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Ariosoma-type *Leptocephali* (Congridae: Bathymyrinae) in the Mentawai Islands region off western Sumatra, Indonesia

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Abstract

Background: *Ariosoma*-type leptocephali of the congrid subfamily Bathymyrinae are typically present in tropical and subtropical regions where they reach large sizes and are often abundant compared to other taxa. Different morphological species types of these larvae have been documented in the Indo-Pacific region, but few have been matched with their adult species, and their life histories are not known.

Results: A sampling survey for leptocephali off western Sumatra, Indonesia, collected 297 *Ariosoma*-type leptocephali of at least 12 different species of both the exterillum gut and non-exterillum gut types that could be distinguished using morphological characteristics. These leptocephali were collected at 23 of 24 stations over deep water but were not caught at two stations over the shelf between Sumatra and Java. They were most abundant in the 15- to 50-mm size range, but six species were also collected with sizes of > 140 mm, some of which were undergoing metamorphosis at sizes of 143 to 324 mm. Larvae of *Ariosoma scheelei* were most abundant, with small larvae of ≤ 25 mm present near Sumatra and the Mentawai Islands and larger larvae also present offshore. The other abundant larval types, sp. 1 and *Ariosoma* sp. 7 showed a different tendency with their small larvae being present more offshore, which suggests different spawning locations possibly linked to differing adult habitats or spawning behaviors.

Conclusions: The presence of at least moderately small leptocephali of most of these species suggests that their adults are present in this region, which indicates that there is a high biodiversity of these small benthic eels on the shelf and slope of the Mentawai Islands region off western Sumatra in the eastern Indian Ocean.

Keywords: Leptocephali; Larval distribution; Marine eels; Congridae; Indian Ocean

Background

One of the largest and often most abundant types of eel larvae, called leptocephali, are the *Ariosoma*-type larvae of congrid eels of the subfamily Bathymyrinae, which have been collected from offshore waters of the world's tropical and subtropical oceans (Smith 1989a; Miller 2002a; Miller and Tsukamoto 2004; Miller et al. 2006b). Adult bathymyrins, however, are mostly small (<500 mm) nocturnal eels that live in shallow marine habitats or over the deeper continental slope and appear to burrow tail

first into the substrate, but little is known about them (Castle 1968; Smith 1989b). This subfamily includes the five currently recognized genera of *Ariosoma*, *Bathymyrus*, *Parabathymyrus*, *Chiloconger*, *Paraconger*, and *Kenyaconger* (Smith and Karmovskaya 2003).

There are two groups of eels within this subfamily: those with leptocephali like *Ariosoma* species and those with leptocephali more similar to other congrids (Smith 1989a). *Ariosoma*-type leptocephali all grow to sizes of at least about 175 mm, and some species can reach up to about 400 mm (Mochioka et al. 1982, 1991; Smith 1989a; Strehlow et al. 1998; Miller et al. 2006b; 2013). These larvae have one to three horizontal rows of myoseptal pigment (a short vertical line of tiny spots on

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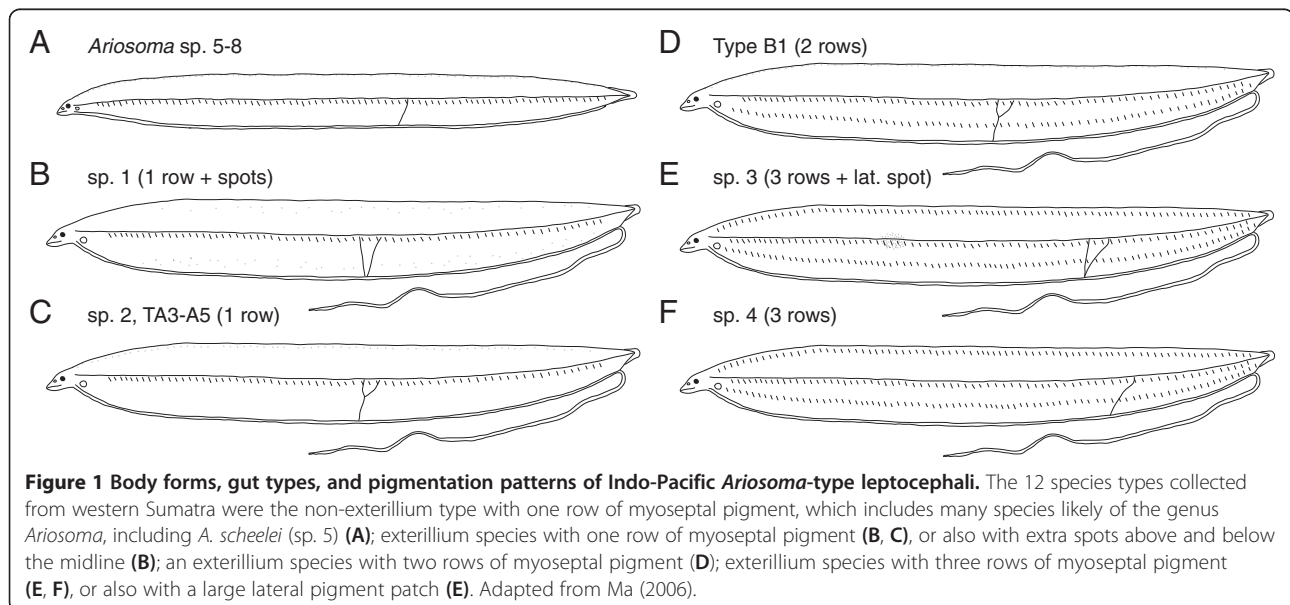
each myoseptum between the myomeres) along the sides of their bodies (Castle 1964, 1968; Blache 1977; Mochioka et al. 1982, 1991; Tabeta and Mochioka 1988; Smith 1989a; Miller and Tsukamoto 2004). As suggested by the morphological features of these larvae, there are two phylogenetically distinct groups of these eels based on mitochondrial DNA (mtDNA) analyses of their leptocephali (Ma 2006), which are represented by larvae that either have a normal gut with the anus located along the ventral surface of the body (non-exterrillium) (Smith 1989a; Mochioka et al. 1991) or have a usually quite long (up to 100% of the body length) exterrillium gut that extends freely away from the body (Mochioka et al. 1982; Smith 1989a) as shown in Figure 1.

Most species of the Bathymyrinae are in the genus *Ariosoma*, and these probably include all non-exterrillium-type larvae and some of those with exterrillium gut larvae. Fewer species are in the genera *Parabathymyrus* and *Bathymyrus*, which like some species of *Ariosoma*, have exterrillium-type larvae (Smith 1989a). *Kenyaconger*, *Chiloconger*, and *Paraconger* are the other genera of the subfamily, and at least *Paraconger* and *Chiloconger* contain species with leptocephali that greatly differ from *Ariosoma*-type larvae by having only a single lateral pigment row similar to many species of the subfamily Congrinae (Smith 1989a). Mitochondrial genome sequences, however, did not suggest that *Paraconger* is closely related to *Ariosoma* (Inoue et al. 2010), so the genera with larvae that differ from *Ariosoma*-type larvae might not actually be true members of the Bathymyrinae. Morphological characters suggest that *Kenyaconger* may fit within the group with *Ariosoma* and the two other genera, but this has not been confirmed (Smith and Karmovskaya

2003). For simplicity in this paper, leptocephali in this study are referred to as *Ariosoma*-type larvae even though they are larvae of at least three genera.

Leptocephali of *Ariosoma*-type larvae were identified to the species level in the western North Atlantic (Smith 1989a), but there are more genera and species in the Indo-Pacific. So, only a few species of non-exterrillium leptocephali were examined at the species level in previous studies (Castle 1964, 1969; Miller et al. 2006b), and only two have been genetically matched with adult species (Ma et al. 2008b). One species that was distinguished as larvae due to its very low range of number of vertebrae is the shallow-water tropical species *Ariosoma scheelei* (Castle 1964, 1969; Miller et al. 2006b). Other ranges of vertebrae likely include mostly different species in different regions, making definitive identification difficult without a clear understanding of adult species present in each region.

A few species of non-exterrillium leptocephali can be quite abundant compared to other species in some areas including subtropical gyres (Miller and McCleave 1994; Miller 1995, 2002a) and in tropical waters such as around Sulawesi Island in the central Indonesian Seas (Miller et al. 2006b), but few studies focused on these types of leptocephali. Castle (1964, 1969) provided some information about the distributions and sizes of a few species or types in the western South Pacific and eastern Indian Ocean. Mochioka et al. (1982, 1991) reported on morphological characteristics and geographic occurrences of *Ariosoma*-type leptocephali in the western Pacific region, but recent studies on assemblages of leptocephali in the Indo-Pacific, except for Miller et al. (2002), did not report species/type-level data for *Ariosoma*-type leptocephali (Wouthuyzen



et al. 2005; Miller et al. 2006a), so information is lacking about the distributions and life histories of these species.

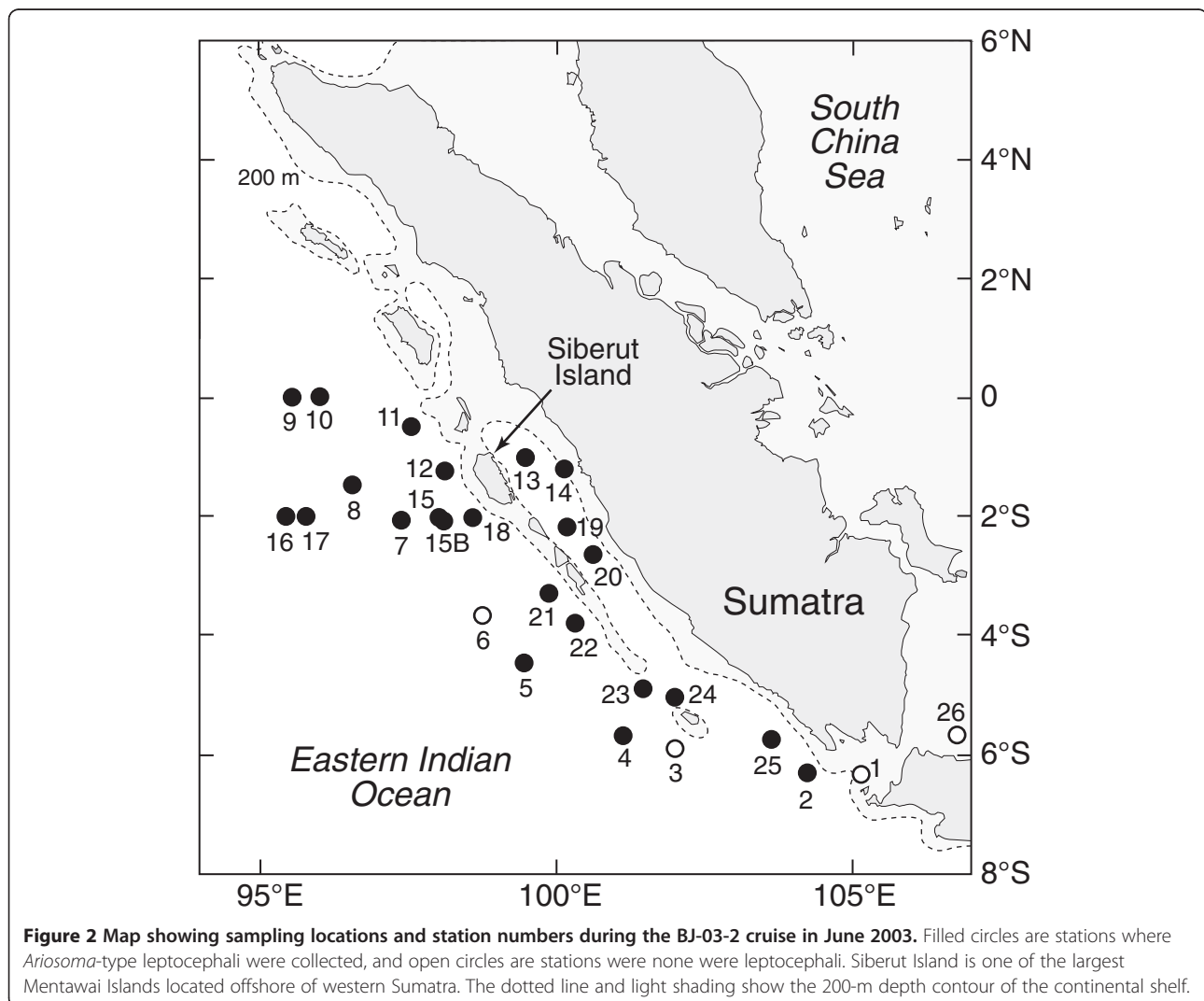
The present study examined the species type composition, distribution, and size of *Ariosoma*-type leptocephali collected during a sampling survey in the Mentawai Islands region off western Sumatra that collected many species of this type of leptocephali. The objectives of this study were to document the possible diversity of this group of marine eels in this area based on the presence of their larvae, briefly examine the life history implications of these catches, and provide information that can be useful for future genetic identification studies to match larvae with their adults for *Ariosoma*-type leptocephali.

Methods

Leptocephali were sampled at 25 stations (stns.) during the BJ-03-2 cruise of the R/V *Baruna Jaya VII* (Research Center for Oceanography of the Indonesian Institute of Sciences) in the eastern Indian Ocean off the western coast

of Sumatra, Indonesia on 5 to 21 June 2003 (Figure 2). Sampling at each station consisted of two tows of an Isaacs-Kidd midwater trawl (IKMT) with a mouth opening of 8.7 m² and a 0.5-mm mesh size. At each station, the IKMT was deployed at night in an oblique tow and a step tow (five horizontal sampling layers), both of which sampled the upper 200 m (see Aoyama et al. 2007 and Miller et al. 2011a for details). An extra tow was made at stn. 15 (stn. 15B), and all the stations were located in areas with water depths of >1,500 m, except for stns. 1, 24, and 26.

Ariosoma-type leptocephali were identified by first categorizing them as having an exterillum gut or not and then matching them to specific types designated by Tabeta and Mochioka (1988) (sp. 1 to sp. 8) and Mochioka et al. (1982) for some rare species (type A3, A4, A5, and B1). Non-exterillum types have only one row of myoseptal pigment, whereas exterillum types can have one, two, or three rows of myoseptal pigment (Figure 1). Two exterillum types also had randomly



spaced small spots above and below the midline (sp. 1) or a large lateral pigment patch (sp. 3). Mochioka et al. (1991) used a different system of names for the types of non-exterillum leptocephali, but we followed Miller and Tsukamoto (2004) and Ma (2006) using sp. 1 to sp. 8 of Tabeta and Mochioka (1988) and the species types of Mochioka et al. (1982) for less common exterillum types. Because non-exterillum species presently appear likely to only be members of the genus *Ariosoma* (Smith 1989a; Ma et al. 2008b), they are in most cases, such as in Table 1, referred to that genus, but it is known that exterillum gut species of leptocephali can belong to other genera, so these are only referred to as 'sp.' or 'type'.

Species types collected during this cruise were distinguished by a combination of patterns of pigmentation (Figure 1) and two meristic counts of myomeres. Briefly, non-exterillum types are mostly only distinguishable by the total myomere count (TM) and the myomere count of the position of the last vertical blood vessel (LVBV). These counts for non-exterillum *Ariosoma* leptocephali of sp. 5, considered to be *A. scheelei* (TM 108 to 128, LVBV 53 to 63), sp. 6 (127 to 134, 64 to 72), sp. 7 (136 to 150, 71 to 77), and sp. 8 (158 to 162, 81 to 85) (Mochioka et al. 1991, western North Pacific ranges) did not overlap much, which enabled separation of the types (Figure 3). Exterillum types have one row (myoseptal pigment) and small spots above and below in sp. 1 (129 to 141, 61 to 66); one row in sp. 2 (131 to 137, 62 to 67); three rows and a large lateral pigment patch in sp. 3 (146 to 155, 89 to 103); three rows in sp. 4 (148 to 161, 89 to 103) (Tabeta and Mochioka 1988), or just one row in types A3 (145 to 151, 68 to 79), A4 (160 to 173, 78 to

91), and A5 (171 to 177, 101 to 104); and two rows in type B1 (151 to 154, 80 to 88) (Mochioka et al. 1982). The larvae classified as type A5 had a lower range of TM compared to those of Mochioka et al. (1982), but their LVBV counts were higher than those of type A4.

Among these 12 species types, only 1 (sp. 5) could be identified as likely being leptocephali of *A. scheelei*, a small tropical eel, the larvae of which are also very abundant in central Indonesian seas (Miller et al. 2006b). It was listed as *Ariosoma* sp. 5 by Tabeta and Mochioka (1988) and as type I by Mochioka et al. (1991), but both were suggested to be *A. scheelei*. Castle (1968) noted that this species has a very low number of vertebrae/myomeres, so because no other *Ariosoma* species appears to have such a low range of vertebrae, the species identification of sp. 5 leptocephali as *A. scheelei* seems certain and that species name was used in the present study.

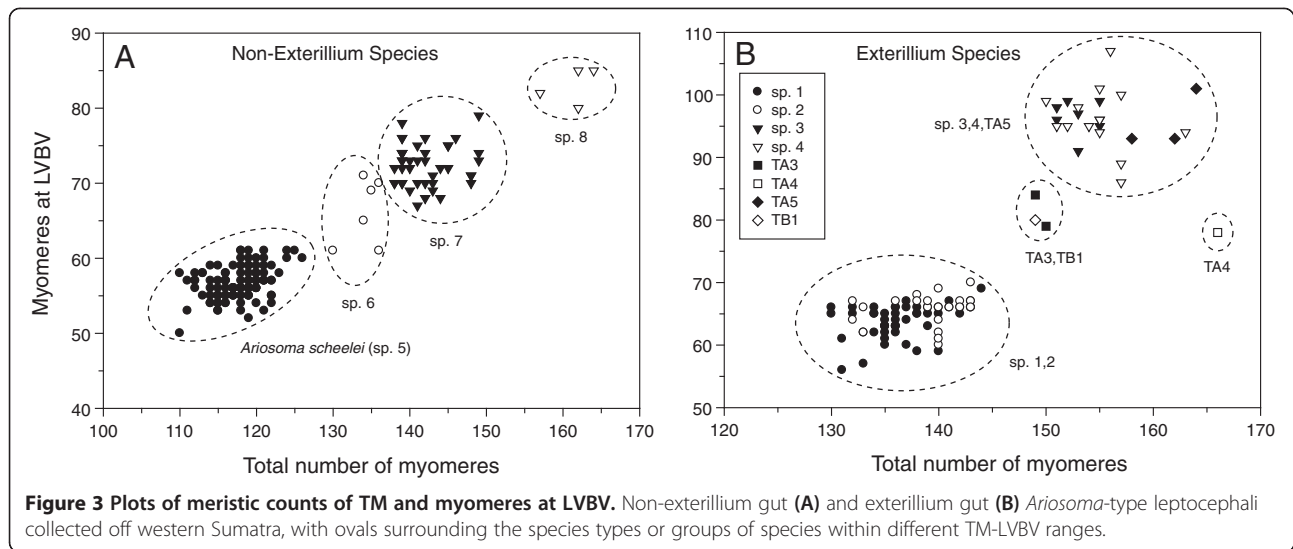
During the BJ-03-2 cruise, the total length (TL) of leptocephali was measured to the nearest 0.1 mm, and they were tentatively identified on board the ship before they were preserved in 10% formalin seawater or 99% ethanol. Formalin-preserved specimens were later reexamined in the laboratory, and the myomere counts were made on specimens that were not damaged. Myomere counts of specimens preserved in ethanol were counted on board the ship, and these specimens were later examined genetically by sequencing about 1,300 sites of their mtDNA 16S ribosomal RNA in the study of Ma (2006) (see Ma et al. 2008a for details of the sequencing analyses). Catch rates of the two size categories of ≤ 25 and > 25 mm were calculated using the number of larvae caught in both tows at a station and the volume of water filtered by the net during

Table 1 Number of each species or type of *Ariosoma*-type leptocephali collected off western Sumatra

Species/type	Gut	TM	LVBV	DNA study ^a	Number of stns.	Size range (meta)	Total
<i>Ariosoma scheelei</i>	N-EX	110-125	50-61	9	22	10.6-175.0	114
<i>Ariosoma</i> sp. 6	N-EX	130-136	61-71	1	5	15.1-79.4 (197.0)	8
<i>Ariosoma</i> sp. 7	N-EX	138-149	70-74	2	12	12.1-220.0 (202.2-324.0)	44
<i>Ariosoma</i> sp. 8	N-EX	157-164	80-85		3	22.2-34.4	4
sp. 1	EXT	130-144	56-69	6	13	13.5-181.0	50
sp. 2	EXT	132-143	60-70	2	9	16.0-60.4	21
sp. 3	EXT	151-155	91-99	3	5	30.0-158.0	7
sp. 4	EXT	150-157	86-107	3	8	18.2-39.6 (143.0)	15
Type A3	EXT	149, 150	79, 84	1	2	27.2, 50.0	2
Type A4	EXT	166	78	1	1	141.5	1
Type A5	EXT	158-164	93-101	1	1	33.4-38.5	3
Type B1	EXT	149	80	1	1	99.3	1
sp. 1 or 2	EXT	133-140	61-67		5	(183.5-232.0)	5
sp.					11	13.2-67.2 (>160-205.0)	22
Total number or range		110-166	50-106	30	22	10.6-324.0	297

N-EX, non-exterillum; EXT, exterillum; TM, total myomeres; LVBV, last vertical blood vessel; stns., stations; meta, metamorphosing larvae.

^aSpecimens genetically examined by Ma (2006).



both tows, which was estimated from the number of flow-meter revolutions and a calibration factor determined at the end of the cruise.

Results

Morphological and genetic types

Morphological characteristics that were examined in the 297 *Ariosoma*-type leptocephali collected during the BJ-03-2 sampling survey off western Sumatra indicated that there were at least 12 different species present among the larvae (Table 1). This number of species was confirmed by the mtDNA sequence analyses of Ma (2006) who found that there were at least 11 species among the larvae sequenced (*Ariosoma* sp. 8 was not among the 30 leptocephali preserved in ethanol) which corresponded to the morphological species types (Table 1).

In total, 170 of the leptocephali were morphologically distinguished as non-exterillium types of *Ariosoma* larvae, with *A. scheelei* (sp. 5) being most abundant ($n = 114$), followed by sp. 7 ($n = 44$), sp. 6 ($n = 8$), and sp. 8 ($n = 4$) (Table 1). There were 105 exterillium-type leptocephali, with sp. 1 ($n = 50$), sp. 2 ($n = 21$), and sp. 4 ($n = 15$) being most abundant, with only 1 to 7 leptocephali of the other exterillium species.

Plots of TM vs. LVBV of the leptocephali showed that non-exterillium species types defined using the TM and LVBV ranges of Mochioka et al. (1991) did not overlap in the distributions of their TM-LVBV points (Figure 3A). Their overall TM counts ranged over about 55 myomeres (110 to 164), with their LVBV counts ranging over 36 myomeres (50 to 85), and being linearly related to the TM ($r^2 = 0.9$, data not shown). The distribution of points suggested that some of the *Ariosoma* sp. 6 larvae with high LVBV counts could actually be *Ariosoma* sp. 7 larvae.

TM and LVBV points of leptocephali of exterillium species overlapped in three areas of the plot (Figure 3B). In the lower range, sp. 1 and sp. 2 overlapped, as did sp. 3, sp. 4, and type A5 in the higher range; and types A3 and B1 were also tightly clustered. Differences in pigmentation patterns were used to distinguish those species with overlapping meristic counts. Type A4 had a low LVBV count relative to its TM count. The TM of the exterillium-type leptocephali were also linearly related to their LVBV, except for within the abundant species and for type A4 ($r^2 = 0.8$, data not shown). The exterillium species were spread out across a higher, narrower range of TM of about 37 myomeres (130 to 166) with wider ranges of TM compared to their LVBV counts within sp. 1 and 2. However, their range of LVBV counts of 51 myomeres (56 to 106) was wider than that of non-exterillium species.

Distribution, size, and abundance

Most *Ariosoma*-type leptocephali collected in the Mentawai Islands region were in the 15- to 50-mm size range, although *A. scheelei* was also present in the 120- to 175-mm size range (Figure 4) up to its likely maximum size (Miller et al. 2006b). Several species including *Ariosoma* sp. 7 were collected at sizes of >175 mm, and most of those were undergoing metamorphosis (Figure 4; see below).

Ariosoma-type leptocephali were collected at all of the stations except for stn. 6 offshore and stns. 1 and 26 that were over the continental shelf between Sumatra and Java (Figures 2, 5, and 6). The distributions of smaller-sized leptocephali of ≤ 25 mm showed differing patterns for some of the common species. Small larvae of *A. scheelei* had the highest catch rates inshore of Siberut Island and near the southernmost Mentawai Islands,

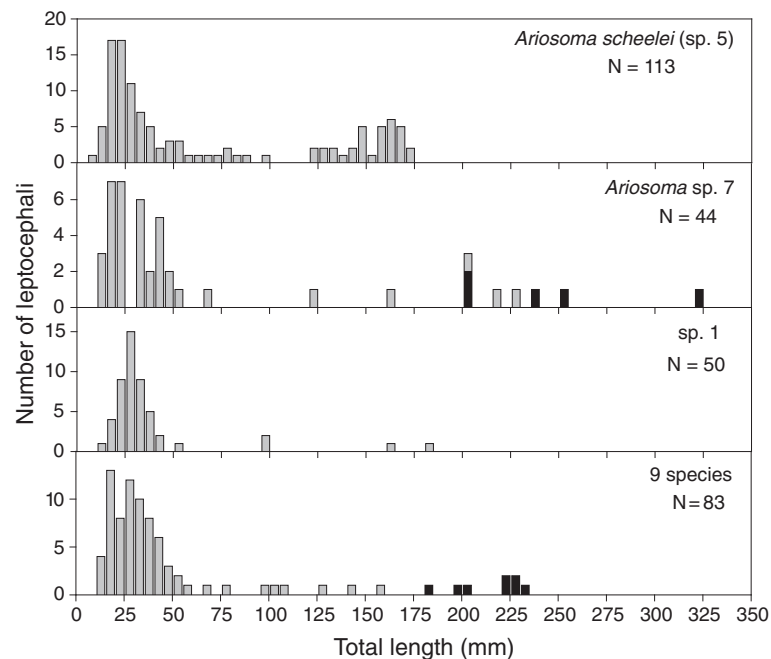


Figure 4 Length-frequency distributions of leptocephali of *Ariosoma*-type leptocephali collected off western Sumatra. The three most abundant species and the remaining nine species pooled together are plotted, with black bars showing metamorphosing leptocephali.

whereas catch rates of sp. 1 and *Ariosoma* sp. 7 were highest at more-offshore stations and were almost completely absent from areas closest to the coast of Sumatra (Figure 5). Smaller larvae of ≤ 25 mm of other species or those that were not identified to a species type were restricted to ten stations, mostly near the islands or in-shore of them. The smallest larvae of < 15 mm were collected at only seven stations near the islands except for a 12.1 mm *Ariosoma* sp. 7 larva that was caught at stn. 8 (Figures 1 and 5).

Larger leptocephali of > 25 mm also showed some differences in distributions among species. Large *A. scheelei* were caught at almost all stations over deep water except for two stations, and they had high catch rates at several offshore stations (Figure 6). Other species were more randomly distributed at some stations, but not others.

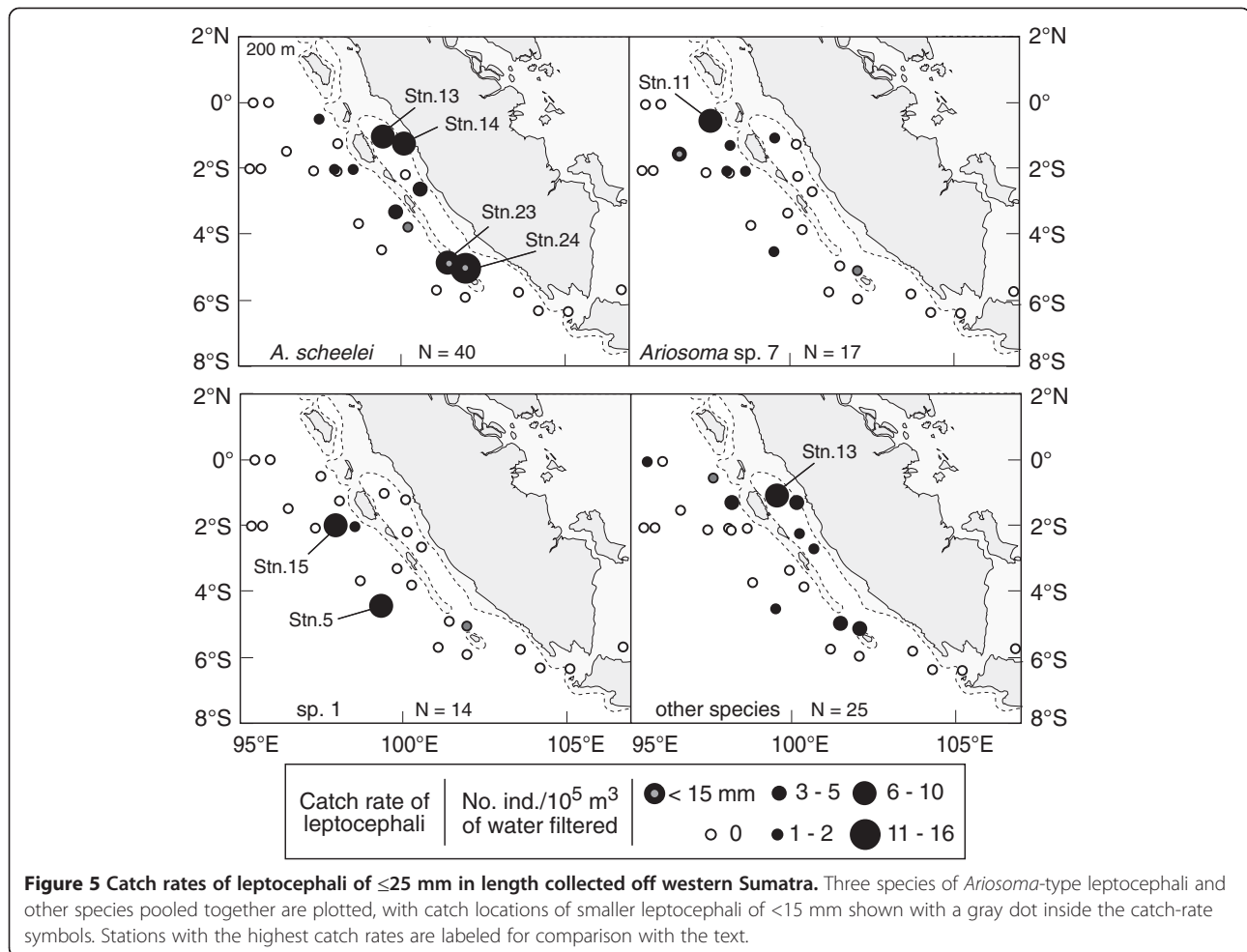
Metamorphosing leptocephali

There were 15 metamorphosing leptocephali (distinguished by loss of teeth and thickening of the head and body) collected at 11 stations, which were all > 175 mm in size (Table 1, Figure 4). Almost 1/2 were caught at stns. 23 to 25 in the southern part of the study area (Figures 2 and 6), and 1 was caught at stn. 17 offshore. These included five *Ariosoma* sp. 7 (202.2 to 252.5 and 324.0 mm), five sp. 1 or sp. 2 (183.5 to 232.0 mm), one sp. 4 (230.0 mm), one *Ariosoma* sp. 6 (197.0 mm), and three unidentified specimens (> 160 to 205.0 mm). These metamorphosing larvae were caught at a few stations

throughout the study area except for the northernmost stations (Figure 6). No metamorphosing *A. scheelei* leptocephali were detected, although the upper size class was large enough to undergo metamorphosis based on collections of *A. scheelei* larvae around Sulawesi Island to the east in the central Indonesian Seas (Miller et al. 2006b). This may have been due in part to the fact that 64% of the larvae of > 120 mm of this species were caught in further offshore stations in the northwestern region of the study area that were not close to their recruitment habitats.

Discussion

This study found that there were at least 12 different species of exterillum and non-exterillum *Ariosoma*-type leptocephali collected off western Sumatra in June 2003. The meristic counts of TM and LVBV used in combination with pigmentation patterns made it possible to distinguish these species according to previously described characteristics and meristic ranges (Mochioka et al. 1982, 1991; Tabeta and Mochioka 1988). The plots of TM and LVBV showed that meristic relationships among the species types within the two groups of leptocephali differed some because non-exterillum species had a wider TM range, but exterillum species had a wider range of LVBV counts. Pigmentation patterns were essential to separate the different species of exterillum-type larvae due to their overlapping meristic counts.

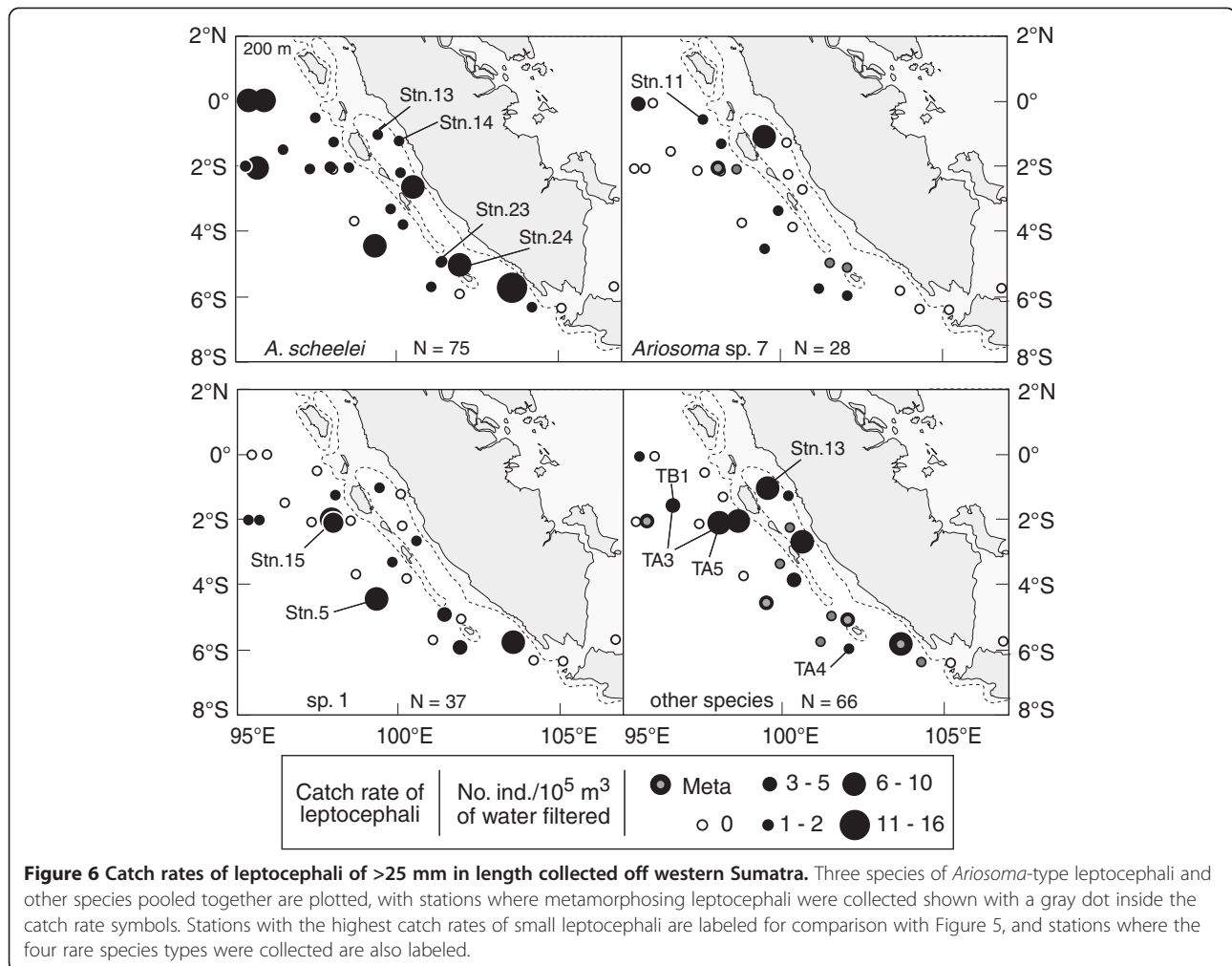


Each of the morphological species types plotted in Figure 3 was genetically confirmed to be distinct species (Ma 2006), except for *Ariosoma* sp. 8, which was not sequenced. However, *Ariosoma* sp. 7 and sp. 3 included two species or mtDNA lineages (Ma 2006). Considering that the meristically distinct *Ariosoma* sp. 8 larvae are quite likely to also be a distinct species, there were at least 12 species and as many as 14 present among the leptocephali collected in this area during the survey of the Mentawai Islands region off western Sumatra.

Only five species of these leptocephali were common during the sampling survey in terms of numbers collected and the number of stations where they were collected (*A. scheelei*, and *Ariosoma* sp. 7, sp. 1, sp. 2, and sp. 4), and these larvae were most abundant in a smaller size range (< 60 mm). *A. scheelei* was the most abundant species off western Sumatra, and it was also the most abundant species of *Ariosoma*-type leptocephali in the central Indonesian Seas in May 2001 in a similar IKMT survey (Wouthuyzen et al. 2005; Miller et al. 2006b). It also seems to be an abundant species in the western South Pacific and western Indian Ocean, and it spawns

off southern Java in the eastern Indian Ocean (Castle 1968), where its larvae were collected during multiple surveys (Castle 1969). *Ariosoma* sp. 7 was the second most abundant non-*exterillum* species off western Sumatra. This type of larvae in the western North Pacific belongs to *Ariosoma major* (Ma et al. 2008a) and is abundant offshore in the subtropical gyre (MJ Miller et al., unpublished data). Off Sumatra, however, these sp. 7 larvae probably belong to *Ariostoma mauritanium* or possibly another species as discussed below, because *A. major* is thought to only be distributed in the East China Sea and Japan region (Asano 1984). *Ariosoma balearicum* appears to be an abundant eel at depths of 30 to 50 m along the southeastern coast of the USA (Walsh et al. 2006), and its leptocephali are also abundant offshore (Miller 1995, 2002a). It is unclear if the relative abundances of each species of leptocephali that were collected off Sumatra are directly related to the abundance of the adults in this region, but it is a possibility.

The 12 to 14 species found morphologically and genetically in the collections of *Ariosoma*-type leptocephali off western Sumatra corresponded well with the 14 species



of adult *Ariosoma* (8 species), *Bathymyrus* (2), *Parabathymyrus* (3), and *Kenyaconger* (1) listed as being present either in the Indian Ocean or in the Indo-Pacific and the Indo-West Pacific region in general (widely distributed species) in FishBase (Froese and Pauly 2000; accessed 15 November 2012). All of these species could be present in the eastern Indian Ocean, considering that these larvae grow for many months reaching large sizes, and they could be transported long distances by ocean currents. It is well documented that water from the Indonesian Seas flows into the eastern Indian Ocean (Hautala et al. 2001; Vranes et al. 2002), and equatorial current jets can transport water in both directions across the northern Indian Ocean (Thompson et al. 2006; Sengupta et al. 2007; Kantha et al. 2008). This makes it likely that some species reported to be present as juveniles or adults in western Indonesia, the South China Sea, or the western Indian Ocean could also be present off western Sumatra.

Except for *A. scheelei* and possibly the presence of *A. mauritanium*, it is premature to attempt to determine possible species matches between adult species and

larval types in the eastern Indian Ocean with any certainty because of a lack of adequate data on geographic distributions and total numbers of vertebrae (TV) data for adults of most species. However, several species known from the area or the regions adjacent to the study area show potential matches with the TM ranges in Figure 3. *A. scheelei* is an abundant shallow-water tropical species with a lower TV range (Castle 1964, 1968), so the identification of *Ariosoma* sp. 5-type leptocephali seems certain as previously concluded (Miller et al. 2006b). *A. mauritanium* (TV, 143) fits *Ariosoma* sp. 7 larvae (138 to 149), and *Ariosoma sokotranum* (136 to 141; western Indian Ocean) (Karmovskaya 1992) also fits the lower TM range of *Ariosoma* sp. 7. Castle (1964) considered non-exterillum leptocephali with TM of 134 to 153 in the western South Pacific and those with 130 to 145 TM in the northwestern Indian Ocean (Castle 1975) to be larvae of *A. mauritanium*. Castle (1969) reported on the distribution and size of these larvae along a latitudinal transect of stations at 110°E that was sampled in multiple seasons in the eastern Indian Ocean. But, leptocephali with the TM range of *A. mauritanium*

may consist of more than one species, and this appears to be the case in the eastern Indian Ocean as indicated by the mtDNA sequencing of Ma (2006) of two specimens of *Ariosoma* sp. 7 from the present study and the TV ranges of two of the adult species that could be present.

For exterillum larvae, *Parabathymyrus karrerae* (TV 156 to 160, western Indian Ocean) fits within the high-TM group of larvae including sp. 3, sp. 4, and type A5 (Karmovskaya 1992). *Bathymyrus smithi* (150 to 155, Mozambique, southern Indonesia) (Castle 1968) fits the TM ranges of type A3 and B1 or the lower TM range of the higher-LVBV exterillum group, as does *Ariosoma ophidiophthalmus* (150 to 153, western Indian Ocean) (Karmovskaya 1992). If *Parabathymyrus brachyrhynchus* (166 to 168) (Smith 1989b) has a species range extending further south from the Philippines, it matches the high TM count of type A4. *P. macrophthalmus* (131 to 134, Japan, South China Sea, and Indonesia) (Hatooka 2000) fits within the lower TM ranges of sp. 1 and sp. 2. Other species reported from the western Indian Ocean, including *Ariosoma nigrimanum*, *Ariosoma bauchotae*, *Bathymyrus echinorhynchus*, *Ariosoma faciatum* (Indo-Pacific), and *Ariosoma anago* (149 to 159, Asano 1984) (Indo-West Pacific), could also possibly be present off western Sumatra (FishBase).

Trawling surveys in this region of the eastern Indian Ocean only reported collections of three species of bathymrid eels of *A. mauritianum*, *A. anago*, and *B. smithi* (Gloerfelt-Tarp and Kailola 2006). However, at least some *Ariosoma* eels are adapted for tail-first burrowing in soft sediments (Smith 1989b; MJ Miller personal observation), so they might not be vulnerable to trawling if they are hiding in the sediment during the day, or they may be able to avoid capture by burrowing when an approaching trawl is detected at night. This is similar to the situation in which these trawl surveys only collected one species of garden eel (Congridae: Heterocongrinae) (Gloerfelt-Tarp and Kailola 2006), which are species that live in burrows, but nine species of garden eel leptocephali were collected in the same survey as the present study (Miller et al. 2011a). Trawling may also be difficult to conduct in various shallow-water habitats with coral structures or other debris where many of these congrid eels live.

Although the actual species level composition of bathymrid leptocephali could not be determined in the present study, it appears that the region around the Mentawai Islands has a high diversity of this group of congrid eels. Considering that 7 of the 12 species of larvae were collected in this area at sizes of <25 mm, and 3 others were collected at 27 to 33 mm (Table 1), it is likely that they were spawned nearby and that juveniles and adults of many of these species live in this area. In comparison, nine species of *Ariosoma*-type leptocephali were collected around Sulawesi Island in the central Indonesian Seas (Wouthuyzen et al. 2005), but only a

minimum of four were reported from the western South Pacific (Miller et al. 2006b). In total, five species were described from the entire western North Atlantic (Smith 1989a), and Blache (1977) described three species from the Gulf of Guinea. The nine species of garden eel leptocephali that were collected off Sumatra in the sampling of the present study is a high proportion of garden eel species known from the Indo-Pacific (Miller et al. 2011a), which also suggests that there is a high biodiversity of various types of congrid eels in this region. Garden eel leptocephali were differently distributed compared to *Ariosoma*-type leptocephali, with many garden eel larvae appearing to have been transported offshore from just north of Siberut Island (Miller et al. 2011a).

Patterns of distribution and sizes of *Ariosoma*-type leptocephali in the present study suggest there are some different life history characteristics among these bathymyrin species. The more-inshore distribution of small larvae of *A. scheelei* compared to those of *Ariosoma* sp. 7 and sp. 1 suggests the possibility of different spawning locations in relation to the shelf and slope. This could be related to different depth distributions of the adults or different movements before spawning. For example, *A. scheelei* and *A. balearicum* can be present in very shallow water that is mostly <100 m, but *A. selenops* and *B. smithi* were collected at 220 to 549 and 470 to 490 m depth ranges, respectively (Castle 1986; Smith 1989b). At least a few species of *Ariosoma* may also make short spawning migrations (Miller 2002a), and some species of *Conger* eels are known to migrate to spawn offshore (McCleave and Miller 1994; Miller et al. 2011b). Although eels such as garden eels and moray eels may spawn within shallow-water habitats (Moyer and Zaiser 1982; Thresher 1984; Ferraris 1985), little is known about the reproductive ecology or species distributions of most marine eels including those of the Bathymyrinae (Miller 2002b, 2009).

The distribution and abundance patterns of the leptocephali in the present study provided no clear information about their spawning locations or larval transport patterns possibly because spawning by each species may occur locally and not in specific spawning areas. Ocean currents and eddy patterns in this region are likely to be complex, making it difficult to estimate larval transport patterns. Surface currents inshore of the Mentawai Islands are thought to be to the southeast parallel to the coast of western Sumatra (Wyrтки 1961), and large eddies move past western Sumatra (Hacker et al. 1998; Vinayachandran et al. 1999; Iskandar et al. 2006). Upwelling sometimes occurs off the coast of western Sumatra that would transport surface water offshore (Susanto et al. 2001). In addition, strong eastward equatorial jets lasting about 10 to 20 days typically occur during May to the northwest of the study area (Thompson et al. 2006; Sengupta et al. 2007; Kantha et al. 2008), which could have a major effect on the

variability of currents and eddies around the Mentawai Islands. These current flows and eddies likely transport leptocephali in a variety of directions during their larval periods in this area.

To better understand the life histories and ecology of these eels and their larvae that grow to large sizes, future research is needed to explore the diversity of species of bathymyrin eels that are present in shelf and slope habitats around the Mentawai Islands and in other parts of the Indo-Pacific. Tissue samples need to be obtained from adult eels that can be used to match *Ariosoma*-type leptocephali with their adult species in each region. Once the species identities of these interesting larvae that grow to very large sizes are known, catch data of leptocephali can be used to learn about the life histories and larval distributions of these poorly known eels that live on continental shelves and slopes around the world.

Conclusions

This study found that there were at least 12 different species of exterillum and non-exterillum *Ariosoma*-type leptocephali that could be morphologically distinguished among the larvae that were collected off western Sumatra in June 2003, and the DNA sequence analyses indicated that there may have been 14 species. Leptocephali of *A. scheelei* were the most abundant, and the adults of this species and most of the other species whose larvae were collected had likely been spawning in the western Sumatra and Mentawai Islands region. A high biodiversity of *Ariosoma*-type eels appears to be present in this region based on these collections of their larvae, and the number of larval species corresponds with the number of adult species that might be present in the Indian Ocean. A variety of future research is needed to better understand these eels and their leptocephalus larvae.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

MJM, SW, JA, SS, YM, TK, and KT participated in the sampling survey off western Sumatra to collect the leptocephali. MJM, MY, and TY worked on examining the leptocephalus specimens and data. TM analyzed the mtDNA sequences. MJM wrote the paper. All authors read and approved the final manuscript.

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