

Dispersal pattern of glass eel stage of *Anguilla australis* revealed by otolith growth increments

Jen-Chieh Shiao¹, Wann-Nian Tzeng^{1,*}, Adrian Collins², Donald John Jellyman³

¹Department of Zoology, National Taiwan University, 1, Sec 4, Roosevelt Rd, Taipei, Taiwan 10617, Republic of China

²Bribie Island Aquaculture Research Centre, 144 North Street Woorim, Bribie Island, Queensland 4057, Australia

³National Institute of Water and Atmospheric Research, PO Box 8602, Christchurch, New Zealand

ABSTRACT: Glass eels of the Australasian shortfin eel *Anguilla australis* (Richardson 1841) were collected from 6 Australian and 2 New Zealand estuaries. Their ages were estimated by counting daily growth increments in the otoliths. According to mean size and age at capture, the glass eels were classified into a northern Australia group or a southern Australia and New Zealand group. The mean length of glass eels increased from 47.6 ± 2.11 mm in northern estuaries to 59.2 ± 3.61 mm in the south. The mean age of glass eels at capture was significantly lower in the north (214 ± 14.6 to 223 ± 17.7 d) than in the south (243 ± 19.7 to 261 ± 22.4 d) ($p < 0.05$). In contrast, the otolith growth rate was greater in the north than in the south. The dramatic increase in increment width and the decline of the Sr:Ca ratios in otoliths were used to determine the timing of metamorphosis from leptocephalus to glass eel stage. The mean ages of leptocephali at metamorphosis were significantly lower in the north (160 ± 14.2 to 161 ± 12.6 d) than in the south (168 ± 14.5 to 189 ± 16.9 d), indicating that faster-growing and earlier-metamorphosed leptocephali recruited to northern Australia and slow-growing and late-metamorphosed leptocephali recruited to southern Australia and New Zealand. In addition, based on current direction and the similarity in age of leptocephali at metamorphosis, age at capture and the period between metamorphosis and estuarine arrival, New Zealand glass eels are unlikely to be transported across Tasman Sea from southern Australia by the East Australian Current, and must reach their destination via a different route(s).

KEY WORDS: Australasian shortfin eel · Otolith · Metamorphosis · Geographic cline

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The Australasian shortfin eel *Anguilla australis* (Richardson, 1841) is a temperate catadromous fish, widely found in the rivers of southeast Australia, Tasmania, New Caledonia, Norfolk Island, Lord Howe Island and New Zealand (Ege 1939). Although previously described by Schmidt (1928) and Ege (1939) as 2 subspecies (*A. australis australis* the Australian subspecies, and *A. australis schmidtii* the New Zealand subspecies), a recent review based on mitochondrial DNA concluded that this designation was invalid and recommended

that the 2 subspecies be merged into a single species (Dijkstra & Jellyman 1999). The spawning grounds of *A. australis* is unknown, but possible sites have been suggested as near New Caledonia (Schmidt 1928), between Fiji and Tahiti (Castle 1963, Aoyama et al. 1999), or further west than this at 150 to 170° W and 5 to 15° S (Jellyman 1987). Despite the uncertainty about its spawning grounds, it is believed that, like larvae of other temperate eels (*A. anguilla*, *A. rostrata* and *A. japonica*), larvae of the Australasian shortfin eel may drift with oceanic currents from their spawning grounds to the continents (Sloane 1984, Jellyman 1987, Arai et al. 1999c).

Since the daily growth increment in otoliths was discovered by Pannella (1971), this ageing technique,

*Corresponding author: E-mail: wnt@ccms.ntu.edu.tw

together with the microchemistry analysis of otoliths, has been extensively used to study the early life history of freshwater eels (Tzeng 1990, Otake et al. 1994, Tzeng & Tsai 1994, Arai et al. 1999a,b,c). Arai et al. (1999c) recently determined the age of *Anguilla australis* on a daily basis and found that the glass eels recruited to Australia (208 ± 17.4 d) were ca 20 to 30 d younger than those recruited to New Zealand (232 ± 19.8 d western coast, 237 ± 20.0 d eastern coast). They considered that the difference in age of glass eels arriving at the coasts of Australia and New Zealand might be due to differences in the migratory routes taken by these 2 stocks (Arai et al. 1999c), but had insufficient data to determine the actual routes. Comparing the daily age of glass eels at metamorphosis and upon estuarine arrival across their dispersal range is a useful technique to help determine the migratory routes of eel larvae (Cheng & Tzeng 1996, Wang & Tzeng 1998, 2000).

The present study examines the microstructure and microchemistry of glass eel otoliths to determine the ages of leptocephali at metamorphosis and of glass eels upon arrival in the Australian and New Zealand estuaries. From a consideration of the size and age of the glass eels, we proceed to consider possible migratory drifting routes from the oceanic spawning grounds to Australia and New Zealand.

MATERIALS AND METHODS

Glass eels of *Anguilla australis* were collected from 6 estuaries on the eastern coasts of Australia in 1997, 1998 and 1999, and from 2 estuaries on the eastern and western coasts of New Zealand in 1996 (Fig. 1). The sampling sites almost covered the dispersal range of *A. australis* along the eastern coast of Australia, except for Tasmania. Table 1 lists the sampling sites, dates and sample size of the glass eels. The glass eels recruiting to Australian estuaries were caught by a Japanese Hell net (12 m × 12 m) and those from New Zealand were sampled using an electric shocker. All glass eels collected were preserved in 95% alcohol. Pigmentation stages were assessed according to pigment distribution on the body surface (Strubberg 1913).

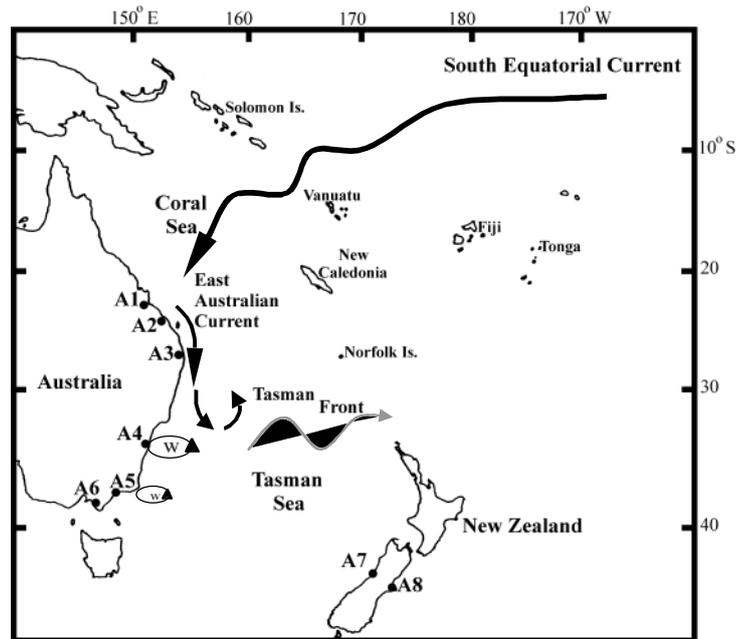


Fig. 1. Sampling sites of *Anguilla australis*. A1: Fitzroy River; A2: Kolan River; A3: Albert River; A4: Port Hacking River; A5: Brodribb River; A6: Tarwin River; A7: Arahura River; A8: Purau Stream

Total lengths were measured to the nearest 0.01 mm before sagittal otoliths were extracted for microchemistry analysis and age determination. The otoliths were embedded in Epofix resin, ground and polished until the core was exposed on the surface. For electron probe microanalysis (Joel JXA-8800M), the polished otoliths were coated with a layer of carbon under a high-vacuum evaporator. Strontium (Sr) and calcium (Ca) concentrations were measured each 2 or 10 μm from the core to the edge of the otoliths with an electron beam of 2 or 10 μm diameter. Accelerating voltage was set at 15 kV and probe current at 3 or 5 nA. The

Table 1. *Anguilla australis* sampling sites, dates and sample sizes collected from 6 Australian estuaries (Sites A1 to A6) and 2 New Zealand estuaries (Sites A7 to A8) (sites are shown in Fig. 1). Numbers in parentheses: numbers of specimens for which ages were determined

Sampling site	Distance upstream (km)	Sampling date	Sample size (n)
Australia			
Fitzroy River (A1)	53	7 Aug, 1998	50 (29)
Kolan River (A2)	14.5	1 & 16 Jul, 1997	70 (33)
Albert River (A3)	42	2 May & 2 Jun, 1997	142 (27)
Port Hacking River (A4)	12	17 Jun & 18 Jul, 1999	35 (26)
Brodribb River (A5)	4.6	11 Jul, 11 Aug & 5 Sep, 1997	138 (35)
Tarwin River (A6)	14	18 Jul, 21 Aug & 19 Sep, 1997	137 (39)
New Zealand			
Arahura River (A7)		22 Aug, 1996	25 (22)
Purau Stream (A8)		29 Aug, 1996	24 (19)

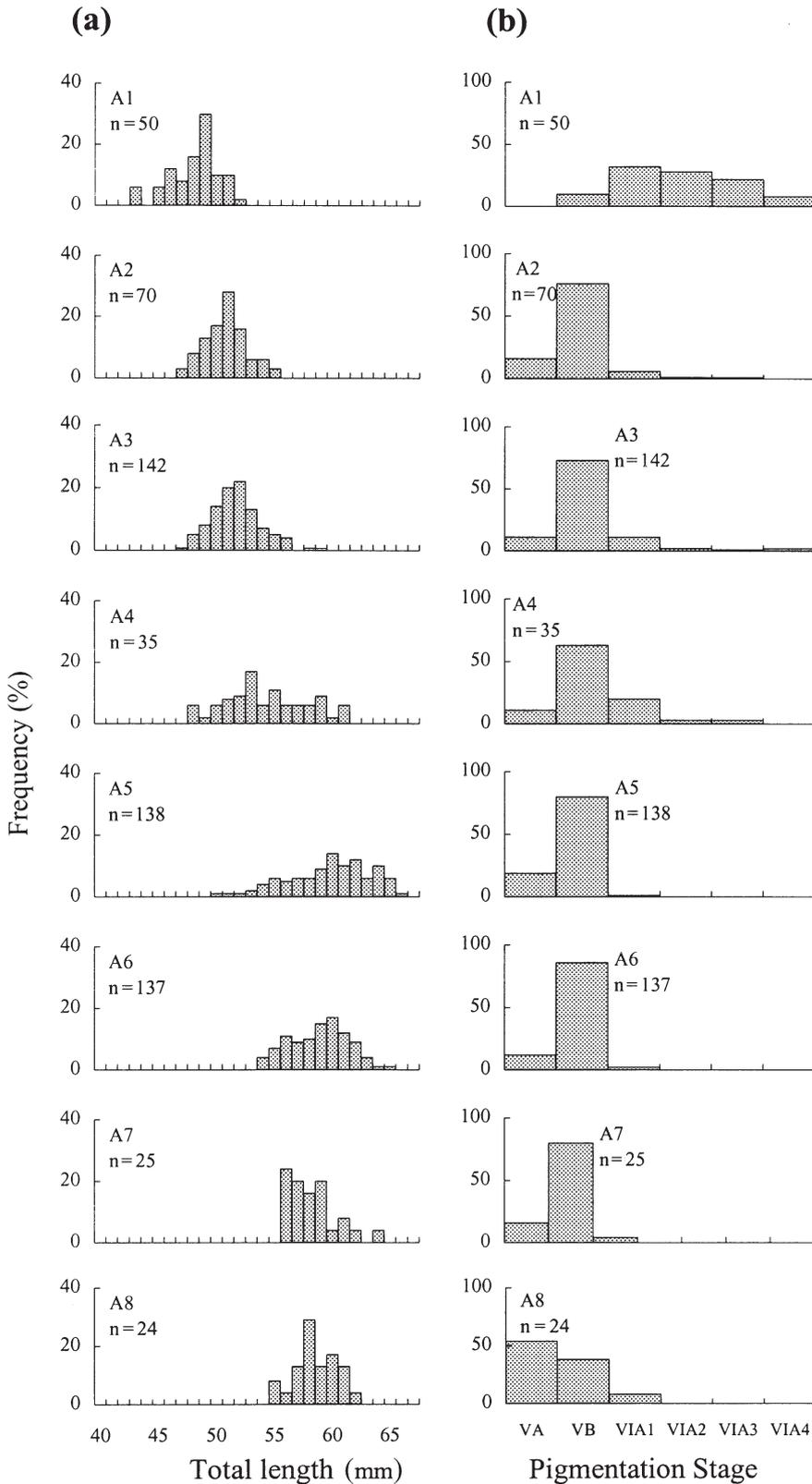


Fig. 2. *Anguilla australis*. Frequency distribution of total length (a) and pigmentation stages (b) of glass eels collected from the 8 estuaries (Sites A1 to A8 are shown in Fig. 1). n = sample size

peak of Sr was counted for 120 s, and background was measured for 20 s on each side, while the peak of Ca was counted for 20 s with 10 s for each background. SrTiO_3 and CaMoO_4 were used as standards for the quantitative analysis of Sr and Ca respectively. The otoliths were then repolished to remove the carbon layer, etched with 0.05 M HCl for 15 s, dried in the oven, and coated with a layer of gold for SEM observation. Photographs were taken at a magnification of $2000\times$ for counting the daily growth increments.

The timing of metamorphosis from leptocephali to glass eels was determined from the drastic increase of increment width coinciding with the decrease in Sr:Ca ratios (Otake et al. 1994, Tzeng & Tsai 1994, Arai et al. 1997, Wang & Tzeng 1998, Arai et al. 1999a,b,c). However, some checks were formed in the otoliths after the glass eels entered the estuaries. The innermost check was called the 'freshwater mark' and the growth increments after this mark were probably deposited during the time that the glass eels were in the estuary (Kawakami et al. 1998). Accordingly, the otolith radii were relegated to 3 stages: R_m (leptocephalus stage), R_s (glass eel stage from metamorphosis to estuarine arrival) and R_e (glass eel stage when present in the estuary) were measured on the SEM pictures. Age at capture (T_i), age at metamorphosis of the leptocephali (T_m), the period between metamorphosis and estuarine arrival (T_s), and the duration of the period spent in the estuary before collection (T_e) were estimated from the counts of daily growth increments in the corresponding radii. Information on the duration of the yolk-sac stage of Australasian shortfin eel is not available, so T_i and T_m could not be adjusted for the period of the yolk-sac stage as for the Japanese and American eels (5 d yolk-sac stage: Cheng & Tzeng 1996, Wang

& Tzeng 1998). To calculate the otolith growth rates of leptocephalus and glass eel stages, the otolith radius of each stage was divided by the corresponding age. The hatching dates of the glass eels were back-calculated from their ages at capture and the sampling dates. Because of preservation effects, the growth increments at the otolith edge, approximately 15 μm , could not be revealed clearly in some New Zealand samples. Therefore, to avoid an underestimate in daily age, the growth increments of the damaged area were estimated from the otolith growth rate and radius in such cases.

The homogeneity of the total length and daily age of glass eels, as well as their otolith radius and growth rate, was tested among estuaries. If the data were normally distributed with equal variance, then Tukey multiple comparison was used; otherwise, a Kruskal-Wallis 1-way ANOVA test on ranks was used.

RESULTS

Total length and pigmentation stage

The total lengths of glass eels of *Anguilla australis* collected from the 8 estuaries ranged from 42.8 to 65.5 mm and showed a geographic cline that increased from north to south (Fig. 2a). Based on size, glass eels were classified into 2 groups: a smaller northern group (Sites A1 to A3, mean 47.6 ± 2.11 to 51.2 ± 3.14 mm) and a larger southern group (Sites A5 to A8, mean 57.8 ± 2.02 to 59.2 ± 3.61 mm), with Site A4 (53.9 ± 3.56 mm) being a median group (Table 2).

The pigmentation stages of glass eels collected from the 8 estuaries were dominated by Stages VA and VB, except at Site A1 which yielded advanced pigmentation stages, VIA1 to VIA4 (Fig. 2b). The glass eels of Stages VA and VB were believed to be the new recruits in the estuary. Arai et al. (1999c) indicated that glass eels kept in freshwater for 10 d after collection develop to Stages VIA1 to VIA4. This suggests that

Table 2. *Anguilla australis*. Homogeneity test (HG) for total length (mean \pm SD) of glass eels collected from the 8 estuaries (A1 to A8). Asterisks shared between estuaries indicate they belong to the same homogeneous group ($p < 0.05$). n = sample size

Sites	n	Mean \pm SD	HG
A1	50	47.6 ± 2.11	*
A2	70	50.2 ± 1.77	**
A3	142	51.2 ± 3.14	**
A4	35	53.9 ± 3.56	**
A7	25	57.8 ± 2.02	**
A8	24	58.0 ± 1.91	*
A6	137	58.4 ± 2.49	*
A5	138	59.2 ± 3.61	*

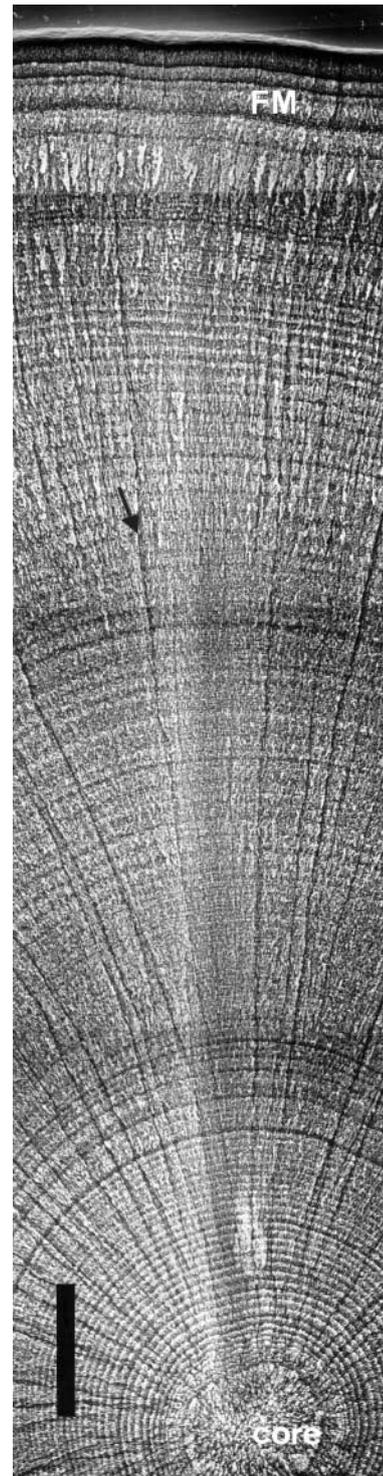


Fig. 3. *Anguilla australis*. Daily growth increments in the otolith of a 53.95 mm total length glass eel collected from Brodribb River (Site A5), Australia. The burned line from the core to the edge of the otolith indicates where Sr and Ca concentration were measured using EPMA. Arrow indicates the abrupt increase of increment width and the appearance of radial aragonite crystals coinciding with decline of Sr:Ca ratios. FM: freshwater mark. Scale bar = 15 μm

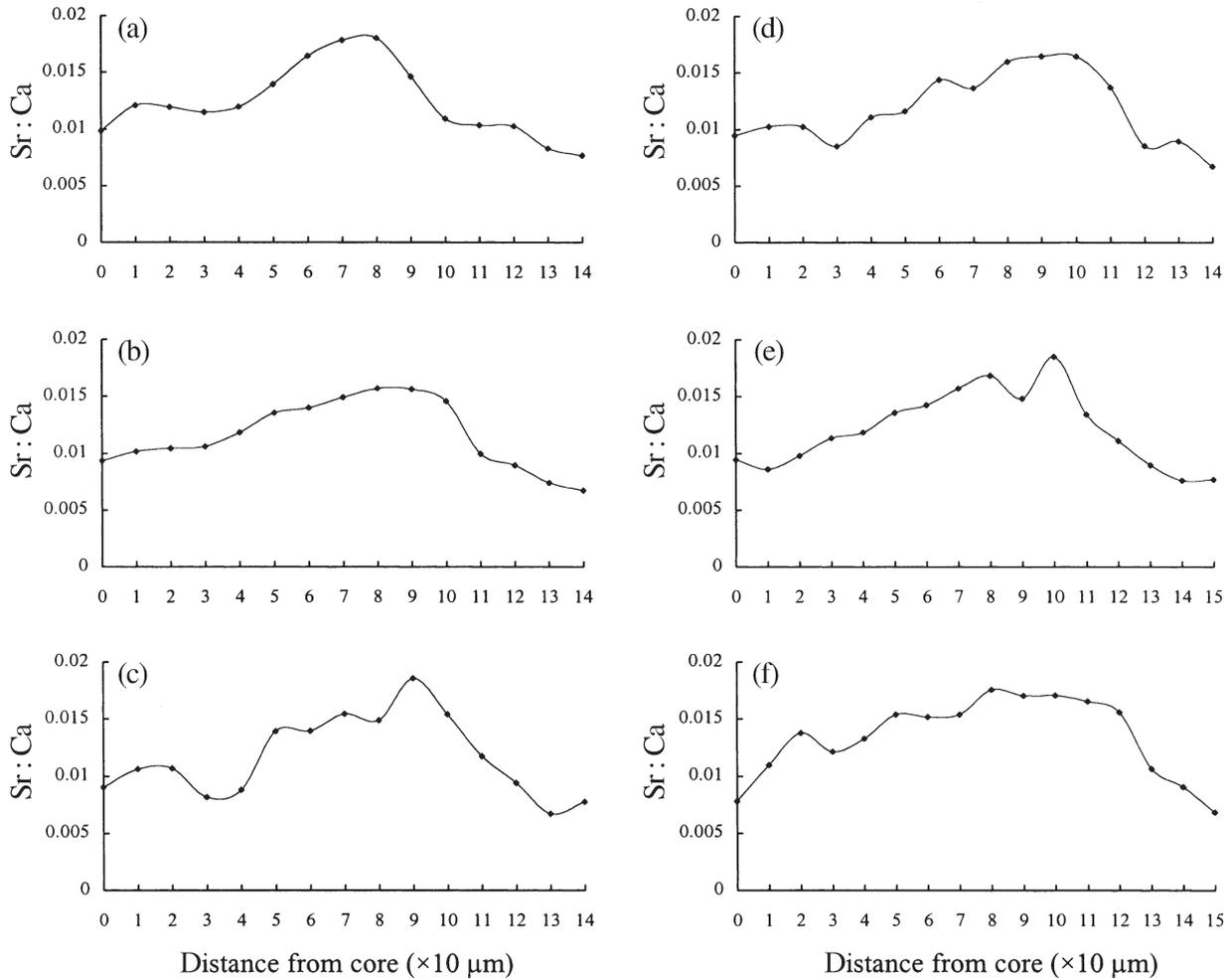


Fig. 4. *Anguilla australis*. Sr:Ca ratios measured along life history transects of glass eel otoliths from the core to the edge. The glass eels were from Albert River (a – c) and from Brodribb River (d – f)

glass eels from Site A1 may remain in the estuary longer than those at other locations.

Otolith microstructure and Sr:Ca ratios

No clear daily growth increment was discernible in the otolith core. Beyond the core, concentric daily growth increments were visible. Increment width increased gradually as the glass eels continued to grow, reaching a peak at ca $0.8 \mu\text{m}$ approximately 40 to 50 d after hatching and then decreasing gradually to ca $0.2 \mu\text{m}$. Then, the aragonite crystal arrangement changed from a concentric to a radial form while increment width abruptly increased to $1 - 1.5 \mu\text{m}$, decreasing again at the edge of the otolith (Fig. 3).

The otolith Sr:Ca ratios along life-history transects were similar among individuals (Fig. 4), being approximately 10×10^{-3} in the otolith core and increasing

gradually with increasing otolith radius to a maximum of about 18×10^{-3} , corresponding to the area where the increment width was narrowest. The Sr:Ca ratios then decreased abruptly to a minimum of approximately 6 to 7×10^{-3} , again at the edge of the otoliths (Fig. 4). The decrease in the Sr:Ca ratio coincided with a drastic increase in increment width. The simultaneous changes in increment width and Sr:Ca ratio indicates metamorphosis from the leptocephalus to the glass eel stage (Otake et al. 1994, Tzeng & Tsai 1994, Arai et al. 1997, Wang & Tzeng 1998, Arai et al. 1999a,b,c).

Ages at metamorphosis, estuarine arrival and duration of stay in the estuaries

The mean ages of the glass eels ranged from 180 to 326 d at capture (T_i), from 130 to 245 d at metamorphosis (T_m), from 15 to 113 d between metamorphosis and

Table 3. *Anguilla australis*. Homogeneity test (HG) for age of glass eels arriving at the 8 estuaries (T_t), age of leptocephalus at metamorphosis (T_m), time between metamorphosis and arrival at the estuaries (T_s), and residence time in the estuary before collection (T_e). Asterisks shared between estuaries indicate they belong to the same homogeneous group ($p < 0.05$). Sample size for each site is shown in parentheses in Table 1. nt: data excluded from homogeneity test because microstructure of otolith edge was damaged and freshwater mark was not discernible

T_t			T_m			T_s			T_e		
Site	Mean \pm SD	HG	Site	Mean \pm SD	HG	Site	Mean \pm SD	HG	Site	Mean \pm SD	HG
A2	214 \pm 14.6	*	A2	160 \pm 12.0	*	A3	43 \pm 10.6	*	A5	6 \pm 7.5	*
A3	217 \pm 16.6	*	A1	160 \pm 14.2	*	A1	45 \pm 11.5	*	A2	8 \pm 8.7	*
A1	223 \pm 17.7	*	A3	161 \pm 12.6	*	A2	46 \pm 10.5	*	A4	8 \pm 8.5	*
A4	243 \pm 19.7	*	A4	168 \pm 14.5	**	A5	57 \pm 12.9	*	A6	9 \pm 8.8	*
A8	246 \pm 14.5	*	A8	180 \pm 8.6	**	A6	63 \pm 14.6	**	A3	12 \pm 7.9	**
A5	247 \pm 23.9	*	A5	183 \pm 20.8	**	A4	67 \pm 13.1	*	A1	19 \pm 10.9	*
A7	258 \pm 19.7	*	A7	188 \pm 11.9	*	A7	70 \pm 15.1 ^a	nt			nt
A6	261 \pm 22.4	*	A6	189 \pm 16.9	*	A8	66 \pm 12.0 ^a	nt			nt

^aData include T_s and T_e

estuarine arrival (T_s), and from 0 to 37 d during their stay in the estuary (T_e). An analysis of variance indicated that mean T_t , T_m and T_s differed significantly among the 8 estuaries ($p < 0.001$). T_t , T_m and T_s were all positively correlated with total length ($p < 0.001$) (Fig. 5), indicating that the total length of glass eels depends on both T_m and T_s .

Table 3 compares the means of T_t , T_m and T_s among the 8 estuaries. The mean T_t of the northern group (Sites A1 to A3) was significantly lower than that of the southern group (Sites A4 to A8). Similarly, the mean T_m in the north (A1 to A3) was also significantly lower than in the southern group (A5 to A8). The mean T_s of A1 to A3 belonged to the same homogeneous group and were significantly lower than at A4 to A6. These data indicate that mean T_t , T_m and T_s tended to

increase from north to south. In other words, the ages of the glass eels (T_t , T_m and T_s) all increased with increasing distance from the spawning ground. In contrast, the mean residence time of glass eels in the estuaries (T_e) was relatively longer at A1 and A3 than at the other sampling sites (Table 3). This was probably because the sampling sites A1 and A3 were 30 to 40 km further upstream than the other estuaries, necessitating a longer migration time.

Growth rate of the otolith

The otolith growth rate of the leptocephali (G_m) was very similar for all groups, but a little faster in the north (e.g. Site A2) than in the south (e.g. Sites A6 and A7).

This indicated that faster-growing leptocephali migrate to the north and slower-growing leptocephali to the south (Table 4). Similarly, the otolith growth rates of glass eels before entering the estuary (G_s) were significantly faster at northern sites (A1 to A3) than at southern sites (A4 to A6).

Hatching dates

The estimated hatching dates of *Anguilla australis* extended from late August to early February for Australian samples, and mid October to middle January for New Zealand samples (Fig. 6). In addition, the hatching dates of glass eels recruiting to the same estuary at different dates overlapped considerably.

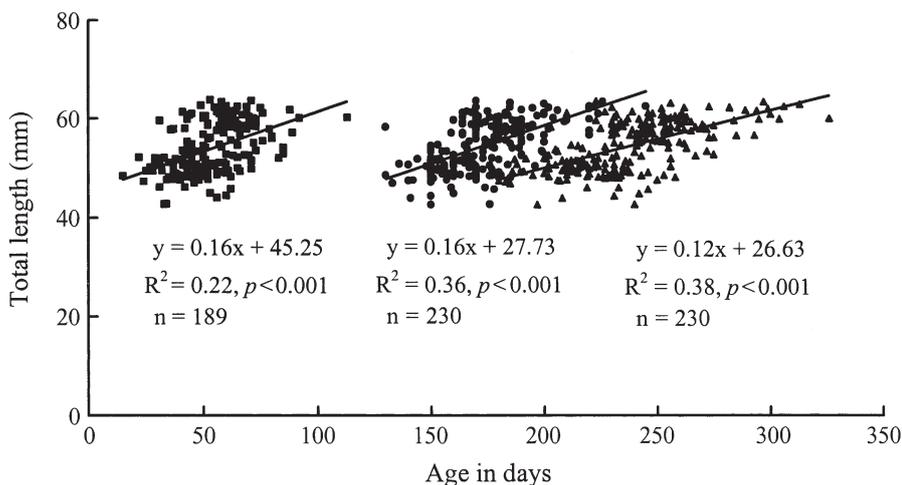


Fig. 5. *Anguilla australis*. Relationships between total length of glass eels and age at capture (T_t , \blacktriangle), age of leptocephali at metamorphosis (T_m , \bullet) and period between metamorphosis and estuarine arrival (T_s , \blacksquare). n = sample size

DISCUSSION

Age upon estuarine arrival in relation to otolith growth rate and age at metamorphosis

We assumed that the growth increments in otoliths of *Anguilla australis* were deposited on a daily basis, as are those of *A. japonica*, *A. rostrata* and *A. celebesensis*, which have been validated (Umezawa et al. 1989, Martin 1995, Arai et al. 2000). The present study found that the Australasian eel *A. australis* took approximately 7 to 9 mo to drift from the spawning grounds to the estuaries of Australia and New Zealand (Table 3), and metamorphosis from leptocephalus to glass eel occurred approximately 5 to 6 mo after hatching. Our estimates of age are similar to those of Arai et al. (1999c), who compared the ages of New Zealand glass eels collected at the same estuaries in 1996. This provides independent confirmation of the ageing technique.

Metamorphosis from the leptocephalus to the glass eel is thought to take place in the open ocean (Tzeng & Tsai 1994, Antunes & Tesh 1997). After metamorphosis, glass eels migrate from the open ocean into the coastal waters and thereafter invade freshwater rivers. The mean otolith growth rate of the leptocephalus stage (G_m) was a little greater in the northern group than in the southern group. However, the mean age at metamorphosis from leptocephali to glass eel was ca 1 mo less in the northern group (Sites A1 to A3, 160 ± 14.2 to 161 ± 12.6 d) than in the southern group (e.g. Sites A5 and A6, 183 ± 20.8 and 189 ± 16.9 d; Table 3). This implies that those leptocephali metamorphosing early would escape from the ocean current earlier and recruit to the northern Australia. Conversely, those leptocephali metamorphosing late would continue to drift with the ocean current further south and recruit to southern Australia.

Since the samples were collected in different years (1996 to 1999), it is possible that varying environmental conditions including oceanic change such as current speed and direction may influence the recruitment of glass eels. To assess this, we compared our data from Albert River (Site A3) in 1997 with published data from the same sampling site in 1996 (Arai et al. 1999c). The mean age of glass eels at metamorphosis and estuarine arrival were 164 ± 18.6 d and 208 ± 17.4 d in the Arai et al. (1999c) study and 161 ± 12.6 d and 217 ± 16.6 d in the present study. This very close agreement of ages for different years indicates that inter-annual variability of age at metamorphosis and recruitment in the same estuary may be minor, and less than variability due to geographic differences.

Effect of oceanic currents on larval dispersal

The East Australian Current (EAC) originates from the South Equatorial Current (SEC) and flows along the eastern seaboard of Australia. Most researchers have assumed that leptocephali travel to Australia on the East Australian Current (Schmidt 1928, Cairns 1941, Sloane 1984, Jellyman 1987, Beumer & Sloane 1990). The geographic cline in the ages of glass eels arriving in Australia found in the present study supports this assumption.

Based on the SEC speed of 0.5 to 0.6 m s⁻¹ (Tchernia 1980) and active swimming of the larvae for only 16 h at night (Umezawa 1991), Arai et al. (1999c) calculated that the time needed for eel larvae to migrate 5000 km from their presumed spawning grounds (Jellyman 1987) to the eastern coasts of Australia was approximately 145 to 173 d. Since larvae passively drift with oceanic currents for 24 h a day, a period of 16 h drift overestimates the time required to reach the continent. Furthermore, Jellyman calculated the distance from

Table 4. *Anguilla australis*. Homogeneity test (HG) for otolith radius (R_m and R_s) and otolith growth rate (G_m and G_s) (mean \pm SD) of glass eels collected from 8 estuaries (A1 to A8). Abbreviations are defined in 'Materials and methods'. Asterisks shared between estuaries indicate they belong to same homogeneous group ($p < 0.05$). Sample size for each site is shown in parentheses in Table 1. nt: data excluded from homogeneity test (see Table 3 legend)

R_m (μm)			G_m ($\mu\text{m d}^{-1}$)			R_s (μm)			G_s ($\mu\text{m d}^{-1}$)		
Site	Mean \pm SD	HG	Site	Mean \pm SD	HG	Site	Mean \pm SD	HG	Site	Mean \pm SD	HG
A3	81 ± 6.1	*	A7	0.50 ± 0.03	*	A1	42 ± 11.7	*	A2	1.05 ± 0.22	*
A1	81 ± 6.6	*	A6	0.51 ± 0.05	*	A3	43 ± 8.5	*	A3	1.03 ± 0.23	*
A2	82 ± 5.9	**	A5	0.51 ± 0.05	**	A5	45 ± 8.1	*	A1	0.98 ± 0.2	*
A4	84 ± 6.9	***	A3	0.52 ± 0.04	**	A6	45 ± 6.4	*	A5	0.81 ± 0.14	*
A7	88 ± 4.8	***	A8	0.53 ± 0.03	**	A2	46 ± 7.4	*	A4	0.76 ± 0.18	*
A5	89 ± 11.6	**	A4	0.53 ± 0.04	**	A4	49 ± 8.1	*	A6	0.75 ± 0.13	*
A8	89 ± 4.2	**	A1	0.53 ± 0.04	**	A7	53 ± 8.3^a	nt	A7	0.75 ± 0.12^a	nt
A6	91 ± 9.2	*	A2	0.54 ± 0.05	*	A8	55 ± 7.8^a	nt	A8	0.83 ± 0.12^a	nt

^aData include R_s and G_s

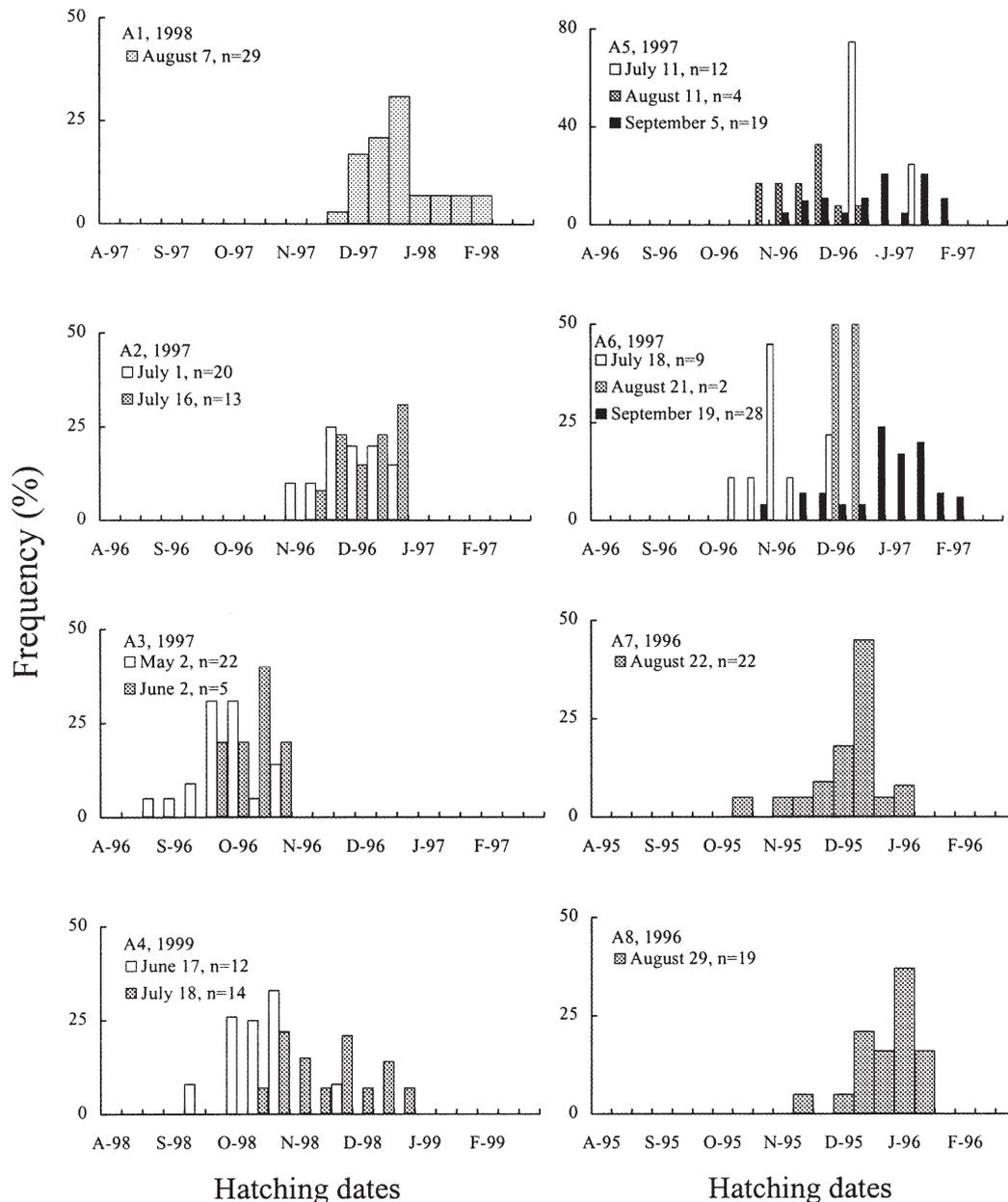


Fig. 6. *Anguilla australis*. Frequency distribution of hatching dates (back-calculated from the sampling dates and ages) of glass eels collected from the 8 estuaries (Sites A1 to A8 are shown in Fig. 1). n = sample size

the spawning grounds to Tasmania to be 7000 km. Hence, the distance from the spawning grounds to northern Australia (Sites A1 to A3) should be 6000 km. Accordingly, approximately 116 to 139 d would be required to transport eel larvae from the spawning area to northern Australia, based on the speed of the SEC (0.5 to 0.6 m s^{-1}) and a whole-day drift (24 h). This estimate was slightly lower than the ages of eels at metamorphosis from leptocephalus to glass eel at Sites A1 to A3 (Table 3). A possible explanation is that the eel larvae may have been indirectly transported by

complex oceanic currents from their spawning ground to the continent.

The ages of the eels at metamorphosis from leptocephalus to glass eel were ca 1 mo greater in the southern than in the northern group (Table 3). During this period, the leptocephali of the southern group would continue to drift on the EAC to southern Australia, while the leptocephali of the northern group would already have metamorphosed to glass eels and have recruited to coastal waters. The difference in the mean ages of leptocephali at metamorphosis to glass eels

was 29 d among the 6 estuaries in Australia. The average velocity of the EAC is 0.3 m s^{-1} (Bramwell 1977), probably reaching speeds as high as 0.52 m s^{-1} (Wyrski 1962). Based on current speed, the EAC could disperse the leptocephali a distance of between 751 and 1303 km over this 29 d period. This distance approximately coincides with the geographic range of the glass eels from the northern to southern estuaries (Sites A3 to A6), and indicates that the EAC plays an important role in transporting the eel larvae from northern Australia to the south.

From about 18°S , the EAC flows generally southward along the east Australian coast, then divides at Latitude 33 to 34°S . A weak branch flows to the south as anticyclonic warm-core eddies (Hamon 1965). The main branch flows offshore to the northeast or north, still as a narrow swift current (Hamon 1965). Further offshore, the remainder of this branch crosses the Tasman Sea southeastward in the general direction of New Zealand, following the Tasman Front (Boland & Church 1981, Gresswell & Legeckis 1986). Based on this circulation pattern, Cairns (1941), Castle (1969) and Aoyama et al. (1999) suggested that the leptocephali of *Anguilla australis* drift with the EAC to the western coast of New Zealand. If the eel larvae are transported by the EAC to the western coasts of New Zealand, the leptocephali must drift at least 1500 km, crossing the Tasman Sea. The surface speed at the Tasman Front is 0.14 m s^{-1} (Wyrski 1962). To drift a distance of 1500 km at speed of 0.14 m s^{-1} requires approximately 120 d. In practice, the ages of leptocephali at metamorphosis (T_m) from the most adjacent trans-Tasman sites (A5 and A7) differed by an average of only 8 d. Thus, it is highly unlikely that recruitment of glass eels to New Zealand is via the east coast of Australia. Furthermore, information on arrival times and sizes of glass eels suggest that arrival in New Zealand is more likely to be from the north than the west (Jellyman 1987, Jellyman et al. 1999, Chisnall et al. 2000). Another possible migration route is transportation by the southwest-flowing portion of the SEC (Jellyman 1987). To validate this possible route, an intensive and successive collection of leptocephali would be required. Likewise, data on ages of glass eels from the north of New Zealand would help confirm whether recruitment to New Zealand is from the north, as suggested by Jellyman (1987) and Jellyman et al. (1999).

Factors affecting duration of glass eel stage

We found that the glass eels from southern Australia and New Zealand spent more time in coastal waters (Table 3) than the northern group. The magnitude and direction of the EAC might influence the timing of

glass eel recruitment. The strong EAC flows continuously and frequently spreads across the continental shelf between 27 and 33°S (Huyer et al. 1988, Middleton et al. 1994). Hence, the EAC off Sites A1 to A3 may carry the glass eels very close to the coast and shorten the time for recruitment to the estuaries. However, offshore at Latitude 34°S , the EAC becomes intermittent and weak, forming irregular and complex eddies. If glass eels were entrained into the complex eddy or northward/northeastward return current (Hamon 1965), they would need additional time to reach the coasts. This might be the reason why the glass eels of the Sites A4 to A5 had a longer residence time in coastal waters.

Growth rate provides another explanation for the difference in the duration of the glass eel stage (G_s) among sampling sites. A lower otolith growth rate was found in southern Australia (Sites A4 to A6) and New Zealand (Table 4) than in the north. In winter, the coastal water temperature in southern Australia and New Zealand (13°C at 35°S) is lower than in northern Australia (20°C at 25°S ; Tchernia 1980). Low temperature and slower growth rate of the glass eels might be one of the reasons causing a delay in recruitment.

Conclusion

The size, age composition and growth rate of otoliths indicated that glass eels recruiting into Australian waters are comprised of 2 groups. The timing of metamorphosis from leptocephalus to glass eel and transportation by the SEC/EAC play an important role in determining the destination of the glass eels. On the other hand, glass eels recruiting to New Zealand probably utilize a different route from the Australian group, since the difference in age at metamorphosis between the leptocephali sampled in Australia and those sampled in New Zealand was not sufficient for the leptocephali to have drifted across the Tasman Sea from eastern Australia to the western coast of New Zealand.

Acknowledgements. This study was financially supported by the National Science Council (NSC89-2611-B-002-004), Republic of China. The authors thank Dr L. Mckinnon for providing specimens from Victoria, Miss C. Y. Lin for assistance in taking SEM photographs, Miss S. Y. Tsai for electron probe microanalysis and the anonymous reviewers for helpful comments.

LITERATURE CITED

- Antunes C, Tesh FW (1997) A critical consideration of the metamorphosis zone when identifying daily rings in otoliths of European eel, *Anguilla anguilla* (L.). *Ecol Freshw Fish* 6:102–107
- Aoyama J, Mochioka N, Otake T, Ishikawa S, Kawakami Y, Castle P, Nishida M, Tsukamoto K (1999) Distribution and

- dispersal of anguillid leptocephali in the western Pacific Ocean revealed by molecular analysis. *Mar Ecol Prog Ser* 188:193–200
- Arai T, Otake T, Tsukamoto K (1997) Drastic changes in otolith microstructure and microchemistry accompanying the onset of metamorphosis in the Japanese eel *Anguilla japonica*. *Mar Ecol Prog Ser* 161:17–22
- Arai T, Limbong D, Otake T, Tsukamoto K (1999a) Metamorphosis and inshore migration of tropical eels, *Anguilla* spp., in the Indo-Pacific. *Mar Ecol Prog Ser* 182:283–293
- Arai T, Otake T, Jellyman DJ, Tsukamoto K (1999b) Differences in the early life history of the Australasian shortfin eel *Anguilla australis* from Australia and New Zealand, as revealed by otolith microstructure and microchemistry. *Mar Biol* 135:381–389
- Arai T, Otake T, Limbong D, Tsukamoto K (1999c) Early life history and recruitment of the tropical eel, *Anguilla bicolor pacifica*, as revealed by otolith microstructure and microchemistry. *Mar Biol* 133:319–326
- Arai T, Limbong D, Otake T, Tsukamoto K (2000) Validation of otolith daily increments in the tropical eel *Anguilla celebesensis*. *Can J Zool* 78:1078–1084
- Beumer J, Sloane R (1990) Distribution and abundance of glass-eels *Anguilla* spp. in East Australian waters. *Int Revue Gesamten Hydrobiol* 75:721–736
- Boland FM, Church JA (1981) The East Australian Current 1978. *Deep-Sea Res* 28A:937–957
- Bramwell M (ed) (1977) The atlas of the oceans. Mitchell Beazley, London
- Cairns D (1941) Life-history of the two species of New Zealand freshwater eel. Part 1. Taxonomy, age and growth, migration and distribution. *N Z J Sci Technol Sect B* 23:53b–72b
- Castle PHJ (1963) Anguillid leptocephali in the southwest Pacific. *Zoology Publ, Vic Univ Wellingt* 33:1–14
- Castle PHJ (1969) Early life history and general distribution of eels. In: Campbell JS (ed) Report on eel seminar. New Zealand Fishing Industry Board, Wellington, p 14–18
- Cheng PW, Tzeng WN (1996) Timing of metamorphosis and estuarine arrival across the dispersal range of the Japanese eel *Anguilla japonica*. *Mar Ecol Prog Ser* 131:87–96
- Chisnall BL, Jellyman DJ, Bonnett ML, Sykes JRE (2000) Studies on glass eels in New Zealand. *NIWA, Wellington, Water and Atmosphere* 8(4):21–22
- Dijkstra LH, Jellyman DJ (1999) Is the subspecies classification of the freshwater eels *Anguilla australis australis* Richardson and *A. a. schmidtii* Phillipps still valid? *Mar Freshw Res* 50:261–263
- Ege V (1939) A revision of the genus *Anguilla* Shaw. A systematic, phylogenetic and geographical study. *Dana-Rep* 3:1–256
- Gresswell GR, Legeckis R (1986) Eddies off southeastern Australia. *Deep-Sea Res* 33:1527–1562
- Hamon BV (1965) The East Australian Current, 1960–1964. *Deep-Sea Res* 12:899–921
- Huyer A, Smith RL, Stabeno PJ, Church JA, White NJ (1988) Currents off south-eastern Australia: results from the Australian coastal experiment. *Aust J Mar Freshw Res* 39:245–288
- Jellyman DJ (1987) Review of the marine life history of Australian temperate species of *Anguilla*. *Am Fish Soc Symp* 1:276–285
- Jellyman DJ, Chisnall BL, Bonnett ML, Sykes JRE (1999) Seasonal arrival patterns of juvenile freshwater eels (*Anguilla* spp.) in New Zealand. *N Z J Mar Freshw Res* 33:249–262
- Kawakami Y, Mochioka N, Morishita K, Toh H, Nakazono A (1998) Determination of the freshwater mark in otoliths of Japanese eel elvers using microstructure and Sr/Ca ratios. *Environ Biol Fish* 53:421–427
- Martin MH (1995) Validation of daily growth increments in otoliths of *Anguilla rostrata* (Lesueur) elvers. *Can J Zool* 73:208–211
- Middleton JH, Coutis P, Griffin DA, Macks A, McTaggart A, Merrifield MA, Nippard GJ (1994) Circulation and water mass characteristics of the Southern Great Barrier Reef. *Aust J Mar Freshw Res* 45:1–18
- Otake T, Ishii T, Nakahara M, Nakamura R (1994) Drastic changes in otolith strontium/calcium ratios in leptocephali and glass eels of Japanese eel *Anguilla japonica*. *Mar Ecol Prog Ser* 112:189–193
- Pannella G (1971) Fish otolith: daily growth layers and periodical patterns. *Science* 173:1124–1127
- Schmidt J (1928) The freshwater eels of Australia with some remarks on the shortfin species of *Anguilla*. *Rec Aust Mus* 16:179–210
- Sloane RD (1984) Invasion and upstream migration by glass-eels of *Anguilla australis australis* Richardson and *A. reinhardtii* Steindachner in Tasmanian freshwater streams. *Aust J Mar Freshw Res* 35:47–59
- Strubberg AC (1913) The metamorphosis of elvers as influenced by outward conditions. *Medd Kommn Havunders Ser Fiskeri* 4(3):1–11
- Tchernia P (1980) Descriptive regional oceanography. Pergamon Mar Ser 3. Pergamon Press, Oxford.
- Tzeng WN (1990) Relationship between growth rate and age at recruitment of *Anguilla japonica* elvers in a Taiwan estuary as inferred from otolith growth increments. *Mar Biol* 107:75–81
- Tzeng WN, Tsai YC (1994) Changes in otolith microchemistry of the Japanese eel, *Anguilla japonica*, during its migration from the ocean to the rivers of Taiwan. *J Fish Biol* 45:671–683
- Umezawa A (1991) Early life history and recruitment mechanism of the eel, *Anguilla japonica*. PhD thesis, The University of Tokyo, Tokyo
- Umezawa A, Tsukamoto K, Tabeta O, Yamakawa H (1989) Daily growth increments in the larval otolith of the Japanese eel *Anguilla japonica*. *Jpn J Ichthyol* 35:440–444
- Wang CH, Tzeng WN (1998) Interpretation of geographic variation in size of American eel *Anguilla rostrata* elvers on the Atlantic coast of North America using their life history and otolith ageing. *Mar Ecol Prog Ser* 168:35–43
- Wang CH, Tzeng WN (2000) The timing of metamorphosis and growth rates of American and European eel leptocephali: a mechanism of larval segregative migration. *Fish Res (Amst)* 1019:1–15
- Wyrтки K (1962) Geopotential topographies and associated circulation in the western south Pacific Ocean. *Aust J Mar Freshw Res* 13:89–105

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: May 10, 2000; Accepted: September 14, 2000
Proofs received from author(s): August 8, 2001