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Comparison of the Early Life History of *Anguilla reinhardtii* and *A. australis* by Otolith Growth Increment

Abstract

The glass eels of *Anguilla reinhardtii* and *A. australis* were collected from the estuaries of eastern Australia. Growth increments and Sr/Ca ratios in otoliths of the eels were examined. The age at metamorphosis from leptocephalus to glass eel stage was determined from where the increment width dramatically increased and the Sr/Ca ratio dropped. The pattern of temporal changes in otolith increment widths and Sr/Ca ratios were similar between species, however the duration of each ontogenetic stage was different. The mean age (± SD) of *A. reinhardtii* (n=119) at metamorphosis was 142.5 ± 12.3 d and at estuarine arrival was181.7 ± 16.5 d and was 173.7 ± 20.5 and 229.2 ± 29.4 d, respectively, for *A. australis* (n=150). The younger ages at estuarine arrival of *A. reinhardtii* suggest that the spawning grounds of this species lie closer to Australia than those of *A. australis*. In addition, the mean total length at recruitment of *A. reinhardtii* (49.4 ± 1.7 mm) was significantly smaller than for *A. australis* (54.6 ± 5.4 mm). However, the growth rates of *A. reinhardtii* (0.25 ± 0.02 mm/d) were significantly faster than for *A. australis* (0.23 ± 0.022 mm/d). The smaller sizes of *A. reinhardtii* at recruitment were likely due to the shorter marine larval period and faster growth rate compared with *A. australis*. The duration of the marine larval period and growth rate may be the principal factors in determining the geographical distribution of both *A. reinhardtii*, which tend to occur in tropical-subtropical waters, and *A. australis*, which dominate in more temperate waters.

Key words: *Anguilla australis*, *Anguilla reinhardtii*, Otolith, Early life history

Along the eastern coasts of Australia and Tasmania, the longfinned eels *Anguilla reinhardtii* and the shortfinned eels *A. australis* are found in a wide variety of wetland habitats [(1)]. Their distribution, invading seasons, size and weight at recruitment of

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the glass eels are well described [2]. *A. reinhardtii* are distributed from 10 – 43°S and most abundant in latitudes 20 – 34°S while *A. australis* occurred from 27 – 44°S and most abundant in latitudes 35 – 44°S [1-3]. The invasions of *A. reinhardtii* glass eel occur on a year round basis in tropical and subtropical regions peaking in the summer and autumn months of January to March. In contrast, the annual invasion of *A. australis* glass eels into temperate waters occurs over a more restricted time frame and peaks in the winter-spring months of July through to September [2].

The possible spawning sites of *A. australis* have been suggested as near New Caledonia[4], between Fiji and Tahiti[5-6], or further west than this at 150 - 170°W and 5 – 15°S[7]. However less attention is focused on *A. reinhardtii*. Recently, a few leptocephali of both species were caught in the vicinity of New Caledonia[6]. Their presence in this region supports the hypothesis that Australian eels spawn in the tropical oceans and larval eels drift in South Equatorial Current (SEC) to eastern Australia[7]. However, since the larvae of both species are transported in the same current, the question arises as to why *A. reinhardtii* predominate in tropical and subtropical waters while *A. australis* predominante in temperate waters. The duration of the marine larval period and growth rate are proposed to be the principal factors affecting the geographical distributions in *A. japonica*[8] and the larval segregative migration in *A. anguilla* and *A. rostrata*[9-10]. *A. australis* was consistently larger and heavier than *A. reinhardtii* at arrival within the same estuaries[2-3], perhaps because of differences in larval duration and/or growth rates between the two species[3].

After the finding of daily growth increment in fish otoliths[11], this ageing method was extensively applied to study the early life history of fish. For example, the ontogenetic stage of eels can be discriminated by otolith microstructure and microchemistry[12-13]. We use this method to estimate the age of the eel at metamorphosis from leptocephalus to glass eel and the age of the glass eel at estuarine arrival along the eastern Australian coast. The objective of this study is to identify the differences in ontogenetic duration and growth rate of the glass eels between species. The results will advance our understanding of the spawning grounds and the geographical distribution of these eels.

Materials and Methods

Sampling design

Glass eels of both *A. australis* and *A. reinhardtii* were collected from the estuaries of the Fitzroy, Albert and Port Hacking Rivers. Only *A. reinhardtii* glass eels were collected from the Barron River while only *A. australis* were collected from the Brodribb and Tarwin Rivers (Fig. 1; Table 1). The specimens collected were immediately preserved in 95% alcohol. The total length of the eels was measured and their pigmentation stage assessed according to the pigment distribution on the body surface[14].

Microchemistry analysis

The sagittal otoliths of glass eels were extracted for microchemistry analysis and age determination. The otoliths were embedded in epofix resin, ground and polished until the core was exposed. For electron probe microanalysis, the polished otoliths were carbon coated under a high vacuum evaporator. Strontium (Sr) and calcium (Ca) concentrations were measured from the core to the edge of otolith at 10 μm intervals with an electron beam of 10 μm in diameter, using an electron probe microanalyzer (JEOL JXA-8900R). The accelerating voltage was set at 15 kV and probe current at 5 nA. The peak concentration of Sr was counted for 90 s with background measurements for 20 s on each side. The peak concentration of Ca was counted for 20 s and each background for 10s. $SrCO_3$ (USNM-R10065) and $CaCO_3$ (USNM-36321) from the Department of Mineral Sciences, National Museum of Natural History, Smithsonian Institution, Washington DC,

USA were used as calibration standards for Sr and Ca respectively.

Age determination and growth rate

After microchemistry analysis, the otolith was polished again to remove the carbon layer, then etched with 0.05 M HCl for 13 - 15s, dried in an oven and coated with gold for SEM observation. SEM photographs were taken of the otoliths at a magnification of 2000 × and used to count their daily growth increments. The age at metamorphosis from leptocephalus to glass eel was determined from the growth increments between the core and where the increment width drastically increased and Sr/Ca ratios abruptly dropped [12-13]. If freshwater checks [15]appeared near the edge of the otolith, the age at estuarine arrival was counted from the first increment to the innermost check, otherwise it was counted to the edge of the otolith. Thus, the age at capture (T_t), estuarine arrival (T_r) and metamorphosis of leptocephalus (T_m) were estimated from the counts of daily growth increments. The hatching date of individual glass eel was back-calculated from the age at capture and the sampling date. The growth rate of the glass eel was estimated from the total length divided by the age at capture. Total lengths, daily ages and growth rates among rivers were tested for homogeneity. 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 (Dunn's method) was used.

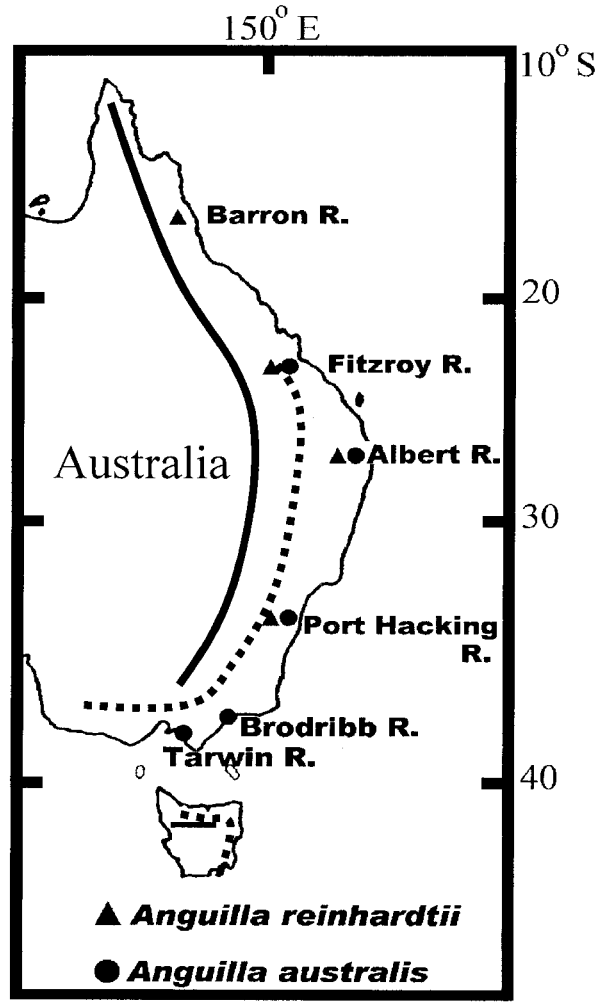

Fig. 1. Eel sampling locations. The distribution of *Anguilla reinhardtii* is indicated by the solid line and *A. australis* by the dashed line.

Table 1. The sampling locations, dates, pigmentation stages and total length of *A. reinhardtii* (LF) and *A. australis* (SF). Numerals in the parenthesis are the sample size for age determination.

Sampling location	Species	Sampling date	Pigmentation stage			Total length (mm)	
			VA	VB	VIA_{I-4}	mean ± SD	range
Barron River	LF (26)	28 Jan, 10 Mar, 26 May 1998	10	15	1	48.0±1.2	45.7-49.9
Fitzroy River	LF (31)	7 Jul 1998	15	14	2	48.7±1.3	46.0-51.0
	SF (29)	7 Aug 1998	0	4	25	47.6±2.1	42.8-51.0
Albert River	LF (33)	10 Nov 1997	0	24	9	49.9±1.4	46.9-52.3
	SF (27)	2 May, 2 Jun 1997	1	22	4	51.1±1.8	48.2-55.9
Port Hacking River	LF (29)	18 Apr 1999	10	18	1	51.0±1.4	47.3-52.7
	SF (26)	17 Jun, 18 Jul 1999	3	16	7	54.4±3.7	47.6-60.9
Brodribb River	SF (31)	11 Jul, 5 Sep 1997	3	25	3	58.8±3.9	49.5-63.8
Tarwin River	SF (37)	18 Jul, 19 Sep1997	7	29	1	59.4±2.1	53.7-63.4
Total	LF (119)		35	71	13	49.9±2.0	45.7-54.8
	SF (150)		14	96	40	54.6±5.4	42.8-63.8

Results

Pigmentation stage and total length

In most rivers, the glass eels were predominantly of pigmentation Stage VA and VB, with few individuals at Stages VIA_I through to VIA_{IV}. However, most *A. australis* from the Fitzroy River were at Stage VIA_I to VIA_{IV} with only 4 individuals at Stage VB (Table 1). The eels of Stages VA and VB were the new recruits, but the eels of VIA_I to VIA_{IV} may have resided in the estuary for a period of time. *A. reinhardtii* ranged from 45.7 - 52.7 mm in total length and *A. australis* from 42.8 - 63.8 mm (Table 1). The mean total lengths of *A. reinhardtii* were significantly smaller than for *A. australis* in the Albert and Port Hacking Rivers ($p < 0.01$, *t*-test) (Table 1). In the Fitzroy River, the mean total lengths of *A. reinhardtii* were significantly larger than *A. australis* ($p = 0.01$, *t*-test) (Table 1).

Changes in increment width and Sr/Ca ratios

The growth increments in otoliths of *A. australis* and *A. reinhardtii* glass eels are shown in Fig. 2. The core of the otolith represents the embryo stage. Beyond the core are the conspicuously concentric growth increments (Fig. 2). The first growth increment is assumed to deposit at the beginning of leptocephalus stage. The increment width increases with growth to 0.8 – 1 μm around 30 d from the beginning of the leptocephalus stage, then declines gradually to about 0.3 μm until metamorphosis. The Sr/Ca ratio at the core is relatively lower, approximately 0.009, then the value gradually increases and peaks (approximately 0.018 - 0.02) at metamorphosis. Beyond the peak, the Sr/Ca ratio dramatically decreases to 0.006 at the edge of the otolith (Fig. 3). The decrease in Sr/Ca is accompanied by an abrupt increase in increment width to 1.5 μm in *A. australis* and 2 μm in *A. reinhardtii*. The decrease in Sr/Ca ratios from peak levels in conjunction with an increase in increment width indicates the metamorphosis from leptocephalus to glass eel[12-13]. Following the

leptocephalus stage is the oceanic glass eel stage. Freshwater checks were found in most otoliths (Fig 2). Between the innermost check and the edge of the otolith, is considered the estuarine glass eel stage and the daily growth increments usually become vague.

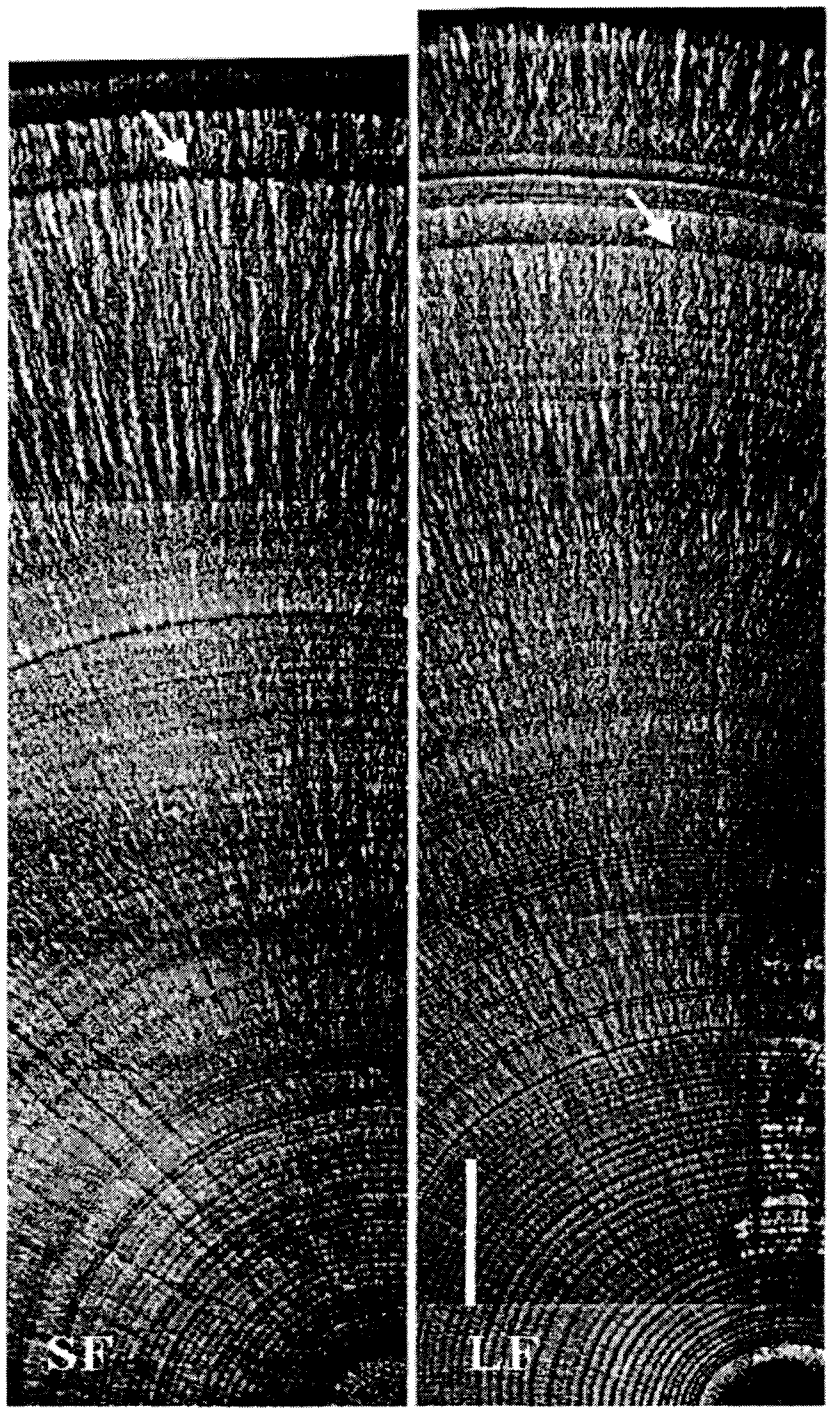

Fig. 2. Daily growth increments in the otolith of *Anguilla australis* (SF), TL: 61.4 mm, Stage: VB from the Brodribb River, and *A. reinhardtii* (LF), TL: 49.3mm, Stage: VB from the Albert River. Arrows: freshwater checks. Bar: 15 μm.

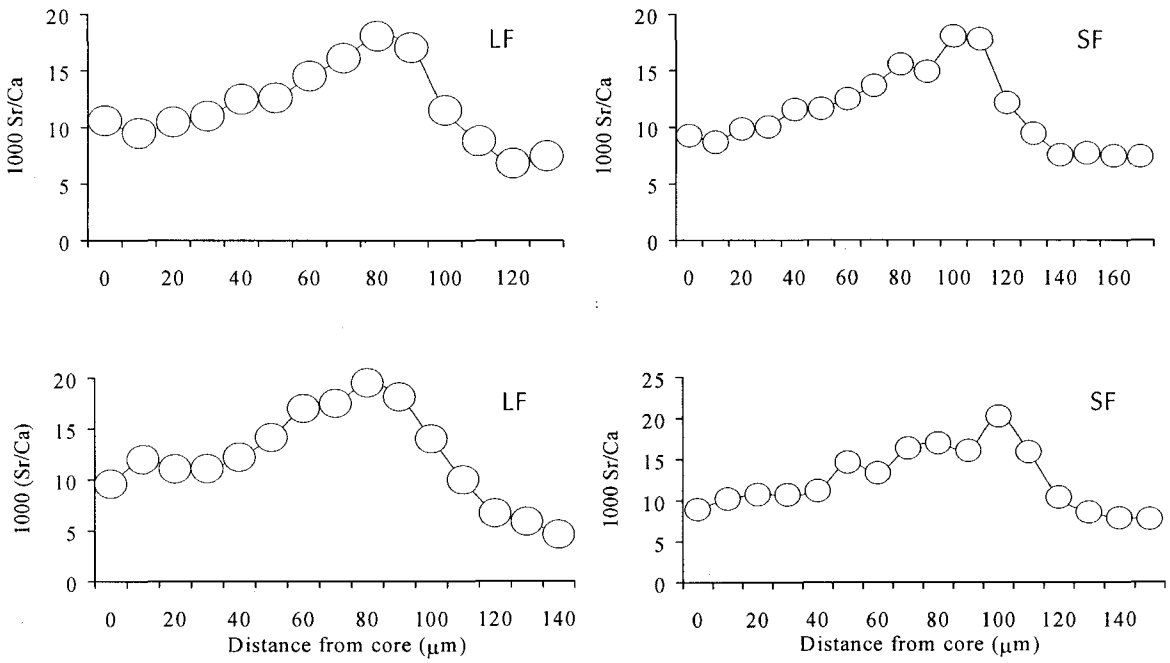

Fig. 3. Temporal changes of Sr/Ca ratios from core to edge of the otoliths in *Anguilla reinhardtii* (LF) and *A. australis* (SF).

Daily age and growth rate

For *A. reinhardtii* collected from the 4 estuaries, the mean ages at metamorphosis from leptocephalus to glass eel (T_m) ranged from 136 - 148 d and the mean ages of glass eels at estuarine arrival (T_r) ranged from 174 - 188 d. The mean T_m of eels from the Albert River was significantly smaller than for the Fitzroy River ($p < 0.05$, Dunn's multiple comparison). Furthermore, the mean T_r of glass eels from the Albert River was significantly smaller than for the Fitzroy and Port Hacking rivers ($p < 0.05$, Dunn's multiple comparison). No significant differences among other rivers were found (Table 2).

The mean T_m of *A. australis* ranged from 160 - 189 d and mean T_r from 204 - 252 d. The mean T_m and T_r of the eels from the Brodribb and Tarwin Rivers were significantly larger than for eels from the Fitzroy and Albert Rivers, with the eels from the Port Hacking River having intermediate values ($p < 0.05$, Dunn's multiple comparison). Between northern and southern rivers, T_m differed approximately 30 d and T_r differed 40 - 50 d (Table 2). For both species, the ages at metamorphosis (T_m) were linearly related with ages at estuarine arrival (T_r) (Fig. 4). This indicates that the leptocephalus metamorphosing at a younger age will arrive at the estuary as a younger glass eel.

T_m and T_r of *A. reinhardtii* from each of the Fitzroy, Albert and Port Hacking Rivers were significantly smaller than for *A. australis* from the same rivers ($p < 0.01$, *t*-test). The difference between these two species was about 10 - 15 d in the Fitzroy River, 20 - 30 d in the Albert River and 20 - 50 d in the Port Hacking River (Table 2). In all three rivers, *A. reinhardtii* grew significantly faster than that of *A. australis* ($p < 0.01$, *t*-test). The mean growth rate was estimated at 0.25 mm/d for *A. reinhardtii* and 0.23 mm/d for *A. australis* (Table 2).

Table 2. Comparison of ages at metamorphosis (T_m), estuarine arrival (T_r) and growth rate (G_r) of the eels. For comparison within species among the rivers, ages with the same letters (i.e. ^{a}, ^{b}, ^{ab}) are not significantly different (at $p < 0.05$, Dunn's multiple comparison).

Location	*Anguilla reinhardtii (LF)*			*Anguilla australis (SF)*			*Difference between species*	
	T_m	T_r	G_r(mm/d)	T_m	T_r	G_r(mm/d)		
Barron River	143.1±11.4^{ab} (130-171)	180.9±16.6^{ab} (151-212)	0.25±0.02					
Fitzroy River	148.2±11.5^{b} (126-177)	188.0±16.0^{b} (153-221)	0.24±0.02	159.6±14.2^{a} (130-180)	204.2±17.9^{a} (169-240)	0.21±0.02	T_m, T_r SF>LF	G_r LF>SF
Albert River	135.9±14.1^{a} (96-175)	173.7±18.9^{a} (140-227)	0.25±0.02	161.1±12.6^{a} (144-190)	204.6±16.6^{a} (175-246)	0.23±0.02	T_m, T_r SF>LF	G_r LF>SF
Port Hacking River	143.3±7.8^{ab} (130-157)	184.9±10.3^{b} (160-203)	0.26±0.02	168.3±14.5^{ab} (130-196)	235.0±21.6^{b} (198-275)	0.22±0.02	T_m, T_r SF>LF	G_r LF>SF
Brodribb River				184.3±21.5^{bc} (150-226)	242.5±24.8^{bc} (185-297)	0.24±0.02		
Tarwin River				189.0±17.3^{c} (160-245)	251.5±25.5^{c} (203-317)	0.23±0.02		
Pooled	142.5±12.3 (96-177)	181.7±16.5 (140-227)	0.25±0.02	173.7±20.5 (130-245)	229.2±29.4 (169±317)	0.23±0.02	*t*-test, $p<0.01$	

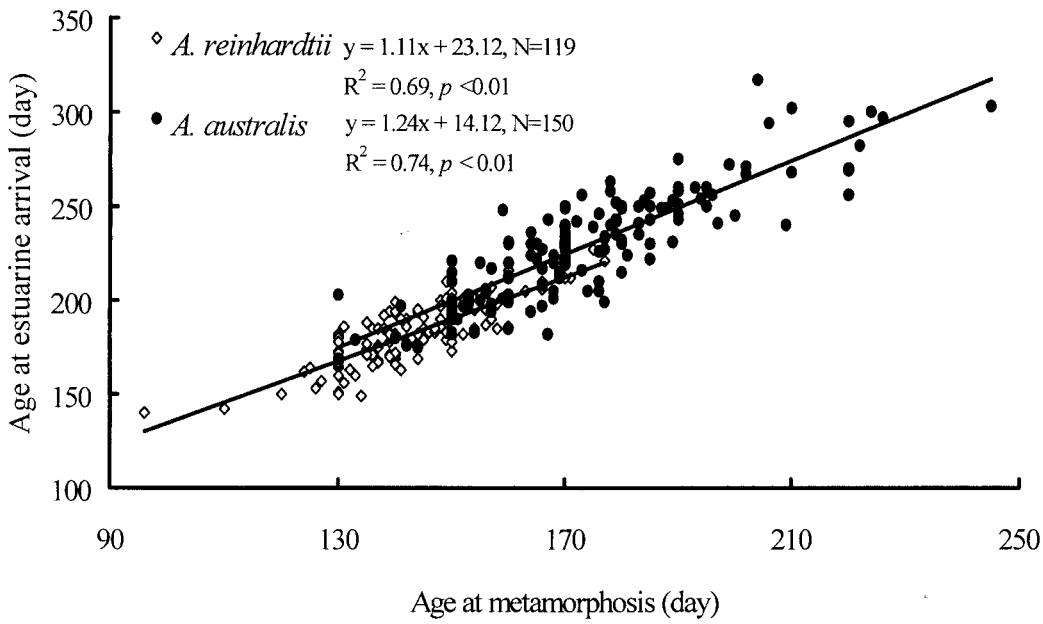

Fig. 4. The relationship between the age at metamorphosis from leptocephali to glass eel and the age of glass eels at estuarine arrival for *Anguilla reinhardtii* and *A. australis*.

Discussion

The age determination of glass eels depends on the daily growth increments in otoliths. The formation of daily growth increments in otoliths has been validated in *A. japonica* at the early leptocephalus stage [16] and in *A. rostrata* [17] and *A. celebesensis* [18] at the glass eel stage. In this study, we assume that otolith growth increments are deposited daily in *A. reinhardtii* and *A. australis*.

The hypothesized drifting routes of larval eels via the South Equatorial Current (SEC) to eastern Australia are widely accepted[6-7, 19]. However, the locations of spawning grounds for *A. reinhardtii* and *A. australis* have yet to be identified. On average, *A. reinhardtii* take approximately 6 months (181.7 ± 16.5 d) to migrate from the spawning grounds to the Australia's eastern coasts (17 - 34°S), with 4 - 5 months in the leptocephalus stage. For *A. australis* to arrive within this area (23 - 34°S), it takes 7 - 8 months (average 204.2 - 235.0 d), and even up to 9 months to reach southern Australia (37 - 38°S). During this period, 5 - 6 months are spent in the marine larval stage (Table 2). The estimated larval ages and current speed are used to deduce the possible spawning grounds of the eels. In the Albert River and Fitzroy River, the mean leptocephalus stages of *A. australis* are about 160 d. The mean SEC speed between the coast of South America and the mid-Pacific is about 0.5 - 0.6 m/s[20]. This current speed was applied to the calculation of larval transport in the western Pacific[6-7, 21], regardless of the spatial heterogeneity in the SEC. According to the recent surveys in the western Pacific, the SEC in this area was about 0.2 - 0.3 m/s[22-25]. Therefore, based on the SEC speed of 0.2 - 0.3 m/s and 160 d drift, the larval eels will be transported about 2,500 – 4,000 km. Thus, the spawning ground of *A. australis* may lie in the areas between Fiji and Samoa.

The *A. reinhardtii* leptocephali were consistently younger (11 - 26 d) than *A. australis* leptocephali. The difference in age between the two species indicates that their spawning grounds must be different. Thus, the spawning site of *A. reinhardtii* may lie about 500 km west of that for *A. australis*. This distance puts the spawning ground of *A. reinhardtii* around or west of Fiji, which is further east than[26] presumption of the Coral Sea. However, this simplified calculation basically ignores the temporal and spatial variability of oceanic currents and assumes a smooth ocean circulation. Furthermore, the active swimming ability of leptocephali is not considered.

Our results support Sloane's[3]conclusion that *A. reinhardtii* has a shorter marine larval duration and younger age at estuarine arrival than does *A. australis* (Table 2, Fig. 4). *A. reinhardtii* also grows faster than *A. australis*. Most *A. reinhardtii* leptocephali are probably able to metamorphose when approaching northern Australia. Close to or over the continental shelf, most *A. reinhardtii* leptocephali metamorphose to glass eels and then recruit to tropical and subtropical areas. On the other hand, *A. australis* has a longer marine larval stage and slower growth rate suitable for a longer migration from more distant spawning grounds to subtropical and temperate areas. *A. australis* glass eels in the Brodribb and Tarwin Rivers (southern Australia) were about 1 month older at metamorphosis and at estuarine arrival than the northern group (Table 2). Shiao et al. [24] recently found that the growth rate of glass eels was slower in southern Australia than in northern Australia. The *A. reinhardtii* inhabiting southern Australia and Tasmania may also have a longer marine larval stage and slower growth rate than their northern counterparts. Marine larval duration and growth rate are evidently important factors affecting the distribution of Australian eels and may also account for the segregation of the American eel (*A. rostrata*) and European eel (*A. anguilla*)[9, 10].

Acknowledgements

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References

1. Beumer, J. P (1996) Freshwater Eels. In 'Freshwater Fishes of South-Eastern Australia' (Ed R M McDowall), pp. 247 (Reed Books, Sydney.)
2. Beumer, J. P., and R. Sloane (1990) Distribution and abundance of glass-eels *Anguilla* spp. in East Australian waters. Internationale revue der gesamten hydrobiology, **75:** 721-736.
3. Sloane, R. D (1984) Invasion and upstream migration by glass-eels of *Anguilla australis australis* Richardson and *A. reinhardtii* Steindachner in Tasmanian freshwater streams. Aust. J. Mar. Freshwat. Res., **35:** 47-59.
4. Schmidt, J. (1928) The freshwater eels of Australia with some remarks on the shortfinned species of *Anguilla.* Records of the Australian Museum, **16:** 179-210.
5. Castle, P. H. J. (1963) Anguillid leptocephali in the southwest Pacific. Zoology Publications, Victoria University of Wellington, **33:** 14p
6. Aoyama, J., N. Mochioka, T. Otake, S. Ishikawa, Y. Kawakami, P. Castle, M. Nishida and K. Tsukamoto (1999) Distribution and dispersal of anguillid leptocephali in the western Pacific Ocean revealed by molecular analysis. Mar. Ecol. Prog. Ser., **188:** 193-200.
7. Jellyman, D. J. (1987) Review of the marine life history of Australian temperate species of *Anguilla. In* 'Symposium of Common strategies of anadromous and catadromous fishes', (Dadswell MJ, Klauda RJ, Moffitt CM, Saunders RL, Rulifson RA, Cooper JE eds.), 276-285 (American Fish Society.)
8. Cheng, P. W. and W. N. Tzeng (1996) Timing of metamorphosis and estuarine arrival across the dispersal range of the Japanese eel *Anguilla japonica.* Mar. Ecol. Prog. Ser., **131:** 87-96.
9. Wang, C. H. and W. N. Tzeng (2000) The timing of metamorphosis and growth rates of American and European eel leptocephali: A mechanism of larval segregative migration. Fish. Res., **46:** 191-205.
10. Arai, T., T. Otake and T. K. sukamoto (2000a) Timing of metamorphosis and larval segregation of the Atlantic eels *Anguilla rostrata* and *A. anguilla,* as revealed by otolith microstructure and microchemistry. Mar. Biol., **137:** 39-45.
11. Pannella, G. (1971) Fish otolith: daily growth-layers and periodical patterns. Science, **173:** 1124-1127
12. Tzeng, W. N. and Y. C. Tsai (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.
13. Arai, T., T. Otake and K. Tsukamoto (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.
14. Strubberg, A. C. (1913) The metamorphosis of elvers as influenced by outward conditions. Meddr Kommn Havunders, Ser. Fish., **4(3):** 1-11.
15. Kawakami, Y., N. Mochioka, K. Morishita, H. Toh and A. Nakazono (1998) Determination of the freshwater mark in otoliths of Japanese eel elvers using microstructure and Sr/Ca ratios. Environ. Biol. Fish., **53:** 421-427.
16. Umezawa, A., K. Tsukamoto, O. Tabeta and H. Yamakawa (1989). Daily growth increments in the larval otolith of the Japanese eel *Anguilla japonica.* Japanese Journal of Ichthyology, **35:** 440-444.
17. Martin, M. H (1995) Validation of daily growth increments in otoliths of *Anguilla rostrata* (Lesueur) elvers. Can. J. Zool., **73:** 208-211.
18. Arai, T., D. Limbong, T. Otake and K. Tsukamoto, (2000b) Validation of otolith daily increments in the tropical eel *Anguilla celebesensis.* Can. J. Zool., **78:** 1078-1084.
19. Tesch, F. W. (1977) 'The Eel: Biology and Management of Anguillid Eels.' 1st Edn. (Chapman and Hall: London.)
20. Tchernia, P. (1980) 'Descriptive regional oceanography.' Pergamon Marine Series 3. (Pergamon Press, Oxford, England)
21. Shiao, J. C., W. N. Tzeng, A. Collins and D. J. Jellyman (2001) Dispersal pattern of glass eel stage of *Anguilla australis* revealed by otolith growth increments. Mar. Ecol. Prog. Ser., **219:** 241-250.
22. Gouriou, Y. and J. Toole (1993) Mean circulation of the upper layers of the western equatorial Pacific ocean. J. Geophys. Res., **98** (C12): 2495-2520.

23. Sprintall, J., and M. J. McPhaden (1994) Surface layer variations observed in multiyear time series measurements from the western equatorial Pacific. J. Geophys. Res., **99** (C1): 963-979.
24. Reverdin, G., C. Frankignoul, E. Kestenare, M. J. McPhaden (1994) Seasonal variability in the surface currents of the equatorial Pacific. J. Geophys. Res., **99** (C10): 20323-20344.
25. Lagerloef, G. S. E., G. T. Mitchum, R. B. Lukas, P. P. Niiler (1999) Tropical Pacific near-surface currents estimated from altimeter, wind, and drifter data. J. Geophys. Res., **104** (C10): 23313-23326.
26. Jespersen, P. (1942) Indo-Pacific leptocephalids of the genus *Anguilla*. Dana Report, **22:** 1-128.