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Contrasting biodiversity of eel larvae across the central Indian Ocean subtropical gyre

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ABSTRACT

The unique semi-enclosed Indian Ocean basin includes large Mascarene Plateau banks, offshore coral-reef islands, seasonal equatorial current jets, and cross-basin westward South Equatorial Current (SEC) flow, making it interesting for studying long larval-duration eel larvae (leptocephali) and regional eel biodiversity. Three surveys for leptocephali (in 2003, 2006, 2010) included sampling west of the Mascarene Plateau (west), a major survey and other stations off Sumatra and Java (east), and 2 cross-basin transects across the SEC. The highest numbers of leptocephali species were observed along Sumatra (2003: ~143 species; 2006: 72 species) and south of Java (2010: 69), with intermediate numbers being collected in the western Indian Ocean (2006: 71; 2010: 53) compared to low numbers in the hydrographically variable offshore zones (2006, 2010: 3–27). The larger continental shelf areas along Sumatra including the Mentawai Islands provide more coral reef and other habitats for species such as congrid, muraenid, ophichthid, and chlopsid eels compared to the Mascarene Plateau banks. Some larvae in these areas get transported offshore, but the majority of offshore larvae were of Nemichthyidae and Serrivomeridae mesopelagic eels that were spawning across the basin. Habitat differences between the southern Mascarene Plateau and Sumatra and southern Indonesia along the edge of the high biodiversity Coral Triangle likely explain the higher biodiversity of eel larvae observed along the western side of the basin, which for the Congridae and Ophichthidae included more species than observed previously within the central Indonesian Seas. In addition to local spawning, seasonal currents likely transport larger larvae towards Sumatra from the north or west and larvae may enter the basin from the Indonesian Throughflow in the east, but it is unknown if equatorial jets or the SEC can transport larvae across the whole basin.

1. Introduction

The Indian Ocean is a unique ocean basin because of its semi-enclosed nature and by having major wind-driven changes in its surface currents in the north (Schott and McCreary, 2001; McPhaden et al., 2015). It also has the South Equatorial Current (SEC) that flows westward across the basin that bifurcates when it reaches Madagascar (Chen et al., 2014; Peng et al., 2015). The basin has various island groups, banks, or large islands in areas such as the Maldives in the north (Jaleel, 2013), Chagos in the north-central area (Shepard et al., 2012; Graham and McClanahan, 2013), Madagascar in the west, and the banks, large islands (Reunion and Mauritius) (Fagoonee, 1990) and island groups of the Mascarene Plateau region (Spalding et al., 2001; Payet, 2005; Turner and Klaus, 2005) (Fig. 1).

The often-narrow continental shelves along the margins of the basin, the benthic habitats of the island groups or banks, and the mesopelagic zone provide habitats for a wide range of marine eels and their close relatives of the Elopomorpha (tarpons, ladyfish, bonefish,

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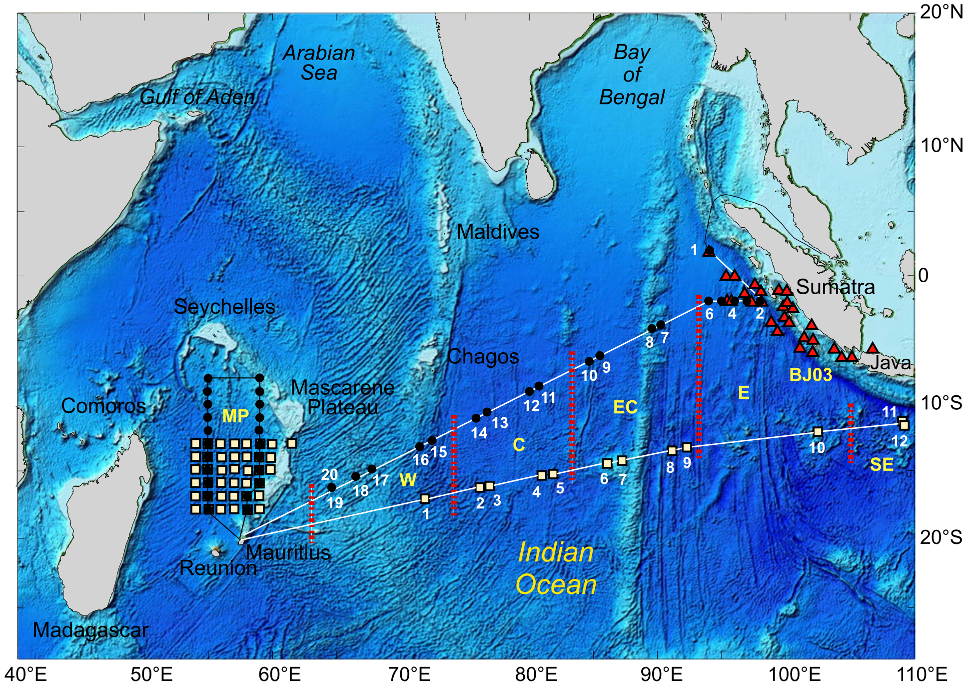

Fig. 1. Map of sampling stations for collecting leptocephali during 3 Indian Ocean research cruises, with offshore stations separated into designated zones (dashed red lines). The R/V *Baruna Jaya* VII survey (BJ03) was conducted in June 2003 off Sumatra (red triangles), with one station being made over the continental shelf in the southwest Java Sea. The R/V *Hakuho Maru* KH-06-4 survey in November 2006 (black circles) started during Leg 1 from off northern Sumatra and extended southwestward to east of the Mascarene Plateau (Stn. 1–20). Leg 2 of KH-06-4 sampled in 2 long transects west of the plateau. The February 2010 KH-09-5 Hakuho Maru survey (squares) started with a grid of stations west of the Mascarene Plateau (Leg 5) and then a transect of stations was sampled (Leg 6) moving eastward (Stn. 1–12). Color shows ocean bathymetry (imagery obtained from the NOAA Marine Geology and Geophysics Center) with dark blue showing deep- and light blue shallow-depths.

notacanths), which all share the common trait of having leptocephalus larvae (Böhlke, 1989a, 1989b; Miller and Tsukamoto, 2004). These larvae are unusual in having laterally compressed transparent bodies and growth to large sizes that gives them longer larval durations than most fish larvae (Smith, 1989; Miller, 2009). The Indian Ocean basin also includes 5 species or subspecies of catadromous anguillid eels that live in freshwater and estuarine habitats on all sides of the basin and on the larger islands, whose spawning areas, larval distributions, and life history characteristics have been studied in the Indian Ocean (Jespersen, 1942; Robinet et al., 2003, 2008; Aoyama et al., 2007; Kuroki et al., 2007; Réveillac et al., 2008, 2009; Pous et al., 2010).

The biodiversity and larval distributions of the leptocephali of marine eels have been studied in a few parts of the Indian Ocean, such as west of the Mascarene Plateau (Miller et al., 2015). Some types of congrid eel larvae were also studied using collections made in the eastern Indian Ocean off Sumatra historically (Castle, 1997) or a during recent survey there (Miller et al., 2011a, 2013). The species composition of leptocephali was also studied in repeated sampling transects across the far eastern part of the Indian Ocean to the northwest of Australia (Castle, 1969). These studies, and those in other parts of the world's major ocean gyres including the north and south Atlantic and Pacific, suggest that the biodiversity of eels indicated by the number of species of leptocephali collected is highest in the Indonesian Seas (see Miller et al., 2016).

Despite the diversity of anguillid and marine eels that inhabit the Indian Ocean region, there is only a very limited understanding of how their life histories interact with the ocean current patterns and complex seasonal changes in circulation in some areas. A spawning area of *Anguilla bicolor bicolor* has been discovered off West Sumatra (Jespersen, 1942; Aoyama et al., 2007) and garden eels of the Heterocongrinae and some congrid eels of the Bathymyrinae (*Ariosoma* and other genera) are among the marine eels that spawn in the nearshore waters there (Miller et al., 2011a, 2013). On the other side of the basin, a wide range of marine eels have been found to spawn in various habitats at or offshore of the Mascarene Plateau to the east of Madagascar (Miller et al., 2015).

The studies of leptocephali in the Indian Ocean and other regions have indicated that most benthic marine eels appear to spawn within or near their benthic habitats or along the edges of continental shelves, but there appear to be differences in how their larvae become dispersed offshore (Miller, 1995, 2009; Miller et al., 2002; Miller and McCleave, 2007). Some *Conger* eels migrate offshore in similar ways as anguillid eels, which exclusively spawn offshore at various distances from their juvenile growth habitats (Aoyama, 2009; Miller et al., 2011b). All species of meso- and bathy-pelagic eels spawn in their open ocean habitats (Miller and McCleave, 1994), but the larvae of all types of species (anguillid, shallow-water, slope, oceanic) mix together in the upper few hundred meters of the ocean (Castonguay and McCleave, 1987a; Miller, 2015; Onda et al., 2017). Larval durations of marine and freshwater eels can vary from several months to more than a year (Miller, 2009; Kuroki et al., 2014), so there is the potential for large-scale dispersal in some parts of the Indian Ocean. However, there have been no studies on leptocephali offshore in the Indian Ocean basin.

The basin is surrounded by the southwestern edge of the high marine biodiversity region referred to as the "Coral Triangle" (Hoeksema, 2007) in the east, the Bay of Bengal in the northeast, the west coast of Australia to the southeast, Madagascar and west Africa in the west and the Arabian Sea in the northwest (Fig. 1). With such diversity of geographic regions in relatively close proximity compared to the size of the Pacific Ocean, the Indian Ocean provides an interesting opportunity to begin to compare the biodiversity and species composition differences among different areas that are often connected by ocean currents.

This is now possible because 3 similar sampling surveys for leptocephali were conducted from about the equator to 20°S in the Indian Ocean with 2 surveys including transects of stations across the basin (Figs. 1 and 2). Many stations were made off Sumatra in 2003 and a transect of stations sampled off Sumatra and across the basin to the west in 2006. A transect of stations was also made from the western part of the basin to south of Java in 2010. These surveys provide the first opportunity to compare the species compositions and distributions of leptocephali found on the western side of the basin, which was studied previously (Miller et al., 2015), to offshore areas (no information), along Sumatra (only information about some congrid larvae; Castle, 1997; Miller et al., 2011a, 2013), and south of Java (Castle, 1969). Therefore, the objective of the present study was to compare the biodiversity, size, and distributions of leptocephali on the two sides and across the basin to begin to evaluate the biogeography and larval

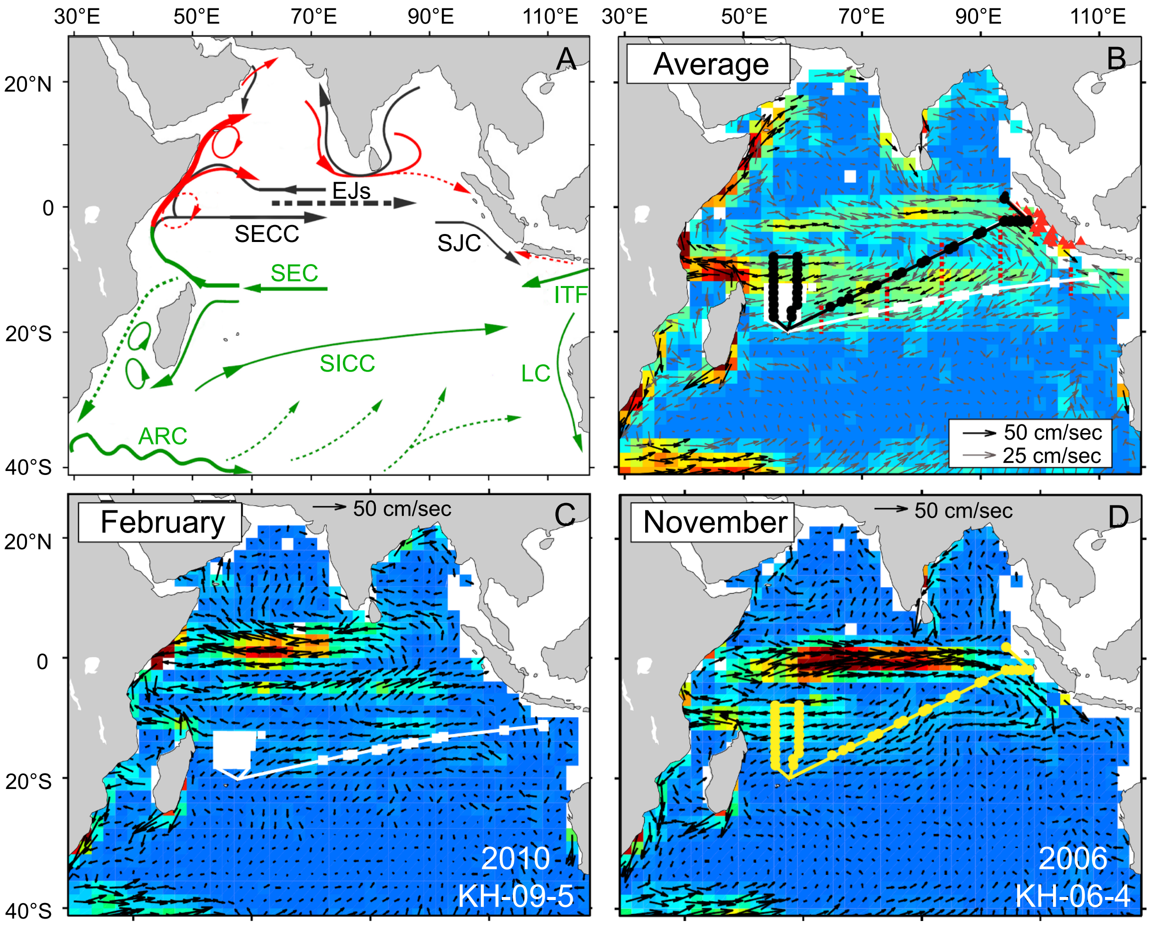

Fig. 2. Maps of the general ocean surface current patterns in the Indian Ocean separated by their seasonal occurrences of all year (green arrows; south of the equator), and winter (black) or summer (red) mostly at or north of the equator (A), the average currents measured by ocean drifters from 1985 to 2013 (B), and the average currents for February (C) and November (D) (modified from Peng et al., 2015), showing all sampling stations of the present study (A; 2003 red; 2006 black; 2010 white; see Fig. 1), and the 2010 (C; white) and 2006 (D; yellow) stations. Color map shading shows kinetic energy (red: high; blue: low) in (B-D). Equatorial Jets (EJs), South Equatorial Countercurrent (SECC), South Java Current (SJC), South Equatorial Current (SEC), South Indian Ocean Countercurrent (SICC), Indonesian Throughflow (ITF), Leeuwin Current (LC), Agulhas Return Current (ARC) are labeled (see Peng et al., 2015 for other current names). The line thickness of current arrows roughly represents the strength of the currents.

dispersal of eels and their close relatives in the central latitudes of the Indian Ocean. The hydrographic structure in the offshore region of the basin was examined with CTD data from the 2 cross-basin transects, and the catches are compared to the surface current flows from the extensive drifter data analyzed by Peng et al. (2015).

2. Methods

2.1. Characteristics of the study area

The central latitudes of the Indian Ocean have westward flow of the South Equatorial Current (SEC) across the basin with some seasonal variations of that basic pattern (Schott and McCreary, 2001; Peng et al., 2015) before the SEC bifurcates at Madagascar (Chen et al., 2014) (Fig. 2A). To the south, there is eastward flow of the shallow South Indian Ocean Countercurrent (SICC) that extends above the southern edge of the deep-reaching SEC flow (Siedler et al., 2006; Palastanga et al., 2007). To the north along the equator, there are alternating-direction shallow equatorial jets (Senan et al., 2003; Sengupta et al., 2007; McPhaden et al., 2015), and below those flows, the Equatorial Undercurrent transports water eastward in some months (Chen et al., 2015; Nagura and McPhaden, 2016). The northern areas of the Indian Ocean have monsoon-related seasonal current patterns (Schott and McCreary, 2001; Peng et al., 2015) that can change much more drastically than the regions south of the equator (Fig. 2A). Upwelling can occur off Sumatra including in the month of November when the 2006 survey was conducted (Susanto et al., 2001).

The sampling area to the west of the Mascarene Plateau was likely dominated by westward SEC flow that passes through the gaps between the plateau banks (New et al., 2007; Pous et al., 2010; Peng et al., 2015). The cross-basin stations in 2006 were also likely within SEC flow (Fig. 2D), but the 2010 stations may have been along the southern margin of SEC flow, except south of Java (Fig. 2C). There is frequently southward flow or large eddies (Hacker et al., 1998; Vinayachandran et al., 1999; Iskandar et al., 2006) off Sumatra (Fig. 2D). To the southeast, there are alternating nearshore flows of the South Java Current or westward flow of the SEC offshore, with contributions of water from the Indonesian Throughflow, which transports water into the Indian Ocean (Schott and McCreary, 2001; Sprintall et al., 2002).

A high-salinity surface maximum area forms in the southern Indian Ocean and other ocean basins where evaporation is higher than precipitation (Gordon et al., 2015). This water is then subducted into the thermocline and forms Subtropical Underwater (STUW) in the Indian Ocean and other ocean basins (O'Conner et al., 2005). The hydrographic sections show water masses consistent with STUW in the western regions (Fig. 3B,E) and this water is also present farther west along the Mascarene Plateau (Miller et al., 2015; Schabetsberger et al., 2016) as seen in the WOCE Atlas sections (http://whp-atlas.ucsd.edu/indian/sections.htm; Accessed 12 December 2017).

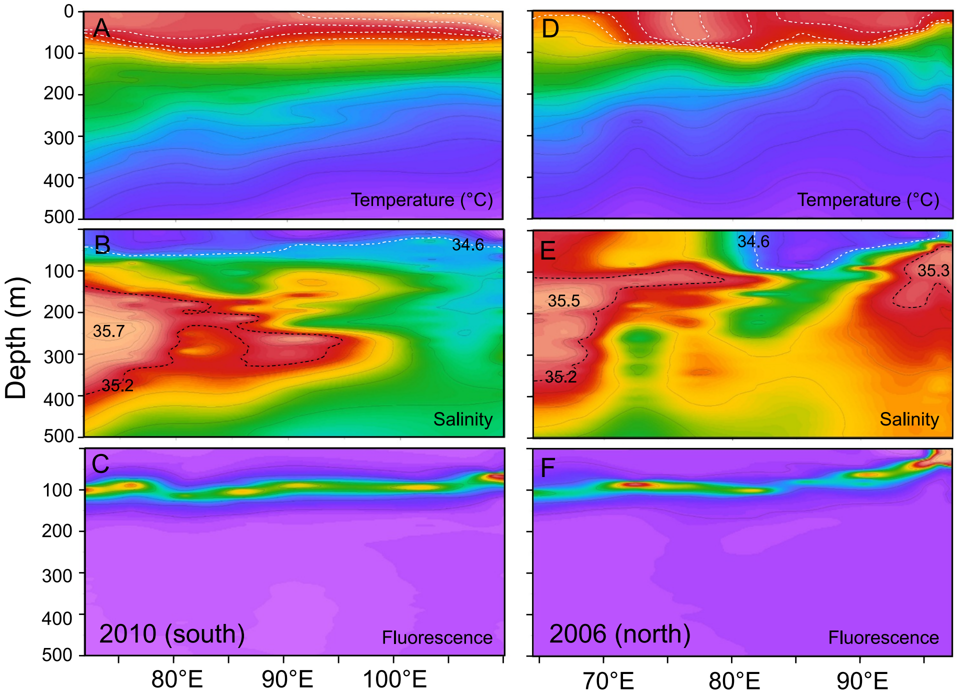

Fig. 3. Hydrographic sections of temperature, salinity, and fluorescence from the February 2010 (A-C) and November 2006 (D-F) transects across the Indian Ocean basin. The 26–29 or 30 °C contours in the surface layer are highlighted (dotted white lines) to compare the temperature structures (1 °C contours intervals), and two salinity contours (0.1 intervals) are labeled along with the maximum salinities. Flourescence values range from 0.05 below the thermocline to 0.65 off Sumatra.

2.2. Surveys for collecting leptocephali

Areas of the eastern and western Indian Ocean were sampled for leptocephali during 3 research cruises that were primarily investigating anguillid spawning areas, and two transects of stations were sampled across the basin at different latitudes (Fig. 1). All 3 surveys used the same type of Isaacs-Kidd Midwater Trawl (IKMT) with an 8.7 m^2 mouth opening and 0.5 mm mesh that was fished in the upper 150 m in either single oblique-tows, or in step-tows that fished horizontally at several depths (*e.g.*, 10 min at 120, 90, 70, 50, 30 m). The BJ-03–2 survey off Sumatra from 5 to 21 June 2003 (subsequently referred to as 2003 or BJ03) was conducted using the R/V *Baruna Jaya* VII of LIPI in Indonesia, which also conducted two previous surveys for leptocephali around Sulawesi Island in the central Indonesian Seas in 2001 and 2002 (Wouthuyzen et al., 2003, 2005, 2009). The 2003 sampling style was the same as the previous surveys that consisted of both an oblique and step tow at each station, with two stations sampled each night (25 stations in 2003). The anguillid (Aoyama et al., 2007; Kuroki et al., 2007) and some congrid eel leptocephali (Miller et al., 2011a, 2013) were studied from the 2003 survey, but the overall assemblage of leptocephali has not been studied. The KH-06–4 survey conducted by the R/V *Hakuho Maru* of Japan in 2006 (referred to as 2006), started off Sumatra and crossed the basin (Leg 1; Stn. 1–20; 12–21 November). Both oblique and step tows were made at each of 2 stations each night. At Stn. 4 and 19 (Fig. 1), only a deep-oblique tow to 4000 m was made, so those stations are excluded from data plots. Then 2 north-south transects were sampled to the west of the Mascarene Plateau (Leg 2; Stn. 21–42; 27 November–3 December), using similar methods, except only one oblique tow was made at each day station and both an oblique and step tow was conducted at night stations (17 oblique tows, 15 step tows). The 2010 KH-09–5 survey of the *Hakuho Maru* (referred to as 2010) started with a tight grid of stations just to the west of the southern banks of the Mascarene Plateau (Leg 5; 29 January-10 February) that had one oblique tow at each day station and one step tow at each night station (24 oblique tows, 16 step tows). Then a partial transect of 1–2 stations per night (1 step tow per station; 15 tows) was made moving east across the basin (Leg 6; 17–24 February). At Stn. 11 and 12 south of Java at the end of the transect, 5 tows mostly had only one step at 30 m for collecting tuna larvae (Stn. 11: 1 standard step tow and a 30-m step tow: Stn. 12: 3 30-m step tows). The leptocephali (2006, 2010) and the isotopic composition of leptocephali and other food web components (2010) were studied from the collections west of the Mascarene Plateau (Feunteun et al., 2015; Miller et al., 2015). During the 3 cruises, temperature, conductivity, depth (CTD) profiles were made at each station, except in the 2010 grid they were made at selected stations, and only one CTD cast was made each night during the 2 basin crossings.

2.3. Identification and comparisons of leptocephali

Leptocephali were sorted fresh from plankton samples, identified, and measured onboard (nearest 1 or 0.5 mm total length). Meristic data (myomere counts) or pigmentation patterns were recorded for some taxa. Specimens were preserved in 10% formalin seawater (2003), in ethanol, or by freezing (2006, 2010). The species identification of most types of leptocephali are not yet known in the Indo-Pacific, but using combinations of body shape, pigmentation and meristic data, different species-types can be separated (Tabeta and Mochioka, 1988; Böhlke, 1989b; Miller and Tsukamoto, 2004). The amount of meristic data obtained sometimes depended on the number of specimens collected, and in 2003 not all specimens were separated into species-types within a family or taxa at a few stations where many Congridae (mostly one-row lateral pigment Congrinae) and Ophichthidae (mostly *Neenchelys*) were collected, and Muraenidae larvae were not separated as clearly using pigmentation patterns as in the later surveys. Although most of these larvae have not been re-examined, the 2003 *Ariosoma*-type and garden eel larvae (*Gorgasia* and *Heteroconger*) were re-examined (including some genetic sequencing), so the number of species of those taxa in 2003 (Miller et al., 2011a, 2013) are more accurate than during other surveys. There are only a few species of the mesopelagic eel species, but their leptocephali are difficult to separate morphologically for the Nemichthyidae and Serrivomeridae. *Nemichthys* larvae were separated into 2 possible species based on lateral pigmentation presence-absence at smaller sizes, and serrivomerids into 2 taxa if total myomere (TM) counts had distinctly different ranges, but TM was not consistently counted for many larvae. These estimates of number of species-types are therefore only approximate for some taxa, but for convenience we will use the phrase “number of species”.

Table 1
Numbers of leptocephali of each species or taxon collected during the 3 sampling surveys separated by geographic sampling zones or stations. The BJ-03-2 survey (BJ03) in June 2003 is separated into all stations off Sumatra, and St. 26 over the continental shelf in the southwest Java Sea, KH-06-4 in November 2006 is separated into west of the Mascarene Plateau (MP), and Indian Ocean transect stations (N: north) separated by west (W), central (C), east-central (EC) and east (E) zones (see Fig. 1), and KH-09-5 is separated into west of the MP, Indian Ocean transect stations (S: south, or single stations listed in W and E) in the same zones, and the 5 tows south of Java at Stn. 11 and 12 (SE in Fig. 1). Numbers in family rows are the numbers of species, and families or single species without their family name are shown in bold.

	MP		W		C		EC		E			S. Java	Java Sea
	2006	2010	N	Stn. 1	N	S	N	S	N	Stn.10	BJ03	Stn.11,12	Stn.26
Anguillidae	**2**	**1**					**1**		**1**		3		
Anguilla bicolor bicolor	1	2							2		41		
Anguilla marmorata	1						1				1		
Congridae	**20**	**17**	**2**	**1**	**5**		**8**		**28**		**40**	**16**	
Ariosoma sp. 1	1				3		6		1		50	3	
Ariosoma sp. 2		1							2		21	5	
Ariosoma sp. 3		1							1		7		
Ariosoma sp. 4	6				1						15		
Ariosoma scheelei	19	1					7		12		114	6	
Ariosoma sp. 6	80	1	1				1		2		8		
Ariosoma sp. 7	13	40					1		4		44	7	
Ariosoma sp. 8	1	3									4	5	
Ariosoma spp.	27	27	1	2	3		1		4		34	105	
Conger	14	65	8						3		14	2	
Gnathophis	42	33			1				4		17	8	
Bathycongrus	2	3					4		19		47	24	
Uroconger							1		43		82		
Congrinae	9	2							6		257	64	
Gorgasia	1	8							12		371	6	
Heteroconger	2								1		104	9	
Gavialiceps									4			8	
Thallassenchelys[a]	3	1							3		7		
sp.	1	6							1		122		
Chlopsidae	**4**	**4**	**1**		**1**		**3**		**5**		**7**	**7**	
Kaupichthys		1					6		9		14	1	
Robinsia catherinae	4	1	1		2		2		1		4		
sp.	9	5					1		14		98	34	
Moringuidae	**1**								1		1	**1**	
Moringua	2								1		7	264	
Muraenidae	**22**	**11**	**1**		**8**	**1**	**9**		**20**		**30**	**13**	**1**
Muraeninae	72	24			6		17		33		160	14	
Uropterygiinae	23	19	1		7	1			7		50	11	
sp.	15	7					1		11		159		3
Ophichthidae	**11**	**10**			**2**		**1**		**10**		**46**	**22**	**x**[b]
Ophichthinae	42	10			2		1		4		120	25	
Myrophinae	5	1							2		60	28	37
Neenchelys spp.	1	2					8		19		404	117	2
sp.	5	3									65		32
Muraenesoscidae											**1**	**1**	**1**
Muraenesox											18	1	15
Nettastomatidae	**3**						**1**		**2**		**4**	**2**	**1**
Nettenchelys/Nettastoma	1						3		2		5		
Saurenchelys/other	2								1		29	2	23
Synaphobranchidae	**2**	**1**	**1**		**1**						**5**	**2**	
Synaphobranchinae	4	1	1		1						1	2	
Illyophinae											5	1	
Derichthyidae	**1**	**2**	**1**			**1**		**1**	**1**			**1**	
Derichthys serpentinus		18				23		3	2				
Nessorhamphus	1	1	1									1	
sp.	2	10											
Nemichthyidae	**2**	**2**	**2**		**3**	**3**	**2**	**3**	**2**	**2**	**2**	**3**	
Nemichthys	61	108	32		45	29	23	17	38	2	51	36	
Avocettina	10	34	10		5	7	9	3	4	1	9	3	
Labichthys						5							
Serrivomeridae	**1**	**2**	**1**	**2**	**1**	**1**	**1**	**1**	**2**		**1**	**1**	
sp.	75	106	7	44	25	149	9	44	15	6	8	16	
Cyema atrum		1	1								3		
Eurypharynx pelecanoides	2	1	1			1		1		2	2		
Monognathidae[c]						1							
Leptocephalus thorianus							1						
Albulidae											2		1
Elopidae											5		
Megalopidae											41		
Notacanthiform	3										5		
Unidentified/Other	3	29			1		2				6	1	
Total	565	575	65	46	102	216	105	68	287	11	2691	809	113
Number of species	71	53	11	3	20	7	27	6	72	4	~143	69	> 6

[a] Has been genetically identified as *Congriscus* (Congridae) (Kurogi et al., 2016).

[b] Species types were not separated.

[c] Formerly referred to *Leptocephalus holti* of the Cyematidae (Poulsen et al., In revision).

The sizes of some abundant taxa of leptocephali were compared statistically to see if there were any obvious seasonal or geographic differences using Kruskal-Wallis tests followed by pairwise Dunn's tests (significance criteria of $p < .05$). Comparisons were made between offshore areas within (west of the plateau, or across the basin) and among years for serrivomerids and *Nemichthys*, and between 2003 off Sumatra, west of the plateau, and at the 2 stations south of Java in 2010 for Muraenidae, Ophichthidae, and *Ariosoma*-type leptocephali.

3. Results

3.1. Species composition across the basin

Combining catches from 3 cruises, a total of 5653 leptocephalus larvae were collected across the central Indian Ocean latitudes (Table 1). Sampling effort differed among regions (lower offshore in the basin), but some clear regional differences were observed in species composition and abundance of taxa of leptocephali. The detailed catch data in Table 1 shows that many more species of larvae of shallow-water and outer-slope eels of the families Congridae, Muraenidae, and Ophichthidae were caught on the two sides of the basin compared to at cross-basin stations.

During the intensive sampling of the June 2003 Sumatra survey there were 2691 leptocephali collected of ~143 species of 17 families of eels and their elopomorph relatives, and 113 larvae of at least 6 species of 5 families were collected at the station located over the continental shelf in the western Java Sea (mostly Ophichthidae, Nettastomatidae, Muraenesoscidae). About half of the larvae off Sumatra were comprised of 40 species the Congridae (N = 1318) (Fig. 4B). This was partly due to the unusually large number of garden eel leptocephali that were collected (Miller et al., 2011a). The next highest proportions of larvae included at least 46 Ophichthidae species (N = 649), and possibly about ≥30 Muraenidae species (N = 369). There were also 7 Chlopsidae species (N = 115), and some Nettastomatidae, Muraenesoscidae, Megalopidae (Elopiformes, ladyfishes), Synaphobranchidae, and notacanthid (Albuliformes, spiny eels) larvae were collected, which were mostly rare or absent in other surveys.

Catches of shallow-water eel larvae were also high at the November 2006 stations off Sumatra and south of Java in February 2010. At Stn. 1–6 off Sumatra, 28 species of congrid leptocephali (N = 122) were collected along with 20 species of muraenids (N = 51) and 24 other species. The congrid leptocephali collected in 2006 sampling near Sumatra included 5 species of *Bathycongrus* and the larvae of *Gavialiceps*, a species not collected elsewhere. The 5 tows at Stn. 11 and 12 south of Java in 2010 collected 809 larvae of 69 species and included big catches of ophichthids (*Neenchelys*, N = 117), Moringuidae (*Moringua*, N = 264), and *Ariosoma* (≥8 species, N = 131). A higher proportion of ophichthid larvae was collected there, and the especially large number of Moringuidae larvae was unique compared to other areas (Fig. 4).

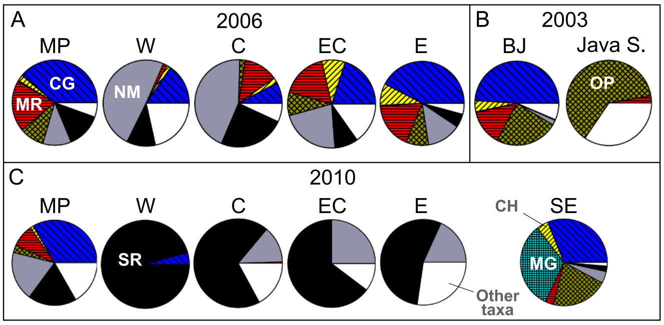

Fig. 4. Proportions of the number of leptocephali of the major families collected in each designated zone of the Indian Ocean (separated as shown in Fig. 1) during the 3 sampling surveys (2003, 2006, 2010), showing the Chlopsidae (CH), Congridae (CG), Moringuidae (MG), Muraenidae (MR), Ophichthidae (OP), Nemichthyidae (NM), Serrivomeridae (SR), and all other taxa pooled together.

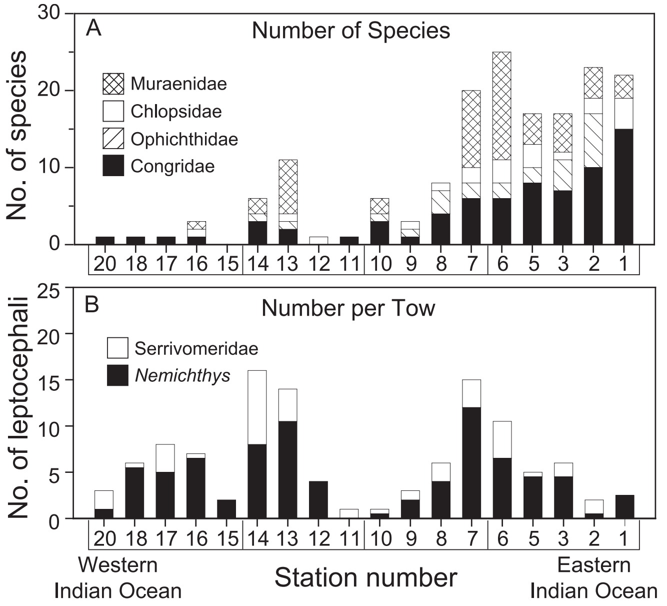

Fig. 5. The number of species of the 4 major families of shallow-water eel leptocephali in the 2006 stations from the eastern Indian Ocean off Sumatra and across the basin to east of the Mascarene Plateau (A), and the number of leptocephali per tow of nemichthyid and serrivomerid mesopelagic eels (B). Designated zones (Fig. 1) are separated with lines between station numbers below the x-axes.

In contrast, the leptocephali of the mesopelagic eels of the Nemichthyidae and Serrivomeridae comprised a low proportion of the leptocephali caught along Sumatra in 2003 and 2006, and south of Java (Fig. 4). Remarkably, only 8 of the more than 2600 larvae in 2003 were serrivomerid leptocephali even though more than half of the stations were made over deep water away from the continental shelf.

The standardized sampling strategy in 2006 started with stations located just offshore of Sumatra and then sampled each night as the ship moved across the basin. This clearly showed a decrease in the number of shallow-water eel species collected as the distance offshore increased (Fig. 5A). Even lower numbers of species were caught at the stations made across the basin in 2010 (Table 1). Only 11–216 leptocephali of 3–27 species were collected within the designated offshore station zones in 2006 and 2010 (Table 1, Fig. 5A), and these catches were usually numerically dominated by serrivomerid and *Nemichthys* larvae (Table 1, Figs. 4, 5). An exception to the rarity of shallow-water eel leptocephali offshore was at Stn. 13 and 14 in the central part of the 2006 transect (Figs. 5, 6D,E). A few *Ariosoma*, *Gnathophis*, ophichthids, chlopsid and 13 muraenid larvae were caught at those 2 stations. Serrivomerids and *Nemichthys* were also abundant there.

Catches of *Nemichthys* and serrivomerid larvae fluctuated across the basin in 2006 (Figs. 5, 6) and also to some degree in the 2010 transect (Table 1, Fig. 7). For example, serrivomerid larvae were abundant at Stn. 1 in 2010, but no *Nemichthys* were caught there. Nemichthyid larvae of *Avocettina* were widely distributed, but were caught in lower numbers, and those of the meso- and bathy-pelagic eels of the Derichthyidae, Eurypharyngidae, Cyematidae, and Monognathidae (formerly *Leptocephalus holti*; Poulsen et al., in revision) were rare, except some *Derichthys serpentinus* were collected west of the Mascarene Plateau in 2010 and 23 were caught in the central stations in the 2010 transect, compared to only 2 being collected off Sumatra in 2006 (Table 1). The locations where larger numbers of species such as *D. serpentinus* and *Avocettina* were collected influenced the relative proportions of the "other taxa" category in Fig. 4, but other species also contributed to that category in some areas (Table 1).

Across the basin to the west of the Mascarene Plateau, 565 larvae of

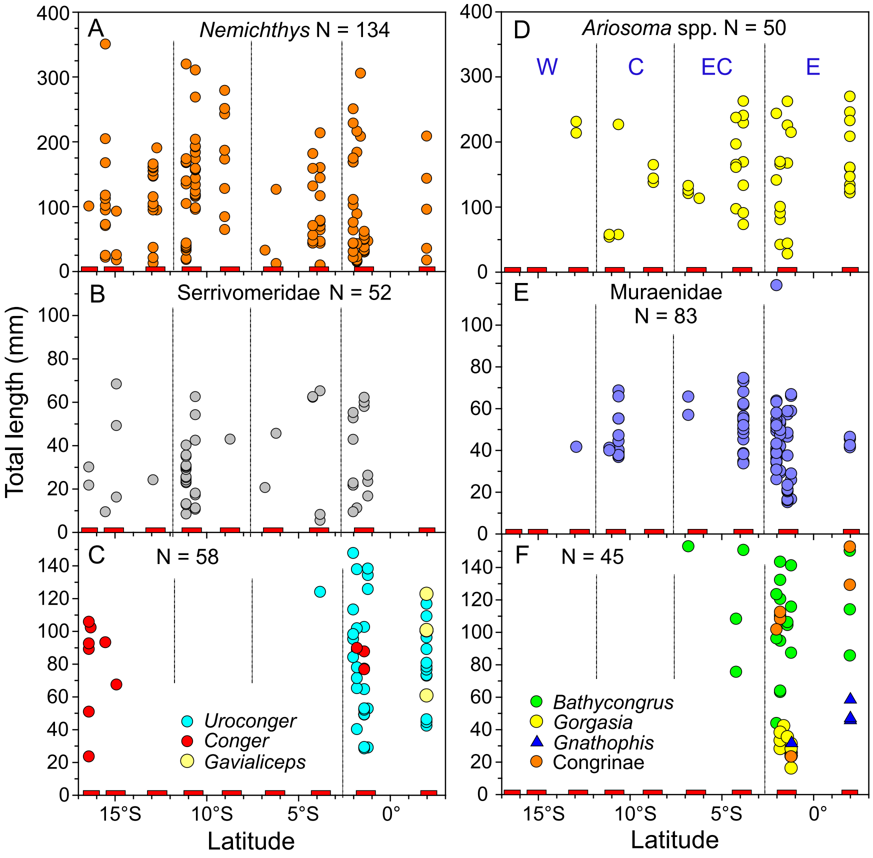

Fig. 6. Plots of individual lengths of 11 taxa of leptocephali collected during the transect of stations from Sumatra to east of the Mascarene Plateau in 2006 with the designated zones (Fig. 1) separated with dashed lines. All taxa except *Nemichthys*, Serrivomeridae, and Muraenidae belong to the family Congridae. Small rectangles above the x-axes show station locations.

71 species of 14 families were collected in the 2006 transects, with 20 species of congrids (N = 221) and 22 species of muraenids (N = 110) being caught; but larvae of the Chlopsidae and Ophichthidae were not diverse in comparison to along the east side of the basin (Table 1). A similar total number of larvae was collected in 2010 (N = 575), but fewer species (53 of 11 families) were caught, mainly due to 50% fewer species of muraenids being identified (see Miller et al., 2015 for a detailed analysis of the two surveys). Combining the two surveys, about 90 species were collected.

3.2. Regional distribution of larval size

Wide sizes-ranges of leptocephali of both shallow-water and mesopelagic eel families were collected west of the Mascarene Plateau in 2006 and 2010 (Miller et al., 2015) and in the other areas (Figs. 6–8). The smallest larvae of ophichthids, muraenids, and chlopsids were collected at the stations closest to the shallow banks of the plateau or off Sumatra in 2003. The sizes of muraenid larvae were different between 2006 (42.4 ± 15.8 mm) and 2003 (mean ± S.D: 32.7 ± 14.5 mm) and 2010 (32.5 ± 16.5 mm) west of the plateau ($p < .001$), but 2003 and 2010 were not different, and 2006 and south of Java in 2010 (45.1 ± 11.7 mm) were not different in the pairwise tests. Ophichthid leptocephali had more similar sizes within the range of 6–150 mm (mean sizes: 47.5–56.0 mm) between the 4 survey areas, but there were differences ($p < .001$) because 2003 was different than 2006 and south of Java. Smaller ophichthid larvae were caught during 2003 than south of Java in 2010 (Fig. 8F,I) and all of the ophichthid larvae south of Java were greater than 28 mm in size (Fig. 8F).

Small *Conger* leptocephali (38 larvae that were 9.2 to ≤ 20 mm, + 24 larger larvae) were collected west of the Mascarene Plateau in 2010, and a wide size-range including a small larva (23.3 mm) was collected east of the plateau at the westernmost 2006 transect stations (Fig. 6C). This suggests that conger eels might make offshore spawning migrations to both the east and west of the plateau.

Wide size-ranges of shallow-water eel larvae were also collected along Sumatra and south of Java (Fig. 8). The greatest number of *Ariosoma*-type leptocephali in that area were about 25 mm (Fig. 8A), which is similar to the size distribution seen in 2003 (Miller et al., 2013). The size of the *Ariosoma* leptocephali showed a steady increase as sampling moved farther offshore in 2006 (Fig. 6D), but some smaller larvae were caught at Stn. 13 and 14 in the central area, where muraenid larvae were also collected (Fig. 6E). The *Ariosoma*-type leptocephali were statistically different in size ($p < .001$) among all areas, except between 2003 and south of Java. The differences resulted from there usually being one or more distinctly abundant size ranges (likely from different spawning periods) that occurred at different sizes among surveys (Fig. 8A, and see Miller et al., 2013, 2015).

Wide size ranges of *Nemichthys* and serrivomerid leptocephali were usually collected in the sampling across the Indian Ocean basin during both 2006 (Fig. 6A,B) and 2010 (Fig. 7). The sizes of the two types of larvae were different among areas though ($p < .001$), except for serrivomerids within each year (west of the plateau v.s. offshore) and the offshore 2010 *Nemichthys* (116.5 ± 69.5 mm) compared to the other areas (52.4–153.6 ± 56.8–75.1 mm). The average size of Serrivomerids was smaller in 2010 (22.9 ± 15.2, 21.6 ± 9.5 mm) than in 2006 (29.3 ± 14.1, 31.5 ± 18.1 mm) both west of the plateau and offshore. The widespread presence of small larvae (minimum serrivomerid size west of the plateau and offshore in 2006 and 2010: 5.3–8.0 mm; *Nemichthys*: 8.5–15.5 mm) indicated those species were likely spawning across most of the basin that was sampled.

3.3. Hydrographic structure and larval catches

The two transects across the Indian Ocean basin included one CTD cast at each station, which enabled the basic hydrographic structure to be examined. Similar upper 500 m temperature ranges were

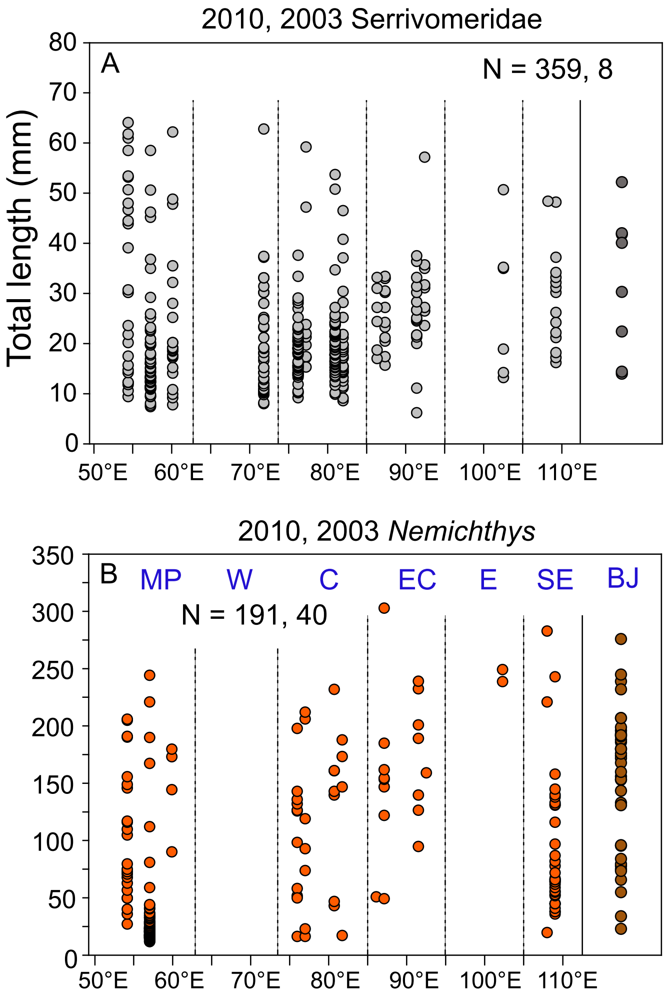

Fig. 7. Plots of the individual lengths of *Nemichthys* and Serrivomeridae leptocephali collected during the 2010 survey west of the Mascarene Plateau (MP, pooled into the 3 longitudinal zones of Miller et al., 2015), in the 2010 transect station zones from the western Indian Ocean to south of Java in 2010, and all the individuals pooled from the 2003 survey (BJ) off Sumatra.

encountered in February 2006 (9–29 °C) and November 2010 (9–30 °C), but the surface mixed layer structure differed between the two years, with warmer water (29–30 °C) being in the eastern side in 2010 and a pool of 29 °C water being crossed at about 76 °E in 2006 (Fig. 3A,D). The main thermocline varied in depth along the two transects within the range of about 75–150 m. The chlorophyll maximum layer was usually at about 100 m or slightly shallower, except in the east, where especially in 2006, levels increased greatly and reached the surface in the area off Sumatra (Fig. 3C,F).

The salinity sections showed the presence of mostly subsurface high-salinity Subtropical Underwater (STUW) in the western ends of the transects reaching 35.5 (2006) and 35.7 (2010) (Fig. 3B,E). A shallower layer of higher-salinity water (35.3) was also present off Sumatra in 2006 and a surface pool of lower-salinity was present down to 100 m farther offshore at about 80–85 °E. A very shallow lens of low-salinity water was at the surface across the 2010 transect that became deeper in the west, and higher-salinity water reached the surface farther to the west in 2006 beyond where the 2010 transect had no stations.

In the 2006 transect, the number of species (~15–25) and the number of collected leptocephali per station (34 – 55) was higher in the areas with a shallow layer of low surface salinity ($<$ 50 m), a shallow high-salinity core, and high fluorescence (Stn. 1–7) than in the stations that were in the more offshore area with a deeper surface layer of low-salinity water and no STUW (Stn. 9–12). More larvae and species were caught at Stn. 13 and 14 in the pool of warmer water (29 °C) that was outside of the zone with low surface salinity, before numbers dropped off again farther west (Figs. 5A, 6D, E). In 2010, there was no obvious pattern of catches in relation to hydrographic structure, except that there were large catches of shallow-water eel larvae south of Java at Stn. 11,12 where there was warmer surface water and higher fluorescence.

4. Discussion

4.1. Contrasting species composition across the basin

The comparisons of leptocephali catches during sampling on both sides of the Indian Ocean and in the 2 transects across the basin provided the first opportunity to evaluate the species composition and distribution of larvae across the central latitudes of the ocean basin. In the west, larvae of the shallow-water eels of the Chlopsidae, Congridae, Muraenidae, and Ophichthidae were clearly more diverse and abundant downstream of the Mascarene Plateau than they were at the stations spread across the basin. Many congrid and ophichthid leptocephali and other shallow-water, outer continental shelf and slope species were also collected off Sumatra in November 2006 and south of Java in February 2010.

However, the larvae of the main 4 shallow-water eel families and other types of continental shelf and slope eels were most diverse at the 2003 stations along Sumatra. The estimated ~143 species of 17 families that were collected there is at least twice as many species as were collected in any other area. Part of that higher number may have been due to the greater sampling effort in 2003 (2 night tows at 25 stations), which probably increased the number of rare species caught. But it also likely reflects a higher number of species being present there, because many night tows were also made west of the Mascarene Plateau. There are many different types of habitats along the coast of Sumatra and around the Mentawai Islands (see maps in Spalding et al., 2001; Miller et al., 2013, 2016), which is an area that likely has the highest marine biodiversity along the Indian Ocean coastlines of Indonesia (Huffard et al., 2012). A variety of species of leptocephali were only collected along Sumatra in 2003. The leptocephali of outer shelf and slope eels of the Nettastomatidae were only abundant off Sumatra or at the one 2003 station in the western Java Sea, and they were rare or absent west of the plateau and across the basin.

In contrast, the leptocephali of mesopelagic eels were rare off Sumatra and were widely distributed at the whole range their sizes across the basin. They were also abundant offshore to the west of the Mascarene Plateau (Miller et al., 2015). Other meso- or bathy-pelagic eel larvae were rare and patchily distributed, with *Derichthys serpentinus* almost exclusively being collected in the 2010 survey, suggesting they spawn seasonally in the Indian Ocean. Small leptocephali of mesopelagic eels are common offshore in subtropical gyres (Castonguay and McCleave, 1987b; Miller and McCleave, 1994; Wippelhauser et al., 1996; Miller et al., 2006; Onda et al., 2017) as they were in the Indian Ocean in the present study because they seem to spawn anywhere in the open ocean.

The pattern of diversity and abundance of the larvae of the different types of eels observed in the Indian Ocean is consistent with where each type lives and spawns, and is also probably influenced by ocean current patterns as discussed below. Although it is not well documented, most shallow-water eels, except a few types of congrids (McCleave and Miller, 1994; Miller, 2002; Miller et al., 2011b), appear to spawn within or along the edges of the habitats where they live. This has been indicated by observations of reproduction-related behavior of moray eels (Moyer and Zaiser, 1982; Ferraris, 1985) and garden eels (Kakizaki et al., 2015) in shallow-water. It has also been indicated by collections of small leptocephali or higher abundances of larvae over the continental shelf or along the shelf-break in a variety of areas (Blache, 1977; Miller et al., 2002; Kimura et al., 2006) and by the absence of

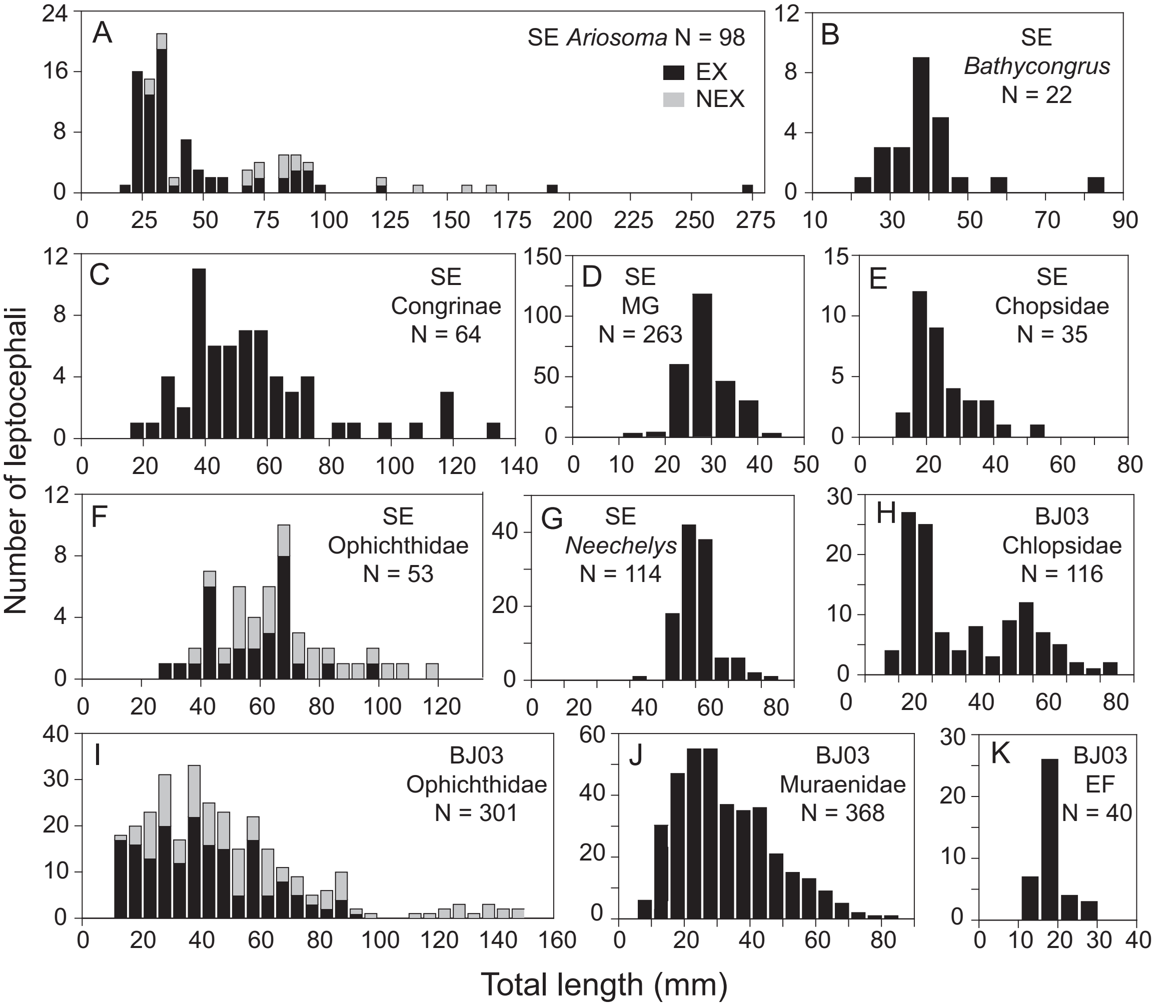

Fig. 8. Length frequency distributions of various taxa of leptocephali collected south of Java in 2010 (SE area) and off Sumatra in 2003 (BJ03) separating non-exterillium gut (NEX) and exterillium gut (EX) *Ariosoma*-type leptocephali (Congridae) (A), Ophichthinae (gray bars) and Myrophinae (black bars) (F), and Ophichthinae (gray bars) and *Neenchelys* (black bars) (I).

their small larvae offshore (Miller, 1995), as was the case in the present study. The two surveys west of the Mascarene Plateau collected small larvae very near the banks or where they had likely been transported offshore (Miller et al., 2015), but none were collected to the east of the banks and farther offshore. The collections off Sumatra included small larvae of most shallow-water families that indicated a wide range of marine eels were spawning there. Some differences in size ranges of leptocephali were detected, which may suggest there are seasonal differences in the amount of spawning of some species, but wide size ranges were usually collected.

One of the most unusual observations of the present study was that the large catches of several types of larvae of shallow-water eels south of Java included big catches of larvae of the burrowing eels of the Moringuidae (spaghetti eels). It is extremely rare to collect many moringuid larvae, and that has not been reported during any previous sampling surveys in the Indo-Pacific (Miller et al., 2002, 2006, 2016; Wouthuyzen et al., 2005; Onda et al., 2017). Perhaps the only other report of an abundant catch of *Moringua* leptocephali was at one station in the Northwest Providence Channel of the northern Bahamas (Miller and McCleave, 2007), but *Moringua* larvae were not abundant offshore in the Sargasso Sea (Miller and McCleave, 1994, 2007; Miller, 1995), and few or none were caught anywhere else in the present study. They were also not abundant in the same area south of Java in a series of transects of widely-spaced stations sampled from Java to northeastern Australia in 1962–1963, when only a few specimens (N = 3) were collected, compared to the much larger numbers of *Ariosoma* and *Gnathophis* leptocephali (75% of the 761 larvae of 62 species of 9 families) and a range of other less-abundant taxa that were collected (Castle, 1969). The 69 species collected south of Java in 2010 also included many *Ariosoma* and other congrids, muraenids, and ophichthids (especially *Neenchelys*).

4.2. Larval catches in relation to ocean structure

The dynamic patterns of ocean currents in the Indian Ocean (Fig. 2A) (Schott and McCreary, 2001; Peng et al., 2015) and the long larval duration of leptocephali (Miller, 2009; Kuroki et al., 2014), suggest that the distribution of leptocephali is likely greatly influenced by current flows in many areas of the ocean basin. This clearly seems to be the case in the offshore area to the west of the Mascarene Plateau where larvae can get transported westward away from the shallow banks by the South Equatorial Current (SEC) or by water recirculated from the north and the large banks of the Seychelles (Miller et al., 2015). Although the SEC is generally present all year, the currents in other areas can differ among February and November and other times of year (Fig. 2; McPhaden et al., 2015; Peng et al., 2015). For example, in November the monthly drifter data analyzed by Peng et al. (2015) indicate eastward equatorial jets flow toward Sumatra and currents then turn to the southeast before turning back offshore to the west (Fig. 2D). But in February there is westward jet-flow just north of the equator and eastward flow of the South Equatorial Countercurrent south of the equator, with no strong flows detected off Sumatra

(Fig. 2C).

The November current flow patterns appear to be consistent with the catches of shallow-water eels in 2006 along Sumatra and with the 2006 hydrographic section. The high catches of especially congrid and muraenid larvae in November 2006 occurred at stations relatively near Sumatra where there could have been water originating from an eastward equatorial jet that usually is strongest in November (McPhaden et al., 2015) or from large eddies that can move past Sumatra (Hacker et al., 1998; Vinayachandran et al., 1999; Iskandar et al., 2006). That area had a distinctive water mass with a shallow core of high-salinity water, which may be consistent with equatorial water from a current jet (see 80 °E and 95 °E WOCE Atlas sections; http://whp-atlas.ucsd.edu/indian/sections.htm; Accessed 12 December 2017). The large size of many of the congrid leptocephali collected off Sumatra in 2006 (*Ariosoma*, *Bathycongrus*, *Uroconger*, and other Congrinae) suggest the possibility that some of those larvae originated from other areas, such as near India and the Bay of Bengal. The ocean current patterns in November and also June (Peng et al., 2015) when the 2003 survey was conducted, support this possibility. However, those species may also be part of the biodiversity of eels along Sumatra, because smaller larvae were also caught there. Species like *Gavialiceps* and *Muraenesox* that were collected in 2003, may mostly be continental shelf species that seem to be rare in the Indonesian Seas, so some of those types of larvae and large congrid or other leptocephali could originate from larger continental shelf areas in the northeastern Indian Ocean. It is unclear though, if complete cross-basin transport of leptocephali is possible due to the long larval durations of eel larvae, as has been considered to be possible for anguillid eels (Gagnaire et al., 2009), but that might be especially likely during the periods when strong equatorial jets occur.

But catches were low farther offshore where there may have been weaker flow and a different water mass than off Sumatra that had a deep pool of low-salinity surface water and no Subtropical Underwater (STUW). The higher catches shallow-water eel larvae at Stn. 13 and 14 in the middle of the basin compared to other offshore stations in 2006 could represent larvae that may have been transported to the southeast from the Chagos banks (Fig. 1), because they were caught in a pool of warmer surface water compared to anywhere else in the transect (Fig. 3C).

Similarly, the abundance of shallow-water eel leptocephali, including some small specimens, south of Java at stations over deep-water not very close to the continental shelf indicates they were transported offshore by currents. It is not clear if this resulted from southeast flow of the South Java Current or westward flow originating from the Indonesian Throughflow (Fig. 2A) that enters the SEC (Schott and McCreary, 2001; Sprintall et al., 2002).

4.3. Biodiversity of eels across the central Indian Ocean

The numbers of species of marine eel leptocephali in each area of the present study are consistent with the regional geography of types of habitats available to eels and the distributional ecology of leptocephali as discussed above. There are no islands on the Mascarene Plateau banks (Saya de Malha and Nazareth banks) east of where sampling occurred in 2006 and 2010 except for on the southmost bank (St. Brandon of the Cargados Carajos Bank), and most parts of the < 50 m banks probably do not reach very close to the surface (Spalding et al., 2001; Payet, 2005; Turner and Klaus, 2005). Therefore, there is likely a limited amount and range of habitat types available for some types of eels there compared to along Sumatra and around the Mentawai Islands where there appears to be high marine biodiversity (Huffard et al., 2012). This may explain the higher number of species collected off Sumatra compared to near the Mascarene Plateau, because various species of eels and their relatives may require specific types of shallow-water habitats such as coral reefs, seagrass beds or soft sediments for burrowing in areas with high enough food resources. One example of this seems to be the leptocephali of tarpon, ladyfish, and bonefish (Adams et al., 2014) that were only collected off Sumatra in 2003. Sumatra is located at the southwestern edge of the high-biodiversity Coral Triangle (Hoeksema, 2007) that has the greatest number of marine fish species (Randall, 1998; Allen and Adrim, 2003; Carpenter and Springer, 2005) and probably the greatest number of marine eel species (Wouthuyzen et al., 2005; Miller et al., 2016).

Although in the Indian Ocean, biodiversity estimates from collections of leptocephali in one area may not always only reflect the species of eels living near where the larvae were collected, the general patterns of geographic differences in numbers of species of leptocephali collected in the present study were similar to patterns seen in other parts of the world. Higher numbers of species and greater abundance of shallow-water eel larvae have been collected over or near the continental shelf or in areas with banks and islands compared to offshore (Miller et al., 1995; Miller et al., 2002; Miller and McCleave, 2007). The total number of about 90 total species of leptocephali collected west of the Mascarene Plateau in the 2 surveys was higher compared to areas in the Atlantic Ocean where there are fewer eel species in general, but was similar to areas such as the western South Pacific (94 species collected in a 1995 survey across the SEC) where there are many islands (Miller et al., 2006). In the offshore Sargasso Sea, only about 50 species have been collected and many of those larvae are transported offshore from the western margin of the gyre (Miller and McCleave, 1994). About 63 species have been collected in the nearby Florida Current region (southern Gulf Stream) (Ross et al., 2007), 77 were collected in the Northwest Providence Channel of the Northern Bahamas (Miller and McCleave, 2007), and 68 were caught near Barbados (Richardson and Cowen, 2004).

The much greater number of species caught along Sumatra in 2003 (~143) is similar to collections in the central Indonesian Seas, because ~136 species leptocephali were collected in various areas around Sulawesi Island in May 2001 (Wouthuyzen et al., 2005), and ~126 species were collected in March during the next leg of the 2010 survey that sampled in the southern Celebes Sea and Tomini Bay of northern Sulawesi Island (Miller et al., 2016). Slightly more species were found off Sumatra in 2003 mainly due to the greater number of congrid (40) and ophichthid (46) species. Fewer species of the Muraenidae and Chlopsidae were collected in 2003 though, compared to in the Indonesian Seas surveys. Distinguishing more species of the Congridae from the 2003 survey than in previous studies was facilitated by detailed analyses of garden eel larvae (9 species; Miller et al., 2011a) and *Ariosoma*-type larvae (12 species; Miller et al., 2013). However, considering the seemingly unique environment of having the Mentawai Islands just offshore of Sumatra and the possibility of transport of larvae from several regions by ocean currents, the waters off Sumatra may have an unusually high biodiversity of marine eels.

Studies on leptocephali in other areas of the Indian Ocean and Indonesian Seas are needed to begin to understand the regional patterns of eel biodiversity and how much exchange of larvae may occur among regions. How far leptocephali can be transported by the persistent flow of the SEC or by seasonally occurring current jets in the Indian Ocean will also be interesting to explore in future studies.

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