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Contrasting assemblages of leptocephali in the western Pacific

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ABSTRACT: To learn about the larval distributions and reproductive ecologies of marine and freshwater eels, the assemblages of anguilliform leptocephali were compared between 2 ecologically different areas along the margins of the western Pacific Ocean using the catch data from 2 sampling surveys targeting leptocephali. The assemblages on the outer shelf and slope of the East China Sea in November and December 2000 were dominated by the leptocephali of 2 abundant taxa of congrid and synaphobranchid eels that had been spawning along the shelf break, and by the leptocephali of 3 other families. The leptocephali of many other families were rare, and catch rates were lower over deeper water to the south. In contrast, assemblages of leptocephali were very diverse and showed a widespread presence of most families over the deep water in close proximity to Sulawesi Island in the Indonesian Seas in May 2001, but there were no high catch rates due to the lack of recent spawning activity offshore. As a result, the northern study area had a higher overall catch rate of leptocephali, but much lower richness, diversity, and evenness of taxa than the southern study area in the Indonesian Seas. Cluster analysis distinguished 3 general assemblages that corresponded mostly to each of the 2 study areas and to a group of stations that were mixed between the 2 study areas. This analysis indicates that assemblages of leptocephali can vary widely depending on the location of sampling and on the eel fauna in each particular area.

KEY WORDS: Leptocephali · Eels · Species assemblages · East China Sea · Kuroshio Current · Indonesian Seas

INTRODUCTION

Various species of eels of the order Anguilliformes inhabit almost all of the different types of marine habitats of the world's oceans, from temperate regions through to the tropics (Castle 1984, Böhlke 1989a). However, relatively little is known about the life histories of most species of eels due to the difficulty in capturing them or observing their behavior. Although juveniles and adults inhabit diverse habitats, ranging from freshwater and shallow marine habitats to the mesopelagic and bathypelagic zones, their larvae, which are called leptocephali, are found almost exclusively in the surface layer of the ocean (Castonguay & McCleave 1987a, Smith 1989). Therefore, studies on their leptocephali are often the best way to learn about the general distribution and reproductive ecology of most species of eels. In addition to the more well-known studies on the leptocephali of the catadromous eels of the genus *Anguilla* (see Tsukamoto 1992, McCleave 1993), there have been studies on the identification and life history characteristics of the leptocephali of marine eels in the Atlantic (e.g. Smith 1974, Blache 1977, Castle 1979, Leiby 1984, Castonguay & McCleave 1987b, Böhlke 1989b, Wippelhauser et al. 1996, Miller 2002) and in the Pacific (e.g. Castle 1965, Tabeta & Mochioka 1988, Mochioka et al. 1991) and Indian Oceans (Castle 1969). There also have been studies on the assemblage structure of leptocephali in the western North Atlantic (Miller & McCleave 1994,

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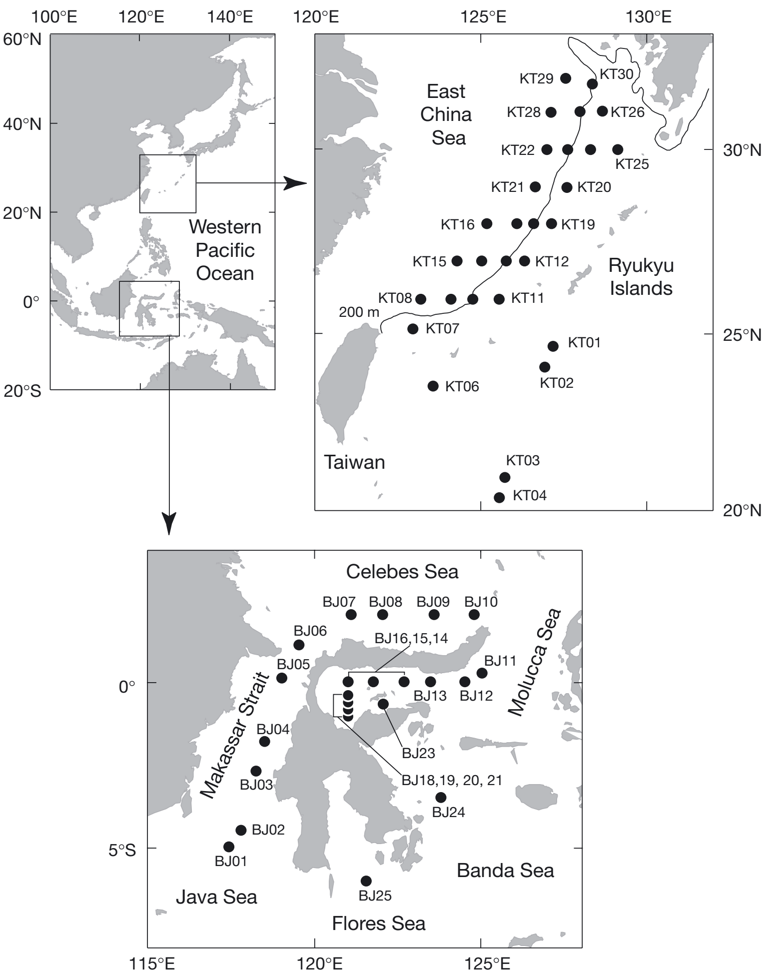

Fig. 1. Study areas where sampling for leptocephali occurred in the western Pacific Ocean, during Cruise KT-00-16 of RV 'Tansei Maru' in the East China Sea region in 2000 and Cruise BJ-01-1 of RV 'Baruna Jaya VII' in the Indonesian Seas around Sulawesi Island in 2001. Stns BJ13 to BJ23 are located in Tomini Bay of Sulawesi Island, which is the large island in the center of the lower map

Miller 1995), but there have not been any studies that have analyzed the assemblages of leptocephali in the western Pacific Ocean.

In this study, we used 2 similar sampling surveys for leptocephali in markedly different zoogeographic regions at about the same longitude along the margin of the western Pacific. The first study area was located at the westernmost edge of the western North Pacific (WNP) and in the East China Sea (ECS), and the second study area was located to the south in the central Indonesian Seas around Sulawesi Island (SLI), Indonesia. A wide variety of marine eels are known from the ECS and surrounding regions (Masuda et al. 1984, Nakabo 2000), and the large shallow shelf area of the ECS is an important area for many different commercial fishes, including several species of marine eels of the order Anguilliformes (Okamura 1986). In contrast, the sampling stations in the southern study area were all located over the deep water basins surrounding SLI, Indonesia.

The Indonesian archipelago is located in the center of the region that is sometimes referred to as the East Indian region (Indonesia, Malaysia, the Philippines, New Guinea), which has been regarded as the center of diversity for marine fishes (Randall 1998, Allen & Adrim 2003). The coral reefs of Indonesia support a rich fauna of marine eels (Allen & Adrim 2003), and the region around SLI has been hypothesized to be where the catadromous eels of the genus *Anguilla* originated, because of the presence of the most likely basal species, *Anguilla borneensis* (Aoyama et al. 2001). In addition, out of the total of 18 members of the Genus *Anguilla* worldwide, there are at least 7 tropical species or subspecies of anguillid eels in the relatively small area of Indonesia (Watanabe 2003), and their leptocephali have been studied in this region by Jespersen (1942).

Because of the lack of knowledge about most eels, studies on the assemblage structure of leptocephali in these 2 areas provide a good opportunity to learn about the characteristics of the eel fauna of different regions of the Pacific Ocean, and to contribute to the relatively limited knowledge about the reproductive and larval ecology of marine eels in general. Our specific objectives in this paper were to directly compare the overall taxonomic composition, relative abundance, richness and diversity, and size of the leptocephali in the 2 areas, and to compare their assemblage structures using multivariate analysis. The findings of these analyses are then discussed in relation to the present state of knowledge about assemblages of leptocephali and the reproductive ecology of eels worldwide.

MATERIALS AND METHODS

Study areas. The first study area was located at the westernmost edge of the WNP and in the ECS between 20 and 32° N (Fig. 1). The Kuroshio Current flows northward along the distinct shelf break of the ECS, and this current is a powerful western boundary current similar to the Florida Current part of the Gulf Stream (Lee et al. 2001). The high velocity region of the Kuroshio in this area has been observed to be ca. 150 km wide, and is located up against the shelf break in the fall season (Kaneko et al. 1990, Yuan et al. 1994). Sampling in the ECS occurred within the warm, lower productivity water of the Kuroshio, across the Kuroshio front and its associated eddies (Qui et al. 1990), and into the colder (Chen et al. 1994), higher productivity (Hama et al. 1997) water over the shelf of the ECS. Sampling also occurred over the much deeper water to the south of the Ryukyu Islands in the WNP.

The eastern ECS region is highly dynamic due to the influence of the Kuroshio Current, making it an interesting area to study the assemblages of leptocephali. Much of the water that enters the Kuroshio probably originates in the North Equatorial Current (NEC) in the WNP (Nitani 1972), and the NEC and Kuroshio appear to transport larvae of the catadromous Japanese eel *Anguilla japonica* from their spawning area in the NEC (Tsukamoto 1992) into the ECS, where they eventually recruit to the coastlines of East Asia (Tsukamoto 1990, T. Otake et al. unpubl.). The NEC bifurcates into the northward flowing Kuroshio and the southward flowing Mindanao Current to the east of the Philippines (Toole et al. 1990, Qu & Lukas 2003). The southward flowing Mindanao current then flows along the east coast of the southern Philippines before entering the Celebes Sea (Lukas et al. 1991).

The second study area was located in the central Indonesian Seas area around Sulawesi Island (SLI), Indonesia between 6° S and 2° N, and included stations over the deep-water basins in the Celebes Sea, Makassar Strait and in the areas on the eastern and southern sides of SLI, which are all 1000 to 5000 m deep. Except for in the Java Sea, the continental shelves around the islands of the Indonesian archipelago are relatively narrow, and the surface currents in the Celebes Sea and Makassar Strait are likely to be dominated by the southward flow of the Indonesian Throughflow from the WNP and wind driven or tidal flow (Wyrtki 1961, Miyama et al. 1995, Hatayama et al. 1996). Because the Indonesian Throughflow appears to be largely fed by flow into the Celebes Sea from the Mindanao Current, the 2 study areas are hydrographically linked by the inflow of water from the NEC southward within the Mindanao Current, and northward within the Kuroshio.

Sampling and identification. Sampling was conducted during a cruise of the RV 'Tansei Maru' (KT-00-16) of the Ocean Research Institute, the University of Tokyo, from 27 November to 7 December 2000 in the ECS, and a cruise of the RV 'Baruna Jaya VII' of the Indonesian Institute of Sciences from 8 to 26 May 2001 around SLI (Fig. 1). Leptocephali were collected during both cruises with identical Isaacs Kidd Midwater Trawls (IKMT), with 8.7 m^2 mouth openings and 1.0 or 0.5 mm mesh.

In the ECS, sampling took place during both day and night (sunrise and sunset occurred at 07:09 and 17:14 h in November at Nagasaki, Japan). Leptocephali were collected in both oblique tows of the IKMT from the surface to 300 m, or to within 20 m of the bottom, and in horizontal step tows within the upper 150 m. Both an oblique and a step tow were made at most stations, but single oblique tows of the IKMT were made at 6 stations (KT01, 02, 03, 04, 13, 27), and a single step tow was made at KT06 and KT12 (Fig. 1; see details in Miller et al. 2002).

Sampling for leptocephali around SLI occurred at 23 stations located in the Java Sea, Makassar Strait, Celebes Sea, Molucca Sea, Tomini Bay, Banda Sea and Flores Sea (Fig. 1) All sampling was done at nighttime from 20:00 to 04:00 h (sunrise and sunset were 05:37 and 18:01 h in May at Jakarta, Indonesia). The IKMT was towed obliquely with 600 m of wire-out to depths of ca. 200 m for ca. 30 min at most stations except for at BJ19 and BJ20. A 60 to 80 min step tow of the IKMT was also made at each station, with a maximum of 450 m of wire-out, which towed horizontally for 10 min at 5 depths of ca. 30, 60, 90, 120 and 150 m.

Leptocephali were sorted fresh from the plankton samples, measured to the nearest 0.1 mm total length, and were either preserved in a 10% formalin-seawater solution or in 99% ethanol after being identified. They were identified to the lowest possible taxonomic level, based on their morphology using Tabeta & Mochioka (1988), Böhlke (1989b), and Castle (1997).

For the analysis in this paper, leptocephali were grouped into the 4 general adult life history categories of eels that can be made at the family level (Castle 1984, Miller & McCleave 1994). These categories are the 'catadromous' fresh water anguillid eels, the completely pelagic 'oceanic' species, which are midwater eels that live primarily in the mesopelagic zone of the open ocean (Derichthyidae, Nemichthyidae, Serrivomeridae), the outer continental shelf or 'slope' species that are deeper water benthic eels (Nettastomatidae, Synaphobranchidae), and the shallow-water 'shelf ' eels that inhabit a wide range of habitats such as coral reefs or other shallow areas with various substrates (Chlopsidae, Congridae, Moringuidae, Muraenidae, Ophichthidae). For simplicity, all taxa will be referred to in the text just by family, subfamily or genus names (without sp. or spp.), even though in most cases there may be more than one species represented by these taxa.

Abundance and diversity. Since fishing effort differed somewhat among individual stations, collection data were standardized by converting them to catch rates. The numbers of individuals at a station were converted to catch rates of the number of leptocephali per 10^5 m^3 of water filtered by the net, using the flow meter revolutions, a calibration factor (m rev^{-1}) and the trawl mouth area (m^2). In this study, catch rates were used as a measure of abundance in the description of the leptocephali assemblages or groups of stations and to show the geographic distribution of the leptocephali of the 4 life history groups of eels. In addition, 2 univariate measures of species diversity, Hill's N1 and N2, were calculated to help compare the assemblages in each study area or group of stations (Hill 1973). Hill's N1 is the exponential of the Shannon-Wiener function (Exp H') and is the index that is most sensitive to changes in rare taxa. Hill's N2 measure of evenness is the reciprocal of Simpson's index (1/D) and is the index that is most sensitive to changes in the more abundant taxa. A justification for this particular choice of measures is provided by Krebs (1989). The catch rates and diversity indices were calculated using the combined data of both oblique and step tows at each station. The catch rates for groups of stations were calculated by pooling the tow volumes and numbers of specimens, but the values of the diversity indices are the average of the values within each particular group of stations. The comparisons of the total lengths of the leptocephali of abundant and/or representative families within each adult life history category were made using the Mann-Whitney rank-sum test.

Multivariate analysis. In order to directly compare the assemblages of leptocephali in the 2 areas, multivariate analysis (cluster analysis and ordination) was performed using the catch rates of leptocephali collected in the oblique IKMT tows that were made during nighttime. Only the night tows were used, because the catches of leptocephali during the day have been found to be significantly lower than at nighttime (Miller & McCleave 1994), and only oblique tows were used because the fishing method of these tows was the same during both cruises. Nighttime oblique tows were made at 20 stations in the ECS and at 21 stations around SLI, and only these stations were compared using cluster analysis with the Bray-Curtis measure and the unweighted pair-group method (UPGMA). Prior to the analysis, taxa were pooled at the genus, subfamily or family level, and then taxa with <2 occurrences were removed. This resulted in 26 taxa being used in the cluster analysis and ordination. The catch rates of taxa at each station were then transformed using a root-root transformation (Field et al. 1982) to scale the values, so the most abundant taxa would not dominate the analysis.

To help evaluate the robustness of the results of the cluster analysis, multidimensional scaling (MDS) was also performed on the same dissimilarity matrix generated for the cluster analysis. MDS helps to visualize the dissimilarity relationships of the assemblages at the various stations, because the distance in the MDS plot has a monotonic relationship to the original distances, so similar assemblages should be shown close together and dissimilar ones far apart. To investigate the underlying reasons for the grouping patterns generated by cluster analysis, SIMPER analysis was employed on the same dissimilarity matrix to determine which taxa most typified the groups identified from the results of the cluster analysis and ordination. A full description of SIMPER is provided by Clarke & Warwick (1994).

RESULTS

Taxonomic composition and abundance of leptocephali

There were 2356 leptocephali of 10 families collected in the ECS region, and 2431 leptocephali of 11 families were collected around SLI, but the relative proportions of the leptocephali of the 4 major life history categories of eels varied considerably between the 2 study areas (Table 1). Over 67% of the total leptocephali in the ECS, and more than 80% of the total around SLI, were shelf species, but the relative proportions of the various taxa were quite different. For example, the leptocephali of the congrid eels *Gnathophis* were the most abundant in the ECS, accounting for 60% of the leptocephali of shelf species, but in contrast, only 17 individuals were observed around SLI. The subfamily Ophichthinae was the only other group of shelf species that was more abundant in the ECS than around SLI. To the south of the ECS in the WNP, the congrids *Ariosoma*, *Gnathophis* and *Conger* consisted of 90% of the shelf species there, and the only 2 chlopsid leptocephali from the entire ECS region were collected at Stn KT06 to the west of Taiwan (Table 1, Fig. 1). The most abundant genera of shelf taxa around SLI were *Ariosoma* and *Neenchelys* (Ophichthidae), and they made up 42% of the shelf species, but in the ECS they made up only less than 5%. The leptocephali of many of the other taxa of the 5 major shelf families such as the Muraenidae, Chlopsidae and Congridae, also were relatively abundant around SLI.

In addition to the very different relative abundances of shelf taxa between the 2 study areas, the composition of slope and oceanic taxa in the 2 areas also were quite different. In the ECS, all except 2 taxa were relatively rare, but around SLI there was a wider variety and greater abundance of these taxa (Table 1). The leptocephali of slope taxa were the second most abundant life history group in the ECS (30% of the total leptocephali) because of the large catches of the synaphobranchid *Dysomma* of the subfamily Ilyophinae. The nettastomatid *Saurenchelys* was also much more abundant in the ECS than around SLI. In the WNP, the

Synaphobranchinae were the only slope leptocephali collected (15% of the total), and no *Dysomma* or *Saurenchelys* were collected (Table 1). Slope taxa were relatively rare around SLI (2.2% of the total), and while oceanic species comprised less than 2% of the total in the ECS, these taxa, such as *Nemichthys* and Serrivomeridae, accounted for ca. 15% of the total from around SLI. The catadromous species, of the genus *Anguilla*, were collected at relatively low abundances in both regions.

Table 1. Numbers (N), proportions (%), and size ranges (TL: total length) of leptocephali collected in the East China Sea region and around Sulawesi Island. Numbers of leptocephali collected at the stations in the western North Pacific (WNP) to the south of the East China Sea are shown in parentheses. Taxa are characterized by their adult life histories as catadromous (CT), shelf (SH), oceanic (OC) or slope (SL)

Taxon	Adult life history	East China Sea N Total	East China Sea N (WNP)	East China Sea %	East China Sea Size range (mm TL)	Sulawesi Island N	Sulawesi Island %	Sulawesi Island Size range (mm TL)
Anguillidae								
Anguilla	CT	9		0.4	51–57	52	2.1	13–51
Chlopsidae								
Chlopsis	SH					52	2.1	9–55
Kaupichthys	SH					97	4.0	20–73
Robinsia	SH					4	0.2	33–49
Thallassenchelys	SH					1	0.0	53–60
Chlopsidae	SH	2	(2)	0.1	55–77	97	4.0	17–68
Congridae								
Ariosoma	SH	65	(15)	2.8	6–239	657	27.0	15–387
Conger	SH	70	(8)	3.0	9–74	108	4.4	14–87
Gnathophis	SH	956	(21)	40.6	7–88	17	0.7	19–75
Gorgasia	SH	2		0.1	13–27	36	1.5	11–53
Heteroconger	SH	4		0.2	11–43	17	0.7	9–69
Uroconger	SH	22		0.9	15–111	99	4.1	10–143
Congrinae	SH	77	(2)	3.3	8–151	117	4.8	10–131
Derichthidae								
Derichthys	OC					9	0.4	20–48
Nessorhamphus	OC					3	0.1	42–48
Moringuidae								
Moringua	SH	3		0.1	16–30	62	2.6	11–55
Muraenidae								
Uropterygiinae	SH	2		0.1	30–53	21	0.9	27–56
Muraenidae	SH	111	(2)	4.7	9–76	286	11.8	8–75
Nemichthyidae								
Avocettina	OC					29	1.2	16–166
Nemichthys	OC	28	(9)	1.2	13–158	183	7.5	13–250
Nettastomatidae								
Nettastomma	SL					1	0.0	88
Nettenchlys	SL	2		0.1	11–12	10	0.4	14–94
Saurenchelys	SL	98		4.2	10–71	13	0.5	18–94
Ophichthidae								
Neenchelys	SH	9		0.4	18–60	178	7.3	15–80
Myrophinae	SH	18		0.8	12–61	23	0.9	27–89
Ophichthinae	SH	253		10.7	8–83	79	3.2	12–134
Serrivomeridae								
Serrivomeridae	OC	6	(1)	0.3	8–33	150	6.2	10–54
Synaphobranchidae								
Ilyophinae	SL	593		25.2	8–43	17	0.7	17–76
Synaphobranchinae	SL	26	(11)	1.1	10–31	13	0.5	21–74
Shelf taxa total		1594		67.7		1951	80.3	
Slope taxa total		719		30.5		54	2.2	
Oceanic taxa total		34		1.4		374	15.4	
Catadromous taxa total		9		0.4		52	2.1	
Total number of specimens		2356	(71)		6–239	2431		8–387

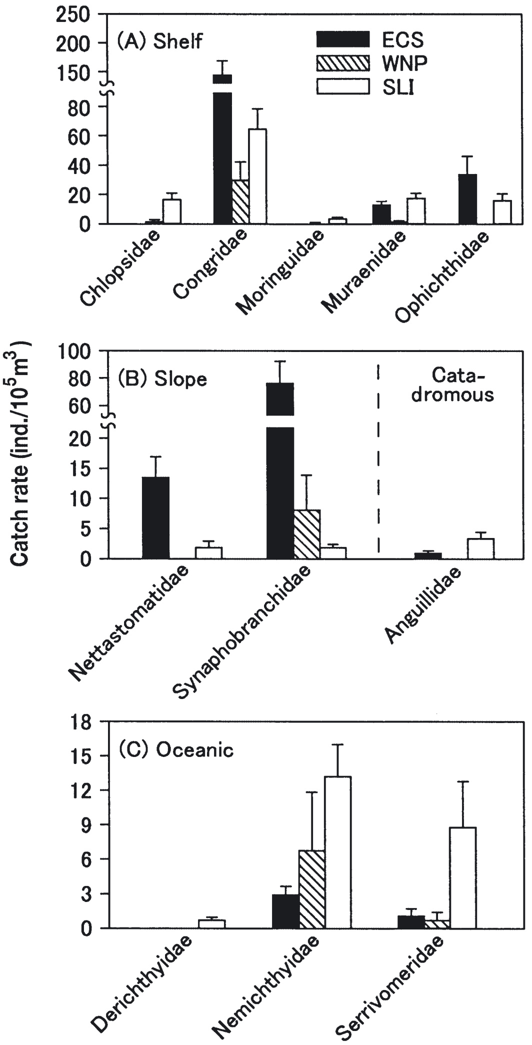

Fig. 2. Catch rates of 11 eel families in the East China Sea (ECS), to the south in the western North Pacific (WNP) and around Sulawesi Island (SLI). Families were characterized by their adult life histories as either (A) shelf, (B) slope or catadromous, and (C) oceanic species

Although the overall number of leptocephali collected around SLI was similar to the ECS region, the total catch rate in the ECS region (249 ind./10^5m^3) was much higher than that around SLI (144 ind./10^5m^3) due primarily to the big catches of *Gnathophis* and *Dysomma* (Fig. 2). After separating out the catch data from the WNP, which had a much lower catch rate (49 ind./10^5m^3), the catch rate in just the ECS was even higher (285 ind/10^5m^3). Leptocephali of the Congridae (144 ind./10^5m^3), Ophichthidae (35 ind./10^5m^3), Synaphobranchidae (76 ind./10^5m^3) and Nettastomatidae (13 ind./10^5m^3) had higher catch rates in the ECS than around SLI or in the WNP. The catch rates of other families in the ECS were lower than they were around SLI, and there were no oceanic species of the Derichthyidae caught there. The catch rates of the few families that were collected in the WNP were low, except for the Congridae (32 ind./10^5m^3).

Geographic distribution of leptocephali

Several geographic patterns were observed in the catch rates of leptocephali of the 4 different life history types of eels at each station in the ECS region (Fig. 3). In the ECS, shelf species had high catch rates at stations on the continental shelf and at some of the northern stations, due to the widespread presence of *Gnathophis*, Ophichthidae, Muraenidae (see Miller et al. 2002), but they had lower catch rates over the continental slope and over the deeper water south of the ECS. In contrast, the slope taxa (mostly *Dysomma*) had a higher catch rate over the continental slope near the 200 m depth contour, and the catches of oceanic taxa were more frequent in the southern part of the study area. The specimens of the catadromous eels *Anguilla japonica* collected in the ECS were in the late stages of metamorphosis into glass eels (T. Otake et al. unpubl.) and were limited to the deep water over the continental slope.

The overall catch rate of the leptocephali of the 4 life history types of eels around SLI did not show many distinct geographic patterns because most taxa were relatively widespread (Fig. 3). The catch rates of shelf species were relatively high throughout the study area around SLI. The oceanic species had the next highest catch rates, and like the slope and catadromous species, they were patchily distributed around the island. The anguillid leptocephali were widely distributed around SLI, with the highest catch rates in Tomini Bay (Fig. 1).

Comparison of sizes of leptocephali

The proportion of small-sized leptocephali collected in the 2 areas was generally greater in the ECS than around SLI for most taxa (Table 1, Fig. 4). The minimum total length (TL) was shorter for many taxa in the ECS due to the apparent spawning of shelf species close to the shelf break (Miller et al. 2002), but the minimum TL for *Anguilla* was smaller near SLI because of spawning activity in Tomini Bay (Aoyama et al. 2003). The various species of congrid leptocephali reach different maximum lengths ranging from ca. 80 to 400 mm (see Böhlke 1989b), so comparisons of the length frequency distributions of *Ariosoma*, which have maximum lengths of over 200 mm, were made

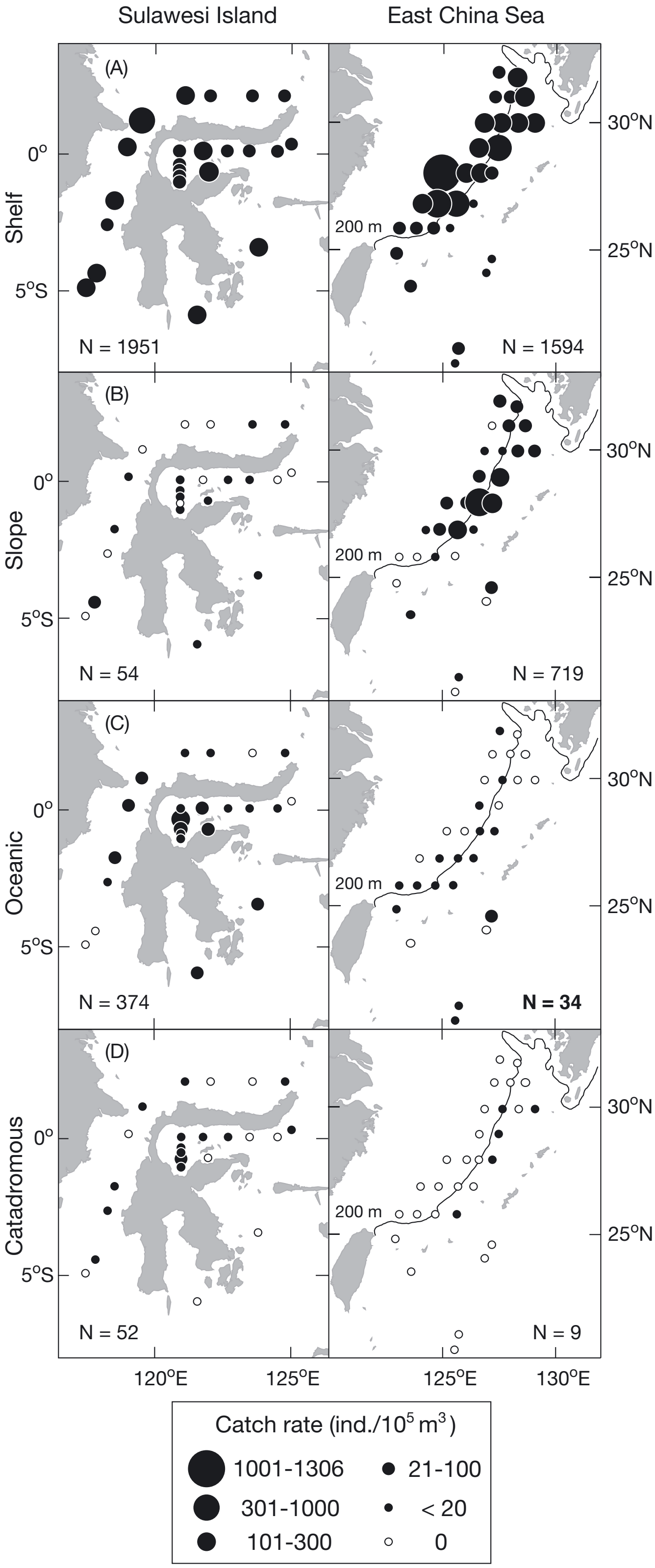

Fig. 3. Geographic distribution and catch rates of leptocephali of the 4 life history categories of eels in the East China Sea region and around Sulawesi Island. Circles represent the abundance of leptocephali expressed as catch-rate values (ind./$10^5 m^3$)

separately from the rest of the congrids that have shorter maximum lengths. The total lengths of the *Ariosoma*, other congrid, nemichthyid, and synaphobranchid leptocephali collected in the ECS region were each significantly different from those around SLI ($p < 0.001$), and these differences were clearly evident in their length frequency plots (Fig. 4). Although

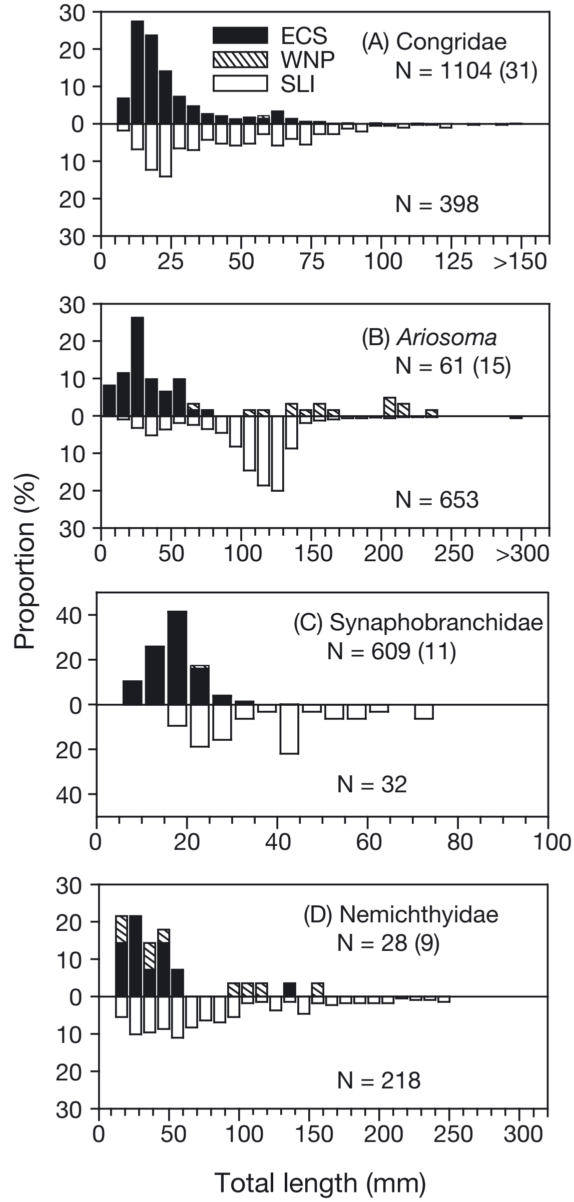

Fig. 4. Comparisons of the length frequency distributions of 4 taxa of leptocephali from in the East China Sea (ECS), to the south in the western North Pacific (WNP) and around Sulawesi Island (SLI). These 4 taxa are representatives of the 3 general life history categories of marine eels that are shelf (Congridae and *Ariosoma*), oceanic (Nemichthyidae), and slope (Synaphobranchidae) eels

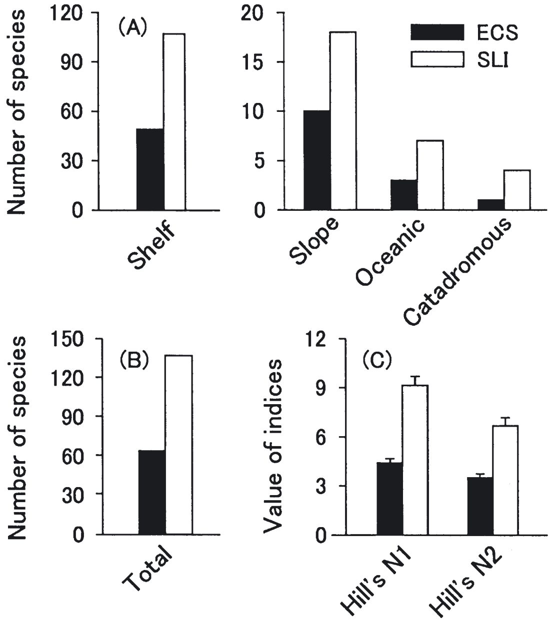

Fig. 5. Number of species of leptocephali (richness) of (A) each of the 4 general life history categories of eels, (B) total species richness of leptocephali, and (C) values of species diversity (Hill's N1) and evenness (Hill's N2) in the East China Sea (ECS) and around Sulawesi Island (SLI)

there were some relatively large congrids, *Ariosoma*, and nemichthyid leptocephali in the ECS region, most of the larger specimens of the latter 2 taxa were caught in the WNP part of the study area (Fig. 4B, D).

Diversity comparisons

The diversity of leptocephali was much greater around SLI, and the number of species of each of the 4 life history categories of eels was also consistently higher there compared to the ECS region (Fig. 5A). Approximately 140 species were collected around SLI, compared to ca. 60 in the ECS region (Fig. 5B). Comparisons between of the diversity indices (Fig. 5C) of the taxa shown in Table 1 show that the average diversity at the stations around SLI (N1 = 9.13) was more than twice as high as in the ECS (N1 = 4.57) and WNP (N1 = 3.56; but with much lower sampling effort), which supported the observations of a much greater number of species around SLI. The index of species evenness around SLI (N2 = 6.67) was also higher than in the ECS (N2 = 3.60) and WNP (N2 = 3.11). This probably reflected the dominance of a few taxa in the ECS (*Gnathophis* and *Dysomma*) that had much higher catch rates than other taxa.

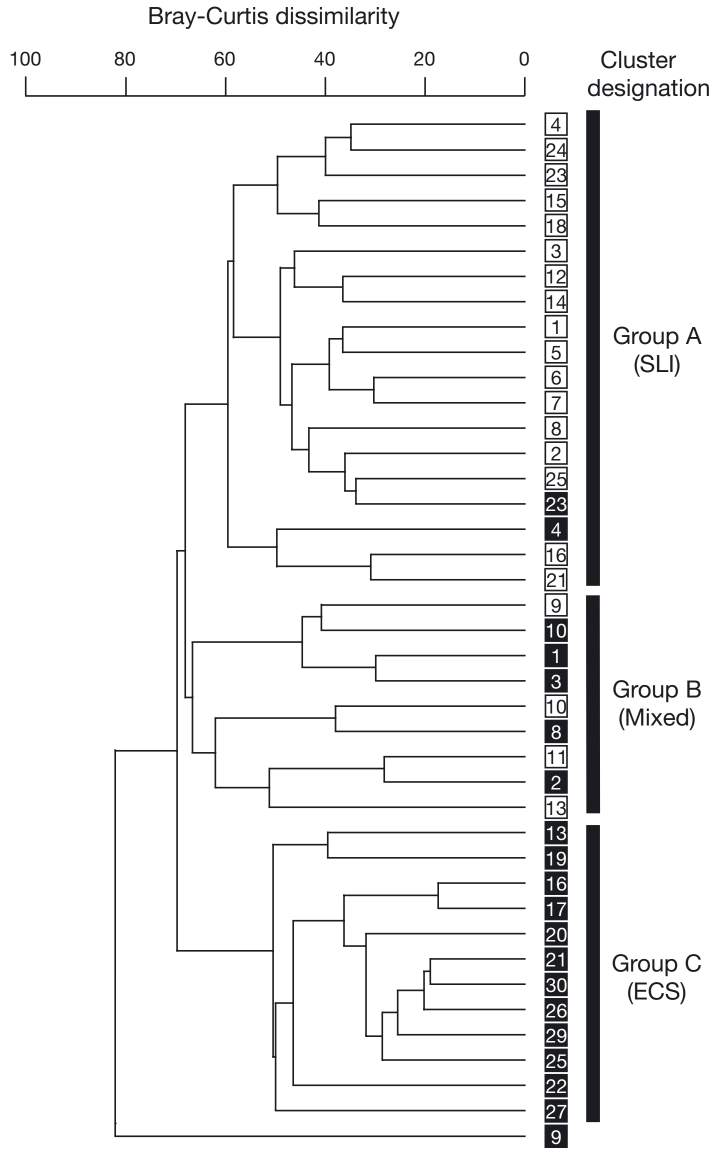

Fig. 6. Bray-Curtis dissimilarity dendrogram of the assemblages of leptocephali at stations (nighttime oblique tows only) in the 2 study areas. Filled squares indicate the stations in the East China Sea region (ECS), and unfilled squares indicate the stations that were around Sulawesi Island (SLI). Numbers within symbols are station numbers

Multivariate analysis of assemblages

Cluster analysis of the leptocephali at individual stations in the 2 study areas resulted in the formation of 3 primary cluster groups of assemblages (Fig. 6) whose stations did not overlap in the MDS plot (Fig. 7), which supports their separation in the dendrogram. All but one of the stations clustered into these 3 cluster groups, which were arbitrarily designated as Group A, B and C. Group A consisted of stations around SLI, except for

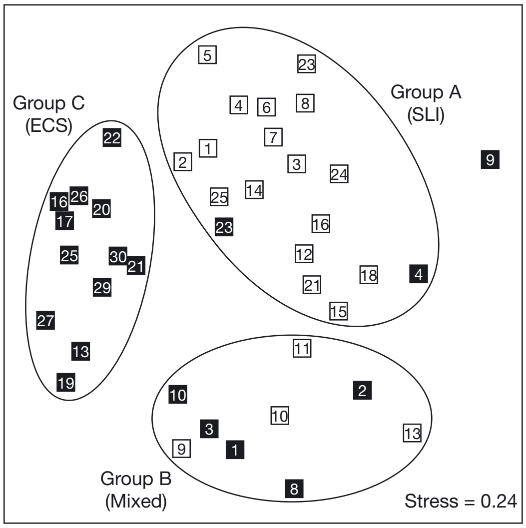

Fig. 7. Multidimensional scaling plot of the assemblages of leptocephali at each station (nighttime oblique tows only) in the 2 study areas. Filled squares indicate the stations in the East China Sea region (ECS), and unfilled squares indicate the stations that were around Sulawesi Island (SLI). Numbers within symbols are station numbers

Stns KT04 and KT23 in the ECS region, and Group C was made up of only stations in the ECS. However, Group B was a mixture of stations from the 2 study areas that were located in the far southern part of the ECS region and in the northeast region around SLI (Fig. 8), which showed an overall lack of any chlopsids, derichthyids, nettastomatids, and serrivomerids (Table 2). Stn KT09 did not cluster within any of the cluster groups due the low catch of only 2 congrid taxa there (Table 2), and it was also an outlier in the MDS plot. The stress value (0.24) of the MDS plot was at an intermediate level because stress values range from poor (0.40), fair (0.20), good (0.10), or excellent (0.05), to perfect (0.00) (Kruskal 1964). The stress value reflects goodness of fit of the plot, and this suggested that the overall between-station dissimilarities did not easily fit into the 2-dimensional space of the MDS plot, or into the pattern of the dendrogram.

The patterns of clustering of the stations within each study area showed some geographic trends, but there was considerable mixing of stations from different areas around SLI. Within Group C, there was mostly just 1 major cluster that consisted only of stations in the northern part of the ECS region (KT20 to KT30), and then 2 other clusters with pairs of stations that were either over the shelf (KT16, KT17) or over the slope (KT13, KT19) along the edge of the Kuroshio (Figs. 1 & 6). In Group A, which was mostly stations from around SLI, some stations in the Celebes Sea and Tomini Bay areas clustered with nearby stations, but there was also considerable mixing of distantly located stations within many of the clusters, suggesting that similar assemblages of leptocephali were located in a variety of areas.

Assemblage characteristics

A SIMPER analysis showed which taxa contributed the most to within-group similarity in the 3 major

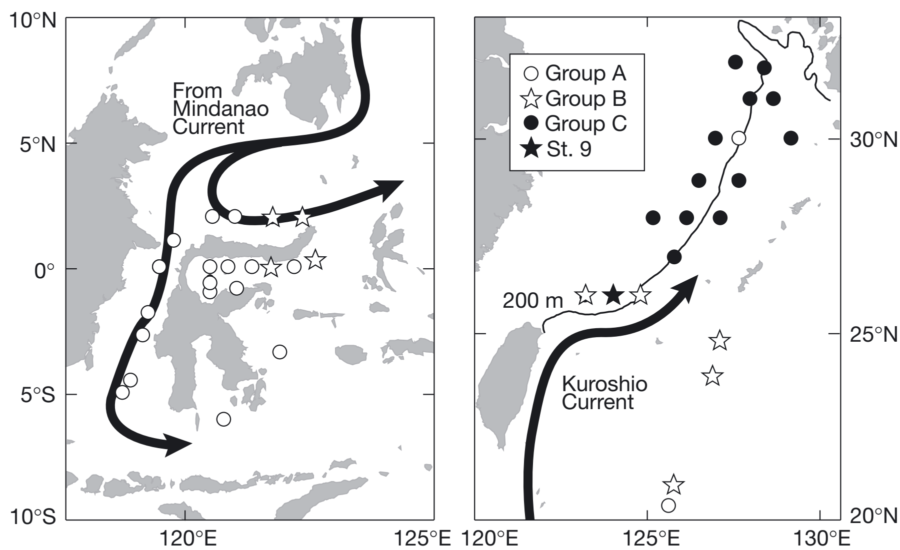

Fig. 8. Geographic distribution of the stations included in the 3 major designated cluster groups detected by cluster analysis at 41 sampling stations in the East China Sea region and around Sulawesi Island. The general flow of surface water in the major current systems in the 2 study areas is also shown

Table 2. Catch rates (ind./10^5 m^3) of taxa collected at stations in the 3 major cluster groups referred to in the text, and at Stn KT09, which was not included in the designated groups. Group A stations were mostly around Sulawesi Island (Baruna Jaya Cruise = BJ) or in the East China Sea region (Tansei Maru cruise = KT). Taxa are characterized by their adult life histories as catadromous (CT), shelf (SH), oceanic (OC), or slope (SL). Taxa are grouped according to family (see Table 1)

Taxon	Adult life history	Group A			Group B		Group C	
		BJ Stns	KT04	KT23	BJ Stns	KT Stns		KT09
Anguilla	CT	1.3		4.9	3.9		0.4	
Chlopsis	SH	1.4						
Kaupichthys	SH	2.9						
Robinsia	SH	0.2						
Chlopsidae	SH	3.6						
Ariosoma	SH	29.0	7.0	14.7	33.0	63.4	4.6	
Conger	SH	5.1	10.6	78.4		10.5	7.5	12.6
Gnathophis	SH	1.3		4.9	4.9	17.0	96.8	
Gorgasia	SH	1.4			4.9			
Heteroconger	SH	1.4			2.4			
Uroconger	SH	5.2		4.9		4.8	3.7	
Congrinae	SH	4.3		4.9	18.2	7.4	5.8	12.6
Derichthys	OC	0.5						
Moringua	SH	3.1			1.6	14.2		
Uropteryginae	SH	0.5			2.4			
Muraenidae	SH	12.6		19.6	6.1	13.2	12.5	
Avocettina	OC	1.1						
Nemichthys	OC	6.3	3.5	4.9		30.3	1.2	
Nettenchlys	SL	0.4						
Saurenchelys	SL	0.7					13.7	
Neenchelys	SH	9.0		9.8			1.2	
Myrophinae	SH	0.9		0.0			0.4	
Ophichthinae	SH	4.9		49.0	10.4	14.2	27.8	
Serrivomeridae	OC	7.8	3.5					
Ilyophinae	SL	0.9					74.4	
Synaphobranchinae	SL	0.4			6.6	42.5	1.2	
Total leptocephali		589	7	40	38	45	605	2

Table 3. Results of the SIMPER analysis showing percentage contributions of typifying taxa (over 5%) to within-group similarities among the major groups of stations generated by cluster analysis. These taxa are characterized by their adult life histories as catadromous (CT), shelf (SH), oceanic (OC), or slope (SL)

Typifying taxon	Adult life history	Group A	Group B	Group C
Ariosoma	SH	19.4	55.3	
Muraenidae	SH	17.1	7.7	13.3
Conger	SH	10.6		
Neenchelys	SH	9.5		
Congrinae	SH	8.2	8.4	
Nemichthys	OC	6.6		
Ophichthinae	SH	5.7	7.4	14.2
Serivomeridae	OC			
Synaphobranchinae	SL		11.2	
Gnathophis	SH		6.9	28.8
Ilyophinae	SL			20.6
Saurenchelys	SL			13.7
Cumulative contribution (%)		76.9	96.8	90.5

groups, and the typifying taxa tended to be those that were most abundant in each group (Table 3). In Groups B and C, the 3 most abundant taxa contributed more than 60% of the within-group similarity, but the contribution of various taxa within Group A was more evenly distributed. *Ariosoma*, Muraenidae, *Neenchelys*, *Conger*, *Nemichthys* and Congrinae all contributed to the similarity within Group A. For Group B, *Ariosoma* was the biggest contributor, but Synaphobranchinae, Congrinae and Muraenidae also contributed to the similarity of the group. Group C was characterized by contributions from *Gnathophis*, *Dysomma*, Ophichthinae, and Muraenidae. Therefore, the SIMPER analysis suggested that Groups B and C had only a few dominant taxa that contributed to the majority of their similarity, but a wider range of taxa were contributing more evenly to Group A due to the absence of extremely dominant taxa, as indicated by the high evenness of this group, as shown in Fig. 5.

Calculations of diversity indices and overall catch rates for each of the 3 cluster groups showed that there

Table 4. Comparison of catch rates (ind./$10^5 m^3$) of the leptocephali of each family of eels, and univariate indices of the assemblage groups in this study and 2 areas of the Sargasso Sea of the western North Atlantic (adapted from Miller & McCleave 1994 using catch data and mean tow volume values). Each family is characterized by their adult life histories as either catadromous (CT), shelf (SH), oceanic (OC), or slope (SL). Southwest data from Cruise CF8303 and CI8901; Northeast data from Cruise CF8305 and CF8503

Taxon	Adult life history	Group A	Group B	Group C	Sargasso Sea (Southwest)	Sargasso Sea (Northeast)
Anguillidae	CT	1.2	0.4	0.2	1.7	11.4
Chlopsidae	SH	7.5			9.2	2.1
Congridae	SH	28.2	7.8	129.3	5.1	0.8
Ariosoma		33.9	10.7	4.7	36.9	9.5
Derichthyidae	OC	0.8			0.1	0.1
Moringuidae	SH	2.4	1.8		3.0	0.6
Muraenidae	SH	15.6	2.4	20.1	3.3	2.3
Nemichthyidae	OC	7.9	3.4	1.2	55.9	22.6
Nettastomatidae	SL	1.6		17.4	0.2	0.1
Ophichthidae	SH	20.7	2.7	52.7	1.6	0.1
Serrivomeridae	OC	5.9			32.3	6.9
Synaphobranchidae	SL	1.3	5.5	55.8	5.2	1.0
Catch rate (ind./$10^5 m^3$)		127.0	34.7	281.5	154.6	57.5
Hill's N1 (Exp *H'*)		7.71	6.02	3.97	5.49	5.48
Hill's N2 (1/D)		6.62	5.71	3.19	4.20	4.18
Total number of specimens		636	83	605	3301	3506
Total number of tows		19	9	12	28	65

were some very clear differences among the groups, in addition to the differences in taxonomic composition (Table 4). The stations that made up Group A had the highest Hill's N1 and N2. In contrast, Hill's N1 and N2 for the stations in the ECS that made up Group C were the intermediate, but these stations had a much higher overall catch rate than the other 2 groups. Group B showed the lowest catch rate and intermediate values for Hill's N1 and N2.

DISCUSSION

The assemblage of leptocephali in the ECS

The assemblages of leptocephali in the ECS region were primarily characterized by the high catch rates of several shelf and slope taxa over the outer continental shelf and slope of the ECS, and the relatively low abundance and richness in the stations over deeper water to the south in the WNP. There were very high catch rates of the leptocephali of the congrid eels *Gnathophis* and of the synaphobranchid eels *Dysomma*, because these 2 taxa appeared to be spawning along the outer shelf and slope in the region (Miller et al. 2002). Other shelf eels such as ophichthids, muraenids and the outer shelf and slope nettastomatid eels were also relatively abundant and widespread over the shelf in the ECS, but all taxa were relatively rare or absent to the south of the ECS in the WNP.

Another interesting finding was the almost complete absence of the leptocephali of the primarily tropical eels of the Chlopsidae and Moringuidae in the ECS region. The lack of some types of shallow water habitats for these eels on the outer shelf and slope of the ECS, and the absence of any nearby islands to the east in the North Equatorial Current region, may explain the low catches of a variety of taxa of leptocephali of shelf eels, such as those of these 2 families. The assemblages of leptocephali farther to the east on the opposite side of the Kuroshio, in close proximity to the coral reef and shallow water habitats of the Ryukyu Islands, may include a wider variety of tropical taxa such as chlopsids and moringuids. However, the surface circulation patterns of the region (Ichikawa & Beardsley 2002) would not likely transport these leptocephali into the areas sampled during this study. Therefore, the assemblages of leptocephali in the ECS region appeared to be primarily a reflection of the spawning activity of shelf and slope eels along the outer shelf of the ECS, and, at least during this season, it appeared that only a few leptocephali of mostly oceanic and catadromous taxa were being transported into the ECS by the Kuroshio.

The assemblage of leptocephali around SLI

The assemblages of leptocephali in the Indonesian Seas region were very diverse and there was a widespread presence of the leptocephali of all the different life history types of eels. Substantial numbers of leptocephali of most of the major eel families were collected, but the leptocephali of the slope and oceanic taxa of the Nettastomatidae, Synaphobranchidae and Derichthyidae were relatively rare compared to the other families. The leptocephali of shelf eels were present at every station, and those of the other 3 life history types were widely distributed around SLI, but were absent at some stations in various areas. There was also a wide range of sizes of many of these leptocephali, indicating that spawning had been occurring in the region over several months.

The primary reasons for this high diversity of leptocephali around SLI are probably the presence of a wide range of different tropical habitats that are suitable for many types of eels, and the likelihood that the tropical environment may allow year-round spawning by some taxa of eels. Therefore, even though the sampling stations around SLI were in the open ocean over water deeper than 1000 m, these stations were still in relatively close proximity to the coastal areas where shelf and slope eels live. There is coral reef and other suitable habitats for shelf eels all around SLI, and because there are no large continental shelf areas in the region, except for in the Java Sea, the shelf break is always very close to the coast, and the slope drops off quickly to water depths of 1000 to 5000 m. Therefore, the strong tides in the region (Hatayama et al. 1996) or wind-driven flow associated with the seasonal monsoon cycle (Wyrtki 1961) probably result in considerable mixing of water among near-shore and offshore areas. This may result in the leptocephali of oceanic, slope, shelf and catadromous species becoming mixed throughout the waters surrounding SLI, which would account for the high diversity of leptocephali that was observed in most areas.

Comparison of assemblages of leptocephali

The contrasting physical and ecological characteristics of the 2 study areas were clearly reflected in the assemblages of leptocephali in each area. In the Indonesian Seas, the patterns of taxonomic composition and relative abundance were very different because there were no collections of large numbers of recently spawned leptocephali like along the shelf break in the ECS. Because of this, the overall catch rates were much higher in the ECS than around SLI, and the proportion of small sized leptocephali was greater. There were some small leptocephali collected along with the larger ones in many areas around SLI, but there were no extraordinarily big catches due to recent spawning like in the ECS. There was, however, a much wider range of taxa for all the life history categories around SLI, due to the presence of the leptocephali of the oceanic and catadromous anguillid eels, which are both known to spawn in the open ocean (Miller & McCleave 1994, Wippelhauser et al. 1996, Tsukamoto et al. 2002), and to the wide variety of leptocephali of shelf eels that mostly appear to spawn over or relatively close to the continental shelf (Moyer & Zaiser 1982, Thresher 1984, Ferraris 1985, Miller 1995, Miller et al. 2002). Some shelf eels, such as ophichthids, may migrate over the continental shelf to deeper water to spawn (Cohen & Dean 1970), or even migrate much farther to spawn offshore as some congrids appear to do (McCleave & Miller 1994, Miller 2002). However, in the Indonesian Seas region, there is no apparent reason for eels to migrate very far to spawn because deep, warm tropical water is close to shore everywhere. Therefore, it appears that the high biodiversity of eels around SLI and the offshore mixing of the different categories of their leptocephali probably account for the much higher richness and diversity of leptocephali observed there in comparison to the ECS region.

These general differences were reflected in the analyses of the assemblage structure of the leptocephali in the 2 study areas, which showed a clear distinction between the majorities of the stations in the 2 areas. The stations of Group A were primarily from around SLI and had higher species diversity and evenness than the stations in Group C from the ECS, but they had a much lower overall catch rate. The lowest catch rate was observed at the stations of Group B, which consisted of stations in the southern ECS, WNP, and stations in the northeast region around SLI. It appears that these stations clustered together because they had assemblages that were unusual in that they had relatively low catch rates, moderate diversity and evenness, with examples such as the slope taxa of the Synaphobranchinae and *Ariosoma* and a few other shelf taxa contributing most to their similarities based on the SIMPER analysis (Table 3, Fig. 8). In the ECS region, the stations of this group were either in the open ocean of the WNP or in the area likely to be directly affected by interaction with the Kuroshio as it first contacts the shelf of the ECS (Fig. 8). Similarly, the stations of this group around SLI were located in relatively close proximity to areas that may be affected by the inflow of water from the WNP. It is unclear if these different assemblages around SLI were affected by the inflow of water from the WNP, but Soewito & Schalk (1990) have suggested that major discontinuities in the larval fish assemblages in the Banda Sea to the east of SLI may have been related to intrusion of water from outside the study area.

It is important to note that these observed differences in the assemblages of leptocephali during this study were detectable even when compared at the higher taxonomic levels of genus or family and, thus, were not caused by differences in the geographic ranges of individual species of eels. Other studies have dealt with larvae identified to the level of family in the western Pacific (Young et al. 1986, Leis 1993), and in the case of eels, this is appropriate because the general ecological category is typically similar at the genus or family level, and this is more meaningful than species level identification. It is especially necessary to examine the assemblage structure of leptocephali primarily at this higher taxonomic level even if the species identifications are known, because in most instances many species of leptocephali are rare in offshore collections, and clustering the random chance-occurrences of rare taxa is ecologically meaningless.

Comparison to the western North Atlantic

The only other studies on assemblages of leptocephali that have used multivariate analyses are those of Miller & McCleave (1994) and Miller (1995), which analyzed collections made with the same kind of IKMT during several cruises in the Sargasso Sea region of western North Atlantic in the February to April season. In the offshore areas of the Sargasso Sea, the leptocephali of oceanic eels, of the Nemichthyidae and Serrivomeridae, and anguillid eels were 3 of the most abundant taxa, because they had been spawning in the Subtropical Convergence Zone of the Sargasso Sea (Kleckner & McCleave 1988, Miller & McCleave 1994, Wippelhauser et al. 1996). The catch rates of both shelf and oceanic species were highest in association with fronts in the southwest region, which was closer to the northern Bahama Islands where most shelf taxa may have originated (Miller & McCleave 1994). Only a limited number of leptocephali of these shelf taxa appeared to get transported farther offshore to the east by the frontal jets, so the farther offshore that sampling occurred, the more impoverished the assemblages of leptocephali became (Miller 1995). The one exception to the finding that shelf species were much less abundant farther offshore was the shelf species *Ariosoma balearicum*, which has been suggested to make spawning migrations from some areas to spawn offshore in the Sargasso Sea (Miller 2002), and is typically one of the most abundant leptocephali there (Miller & McCleave 1994). Another pattern similar to the Sargasso Sea region was found in the overall diversity and abundance of tropical shelf taxa, which were greatest close to the southern coast of Java, as they were closer to the northern Bahamas.

A comparison of the characteristics of the 3 general assemblages identified by the cluster analysis of this study and the leptocephali collected in the Sargasso Sea showed that there were some similarities between the various areas, but also some differences. We used the data in Miller & McCleave (1994) to calculate the approximate catch rates and diversity indices for comparison to the values from the ECS and around SLI (Table 4). The assemblage of Group A (stations mostly around SLI) showed similar catch rates of shelf taxa such as chlopsids, *Ariosoma*, and moringuids to those observed in the southwest Sargasso Sea, but catch rates of serrivomerids and synaphobranchids were more similar to the more offshore areas of the northeast Sargasso Sea. The mixed stations of Group B had catch rates that were similar to those in the southwest Sargasso Sea for congrids, ophichthids and synaphobranchids, but were similar to those of *Ariosoma*, moringuids, and muraenids in the northeast Sargasso Sea. The high catch rates of some congrids, nettastomatids, ophichthids, and synaphobranchids of Group C in the ECS differed markedly from those in the Sargasso Sea region, where the anguillids, nemichthyids, and serrivomerids had much higher catch rates than almost all the areas of this study. The overall catch rates and diversity and evenness values were most similar between Group B of this study and the farther offshore area in the northwest Sargasso Sea (Table 4). However, the assemblage structure in the Sargasso Sea, and probably the ECS, may vary somewhat on a seasonal basis, because some eels such as the anguillids and possibly *Gnathophis* and *Dysomma* do not spawn year round, as some tropical eels appear to.

The findings of this and the previous studies indicate that assemblages of leptocephali can vary markedly based on the geography and ocean currents of a particular region, and on the taxonomic composition and spawning areas of the eels living there. However, the seasonal differences in most of these assemblages have yet to be determined, so more research in a variety of seasons and other locations is needed. Future research on the leptocephali collected in the 2 areas of this study will examine their detailed life history characteristics, and surveys in both regions during different seasons will enable comparisons of the seasonality of spawning of the various taxa of eels in both subtropical and tropical regions. Sampling surveys that compare the assemblages of leptocephali along transects from deep water to over the shelf in tropical and other areas are also needed to clarify the exact spawning locations of the wide range of eels that inhabit the various types of habitats in the world's oceans.

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