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The Processes of Onshore Migration of the Japanese Eel *Anguilla japonica* as Revealed by Otolith Microstructure

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1. Introduction

The anguillid eel is a catadromous fish that spawns in the ocean and grows in rivers (Tesch 1977). There are 15 species and 3 subspecies in the world (Castle and Williamson 1974), most of which breed in tropical waters (Schmidt 1922, 1925, Ege 1939). The transparent leaf-like leptocephalus larvae are transported by subtropical currents from spawning areas and metamorphose into glass eels on the continental shelf. Glass eels drift with the coastal current to the estuary and become pigmented elvers. Most elvers migrate upstream to become yellow eels. The Japanese eel resides in rivers for 5 to 10 years until silvering and beginning sexual maturation, after which they migrate to the sea to spawn during autumn (Tzeng et al. 2000a). Otolith microchemistry studies have indicated that some yellow eels do not migrate into rivers but stay in marine and estuarine waters until their spawning migration (Tsukamoto et al. 1998; Tzeng et al. 2000b) (Fig.1).

The migration history of the eel between the spawning ground and the estuary remains speculative because field collections of leptocephali and marine glass eels are expensive and difficult (Tsukamoto and Umezawa 1990; Tsukamoto 1992; Liao et al. 1996). Daily growth increments in the otoliths of teleost fishes were first discovered and used to determine age by Pannella (1971). The trace element composition of the increments can be used to reconstruct the environmental history of many fishes (Campana and Neilson 1985; Radtke and Shafer 1992; Campana 1999). Since Tabeta et al. (1987) described the daily growth increments in the otoliths of the Japanese eel *Anguilla japonica*, otolith microstructure has been widely used to study the early life history of anguillid eels (Tzeng 1990; Tsukamoto 1990; Lecomte-Finiger 1992; Tzeng and Tsai 1992, 1994; Tzeng 1996a; Cheng and Tzeng 1996; Wang and Tzeng 1998, 2000; Arai et al. 2000). Recently, Cieri and McCleave (2000) argued

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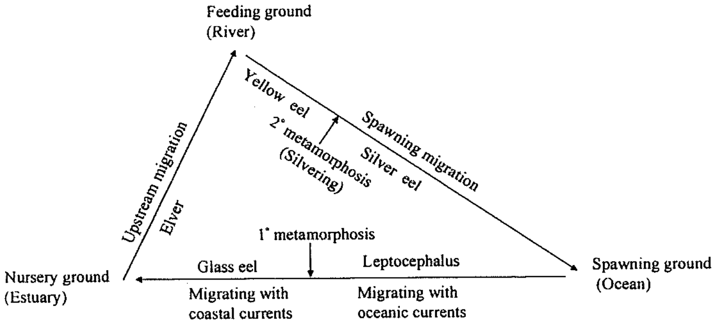

Fig. 1. A migratory model for anguillid eels

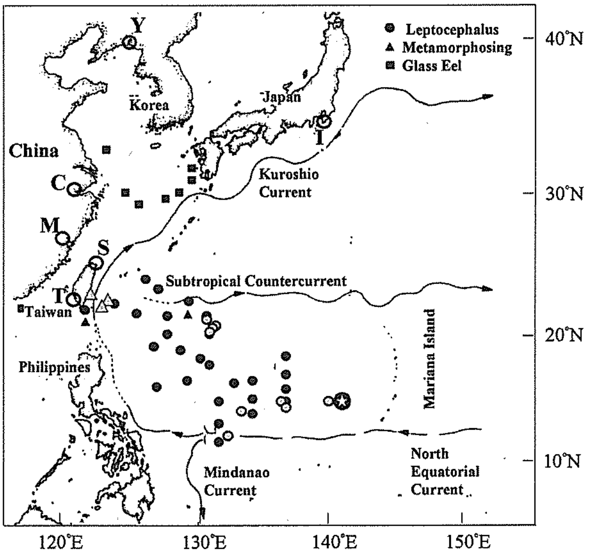

Fig. 2. Distribution and dispersal of leptocephali and marine glass eels of the Japanese eel *Anguilla japonica* (*solid symbols*, collected by Japan; data from Tsukamoto and Umezawa 1990; Tsukamoto 1992; *gray symbols*, collected by Taiwan; data from Liao et al. 1999 and unpublished; *star*, the presumed spawning ground). Elvers for otolith examination were collected from six estuaries in Taiwan, China, and Japan (*open circles*: *C*, Chyan-Tarng River; *I*, Ichinomiya River; *M*, Ming-Chiang River; *S* (S_1, S_2), Shuang-Shi River; *T* (T_1, T_2), Tung-Kang River; *Y*, Ya-Lu River). (See Cheng and Tzeng 1996)

that the daily growth increments in otoliths of the American eel, *A. rostrata,* might be underestimated in the metamorphic zone, thus biasing total counts of the increments from the primordium to otolith edge.

We reappraised the otolith increments of Japanese eel elvers by sections to avoid the error that might be concealed in the metamorphic zone. Thus, we first counted the increments from the primordium to the metamorphosis check to estimate the age at metamorphosis from leptocephalus to glass eel (T_m), and then counted the increments from the metamorphosis check to the otolith edge to estimate the time from metamorphosis to estuarine arrival ($T_{\text{r-m}}$). Then, we compared the estimates of T_{m} and $T_{\text{r-m}}$ for Japanese eel elvers from six estuaries in Taiwan, China, and Japan to examine the effect of oceanic currents on the dispersal of eels during their migration from spawning ground to estuary (Fig. 2).

2. Life History Events as Recorded in the Otolith

The structure of the growth increments in elver otoliths changed with fish growth, and obvious growth checks appeared during life history stage transitions (Fig. 3); this allowed us to measure the duration of each life history stage of the fish by counting the growth increments in each otolith section (Tzeng 1990; Tzeng and Tsai 1992; Cheng and Tzeng 1996; Wang and Tzeng 1998). Scanning electron microscope photographs of the otolith growth increments in an American eel *A. rostrata* elver are shown in Fig. 3. The primordium of the elver otolith was amorphous, and no distinct daily growth increments were discernible between the hatching check (HC) and the first feeding check (FFC). The nucleus, from the primordium to FFC, was deposited in the yolk sac stage. Beyond the FFC, there were distinct daily growth increments. The otolith crystalline arrangement changed from a circular to a radial form at approximately two-thirds of the total radius distance from the primordium. Also, the increment widths at the transition boundary became very narrow. The changes in crystalline pattern and increment width yielded a distinct check that was interpreted as the metamorphosis check (MC). Such

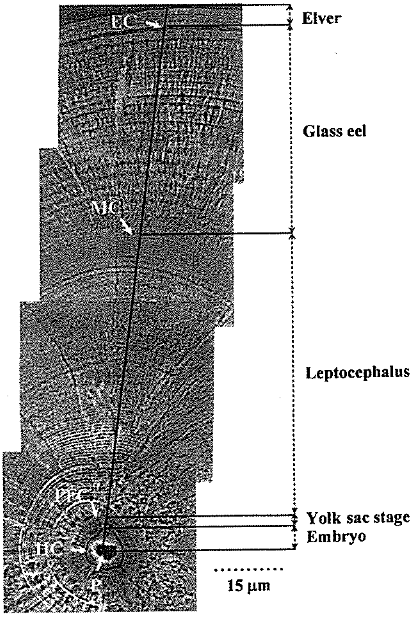

Fig. 3. Daily growth increments and growth checks in otolith of an American eel *A. rostrata* elver (*P*, primordium; *HC*, hatching check; *FFC*, first feeding check; *MC*, metamorphosis check; *EC*, elver check). (Modified from Wang and Tzeng 1998). *Bar* 15 μm

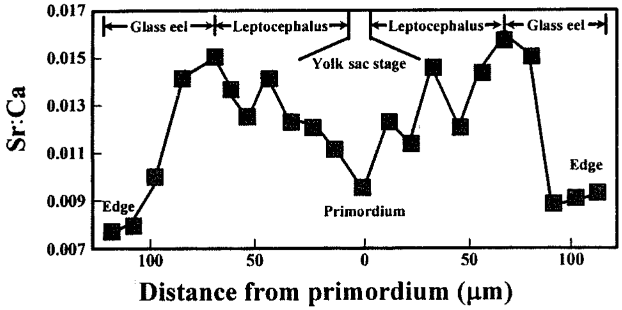

Fig. 4. Temporal changes in Sr:Ca concentration ratios from primordium to the otolith edge of a Japanese eel *Anguilla japonica* elver. (Modified from Tzeng and Tsai 1994)

changes reflect different developmental stages of the fish. The zone from the FFC to the MC, which was deposited during the leptocephalus stage, had daily growth increments that were wide and clear at the beginning of the stage but that became undistinguishable and almost uncountable across the MC check. These changes indicated that the growth of the leptocephalus was fast in the early stage and then gradually slowed. From the MC to the otolith edge, the crystalline arrangement became radial in form and had wide increments, indicating that growth was faster after metamorphosis.

The age at metamorphosis from leptocephalus to glass eel (T_m) and the time from metamorphosis to estuarine arrival (T_{r-m}) of the Japanese eel were estimated from the counts of growth increments in otoliths between the checks (see Fig. 3). The T_m and T_{r-m} were calculated as follows:

$$T_m = N_o + N_m$$
$$T_{r-m} = N_{r-m}$$

where N_o is the duration of yolk sac stage that has no discernible daily growth increments, but it was estimated at approximately 5 days (Yamamoto and Yamauchi 1974; Yamauchi et al. 1976; Tzeng 1990; Tzeng and Tsai 1994). N_m and N_{r-m} are the numbers of growth increments from FFC to MC and from MC to the elver check (EC), respectively. EC was deposited when the glass eel met freshwater in the estuary (Fig. 3).

The Sr:Ca concentration ratios in the otoliths of the elvers of the Japanese eel *A. japonica* were approximately 9×10^{-3} in the primordium, then gradually increased with otolith growth, reaching a maximum $16–17 \times 10^{-3}$ near the MC. Beyond the MC check, the Sr:Ca ratio sharply decreased (Fig. 4). The drastic change in otolith Sr:Ca ratios was thought to correspond to both the time of metamorphosis from the leptocephalus to the glass eel and the time of migration from oceanic to coastal waters (Tzeng and Tsai 1992, 1994; Otake et al. 1994; Tzeng 1996a; Arai et al. 1997).

3. Two-Stage Transport Hypothesis

The distribution areas of the Japanese eel *A. japonica* at the stages of leptocephalus and glass eel were obviously different (see Fig. 2). The Kuroshio Current seems the approximate boundary between the distributions of the eels at these two stages. The leptocephali were distributed in the oceanic waters and were passively transported from the spawning ground to the continental shelf edge of northern East Asia. In contrast, glass eels were distributed in the coastal waters. Therefore, the timing of metamorphosis from the leptocephalus to the glass eel stage appears to occur when larvae are leaving the Kuroshio Current to enter coastal waters. Accordingly, we hypothesized two-stage transportation for larval dispersal of the Japanese eel from the spawning ground to the estuary (see Fig. 1).

4. The Timing of Metamorphosis Determines Dispersal Distance

The leptocephalus was passively transported by the North Equatorial Current and Kuroshio Current from the spawning ground to the continental shelf waters of the East Asian countries of Taiwan, China, Korea, and Japan, and then the glass eels exit the Kuroshio Current and migrate with coastal currents to estuaries. To validate the effect of oceanic currents on larval dispersal we collected elvers from six

Table 1. Mean (±SD) total length (mm), ages of *Anguilla japonica* leptocephali at metamorphosis (T_m in days) and time between metamorphosis and estuarine arrival (T_{r-m} in days) for the elvers collected at the six estuaries in Taiwan, China, and Japan

Sampling site	Sampling date	*n*	Total length	T_m	T_{r-m}
Taiwan					
T1 (South)	30 Dec 1992	30 (16)	57.0±2.0	117.7± 14.3	39.2±6.8
T2	24 Mar 1993	30 (14)	56.1±2.4	121.4± 12.0	42.9±6.2
S1 (North)	30 Dec 1992	30 (12)	56.8±2.3	125.9± 14.7	31.7±7.6
S2	17 Feb 1993	30 (13)	55.9±2.2	115.8± 8.1	38.9±5.8
China					
M	1 Mar 1993	30 (20)	55.1±1.9	128.4± 6.9	34.5±3.6
C	17 Feb 1993	30 (23)	55.6±1.9	137.9± 11.3	38.6±5.7
Y	3 May 1993	30 (23)	58.3±1.8	135.5± 11.3	42.8±7.4
Japan					
I	10 Jan 1994	30 (10)	57.4±2.3	137.0± 12.9	45.0±9.2

T(T1, T2), Tung-Kang River; S(S1, S2), Shuang-Shi River; M, Ming-Chiang River; C, Chyan-Tarng River; Y, Ya-Lu River; I, Ichinomiya River

Numerals in parentheses are the sample size for otolith aging

Source: Data from Cheng and Tzeng (1996) estuaries in Taiwan, China, and Japan (see Fig. 2). The age of the Japanese eel at metamorphosis from the leptocephalus to the glass eel stage (T_m) was found to increase with the distance from the spawning ground and to be a key determinant of their ultimate destination. Early-metamorphosing leptocephali recruited to the south of their dispersal range and late-metamorphosing leptocephali recruited to the north (Table 1). The difference in mean T_m between Taiwan (116 days) and Japan (137 days) was 21 days (Δt). If the leptocephali were transported by the Kuroshio at a velocity (v) of 2.5 knots or 96 km day^{-1} (Nitani 1972), the dispersal distance of the leptocephali (d) for the different times can be estimated as follows:

$$\begin{aligned} d &= v \times \Delta t \\ &= 96 \text{ km day}^{-1} \times 21 \text{ days} \\ &= 2016 \text{ km} \end{aligned}$$

This distance approximately equals that from Taiwan to Japan and indicates that the timing of the metamorphosis of the leptocephalus and the Kuroshio Current play important roles in the long-distance dispersal of the Japanese eel.

5. Onshore Migration of Glass Eels in Association with Coastal Currents

After metamorphosis from leptocephali to glass eels, the migration of the Japanese eel is probably influenced less by the Kuroshio Current and more by the coastal currents. Elvers recruited to the estuaries of Taiwan from November through March when the northeasterly monsoon-driven China Coastal Current flowed from north to south (Chu 1963; Tzeng 1985). The coastal current prevailed in the west and the Kuroshio Current in the east of Taiwan. Elver catches were more abundant along

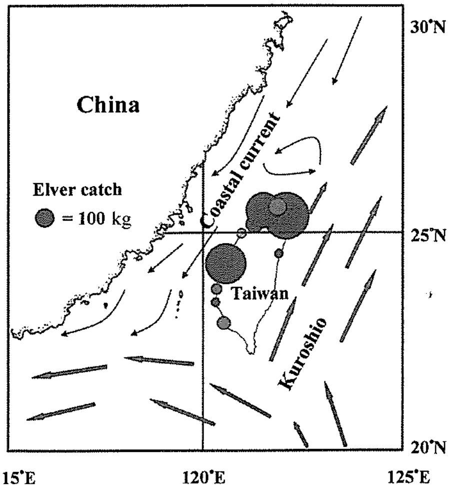

Fig. 5. Relationship between oceanic currents and elver catches in Taiwan during January. (Modified from Tzeng 1996b)

the western than eastern coasts of Taiwan (Fig. 5), implying that glass eels migrated with the cold China Coastal Current to the western coast of Taiwan.

To further validate this conclusion, we examined the daily growth increments in otoliths of elvers collected both from the Shungshi River estuary in the north of Taiwan on 30 December 1992 and 17 February 1993 (S_1, S_2) and from the Tungkang River estuary in southwestern Taiwan on 30 December 1992 and 24 March 1993 (T_1, T_2) (see Fig. 2). The number of daily growth increments from the metamorphosis check to the otolith edge (T_{r-m}) indicated that the age of elvers was approximately 4 to 7 days greater in the southern (T_1 and T_2) than the northern estuaries (S_1 and S_2) (see Table 1). This result indicated that the Japanese eel elvers were transported by the China Coastal Current from the north to the western coast of Taiwan.

6. Discussion

The structure of growth increments in eel otoliths and the Sr:Ca ratios in the increments drastically changed at metamorphosis from the leptocephalus to the glass eel stage. Similar to other teleost fishes, the increments in the otoliths of eels were deposited daily (Tsukamoto 1989; Martin 1995; Cieri and McCleave 2001). We were able to determine the age of leptocephali at metamorphosis by counting the otolith increments from the primordium to the metamorphosis check (Otake et al. 1994; Tzeng and Tsai 1994; Tzeng 1996a; Cheng and Tzeng 1996; Arai et al. 1997; Wang and Tzeng 1998). The accuracy and precision of the age estimates depends on the reliability of daily increment deposition.

Recently, Cieri and McCleave (2000) argued that the daily growth increment in otoliths of the American eel might be underestimated in the metamorphic zone. However, we found that the daily age of the metamorphosing leptocephali collected in the eastern waters of Taiwan (Liao et al. 1999) was very close to that estimated from the otolith of elvers (Cheng and Tzeng 1996). Thus, the age of the leptocephalus at metamorphosis is reliable when backcalculated from elver otolith increments.

The Japanese eel is a panmictic population (Sang et al. 1994) that spawns in the waters to the west of the Mariana Islands (Tsukamoto 1992) and is widely distributed from Taiwan to Japan (Tesch 1977). The distance from the spawning ground to the growth habitats of northwestern Pacific countries is approximately 2000–5000 km. The leaf-like leptocephalus larvae are suitable for long-distance dispersal by oceanic currents. Thus, the duration of the leptocephalus stage is a key factor determining their ultimate destination. This study found that a difference of 21 days in the mean ages of leptocephali at metamorphosis to glass eels allowed this species to disperse from Taiwan to Japan. Thus, the timing of leptocephalus metamorphosis was an important determinant of the distribution of this species. The mechanism determining the timing of metamorphosis is not clear but is probably related to larval growth and the accessibility of the continental shelf.

The leptocephali are mainly distributed in oceanic waters and the glass eels in coastal waters (see Fig. 2). Thus, the migratory behavior associated with current systems differed completely between the leptocephalus and glass eel stages. The Japanese eel leptocephali are transported by the North Equatorial and Kuroshio Currents from the spawning ground to the continental shelf, and the China Coastal Current transported the glass eels around Taiwan. The continental shelf was probably a cue to induce metamorphosis in the leptocephali. The leptocephali must grow fully to a certain size; otherwise, they cannot metamorphose into glass eels (Tsukamoto and Umezawa 1990). For example, the leptocephali of the Japanese eel migrate with the North Equatorial Current through Philippine waters, but glass eels are seldom found there (Tabeta et al. 1975, 1976). The Japanese eel spawns in the waters west of the Mariana Islands (15-°N, 140-°E), and their larvae drift with the North Equatorial Current at a speed of 20 to 32 cm s^{-1} (Kimura et al. 1994). Depending upon the speed of the current and the distance involved, larvae arrive in Philippine waters approximately 55 to 87 days after hatching. The age of leptocephali at metamorphosis for the elvers collected at the six estuaries of Taiwan, China, and Japan averaged 116 to 137 days (Cheng and Tzeng 1996). The leptocephali that arrive in Philippine waters are apparently too young to metamorphose and migrate toward estuaries.

Liao et al. (1999) collected two fully-grown Japanese eel leptocephali with total lengths of 56 and 62 mm at the ages of 132 and 130 days after hatching respectively, in the eastern waters of Taiwan (23°26'–55'N, 122°36'–55'E) on 9 November 1998. Based on their age at metamorphosis (116–137 days) and capture location, the latitude where leptocephali may metamorphose to glass eels was estimated to be over the continental shelf near or beyond Taiwan.

After metamorphosis, the glass eels left the Kuroshio Current and migrated with coastal currents toward estuaries. Upon arrival at an estuary, the glass eels became elvers. The China Coastal Current is a cold current and prevails in the winter, decreasing the water temperature on the western coast of Taiwan (Chu 1963). The catch of elvers in the estuaries along the western coast increased as the water temperature decreased in winter (Tzeng 1985) (see Fig. 5). These synchronous events indicate that the coastal current may play an important role in the process of onshore migration of the eel. On the other hand, the time from metamorphosis to estuarine arrival for elvers collected in southern Taiwan was longer than for those collected in northern Taiwan. This result also supports the hypothesis that elvers along the western coasts of Taiwan are being carried by the China Coastal Current from the north (Tzeng 1985; Tzeng and Tsai 1992; Cheng and Tzeng 1996).

Acknowledgments. This study was financially supported by the National Science Council of the Republic of China (Project No. NSC89-2611-B-002-004 and NSC90-2611-M-002-019-OP4). The author is grateful to Mr. Brian M. Jessop and anonymous reviewers for helpful comments on previous drafts of the manuscript.

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