor pacifica*. SEM photographs showing otolith microstructure of a glass eel (TL: 49.9 mm) collected in the mouth of the Dumoga River on 5 June 1996. A–D For explanation of parts see Fig. 2. Scale bar: 10  $\mu$ m

#### Age and hatching date

Glass eels collected on 5 June and 22 July 1996 were aged as  $173 \pm 13.3$  d (range: 151 to 195 d) and  $159 \pm 24.5$  d (range: 124 to 202 d), respectively (Table 1). The lack of any significant difference in the age of the glass eels ( $p > 0.05$ ) suggested that the age at recruitment was the same in the two sample groups.

The hatching dates of the glass eels collected on 5 June and 22 July were estimated as 14 December 1995 ( $\pm 13$  d SD) (range: 22 November 1995 to 5 January 1996), and 12 February 1996 ( $\pm 25$  d SD) (range: 1 January 1996 to 19 March 1996), respectively (Table 1). Because these hatching dates differed significantly ( $p < 0.05$ ), it is likely that the glass eels born earlier in the spawning season also migrated earlier to the river mouth.

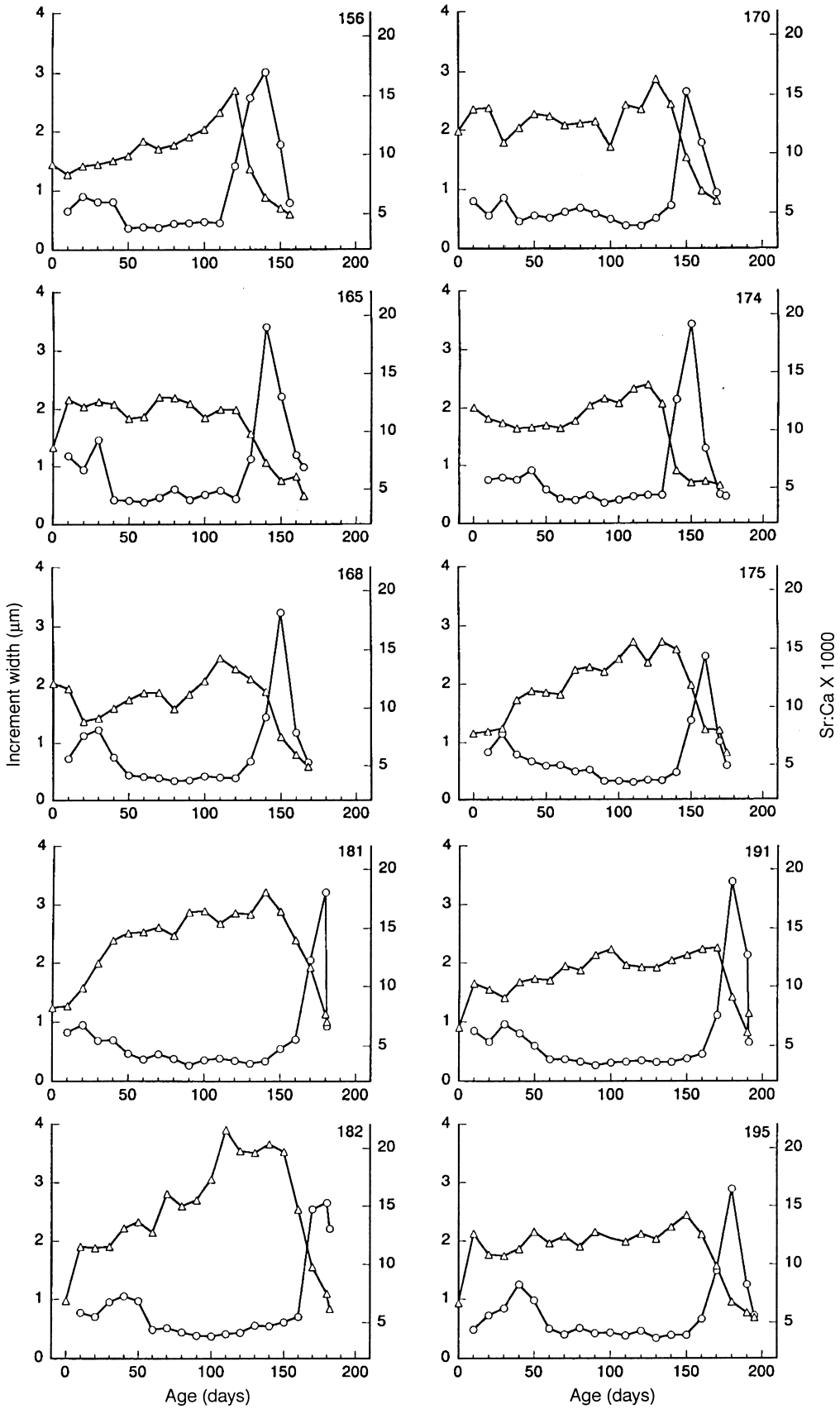
#### Otolith growth pattern

Changing patterns in the otolith increment widths along the life-history transect from the core to the edge are shown in Figs. 3A to D, 4 and 5. The patterns represented four phases, with drastic changes occurring in the last two phases. Otolith increment widths increased between the hatch check and age 20 to 50 d (first phase) (Figs. 2, 3A, B), thereafter becoming constant or gradually decreasing until age 90 to 160 d, average width being  $0.47 \pm 0.11$   $\mu$ m (mean  $\pm$  SD) (second phase) (Figs. 2, 3B, C). Beyond age 101 to 172 d ( $135 \pm 18.2$  d; mean  $\pm$  SD), increment widths increased sharply to a maximum, being  $2.8 \pm 0.6$   $\mu$ m (mean  $\pm$  SD) (Figs. 2, 3C) at age 120 to 200 d (third phase). Increment widths thereafter decreased rapidly (fourth phase) (Figs. 2, 3D). Younger specimens, i.e. younger migrants, tended to undergo the drastic width increases of the third phase at an earlier age (Fig. 6), being coincident with a drop in otolith Sr:Ca ratios. The duration of the third phase was 20 to 40 d, independent of the age at recruitment.

#### Otolith Sr:Ca ratios

Otolith Sr:Ca ratios showed dramatical changes along the life-history transect (Fig. 4). Averaging  $9.0 \times 10^{-3}$  in

▶  
**Fig. 4** *Anguilla bicolor pacifica*. Profiles of otolith incremental widths from the core to the edge (○) and otolith Sr:Ca concentration ratios measured with a wavelength-dispersive electron microprobe from the core to the edge (△). Each graph represents an individual otolith; each point represents the average of data for every 10 d. Numbers at the upper right indicate age (d). Specimens were collected at the mouth of the Dumoga River on 5 June 1996



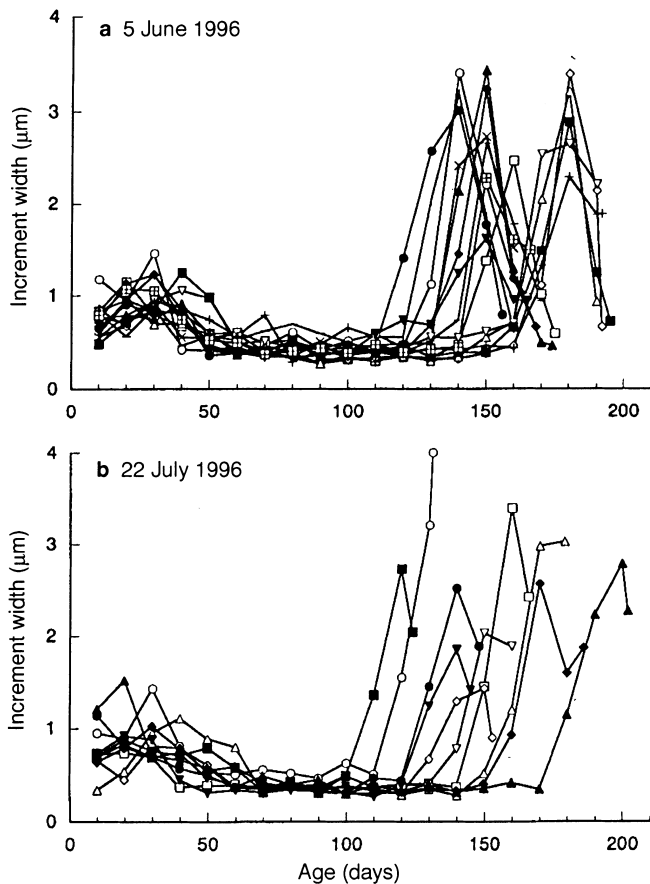


Fig. 5 *Anguilla bicolor pacifica*. Profiles of otolith incremental widths from the core to the edge. Each point represents the average of data for every 10 d. Sampling date at upper left

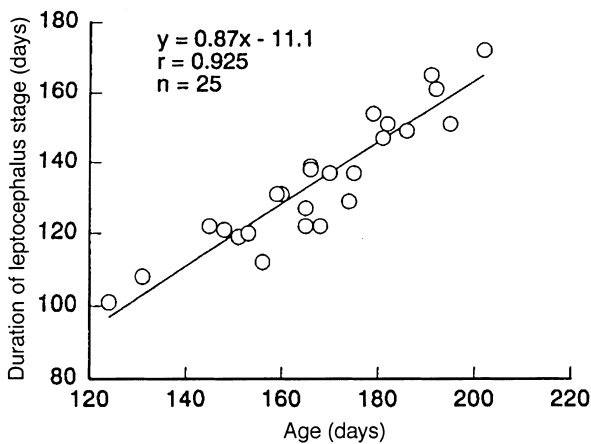


Fig. 6 *Anguilla bicolor pacifica*. Relationship between total age (d) and duration of leptocephalus stage (d)

the core, ratios dropped slightly around age 20 to 60 d, but subsequently increased to a maximum level, averaging  $15.6 \times 10^{-3}$ , around age 110 to 170 d. A marked decrease thereafter to the edge was coincident with the rapid increase in growth increment widths (third phase of otolith growth). The minimum average value of

$5.7 \times 10^{-3}$  was recorded in the outermost region of the otolith.

## Discussion

Otolith growth patterns in the *Anguilla bicolor pacifica* glass eels comprised four phases, the last two, characterized by drastic growth changes, overlapping completely a drop in otolith Sr:Ca ratios. Such a fluctuation pattern associated with Sr:Ca ratios matched that found in otoliths of *A. japonica* (Otake et al. 1994; Arai et al. 1997). The coincidental changes recorded in otolith growth and Sr:Ca ratios have been considered an indication of the beginning of metamorphosis, the latter being completed before increment widths reached their maximum level, i.e. during the third phase of otolith growth (Arai et al. 1997). Otake et al. (1997) observed the same phenomenon in *Conger myriaster*. Such relationships between otolith growth, otolith Sr:Ca ratios and metamorphosis seem, therefore, to be common in anguillid fishes. The onset of metamorphosis in *A. bicolor pacifica* apparently occurs in the age period 101 to 172 d ( $135 \pm 18.2$  d; mean  $\pm$  SD), the duration of metamorphosis overall being estimated as 20 to 40 d, and independent of the individual age at recruitment, a similar situation to that in *A. japonica* (Arai et al. 1997).

The total length of *Anguilla bicolor pacifica* at recruitment ( $48.9 \pm 1.5$  mm; mean  $\pm$  SD) was 10 to 20 mm less than that of temperate *Anguilla* species, such as *A. anguilla* (68 mm) (Lecomte-Finiger 1992) and *A. japonica* (57 mm) (Umezawa 1991; Cheng and Tzeng 1996), although all were characterized by the same pigmentation stage (Stage VA). *A. marmorata*, a tropical eel, has also been reported to be of small size (47.0 to 51.8) upon its arrival at river mouths in tropical areas (Budimawan 1997). Furthermore, a difference in the sizes of fully-grown leptocephali has also been found between tropical and temperate species. The total lengths of fully-grown leptocephali of the temperate eels *A. anguilla*, *A. japonica* and *A. rostrata* were 75 mm (Jespersen 1942; Tesch 1977), 60 mm (Tabeta and Konishi 1986) and 70 mm (Kleckner and McCleave 1985), respectively. In contrast, the maximum *A. bicolor pacifica* leptocephalus size that we have recorded is only 54 mm TL (Arai et al. unpublished data). Furthermore, the total lengths of fully-grown leptocephali of Indo-pacific tropical eels have been reported as averaging 50 mm TL (Jespersen 1942). The growth rate of *A. bicolor pacifica* leptocephali, according to our age determination, was estimated to range from 0.31 to 0.54 mm d<sup>-1</sup>. *A. marmorata* apparently grow 0.58 to 0.62 mm d<sup>-1</sup>, estimated from the duration of the leptocephalus stage (81 to 86 d) (Budimawan 1997) and the fully-grown leptocephalus size in that species reported by Jespersen (1942). Estimated growth rates of tropical eel leptocephali were varied, and covered the overall range reported for temperate eels such as *A. anguilla* and *A. rostrata* (0.33 to 0.44 mm d<sup>-1</sup>)

(Castonguay 1987) and *A. japonica* (0.56 to 0.59 mm d<sup>-1</sup>) (Umezawa and Tsukamoto 1990; Tsukamoto et al. 1992). The smaller size at recruitment of tropical eels, including *A. bicolor pacifica*, seems to be related to the shorter duration of the leptocephalus stage in those species.

*Anguilla bicolor pacifica* leptocephali are believed to take about 5 to 6 months to migrate from their spawning area to the estuarine parts of North Sulawesi Island. Such duration is longer than that of *A. marmorata*, which migrates for only 3 to 4 months (Budimawan 1997). In temperate eels, which migrate via oceanic current systems, the duration of migration seems to be related to the distance and complexity of the current systems between the spawning areas and their destinations. According to Jespersen (1942) and Tesch (1977), the spawning areas of tropical eels, including *A. bicolor pacifica*, distributed around North Sulawesi Island are situated in the Celebes and Molucca Seas, close to their distribution area (Fig. 1). Therefore, the rather long migration period of *A. bicolor pacifica* relative to the short direct distance migrated may be due to the complicated current systems around North Sulawesi Island. Alternatively, the spawning area might be situated more distantly. The waters off the southwestern coast of Sumatra Island are supposedly the spawning area for tropical eels distributed along the nearby southwestern coasts of Sumatra and Java Islands (Jespersen 1942). The occurrence of leptocephali from preleptocephalus to metamorphosing stages, inclusive, in the waters off Sumatra (Jespersen 1942) support that supposition. This situation is quite different to that of temperate eels, suggesting that the migration mechanisms of the latter differ from those of tropical eel larvae. Further information on the geographical distribution, age and growth of tropical eel leptocephali, and the oceanography of Indonesian seas is necessary to more clearly determine the spawning areas and migration mechanisms of tropical eels.

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