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Distribution, Diversity, and Abundance of Garden Eel Larvae off West Sumatra, Indonesia

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Michael J. Miller, Sam Wouthuyzen, Tao Ma, Jun Aoyama, Sasanti R. Suharti, Yuki Minegishi, and Katsumi Tsukamoto (2011) Distribution, diversity, and abundance of garden eel larvae off west Sumatra, Indonesia. *Zoological Studies* **50**(2): 177-191. Garden eels of the subfamily Heterocongrinae (family Congridae) are long, slender, planktivorous eels that live in colonies in shallow sandy tropical marine habitats, but little is known about their early life history because their leptocephali are rarely collected. This study examined the species composition, distribution, and size of a large collection of garden eel leptocephali in Indonesian waters off west Sumatra on both sides of the Mentawai Is. in June 2003 to learn about the diversity and larval ecology of garden eels in this region of the Indian Ocean. 371 *Gorgasia* and 104 *Heteroconger* leptocephali were collected, which may have included about 9 species of the 2 genera. Based on vertebral counts of adult garden eel species from the eastern Indian Ocean region, the leptocephali of *G. maculata*, *G. preclara*, *G. taiwanensis*, *H. hassi*, *H. obscurus*, and *H. tomberua* may have been collected, but adults of the last species have not been reported from the region. At least 2 other species of *Heteroconger* and another species of *Gorgasia* leptocephali were also collected. Leptocephali of *G. preclara*, *G. taiwanensis*, and *H. tomberua* appeared to be the most abundant in the collections. Wide size ranges of *Gorgasia* (9-68 mm) and *Heteroconger* (14-104 mm) leptocephali were collected, but no metamorphic specimens were caught. The smallest sizes and the greatest abundances were collected in the northern region of the study area near the most extensive areas of continental shelf along west Sumatra, suggesting that many garden eel leptocephali had been transported offshore by strong currents. A similar widespread distribution of garden eel leptocephali was present off west Sumatra in Sept.-Nov. 1929, which suggests garden eels and their larvae may typically be abundant there. http://zoolstud.sinica.edu.tw/Journals/50.2/177.pdf

Key words: Leptocephali, Marine eels, Spawning, Recruitment, Indian Ocean.

Garden eels of the congrid subfamily Heterocongrinae are present in shallow coastal marine habitats in tropical regions around the world (Smith 1989a), and 28 species have been described that are separated into 2 genera, *Heteroconger* and *Gorgasia* (Castle and Randall 1999, Greenfield and Niesz 2004, Allen and Erdmann 2009). Juvenile and adult garden eels are considerably different in their body forms and life histories compared to other types of marine eels, because their bodies protrude out of semi-permanent burrows arranged in colonies, and they have a specialized tail that helps them burrow tail first into the sand (Smith 1989a, Tyler and Smith 1992, Castle and Randall 1999, De Schepper et al. 2007). These colonies are often observed by divers as a "garden of eels" with their heads and upper bodies extending out the sand while they feed during the daytime (Smith 1989a). Garden eel colonies can sometimes be quite large and some

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include male-female pairs of eels (Clark et al. 1990, Tyler and Luckhurst 1994). They protrude out of their burrows to feed on plankton that drifts past, and their colonies are located at depths from a few meters to about 50 m and deeper in areas that typically have steady current flows (Smith 1989a). They have been found to feed on a variety of planktonic organisms ranging from copepods to gelatinous zooplankton (Smith 1989a, Vigliola et al. 1996). This feeding and burrowing style is very different from most other marine eels that are only seen at night, because with the exception of some moray eels of the family Muraenidae (Gilbert et al. 2005) and ophichthid eels that mimic sea snakes (Randall 2005), other marine eels are rarely observed during the daytime.

Garden eels also appear to differ from many other types of marine eels in their style of reproduction. Unlike a few other congrid eels that are thought to make offshore spawning migrations (McCleave and Miller 1994, Miller 2002) or spawn near the edge of the continental shelf (Castle and Robertson 1974, Miller et al. 2002, Kimura et al. 2006), garden eels appear to spawn within their colonies with no spawning migration (Thresher 1984, Smith 1989a). This type of local spawning, which results in their leptocephali originating over the shelf areas where they live, has likely contributed to their leptocephali being rare or absent in offshore collections that targeted leptocephali compared to other species in the western North Atlantic and western South Pacific (Miller 1995 2009, Miller et al. 2006a, Miller and McCleave 2007). There have been a few studies that specifically examined garden eel leptocephali (Raju 1974, Castle 1997, Smith 2002), but no detailed studies have focused on their larval distributions.

The most extensive study on garden eel leptocephali was by Castle (1997) using specimens collected by the Carlsburg Foundation's Round the World Oceanographical Expedition that sampled for leptocephali in the Indo-Pacific region (Jespersen 1942). Garden eel leptocephali were collected in the eastern Indian Ocean off west Sumatra at many of the numerous stations that were sampled there in Sept.-Nov. 1929. Castle (1997) showed that these leptocephali were widespread in the region (Fig. 1) and reported that *Heteroconger hassi* and *Gorgasia maculata* leptocephali could be identified based on their morphological features. However, the overlapping ranges of meristic characters of adults of these species prevented other garden eel leptocephali from being identified to the species level. Garden eel leptocephali were also collected more recently during a 2001 survey around Sulawesi I. in the central Indonesian Seas when 53 specimens of as many as 8 species were collected (Wouthuyzen et al. 2005), but the possible species composition, distribution, and larval ecology were not examined.

The present study analyzed a large number of garden eel leptocephali that were collected off west Sumatra in June 2003 to learn about the possible species composition and larval ecology of garden eels in the eastern Indian Ocean. This is a region of the world where as many as 15 species of garden eels have been reported (Castle and Randall 1999, Allen and Adrim 2003), but there is little published information available about these eels. In this paper, we describe the distribution, abundance, size, and possible species composition of garden eel leptocephali collected during the 2003 sampling survey off west Sumatra and discuss the possible biological and physical factors that may affect their distribution and abundance in this area.

MATERIALS AND METHODS

Leptocephali were collected during the BJ-03-2 cruise of the *R/V Baruna Jaya VII* of the Research Center for Oceanography of the Indonesian Institute of Sciences (Jakarta, Indonesia) on 5-21 June 2003. Sampling occurred at 25 stations (Stns.) in the eastern Indian Ocean off the west coast of Sumatra, Indonesia (Fig. 2) and at 1 station over the shallow continental shelf in the southwestern Java Sea. Sampling for leptocephali at each station consisted of 2 tows of an Isaacs Kidd Midwater Trawl (IKMT), which is a large pelagic trawl that has a mouth opening of 8.7 m^2 and 0.5 mm mesh size. An extra tow was subsequently made at Stn. 15 (Stn. 15B). All sampling was done at night, and at each station a 30 min oblique tow to a depth of about 200 m was made, along with a 60-80 min step tow, which was towed horizontally for 10 min at 5 depths of about 30, 60, 90, 120, and 150 m. Profiles of temperature and salinity (CTD) were made at each station to a depth of 500 m. All stations were located in areas with water depths of > 1500 m, except for Stns. 1, 24, and 26. Aoyama et al. (2007) showed the presence of lower-salinity water inshore of the Mentawai Is. and in the southern part of the study area. Aoyama et al. (2007) reported on the distribution of anguillid leptocephali from this survey, and Kuroki et al. (2007) analyzed the age and growth of the *Anguilla bicolor bicolor* leptocephali that were collected.

Garden eel leptocephali that were collected were identified to genus or species level following Castle (1997), and their total length was measured

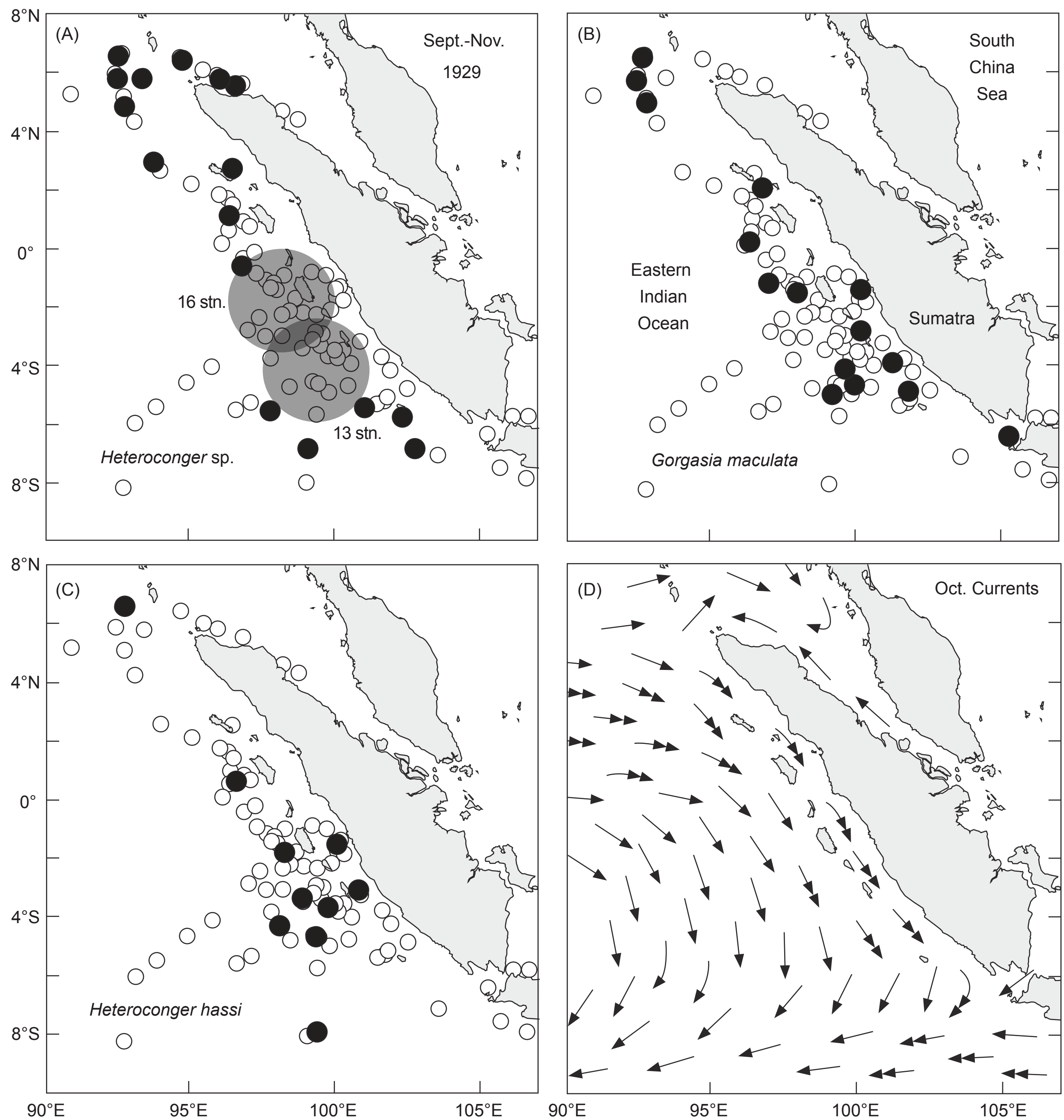

Fig. 1. Map of sampling stations where some species of garden eel leptocephali were collected off west Sumatra in Sept.-Nov. 1929 during the Carlsberg Foundation's Round the World Oceanographical Expedition in the Indo-Pacific and Indian Oceans (A-C). Station locations are adapted from Jespersen (1942), and the approximate locations of leptocephalus catches are adapted from Castle (1997). Black circles show individual stations where leptocephali were collected, and shaded ovals show regions with multiple stations where leptocephali were collected (stations are not individually distinguished). Stations outside of the shaded ovals where these species were not collected are shown as white circles. Other garden eel leptocephali were collected, but were not plotted by Castle (1997). Surface currents in the region during Oct. were adapted from Wyrtki (1961), with stronger currents shown with double arrowheads (D).

before being preserved in 10% formalin-seawater or 99% ethanol. The larval forms of most species of garden eels in the Indo-Pacific region have not been identified yet, but leptocephali of this congrid subfamily are distinctly different from those of the other subfamilies because of their short gut and patterns of lateral pigmentation. Their unique combination of morphological features also separates them from other families of marine eel leptocephali (Miller and Tsukamoto 2004), so all the garden eel leptocephali that were collected could be assigned to one of 2 genera, except for a few small or damaged specimens. Larvae of the 2 species of *Heteroconger* from the western North Atlantic have a single row of lateral pigment along the midline (Smith 1989b), but the leptocephali of this genus in the Indo-Pacific have either a single row of lateral pigment along the midline in various species that have not been matched with their adults, or have small pigment spots all over the body as described for *H. hassi* by Castle (1997). Leptocephali of *Gorgasia* were more difficult to match with their adults than were those of *Heteroconger* because their pigmentation consists of various patterns of small myoseptal pigment

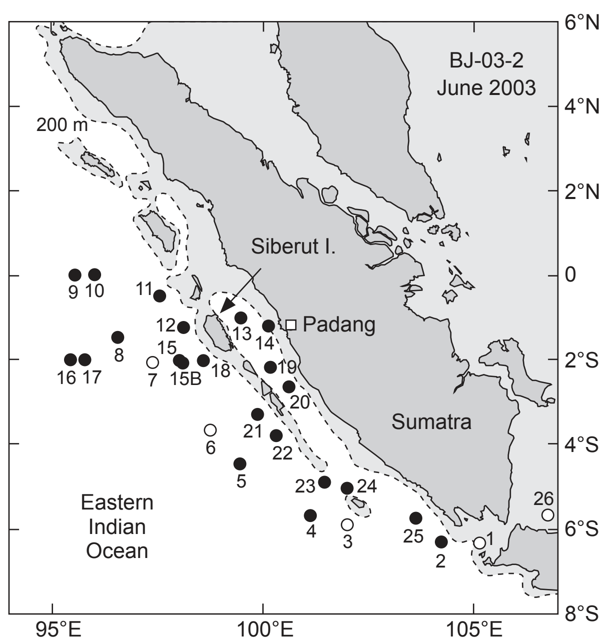

Fig. 2. Map showing sampling locations and station numbers during the BJ-03-2 cruise of the *R/V Baruna Jaya VII* in the Indian Ocean off west Sumatra in June 2003. Filled circles are stations where garden eel leptocephali were collected, and open circles are stations were none were collected. Siberut I. is one of the largest of the Mentawai Is. located offshore of west Sumatra. The dotted line and light shading show the 200 m depth contour of the continental shelf.

spots along and below the midline (Castle 1997, Smith 2002).

There are at least 23 species of garden eels in the Indo-Pacific (Castle and Randall 1999, Smith 1999, Allen and Adrim 2003, Greenfield and Niesz 2004, Allen and Erdmann 2009), but except for a few species, the ranges of total number of vertebrae (TV) of the adults overlap too much to separate their leptocephali using that information (Castle 1997, Castle and Randall 1999). To tentatively evaluate the species composition of garden eel leptocephali collected in the present study, several types of information were used. The pigmentation and counts of the total number of myomeres (TM, muscle segments in the body that correspond to the TV in adults) that were made on most of the collected specimens were directly compared to the larval species distinguished in this area by Castle (1997) and also were compared to the TV ranges of the adult species reported from the margin of the eastern Indian Ocean by Castle and Randall (1999) and Allen and Adrim (2003) as shown in table 1. The TM data of the leptocephali were also evaluated using the TM counts of the 59 garden eel leptocephali preserved in ethanol during the sampling survey (12.3% of the total collected), which were later genetically examined using about 1336 sites of their mitochondrial (mt)DNA 16S ribosomal (r)RNA sequences by Ma (2006). These 59 leptocephali (37 *Gorgasia* and 22 *Heteroconger*) from 20 different stations (with 1-21 specimens per station) were genetically distinguished into 5 *Heteroconger* and 4 *Gorgasia* mtDNA lineages by Ma (2006) that appear to correspond to different species, but the details of that analysis will be the subject of a separate study.

In the present study of all the garden eel leptocephali collected during the survey, an effort was made to obtain TM data from as many specimens as possible, but only subsamples of TM counts were made from stations with the highest catches due to time constraints and the difficulty of obtaining accurate counts from smaller-sized or damaged leptocephali. This resulted in TM data being obtained from 70% of all specimens from the survey. However, it should be noted that TM counts of the larvae may be less accurate than TV counts of adults due to the difficulty in counting the tiny myomeres in the tail of each leptocephalus, and also that most of the TV ranges of adults are not complete due to small sample sizes. Ranges of the TV of eel species may also vary somewhat in different regions, as they have been found to in anguillid eels with multiple populations (Watanabe et al. 2008). Because of these factors, the heavy overlap in the TV ranges of many of the adult species in the region, and the non-systematic selection of the specimens preserved in ethanol that were later examined genetically by Ma (2006), this study will only generally evaluate the possible species identity of the garden eel leptocephali that were collected, and will analyze their distribution, catch rates, and life history characteristics primarily at the genus level of identification.

RESULTS

Species composition and abundance

Among the 479 garden eel leptocephali collected off western Sumatra during the June 2003 survey, 371 were distinguished as *Gorgasia* and 104 as *Heteroconger* based on the different types of lateral pigmentation of the 2 genera. Comparisons of the pigmentation and TM counts of the collected larvae to the species descriptions of garden eel larvae in Castle (1997) and the TV of adults in Castle and Randall (1999) indicated there were leptocephali collected during the survey that appeared to match with 6 adult species (Fig. 3). These species were *G. maculata*, *G. prelara*, *G. taiwanensis*, *H. hassi*, *H. obscurus*, and *H. tomberua* (Fig. 3). All of these adult species except for *H. tomberua*, have been reported to be present along the eastern margin of the Indian Ocean (Table 1). In other cases; however, such as the *Heteroconger* leptocephali with about 155-180 TM and 1 row of lateral pigment, there are 5 adult species of the genus reported from the region that have TV numbers within that range.

The heavy overlap of vertebral ranges of the adult species of *Heteroconger* made it difficult to determine how many species of leptocephali may have been collected using just morphology; but using all available information it appears at least 5 species were present in the collections. Leptocephali of *H. hassi* have 165-183 TM and pigment spots all over the body, which easily distinguishes them from other species in the genus (Castle 1997). Only 3 leptocephali of *H. hassi* were collected in this study, and only a few were collected in 1929 (Fig. 1C). Up to 8 species of *Heteroconger* leptocephali with 1 row of lateral pigment could have been collected in 2003 though, simply based on the wide range of TM (143-233) and the TV ranges of adults in the region (Fig. 3). Excluding *H. hassi*, there are 6 adult species of *Heteroconger* with TV counts between 142-177

Table 1. List of species of adult garden eels (Congridae, subfamily Heterocongrinae) that are possibly present in the southern Indonesia region adjacent to the eastern Indian Ocean. Ranges of total number of vertebrae are based on Castle and Randall (1999), and species ranges and collection localities are based on Castle and Randall (1999) and Allen and Adrim (2003). Specific collection reports from areas adjacent the eastern Indian Ocean are shown in parentheses. PNG, Papua New Guinea; W, western; and Isl., Island.

Species	Known range	No. of vertebrae
Heteroconger		
H. enigmaticus Castle and Randall	Central Indonesia, (Flores, Timor)	154-163
H. hassi (Klausewitz and Eibl-Eibesfeldt)	Widespread Indo-Pacific, (Sumatra)	164-175
H. lentiginosus Böhlke and Randall	Indonesia, Society Isl., Marquesas, (Bali)	173-176
H. perissodon Böhlke and Randall	Philippines, Indonesia, (Bali)	173-176
H. polyzona Bleeker	Indonesia, PNG, Vanuatu, Okinawa	153-159
H. obscurus (Klausewitz and Eibl-Eibesfeldt)	Nicobar Isl.	144
H. taylori Castle and Randall	PNG, Ambon, (Bali)	169-172
H. tomberua Castle and Randall	Fiji	186-208
H. tricia Castle and Randall	Central Indonesia, (Flores)	210
Gorgasia		
G. barnesi Robison and Lancraft	Indonesia, PNG, Solomon Isl., Vanuatu, (Flores)	201-219
G. japonica Abe, Miki and Asai	Indonesia, Japan, Taiwan, New Zealand, (Bali)	187-196
G. maculata Klausewitz and Eibl-Eibesfeldt	W. Indian Ocean to Solomon Isl., (Nicobar Isl., Flores)	167-178
G. naeocepaea (Böhlke)	Mindanao Isl. of the Philippines	177
G. preclara Bohlke and Randall	East Africa and Maldives Isl. to W. Pacific, (Bali)	144-152
G. taiwanensis Shao	Indonesia, Taiwan, Japan, (Bali)	156-167

(*H. enigmatus*, *H. lentiginosus*, *H. obscurus*, *H. perissodon*, *H. polyzona*, and *H. taylori*, Table 1), but leptocephali with TM counts in this range were not abundant (Fig. 3). Ma (2006) detected 2 larval species of *Heteroconger* with 1 row of lateral pigment within part of this TM range using genetic sequences (Fig. 3), but it is unclear if more species within this TM range may have been collected. The leptocephali in the 143-155 TM range may have been *H. obscurus*, which has the lowest TV count. That species is only known from the Nicobar Is. just northeast of Sumatra (Table 1). The leptocephali in the very high range of 218-233, that genetically represented another species, did not match the TV range of an adult species in the region, except possibly *H. trica* (with a TV of 210).

One species of *Heteroconger* larvae appeared to be the most abundant off west Sumatra, because the greatest number of *Heteroconger* leptocephali in June 2003 were within the 185-200 TM range (Fig. 3). *Heteroconger* leptocephali with a 188-208 TM range were collected at about 45 stations in this region in 1929 (Castle 1997) and are shown in figure 1A as *Heteroconger* sp. Castle and Randall (1999) suggested that these leptocephali could be *H. tomberu* (with a TV of 186-208), the adults of which were only collected in Fiji so far.

The *Gorgasia* leptocephali that were collected in 2003 had a more narrow range of TM, and there are fewer possible adult species reported from the region (Table 1, Fig. 3). The TM data and genetic analysis indicated that 4 different species of leptocephali may have been collected. *Gorgasia maculata* leptocephali have 164-183 TM (Castle 1997) and appeared to be among the

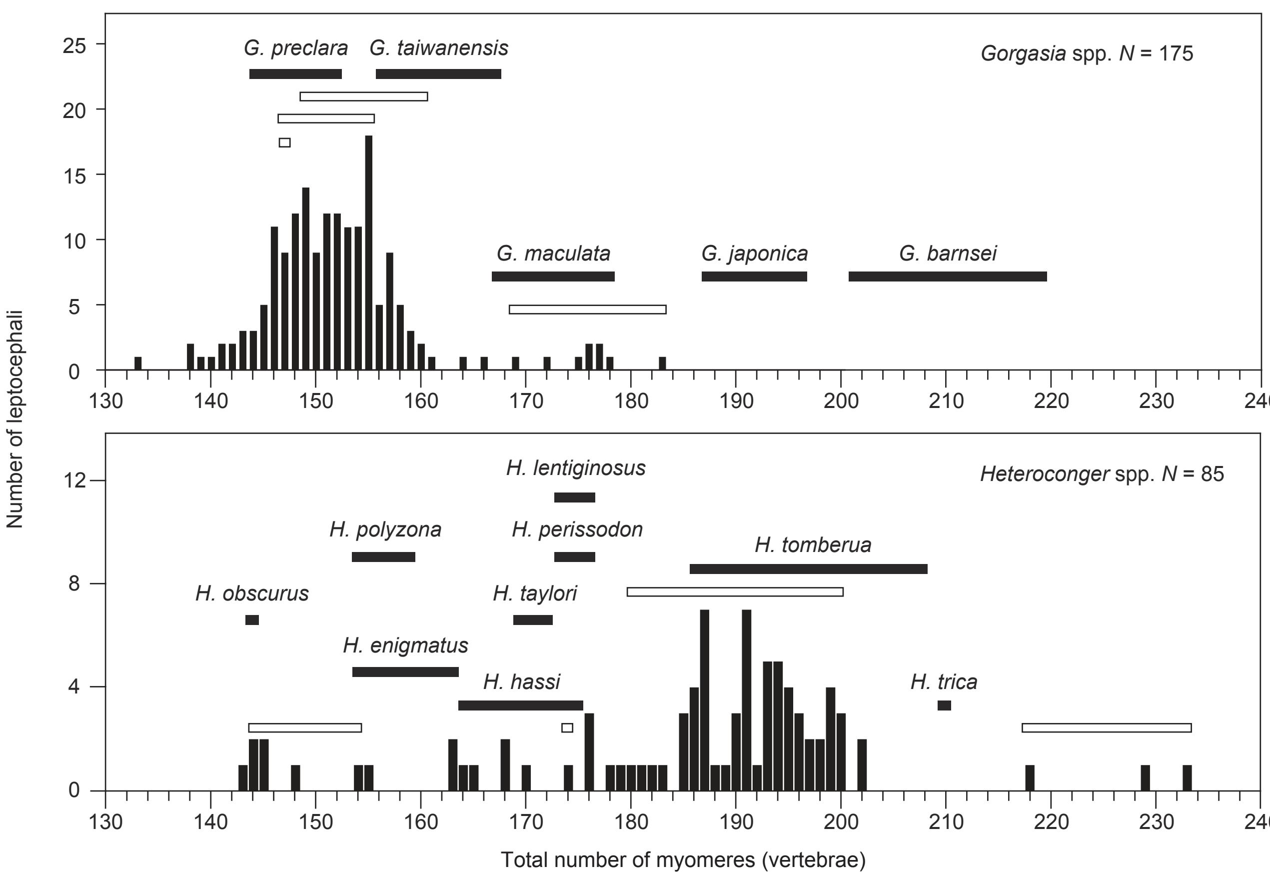

Fig. 3. Frequency distributions of the total number of myomeres (TM) of garden eel leptocephali collected off west Sumatra during the BJ-03-2 sampling survey (sample sizes are for TM data only). Also shown are the ranges of the total number of vertebrae (TV) (horizontal black bars) for adult species of each genus (from Castle and Randall 1999; see Table 1) reported from areas adjacent to the eastern Indian Ocean (Sumatra, and the Nicobar, Bali, Flores, and Timor islands), and for *H. tomberua* that has only been collected in Fiji. TM ranges are also shown (horizontal white bars) for the apparent species of *Gorgasia* leptocephali and *Heteroconger* leptocephali with 1 row of lateral pigment (i.e., excluding *H. hassi*) that were detected in the genetic analysis by Ma (2006) of ethanol-preserved specimens from the survey.

Gorgasia leptocephali collected in 2003 based on the myomere counts and the TV ranges of adults in the region (Table 1, Fig. 3). They did not appear to be the most abundant species though, and the leptocephali of this species also seemed to be widely distributed at low abundances in 1929 (Fig. 1B). *Gorgasia preclara* has a lower TV range (about 144-152) than other members of the genus (Castle and Randall 1999), so this species also appeared to be present based on TM counts and the genetic analysis, and may have been one of the abundant species of garden eel leptocephali (Fig. 3). Castle and Randall (1999) noted that *Gorgasia* leptocephali with 141-155 TM were quite abundant in the 1929 collections, and concluded that most of those were *G. preclara*. *Gorgasia* leptocephali with slightly higher TM counts were genetically indicated to be a separate species though, and their TM range overlapped with that of *G. taiwanensis*, which was reported from Bali, to the southeast of the study area (Table 1, Fig. 3). A 3rd species of leptocephalus with 147 TM that was caught offshore at Stn. 5 (Fig. 3) was genetically detected by Ma (2006), but this specimen was 68.0 mm in TL, so it could have been transported into the study area from elsewhere. Including this apparently different species of leptocephalus, there is evidence of 4 species of *Gorgasia* and 5 species of *Heteroconger* leptocephali being collected off western Sumatra in 2003.

Distribution and catch rate

Garden eel leptocephali were collected at 21 of the 26 stations and were only absent at 3 of the offshore stations and the 2 stations over the continental shelf near Java I. (Figs. 2, 4). Both genera of leptocephali were widely distributed, and each was collected at 17 of the 26 stations. The biggest catches of *Gorgasia* and *Heteroconger* both occurred near Siberut I. (see Fig. 2) at latitudes of 1°-2°S (Fig. 4), but there were some differences in their distribution and abundance patterns. The highest catch rate of the survey was of *Gorgasia* at Stn. 12 (280 individuals (ind.)/10^5 m^3), and the 2nd highest was of *Gorgasia* at Stn. 11 (68 ind./10^5 m^3) just to the northwest (Fig. 4). Station 13 on the other side of Siberut I. and Stn. 22 to the south also had higher catch rates of *Gorgasia* than the other stations. *Heteroconger* leptocephali were more abundant only at the 3 stations closest to Siberut I. (Stns. 12, 13, and 18; 19-32 ind./10^5 m^3) (Fig. 4). Single individuals of *Heteroconger* leptocephali were collected at 3

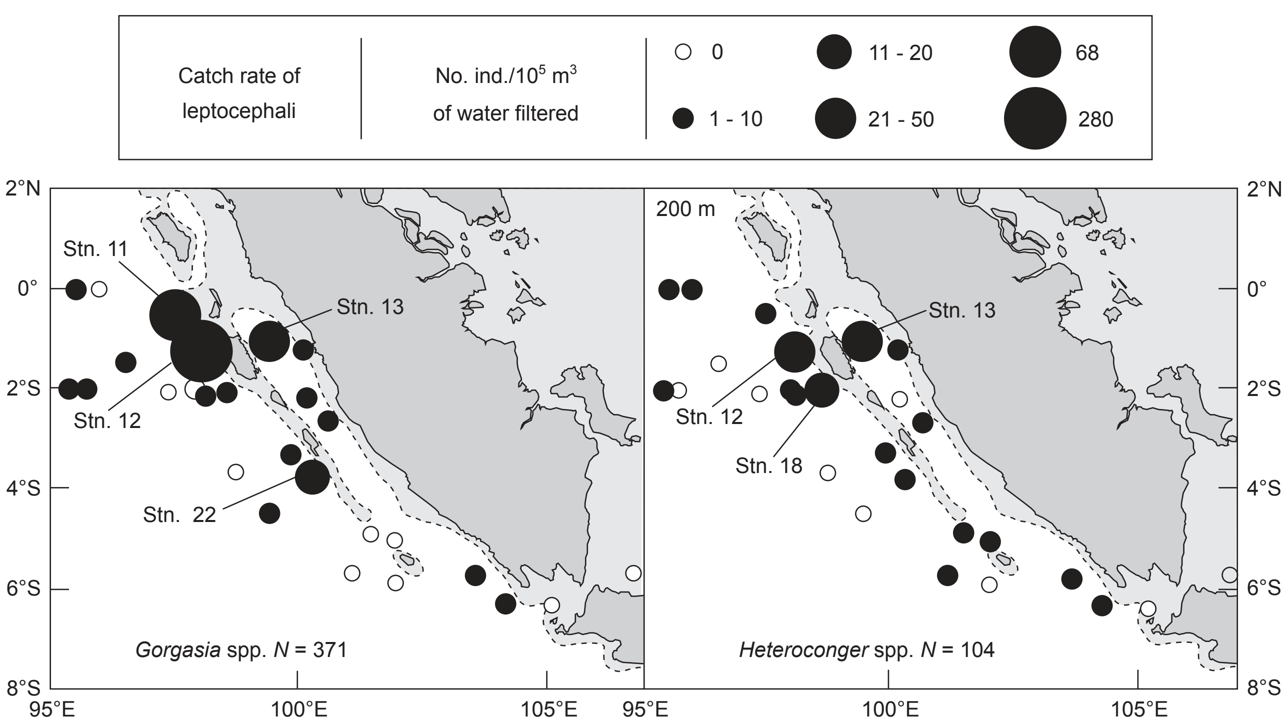

Fig. 4. Catch rates of *Gorgasia* and *Heteroconger* leptocephali at each station of the BJ-03-2 cruise. Data are plotted as the number of individuals (ind.) per amount of water filtered by the trawl. High-catch stations referred to in the text are shown, and the dotted lines and shading show the location of the 200 m depth contour of the continental shelf.

of 4 stations from 5°-6°S at the southern end of the Mentawai Is., where no *Gorgasia* leptocephali were collected. Despite the greater abundance of *Gorgasia* at 3 of the stations, catch rates of the 2 genera of leptocephali at the 26 stations were not statistically different (*U*-test, $p > 0.6$).

Size of leptocephali

Wide size ranges of both *Gorgasia* and *Heteroconger* leptocephali were collected, with most specimens being about 10-70 mm. *Gorgasia* leptocephali were most abundant in the 10-30 mm range, but *Heteroconger* leptocephali were most abundant at 35-60 mm and had a higher maximum size range than *Gorgasia* (Fig. 5). *Heteroconger hassi* specimens were 23.1, 86.0, and 107.4 mm (Stns. 13, 15, and 12, respectively, Fig. 6), and the average total length (± S.D.) of the other *Heteroconger* leptocephali was 47.3 ± 14.2 (range,14.0-93.7) mm. *Gorgasia* leptocephali had an average total length of 25.4 ± 9.9 (range, 9.2-68.0) mm. The smallest leptocephali of *Gorgasia* were collected at Stns. 8, 11, 12, 14, and 19, and the smallest *Heteroconger* specimens were collected at Stns. 11 and 12 (Fig. 6). These stations were all near the latitude of Siberut I. The small leptocephali were most abundant at Stns. 11 and 12 near the largest area of shallow continental shelf along the coast of Sumatra (Figs. 6, 7).

The length frequency distributions of garden eel leptocephali at stations with the largest catches showed some different patterns for the 2 genera. *Gorgasia* leptocephali at the 3 high-catch stations showed similar sizes at Stns. 11 and 12, but those at Stn. 13, located inshore of Siberut I., were considerably larger (Fig. 7). Total lengths at these 3 stations were statistically different (ANOVA, $p < 0.001$), with Stn. 13, with much larger individuals (average, 45.3 ± 5.1 mm; range, 38.2-65.2 mm), being different from the other 2 stations ($p < 0.001$); but Stns. 11 (average, 19.7 ± 4.5 mm; range, 12.0-29.4 mm) and Stn. 12 (average, 22.1 ± 5.6 mm; range, 9.2-45.2 mm) were also significantly different from each other ($p < 0.01$) in post-hoc pairwise comparisons (Tukey's test). The length frequency distributions of the largest catches of *Heteroconger* at 2 of the same 3 stations showed wider size ranges (Fig. 7). There were significant differences among the lengths of the *Heteroconger* leptocephali at Stns. 12 (average, 38.2 ± 13.7 mm; range, 14.0-67.0 mm), 13 (55.1 ± 9.9 mm; 26.7-93.7 mm), and 18 (51.9 ± 8.9 mm; 37.2-65.0 mm) (Kruskal-Wallis, $p < 0.001$), but Stns. 12 and 13 were not significantly different from each other in the pairwise comparisons (Dunn's test, $p > 0.05$) due to their wide size ranges.

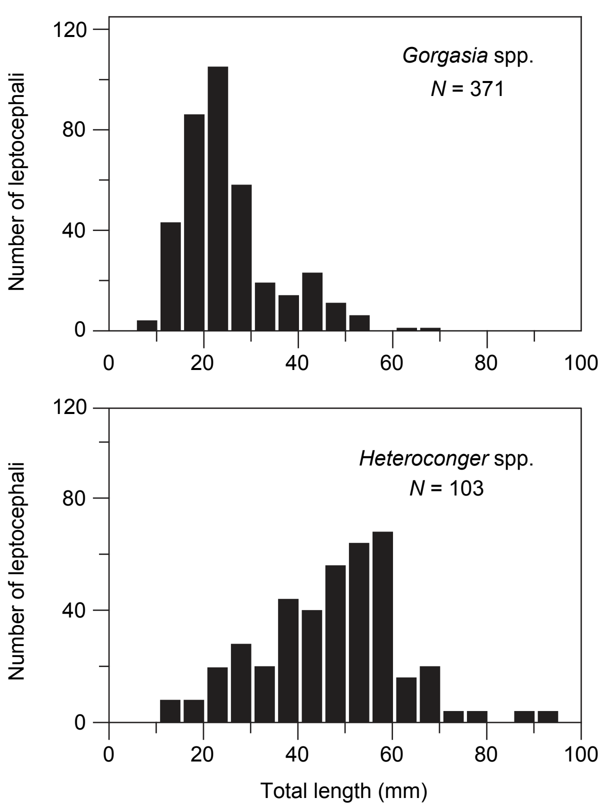

Fig. 5. Length frequency distributions of *Gorgasia* and *Heteroconger* leptocephali collected at all stations during the BJ-03-2 cruise.

DISCUSSION

Distribution of leptocephali

The collections of garden eel leptocephali in the present study and during the historical survey in Sept.-Nov. 1929 (Fig. 1; Castle 1997) indicate that these leptocephali may frequently be abundant just offshore of west Sumatra and around the Mentawai Is. In June 2003, both *Gorgasia* and *Heteroconger* leptocephali were widely distributed, and both genera were most abundant at some of the stations near Siberut I. Comparatively few were collected at the stations farther offshore or at stations in the southern half of the study area, as also seemed to be the case in 1929. In 2003, the smallest-sized leptocephali were collected near Siberut I., but wide size ranges of leptocephali of both *Gorgasia* and *Heteroconger* were also caught at some of the stations there. The smallest specimens at these stations were about 9-12 mm, and based on growth studies of a few other taxa of leptocephali could have been about 10-20 d old (Ma et al. 2005, Kuroki et al. 2006). Mostly larger-sized leptocephali were collected at the stations farther offshore and in the southern part of the study area.

These patterns of distribution and size suggest that the largest number of colonies of garden eels, or the most offshore transport away from the continental shelf prior to the survey, was in the region near Siberut I. The lack of specimens < 9 mm in the 2003 survey also supports the hypothesis that garden eels spawn without moving away from their colonies on the continental shelf, because all of the stations where garden eel leptocephali were collected were over water

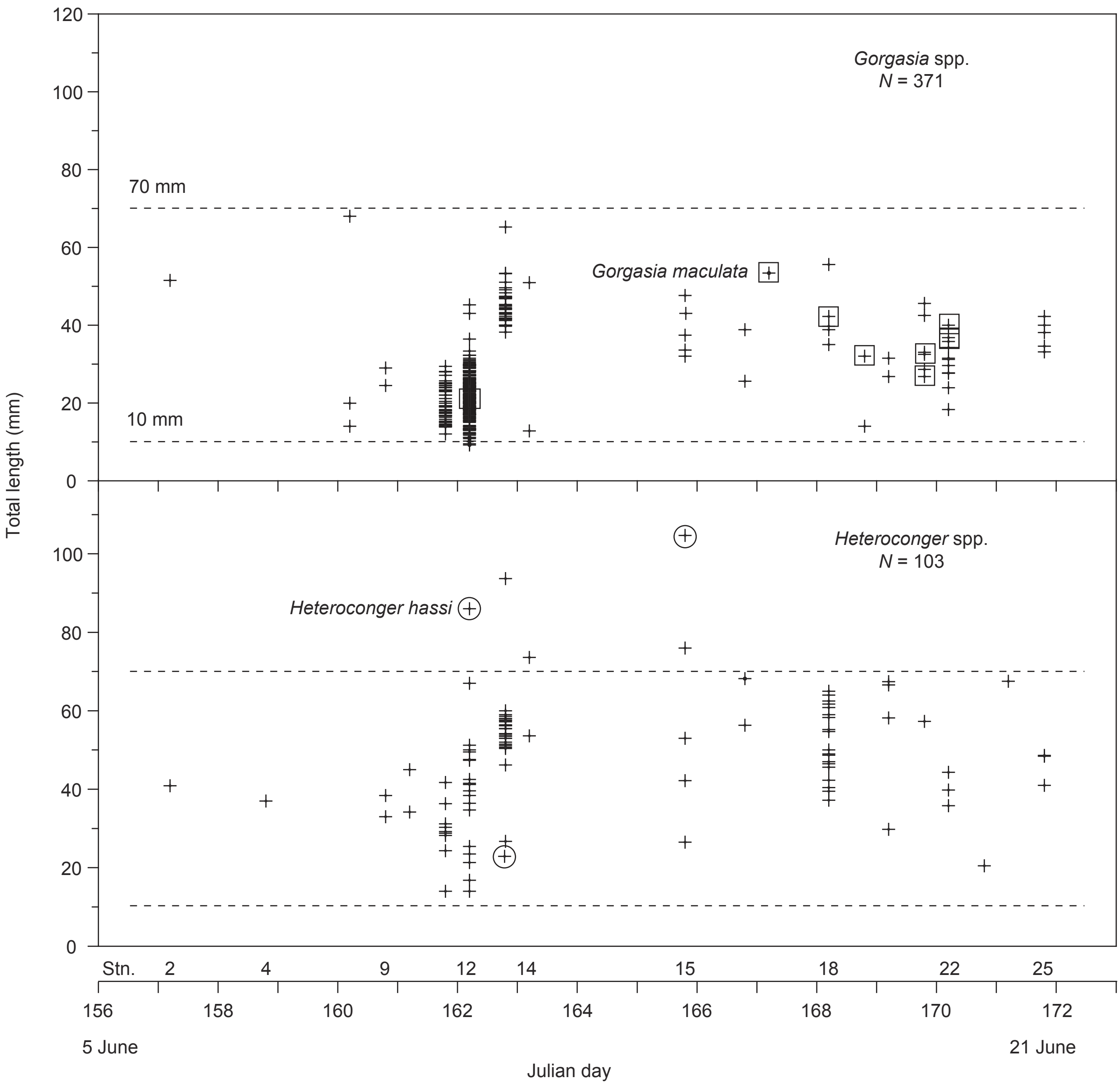

Fig. 6. Lengths of individual *Gorgasia* and *Heteroconger* leptocephali collected at each station plotted by the day of the year (Julian day) when they were captured, with representative station numbers and actual dates of the 1st and last stations of the BJ-03-2 cruise labeled. Larvae of 1 species of each genus that were identified morphologically are shown as circles or squares. Dashed lines at 10 and 70 mm are for easy comparison of lengths between stations and panels.

at least 1500 m deep. This is consistent with observations of courtship and apparent spawning behavior of *G. sillneri* within its colonies (see Thresher 1984). The abundance of garden eel leptocephali near Siberut I. may be the result of many garden eels living on the large area of the continental shelf that extends out from western Sumatra just to the north of the island (Fig. 7). This large shelf area includes some small islands and shallow banks that are < 30 m deep, so there is probably a large amount of suitable habitat for garden eels.

The outer edge of this large bank is surrounded by deep water on 3 sides, so strong currents crossing the bank could easily carry small leptocephali out over deeper water. As seen in Oct. (Fig. 1D), the typical surface currents inshore of the Mentawai Is. are thought to be to the southeast parallel to the coast of west Sumatra (Wyrtki 1961). If part of this southeast-flowing current turns to the west as it crosses the shallow protrusion of the continental shelf to the north of Siberut I., many small leptocephali may get transported offshore. Most leptocephali are distributed in the upper 100 m at night in the open ocean and sometimes deeper during the day (Castonguay and McCleave 1987, Miller 2009), so surface currents can transport them long distances, especially because some taxa of leptocephali have larval durations of 3 mo to almost a year (Marui et al. 2001, Ma et al. 2005, Kuroki et al. 2006). This long larval duration and offshore transport and mixing of leptocephali from different areas or spawning events by currents and eddies could have caused the distribution patterns of garden eel larvae observed off west Sumatra in this study and in the previous study in 1929.

Although there were some differences in size ranges between the 2 genera of leptocephali and among some stations, the exact spawning locations and larval drift patterns are not clear from these catch data. The size ranges of leptocephali at Stns. 11 and 12 were smaller than those at Stn. 13, which is inshore of Siberut I. This suggests that there had been stronger offshore transport prior to the survey than there was into the area

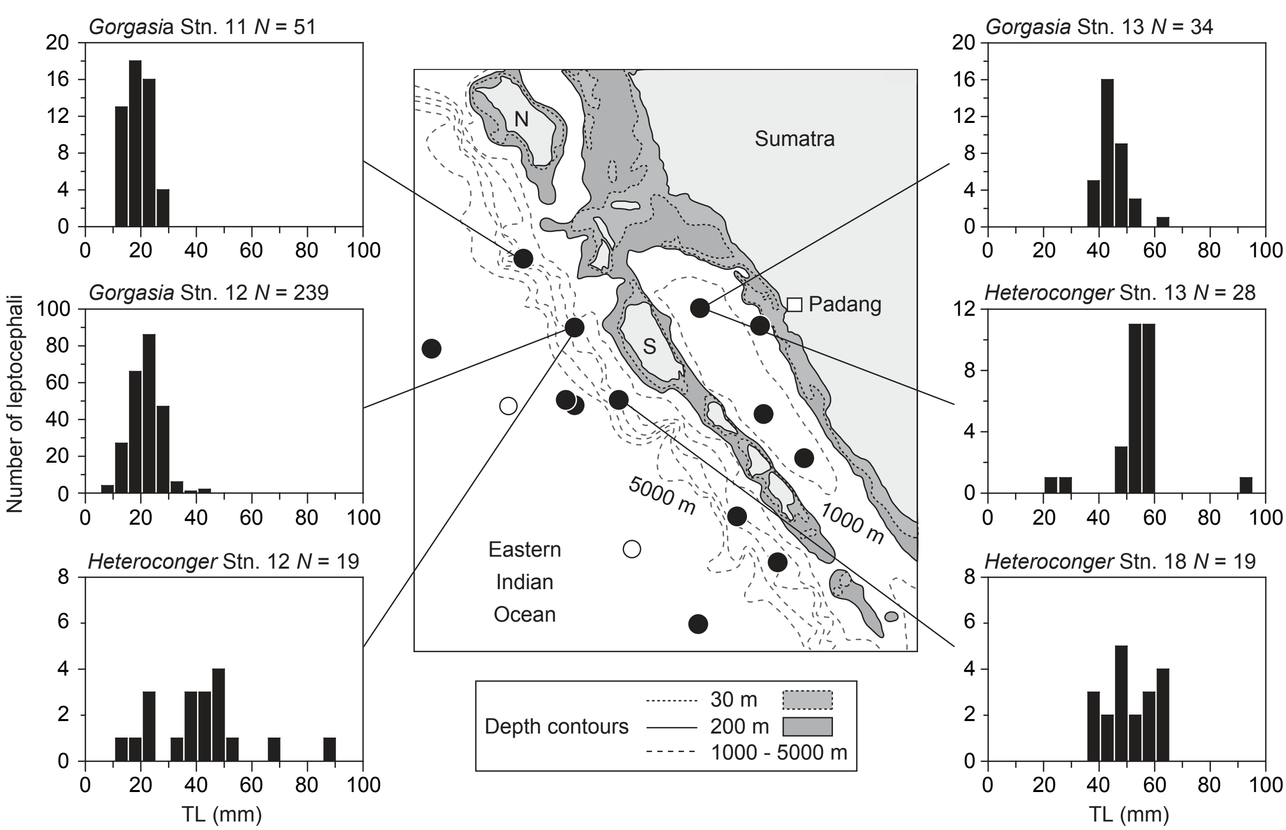

Fig. 7. Length frequency distributions of *Gorgasia* and *Heteroconger* leptocephali collected at 4 high-catch stations during the BJ-03-2 cruise, shown in relation to ocean depths in the northern part of the study area. The 2 shallowest depth contours are shown with shading. N, Nias I.; S, Siberut I.

inshore of the Mentawai Is. Upwelling off the coast of west Sumatra has been reported, which would transport surface water offshore, but this activity appears to be strongest later in the year in Oct. (Susanto et al. 2001).

Offshore transport may frequently occur in this area because the northern Indian Ocean is a unique region of the world's oceans that has drastic changes in current patterns caused by shifts in the winds associated with the regional monsoon cycle (Schott and McCreary 2001). One factor in the eastern Indian Ocean that would influence the currents at the edge of the continental shelf appears to be large eddies that move past Sumatra (Hacker et al. 1998, Vinayachandran et al. 1999, Iskandar et al. 2006). These currents and eddies are likely created in part by strong seasonal offshore equatorial current jets that include periods of intense eastward surface flows lasting about 10-20 d, mostly during the northern hemisphere spring and fall (Senan et al. 2003, Masumoto et al. 2005, Sengupta et al. 2007, Kantha et al. 2008). These strong current jets could have a major effect on the variability of the flow of water around the Mentawai Is. and the large shelf area north of Siberut I. Strong eastward equatorial jets appear to typically occur during May (Thompson et al. 2006, Sengupta et al. 2007, Kantha et al. 2008). The eastward jet in May 2003 just before the survey in June appears to have been brief compared to some years, but it was also followed by an unusually strong westward current flow in June (Kantha et al. 2008), which could have also contributed to the advection of leptocephali to offshore areas.

Diversity and abundance of garden eels off Sumatra

The large catches and many species of garden eel leptocephali in this region and reports of many adult species in nearby areas suggest that continental shelf habitats of west Sumatra and the Mentawai Is. are inhabited by a variety of species of garden eels. The morphology and genetic sequence data of the leptocephali indicated that at least 9 species of garden eel leptocephali were collected in 2003. This presence of such a large number of species of larvae is consistent with reports of a wide variety of adult garden eel species in the eastern Indian Ocean region (Table 1). There have been 5 species of *Gorgasia* (*G. barnsei*, *G. japonica*, *G. maculata*, *G. preclara*, and *G. taiwanensis*) and 8 species of *Heteroconger* (*H. enigmaticus*, *H. hassi*, *H. lentiginosus*, *H. obscurus*, *H. perissodon*, *H. polyzona*, *H. taylori*, and *H. trica*) reported from either Sumatra or Bali in southern Indonesia, East Timor (east of Bali), or the Nicobar Is. (northeast of Sumatra) by Castle and Randall (1999) and Allen and Adrim (2003), which are all areas adjacent to the eastern Indian Ocean. Only a few specimens of some of these species have been collected as adults and examined though (Castle and Randall 1999), so little information is available about their habitat use and relative abundances. In addition, there also appears to be another species of *Gorgasia* in the region that has been collected much further to the north in the Andaman Is. in the Bay of Bengal, which has 170-179 vertebrae and appears to be a species similar to *G. galzini* from the Pacific (Allen and Erdmann, in prep.).

The TM counts of this and the previous study (Castle 1997) suggest that *G. preclara* and *H. tomberua* are abundant species of garden eel leptocephali in the region. The present study and the recent report of adults of *G. taiwanensis* at Bali (Allen and Adrim 2003) indicate that there were likely 2 abundant species of *Gorgasia* leptocephali present off Sumatra in June 2003. Adults of *H. tomberua* have only been collected in Fiji up to now (Castle and Randall 1999), so further research is needed to identify the species of adult *Heteroconger* with a TV range of about 186-208 that seems to be present near the Mentawai Is. to determine if it is actually *H. tomberua* or a new species. Leptocephali of *G. maculata* and *H. hassi* were present in smaller numbers during both surveys (Figs. 1, 6), and it appears likely that *H. obscurus* larvae were also collected.

The 13 garden eel species reported from the southern Indonesia region and the collection of about 9 species of leptocephali in the present study suggest that there is a remarkable diversity of garden eels living sympatrically on the continental shelf areas of the Mentawai Is. and along west Sumatra. In comparison, up to 13 species of garden eels have been reported from the entire Indonesian archipelago (Castle and Randall 1999, Allen and Adrim 2003, Allen and Erdmann 2009, Table 1), and at least 13 species were thought to be present across the entire western Central Pacific region (Smith 1999). Only 23 species are known from the Indo-Pacific as a whole (Castle and Randall 1999, Greenfield and Niesz 2004, Allen and Erdmann 2009), so the eastern margin of the Indian Ocean may have a higher diversity of garden eels compared to most regions of the world.

The abundance of garden eel leptocephali off west Sumatra relative to those of other species of leptocephali also appeared to be high compared to other regions. Off Sumatra in 2003, garden eel leptocephali comprised 17.4% of the 2743 total leptocephali of 12 families of anguilliform eels collected during the survey, which included 43 anguillid leptocephali of 3 species (Aoyama et al. 2007). In comparison, only 2.0% of the 2575 anguilliform leptocephali collected at 25 stations around Sulawesi I., Indonesia, in May 2001 were garden eel leptocephali (Wouthuyzen et al. 2005). Similar or even lower proportions were reported in other large collections of leptocephali in tropical (4.4% of 4511 leptocephali, Richardson and Cowen 2004) and subtropical (0.03% of 4336 leptocephali, Miller 1995; 0.02% of 2356 leptocephali, Minagawa et al. 2004) areas. Only 2.6% of the 1560 leptocephali collected in the Northwest Providence Channel of the northern Bahamas were garden eels, and included only 1 or possibly 2 species of *Heteroconger* (Miller and McCleave 2007). In the Florida Current stations of the same survey, 2.4% of 672 leptocephali were *Heteroconger*, but none of the 2115 leptocephali collected offshore in the Sargasso Sea were garden eels (Miller and McCleave 2007). A very low percentage of garden eel leptocephali (0.38%) was also present among the 2362 leptocephali collected in offshore areas of the western South Pacific (Miller et al. 2006a). The reason for the higher relative abundance of garden eel leptocephali off Sumatra could be due to a greater number of garden eel colonies in the area, or as discussed above, the geography of the colony locations in relation to the flow patterns of strong currents may result in more larvae being transported offshore compared to other regions.

Ecology and recruitment mechanisms

Although garden eel leptocephali were abundant off west Sumatra, studies on assemblages of leptocephali in other regions of the world suggest that this particular type of leptocephali are not typically transported far offshore into ocean gyres as much as are many other species of marine eel leptocephali. Extensive sampling in offshore areas of the Sargasso Sea showed that few or no garden eel leptocephali were caught there, even though many other taxa of leptocephali of coastal eels were transported far offshore (Miller 1995, Miller and McCleave 2007). This pattern was also similar to that seen for most ophichthid leptocephali caught in the region (Miller 1995, Miller and McCleave 2007), which suggests that leptocephali of these 2 taxonomic groups may have behavioral mechanisms to facilitate retention near their adult habitats (Miller 2009).

The lack of many garden eel leptocephali > 70 mm in the present study and the absence of metamorphosing larvae may indicate that large garden eel leptocephali are less vulnerable to being transported offshore. The likely maximum size of most garden eel leptocephali may be around 100-110 mm (Raju 1974, Castle 1997). Because leptocephali of that size appear to be able to swim quite well (Miller and Tsukamoto 2004, Wuenschel and Able 2008), active swimming or other types of behavior may contribute to the retention of larger garden eel leptocephali near the edge of the continental shelf (Miller 2009). The consistent rarity of garden eel leptocephali in offshore areas also suggests that even if they are transported away from the continental shelf, they may attempt to swim back to shelf areas. This was suggested for larvae of coral reef fishes (Leis and Carson-Ewart 2003, Fisher 2005, Leis 2006), and it is possible that directional swimming is used by garden eel leptocephali to return to coastal areas. This would reduce the potentially huge losses of their larvae as a result of being transported away from adult colonies on the shelf by local currents, or from sporadic strong current events as discussed above.

A few large *Heteroconger* leptocephali were collected offshore in 2003 though, which may have been ready to begin metamorphosis. Remarkable changes in morphology occur during metamorphosis from the leptocephalus to the glass eel stage (Bell et al. 2003, Otake 2003, Miller and Tsukamoto 2004, Miller 2009), which makes metamorphosing specimens easy to detect when collected. Raju (1974) described a few specimens of metamorphosing garden eel leptocephali (100-110 mm long) that were collected along the eastern margin of the tropical Pacific. However, it is unclear what stimuli initiate this process in eel larvae (Miller 2009). The rarity of metamorphosing specimens of garden eel leptocephali over deep waters in this and previous studies (Miller 1995, Wouthuyzen et al. 2005, Miller et al. 2006a, Miller and McCleave 2007) suggests that they may typically require contact with environmental conditions associated with the continental shelf to trigger metamorphosis, as was discussed in relation to other congrid leptocephali (Miller et al. 2006b).

A complete perspective of the larval ecology of garden eels was not obtained in the present study, because no stations were sampled very close to or over the continental shelf, where metamorphosing larvae or recently spawned leptocephali would likely be found. Like garden eels, some other shallow-water eel species may spawn over the shelf, such as moray eels (Moyer and Zaiser 1982, Thresher 1984, Ferraris 1985) and ophichthid eels (Fahay and Obenchain 1978), and their leptocephali may also have behavioral mechanisms to remain near their continental shelf recruitment areas. This was suggested by regular pulses of recruitment of leptocephali such as ophichthids that occur over shallow banks in the northern Bahamas (Thorrold et al. 1994). The cyclic pattern of recruitment might indicate that leptocephali wait just offshore until the onset of metamorphosis, and then began a rapid ingress onto the shelf at certain periods of the lunar cycle (Miller 2009). It is not known if garden eel leptocephali use this type of recruitment strategy or not, since studies have not examined the recruitment of leptocephali at the species level.

Future studies should sample over the shelf, near the shelf break, and over deep water to help understand the larval distributions and recruitment mechanisms of garden eels and other shallow-water marine eels that spawn without migrating offshore. Data from the present study indicate that some species may be more abundant than others near Siberut I., but there are no data available on the relative abundances or habitat use of adult garden eels in this area. Surveys of garden eel colonies by divers along west Sumatra and genetic studies of the adults and larvae will be useful to help evaluate the apparently high diversity of garden eels along the margin of the eastern Indian Ocean and to increase our understanding of these remarkable planktivorous eels.

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