Journal of Fish Biology (1992) **40**, 845–857

Otolith microstructure and daily age of *Anguilla japonica*, Temminck & Schlegel elvers from the estuaries of Taiwan with reference to unit stock and larval migration

W.-N. TZENG AND Y.-C. TSAI

Department of Zoology, College of Science, National Taiwan University, Taipei, Taiwan 10617, Republic of China

(*Received 15 July 1991, Accepted 19 October 1991*)

To test the hypothesis that the Japanese eel, *Anguilla japonica*, elvers in the eastern and western coasts of Taiwan are recruited from two different spawning grounds and to increase the knowledge of the early life history of the eel, the otolith microstructure and daily age of elvers collected from five estuaries in the coast of Taiwan during December 1989 through February 1990 were examined by scanning electron microscopy. The total length of elvers at arrival in the estuaries was similar among estuaries, averaging *c*. 56·0 mm and showed a seasonal decrease. The maximum radius of the sagittal otolith of elvers ranged from 124·46 to 181·82 μm with a mean of 143·15 ± 12·72 μm. The otolith from centre to edge included an organic-rich primordium (9·20 ± 2·02 μm in diameter), a diffusively calcified core (20·94 ± 1·99 μm), and the daily growth increments; these three layers were probably deposited during the embryonic, yolk sac and feeding period respectively. The growth rate of the otolith was higher at the beginning of early life (0·5–1·0 μm day^{-1}), lowest at approximately 100-days old (<0·5 μm day^{-1}), and highest 1 month before arrival at the estuary (> 1·0 μm day^{-1}). The mean age for elvers arriving in the estuaries of the coasts of Taiwan was approximately 170·4 ± 21·02 days. Neither the growth pattern of the otolith nor the age of elvers arriving in the estuary were significantly different among estuaries, indicating that the elvers in both eastern and western Taiwan were probably recruited from the same spawning ground. The growth pattern of the otolith in relation to larval migration was analysed.

Key words: *Anguilla japonica*; elver; otolith growth increment; daily age; early life history; spawning ground; larval migration.

I. INTRODUCTION

The Japanese eel, *Anguilla japonica*, Temminck & Schlegel, is one of the most important cultured species in Taiwan. For cultivation purposes, large numbers of elvers are caught from the estuary during upstream migration in the period November to March (Chen, 1975; Tzeng, 1983*a*, 1985). Aquaculture of eels has been commercially successful in Taiwan since 1963 (Tzeng, 1983*b*), however the knowledge of the early life history of this species, e.g. spawning areas and season, distribution and migration of leptocephali and elvers, is limited (Tanaka, 1975; Tabeta *et al*., 1987; Kajihara, 1988; Ozawa *et al*., 1989; Tsukamoto, 1990). The spawning ground of the Japanese eel was first presumed to be in the waters south of Okinawa and east of Taiwan (Matsui, 1957). However, based on the distribution of elvers along the coast of Taiwan and their transportation by the Kuroshio current, a local spawning ground in the waters southwest of Taiwan was proposed (Kuo, 1971). Recent investigations on the distribution of leptocephali and ageing studies on leptocephali and elvers indicate that the exact spawning ground is located in the waters east of the Philippines between the North Equatorial Current

0022–1112/92/060845 + 13 $03.00/0

at about 10° N and the Subtropical Countercurrent at about 20° N (Kajihara, 1988; Ozawa *et al.*, 1989; Tsukamoto *et al.*, 1989; Tsukamoto, 1990).

Since Pannella (1971) detected primary growth increments in otoliths of fish, larval ageing techniques based on examination of otolith microstructure have been widely used to study the early life history of fish (Campana & Nielson, 1985). The growth increments in otoliths of both newly hatched larvae and elvers were found to be deposited on a daily schedule (Umezawa *et al.*, 1989; Lee & Lee, 1989; Tsukamoto, 1989). The daily age of anguillid leptocephali and elvers can thus be examined from otolith growth increments (Tabeta *et al.*, 1987; Tsukamoto *et al.*, 1989; Umezawa & Tsukamoto, 1990). This permitted the time required for migration of the eel larvae from the spawning ground to the coasts, and the spawning season of the eel, to be estimated (Tsukamoto, 1990; Tzeng, 1990). Changes in the growth pattern of the otolith have been related to environmental conditions in juvenile chinook salmon (*Oncorhynchus tshawytscha* Walbaum) (Neilson *et al.*, 1985) and in the European eel, *Anguilla anguilla* (Linnaeus), elvers (Lecomte-Finiger & Yahyaoui, 1989).

This paper compares the daily age of elvers among the estuaries of Taiwan based on examination of the otolith microstructure and then tests the hypothesis that the elvers in the estuaries of Taiwan are recruited from two different spawning grounds. The migratory history of the eel larvae as indicated from the otolith microstructure was also analysed.

II. MATERIALS AND METHODS

A total of 1108 *Anguilla japonica* elvers was collected from the estuaries of Su-Ao (SA), Shuang-Hsi (SH), Sha-Lung (SL), Li-Shui (LS) and Tung-Kang (TK) on the eastern and western coasts of Taiwan during the period from December 1989 to February 1990 (Fig. 1). Elvers collected were immediately fixed with 95% alcohol, and total length was measured to the nearest 0·1 mm 1 week post-fixation. The pigmentation stage of the elvers was determined according to the distribution of pigments on the body surface (Strubberg, 1913; Bertin, 1956). Twenty-five elvers at the early pigmentation stage from the samples of SA on 22 December 1989 and from SL, LS, TK on 22 and 23 January 1990 were used to examine their otolith microstructure. Because the fishing season in SA was closed earlier than in other places, the elvers from different sampling sites were not available on the same date.

The microstructure of the sagittal otolith of elvers sectioned in the frontal plane was examined by scanning electron microscopy (SEM) photographs (Hitachi S-520) at 2000 ×. Preparation of the otoliths for SEM were described previously (Tzeng, 1990). The otolith radius and increment width were measured along the maximum otolith radius. The daily age of elvers after hatching was estimated by the number of otolith growth increments with an additional 5-day yolk sac larval period (Tzeng, 1990).

The tests of difference of total length–frequency distribution of the elvers between month and estuaries were conducted both by two-way analysis of variance (ANOVA) and by Scheffe's multiple range analysis (Sokal & Rohlf, 1981). The test of difference of daily age of the elvers among estuaries was conducted using Kruskal–Wallis one-way ANOVA by rank (Siegel, 1956).

III. RESULTS

PIGMENTATION STAGE AND TOTAL LENGTH

The pigmentation stages of elvers collected from five estuaries during the period from December 1989 to February 1990 were dominated by stages VA and VB, with other advanced stages being relatively few (Table I). The elvers of stages VA and

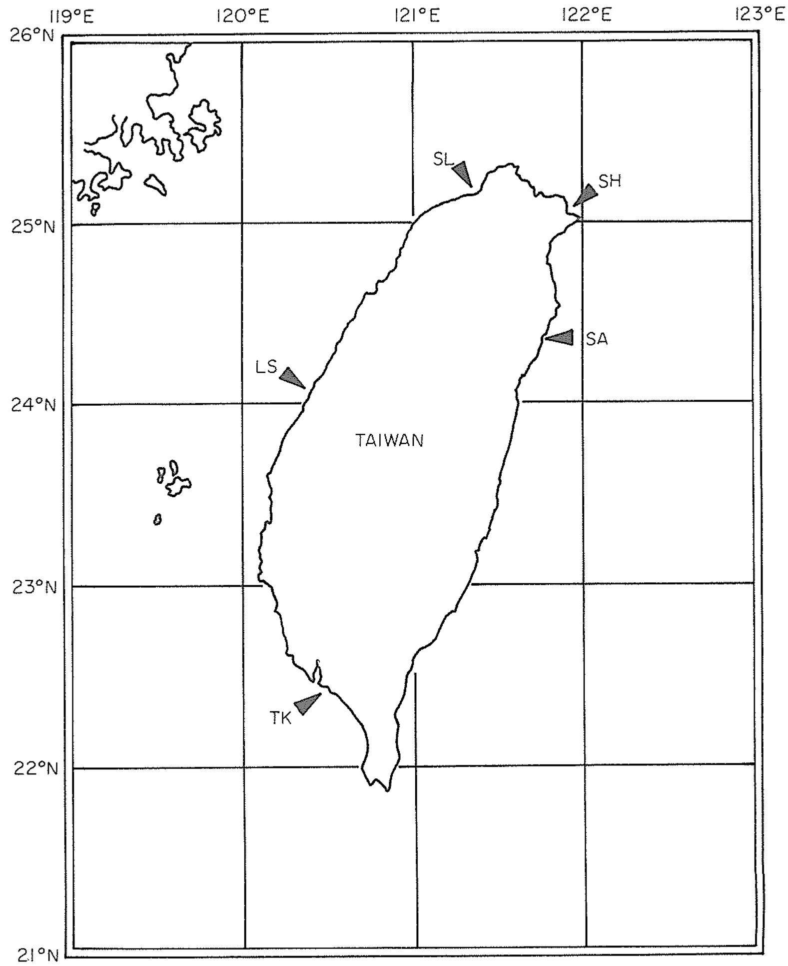

FIG. 1. Map showing sampling locations of *Anguilla japonica* elvers from five estuaries in the coast of Taiwan. LS, Li-Shui; SA, Su-Ao; SH, Shuang-Hsi; SL, Sha-Lung; TK, Tung-Kang.

VB were believed to be the new recruits in the estuary. The proportion of elvers with advanced pigmentation stages increased slightly in the later fishing season.

Individual total lengths of the elvers ranged from 49·0 to 64·5 mm, with means ranging from 53·88 to 57·20 mm, and an overall mean of 56·0 mm (Fig. 2). Two-way ANOVA indicated that the mean total length of elvers was significantly different between sampling periods and locations ($P<0{\cdot}001$). Scheffe's multiple range comparison indicated that mean total length of the elvers among different sampling locations in the early fishing season (December and January) were more homogeneous than those in the later fishing season (February) (Table II). The mean total length of the elvers from SL, LS and TK appeared to be smaller in the later fishing season (Fig. 2).

DIMENSION AND MICROSTRUCTURE OF OTOLITHS

Sagittae are the largest of the three pairs of elver otoliths. The maximum radius of the sagittal otoliths in the frontal section of 17 elvers ranged from 124·46 to

TABLE I. Pigmentation stages of *Anguilla japonica* elvers collected from five different estuaries in the coasts of Taiwan on 22 December 1989 and 22 and 23 January 1990. Sampling sites SA, SH, SL, LS and TK as Fig. 1, pigmentation stages after Strubberg (1913)

Sampling site	Date	Sample size	No. fish in pigmentation stage					
			Va	Vb	VIa1	VIa2	VIa3	VIa4
SA	Dec. 1989	98	98					
SH	Dec. 1989	40	40					
	Jan. 1990	88	65	16	6	1		
SL	Dec. 1989	93	93					
	Jan. 1990	99		79	16	4		
	Feb. 1990	99	72	18	2	3	3	1
LS	Dec. 1989	100	61	38	1			
	Jan. 1990	99	68	31				
	Feb. 1990	100	46	46	8			
TK	Dec. 1989	93	35	58				
	Jan. 1990	100	100					
	Feb. 1990	99	15	70	13	1		
Total		1108	693	356	46	9	3	1

181·82 μm with a mean of 143·15 ± 12·72 μm. The otolith is elliptical and the shape changes with growth. The growth of otoliths in the anterior–posterior direction is faster than in other directions. The growth increment is thus best discernible in an anterior–posterior direction (Fig. 3).

The primordium of the otolith was substantially composed of an organic material (probably fibroprotein otolin), and appeared deep after EDTA-etching [Figs 3, 4(a)]. The primordium measured from four well-sectioned otoliths was approximately 9·20 ± 2·02 μm and 7·60 ± 1·99 μm in diameter along their long and short axes, respectively. The core was constituted by well-calcified crystal substances arranged in radial form [Figs 4(a, b)]. The core was approximately 20·94 ± 1·99 and 17·31 ± 1·47 μm in diameter along the long and short axes, respectively. The daily growth increments began outside these structures (Figs 3, 4). A daily growth increment was a bipartite structure, composed of one carbonate-rich incremental zone (light band) and one organic-rich discontinuous zone (dark band), deposited on a daily schedule (Degens *et al.*, 1969; Tanaka *et al.*, 1981; Campana & Neilson, 1985). The number of daily growth increments was used to estimate the daily age of the elvers. A deeply-etched ring separated the first growth increment and the core [Fig. 4(b)]. This indicated that there was a distinctive transition of growth history of the otolith during this period. The width of the daily growth increments changed with time: they became wide, indicating fast-growing periods [FGI; Figs 4(b, d)]; narrow, indicating slow-growing periods [SGI; Figs 4(c, d)]; there was also a deeply-etched growth check during the slow-growing period [Fig. 4(c)]. Sometimes, no increments were discernible in the distal side of the otolith during a slow-growing period [Fig. 4(d)]. The daily growth increments widened distinctively again near the edges of the otolith both on the anterior–posterior and distal sides [Figs 3, 4(d)].

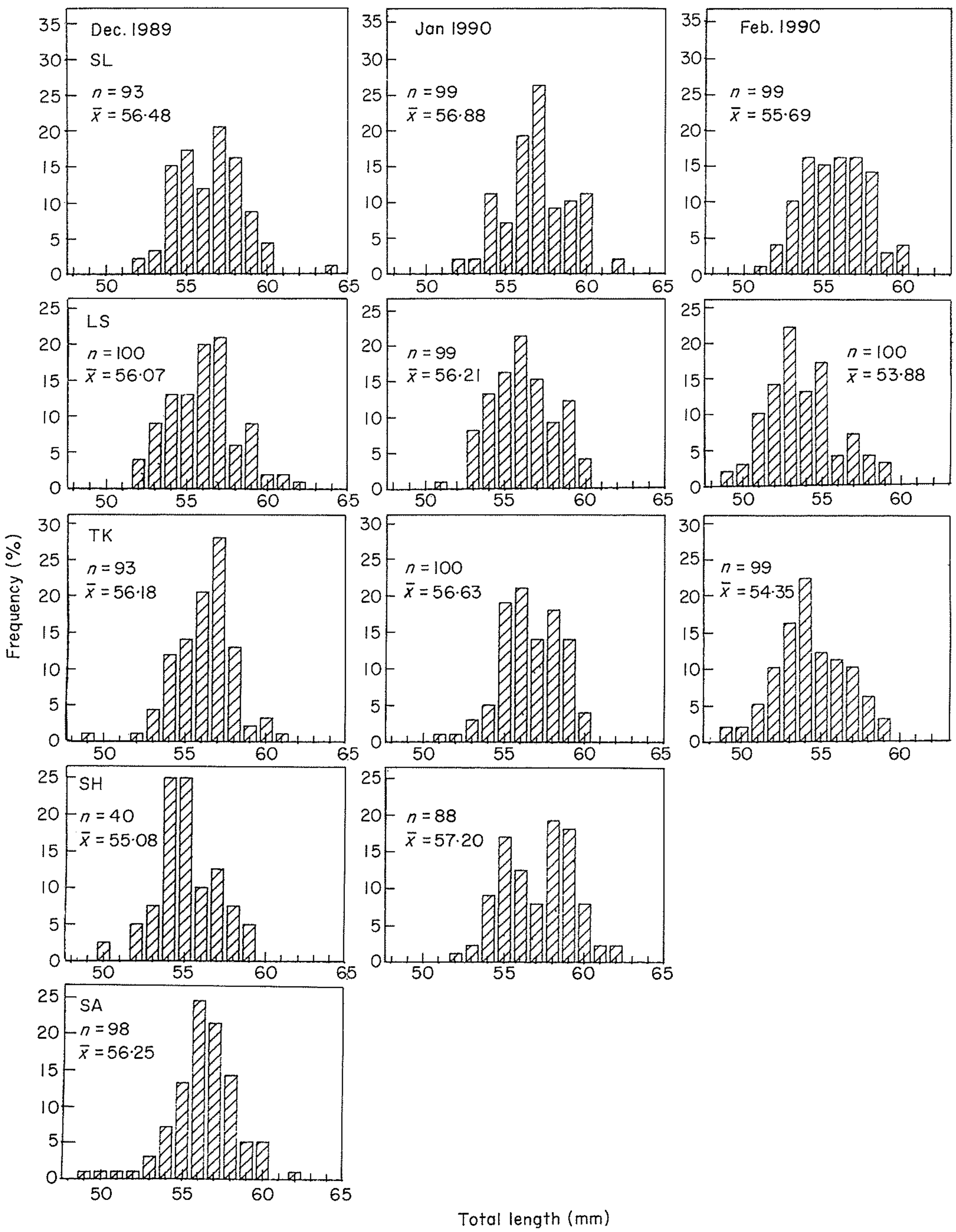

FIG. 2. Frequency distribution of total length of elvers collected from SL, LS, TK, SH and SA, December 1989–February 1990. The sampling sites and dates as in Table I.

GROWTH HISTORY AS INDICATED FROM OTOLITHS

The growth history of the elver may have influenced the change of the width of daily growth increments in otoliths. The first 60 daily growth increments were

TABLE II. Homogeneous test of mean total length, by Scheffe's multiple range analysis, of *Anguilla japonica* elvers collected from five different estuaries on 22 December 1989, and 22 and 23 January 1990. Sampling sites SA, SH, SL, LS and TK as in Fig. 1

Rank	Sampling site	Sampling date	Sample size	Mean total length (mm)	Homogeneous group
1	LS	Feb. 1990	100	53·88	*
2	TK	Feb. 1990	99	54·35	*
3	SH	Dec. 1989	40	55·08	*
4	SL	Feb. 1990	99	55·69	*
5	LS	Dec. 1989	100	56·07	**
6	TK	Dec. 1989	93	56·18	*
7	LS	Jan. 1990	99	56·21	*
8	SA	Dec. 1989	98	56·25	**
9	SL	Dec. 1989	93	56·48	***
10	TK	Jan. 1990	100	56·63	**
11	SL	Jan. 1990	99	56·88	**
12	SH	Jan. 1990	88	57·20	*

wider in a particular elver collected from Sha-Lung, north Taiwan on 22 January 1990 (Fig. 3). If otolith growth was proportional to body growth, this implied that the growth rate of the fish was higher during the first 2 months of the early life history, and then growth increments became narrow and thus the growth rate decreased gradually to a minimum at approximately 100 days old. In this slow-growing period, the growth of the otolith was interrupted, as indicated by a deeply etched growth check in Figs 3, 4(c). This growth check was observed frequently in the otoliths of elvers, and its formation period considered to correspond to the period of metamorphosis from leptocephalus to elver (Lecomte-Finiger & Yahyaoui, 1989). The increments then widened, implying that growth became extremely fast 2 months before arrival at the estuary (Fig. 3). In conclusion, the growth rate of the otolith was higher, 0·5–1·0 μm day^{-1} at the beginning of early life, lowest (usually $<0·5$ μm day^{-1}) at approximately 100 days old, and highest ($>1·0$ μm day^{-1}) 1 month before arrival at the estuary. However, it is emphasized that this relationship between otolith growth and body growth has not yet been validated, and that in two other species otolith growth and body growth had been shown to be uncoupled (Mosegaard *et al.*, 1988; Wright *et al.*, 1990).

DAILY AGE AND BIRTH DATE

The mean daily ages of elvers collected from estuaries SA, SL, LS and TK on 22 December 1989 and 22 and 23 January 1990 were estimated to be $169·3 \pm 14·9$, $175·6 \pm 27·8$, $165·6 \pm 22·6$ and $171·7 \pm 26·2$ days, respectively (Table III). Kruskal–Wallis analysis indicated that these mean daily ages were not significantly different among estuaries ($P > 0·5$).

The birth date of the elvers back-calculated from the daily ages was from mid-June to late July for those collected from SA on 22 December 1989, from late June to early September for those from SL and LS collected on 22 January 1990 and from early July to late September for those collected from TK on 23 January

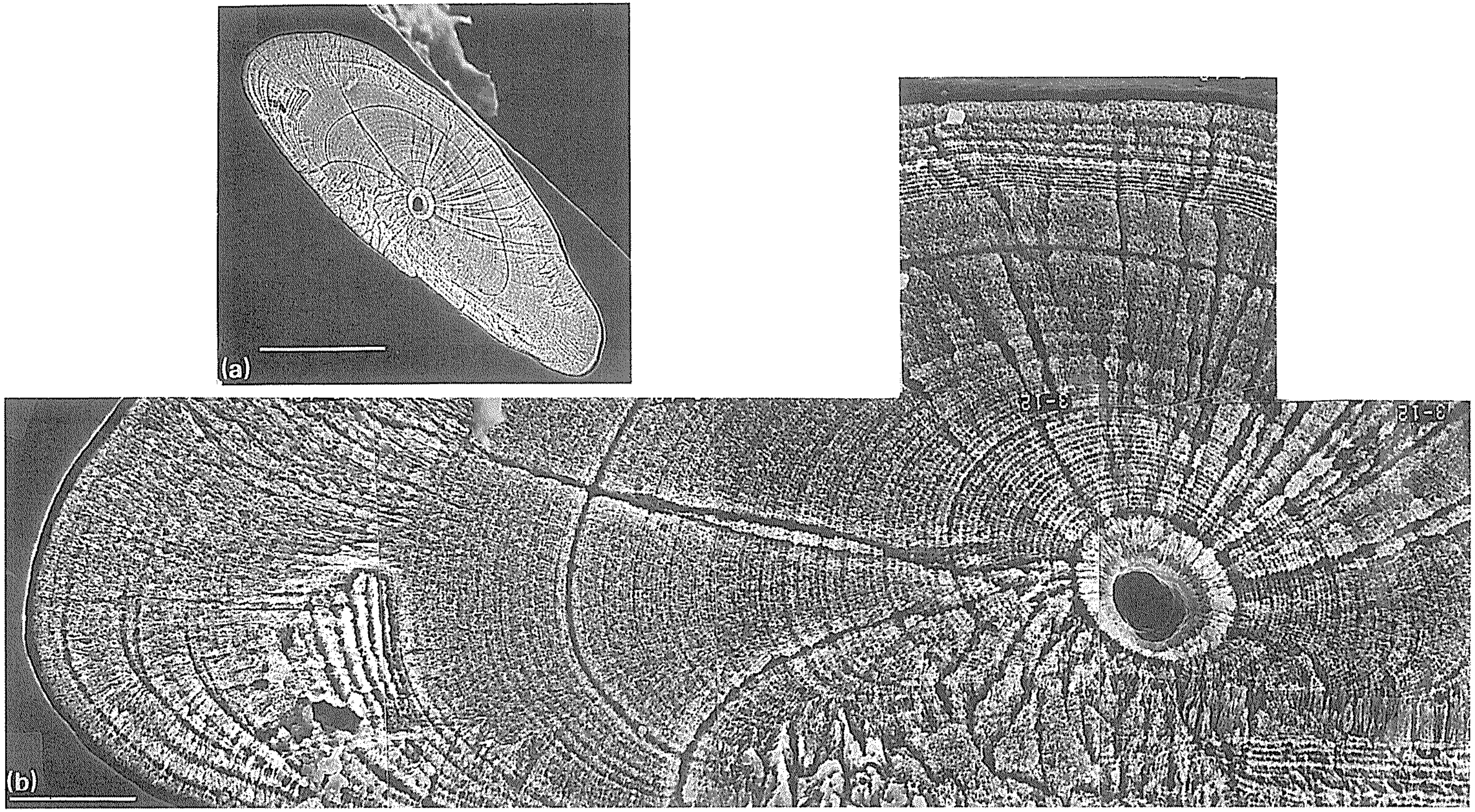

FIG. 3. Scanning electron micrographs illustrating microstructural growth pattern of sagittal otolith of a 54·31 mm T.L. elver collected from Sha-Lung estuary, north Taiwan on 22 January 1990 (a). Daily growth increments in the distal and posterior sides of the otolith were enlarged (b). Scale bar = 75 μm (a), 15 μm (b).

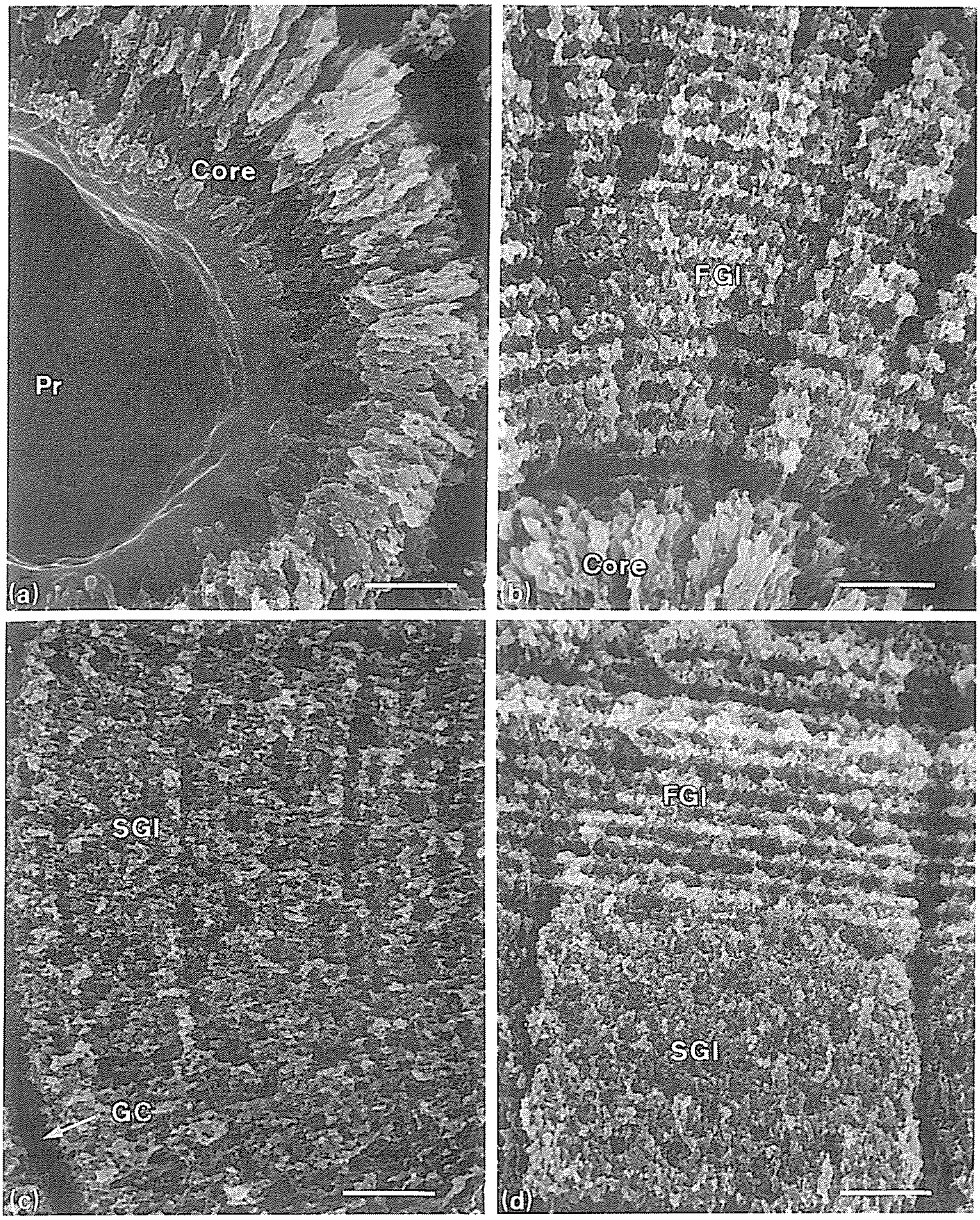

FIG. 4. Scanning electron micrographs illustrating microstructure of the daily growth increments in sagittal otoliths enlarged from Fig. 3. (a) Showing primordium (Pr) and core. (b) Fast-growing daily growth increments (FGI) adjacent to the core in the distal side of the otolith. (c) Slow-growing daily growth increments (SGI) and a growth check (GC) in the posterior side of the otolith. (d) Daily growth increments in the distal side of the otolith deposited from slow- to fast-growing. Scale bar = 2·0 μm.

1990. The birth dates of the elvers among the estuaries were similar, ranging from mid-June to late September.

The time required for migration from the spawning ground to the coasts of Taiwan was similar among estuaries irrespective of sampling site (Table III). This

TABLE III. Daily age and birth date of elvers collected from four different estuaries (SA, SL, LS and TK) in the eastern and western coasts of Taiwan on 22 December 1989 and 22 and 23 January 1990

Sampling site	Date	Sample size	Total length (mm)	Otolith radius (μm)	Age (days)	Birth date
SA	22 Dec. 1989	9	56·39 ± 1·39	141·25 ± 8·85	169·3 ± 14·9	18 Jun.–24 Jul.
SL	22 Jan. 1990	5	56·66 ± 2·84	129·44 ± 10·21	175·6 ± 27·8	26 Jun.–9 Sep.
LS	22 Jan. 1990	5	56·20 ± 2·21	165·85 ± 22·77	165·6 ± 22·6	10 Jul.–3 Sep.
TK	23 Jan. 1990	6	56·80 ± 2·15	130·43 ± 14·00	171·7 ± 26·2	7 Jul.–22 Sep.

implies that the elvers from the estuaries of Taiwan may originate from the same spawning ground.

IV. DISCUSSION AND CONCLUSIONS

The mean total lengths of elvers were almost homogeneous among estuaries for those collected in the early fishing season (December and January), but mean lengths decreased in the late fishing season (February). The seasonal decrease in total length of elvers probably led to the significant difference in mean length among estuaries (Fig. 2 and Table II). The seasonal decrease in length of elvers during upstream migration is a very common feature in anguillid species; two mechanisms have been suggested: (1) length decreased as pigmentation progressed in response to rising temperature, and (2) the elvers arriving later were shorter (Strubberg, 1913; Boëtius, 1976; Tzeng, 1985; Haro & Krueger, 1988). It has also been reported that the mean total length of the American eel, *Anguilla rostrata* (LeSueur), elvers increased with increasing distance from the spawning area (Haro & Krueger, 1988), however, this tendency was not obvious in the elvers from the coasts of Taiwan (Fig. 2). This is probably because of the difference in latitude from south to north of Taiwan is not large.

The primordium, core and daily growth increments were visible on the sagittal otoliths of elvers. The diameters of the primordium and core were $9{\cdot}20 \pm 2{\cdot}02$ µm and $20{\cdot}94 \pm 1{\cdot}99$ µm on the long axis, which are close to the diameters of otoliths of reared larvae at hatching (8·3 µm) and at 6 days old ($24{\cdot}0 \pm 1{\cdot}48$ µm) (Umezawa *et al.*, 1989). In addition, the reared larvae completed yolk sac absorption at 5 days old (Umezawa *et al.*, 1989). This fact indicated that the primordium, core and daily growth increments were probably deposited during embryonic, yolk sac periods and after feeding, respectively.

The age of the elvers in the present study was estimated to be $170{\cdot}4 \pm 20{\cdot}6$ days, which was higher than those of previous studies in this area, $112{\cdot}9 \pm 9{\cdot}4$–$156{\cdot}5 \pm 13{\cdot}5$ days (Tabeta *et al.*, 1987; Umezawa & Tsukamoto, 1990; Tzeng, 1990). The age of elvers arriving at the estuaries was reported to be inversely related to mean growth rate in the larval stage, and became greater among those arriving later (Tzeng, 1990). The age of elvers from Taiwan was about 1–2 months younger than those from Japan (averaged 218 ± 29 days) (Tsukamoto, 1990), even though the estimated birth date of the elvers was similar between Taiwan and Japan. Also the timing of the peak catch of elvers arriving at the estuary was approximately 1–2 months earlier in Taiwan than Japan (Tzeng, 1983*a*, 1985; Tsukamoto, 1990), which corresponded to the difference in age of elvers arriving at estuaries in the two countries. This indicates that the elvers from both countries are probably recruited from the same spawning ground, and that the elvers arrive first at the estuaries of Taiwan because the eel larvae are transported northward by the current.

The spawning ground of Japanese eels was first proposed by Matsui (1957) to be in the waters south of Okinawa and east of Taiwan. However, recent studies indicate that the spawning ground is more likely located to the east of the Philippines, i.e. in the waters between the westward North Equatorial Current at about 10° N and the eastward Subtropical Countercurrent at about 20° N (Ozawa *et al.*, 1989; Tsukamoto, 1990). The elvers were more abundant on the northern and western coasts than on the eastern coast of Taiwan, and thus a local spawning ground in the waters southwest of Taiwan was suggested to explain this distribution (Kuo, 1971; Chen, 1975). The elvers from the eastern coast of Taiwan were proposed to be recruited from Matsui's (1957) presumed spawning ground, and those from the western coast from a local spawning ground in the waters southwest of Taiwan. If this were true, the elvers from the eastern coast of Taiwan (e.g. SA) should be at least 72 days older than those from the west (e.g. LS and TK) (Table III) because the leptocephali which migrate from the spawning ground in the east of the Philippines to the adjacent waters of Taiwan would require 72 days (Tsukamoto *et al.*, 1989). However, the age of the elvers was not significantly different between the eastern and western coasts of Taiwan (Table III). Therefore, the assumption that the elvers on the eastern and western coasts of Taiwan were recruited respectively from two different spawning grounds seemed not to be true. The local spawning ground of Japanese eels in the waters southwest of Taiwan, proposed by Kuo (1971) and Chen (1975), seems not to exist.

The otolith is an information storage structure, in which the daily growth increment is not only used for dating, but also for recording some aspects of the growth history of the fish. The changing pattern of the daily growth increment in the otolith of elvers, has led to speculation about the migratory history of the elvers (Tabeta *et al.*, 1987). A theoretical growth model of the elvers of the European eel has also been proposed, based on the microstructure of their otoliths (Lecomte-Finiger & Yahyaoui, 1989). The elver shown in Fig. 3 was estimated to be 205 days old and its growth history was speculated from the otolith microstructure as follows: the larva first drifted with the North Equatorial and Kuroshio current away from the spawning ground. During this period, it is a willow-leaf-shaped leptocephalus which is an energy-saving body shape and most suitable for drifting migration. At approximately 100 days old the leptocephalus left the strong Kuroshio current, at this time the growth of its otoliths slowed down and even recorded a growth check [Figs 3, 4(c)]. Although we have not tested or validated this, the check seems to be a mark of metamorphosis (Lecomte-Finiger & Yahyaouri, 1989). Eel larvae may take approximately 1 month to metamorphose from leptocephalus to elver (Tabeta *et al.*, 1987; Tsukamoto, 1990), and this larva seems to have had to expend a great deal of energy for morphological change and to leave the strong Kuroshio current, so that the growth of its otolith almost stopped. After the elvers entered the coastal waters, the growth rate of the otoliths increased and the elvers seemed to live in the coastal waters for at least 1–2 months as indicated from the counts of daily growth increments after metamorphosing. The elvers then moved into the inland water to make their upstream migration. In the estuaries of Taiwan, the numbers of elvers migrating upstream reach a peak in the spring tide when monthly water temperature is at its lowest (Tzeng, 1985). The fish experience two widely differing environments: before metamorphosing they drifted with the warm oceanic currents (mainly the North Equatorial Current and Kuroshio) and after metamorphosing they migrate with cold coastal water. The dramatic changes in the migratory history of the eel larva seemed to be faithfully written down on the otolith of the fish.

This study was conducted with the financial support of the National Science Council, Republic of China (project Nos. NSC 79-0211-B002-09 and NSC 80-0209-B002-04). The authors are grateful to Mr W. C. Chen for specimen collection, Misses C. I. Lin and S. H.

Jen for assistance in taking SEM photographs and to Dr J. E. Thorpe and an anonymous reviewer for helpful comments.

References

Bertin, L. (1956). *Eels—A Biological Study*. London: Cleaver-Hume Press.

Boëtius, J. (1976). Elvers, *Anguilla anguilla* and *Anguilla rostrata* from two Danish localities. I. Size, body weight, developmental stage and number of vertebrae related to time of ascent. *Meddelelser fra Danmarks Fiskeri-og Havundersøgelser* **7,** 199–220.

Campana, S. E. & Neilson, J. D. (1985). Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Science* **42,** 1014–1032.

Chen, T. S. (1975). Preliminary study of the elver of *Anguilla japonica* in Taiwan. *China Fisheries Monthly* **268,** 11–19.

Degens, E. T., Deuser, W. G. & Haedrich, R. L. (1969). Molecular structure and composition of fish otoliths. *Marine Biology* **2,** 105–113.

Haro, A. J. & Krueger, W. H. (1988). Pigmentation, size, and migration of elvers (*Anguilla rostrata* (LeSueur)) in a coastal Rhode Island stream. *Canadian Journal of Zoology* **66,** 2528–2533.

Kajihara, T. (1988). Distribution of *Anguilla japonica* leptocephali in western Pacific during September 1986. *Bulletin of the Japanese Society of Scientific Fisheries* **54,** 929–933.

Kuo, H. (1971). Approach of eel elvers to the land in Taiwan. *Aquaculture (Yoshoku)* **1,** 52–56.

Lecomte-Finiger, R. & Yahyaoui, A. (1989). Otolith microstructure analysis in the study of the early life history of the European eel *Anguilla anguilla*. *Compte rendu Académie des Sciences, Paris* **308,** Serie III, 1–7.

Lee, T. W. & Lee, K. S. (1989). Daily growth increments and lunar pattern in otolith of the eel, *Anguilla japonica*, in the freshwater. *Bulletin of the Korean Fisheries Society* **22,** 36–40.

Matsui, I. (1957). On the records of a leptocephalus and catadromous eels of *Anguilla japonica* in the waters around Japan with a presumption of their spawning places. *Journal of Shimonoseki College of Fisheries* **7,** 151–167.

Mosegaard, H., Svedäng, H. & Taberman, K. (1988). Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. *Canadian Journal of Fisheries and Aquatic Sciences* **45,** 1514–1524.

Neilson, J. D., Geen, G. H. & Bottom, D. (1985). Estuarine growth of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) as inferred from otolith microstructure. *Canadian Journal of Fisheries and Aquatic Sciences* **42,** 899–908.

Ozawa, T., Tabeta, O. & Mochioka, N. (1989). Anguillid leptocephali from the western north Pacific east of Luzon in 1988. *Bulletin of the Japanese Society of Scientific Fisheries* **55,** 627–632.

Pannella, G. (1971). Fish otoliths: daily growth layers and periodical patterns. *Science* **173,** 1124–1127.

Siegel, S. (1956). *Nonparametric Statistics*. New York: McGraw-Hill.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*, 2nd edn. San Francisco: W. H. Freeman.

Strubberg, A. C. (1913). The metamorphosis of elvers as influenced by outward conditions. *Meddelelser fra Kommissionen for Havundersøgelser Series Fiskeri* **4,** 1–11.

Tabeta, O., Tanaka, K., Yamada, J. & Tzeng, W. N. (1987). Aspects of the early life history of the Japanese eel *Anguilla japonica* determined from otolith microstructure. *Bulletin of the Japanese Society of Scientific Fisheries* **53,** 1727–1734.

Tanaka, K., Mugiya, Y. & Yamada, J. (1981). Effects of photoperiod and feeding on daily growth patterns in otoliths of juvenile *Tilapia nilotica*. *Fishery Bulletin U.S.* **79,** 459–466.

Tanaka, S. (1975). Collection of leptocephali of the Japanese eel in waters south of the Okinawa Islands. *Bulletin of the Japanese Society of Scientific Fisheries* **41,** 129–136.

Tsukamoto, K. (1989). Otolith daily growth increments in the Japanese eel. *Bulletin of the Japanese Society of Scientific Fisheries* **55**, 1017–1021.

Tsukamoto, K., Umezawa, A., Tabeta, O., Mochioka, N. & Kajihara, T. (1989). Age and birth date of *Anguilla japonica* leptocephali collected in western north Pacific in September 1986. *Bulletin of the Japanese Society of Scientific Fisheries* **55**, 1023–1028.

Tsukamoto, K. (1990). Recruitment mechanism of the eel, *Anguilla japonica*, to the Japanese coast. *Journal of Fish Biology* **36**, 659–671.

Tzeng, W. N. (1983a). Seasonal and long-term changes of the catch of Anguillid elvers in Taiwan. *Journal of Fisheries Society of Taiwan* **10**, 1–7.

Tzeng, W. N. (1983b). Species identification and commercial catch of the Anguillid elvers from Taiwan. *China Fisheries Monthly* **366**, 16–23.

Tzeng, W. N. (1985). Immigration timing and activity rhythms of the eel, *Anguilla japonica*, elvers in the estuary of northern Taiwan with emphasis of environmental influences. *Bulletin of the Japanese Society of Fisheries Oceanography* **47/48**, 11–28.

Tzeng, W. N. (1990). Relationship between growth rate and age at recruitment of *Anguilla japonica* elvers in a Taiwan estuary as inferred from otolith growth increments. *Marine Biology* **107**, 75–81.

Umezawa, A., Tsukamoto, K., Tabeta, O. & Yamakawa, H. (1989). Daily growth increments in the larval otolith of the Japanese eel, *Anguilla japonica*. *Japanese Journal of Ichthyology* **35**, 440–444.

Umezawa, A. & Tsukamoto, K. (1990). Age and birth date of the glass eel, *Anguilla japonica*, collected in Taiwan. *Bulletin of the Japanese Society of Scientific Fisheries* **56**, 1199–1202.

Wright, P. J., Metcalfe, N. B. & Thorpe, J. E. (1990). Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L: evidence against coupling. *Journal of Fish Biology* **36**, 241–249.