

Early life history and oceanic migration of the eel, *Anguilla japonica**

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Abstract: The first attempt to outline the whole aspects of early life history and migration mechanisms of the eel *Anguilla japonica* was made by synthesizing the recent information on the otolith microstructure of 1045 fish and the offshore collection data of 110 leptocephali and 9 glass eels. Waters east of Philippine, 10°-20°N, 140°-150°E, were one of the most possible spawning areas of *A. japonica*. Age determinations of leptocephali and glass eels showed that *A. japonica* spawned in April-November with a peak in August. Larvae grew linearly at 0.56mm/d until 45mm in TL and 74d in mean age. Analysis of otolith increment width showed that metamorphosis occurred at 85 d and 61.3mm corresponding to a zone of wider increments (2-4 µm) in the sagitta. Metamorphosis lasted for 12 days with body shrinkage at -0.22mm/d. A negative linear relationship between age at metamorphosis and otolith growth rate suggested that leptocephali with a larger growth rate began to metamorphose at a younger age. Leptocephali were slowly transported northwestward in complicated eddies from spawning area to the origin of the Kuroshio Current for 2-3 months. Larvae were entrained by the strong Kuroshio Current and transported northward for 2-27 days to exit from it after completion of metamorphosis. Fish metamorphosing at a younger age were transported a shorter distance and exit from it at lower latitude. More glass eels recruited at a full and new moon than at other lunar phases. Age at metamorphosis was positively correlated with age at recruitment. Age at recruitment to the estuary or the time required for oceanic migration was 4-7 months and gradually increased with the sampling date or the recruitment timing, whereas body size of the glass eel was roughly constant, about 55-60mm TL. Birth date and recruitment timing positively correlated. Thus, the earlier-born fish or fish with the larger growth rate metamorphosed and recruited earlier at lower latitude, at a younger age and with more advanced pigmentation, but with a constant body size.

1. Introduction

Migration study is one of prerequisites to determine the recruitment mechanism of a fish. In spite of its commercial importance in Eastern Asia, the recruitment mechanism of a catadromous eel, *Anguilla japonica* Temminck et Schlegel, is poorly known, since knowledge of the early life history and larval migration of this species is still lacking, e.g. its spawning place and season, larval growth and metamorphosis, larval transportation and inshore migration.

The objective of this study is to outline the whole aspects of early life history and migration mechanisms of *A. japonica* from

its spawning ground offshore to coastal waters by synthesizing the recent information based mainly on the otolith microstructure and the offshore collection data of larvae.

2. Materials and Methods

For 9 years from 1982 to 1990, a total of 1012 glass eels*** and elvers*** were collected at 13 stations in Taiwan, Korea and Japan (TSUKAMOTO, 1990; UMEZAWA, 1991). Thirty three leptocephali*** obtained in eastern waters off the Philippines and Taiwan in 1986 and 1990 were also analyzed (KAJIHARA,

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*** "Leptocephalus" means larva before and during metamorphosis, while "glass eel" is a juvenile after metamorphosis without pigmentation except the spots at skull, rostral and caudal regions (stage IV-V after BERTIN, 1956). "Elver" has more developed pigmentation (stage VI).

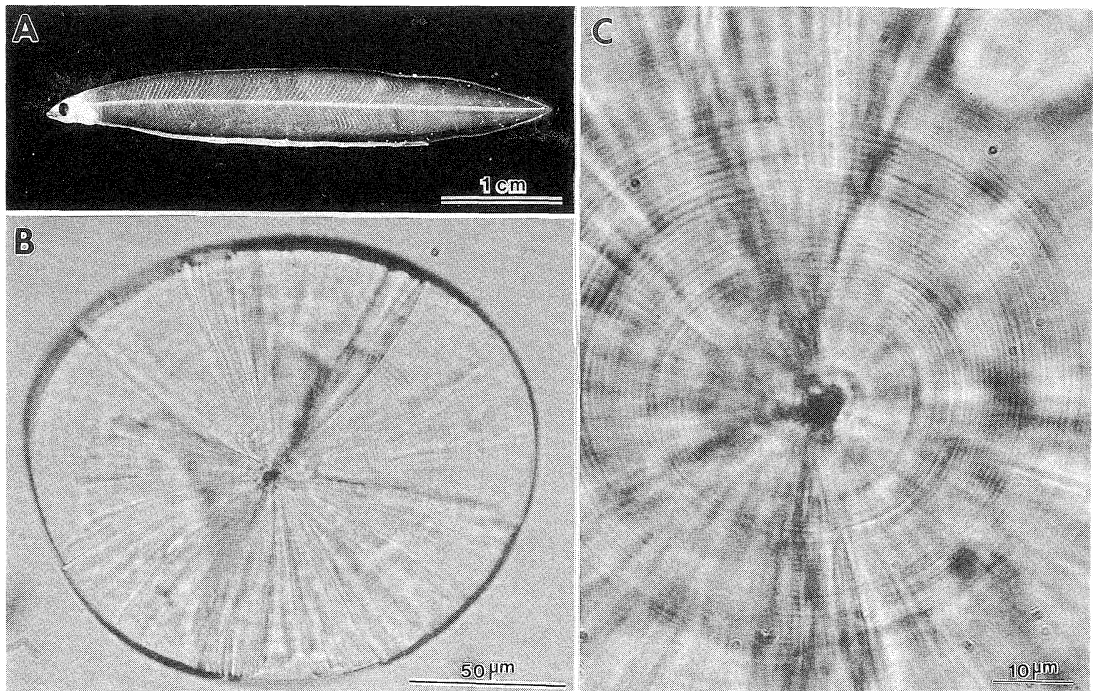


Fig. 1. A: *Anguilla japonica* leptocephalus of 41.0 mm in TL (Specimen No. 10) collected at 18°59.1'N, 129°13.5'E, 23 September 1986. B: Sagitta of *A. japonica* leptocephalus of 45.9 mm in TL, 78 d old (Specimen No. 17). C: Central region of sagitta of *A. japonica* leptocephalus. Otolith daily increments are shown around the core of 5–10 μ m diameter (dark region in the center).

1988; OZAWA *et al.*, 1991, TSUKAMOTO *et al.*, 1992).

Sagittal otoliths were extracted and mounted distal side up on a glass microscope slide with a drop of epoxy resin. They were ground with emery paper #1200–#12000 to just before the sagittal plane with the otolith core, and etched in 1 % HCl solution for 1–3s. A bipartite structure of a narrow opaque band (discontinuous zone) and adjacent wider translucent band (incremental zone) was regarded as one otolith increment or ring (Fig. 1). Increments were traced at $\times 900$ –1500 under a light microscope with a camera lucida (TSUKAMOTO, 1989). Fish were aged by counting daily increments outside the hatch ring of 8.3 μ m diameter (UMEZAWA *et al.*, 1989). The birth date of each specimen was backcalculated from the estimated age and the date of sampling. Changes in increment width from the otolith core to the edge

were also examined based on the increment trace of some 300 glass eels and elvers and of 33 leptocephali by measuring the radius of each increment along the 'longest radius' of an otolith (UMEZAWA, 1991, see Fig. 1).

3. Results and Discussion

Breeding place

Spawning areas of the Atlantic eel were outlined in the early part of this century by SCHMIT (1922, 1925), whereas that of the Japanese eel in the Pacific Ocean has not yet been determined. Relatively little is known of *A. japonica* leptocephali compared to Atlantic eels; *i. e.* the number of *A. japonica* leptocephali collected is only 110 individuals (MATSUI *et al.*, 1968; TABETA and TAKAI, 1975a, b; TANAKA, 1975; TAKAI and TABETA, 1976; TABETA and KONISHI, 1986; KAJIHARA, 1988; OZAWA *et al.*, 1989; OZAWA *et al.*, 1991; TSUKAMOTO *et al.*, 1992) and its smallest recorded

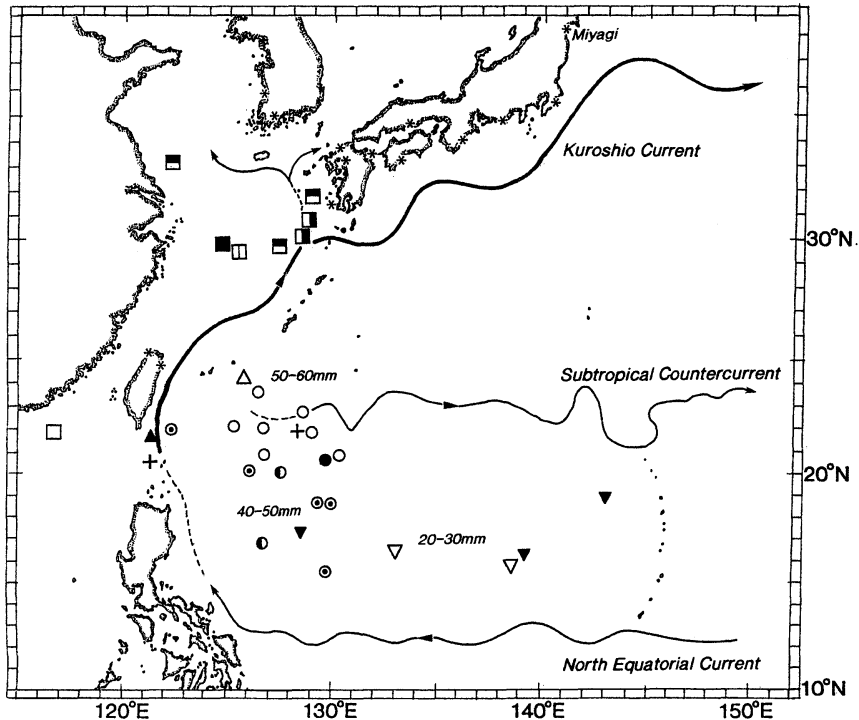


Fig. 2. Larval migration and recruitment of *A. japonica* to coastal waters. Squares indicate offshore collections of glass eels (solid square, SHOJIMA, 1966; square with vertical bar, SHOJIMA, 1967; solid half upside, TSUKAHARA, 1971 cited in TABETA, 1981; open square, TABETA and TAKAI, 1973; solid half rightside, SHOJIMA, 1990). Crosses are metamorphosing larvae (TABETA and TAKAI, 1975a; TANAKA, 1975 cited in TABETA and TAKAI, 1975b). Other symbols indicate leptocephali (solid triangle, MATSUI *et al.*, 1968; open circle, TANAKA, 1975; semi solid circle, TAKAI and TABETA, 1976; open triangle, TABETA and KONISHI, 1986; double circle, KAJIHARA, 1988; inverted triangle, OZAWA *et al.*, 1989; inverted solid triangle, OZAWA *et al.*, 1991; solid circle, TSUKAMOTO *et al.*, 1991). Numerals indicate TL, Asterisks show the sampling locations of glass eels recruited to the coastal waters.

size at capture was 19.5 mm TL (OZAWA *et al.*, 1991), while more than twenty thousand Atlantic eels have been obtained (BÖETIUS and HARDING, 1985; KLECKNER and McCLEAVE, 1985) and its minimum size was as small as 3.9 mm TL, corresponding to 4 days after hatching (WIPPELHAUSER *et al.*, 1985).

Developing leptocephali of *A. japonica* of about 50–60mm in TL were collected in eastern waters of Taiwan, 20°14'–23°40' N, 125°01'–130°00' E in November–December (TANAKA, 1975; Fig. 2). In the more southern waters, east of Luzon, 15°56'–22°02' N, 122°25'–129°37' E, smaller larvae of

ca. 30–50mm with an age of 67–78 days after hatching were collected in September (KAJIHARA, 1988; TSUKAMOTO *et al.*, 1989). Based on these results and the water flow in this area, the breeding of *A. japonica* was predicted to occur in June or July farther east than has been surveyed to date (KAJIHARA, 1988; TSUKAMOTO *et al.*, 1989). In fact, smaller larvae of ca. 20–30mm were collected in a more eastern area, 15°46'–16°22' N, 132°59'–138°43' E in June–July (OZAWA *et al.*, 1989). More recently, 21 small leptocephali of ca. 20mm were obtained in only one haul at 16°17' N, 139°12' E (OZAWA

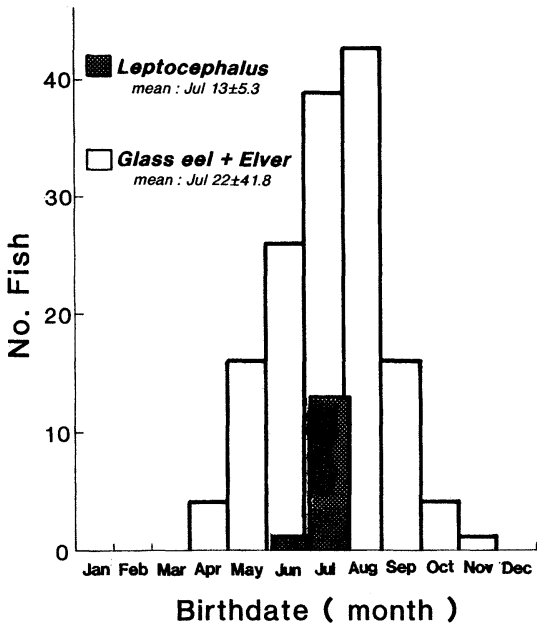


Fig. 3 Birth dates of the glass eels and elvers collected at the estuaries of the Japanese coast (TSUKAMOTO, 1990). Heavily shaded area shows the birth date distribution of leptocephali collected in the Western North Pacific (TSUKAMOTO *et al.*, 1989).

et al., 1991: Fig. 2). A wider area, especially to the east (10° – 20° N, 140° – 150° E) should be investigated in May–July to determine the spawning area of *A. japonica*.

Spawning season

The age of the glass eel upon arrival at the Japanese coast was roughly constant, 218 ± 29 d (mean \pm SD) for 149 individuals (TSUKAMOTO, 1990). Glass eels arrived at Taiwan at an age of 100–140 d (40 fish; UMEZAWA and TSUKAMOTO, 1990) and 95–175 d (61 fish; TZENG, 1990). The birth date estimated for each individual ranged from April to November and the mean was 22 July (Fig. 3; TSUKAMOTO, 1990). Later examination of 1012 glass eels including samples from Taiwan, Japan and Korea showed that the age at recruitment (age upon arrival at the coast) was 117 ± 12.7 d (about 4 months) and the birth date ranged from June to November with the peak in August (UMEZAWA, 1991). Although the estimated ages at

recruitment were different among investigators, the peak of the hatch date (August) coincided with one another (Fig. 3). Age determination of *A. japonica* leptocephali collected in the Western North Pacific in September 1986 showed that their birth dates ranged from 28 June to 18 July 1986 with a peak in mid July (TSUKAMOTO *et al.*, 1989). The estimated birth date was consistent with that of the glass eel (Fig. 3). The birth date can be regarded about the same as the spawning time since the duration of the egg stage of this species was less than 2 days (YAMAMOTO *et al.*, 1974; SATO, 1979). Therefore, it can be summarized from these results that *A. japonica* spawns in summer and the offspring takes ca. 4–7 months to migrate from the spawning area to the estuaries of East Asia. This is in striking contrast to the common belief *Anguilla japonica* spawns in winter and that the larvae take 1 year to recruit to the Japanese coast (MATSUI, 1952; TABETA, 1981).

The long estimated duration of the spawning season (*e.g.* April–November; 7 months in TSUKAMOTO, 1990) should not be caused by the counting error in age determination since the latter did not exceed 10 % (about 20 days at most for glass eel). Multiple subpopulations of adult eel might prolong the duration of estimated spawning season.

The reported peak spawning of Atlantic eels was February and April for *A. rostrata* and *A. anguilla*, respectively (HARDEN JONES, 1968; BÖETIUS and HARDING, 1985; WIPPELHAUSER *et al.*, 1985), which is earlier than that of *A. japonica* estimated here. Assuming that otolith increments were formed daily, the birth dates of the leptocephali collected in the southwestern Sargasso Sea in August 1984 were estimated to be May–June 1984 for both *A. rostrata* (mean TL, 34mm) and *A. anguilla* (32mm) larvae (CASTONGUAY, 1987). *A. rostrata* (mean TL, 36.8mm) and *A. anguilla* (53.6mm) collected in the Atlantic Ocean and the Mediterranean Sea in December 1989 and January 1990 hatched in September–October 1989 (TSUKAMOTO *et al.*, 1991). Further age determinations, coupled with experimental validation of the frequency of otolith increment formation, will be needed to explain this

disparity.

Silver eels of both *A. japonica* and *A. anguilla* begin their downstream migration in autumn. Based on their estimated spawning dates, the migration of silver eels from freshwater to the breeding place takes ca. 10 months for *A. japonica*, whereas *A. anguilla* requires only ca. 6 months to the Sargasso Sea, if it is assumed that the peak spawning is in April.

Growth

Age and body length of artificially hatched preleptocephali (2–6mm, 0–6d) and field collected developing leptocephali (ca. 20–50 mm, 25–78d) were linearly related, suggesting that early growth of eel larvae was linear with a growth rate of 0.56mm/d (Fig. 4, TSUKAMOTO *et al.*, 1989; UMEZAWA and TSUKAMOTO, 1992a). After metamorphosis, the body lengths of glass eels and elvers became relatively constant, ca. 60mm (UMEZAWA and TSUKAMOTO, 1992a). When examined in detail however, glass eels shrank 0.22mm/d (UMEZAWA and TSUKAMOTO, 1992b; see below) and body lengths of elvers increased 0.09mm/d till ca. 150 d (UMEZAWA and TSUKAMOTO, 1992a).

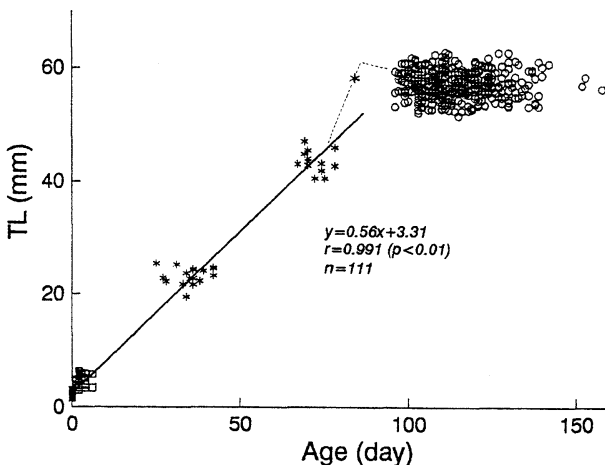


Fig. 4 Early growth of *A. japonica*. Asterisks indicate leptocephali collected offshore, and circles, glass eels and elvers at recruitment. Squares are preleptocephali artificially hatched. Solid line was fitted to data of preleptocephali and leptocephali. Dashed lines were drawn by hand between leptocephalus and glass eel stages.

The growth rate of glass eels recruited to Taiwan was estimated with otolith increments as being 0.35–0.60mm/d (TZENG, 1990), a value which would have included the shrinkage period during metamorphosis.

The growth rate of Atlantic eel leptocephali (both of *A. rostrata* and *A. anguilla*) was estimated via otolith microstructure as being 0.38mm/d (CASTONGUAY, 1987), a value which is smaller than that of *A. japonica*. However, a more recent otolith examination showed that growth rates of *A. rostrata* (0.46 mm/d) and *A. anguilla* (0.62mm/d) were similar to that of *A. japonica* (TSUKAMOTO *et al.*, 1991a). BÖETIUS and HARDING (1985) concluded that there was no differential growth rate in 0-group leptocephali of *A. rostrata* and *A. anguilla*. However, estimates of growth rates based on regressions of TL on date of capture are indirect and have tendency to underestimate (CASTONGUAY, 1987). In fact, the larval growth of the Atlantic eels previously reported (0.17–0.24mm/d; BOETIUS and HARDING, 1985; KLECKNER and McCLEAVE, 1985; WIPPELHAUSER *et al.*, 1985) was much lower than that estimated from otolith examination (0.38–0.62mm/d: CASTONGUAY, 1987; TSUKAMOTO *et al.*, 1989; TSUKAMOTO *et al.*, 1991; UMEZAWA and TSUKAMOTO, 1992a;). Future research should include intensive age determination of a wide range of lengths of specimens collected from various area in the north Atlantic and the Mediterranean Sea at different times of the year.

Metamorphosis

The change in otolith increment width from the center to the edge showed a similar pattern in both *A. japonica* glass eels and elvers examined (TABETA *et al.*, 1987; UMEZAWA and TSUKAMOTO, 1992b): the width was roughly constant, ca. 1 μ m, from 0 d until 74 d increasing rapidly to a peak of ca. 4 μ m at 85 d, and then decreasing to be constant again from 97 d until the otolith edge (Fig. 5). Every glass eel and elver examined, even the youngest glass eel (95d, 58.8 mm), had such a "Wide Increment Zone (WIZ)", whereas there was no such WIZ in every leptocephalus at developing

stage. This suggests that the WIZ is formed during metamorphosis from the leptocephalus to the glass eel (Fig. 5). The largest leptocephalus examined (58.2mm, 84d) had several wide increments at the peripheral part of the otolith, suggesting that this specimen was just starting to form a part of the WIZ. In Fig. 4, this fish had a positive residual on the growth regression line for leptocephali, which suggests that leptocephali might grow rapidly at the end of the developing stage until the beginning of metamorphosis, although this assumption was based on only 1 specimen. Otolith radius ($Y: \mu\text{m}$) and total length ($X: \text{mm}$) were linearly related in the leptocephali ($Y=1.89X-1.60$, $r=0.988$, $N=110$; UMEZAWA and TSUKAMOTO, 1992a). Glass eels and elvers also presented a linear relationship but with a different regression coefficient ($Y=2.89X+7.99$, $r=0.875$, $n=1349$; UMEZAWA and TSUKAMOTO, 1992a). These considerations lead to the conclusion that leptocephali begin to metamorphose at the mid point of WIZ of

the largest increment width, at a mean age of 85d, and that body size shrinks afterwards (Fig. 5). Assuming that the latter half of the WIZ represents metamorphosis, it lasts for 12 d. Duration of metamorphosis estimated in the study does not differ from that of beach conger *Conger japonicus*, 11-14d (OCHIAI *et al.*, 1978). The total length of glass eel ($Y: \text{mm}$) and the days (X) after the mid point of WIZ or the beginning of metamorphosis showed a negative linear relationship ($Y=-0.22X+61.3$, $r=0.519$, $n=40$; UMEZAWA and TSUKAMOTO, 1992b). The equation suggests that the size of the leptocephalus at the maximum developing stage would be 61.3mm in TL and the eel shrank at 0.22mm/d in length after the beginning of metamorphosis until the elver stage (Fig. 5). This estimation is consistent with the collection data: the largest size of leptocephalus ever collected was 59.2mm in TL (TABETA and KONISHI, 1986), the 4 metamorphosing larvae ranged from 52.0 to 60.2mm, 9 glass eels collected at

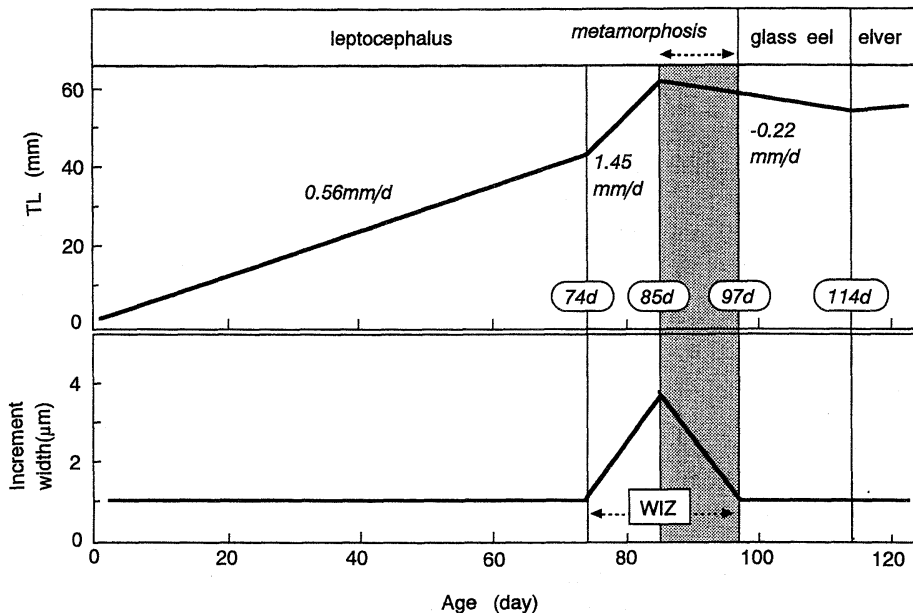


Fig. 5 Correspondence between early growth pattern of *A. japonica* and change in otolith increment width against age, or increment number from the inside to the edge. A zone of wide increments (WIZ) occurred between 74 and 97 d in a series of otolith increment width from the core to the edge. Metamorphosis started at 85 d or the mid point of WIZ showing the largest value of increment width.

open sea, 53.0–61.2mm (SHOJIMA, 1966, 1967; TSUKAHARA, 1971; TABETA and TAKAI, 1973; TABETA, 1981; SHOJIMA, 1991), and 260 glass eels obtained at surf zone of Kanagawa, Japan, 52.1–62.4mm (UMEZAWA, 1990). There was a negative linear relationship between age at metamorphosis (the mid point of the WIZ) and otolith growth rate (UMEZAWA and TSUKAMOTO, 1992b). This shows that leptocephali with a larger growth rate begin to metamorphose at a younger age, since otolith growth is positively related to body growth (see above).

The leptocephalus phase of *A. rostrata* is believed to last for 10–12 months (SCHMIDT, 1922), or 8–12 months (KLECKNER and McCLEAVE, 1985). *A. anguilla* is supposed to metamorphose into the glass eel stage 2.5–3 years after hatching (SCHMIDT, 1922, 1925), 3–4 years (UTRECHT and HOLLEBOOM, 1985), or 12–15 months (BÖETIUS and HARDING, 1985). LIEW (1974) suggested that *A. rostrata* spent 2 years in the sea, and *A. anguilla*, 3 years. A metamorphosing leptocephalus of *A. anguilla* (63.0mm TL) collected in the Mediterranean Sea in January 1990 had only 102 increments (presumed daily) in the otolith (TSUKAMOTO *et al.*, 1991), suggesting a much shorter duration (3–4 months) of leptocephalus stage than has been previously reported (TSUKAMOTO *et al.*, 1991). The duration of the leptocephalus phase and the time required for oceanic migration vary greatly among *A. japonica* and both Atlantic species. Such disparity could well be the subject of future research.

Oceanic migration

The process and mechanism of oceanic migration by eels is poorly known (OZAWA *et al.*, However, it can be assumed at least from the present collection data on *A. japonica* leptocephali that spawning may occur in the waters east of the Philippines (see above, Fig. 2). Accordingly, oceanic migration of the eel from the spawning area to an estuary can be roughly divided into three periods: (1) long drift from the spawning area to the origin of the Kuroshio current, (2) rapid northward transport in the Kuroshio, and (3) inshore migration toward the estuary after the exit from the Kuroshio.

Long Drift: Ocean circulation is complex in waters east of Taiwan and the Phillipines, lat. 15°–25°N and long. 125°–135°E (NITANI, 1972; HASUNUMA and YOSHIDA, 1978), where the eel spends its leptocephalus stage. Based on the dynamic topography of the sea surface relative to the 1000 db surface (HASUNUMA and YOSHIDA, 1978), small leptocephali (20–30mm TL) were caught in the southern slope of the north equatorial ridge of the geopotential anomaly, or near the northern boundary of the North Equatorial Current (see Fig. 2). Old leptocephali just before metamorphosis (*e. g.* 77–87d, 50–60mm) and metamorphosing larvae were recorded just east of the origin of the Kuroshio (Fig. 2). The eel larvae might be slowly transported northwestward in complicated eddies from the spawning area to the origin of the Kuroshio (OZAWA *et al.*, 1992). Duration of the drift in this area is supposed to be 2–3 months before metamorphosis (UMEZAWA and TSUKAMOTO, 1992b). If it is assumed that the spawning area is located 10°–20°N, 140°–150°E, larvae would drift through 2000–3000 km in distance at ca. 40 km/d.

Kuroshio Transport: All of the leptocephali which have been collected were found east of the Kuroshio, whereas glass eels collected offshore were recorded west of the Kuroshio (Fig. 2; SHOJIMA, 1966 1967; TSUKAHARA, 1971; TABETA and TAKAI, 1973; SHOJIMA, 1990). Although no eel larvae have ever been collected in the Kuroshio, it is probable that larvae which arrived at waters just southeast of Taiwan, the beginning of the Kuroshio (NITANI, 1972), would be entrained by the strong Kuroshio and transported northward. Timing and developmental stage at the time of entrainment to the current would vary in each individual because the transport in eddies during long drift would be entirely passive and indefinite. However, the exit from the Kuroshio may occur at the same stage in all individuals, *i. e.* during or just after metamorphosis. Buoyancy would be lost during metamorphosis because of decreases in the area of the body surface

and water content (CALLAMAND, 1943) and increases in specific gravity (SINHA and JONES, 1975; HICKMAN, 1981). *Conger japonicus* began active swimming when metamorphosis started (OCHIAI *et al.*, 1978). The records of offshore catches of glass eels and metamorphosing leptocephali (Fig. 2) suggest that the eel, in general, begins metamorphosis in or just east of the Kuroshio, and completes it in the current (UMEZAWA and TSUKAMOTO, 1992b) or in the marginal waters of the continental shelf (TABETA and TAKAI, 1973).

Kuroshio Transport Distance, the distance an eel might be transported by the Kuroshio from its origin (0 km) to a point of exit, varies from 250 km to 3000 km for fish recruited to Taiwan and Miyagi in Japan (the northernmost sampling station in Fig. 2), respectively. Since the velocity of the Kuroshio is ca. 2–3 kt (NITANI, 1972), the duration of Kuroshio transport is estimated to be 2–27 days. The Kuroshio Transport Distance and age at metamorphosis of fish collected at each coastal station showed a positive linear relationship except for samples from Korea and Miyagi whose stations do not face the Kuroshio directly. This suggests that fish metamorphosing earlier would be transported a shorter distance and exit from the current at a lower latitude.

Inshore Migration: How the eel migrates inshore after exit from the Kuroshio is unclear. Since a total of 9 glass eels has ever been collected offshore (Fig. 2), there is insufficient information to explain the process of inshore migration of a billion glass eels recruiting to coastal waters of East Asia. Although glass eels collected offshore were recorded at comparatively shallow depths near the surface (SHOJIMA, 1990), there remains the possibility that settlement to the bottom occurred after metamorphosis, followed by movement inshore along the sea bed. However, the glass eel at recruitment had no characteristic microstructure in the otolith, *e. g.* check, corresponding to the settlement to the sea bed accompanied by a drastic decrease in environmental temperature of about 20°C.

Otolith examination suggests that mean

duration between metamorphosis and recruitment to a coast is 20–32 days (UMEZAWA and TSUKAMOTO, 1992b). Assuming that the cruising speed of glass eels (60 mm TL) is 120 mm/s (2 TL/s), and that active swimming occurs only 16 h at night since the eel is nocturnal (UMEZAWA, 1991), it was calculated that a glass eel might migrate 138–221 km distance by itself after exit from the Kuroshio following metamorphosis. This estimation might explain a distance of 56–206 km from the Kuroshio flow axis to each sampling station along the coast. However, the situation may not be so simple because the eel would not swim directly to a coast, and countercurrents of the Kuroshio and complicated coastal currents might affect the inshore migration.

The utilization of tidal current in the entry to estuaries was reported in *A. rostrata* (McCleave and KLECKNER, 1982; McCleave and WIPPELHAUSER, 1987) and *A. anguilla* (CREUTZBERG, 1958). Similarly, the recruitment of *A. japonica* to the estuary might be controlled by a tidal rhythm. Birth dates of the glass eels on arrival to the coast increased in stepwise following the sampling date, and the duration of each step was about 14 d which coincided with the half of lunar phase (UMEZAWA, 1991). Age at recruitment and tidal range were negatively correlated. Furthermore, CPUE and tidal range showed a positive linear relationship. These results suggested that the glass eels recruited to the coast at the full or new moon, and

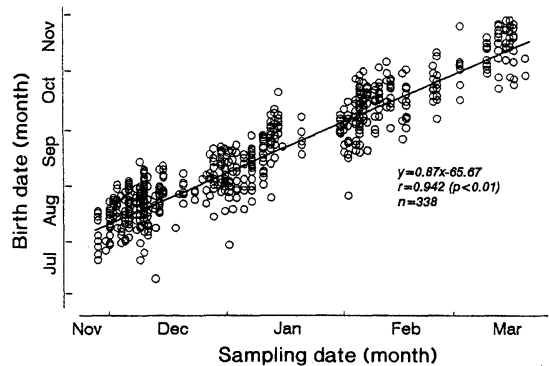


Fig. 6 Relationship between sampling date and birth date of glass eels collected on the Japanese coast.

stayed there until the next spring tide (UMEZAWA, 1991).

Migration mechanism

Clear correspondence was observed between birth date and the time of arrival at the coast (Fig. 6; TSUKAMOTO, 1990; UMEZAWA, 1991). A similar relationship was confirmed in fish recruited to Taiwan (TZENG, 1990). The age at metamorphosis was positively correlated with the age at recruitment to the coastal waters of Taiwan and Japan (Fig. 7; UMEZAWA and TSUKAMOTO, 1992b). The age of glass eels or the time required for oceanic migration increased gradually with the date of recruitment (TSUKAMOTO, 1990). However, the body size at recruitment was roughly constant, about 55–60 mm TL (TZENG, 1990; UMEZAWA, 1991). The growth rate of glass eels recruited to Taiwan was inversely correlated with age at recruitment, suggesting that fast-growing larvae took a shorter time for oceanic migration than slow-growing larvae (TZENG, 1990). Pigmentation developed at a lower latitude (TSUKAMOTO, 1990). Thus, the migration mechanism of the eel *A. japonica* can be summarized as follows: The earlier-born fish or fish with a faster growth rate metamorphose and recruit earlier, at a younger age to the lower latitude with the more advanced pigmentation, but with a constant body size (Fig. 8; TSUKAMOTO, 1990; UMEZAWA, 1991).

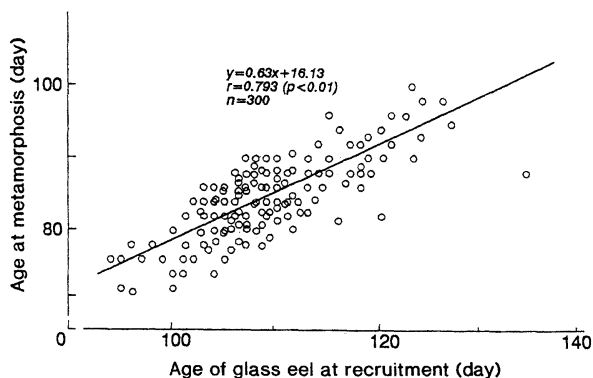


Fig. 7. Relationship between the age at metamorphosis (the mid point of WIZ) estimated by otolith microstructure and the age at recruitment in the glass eels collected in the coastal waters of Taiwan and Japan.

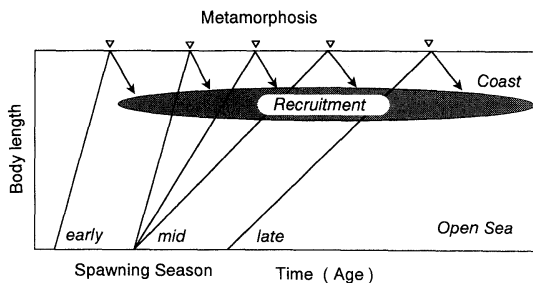


Fig. 8. Migration mechanism of *Anguilla japonica*, with special reference to the correspondence among birth date, growth rate and timing of recruitment. Solid lines with arrows each represent a diagrammatic growth curve of an individual for each timing of birth.

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References

- BERTIN, L. (1956): Eels: A biological study, pp. 192, Cleaver-Hume Press Ltd., London.
- BÖETIUS, J and E. F. HARDING (1985): A re-examination of Johannes Schmidt's Atlantic eel investigations. *Dana* 4, 129–162.
- CALLAMAND, O. (1943): L'Anguille Européenne, Les bases physiologiques de sa migration. *Ann. Inst. Ocean.*, 21, 361–440.
- CASTONGUAY, M. (1987): Growth of American and European eel leptocephali as revealed by otolith microstructure. *Can. J. Zool.*, 65, 875–878.
- CREUTZBERG, F. (1958): Use of tidal streams by migrating elvers (*Anguilla vulgaris* Turt.). *Nature, Lond.*, 181, 857–858.
- HARDEN JONES, F. R. (1968): Fish migration. pp. 325, E. Arnold Ltd. London, England.
- HASUNUMA, K. and K. YOSHIDA (1978): Splitting of the subtropical gyre in the Western North Pacific. *Journal of the Oceanographical Society of Japan*, 34, 160–172.
- HICKMAN, R. A. (1981): Densities and swimbladder development of juvenile American eels, *Anguilla rostrata* (Lesuer) as related to energetics of migration. *J. Fish. Biol.*, 18, 507–517.
- KAJIHARA, T. (1988): Distribution of *Anguilla japonica* leptocephali in Western Pacific during September 1986. *Nippon Suisan Gakkaishi*, 54, 929–933.

- KLECKNER, R. C. and J. D. McCLEAVE (1985): Spatial and temporal distribution of American eel larvae in relation to North Atlantic Ocean current systems. *Dana* **4**, 67-92.
- LIEW, P. K. L. (1974): Age determination of American eels based on the structure of their otoliths, pp. 124-136. *In* T. B. Bagenal (ed): *The Proceedings of an International Symposium on the Aging of Fish*. Unwin Brothers Ltd., Surrey, England.
- MATSUI, I. (1952): Morphology, ecology and culture of the Japanese eel. *J. Shimonoseki Coll. Fish.*, **2**, 1-245.
- MATSUI, I., T. TAKAI and A. KATAOKA (1968): Anguillid leptocephalus found in the Japan current and its adjacent waters. *J. Shimonoseki Univ. Fish.*, **17**, 17-23.
- MCCLEAVE, J. D. and R. C. KLECKNER (1982): Selective tidal stream transport in the estuarine migration of glass eels of the American eel (*Anguilla rostrata*). *J. Cons. int. Explor. Mer.*, **40**, 262-271.
- MCCLEAVE, J. D. and G. S. WIPPELHAUSER (1987): Behavioral aspects of selective tidal stream transport in juvenile American eels (*Anguilla rostrata*). *Amer. Fish. Soc. Symp.*, **1**, 138-150.
- NITANI, H. (1972): Beginning of the Kuroshio. pp. 129-163. *In* H. Stommel and K. Yoshida (ed.): *Kuroshio: its physical aspects*. University of Tokyo Press, Tokyo.
- OCHIAI, A., T. IKGAMI and Y. NOZAWA (1978): On the metamorphosis and identification of the leptocephali of the congrid eel, *Conger japonicus*, from Tosa Bay, Japan. *Japan. J. Ichthyol.*, **25**, 205-210.
- OZAWA, T., O. TABETA and N. MOCHIOKA (1989): Anguillid leptocephali from the Western North Pacific east of Luzon, in 1988. *Nippon Suisan Gakkaishi*, **55**, 627-632.
- OZAWA, T., F. KAKIZOE, O. TABETA, T. MAEDA and Y. YUWAKI (1991): Japanese eel leptocephali from three cruises in the Western North Pacific. *Nippon Suisan Gakkaishi*, **57**, 1877-1881.
- OZAWA, T., F. KAKIZOE, O. TABETA, T. MAEDA and Y. YUWAKI (1992): Larval growth and drift of Japanese eel *Anguilla japonica* estimated from leptocephali collection. *Nippon Suisan Gakkaishi*, **58**, 15-23.
- SATO, H. (1979): Aiming the complete rearing of the eel. *Iden (Hereditiy)*, **33**, 23-30.
- SCHMIDT, J. (1922): The breeding places of the eel. *Phil. Trans. R. Soc.*, **211**(B), 179-208.
- SCHMIDT, J. (1925): The breeding places of the eel. *Ann. Rep. Smithsonian Inst.*, **1924**, 279-316.
- SINHA, V. R. and J. W. JONES (1975): *The European freshwater eel*. pp. 146, Liverpool University Press, Liverpool.
- SHOJIMA, Y. (1966): Report on a capture of an elver of Japanese eel, *Anguilla japonica* TEMMINCK et SCHLEGEL, in the East China Sea. *Nippon Suisan Gakkaishi*, **32**, 41-44.
- SHOJIMA, Y. (1967): Record of Japanese eel elver found in the offshore of the East China sea for the second time. *Zool. Mag.*, **76**, 167-171.
- SHOJIMA, Y. (1990): Elvers in the East China Sea. *Suisan Gijutsu to Keiei (Techniques and Management in Fisheries)*, **36**, 18-28.
- TABETA, O. (1981): On the early life history of Japanese eel with reference to the spawning ground. *Kaiyo to seibutsu (Aquabiology)*, **3**, 412-417.
- TABETA, O. and Y. KONISHI (1986): An anguillid leptocephalus *Anguilla japonica* from the waters south of Miyako Island, Okinawa, Japan. *Nippon Suisan Gakkaishi*, **52**, 1935-1937.
- TABETA, O. and T. TAKAI (1973): An elver of *Anguilla japonica* found in the northern part of the South China Sea. *J. Shimonoseki Univ. Fish.*, **22**, 1-5.
- TABETA, O. and T. TAKAI (1975a): Leptocephalus of *Anguilla japonica* found in the waters south of Taiwan. *Japan. J. Ichthyol.*, **22**, 100-103.
- TABETA, O. and T. TAKAI (1975b): Leptocephali of *Anguilla japonica* found in the waters south of the Okinawa Island. *Nippon Suisan Gakkaishi*, **41**, 137-145.
- TABETA, O., K. TANAKA, J. YAMADA and W. N. TZENG (1987): Aspects of the early life history of the Japanese eel *Anguilla japonica* determined from otolith microstructure. *Nippon Suisan Gakkaishi*, **53**, 1727-1734.
- TAKAI, T. and O. TABETA (1976): Anguillid leptocephali. pp. 12-13. *In* T. Ishii (ed.): *Preliminary report of the Hakuho Maru KH-75-1*. Ocean Research Institute, University of Tokyo, Tokyo.
- TANAKA, S. (1975): Collection of leptocephali of the Japanese eel in waters south of the Okinawa Island. *Nippon Suisan Gakkaishi*, **41**, 129-136.
- TSUKAHARA, H. (1971): Approach of eel elvers to the land. *Yoshoku (Aquaculture)*, **4**, 56-59.
- TSUKAMOTO, K. (1989): Otolith daily growth increments in the Japanese eel. *Nippon Suisan Gakkaishi*, **55**, 1017-1021.
- TSUKAMOTO, K. (1990): Recruitment mechanism of the eel, *Anguilla japonica*, to the Japanese coast. *J. Fish. Biol.*, **36**, 659-671.

- TSUKAMOTO, K., A. UMEZAWA, O. TABETA, N. MOCHIOKA and T. KAJIHARA (1989): Age and birth date of *Anguilla japonica* leptocephali collected in Western North Pacific in September 1986. Nippon Suisan Gakkaishi, **55**, 1023-1028.
- TSUKAMOTO, K., T. Otake, A. UMEZAWA, S. TATENO and Y. AKIMOTO (1991): Age and growth of the Atlantic eels leptocephali. In T. Nemoto (ed.): Preliminary report of the Hakuho Maru Cruise KH-89-2. Ocean Research Institute. University of Tokyo, Tokyo, 74-83.
- TSUKAMOTO, Y., A. UMEZAWA, K. TSUKAMOTO and M. OKIYAMA (1992): Fully grown leptocephalus of Japanese eel, *Anguilla japonica*, collected from Western Pacific. Nippon Suisan Gakkaishi. submitted.
- 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. (1991): Early life history and recruitment mechanism of the eel, *Anguilla japonica*. pp. 173. Doctoral dissertation, University of Tokyo, Tokyo.
- UMEZAWA, A. and K. TSUKAMOTO (1990): Age and birth date of the glass eel, *Anguilla japonica*, collected in Taiwan. Nippon Suisan Gakkaishi, **56**, 1199-1202.
- UMEZAWA, A. and K. TSUKAMOTO (1992a): Larval growth of the Japanese eel, *Anguilla japonica*. Journal Fish Biology. submitted.
- UMEZAWA, A. and K. TSUKAMOTO (1992b): Metamorphosis and oceanic migration of eel larvae, *Anguilla japonica*. Journal Fish Biology, submitted.
- UMEZAWA, A., K. TSUKAMOTO, O. TABETA and H. YAMAKAWA (1989): Daily growth increments in the larval otolith of the Japanese eel, *Anguilla japonica*. Japan. J. Ichthyol., **35**, 440-444.
- UTRECHT, W. L. VAN and M. A. HOLLEBOOM (1985): Notes on eel larvae (*Anguilla anguilla* Linnaeus, 1758) from the central and eastern north Atlantic and on glass eels from the European continental shelf. Bijdragen tot de Dierkunde, **55**, 249-262.
- WIPPELHAUSER, G. S., J. D. McCLEAVE and R. C. KLECKNER (1985): *Anguilla rostrata* leptocephali in the Sargasso Sea during February and March 1981. Dana, **4**, 93-98.
- YAMAMOTO, K. and K. YAMAUCHI (1974): Sexual maturation of Japanese eel and production of eel larvae in the aquarium. Nature, **251**, 220-221.