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Evidence of a Spawning Area of *Anguilla marmorata* in the North Equatorial Current of the Western North Pacific

Abstract

Leptocephali that appear to be predominantly *Anguilla marmorata* have been consistently collected in the same area of the North Equatorial Current (NEC) in the western North Pacific during three consecutive cruises in June and July of 1991 (N = 28), 1994 (N = 20), and 1995 (N = 27). These *A. marmorata* type leptocephali were collected between 131°E to 142°E and 13°N and 20°N, to the west of the Mariana Islands, in 20 tows in 1991, in 14 tows in 1994 and in 17 tows in 1995, indicating a widespread presence, but a relatively low abundance. Six of these specimens (16.3-36.0 mm TL) from the 1995 cruise, which were of the typical size range of these leptocephali, have been genetically confirmed as the longfin species *A. marmorata* by Aoyama et al.⁽¹⁾ The consistent presence of recently spawned *A. marmorata* type leptocephali (9-20 mm) in all three years suggests that the western region of the NEC is the spawning area of the northern population of *A. marmorata* that has been identified genetically by Ishikawa⁽²⁾. These leptocephali would then be transported westward by the NEC and could either be transported north into the Kuroshio Current and toward Taiwan and Japan, or south toward the southern Philippines and into the Celebes Sea by the Mindanao Current. The presence of other genetically distinct populations of *A. marmorata*⁽²⁾, the presence of *A. marmorata* leptocephali in the equatorial region to the southeast and in the western South Pacific⁽¹⁾, and the patterns of surface circulation in the western Pacific, indicate that unlike temperate anguillid species, this species appears to have multiple spawning areas.

Key words: *Anguilla marmorata*, Leptocephali, Spawning area, North Equatorial Current

Anguilla marmorata is a tropical anguillid eel that is widely distributed throughout most of the western Pacific and Indian Oceans. It has been reported from the southern coast of Japan, Taiwan, southeastern China, throughout the Indo-Pacific region, New Caledonia, the islands of Polynesia and French Polynesia, and in the eastern and southwestern Indian Ocean⁽³⁾. However, in contrast to temperate species

such as the Japanese eel *Anguilla japonica* and the Atlantic eels *Anguilla rostrata* and *Anguilla anguilla*, relatively little is known about the life history of *A. marmorata*. This species has recently been found to consist of several regional populations based on genetic analysis, including a distinct North Pacific population as well as several South Pacific and Indian Ocean populations⁽²⁾, so it presumably has several different spawning areas throughout the western

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Pacific and Indian Oceans. In fact, genetically identified *A. marmorata* leptocephali have been collected in widely separated areas of the North and South Pacific Oceans during the same research cruise, clearly indicating that there are at least two spawning areas in the western Pacific Ocean⁽¹⁾.

There appears to be an extended spawning period for *A. marmorata* in the western Pacific based on the wide size range of leptocephali that have been collected during the same season⁽¹⁾ and on the recruitment patterns and back-calculated spawning dates of glass eels. A pattern of almost year-round recruitment also has been observed in *A. marmorata* glass eels collected along Sulawesi Island in Indonesia⁽⁴⁾. Almost year-round spawning also has been indicated by back-calculated spawning dates and the seasonal occurrence of glass eels recruiting to freshwater on to Sulawesi Island⁽⁵⁾ and also in southern Japan⁽⁶⁾. In addition, back-calculated spawning dates from analyses of otolith microstructure in various samples of *A. marmorata* glass eels^(7, 8) and leptocephali⁽⁹⁾ have indicated a wide range of spawning times for this species.

Until the recent advent of molecular techniques for genetic identification of anguillid eels^(1,10), identification of some of the leptocephali of both temperate and tropical eels has been difficult due to overlap in the ranges of number of myomeres. However, the development of these molecular techniques for genetically identifying anguillid eels has enabled definitive identification of leptocephali collected in offshore areas of the western Pacific Ocean. The recent identification of relatively small (16.3-36.0 mm TL) leptocephali of *A. marmorata* in the North Equatorial Current (NEC) in the western North Pacific⁽¹⁾ has provided support that the leptocephali that have been consistently collected there during three research cruises of the RV Hakuho Maru of the Ocean Research Institute of the University of Tokyo, during the summer and early fall season of 1991, 1994, and 1995, are *A. marmorata*. In this paper we present data on the distribution, size and morphology of these leptocephali in relation to

surface circulation patterns in the western Pacific that indicates the western North Equatorial Current area is one of the spawning areas of this species.

Materials and Methods

Leptocephali were collected during three cruises of the RV Hakuho Maru of the Ocean Research Institute of the University of Tokyo during the June to September season (Table 1). The 1991 cruise sampled in a large grid of stations that extended from 10–22°N and from 131 to 155°E (Fig. 1). The 1994 cruise sampled in a smaller grid within the larger 1991 sampling area, from 13–17°N and from 134–141°E. In contrast, the 1995 cruise sampled within a similar area as the 1994 cruise at two different periods⁽¹⁾ with the cruise track extending southeastward and into the South Pacific Ocean before returning to the study area described here.

Leptocephali were collected with a 3 m Issacs-Kidd Midwater Trawl that had an 8.7 m² mouth opening with 0.5 mm mesh, in both oblique tows from the surface to 300 m and in horizontal step tows within the upper 150 m. Specimens were sorted fresh from the plankton, measured to the nearest 0.1 mm total length (TL), and meristic characters such as the total number of muscle segments, or myomeres, preanal myomeres, predorsal myomeres, and the number of myomeres until the last vertical blood vessel were counted. Specimens were then either preserved in formalin or in 95% ethanol.

Results and Discussion

Distribution of leptocephali

The *A. marmorata* type leptocephali collected during the three cruises, 1991 (N = 28), 1994 (N = 20), and 1995 (N = 27), were located in an area between 131°E to 142°E and 13°N and 20°N, to the west of the Mariana Islands, in 20 tows in 1991, in

14 tows in 1994 and in 17 tows in 1995 (Fig. 1). For convenience, these leptocephali will be subsequently referred to as *A. marmorata* leptocephali based on the genetic identification of some specimens and the other factors discussed below, although the possibility that some belong to other species cannot be completely ruled out without genetic data. The specimens were collected in the three westernmost transects of the 1991 cruise,

but not in three transects to the east. The sampling areas of the 1994 and 1995 cruises were limited to the area to the west of the Mariana Islands and *A. marmorata* leptocephali were collected at many stations throughout the area. These collections were in an overlapping area with the distribution of *A. japonica* leptocephali in the 1991 cruise⁽¹⁾, which indicates that both species appear to spawn within the western NEC.

Table 1. Sampling dates during the three cruises that collected *Anguilla marmorata* leptocephali in the North Equatorial Current Region of the western North Pacific and the average and range of total length and total number of myomeres of the specimens from each cruise.

	<i>KH-91-4</i>	<i>KH-94-2</i>	<i>KH-95-2</i>		
			<i>Leg 1</i>	<i>Leg 4</i>	<i>1995 Total</i>
Sampling dates	17 Jun – 18 Jul	19 Jun – 6 Jul	16 - 25 Jul	16 – 23 Sep	
Total number of specimens	28	20	20	7	27
Avg. total length (mm) ± standard deviation	22.2 ± 13.0	26.2 ± 7.8	23.0 ± 8.4	28.2 ± 11.4	24.4 ± 9.3
Range of total length (mm)	9.6 – 56.0	10.5 – 43.3	9.7 – 39.6	14.3 – 43.1	9.7 – 43.1
Avg. total myomeres ± standard deviation	103.3 ± 1.7	103.0 ± 1.8	105.0 ± 8.2	103.0 ± 1.6	104.5 ± 2.5
Range of total myomeres	100 – 108	100 – 106	101 – 109	101 – 106	101 – 109

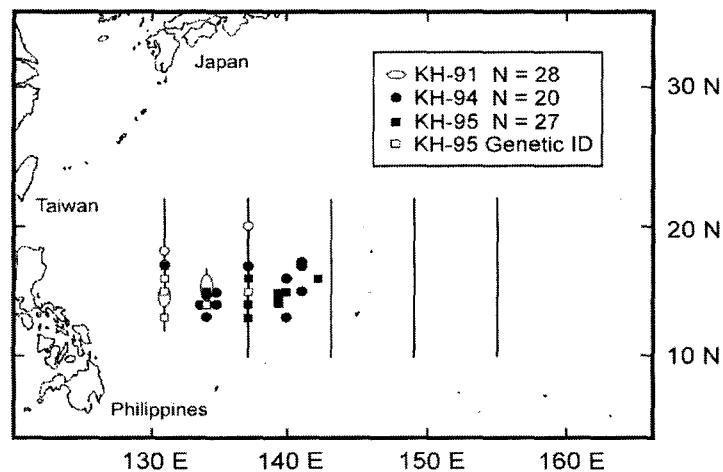


Fig. 1. Map showing the locations where *Anguilla marmorata* leptocephali were collected during three cruises in the North Equatorial Current region of the western North Pacific. The lines represent transects of negative stations during the 1991 cruise. The specimens identified using genetic analysis⁽¹⁾ are indicated by open squares, but are included in the sample size for other 1995 specimens.

Size and morphological characteristics of leptocephali

The size ranges and ranges of total myomeres were similar between years, and these leptocephali had the same general morphological features as all anguillid leptocephali. They lacked any pigment and had the typical body shape of anguillid leptocephali (Fig. 2). The size ranges of the *A. marmorata* leptocephali were similar between all three years, with lengths ranging from 9.6 to 56.6 mm TL (Fig. 3). Specimens as small as 9 - 10 mm TL were collected in all three years (Table 1). These specimens had similar

average numbers of total myomeres among years (103.0-104.5), and all ranged between 100 and 109 total myomeres (Table 1, Fig. 4), which is characteristic of *A. marmorata*. Thus, similarly sized leptocephali that have the characteristics of *A. marmorata* were present in all three years in the region that was sampled. Six of these specimens (16.3-36.0 mm TL) from the 1995 cruise, which were of the typical size range of these leptocephali, have been genetically confirmed as *A. marmorata* by Aoyama et al.⁽¹⁾, and three other larger specimens (49.6-50.5 mm TL) were genetically identified as *Anguilla bicolor pacifica*.

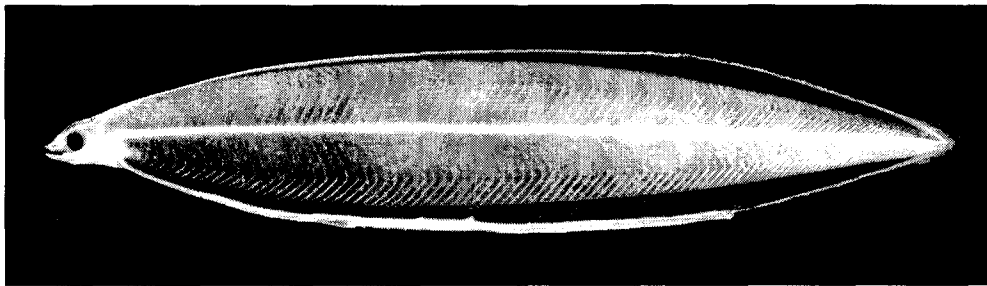


Fig. 2. A photograph of a 55.5 mm TL *Anguilla marmorata* leptocephali collected on 15 July during the 1991 cruise. Photograph courtesy of Noritaka Mochioka.

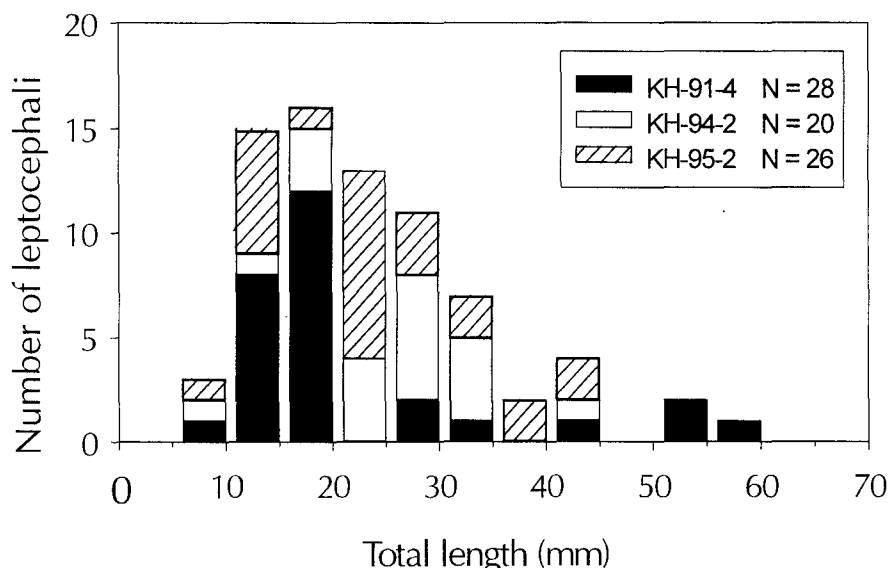


Fig. 3. Length frequency distributions of *Anguilla marmorata* leptocephali collected in three different years in the western North Pacific.

Although these shortfin (*A. bicolor pacifica*) and longfin *A. marmorata* leptocephali have overlapping ranges of total myomeres/vertebrae⁽³⁾, they can be separated based on the number of ano-dorsal myomeres⁽¹²⁾ at lengths greater than 20 mm. In our collections, 63% of the specimens of this larger size were the longfin type, and all 23 of the *A. bicolor pacifica* shortfin leptocephali collected in the study area during two of the cruises were greater than 40 mm TL, with most being collected to the northeast or at the southern

edge of the study area. Therefore, in contrast to the longfin eel, *A. marmorata*, there is no evidence that *A. bicolor pacifica* spawns in the study area during the summer or fall season. Another longfin species, *Anguilla celebesensis*, also has a similar range of vertebrae as the other two species, but their leptocephali have not been genetically identified in the NEC region. In addition, the adult range of *A. marmorata* extends farther north than *A. celebesensis*, which is only found as far north as the Philippines⁽³⁾.

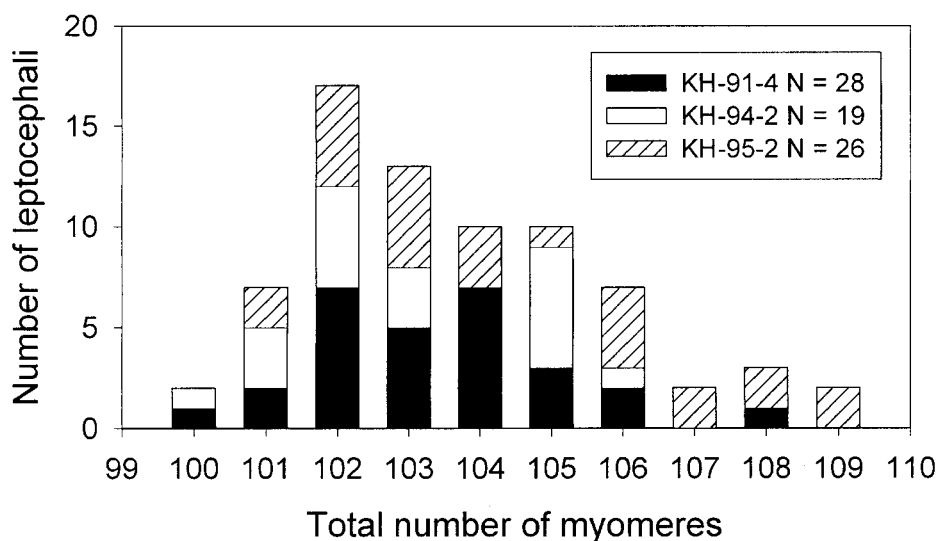


Fig. 4. Myomere frequency distribution of *Anguilla marmorata* leptocephali collected in three different years in the western North Pacific.

Spawning and recruitment in the western North Pacific

The presence of *A. marmorata* leptocephali in the western NEC area to the west of the Mariana Islands in three different years strongly suggests that this area is a spawning area of this species. Leptocephali were collected throughout the area to the west of 142°E, but not at stations farther to the east. Leptocephali were present at stations at the southwestern edge of the sampling area, so the

western and southern extent of this spawning area has not been determined sufficiently.

The area of the western North Pacific where *A. marmorata* leptocephali have been consistently collected is within the NEC and typically has westward surface flow during the summer season⁽¹³⁻¹⁵⁾ and throughout the year⁽¹⁶⁾. The northern part of this westward flow turns north (Fig. 5) and enters the northward flow of the Kuroshio Current northeast of Taiwan⁽¹⁷⁾. The southern part of the NEC enters the southward flow of the Mindanao Current^(18, 19). The

Mindanao Current flows south along the eastern side of the southern Philippines and then at least part of it enters the Celebes Sea^(20, 21) (Fig. 5).

Therefore, leptocephali originating in this spawning area in the western NEC could be transported to all of the areas that *A. marmorata* is known to recruit to in the North Pacific. This species is known to recruit to the east coast of the southern half of Japan, Taiwan, parts of southeastern China, the Philippines and Sulawesi Island, Indonesia^(3, 4, 7, 22, 23). Individuals from each of these areas have been found to be part of a northern subpopulation of this species that is genetically different from individuals from other areas to the south and southwest, and in the Indian Ocean⁽²⁾. Thus the surface current patterns of the western North Pacific (Fig. 5) appear to be capable of transporting *A.*

marmorata leptocephali from the NEC spawning area to all the areas that have been found to be part of the northern population. This suggests that Jespersen's⁽¹³⁾ speculation about the spawning area of tropical eels in the Indo-Pacific being near the Celebes or Sulu Seas, although still potentially true for *A. bicolor pacifica* and *A. celebescensis*, is not true in the case of *A. marmorata*, based on this study and recent genetic studies. The presence of other genetically distinct populations of *A. marmorata*, the collection of *A. marmorata* leptocephali in the equatorial region further south and east as well as in the western South Pacific⁽¹⁾, and the patterns of surface circulation in the western Pacific, indicate that unlike temperate anguillid species, this species appears to have multiple spawning areas and potentially different recruitment mechanisms.

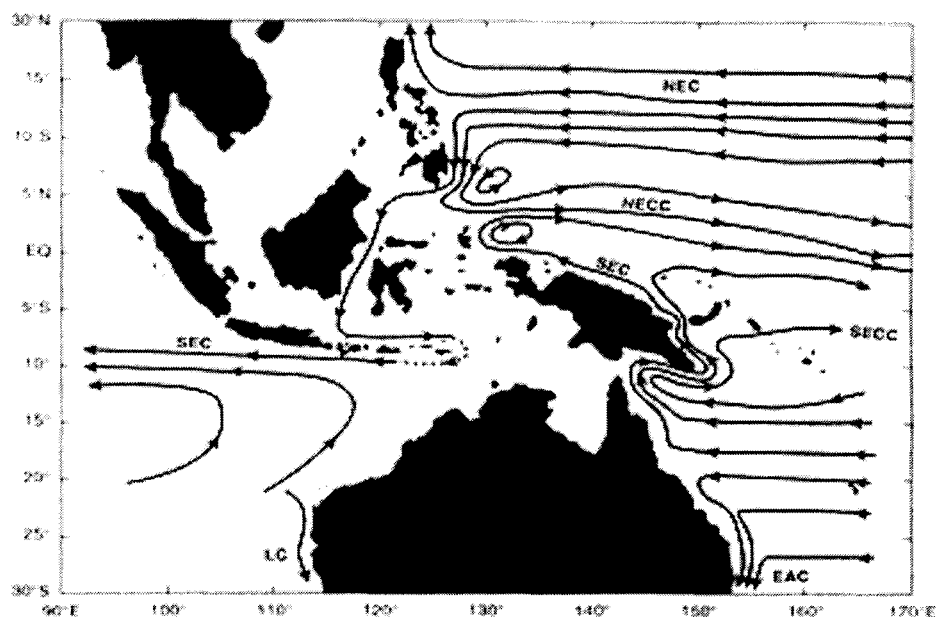


Fig. 5. Diagram showing the general surface circulation features of the southwest Pacific Ocean, after Godfrey⁽²¹⁾, with the North Equatorial Current (NEC), North Equatorial Countercurrent (NECC) and South Equatorial Current (SEC) labeled.

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References

1. Aoyama, J, N. Mochioka, T. Otake, S. Ishikawa, Y. Kawakami, P. H. J. Castle, M. Nishida and K. Tsukamoto (1999) Distribution and dispersal of anguillid leptocephali in the western Pacific Ocean revealed by molecular analysis. *Mar. Ecol. Prog. Ser.*, **188**: 193-200.
2. Ishikawa, S. (1998) Molecular study on the population structure of *Anguilla marmorata*. Ph. D. Dissertation, The University of Tokyo.
3. Ege, V. (1939) A revision of the Genus *Anguilla* Shaw. *Dana Rep.*, **16**(13): 8-256.
4. Arai, T., J. Aoyama, D. Limbong and K. Tsukamoto (1999a) Species composition and inshore migration of tropical eels, *Anguilla* spp., recruiting to the estuary of the Poigar River, Sulawesi Island. *Mar. Ecol. Prog. Ser.*, **188**: 299-303.
5. Arai, T., J. Daniel, T. Otake and K. Tsukamoto. Recruitment mechanisms of tropical eels, *Anguilla* spp., and implications for the evolution of oceanic migration in the genus *Anguilla*. *Mar. Ecol. Prog. Ser.*, (in press).
6. Mochioka, N., T. Yamamoto, K. Hirano, and O. Tabeta (2000) Inshore migration and hatching season of the tropical eel *Anguilla marmorata* immigrating to the Pacific coast of Kyushu, Japan. Abstracts of the 3rd East Asian Symposium on Eel Research-Sustainability of Resources and Aquaculture of Eels, Taiwan Fisheries Research Institute, November 16-18, 2000, Keelung, Taiwan, 23.
7. Arai, T., D. Limbong, T. Otake and K. Tsukamoto (1999b) Metamorphosis and inshore migration of tropical eels, *Anguilla* spp., in the Indo-Pacific. *Mar. Ecol. Prog. Ser.*, **182**: 283-293.
8. Marui, M., T. Arai, M. J. Miller, D. J. Jellyman and K. Tsukamoto (2001) Comparison of early life history between New Zealand temperate eels and Pacific tropical eels revealed by otolith microstructure and microchemistry. *Mar. Ecol. Prog. Ser.*, **213**: 273-284.
9. Arai, T., J. Aoyama, S. Ishikawa, M. J. Miller, T. Otake, T. Inagaki and K. Tsukamoto.(2001) Early life history of tropical *Anguilla* leptocephali in the western Pacific Ocean. *Mar. Biol.*, **138**: 887-895.
10. Aoyama, J., S. Watanabe, M. Nishida and K. Tsukamoto (2000) Discrimination of catadromous eel species, genus *Anguilla*, using PCR-RFLP analysis of the mitochondrial 16SrRNA domain. *Trans. Am. Fish. Soc.*, **129**: 873-878.
11. Tsukamoto, K. (1992) Discovery of the spawning area for the Japanese eel. *Nature*, **356**: 789-791.
12. Jespersen, P. (1942) Indo-Pacific leptocephali of the genus *Anguilla*. *Dana Rep.*, **22**: 1-128.
13. Kaneko, I., Y. Takatsuki, H. Kamiya and S. Kawae (1998) Water property and current distributions along the WHP-P9 section (137 -142°E) in the western North Pacific. *J. Geophys. Res.*, **103**: 12,959-12984.
14. Kawabe, M. and K. Taira (1998) Water masses and properties at 165°E in the western Pacific. *J. Geophys. Res.*, **103**: 12, 941-12, 958.
15. Wijffels, S. E., M. M. Hall, T. Joyce, D. J. Torres, P. Hacker and E. Firing (1998) Multiple deep gyres of the western North Pacific: a WOCE section along 149°E. *J. Geophys. Res.*, **103**: 12, 985-13, 009.
16. Reverdin, G., C. Frankignoul, E. Kestenare and M. J. McPhaden (1994) Seasonal variability in the surface currents of the equatorial Pacific. *J. Geophys. Res.*, **99**: 20, 323-20, 344.
17. Fine, R. A., R. Lukas, F. M. Bingham, M. J. Warner and R. H. Gammon (1994) The western equatorial Pacific: A water mass crossroads. *J. Geophys. Res.*, **99**: 25, 063-25, 080.
18. Lukas, R., E. R. Firing, P. Hacker, P. L. Richardson, C. A. Collins, R. Fine and R. Gammon (1991) Observations of the Mindanao Current during the western Equatorial

- Pacific Ocean Circulation Study. *J. Geophys. Res.*, **96**: 7089-7104.
19. Qu, T., H. Mitsudera and T. Yamagata (1998) On the western boundary currents in the Philippine Sea. *J. Geophys. Res.*, **103**: 7537-7548.
20. Miyama, T., T. Awaji, K. Akitomo and N. Imasato (1995) Study of seasonal transport variations in the Indonesian seas. *J. Geophys. Res.*, **100**: 20, 517-20, 541.
21. Godfrey, J. S. (1996) The effect of the Indonesian throughflow on ocean circulation and heat exchange with the atmosphere: A review. *J. Geophys. Res.*, **101**: 12, 217-12, 237.
22. Yu, H. T., C. S. Yu and W. N. Tzeng (2000) Species composition of the anguillid evers in estuaries of Taiwan - an application of molecular genetics. Abstracts of the 3rd East Asian Symposium on Eel Research-Sustainability of Resources and Aquaculture of Eels, Taiwan Fisheries Research Institute, November 16-18, 2000, Keelung, Taiwan, 45.
23. Tabeta, O., I. E. Setiawan and N. Mochioka (2000) Glass eels from Hainan Island and Guangdong Province, southern China. Abstracts of the 3rd East Asian Symposium on Eel Research-Sustainability of Resources and Aquaculture of Eels, Taiwan Fisheries Research Institute, November 16-18, 2000, Keelung, Taiwan, 32.