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SHORT COMMUNICATION

Seasonality of spawning by tropical anguillid eels around Sulawesi Island, Indonesia

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Abstract Remarkably little is known about the life histories of the many tropical anguillid eels distributed across the Indo-Pacific region, and since the Danish expedition to study eels in the region in 1928 and 1929, research on these eels has only begun again in recent years. Sampling for anguillid leptocephali in the Indonesian Seas has been carried out recently to learn about the spawning ecology and larval distributions of tropical eels there. The leptocephali of *Anguilla marmorata*, *Anguilla bicolor pacifica*, *Anguilla borneensis*, *Anguilla interioris*, and *Anguilla celebesensis* were collected around Sulawesi Island both in May 2001 and October of 2002. The development of genetic identification techniques has enabled these leptocephali to be identified to species, and their distributions and sizes during different seasons indicated that there are differing life history patterns among sympatric species in the region. *A. celebesensis* was found to have been spawning in Tomini Bay of northeastern Sulawesi Island in March and April 2001, but apparently, no spawning had occurred in the late summer and fall of 2002. Studies on anguillid glass eels have suggested that tropical anguillids may spawn throughout much of year, but our research on leptocephali in Tomini Bay and data on the downstream migration of tropical anguillids in the major tributary to Tomini Bay indicate that *A. celebesensis* may have a distinct seasonal pattern of spawning possibly related to the regional monsoon cycles. This is the first evidence of seasonality of spawning in tropical anguillid eels whose life histories are only just beginning to be revealed.

Keywords *Anguilla* · Eels · Leptocephali · Seasonal spawning · Sulawesi Island

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Introduction

The mystery of where temperate anguillid eels spawn in the open ocean has fascinated biologists ever since the discovery of the spawning area of the Atlantic eels in the Sargasso Sea (Schmidt 1922). This finding was followed by the discovery of the spawning area of the Japanese eel, *Anguilla japonica*, in the western North Pacific (Tsukamoto 1992). During the last century, these discoveries about the spawning areas of temperate eels were accompanied with studies about their life history and freshwater ecology, which indicated that temperate anguillids have well-defined spawning seasons and that they make long migrations out into the open ocean to spawn (Tesch 2003).

In comparison, there has been very little research on the 12 species of tropical anguillids, which outnumber the six temperate species. The region of the Indonesian Seas around Sulawesi Island is unique because the freshwater habitats are inhabited by five species of tropical anguillids, which is more than anywhere else in the world (Ege 1939; Watanabe et al. 2004). The genus *Anguilla* may have originated in the Indonesian region because phylogenetic analyses indicate the endemic tropical species *Anguilla Borneensis* from eastern Borneo (Kalimantan) is one of the most basal species of the genus (Aoyama et al. 2001; Minegishi et al. 2005).

The tropical anguillid eels found in the Indonesian Seas region have differing species ranges, but most overlap in the region around Sulawesi Island. The most widespread anguillid is the giant mottled eel, *Anguilla marmorata*, which has several populations from the western Indian Ocean, through the Indonesia region, north to southern Japan, and across the western South Pacific (Ishikawa et al. 2004; Minegishi et al. 2008). The other common species in the Sulawesi Island region is the Indonesian mottled eel, *Anguilla celebesensis*, which has a restricted range in the central Indonesian Seas region and the Philippines. *Anguilla bicolor pacifica* is widely distributed throughout the northern Indonesian Seas and on some islands of the western North Pacific. *Anguilla interioris* is known from northern New Guinea but may be more widely distributed than previously thought.

Until recently, remarkably little was known about the spawning areas and larval distributions of tropical anguillids. The Danish Round the World Expedition from 1928 to 1930 collected many leptocephali off west Sumatra (Fig. 1), indicating that *Anguilla bicolor bicolor* spawned there (Jespersen 1942). However, only large anguillid leptocephali were collected in the Indonesian Seas region and near northern New Guinea (Fig. 1), so spawning areas could not be determined (Jespersen 1942). Another problem was the overlapping ranges of meristic characters, which prevented most species identifications from being made. However, recent advances in molecular genetic techniques have made it possible to clearly identify anguillid leptocephali (Aoyama et al. 2003), and these techniques have been used recently in early life history studies of tropical anguillids.

Information about the life histories of tropical anguillids has begun to be obtained from sampling surveys for leptocephali, otolith studies, and research on the adults. Catches of leptocephali have indicated that the northern population of *A. marmorata* migrates from northern Indonesia, the Philippines, and southern East Asia to spawn in the North Equatorial Current region of the western North Pacific (Miller et al. 2002). There have been studies on the recruitment patterns and ages of glass eels (e.g., Arai et al. 2001; Sugeha et al. 2001), and the ages and hatching dates of leptocephali have been determined using otolith microstucture (Kuroki et al. 2006). All stages of *A. marmorata* also have been studied recently on Sulawesi Island (Sugeha 2003). In February 2000, a sampling survey for anguillid leptocephali in the Celebes and Sulu Seas by the R/V Hakuho Maru collected several small leptocephali of *Anguilla borneensis* and *A. celebesensis* in the Celebes Sea, indicating the presence of a spawning area of these two tropical eels there (Aoyama et al. 2003).

In 2001, a wider area around Sulawesi Island was surveyed for leptocephali during a cruise of the R/V Baruna Jaya VII in May, and a spawning area of *A. celebesensis* was discovered in Tomini Bay of northern Sulawesi Island (Aoyama et al. 2003). In late September and early October

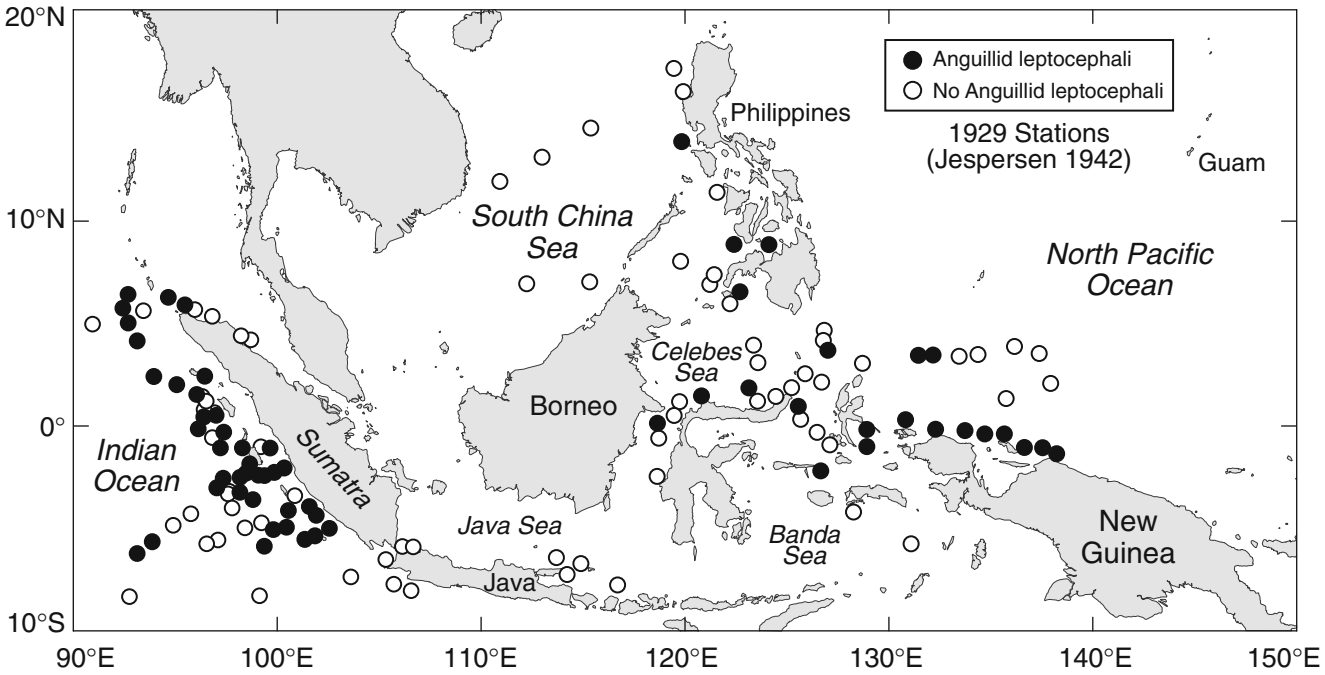

Fig. 1 Map of the stations where anguillid leptocephali were collected in the Indonesian Seas region during the Carlsberg's Round the World Expedition in 1929. Stations where leptocephali were collected are shown with *black circles*, and stations where none were collected are shown with *white circles* [adapted from Jespersen (1942)]

2002, a second sampling survey was conducted by the Baruna Jaya VII in the same region to collect anguillid leptocephali in a different season.

In this paper, we report the finding of a pattern of seasonal spawning by *A. celebesensis* in Tomini Bay based on the 2001 and 2002 surveys for leptocephali there in two different seasons. The collections of four species of anguillid leptocephali around Sulawesi Island are compared between the two seasons, and the implications of the catches of leptocephali are discussed in relation to data on the downstream migration of tropical silver eels into Tomini Bay.

Materials and methods

The methodology, oceanographic conditions, and other leptocephali collected during the BJ-01-1 sampling survey

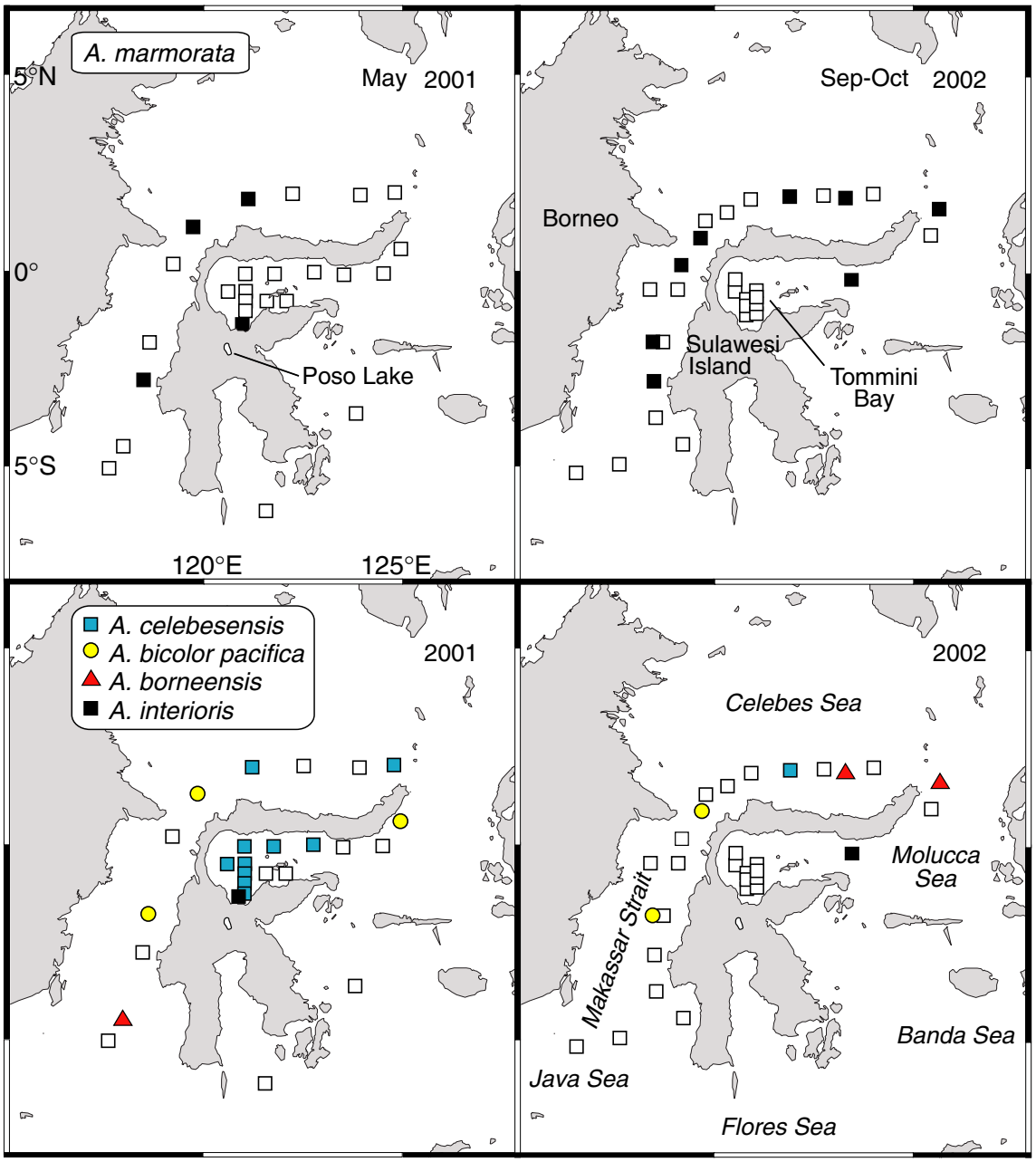

Fig. 2 Map of the area around Sulawesi Island, Indonesia showing the sampling stations (*open squares*) and the locations where *Anguilla marmorata* leptocephali were collected (*black squares*) during BJ-01-1 cruise in May 2001 (*upper left*, including a glass eel in Tomini Bay) and during BJ-02-4 in September and October (*upper right*, including a glass eel in the Celebes Sea), and where *A. bicolor pacifica*, *A. celebesensis*, *A. interioris*, and *A. borneensis* leptocephali were collected in the same two cruises (*lower panels*)

by the R/V Baruna Jaya VII of the Research Center for Oceanography of the Indonesian Institute of Sciences around Sulawesi Island during 12–26 May 2001 are described elsewhere (Wouthuyzen et al. 2005; Miller et al. 2006), but briefly, 25 stations were sampled using the large mouth opening Isaacs Kidd Midwater Trawl (IKMT). Two tows (one oblique, one step tow) of the IKMT (8.7 m^2 mouth opening, 0.5 mm mesh) were made at each station. During the BJ-02-4 Baruna Jaya VII cruise in 2002, leptocephali were collected with the IKMT using the same techniques (except only one step or oblique tow was made at all but two stations, which had both) between 26 September and 17 October. Sampling occurred at 34 stations (36 tows) that were all located in areas >1,000 m deep except in the Java Sea. Leptocephali were sorted fresh from the plankton samples, and their total length and other characters were measured before preservation in 99% ethanol for later genetic identification (Aoyama et al. 2003).

Results

There were 27 anguillid leptocephali and one glass eel collected during the BJ-02-4 cruise in 2002, which were genetically identified as 18 *A. marmorata*, three *A. bicolor pacifica*, three *A. interioris*, two *A. borneensis*, and one *A. celebesensis*. A 48.6-mm *A. marmorata* glass eel was also collected in the southern Celebes Sea. The size range of the leptocephali collected in 2002 was 33.1–49.5 mm, and they were collected at four stations in Makassar Strait, two stations in the Celebes Sea, and two stations in the Molucca Sea (Fig. 2).

Similar species were collected during the survey the year before, but there was a distinct difference in the catches of leptocephali in Tomini Bay of Sulawesi Island. During the BJ-01-1 cruise in May 2001, a total of 52 leptocephali of the same five species as in 2002 were collected, except that one *A. marmorata* glass eel was also collected in Tomini Bay (Aoyama et al. 2003). The *A. marmorata* and *A. bicolor pacifica* leptocephali were all large (33–50 mm) and widely distributed in both surveys (Fig. 2). The less-abundant species such as *A. bicolor pacifica* and *A. borneensis* were also widely distributed in both years. During 2002, one specimen of *A. celebesensis* (36.4 mm) was collected in the Celebes Sea, and two leptocephali of this species (31, 37 mm) were also collected there in 2001. However, during 2001, many *A. celebesensis* leptocephali of two size classes were collected in Tomini Bay (13–23, 30–48 mm). In contrast, despite similar sampling effort in the same regions of Tomini Bay, no *A. celebesensis* were collected there in 2002, which indicated that there had been no spawning in the bay during the previous months (Fig. 2).

Discussion

The findings of this study provided the first opportunity to examine the seasonal distribution and species composition of leptocephali of tropical eels in the central Indonesian Seas. The sampling surveys in 2001 and 2002 around Sulawesi Island found that anguillid leptocephali were widely scattered around the island and that the leptocephali of *A. borneensis*, *A. bicolor pacifica*, *A. celebesensis*, and *A. marmorata*, were collected in both years during two different seasons. These are the same species that have been reported from the freshwater areas of the surrounding landmasses. The small leptocephali (8–13 mm) of *A. borneensis* and *A. celebesensis* collected in the Celebes Sea in February of 2000 and the larger ones collected there in both 2001 and 2002 indicate that the Celebes Sea is a spawning area of these tropical eels. The eels that live near the freshwater habitats likely spawn there after a relatively short spawning migration compared to temperate anguillids (Aoyama et al. 2003).

However, in 2001, *A. celebesensis* was found to also have a different local spawning area in Tomini Bay. The presence of leptocephali as small as 13 mm in May of 2001 indicated that *A. celebesensis* had been spawning in the southern part of Tomini Bay prior to the cruise, and the larger size class showed there was also another spawning event in the bay in preceding months. This type of pattern of multiple local spawning areas differs drastically from the single large panmictic spawning areas of temperate anguillids (Tsukamoto et al. 2002).

The back-calculated hatching dates of the leptocephali in Tomini Bay ranged from late February to early May of 2001 according to the number of daily rings in their otoliths

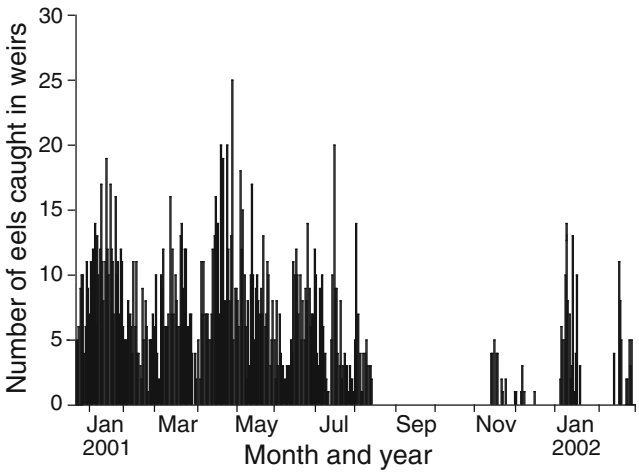

Fig. 3 Catches of downstream migrating silver eels at the outlet of Poso Lake from December 2000 to February 2002. The Poso River flows into Tomini Bay where *Anguilla celebesensis* was found to be spawning between late February and early May 2001 [adapted from Sugeha (2003)]

(Kuroki et al. 2006). *A. celebesensis* leptocephali may reach their maximum size and begin to metamorphose between ages of about 70 and 120 days old (Arai et al. 2001), so this suggests that in October of 2002, when leptocephali were absent, there had been no spawning of *A. celebesensis* in Tomini Bay for at least about 3–4 months prior to the cruise. This absence of spawning prior to the 2002 survey provides the first clear suggestion of seasonality of spawning in a tropical anguillid species. Temperate anguillids typically have clearly seasonal patterns of downstream migration, spawning in the open ocean, and recruitment of glass eels (Tesch 2003), but tropical species have shown much wider ranges of recruitment times of glass eels and back-calculated hatching dates (e.g., Arai et al. 2001; Sugeha et al. 2001; Kuroki et al. 2006).

However, further evidence of a seasonal pattern of spawning of *A. celebesensis* in Tomini Bay comes from catch data of anguillid silver eels collected at seven large weirs across the outlet of Poso Lake (Fig. 2) in the center of Sulawesi Island (Sugeha 2003). The Poso River flows into the southern part of Tomini Bay and is the largest drainage and potential source of silver eels adjacent to the bay. Catch data from the weirs showed that silver eels were mostly a mix of *A. celebesensis* and *A. marmorata* and that they had been moving out of the lake at least from late December 2000 to mid-August 2001 (Fig. 3) during an overlapping period of time when spawning by *A. celebesensis* was occurring in the bay in 2001. Outmigration from the lake stopped, however, from mid-August to early November of 2001. If a similar stop in outmigration occurred during the same period in 2002, it would be consistent with the apparent absence of spawning detected by the larval survey in the bay in October 2002. The weir data in 2001 and larval sampling in 2002 both suggest that migration and spawning of *A. celebesensis* in Tomini Bay stopped for a several month period in each year, which may correspond with the dry season on Sulawesi Island that is controlled by the regional tropical monsoon cycle.

Interestingly, the back-calculated hatching dates of *A. marmorata* and *A. bicolor pacifica* leptocephali from both the Indonesian Seas and offshore show a similar gap in hatching dates from mid-August to the end of October like that seen for *A. celebesensis* (Kuroki et al. 2006). This suggests that there is a general pattern of cessation of downstream migration of tropical anguillids during the dry season. The wide variations in recruitment times of glass eels observed may be due to widely varying transport patterns of leptocephali in these tropical areas with many eddies and seasonally shifting wind patterns. This is supported by the fact that each species has shown peaks in recruitment in particular seasons of several different years (Sugeha et al. 2001), which may correspond to the larvae that have direct migrations back to coastal recruitment areas.

Little is known about the spawning periodicity of tropical anguillid eels or marine eels in the Indo-Pacific though, despite the many species living there (Wouthuyzen et al. 2005; Kuroki et al. 2006; Miller et al. 2006). It is known that the Japanese eel appears to spawn during new moon periods within their spawning season (Tsukamoto et al. 2003), and at least some species of small tropical marine eels of the family Chlopsidae (false morays) appear to spawn during full moon periods, perhaps all year-round (Lee et al. 2008). However, similar to temperate anguillids whose spawning and recruitment is timed in relation to the seasonal cycle of temperature, some temperate or subtropical marine eels may not spawn during the winter months even if similar species may spawn year-round in more tropical areas (Minagawa et al. 2007).

Although the findings of the present study around Sulawesi Island are interesting, much more research on the reproductive ecology and spawning patterns of tropical anguillids is needed to fully understand these mysterious fishes. Research on the freshwater ecology of tropical eels is also desperately needed to learn even the most basic biological information about each species. This type of information is critical to assist efforts to conserve these species before they experience the declines that have been observed in temperate eel species worldwide in recent years.

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