

Larval duration of the tropical eel *Anguilla celebesensis* from Indonesian and Philippine coasts

Takaomi Arai^{1,*}, Michael J. Miller², Katsumi Tsukamoto²

¹Otsuchi Marine Research Center, Ocean Research Institute, The University of Tokyo, 2-106-1 Akahama, Otsuchi, Iwate 028-1102, Japan

²Ocean Research Institute, The University of Tokyo, Minamidai, Nakano, Tokyo 164-8639, Japan

ABSTRACT: A comparative study of the otolith microstructure of glass eels *Anguilla celebesensis* from the Indonesian and Philippine coasts determined the timing of metamorphosis and age at recruitment to freshwater habitats; 2 samples from Indonesia were analyzed and statistically compared with a previously published sample analyzed using the same techniques. Ages at metamorphosis and at recruitment were, respectively: 98 ± 7.2 d (mean \pm SD) and 122 ± 7.2 d for specimens from the Poso River in Indonesia; 90 ± 13.6 and 112 ± 14.2 d for specimens from the Poigar River in Indonesia; and 124 ± 12.0 and 157 ± 13.7 d for specimens from the northern Philippines. The average duration of metamorphosis was very similar (15 to 17 d) in all specimens. A close linear relationship was found between age at metamorphosis and age at recruitment. These findings and the regional geography of the islands and ocean currents suggest that *A. celebesensis* has several spawning areas and potentially isolated populations in the region, as has been suggested for another, more widely distributed tropical anguillid, *A. marmorata*.

KEY WORDS: Glass eels · Otolith microstructure · Metamorphosis · Recruitment · Ocean currents

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INTRODUCTION

Freshwater eels of the genus *Anguilla* are catadromous, and migrate between their freshwater growth habitats and offshore spawning areas. All anguillids and other eels have a leptocephalus larva, and metamorphosis from the leptocephalus to the glass eel is one of the most interesting ecophysiological phenomena in their life histories. The timing of metamorphosis and the duration of the leptocephalus stage seem to constitute an important biological key in determining the geographic distribution of anguillid eels (Tsukamoto & Umezawa 1994). Therefore, in the long term their larval migration in the world ocean may have had a major influence on the worldwide distribution of the genus *Anguilla* and the patterns of speciation of this remarkable group of fishes (Tsukamoto 1994, Tsukamoto & Aoyama 1998).

Worldwide, 15 species of *Anguilla* have been reported, with 10 being known from tropical regions (Ege 1939). Of the tropical species/subspecies, 7 occur in the

western Pacific around Indonesia (Ege 1939, Castle & Williamson 1974), and recent phylogenetic studies indicate that tropical species are probably more closely related to the ancestral form than their temperate counterparts (Aoyama et al. 2001). Tropical anguillid eel species differ from temperate species in that some species such as *A. marmorata* appear to have multiple populations and spawning areas (Ishikawa 1998, Arai et al. 2001a, Miller et al. 2002), have shorter larval durations (Arai et al. 2001b, Marui et al. 2001), and show evidence of potentially year-round spawning and recruitment (Arai et al. 2001b, Sugeha et al. 2001). Thus, the study of the early life history and recruitment of tropical eels could provide valuable information that will increase our understanding of the nature of the ancestral catadromous migration of freshwater eels and how the large-scale migration of temperate species became established.

In the present study, we examined the otolith microstructure in the glass eel stage of *Anguilla celebesensis* collected during recruitment to 3 oceanographi-

*Email: arai@wakame.ori.u-tokyo.ac.jp

cally isolated areas of the Indonesian Seas and the western North Pacific. This species is less widely distributed than *A. marmorata*. It is only found in and around the central Indonesian Seas region, from East Timor northwards past Sulawesi Island and the Philippines, and (to a lesser extent) around Taiwan (Tzeng 1983), and as far east as western New Guinea (Ege 1939). We determined the timing and duration of metamorphosis, age at recruitment and hatching date of specimens collected from 2 sites on opposite sides of Sulawesi Island in Indonesia. For comparison, we include the data from a previously published analysis of the otolith microstructure of specimens collected at the northern edge of the Philippines (Arai et al. 1999a). These data form the basis of a discussion on the spawning locations and the larval migration of *A. celebesensis* in relation to the major surface currents in the region.

MATERIALS AND METHODS

Fish and otolith analyses. Glass eels *Anguilla celebesensis* were collected at night during new moon with scoop nets at the mouth of the Poigar River on Sulawesi Island, Indonesia, on 7 July 1997 and at the mouth of the Poso River, on the same island, on 15 July 1999 (Fig. 1). The glass eels were preserved in 99% ethanol immediately after collection. Total lengths were measured to the nearest 0.1 mm, and pigmentation stages were determined according to Bertin (1956). Sagittal otoliths were extracted from each fish, embedded in epoxy resin (Struers, Epofix) and mounted on glass slides. The otoliths were ground to expose the core in the sagittal plane, using a grinding machine equipped with a diamond cup-wheel (Struers, Discoplan-TS), and further polished with 6 μm and subsequently 1 μm diamond paste on an automated polishing wheel (Struers, Planopol-V). They were then cleaned in an ultrasonic bath and rinsed with deionized water, and were etched with 0.05 M HCl and vacuum coated with Pt-Pd in an ion-sputterer for scanning electron microscope observations (SEM, Hitachi S-4500) as described by Arai et al. (1997, 1999a,b) (Fig. 2). Since otolith increments in *A. celebesensis* are deposited daily (Arai et al. 2000), we considered the number of increments to be equal to the age in days for *A. celebesensis* (Table 1).

Previously reported otolith data (Arai et al. 1999a) are included for comparison and originate from specimens collected with scoop nets at the mouth of the Cagayan River in the Philippines on 24 September 1994. Thus, a total of 43 specimens (30 specimens from Indonesia, 13 specimens from the Philippines) comprised the samples in the present study (Table 1).

Interpretation of growth history. Based on previous data for otolith increment width and Sr:Ca ratios of *Anguilla japonica*, *A. rostrata*, *A. australis*, *A. bicolor pacifica*, *A. celebesensis*, *A. marmorata* and *A. bicolor bicolor*, *A. anguilla*, and *A. dieffenbachii* (see Arai et al. 2001b, Marui et al. 2001), the age at which a marked increase in otolith increment width occurred coincident with a drop in Sr:Ca ratios was regarded as the onset of metamorphosis in each specimen examined here. The duration of the metamorphosis stage was regarded as the period between the onset of a marked increase in otolith increment width and the maximum width recorded. Total age (age at recruitment) was recorded as the number of increments between the hatch check and the otolith edge (Table 1).

Statistical analyses. Differences among data were tested by an analysis of variance (ANOVA) and afterwards with Scheffé's multiple-range test for pairwise comparisons. The significance of the correlation coefficients and regression slopes was tested with Fisher's Z-transformation and an analysis of covariance (ANCOVA) (Sokal & Rohlf 1995).

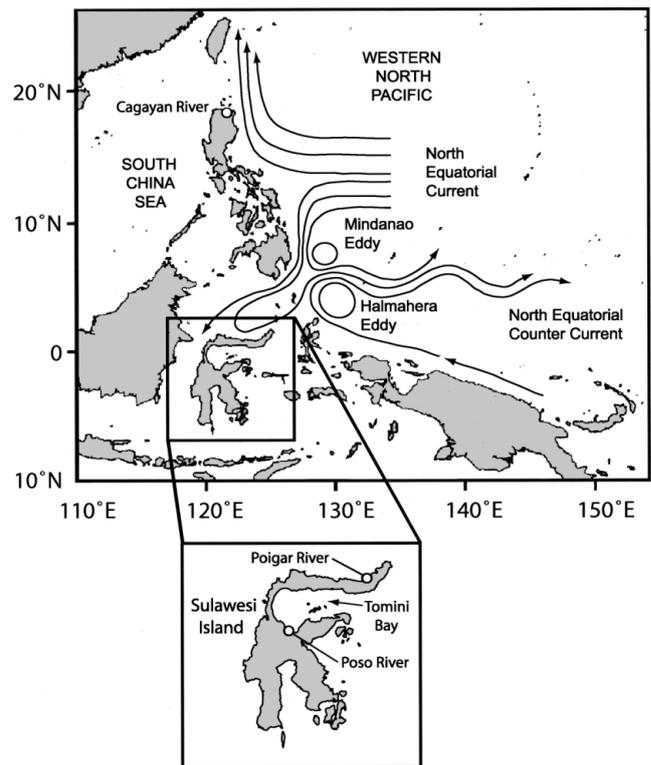


Fig. 1. Map of study area showing sampling sites (O) in the northern Philippines, and on Sulawesi Island in Indonesia (inset), and general surface currents that affect the areas around the sampling sites (after Toole et al. 1990, Lukas et al. 1991, and Wijffels et al. 1995)

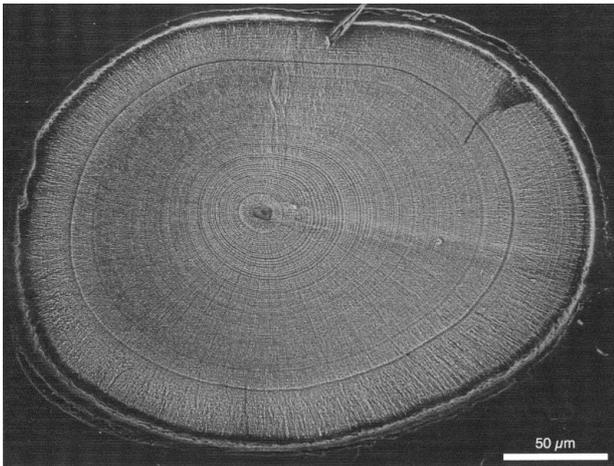


Fig. 2. *Anguilla celebesensis*. Scanning electron micrograph photograph showing otolith growth increments of glass eel (total length = 49.1 mm) collected at mouth of Poigar River on 7 July 1997

RESULTS

Size and stage at recruitment

The total lengths (mean \pm SD) of the specimens of *Anguilla celebesensis* from the Poso and Poigar Rivers (Indonesia) and from the Cagayan River (Philippines) were 50.6 ± 1.3 mm (range: 49.2 to 53.2 mm), 52.8 ± 1.9 mm (range: 50.0 to 56.2 mm) and 51.2 ± 1.7 mm (range: 48.4 to 54.6 mm), respectively (Table 1). A significant difference in total length was found among the 3 sites (ANOVA, $p < 0.01$), with the lengths of the specimens from the Poso and Poigar Rivers being significantly different ($p < 0.05$), but not between either of the Indonesian samples and the Philippines sample ($p > 0.05$).

The mean (\pm SD) radius of the otoliths of the specimens of *Anguilla celebesensis* from the Poso and Poigar Rivers and from the Cagayan River was 132 ± 7.0 μ m (range: 121 to 139 μ m), 124 ± 8.8 μ m (range: 104 to 138 μ m) and 163 ± 7.4 μ m (range: 156 to 182 μ m),

respectively (Table 1). A significant difference in otolith radius was found among the 3 sites (ANOVA, $p < 0.0001$), with pairwise differences being found between the sample from the Philippines and both samples from Indonesia ($p < 0.0001$), but not between the 2 Indonesian samples ($p > 0.05$).

Pigmentation in all specimens except those from the Philippines was poorly developed and was limited to the caudal, skull, or rostral regions of the body, indicating that they were at Stages VA or VB (according to Bertin 1956). Advanced pigmentation in the Philippines specimens was visible along the entire dorsal region of the body. They were therefore classified as Stages VIA_{II} or VIA_{IV}; i.e. at the beginning of transition to the elver stage.

Timing and duration of metamorphosis

Age at onset of metamorphosis (mean \pm SD) of *Anguilla celebesensis* from the Poso and Poigar Rivers and from the Cagayan River was 98 ± 7.2 d (range: 87 to 115 d), 90 ± 13.6 d (range: 74 to 115 d) and 124 ± 12.0 d (range: 104 to 147 d), respectively (Table 1). A significant difference in age at onset of metamorphosis was found among the 3 sites (ANOVA, $p < 0.0001$), with pairwise differences being found between the Philippines sample and both samples from Indonesia ($p < 0.0001$), but not between the 2 Indonesian samples ($p > 0.05$).

The duration of metamorphosis (mean \pm SD) of *Anguilla celebesensis* from the Poso and Poigar Rivers and from the Cagayan River was 15 ± 2.2 d (range: 12 to 18 d), 17 ± 2.9 d (range: 12 to 25 d) and 17 ± 3.2 d (range: 12 to 24 d), respectively (Table 1). The mean duration of metamorphosis did not differ among the 3 samples (ANOVA, $p > 0.1$).

Age at recruitment

Age at recruitment (mean \pm SD) of *Anguilla celebesensis* from the Poso and Poigar Rivers and from the

Table 1. *Anguilla celebesensis*. Total length, otolith radius, age at onset of metamorphosis, duration of metamorphosis stage, age at recruitment and hatching date (mean \pm SD, range). N: no. of specimens

Sampling location	Poso River (N = 10)	Poigar River (N = 20)	Cagayan River (N = 13)
Total length (mm)	50.6 ± 1.3 , 49.2–53.2	52.8 ± 1.9 , 50.0–56.2	51.2 ± 1.7 , 48.4–54.6
Otolith radius (μ m)	132 ± 7.0 , 121–139	124 ± 8.8 , 104–138	163 ± 7.4 , 156–182
Age at onset of metamorphosis (d)	98 ± 7.2 , 87–115	90 ± 13.6 , 74–115	124 ± 12.0 , 104–147
Duration of metamorphosis stage (d)	15 ± 2.2 , 12–18	17 ± 2.9 , 12–25	17 ± 3.2 , 12–24
Age at recruitment (d)	122 ± 7.2 , 112–132	112 ± 14.2 , 92–139	157 ± 13.7 , 130–177
Hatching date	15 Mar 1999 \pm 7.2 7–25 Mar 1999	15 Feb 1997 \pm 14.2 19 Jan–7 Mar 1997	20 Apr 1994 \pm 13.7 31 Mar–17 May 1994

Cagayan River was 122 ± 7.2 d (range: 112 to 132 d), 112 ± 14.2 d (range: 92 to 139 d) and 157 ± 13.7 d (range: 130 to 177 d), respectively (Table 1). A significant difference in age at recruitment was also found among the 3 sites (ANOVA, $p < 0.0001$), along with pairwise differences between the Philippines sample and both Indonesian samples ($p < 0.0001$), but not between the 2 Indonesian samples ($p > 0.05$). Close linear relationships were apparent between age at metamorphosis and age at recruitment in all samples (Fisher's Z-transformation, $p < 0.0001$) (Fig. 3).

Hatching date

The estimated hatching dates (back-calculated from the sampling date and age of each specimen collected from the Poso and Poigar Rivers in Indonesia and the Cagayan River in the Philippines) were from 7 March to 25 March 1999, from 19 January to 7 March 1997, and from 31 March to 17 May 1994, respectively (Table 1).

DISCUSSION

In this and previous studies, the size of tropical glass eels has been typically observed to be smaller at recruitment than that of temperate glass eels. The average total lengths of *Anguilla celebesensis* at recruitment in this study (50.6 to 52.8 mm) were 10 to 20 mm shorter than those of temperate anguillid species such as *A. anguilla* (68 mm) (Lecomte-Finiger 1992) and *A. japonica* (57 mm) (Cheng & Tzeng 1996, Arai et al. 1997), even though all 3 species were at the same pigmentation stage, i.e. Stages VA or VB. Arai et al. (1999a,b, 2001b, 2002a,b) also reported small average sizes for tropical glass eels (44.7 to 52.6 mm in *A. celebesensis*, 49.4 mm in *A. bicolor bicolor*, and 48.6 to 51.5 mm in *A. bicolor pacifica*) that were similar to those of *A. celebesensis* when they arrive at river mouths in tropical areas. Differences in the total lengths of fully grown leptocephali have also been found between tropical and temperate species. The total lengths of fully-grown leptocephali of the temperate eels *A. anguilla*, *A. rostrata* and *A. japonica*, were estimated as 75 mm (Jespersen 1942), 70 mm (Kleckner & McCleave 1985) and 60 mm (Tabeta & Konishi 1986), respectively, while those of tropical species collected in the Indo-Pacific region have been reported as being around 50 mm (Arai et al. 2001a). However, 2 species, *A. rostrata* (Wang & Tzeng 2000) and *A. australis* (Shiao et al. 2001), which recruit over a wide latitudinal range from subtropical to temperate regions, have shown a cline in the total length of glass

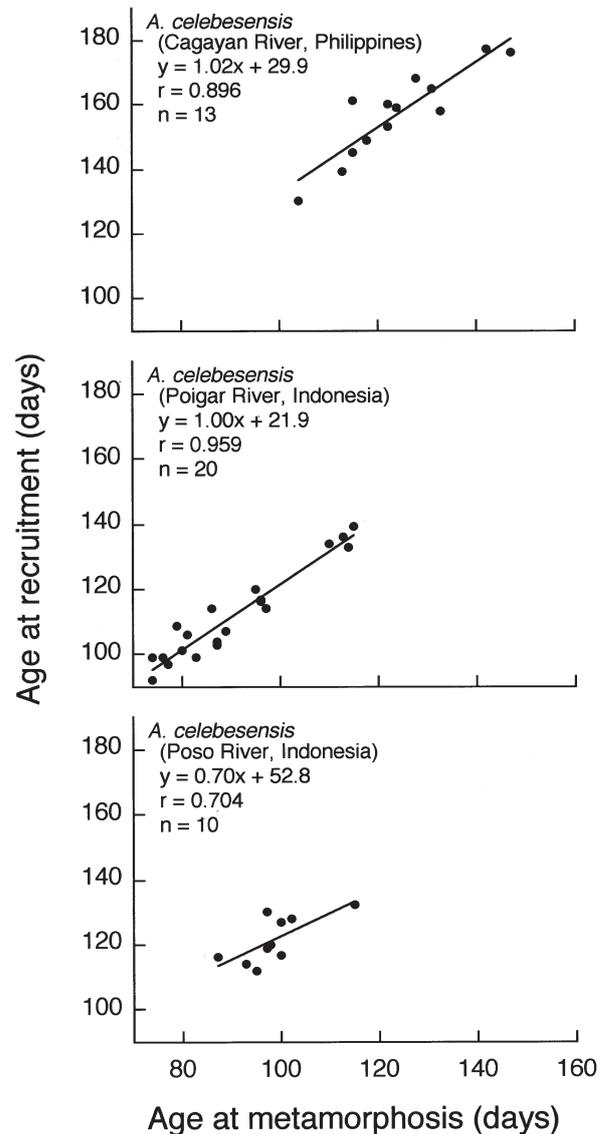


Fig. 3. *Anguilla celebesensis*. Relationship between age at metamorphosis and age at recruitment of glass eels collected from coasts of Sulawesi Island, Indonesia, and the northern Philippines

eels that appears to correlate to the distance from their spawning areas, with the size ranges at the lower latitudes (41 to 55 mm) being similar to those of tropical species.

The linear relationship between age at metamorphosis and age at recruitment in this and previous studies has clearly shown that glass eels that metamorphose at an earlier age also tend to migrate to coastal regions at a younger age, indicating that early metamorphosing larvae recruit earlier (Fig. 3). The same linear relationship has been found for glass eels of the other tropical species *Anguilla bicolor pacifica*, *A. marmorata*, *A. bicolor bicolor*, and the temperate species *A. japonica*,

A. australis, *A. anguilla*, *A. rostrata* and *A. dieffenbachii* (eg. Tsukamoto & Umezawa 1994, Arai et al. 1999a,b, 2001b, 2002a,b, Marui et al. 2001). This relationship between the timing of metamorphosis and the inshore migration of glass eels seems to be typical for anguillid eels, so metamorphosis must be a key factor during larval migration that is related to the timing of the inshore migration of glass eels.

An interesting finding of this study was that the age at metamorphosis and age at recruitment of *Anguilla celebesensis* that recruit to the Philippines and to northern Indonesia appear to be different. *A. celebesensis* collected at the Cagayan River in the Philippines on 24 September 1994, which metamorphosed and recruited on average (mean \pm SD) at 124 ± 12.0 and 157 ± 13.7 d, respectively, had early life-history parameters 26 to 45 d longer than those of *A. celebesensis* collected from the Poigar River on 7 July 1997 (90 ± 13.6 and 112 ± 14.2 d) and the Poso River on 15 July 1999 (98 ± 7.2 and 122 ± 7.2 d). These findings are similar to those of a previous study (Marui et al. 2001) for *A. celebesensis* glass eels from the Poigar River collected on 13 October 1996 (metamorphosis: 87 ± 15.7 d; recruitment: 112 ± 15.0 d; $N = 14$) and for 3 glass eels collected at the southern tip of Mindanao Island in the Philippines on 30 January 1998 (98, 95, 120 d and 127, 138, 151 d, respectively). In fact, the average age at metamorphosis of glass eels that recruited to the Poigar River in 1997 ranged from 84 to 95 d throughout the year (Arai et al. 2001a), suggesting that *A. celebesensis* glass eels recruiting to the Poigar River may consistently have a shorter larval duration than those that recruit to the Philippines. The *A. celebesensis* glass eels from both the Poso and Poigar Rivers have early life-history parameters that are shorter than those of any other anguillid glass eels studied (see Arai et al. 2001b, Marui et al. 2001), which suggests that the distance between their spawning areas and the Poso and Poigar Rivers in Indonesia may be much shorter than between the spawning area and the recruitment area of *A. celebesensis* in the Philippines.

The patterns of surface circulation around the Philippines and northern Indonesia make it difficult to develop a hypothesis as to how the 3 samples of glass eels could have originated from the same spawning population. The surface circulation of the eastern side of the Philippines and the Celebes Sea is primarily influenced by water from the westward-flowing North Equatorial Current (NEC) that predominates between about 5 to 17° N in the western North Pacific (Reverdin et al. 1994, Kaneko et al. 1998, Kawabe & Taira 1998) because this water flows both north and south (Toole et al. 1990) when it reaches the east coast of the Philippines (Fig. 1). The northern part flows north past the northern Philippines to enter the northward flow of the

Kuroshio Current northeast of Taiwan, and the southern part turns south to create the southward flow of the Mindanao Current (Wijffels et al. 1995, Qu et al. 1998). The Mindanao Current flows south along the eastern side of the southern Philippines and reaches the Mindanao Eddy region at the mouth of the Celebes Sea, and then at least part of it enters the Celebes Sea (Lukas et al. 1991, Miyama et al. 1995), while another part enters the North Equatorial Countercurrent, which flows to the east. Therefore, the only place where *Anguilla celebesensis* could spawn and recruit to all 3 areas sampled during the present study would be the western NEC region, which has recently been reported to be a spawning area for *A. marmorata* (Miller et al. 2002).

However, if all *Anguilla celebesensis* were spawning in this region, based on the distances from the NEC to the sampling locations in both areas, the glass eels recruiting to northern Indonesia should be older than those in the northern Philippines, but this was not the case. The age data from the glass eels sampled in northern Indonesia and the Philippines in this and previous studies and the ocean current patterns of the region suggest that these glass eels came from at least 2, or more likely 3, spawning areas. Although it is theoretically possible that the *A. celebesensis* glass eels from the Poigar and Poso Rivers on opposite sides of Sulawesi Island could have come from a spawning area near the mouth of the Celebes Sea, recent data on the distribution of leptocephali of this species indicate that spawning occurs in both the Celebes Sea and in Tomini Bay, where the Poso River reaches the sea (Aoyama et al. 2003).

The fact that the life-history parameters of the *Anguilla celebesensis* glass eels from the Cagayan River in the northern Philippines (which metamorphosed and recruited on average at 124 ± 12.0 and 157 ± 13.7 d, respectively) do not differ significantly from the corresponding parameters (120 ± 13.0 and 154 ± 13.5 d) for *A. marmorata* collected in the Cagayan River (Arai et al. 1999b), suggests that the *A. celebesensis* that recruited to the northern Philippines might have been transported from somewhere in the same region of the NEC as the spawning area of *A. japonica* (Tsukamoto 1992) and the northern population of *A. marmorata* (Ishikawa 1998), which has recently been identified on the basis of the consistent presence of leptocephali there (Miller et al. 2002), some of which have been genetically identified (Aoyama et al. 1999). Both species have been collected in relatively large numbers (800 to 1000 elvers) in the Cagayan River estuary in some years (Tabeta et al. 1976). Therefore, although *A. celebesensis* has not been genetically identified from the NEC in the summer or early fall, it is possible that it was not detected

among the *A. marmorata* leptocephali because of the similar morphology of these 2 species. It is also possible that *A. celebesensis* has a different spawning season in the NEC than *A. marmorata*, which also appears to have a very different pattern of recruitment that includes areas from southern Japan to northern Indonesia (Ishikawa 1998, Yamamoto et al. 2001, Miller et al. 2002). Another alternative is that this apparent northern population of *A. celebesensis* in the Philippines and possibly Taiwan may spawn over deep water in the northern South China Sea; however, it is difficult to evaluate this hypothesis at present.

However, if *Anguilla celebesensis* does spawn in the NEC along with the other 2 species, this would be an extremely interesting discovery, since it would indicate that 3 species with apparently different recruitment patterns all utilize the same westward flowing current and then differentially recruit to very specific areas. Further otolith analysis of glass eels of *A. celebesensis* from various areas of the Philippines and Taiwan in combination with genetic population studies are needed along with year-round sampling of leptocephali in the NEC to resolve these interesting questions about the life history and population structure of *A. celebesensis* in the western North Pacific and Indonesian Seas.

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