

Vertical distribution and assemblage structure of leptocephali in the North Equatorial Current region of the western Pacific

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ABSTRACT: The ecology of leptocephali is poorly understood. We investigated their nighttime vertical distributions and assemblage structure in the North Equatorial Current (NEC) region of the western Pacific in October and November 2013. Of the 1372 collected leptocephali of about 66 species, the most abundant taxa were Serrivomeridae, Nemichthyidae, *Conger*, and Anguillidae that were spawned offshore and *Ariosoma*, Muraenidae, and Chlopsidae larvae that had been transported offshore. Horizontal towing along the 141° E transect indicated that all species of leptocephali were more abundant at 50–100 m near or above the top of the thermocline than at 150–200 m. Towing in the other areas indicated that *Ariosoma*, *Avocettina*, *Nemichthys*, and Serrivomeridae leptocephali were more abundant in the surface mixed layer at 30–50 m, while *Anguilla*, *Conger*, *Derichthys*, Chlopsidae, Muraenidae, and Ophichthidae leptocephali were more abundant near the top of the thermocline at 70–100 m. Leptocephali were most abundant and diverse in the western 131° E transect, and 3 main assemblage groups of leptocephali were detected based mostly on the distributions of oceanic, anguillid, and congrid taxa. Anguillid and conger eels were spawning in specific areas after offshore migrations, and *Avocettina*, *Nemichthys*, and Serrivomeridae had spawned over wide areas. The vertical distribution patterns support the hypothesis that nighttime vertical distributions of leptocephali are influenced by the thermocline. The assemblage structure of the NEC region appears to be a reflection of the taxa spawning offshore and other leptocephali being transported offshore by countercurrents and gyre recirculation.

KEY WORDS: Leptocephali · Vertical distribution · Assemblage structure · North Equatorial Current · Spawning area

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INTRODUCTION

The order Anguilliformes includes 15 families with about 140 genera and >900 species (Nelson 2006, Eschmeyer & Fong 2016). Most anguilliform eels are

marine species that are widely distributed in all types of coastal habitats including coral reefs, continental shelf and slope, deep benthic habitats, and the offshore mesopelagic zone (Böhlke 1989, Miller & Tsukamoto 2004). However, little is known about eel

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life histories due to the difficulty in capturing them, observing their behaviors, and identifying the species of their larvae, which are called leptocephali.

Leptocephali have transparent bodies and long larval durations, and they reach larger sizes before metamorphosis than other fish larvae (Smith 1989). Although juvenile and adult eels inhabit diverse habitats, leptocephali are present almost exclusively in the ocean surface layer in tropical and subtropical regions (Castonguay & McCleave 1987a, Smith 1989, Miller 2009). Thus, studies on leptocephali are a useful way to understand the biodiversity and spawning ecologies of eels and their larval dispersal patterns.

Oceanic eels such as those of the Serrivomeridae, Nemichthyidae, and Derichthyidae live in the mesopelagic zone and are widely distributed offshore in the Atlantic, Pacific, and Indian oceans, where collections of their small leptocephali indicate they spawn (Castonguay & McCleave 1987b, Wipplhauser et al. 1996, Miller et al. 2006a, 2015a). Marine eels that live in inshore areas and on the continental shelf, such as of the Congridae, Muraenidae, and Ophichthidae, seem to mostly spawn close to their adult habitats (Miller et al. 2002, Miller & McCleave 2007). In contrast, eels of the genus *Anguilla* (catadromous freshwater eels of the Anguillidae) and at least some species of the genus *Conger* (Congridae) migrate to spawn offshore, and their juvenile growth stages occur in either freshwater and estuaries or in coastal and continental shelf waters, respectively (McCleave & Miller 1994, Aoyama 2009, Miller et al. 2011a, Tsukamoto et al. 2011, Kurogi et al. 2012). In addition to research on the distribution of small leptocephali to find the spawning areas of eels, there have been studies on the species compositions and assemblages of leptocephali in the western North Atlantic Ocean (Miller & McCleave 1994, 2007, Miller 1995, 2015, Richardson & Cowen 2004, Ross et al. 2007), the Indian Ocean (Miller et al. 2015a), and the Indonesian seas (Minagawa et al. 2004, Wouthuyzen et al. 2005, Miller et al. 2016).

In the Pacific Ocean, the species compositions and assemblage structure of leptocephali have been investigated in areas such as the East China Sea (Miller et al. 2002, Minagawa et al. 2004), coastal Japan (Kimura et al. 2006), the Kuroshio-Oyashio transitional region (Takahashi et al. 2008), and the western South Pacific (Miller et al. 2006a). There has also been extensive sampling for leptocephali offshore in the North Equatorial Current (NEC) region of the western North Pacific (WNP) in the spawning area of the Japanese eel *Anguilla japonica* (Shinoda

et al. 2011, Tsukamoto et al. 2011, Aoyama et al. 2014). However, the assemblage structure of leptocephali in the NEC region has previously not been studied.

In contrast to studies on the horizontal distribution and assemblage structure of leptocephali, there have been only a few studies on their vertical distribution. Leptocephali of most eels reside in the upper 100 m at night, although larvae of some species move deeper during daytime (Castonguay & McCleave 1987a, Kajihara et al. 1988, Otake et al. 1998, Miller 2015). These previous studies have suggested that the nighttime vertical distributions of leptocephali are influenced by the thermocline. However, there is only limited information on the vertical distribution of leptocephali in the NEC region of the WNP (Otake et al. 1998).

Understanding the vertical distribution of eel larvae is important because unlike most other fish larvae, leptocephali appear to primarily feed on particulate organic matter (POM) such as marine snow. This has been indicated by observations of their gut contents and their isotopic compositions (Otake et al. 1993, Mochioka & Iwamizu 1996, Miller et al. 2011b, 2013, Feunteun et al. 2015). Leptocephali appear to feed more during the daytime or crepuscular periods, although this has not been quantified (Miller et al. 2011b). In addition, their feeding ecologies may differ among species, because stable isotope studies show that species that grow to larger sizes (Nemichthyidae and *Ariosoma*-type congrids) have different isotopic signatures than those with smaller maximum sizes such as *Anguilla* (Miyazaki et al. 2011, Feunteun et al. 2015, Liénart et al. 2016). Those findings suggest that leptocephali may feed on different types of POM or they feed at different depths, but their feeding times and depths are not known.

Most aspects of the biology and ecology of leptocephali are not well understood, although they appear to be adapted for predator avoidance due to their transparency and behavioral characteristics (Smith 1989, Miller 2009, Miller et al. 2015b). Understanding the distributional ecology of leptocephali in both horizontal and vertical dimensions is important for understanding their ecology and also their intra- and inter-specific interactions, which may influence the early survival and growth of the commercially important *Anguilla* and *Conger* eels. The objectives of the present study were to evaluate the assemblage structure of leptocephali in the western NEC region and to investigate the nighttime vertical distributions of leptocephali in relation to the thermocline.

MATERIALS AND METHODS

Hydrographic characteristics of the study area

There are several major surface currents in the WNP that transport water in various directions at the depths where leptocephali live. The NEC flows westward from about 8° to 17° N (Kaneko et al. 1998, Hsu et al. 2017) to the east coast of the Philippine Islands and then bifurcates into a northward flow entering the Kuroshio Current and a southward flow of the Mindanao Current (Fig. 1; Toole et al. 1988, Qiu & Chen 2010a). This study included sampling in 4 transects of stations across the latitudes of the NEC (Fig. 1B). The NEC has the North Equatorial Coun-

tercurrent to the south (Fig. 1A) and alternating bands of east and west flow to the north (Kaneko et al. 1998). The Subtropical Countercurrent is usually present to the north of the NEC region from about 18° to 25° N (Hasunuma & Yoshida 1978, Qiu & Chen 2010b), but eastward flow at those latitudes may consist of more than one countercurrent related to different fronts (Kaneko et al. 1998, Aoki et al. 2002, Kobashi et al. 2006). Three stations were established in the Subtropical Countercurrent region (Fig. 1B).

There are some water masses that are characterized by salinity in the NEC region (Fig. 2; Kimura & Tsukamoto 2006). There is low-salinity water of less than about 34.5 in the upper 100 m that is formed by precipitation (Kimura et al. 2001, Aoyama et al. 2014)

and high-salinity water of about 35.0 or higher just below that. The high-salinity water is Subtropical Underwater (STUW), which is present in many regions worldwide (see Schabetsberger et al. 2016). The low-salinity water often forms a front that appears to influence the spawning latitude of the Japanese eel (Kimura et al. 2001, Aoyama et al. 2014). Water temperature in the NEC region shows less distinct latitudinal structure, with the top of the thermocline at depths from about 50 to 100 m (Fig. 2; Kimura & Tsukamoto 2006, Aoyama et al. 2014).

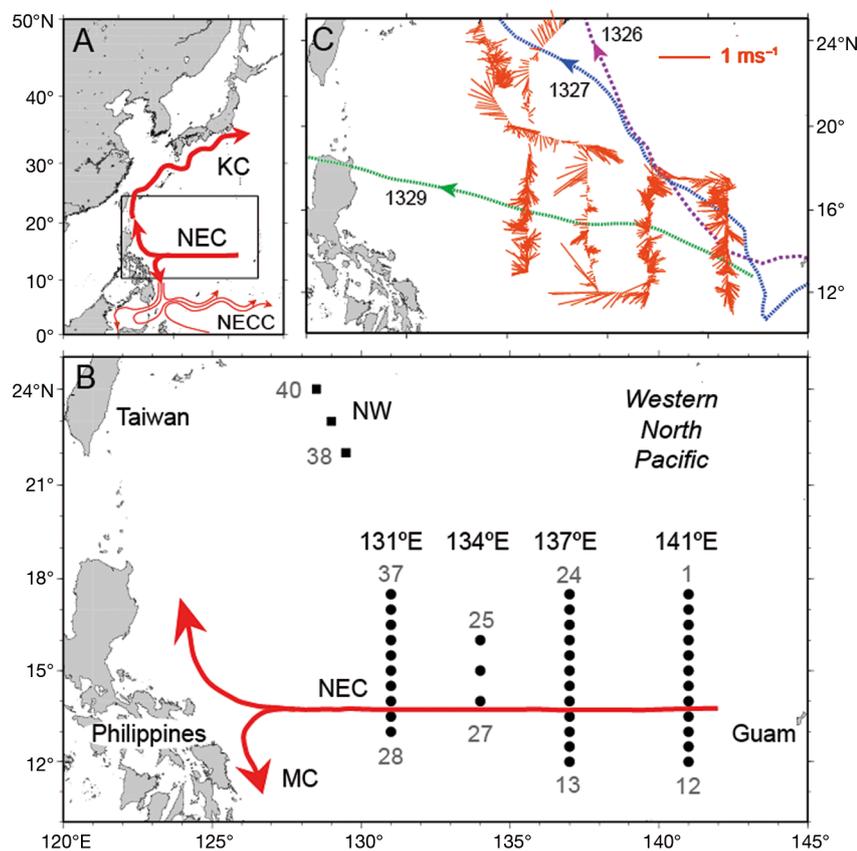


Fig. 1. (A) Location of the study area (rectangle) in the western North Pacific, (B) Isaacs-Kidd midwater trawl sampling stations during the R/V 'Hakuho Maru' KH-13-6 research cruise in the North Equatorial Current (NEC) and 3 stations to the northwest (NW area) in October and November 2013, and (C) the acoustic Doppler current profiler current vectors that were measured at 42 m during the cruise. The tracks of 3 typhoons that crossed the study area, typhoons 1326 (crossed 141° E on 11 October 2013), 1327 (crossed 141° E on 19 October 2013), and 1329 (crossed 141° E on 28 October, 137° E on 29 October, 134° E on 29 October, and 131° E on 30 October 2013), are shown in (C) (storm track data were obtained from Japan Meteorological Agency). General patterns of major ocean currents are shown for the Mindanao Current (MC), North Equatorial Countercurrent (NECC), and Kuroshio Current (KC), but the NEC flows through a wider zone of latitude (~8° to 17° N) than shown by arrows

Observation and sampling methods

Oceanographic observations and sampling of leptocephali in the NEC and the area to the northwest (NW area) were conducted during the KH-13-6 research cruise of the R/V 'Hakuho Maru' (Japan Agency for Marine-Earth Science and Technology) from 17 October to 28 November 2013 (Fig. 1). A grid of sampling stations in 4 transects from 12° to 17.5° N was originally planned to cross the entire western NEC region. However, typhoons crossing the study area reduced the number of stations. Three typhoons crossed some of the transect lines before they were sampled (Fig. 1C). Two complete transects with stations spaced at 0.5° along 137° E and 141° E and a mostly complete

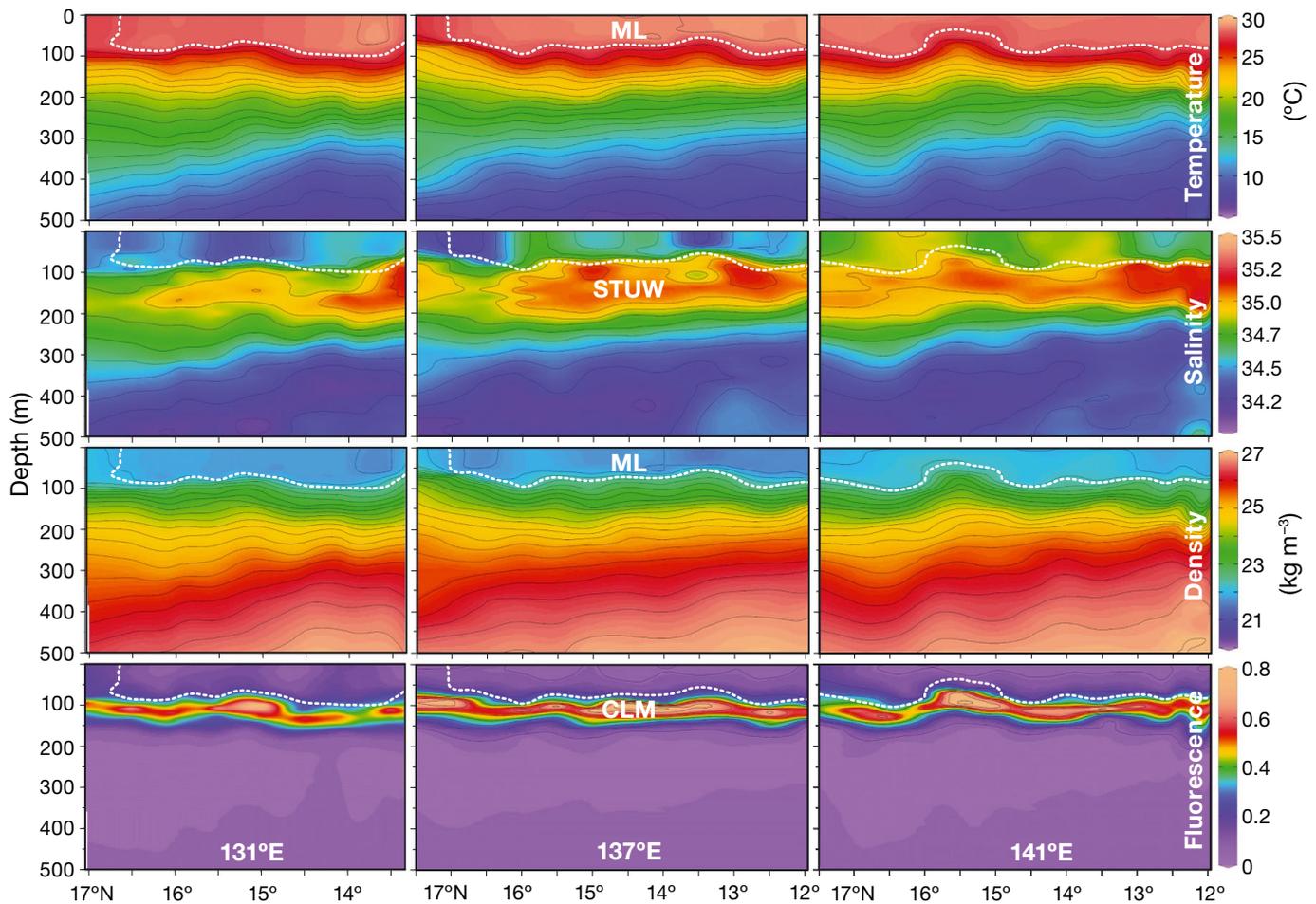


Fig. 2. Vertical profiles of temperature, salinity, density, and fluorescence (reflecting chlorophyll concentrations) in the upper 500 m of the 3 major transects of the sampling survey. ML: mixed layer; STUW: Subtropical Underwater; CLM: chlorophyll maximum. White dashed line: 28°C isotherm

transect along 131°E were sampled (Stns 1 to 40; Fig. 1B). Only 3 stations were sampled along the planned 134°E transect, and 3 stations were sampled in the NW area where the Subtropical Countercurrent could be.

Oceanographic conditions including temperature, salinity, fluorescence, and current velocity were observed using a CTD profiler and an acoustic Doppler current profiler (ADCP). CTD observations were conducted mainly from the surface to 1000 m during daytime, except at northernmost 131°E stations during bad weather. Current velocity at 42 m was averaged every 30 min and plotted as current vectors (Fig. 1C).

Leptocephali were collected at 40 stations in 80 tows of the Isaacs-Kidd midwater trawl (IKMT) that had an 8.7 m² mouth opening and 0.5 mm mesh. The IKMT was fished in step tows that each included 30 min of horizontal towing at 2 depth layers with a

ship speed of 0.8 to 1.5 m s⁻¹ and wire speed of 0.5 to 1.0 m s⁻¹. The step towing was conducted during nighttime from 20:00 to 04:00 h at 2 tows per station. The IKMT was towed horizontally at both 50 and 100 m in one tow and at 150 and 200 m in a second tow at stations along the 141°E transect to evaluate leptocephalus abundance in deeper layers of their possible distributions. Because all taxa were most abundant in the upper depth layers in that transect, the data for all species were pooled together for comparison and presentation of the data. At other stations, the IKMT was towed horizontally at 30 and 50 m in one tow and at 70 and 100 m in a second tow to compare abundances in shallow and deeper layers in the upper 100 m. The mouth of the IKMT remained open as it moved from the surface to fishing depths and between steps, so some leptocephali could have been caught at shallower depths than the horizontal towing depths.

Leptocephali were sorted fresh from plankton samples and were measured to the nearest 0.1 mm total length (TL) after morphological identification to the lowest possible taxonomic level using Tabeta & Mochioka (1988) and Miller & Tsukamoto (2004). DNA sequence identifications of species such as the anguillid larvae are not available for this study. Leptocephali can be grouped into 5 general adult life histories: catadromous anguillid eels; migratory marine eel *Conger* species, including *C. myriaster* that migrates offshore to spawn; mesopelagic oceanic eels of the Derichthyidae, Nemichthyidae, and Serrivomeridae; outer continental shelf or slope species that are deep-water benthic eels such as Nettastomatidae and Synphobranchidae; and shallow-water shelf eels such as other congrid species, Chlopsidae, Moringuidae, Muraenidae, and Ophichthidae (Table 1). In this study, taxa will be referred to in the text usually by family or genus names (without sp. or spp.).

Data analysis

For standardized comparisons of leptocephali catches among stations, the number of leptocephali collected at each station was converted into a catch rate based on the amount of water filtered by the net. Catch rates were calculated as the number of individual leptocephali per 10^4 m^3 of water filtered by the net, using the flowmeter revolutions, a calibration factor (m rev^{-1}), and the IKMT mouth opening (m^2). The 141°E transect tows that fished at 150 and 200 m were excluded from catch rate calculations because few leptocephali were collected at those depths. To investigate the assemblages of leptocephali, taxonomic richness and the Shannon-Wiener index (H') were used. The Shannon-Wiener index is recognized as a classic indicator of species diversity (Spellerberg & Fedor 2003). The diversity index was calculated using the numbers of individuals of taxa along each transect and the NW area or was calculated for individual stations. To investigate the vertical distribution of leptocephali in the NEC, the catch rates were compared between the shallower and deeper layers using either parametric (paired t -test) or non-parametric (Wilcoxon signed-rank test) methods. Statistical comparisons of TL values from each depth for taxa with large enough sample sizes (≥ 20 ind. per depth) were made using either parametric (t -test) or non-parametric (U -test or Kruskal-Wallis test) methods and were followed by pairwise tests (Bonferroni correction). Comparisons were made among 2 or 4 different depths: 30–50, 50–100, 70–100, and 150–200 m.

Multivariate analyses were conducted to examine the assemblage structure of leptocephali in the western 3 transects and the NW area but not in the 141°E transect because towing was deeper there. For the cluster analysis, the 16 most abundant taxa were used, with some taxa being pooled at the family level as in previous studies, because the life history category/family of rare species is more meaningful than the individual species (Miller et al. 2006a, 2015a). The cluster analysis of the catch rates of 16 taxa used the Bray-Curtis index with the Ward's method, and multidimensional scaling (MDS) was performed using the same dissimilarity matrix (Clarke & Ainsworth 1993). A similarity percentage (SIMPER) analysis was calculated as the percentage contribution of taxa to assemblage dissimilarity between groups as well as the percentage contribution of the 16 taxa to assemblage similarity within each group (Clarke 1993). To decrease the heterogeneity in taxonomic abundance between groups, the station catch rates of each taxa were increased by 0.5 and were transformed using a root-root transformation before the cluster analysis, MDS, and SIMPER analysis were performed (Field et al. 1982, Yamamura 1999). The statistical and multivariate analyses were conducted using the R statistical package version 3.2.3 (R Foundation for Statistical Computing) and used the packages MASS version 7.3–45 and vegan version 2.4.

RESULTS

Oceanographic conditions in the study area

The temperature in the upper 100 m in the NEC region was above 26°C and was 28 to 29°C in the mixed layer above the thermocline (Fig. 2). The top of the thermocline was usually between 50 and 70 m in most of the study area. It was shallower from 15° to 16°N in the 141°E transect. Therefore, the mixed layer was usually formed from the surface to 50–70 m. The 2 typhoons that crossed 141°E before the northern stations in that transect were sampled appeared to cause upwelling of the thermocline (Fig. 2). That may also have caused phytoplankton blooms or higher levels of primary production, which might also have occurred in the central part of the 131°E transect after another typhoon crossed there (Fig. 2). Temperature in the upper 100 m was mainly 24 to 27°C in the NW area, and temperature in the surface layer was about 1 to 5°C lower in the NW area than in the NEC region.

Table 1. Number (N), relative abundance (%), and total length (TL) range of leptocephali collected at stations along each transect and the NW region. Taxa are characterized by their life histories as catadromous (CT), migratory marine eel (MM), shelf (SH), slope (SL), or oceanic (OC)

Taxon	Life history	NW area		North Equatorial Current								Total		TL range
				131°E		134°E		137°E		141°E				
		N	%	N	%	N	%	N	%	N	%	N	%	
Anguillidae (≥3 spp., N = 66)														
<i>Anguilla japonica</i>	CT	4	3.0	4	0.8	1	0.5	3	1.0	1	0.5	13	0.9	26.3–56.9
<i>Anguilla marmorata</i>	CT			9				14				23	1.7	13.0–45.0
<i>Anguilla marmorata/luzonensis</i>	CT							27				27	2.0	8.8–15.3
<i>Anguilla bicolor pacifica</i>	CT							1				1	0.1	48.5
<i>Anguilla</i> spp.	CT							1	0.3	1	0.5	2	0.1	5.8–9.3
Chlopsidae (8 spp., N = 63)														
<i>Chlopsis</i> spp.	SH	1	0.7	4	0.8	3	1.4	3	1.0			11	0.8	37.5–56.4
<i>Kaupichthys</i> spp.	SH	2	1.5	16	3.1	5	2.4	1	0.3	4	2.0	28	2.0	15.4–76.0
<i>Robinsia</i> spp.	SH	2	1.5	1	0.2	2	0.9	1	0.3	4	2.0	10	0.7	19.6–97.0
<i>Chlopsidae</i> spp.	SH	4	3.0	6	1.2	2	0.9			2	1.0	14	1.0	38.5–71.2
Congridae (12 spp., N = 535)														
<i>Ariosoma</i> sp. 3	SH			1	0.2			1	0.3			2	0.1	171.0–218.0
<i>Ariosoma</i> sp. 4	SH	4	3.0	4	0.8	14	6.6	5	1.6	2	1.0	29	2.1	63.0–176.0
<i>Ariosoma</i> sp. 5	SH	1	0.7	30	5.9	45	21.3	15	4.8	1	0.5	92	6.7	82.0–193.0
<i>Ariosoma</i> sp. 6	SH	13	9.6	12	2.3	14	6.6	10	3.2			49	3.6	78.0–301.5
<i>Ariosoma majus</i> (sp. 7)	SH	10	7.4	7	1.4	4	1.9	5	1.6	6	3.0	32	2.3	68.5–312.0
<i>Ariosoma</i> spp.	SH	3	2.2	3	0.6	2	0.9	3	1.0			11	0.8	84.0–127.0
<i>Conger</i> spp.	MM	3	2.2	210	41.1	24	11.4	14	4.5	2	1.0	253	18.4	8.8–67.0
<i>Gnathophis</i> spp.	SH	33	24.4	24	4.7					2	1.0	59	4.3	21.8–75.6
<i>Gorgasia</i> spp.	SH			1	0.2	1	0.5					2	0.1	26.8–31.7
<i>Heteroconger</i> spp.	SH					1	0.5					1	0.1	87.6
<i>Congridae</i> spp.		2	1.5			1	0.5	2	0.6			5	0.4	79.9–88.0
Derichthidae (2 spp., N = 29)														
<i>Derichthys</i> spp.	OC			4	0.8	6	2.8	6	1.9	3	1.5	19	1.4	9.2–38.0
<i>Nessorhamphus</i> spp.	OC							1	0.3	4	2.0	5	0.4	20.0–82.3
<i>Derichthidae</i> spp.	OC							5	1.6			5	0.4	12.2–15.4
Moringuidae (1 spp., N = 2)														
<i>Moringua</i> sp.	SH			2	0.4							2	0.1	41.4–45.7
Muraenidae (≥31 spp., N = 94)														
<i>Uropterygiinae</i> spp.	SH	2	1.5	6	1.2	3	1.4	4	1.3	2	1.0	17	1.2	25.9–81.5
<i>Muraeninae</i> spp.	SH	11	8.1	40	7.8	11	5.2	5	1.6	10	5.0	77	5.6	30.3–75.0
Nemichthyidae (3 spp., N = 85)														
<i>Avocettina</i> spp.	OC	2	1.5	1	0.2	7	3.3	3	1.0	4	2.0	17	1.2	7.0–113.5
<i>Nemichthys</i> spp.	OC	23	17.0	22	4.3	10	4.7	8	2.6	5	2.5	68	5.0	8.2–151.5
Nettastomatidae (1 spp., N = 1)														
<i>Saurechelys</i> sp.	SL	1	0.7									1	0.1	
Ophichthidae (2 spp., N = 9)														
<i>Neenchelys</i> sp.	SH			1	0.2	1	0.5					2	0.1	70.0–71.7
<i>Myrophinae</i> sp.	SH	5	3.7	2	0.4							7	0.5	51.0–60.3
Sacopharngiform (1 spp., N = 1)														
<i>Sacopharngiform</i> sp.	OC									1	0.5	1	0.1	8.6
Serrivomeridae (≥1 spp., N = 465)														
<i>Serrivomeridae</i> spp.	OC	7	5.2	101	19.8	53	25.1	171	54.6	133	65.8	465	33.9	6.0–85
Synaphobranchidae (1 spp., N = 1)														
<i>Ilyophinae</i> sp.	SL	1	0.7									1	0.1	116.8
Unidentified/preleptocephali														
Total leptocephali		135	0.7	511		211	0.5	4	1.3	15	7.4	21	1.5	
Shelf taxa total		91	67.4	160	31.3	108	51.2	53	16.9	33	16.3	445	32.4	
Slope taxa total		2	1.5	0	0.0	0	0.0	0	0.0	0	0.0	2	0.1	
Oceanic taxa total		32	23.7	128	25.0	76	36.0	194	62.0	150	74.3	580	42.3	
Catadromous/migratory marine taxa total		7	5.2	223	43.6	25	11.8	60	19.2	4	2.0	319	23.3	
No. of taxa		29		45		26		22		26		66		
<i>H'</i> (Shannon-Wiener index)		3.95		3.26		3.47		2.39		1.99				
No. of tows		3		10		3		12		12		40		

Although the average current flow direction at 42 m was westward in the NEC region based on the ADCP measurements, there was a complicated pattern of current vectors (Fig. 1C). The westward current velocity along the 141° E transect line was strong around 14° to 17° N. Strong westward flows were also found around 17° to 18° N in the 134° E line and in the low-latitude area. The presence of large eddies or eastward countercurrents were also suggested by the ADCP data, which appears to be typical of the NEC region (Kaneko et al. 1998).

Taxonomic composition of leptocephali

There were 1372 leptocephali of at least 12 families and at least 66 species that were collected in the present study (Table 1), with 73% of the specimens belonging to the families Congridae (N = 535) and Serrivomeridae (N = 465). Congridae leptocephali included at least 5 genera and about 12 species, with *Conger* (N = 253), *Ariosoma* (6 species; N = 215), and *Gnathophis* types (3 species; N = 59) being the most abundant taxa. The few garden eel leptocephali (2 species, N = 3) were the only other congrid leptocephali identified. Serrivomerid leptocephali were abundant, but it is not possible yet to morphologically distinguish different species that may have been present. The leptocephali of the Muraenidae (≥ 31 species; N = 94), Nemichthyidae (3 species; N = 85), Anguillidae (≥ 3 species; N = 66), and Chlopsidae (8 species; N = 63) were also collected in substantial numbers. Derichthyidae, Moringuidae, Ophichthidae, Nettastomatidae, and Synphobranchidae leptocephali were rare, and each had only from 1 to 29 larvae collected of 1 to 2 species.

The number of species was greatest along 131° E (≥ 45), and there were at least 23 to 29 species collected in the other 3 transects to the east or in the NW area (Table 1). The 131° E transect had the most species partly because about 18 muraenid species were collected there, compared to 8–11 species in the other areas, and rare species such as *Moringua*, Ophichthidae, and *Gorgasia* (garden eels) were also caught there.

Geographic distribution of leptocephali

Leptocephali were abundant along the 131° E transect because of large catches of serrivomerids, *Conger*, muraenids, *Ariosoma* sp. 5, and *Kaupichthys* (Table 1), but serrivomerids were abundant at some

stations across the study area except in the NW area and at a few other stations (Fig. 3). *Ariosoma*, serrivomerid, and *Conger* leptocephali were abundant in the 3 stations of the 134° E transect. The various species of *Ariosoma* were widely distributed, but like *Conger* leptocephali, they were most abundant in the northwestern transect areas and NW area in the case of *Ariosoma* (Fig. 3). *Gnathophis*, chlopsids, muraenids, and ophichthids were also most abundant in the northwesternmost transect stations or in the NW area, and ophichthids were absent in the 2 easternmost transects. Anguillid and derichthyid leptocephali were most abundant in the 137° E transect. To various degrees, *Avocettina*, *Nemichthys*, and chlopsids were present at northern stations of the 4 transects and were absent at many southern stations. Oceanic species of *Derichthys* leptocephali were caught in more central transect areas, and the few *Nessorhamphus* leptocephali were caught in southeastern parts of the 2 eastern transects (Fig. 3).

Size distribution of leptocephali

Small anguillid leptocephali (≥ 5.8 mm) were caught from 14° to 15° N in the eastern 2 transects (Figs. 4 & 5). The smallest *Conger* leptocephali (8–15 mm) were caught at a wider range of latitudes (14° to 17° N) and were restricted to the 2 western transects (Figs. 4 & 5). In contrast, small serrivomerid and nemichthyid leptocephali (6–15 mm) were widely distributed in both latitude and longitude across the transects and the NW area, indicating widespread spawning. No leptocephali <15 mm were collected of shelf families (excluding *Conger*), although a few 15–25 mm chlopsids were caught in the northern 141° E stations (Figs. 4 & 5).

Different distribution patterns of larger sizes of leptocephali were also observed across the study area. Serrivomerid leptocephali were uniformly distributed from small to near-maximum sizes of 60–70 mm both latitudinally and longitudinally. *Anguilla*, *Nemichthys*, and *Conger* leptocephali tended to have larger sizes in the west, whereas both minimum and maximum sizes of *Ariosoma* leptocephali increased to the east, except in the NW area, where narrower sizes were observed. Muraenidae leptocephali were >25 mm and had sizes up to their maximum size range of <80 mm except in the south, and minimum sizes increased towards the east until the 141° E transect, where the smallest larvae were caught. *Gnathophis* leptocephali in the northwestern areas were all ≥ 40 mm, and the only 2 larvae <40 mm were collected in the 141° E transect.

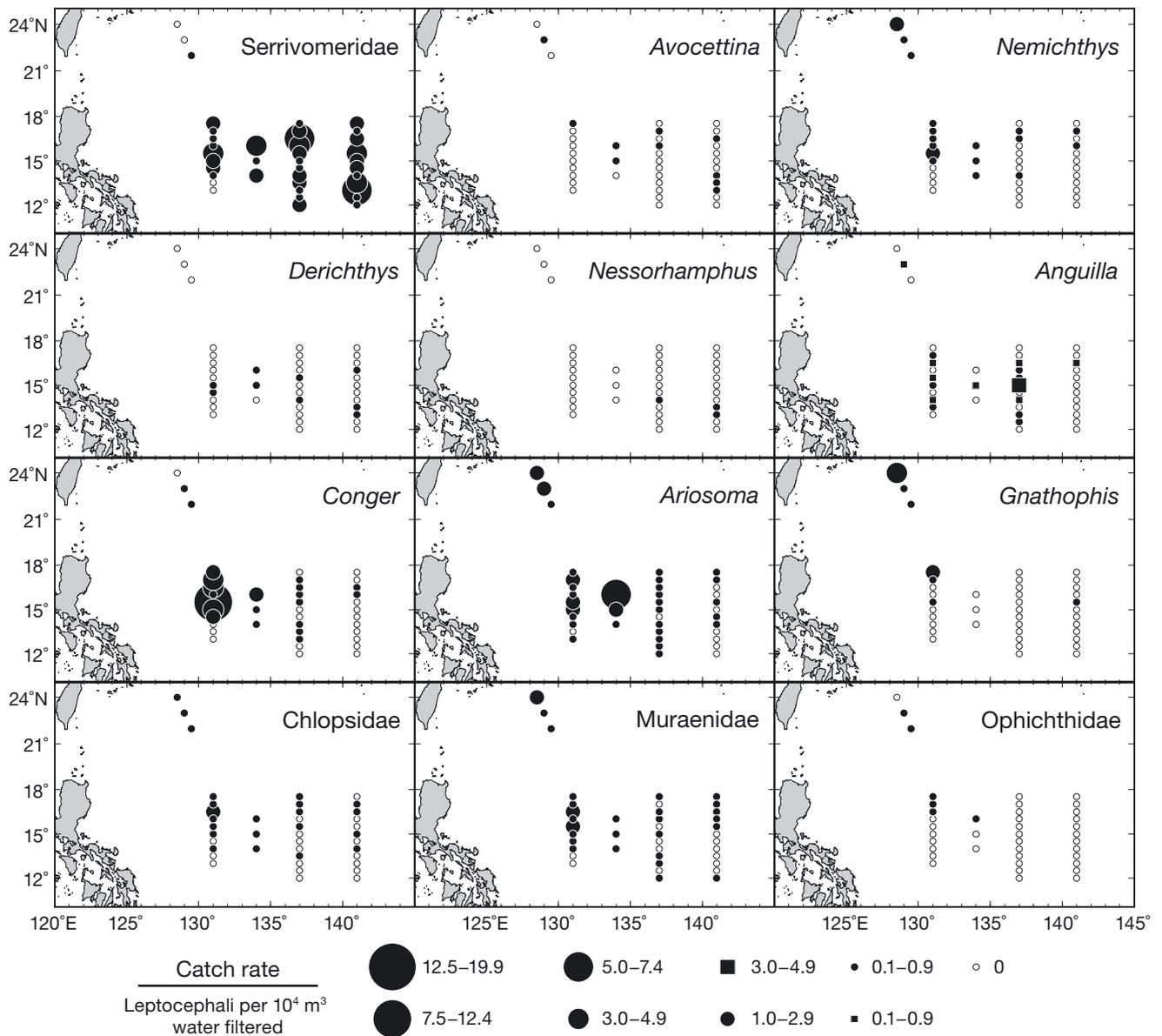


Fig. 3. Catch rates (ind. 10^4 m^{-3}) of the main taxa of leptocephali collected during the KH-13-6 sampling survey. Squares indicate stations where *Anguilla japonica* leptocephali were collected during the cruise

Vertical distribution of leptocephali

Along the eastern 141°E transect, the catch rate of total leptocephali in the 50–100 m depth layer above or within the top of the thermocline was about 3 times greater and significantly different than that in the 150–200 m depth layer below the top of the thermocline (paired t -test, $p < 0.001$) (Fig. 6). Some leptocephali collected in tows that targeted 150–200 m depth layers could have been collected at depths $< 150 \text{ m}$, as the net went down to and up from those depths. However, the proportions of lepto-

cephali collected in the deeper layer compared to total numbers of each taxa were not the same (Fig. 7), which suggests at least a few leptocephali could have been caught at the deeper depths. For example, none of the 247 *Conger* and only 1 of the 204 *Ariosoma* (0.5%) leptocephali were caught in tows that fished at 150–200 m, but 25 of the 457 (5.5%) serrivomerid larvae were caught in the deeper tows.

In the other sampling stations in the NEC, serrivomerid and *Nemichthys* leptocephali had higher and significantly different catch rates in the 30–50 m depth-layer tows usually above the thermocline than

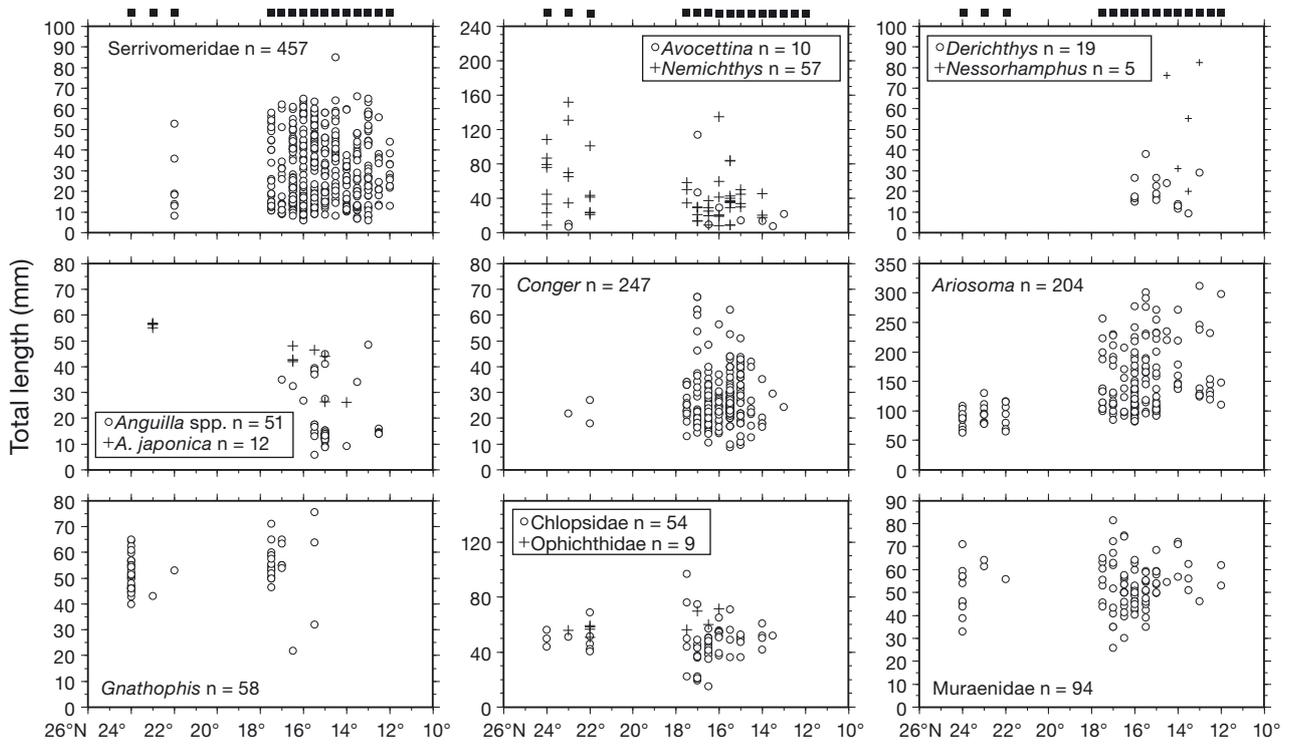


Fig. 4. Total length of individual leptocephali of the main taxa collected at each latitude during the KH-13-6 sampling survey. Black squares at the top of the panels show latitudes where stations were in the North Equatorial Current transects or the NW area

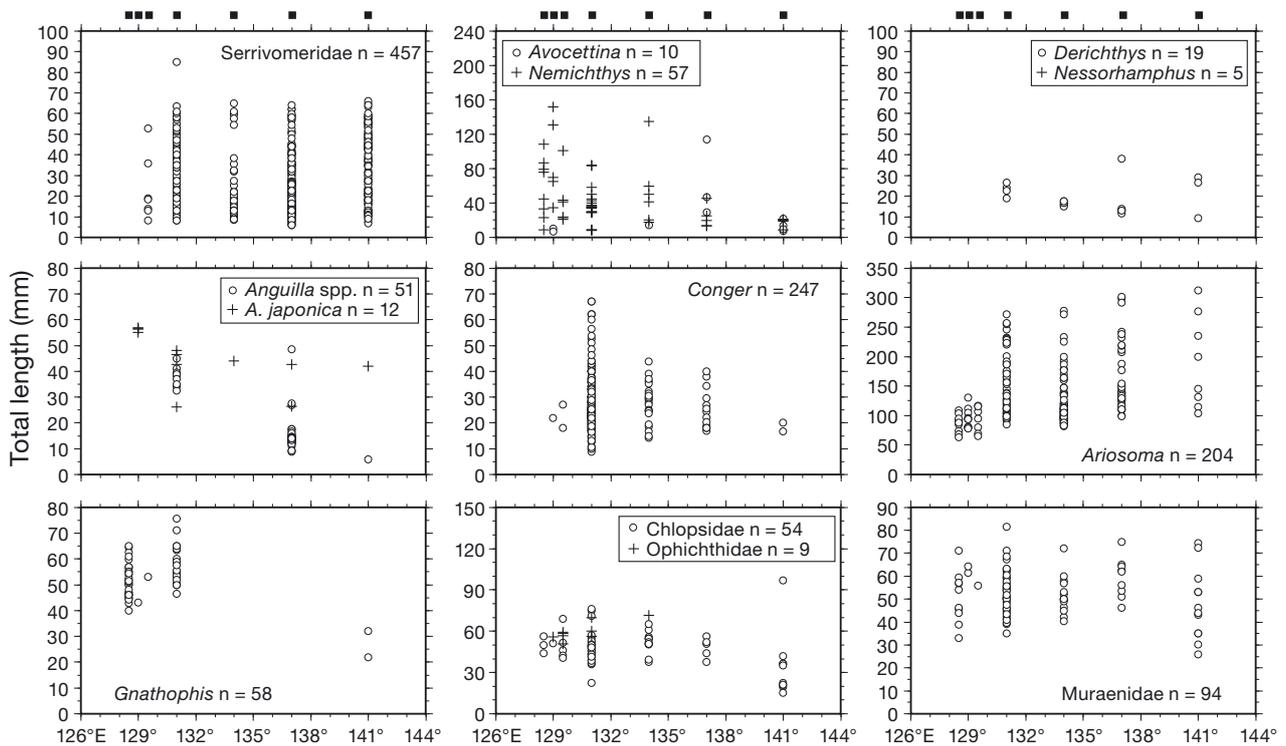


Fig. 5. Total length of individual leptocephali of the main taxa collected at each longitude during the KH-13-6 sampling survey. Black squares at the top of panels show longitudes where stations were in the NW area or in the 4 transects across the North Equatorial Current

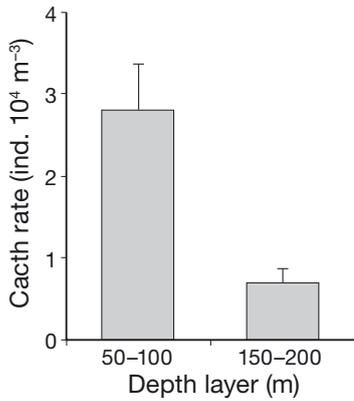


Fig. 6. Average catch rates of leptocephali in Isaacs-Kidd mid-water trawl deployments that towed horizontally at 50 and 100 m or at 150 and 200 m along the 141° E transect line during the KH-13-6 sampling survey. Vertical bars indicate SE

in the 70–100 m depth-layer tows within or near the top of the thermocline (Wilcoxon signed-rank test, $p < 0.05$) (Fig. 8). The catch rates of *Avocettina* and *Ariosoma* were also higher in the shallower layer than in the deeper layer, although they were not significantly different (Wilcoxon signed-rank test, $p >$

0.05). For other taxa, more leptocephali were caught in the 70–100 m depth-layer tows, with *Derichthys*, *Anguilla*, *Conger*, and Muraenidae catch rates being significantly higher in the deeper layers than the shallower 30–50 m layers (Wilcoxon signed-rank test, $p < 0.05$). The catch rates of the other taxa were also higher in the deeper layer than in the shallower layer but not significantly (Wilcoxon signed-rank test, $p > 0.05$).

Generally, similar-sized larvae were collected at the different depths, but there were some differences (Fig. 7). The statistical comparisons of the larval sizes at 3 depth ranges found that serrivomerid sizes were significantly different among depths (Kruskal-Wallis, $p < 0.001$), with 2 pairwise comparisons being significantly different between 30–50 and 50–100 m and between 50–100 and 70–100 m (Bonferroni test, $p < 0.001$). *Ariosoma* sizes were significantly different between 30–50 and 70–100 m depths (*U*-test, $p < 0.001$), although *Conger*, *Gnathophis*, Chlopsidae, and Muraenidae showed no significant differences between those depths ($p > 0.05$). The smallest sizes of *Ariosoma* and a narrower size range of *Conger* larvae were caught in the

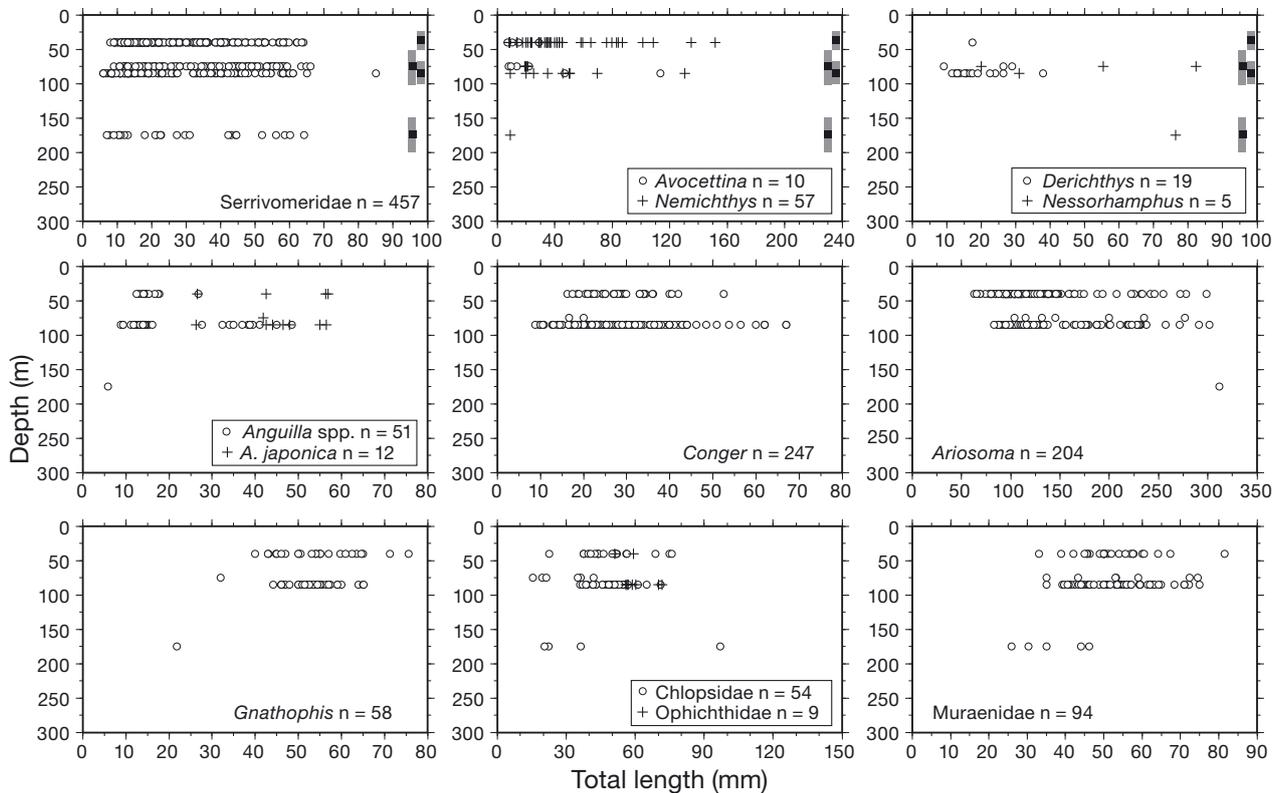


Fig. 7. Sizes of individual leptocephali collected at each depth range plotted at the average depth of each type of Isaacs-Kidd midwater trawl deployment during the KH-13-6 sampling survey. Gray bars in the upper right of top panels show ranges of depths of each type of deployment, and black squares show average depths where data are plotted

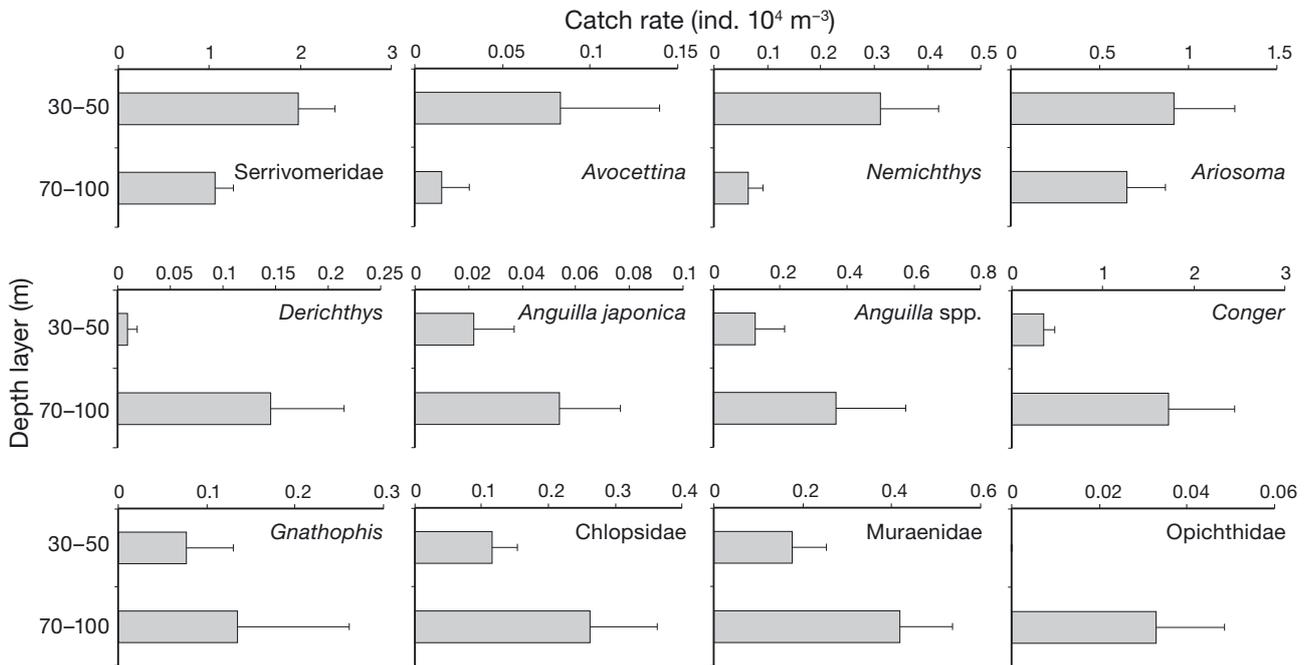


Fig. 8. Average catch rates of the main taxa of leptocephali collected in Isaacs-Kidd midwater trawl deployments that towed horizontally at 30 and 50 m or at 70 and 100 m in the 3 western transects during the KH-13-6 sampling survey. Horizontal bars indicate SE

shallowest layer. The smallest anguillid, muraenid, and *Gnathophis* larvae may have been caught at the deepest layer.

Assemblage analysis

The cluster analysis and MDS analysis of 16 taxa detected some clear patterns of assemblage structure that partly corresponded to the geography of the station locations (Fig. 9). The stations in the dendrogram were separated into 3 clusters and 1 individual station that were defined as cluster groups A, B, and C and Stn 40 in the NW area. Group A consisted mainly of northern 131° E transect stations (Fig. 9C). Group B included stations in the middle or northern parts of the transects and 2 NW area stations. Group C consisted of 137° E transect stations and southern 131° E stations. Group A stations did not overlap with other stations in the MDS plot, although a few stations of groups B and C overlapped slightly (Fig. 9B).

The SIMPER analysis indicated how much each taxon contributed to the assemblage structure of the cluster analysis by showing the percent contributions of each taxon in the groups (Table 2). The Group A assemblage was characterized by a high abundance of leptocephali due to large catches of serrivomerids

(16.3% contribution), *Conger* (13.5%), *Ariosoma* sp. 5 (13.2%), and *Gnathophis* (10.3%) that were the top contributors to within-group similarity. The top contributors of the Group B assemblage were Serrivomeridae (21.6%), *Nemichthys* (10.0%), *Conger* (9.3%), and *Ariosoma* sp. 5 (9.5%). In contrast to the 10 to 11 contributing taxa of other groups, Group C only had 7 contributing taxa of *Anguilla marmorata* (31.0%), Serrivomeridae (25.6%), *Ariosoma* sp. 5 (12.1%), *Ariosoma* sp. 6 (7.3%), Muraenidae (4.9%), and Chlopsidae (4.0%), with the group having a low overall catch rate. Stn 40 did not cluster with other stations, probably due to high contributions of *Gnathophis* (44.3%), *Nemichthys* (17.9%), Muraenidae (14.9%), and *Ariosoma majus* (11.9%) and an absence of serrivomerids.

The species diversities (H') were higher (3.26 to 3.95) in the western areas (NW area, 131° E, 134° E) than in the 2 eastern transects (2.39 for 137° E and 1.99 for 141° E) (Table 1, Fig. 10), possibly due to the abundance of oceanic taxa and lower numbers of shelf taxa along 137° E and 141° E. The NW area had the highest diversity because many shelf taxa including ophichthid leptocephali and the only nettastomatid and synphobranchid larvae were caught there. The lowest diversities were found at the stations in the southern half of the 141° E transect (Fig. 10).

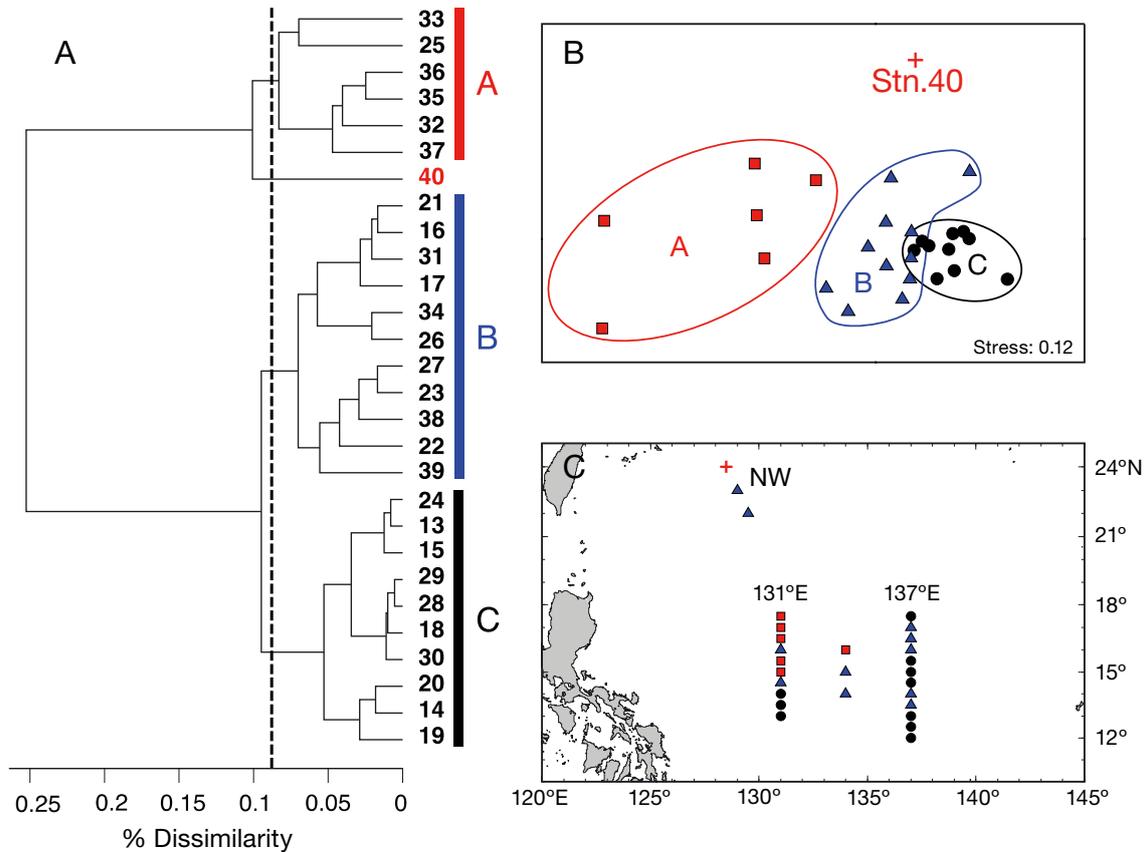


Fig. 9. (A) Results of the multivariate analyses of 16 taxa of leptocephali, with the 3 main cluster groups of stations labeled in the dendrogram; (B) MDS plot, with cluster group stations enclosed in ovals; and (C) locations of cluster group stations indicated on the map, with symbols as shown in (B)

Table 2. Number of specimens of leptocephali of 14 taxa in each cluster group and percent contributions (CTB) of taxa to within-group similarity of each cluster group from SIMPER analysis. Only taxa contributing over 4% are shown. No CTB values were calculated for Stn 40 because it did not group with other stations

Family	Taxon	Group A		Group B		Group C		Stn 40	
		N	% CTB	N	% CTB	N	% CTB	N	% of total
Anguillidae	<i>Anguilla japonica</i>	3		7	4.4	2			
	<i>Anguilla marmorata</i>	8		1		41	31.0		
Chlopsidae		34	6.2	13	5.2	3	4.0	3	4.5
Congridae	<i>Ariosoma</i> sp. 4	14	7.3	10	5.4	2		1	1.5
	<i>Ariosoma</i> sp. 5	58	13.2	20	9.5	13	12.1		
	<i>Ariosoma</i> sp. 6	20	5.8	21	8.1	6	7.3	2	3.0
	<i>Ariosoma majus</i>	9		6		3	4.1	8	11.9
	<i>Conger</i>	212	13.5	37	9.3	2			
	<i>Gnathophis</i>	24	10.3	2				31	46.3
Derichthyidae	<i>Derichthys</i>	7	4.1	8	5.3	1			
Muraenidae		50	6.2	17	5.0	5	4.9	10	14.9
Nemichthyidae	<i>Avocettina</i>	2		11	6.1				
	<i>Nemichthys</i>	24	4.9	27	10.0			12	17.9
Serrivomeridae		115	16.3	164	21.6	53	25.6		
Total no. of ind.		584		350		131		67	
No. of tows		6		11		10		1	
Total catch rate (ind. 10 ⁴ m ⁻³)		10.4		3.8		1.6		8.0	

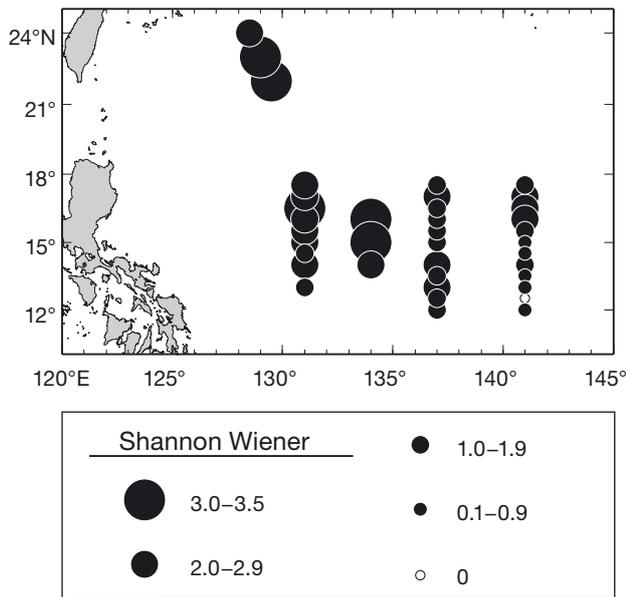


Fig. 10. Individual-station Shannon-Wiener species diversity index values calculated using the numbers of leptocephali of each taxon collected at the stations of the KH-13-6 sampling survey

DISCUSSION

Assemblages of leptocephali in the NEC

The present study presented a unique opportunity to examine the assemblage structure of leptocephali in the NEC of the WNP from both latitudinal and longitudinal perspectives. Extensive sampling for leptocephali occurred in this region in previous years (Shinoda et al. 2011), but sampling was focused on the geography of spawning by anguillid eels near the West Mariana Ridge (Tsukamoto et al. 2011, Aoyama et al. 2014) and not on leptocephali assemblages across the wider NEC region. The previous sampling efforts revealed that *Conger myriaster* that lives in East Asia migrates offshore to spawn in the NEC region (Miller et al. 2011a, Kurogi et al. 2012) in a similar way as *Anguilla japonica* and *A. marmorata* that spawn there (Kuroki et al. 2009, Tsukamoto et al. 2011). *A. luzonensis* may also spawn offshore in the NEC (Kuroki et al. 2012). The present study also detected offshore spawning of anguillid and conger eels in the NEC region and revealed that other eel taxa show a variety of distribution patterns across the region.

The multivariate analyses and plots of catch rates indicated that the northern parts of the 2 western transects formed an assemblage group primarily due

to the abundance of *Conger*, *Ariosoma*, and shelf species. Other stations mostly in the central part of the NEC region formed another assemblage that included oceanic species and also *Conger* and *Ariosoma*. The third assemblage included fewer taxa with high contributions of anguillid and serrivomerid leptocephali. Stn 40 had a distinct assemblage primarily due to many *Gnathophis* and *Nemichthys* leptocephali being collected there.

This general pattern of leptocephali distribution and abundance showed similarities with assemblages in other regions. In the Sargasso Sea of the western North Atlantic, the abundance and number of species of shelf leptocephali was higher in the southwestern part of the subtropical gyre (Miller & McCleave 1994, 2007, Miller 1995), as they were in the same part of the WNP gyre (northwestern parts of the transects) in the present study. Oceanic species of serrivomerid and nemichthyid leptocephali were widely distributed in both study areas. Transects across the western South Pacific also found diverse assemblages either with many shelf species, dominated by serrivomerids, or with low diversity (Miller et al. 2006a). The number of species collected in our study was a little higher compared to Sargasso Sea offshore collections (Miller & McCleave 1994) but was considerably lower than in the Indonesian seas, where about twice as many species of marine eel leptocephali have been collected (Wouthuyzen et al. 2005, Miller et al. 2016).

The hydrographic sections did not reveal clear patterns apparently related to the assemblage structure of leptocephali, and the temperature, density, and chlorophyll structure was similar across all the transects. There was surface-layer low-salinity water and subsurface STUW variation, but there was no obvious linkage with the distribution and abundance of leptocephali in the study area. The diversities and abundances of leptocephali are generally related to the geography of where the sampling occurs in relation to the spawning locations of eels near shore and the offshore transport of their larvae as well as the spawning of other species offshore, as is discussed more in the last section of the 'Discussion'.

Vertical distribution of leptocephali

Nighttime horizontal towing in the western NEC region showed that leptocephali were more abundant in the upper 100 m compared to at 150–200 m and that their vertical distribution patterns in the upper 100 m differed between some taxa. Previous studies

that used discrete depth sampling gear in the Sargasso Sea also showed that leptocephali are rare below 100 m at night (Castonguay & McCleave 1987a, Miller 2015). Horizontal towing at night also showed this to the west of our study area in September 1986 (Kajihara et al. 1988). Our sampling showed that some species were most abundant at 30–50 m but that others were more abundant at 70–100 m. Previous studies found similar differences among taxa (Castonguay & McCleave 1987a, Miller 2015).

Anguilla leptocephali in our study in the NEC region were most abundant at 70–100 m, and they were most abundant at 50 and 80 m in the study by Kajihara et al. (1988). But they can be abundant shallower such as at 0–30 m in some locations (Miller 2015), and they show ontogenetic changes in depth distribution to be exclusively in the upper 100 m at night and deeper during the day as they grow larger (Castonguay & McCleave 1987a, Otake et al. 1998). Anguillid leptocephali may also reach deeper depths as they approach continental shelf areas (Tesch 1980).

Derichthyidae leptocephali seem to be consistently more abundant in deeper layers compared to shallower ones even though the exact depths sampled varied among studies. They were not abundant in our study, but most were caught at 70–100 m, and they were caught deeper compared to shallower in the Sargasso Sea (Castonguay & McCleave 1987a, Miller 2009). In contrast, *Nemichthys* and *Avocettina* may be typically present in upper layers, as they were in the NEC, compared to deeper depths, although their depths may vary with size (Castonguay & McCleave 1987a, Miller 2009, 2015). *Ariosoma* leptocephali have consistently been more abundant in the shallower layer in our sampling and previous studies (Castonguay & McCleave 1987a, Miller 2009, 2015). Mochioka et al. (1991) reported that *Ariosoma* leptocephali were abundant from the surface to 20 m in the Pacific Ocean, and they are the most common leptocephali collected in net tows at the surface (<1 m; Miller et al. 2006b). Serrivomerid leptocephali were abundant in our collections, and they had higher catch rates in 30–50 m tows than at deeper depths, which is similar to their <70 m distribution in the northern Sargasso Sea (Miller 2009). However, 2 species of serrivomerids had different nighttime vertical distributions in the southern Sargasso Sea (Castonguay & McCleave 1987a). Muraenid leptocephali have shown different vertical distribution patterns, such as deeper in our study and one other (Castonguay & McCleave 1987a) or shallower elsewhere (Miller 2015). The reasons for the variations in vertical distributions of leptocephali are not known but

are beginning to be evaluated, as described in the next subsection.

Distributional ecology of leptocephali

The catches of leptocephali along the southwestern and western parts of the WNP subtropical gyre were evaluated from both horizontal and vertical perspectives. In the horizontal dimension, the study area location indicates that various factors likely contributed to the species composition and sizes of leptocephali. Because the hydrographic structure across the latitudes that were sampled was relatively uniform, the factors affecting the geographic patterns of distribution of the different types of leptocephali are likely more related to interactions between the life histories of the different types of eels and the ocean circulation in the region. One factor is that the anguillid and conger eels that live in freshwater or continental shelf habitats had migrated offshore and spawned in the westward-flowing NEC that would transport their larvae towards their recruitment areas. This also occurs in other areas where their small leptocephali have been collected offshore like they were in the present study (McCleave & Miller 1994, Kuroki et al. 2008, Aoyama 2009, Miller et al. 2011a). A second factor is that oceanic eels were spawning offshore in wide areas of the WNP before our sampling survey based on the presence of their small larvae, especially in the case of serrivomerids, as was also observed in other areas (Castonguay & McCleave 1987b, Miller & McCleave 1994, Wippelhauser et al. 1996, Miller et al. 2006a, 2015a).

Another observation was that leptocephali of shelf eels that do not spawn offshore were more diverse and abundant in the northwestern transect areas even though they were not close to any landmasses. Those types of eels spawn over or along the East China Sea continental shelf, along the Pacific coast of Japan, and in similar areas worldwide but not in offshore areas (Miller 1995, Miller et al. 2002, 2015a, Kimura et al. 2006). The largest NEC catch rates of their leptocephali occurred near or north of 16° N along the northern margin of the NEC and where there could be eastward countercurrents. Eastward flow at the northern edge of the NEC has been seen in ADCP (Kaneko et al. 1998, Kashino et al. 2009) and geostrophic current (Qiu & Chen 2010a, Hsu et al. 2017) plots, which could transport leptocephali offshore, as occurs in the Sargasso Sea (Miller 1995). Fronts that could have eastward countercurrents have also been seen in other types of datasets

(Kobashi et al. 2006). Our ADCP data showed some eastward current vectors at various latitudes of the transects from about 15° to 17° N. Another possible factor affecting leptocephali distribution is that WNP dynamic height plots that show the basic structure of the Kuroshio subtropical gyre (Kobashi et al. 2006, Qiu & Chen 2010a,b) suggest that some water recirculates in a clockwise pattern within the western gyre. Eddies to the east of Taiwan may also influence the movement of water offshore (Chang et al. 2015). Other sources of leptocephali moving offshore could be westward transport of leptocephali from the Mariana ridges where marine eels live (West Mariana Ridge including shallow seamounts and the Mariana Ridge including Guam and Saipan islands).

High catches of *Gnathophis* and *Ariosoma* in the NW area were likely related to spawning locations of these eels near the edges of the Kuroshio Current and recirculation of their leptocephali. *Gnathophis* spawn over the East China Sea shelf break along the western edge of the Kuroshio (Miller et al. 2002) and in other places along the continental shelf of Japan (Kimura et al. 2006), which results in offshore transport of their leptocephali (Takahashi et al. 2008). Some *Ariosoma* eels also appear to spawn along the Kuroshio in the East China Sea (Watanabe et al. 2016), and *A. balearicum* that live adjacent to the Sargasso Sea appear to migrate a short distance to the eastern side of the Gulf Stream to spawn, with their larvae being recirculated into the Sargasso Sea gyre (Miller 2002). Small *Ariosoma* leptocephali also only appear to be present at the edges of the WNP (Mochioka et al. 1991), and phyllosoma (lobster) larvae distributed within the upper 100 m in the Kuroshio recirculation region can be transported to the area east of Taiwan (Miyake et al. 2015). Therefore, it is possible that Kuroshio recirculation might bring some leptocephali such as *Ariosoma* into the study area. Sampling stations spread more widely will be needed to fully evaluate how leptocephali are transported offshore into the NEC region.

Similarly, more precise vertical dimension sampling of leptocephali will be needed to better understand where they reside at night. Our sampling showed different vertical distributions among taxa within the upper 100 m at night, but each tow sampled 2 depth layers (30 and 50 m or 70 and 100 m), so we could not determine exact depths where leptocephali were collected in each net deployment. However, based on the hydrographic sections, it appears that some species tended to reside above the thermocline in the warm water mixed layer (<50 m), and others tended to reside within or just above the ther-

mocline (70–100 m). Both depth layers are in the lower-salinity water above the STUW and above the highest chlorophyll concentrations in the lower thermocline.

One possibility is that leptocephali may reside in the warm water above the thermocline at night to facilitate growth (Miller 2015). Leptocephali seem likely to feed visually during daytime or crepuscular periods, because their food source appears to be POM or marine snow (Otake et al. 1993, Mochioka & Iwamizu 1996, Miller et al. 2011b), and most visible gut contents have been observed in larvae collected during daylight hours (Miller et al. 2011b). Marine snow concentrations may often be highest just below the surface mixed layer (Lampitt et al. 1993, Pilskaln et al. 2005), so some leptocephali may prefer to stay near the higher food concentrations even if they do not feed at night.

The finding of some taxa of leptocephali being more abundant at different depths may partly help explain some findings of studies on the stable isotopic compositions of leptocephali. In the NEC, stable isotope compositions of *Anguilla japonica* leptocephali differed from those of *Ariosoma majus* (sp. 7) leptocephali (Miyazaki et al. 2011). One possible explanation for the difference is that the large *Ariosoma* leptocephali could have originated from outside of the NEC area, where the isotopic characteristics of the biological community might be different, as reported in other fish species (Miyazaki et al. 2011, Lorrain et al. 2015). However, similar differences in isotopic compositions among taxa of leptocephali were also detected in the western Indian Ocean (Feunteun et al. 2015) and western South Pacific (Lié-nart et al. 2016). There appear to be 2 groups of leptocephali: species with lower nitrogen isotope ($\delta^{15}\text{N}$) signatures (*Ariosoma*, *Nemichthys*, *Avocettina*) and others with slightly higher $\delta^{15}\text{N}$ signatures (*Anguilla*, other Congridae, and Muraenidae) (Feunteun et al. 2015). The reasons for different isotopic signatures are not known, but leptocephali feeding at different depths on different types of POM is one possible explanation (Miyazaki et al. 2011, Feunteun et al. 2015). Interestingly, the species of leptocephali with lower $\delta^{15}\text{N}$ values are those that grow to larger sizes (>150 mm) than other leptocephali. Those 3 taxa (*Ariosoma*, *Nemichthys*, *Avocettina*) all showed higher abundances in the 30–50 m depth range in our sampling, although serrivomerids that are in the high $\delta^{15}\text{N}$ value group also were more abundant in the shallower layers.

There is presently not enough information available to evaluate possible relationships between the

vertical distributions of leptocephali and their feeding ecologies, so future research needs to investigate the fine-scale vertical distributions of each taxon along with studies on the diets and isotopic compositions in relation to the physical and biological structures of the communities where they live. More knowledge about the assemblage structure in the NEC region of the WNP will also be gained if sampling is extended over a larger area both latitudinally and longitudinally. Information from these types of future studies will help to provide a better understanding of the abundances and distributions of leptocephali and their role in oceanic communities, POM cycling, and the ocean carbon cycle.

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