

Year-round spawning by a tropical catadromous eel *Anguilla bicolor bicolor*

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Abstract Remarkably little is known regarding the spawning area, spawning ecology or life history after recruitment of tropical eels to coastal areas across the Indo-Pacific region. In contrast, eel species in temperate areas, including the American, Australasian, European and Japanese eels, are known to have well-defined spawning and recruitment seasons, and spawning migrations generally take place during autumn months. Using monthly collections and analyses of both gonadosomatic index and gonad histology, we determined that the final stage of maturation for seaward spawning migration occurred throughout the year and year-round spawning and recruitment were evident in the tropical coastal areas from the open ocean. This non-seasonal spawning ecology is notably different from that of temperate catadromous eels. The unique year-round spawning ecology of *Anguilla bicolor bicolor* may facilitate mating between adult eels from different year classes (cohorts) or from different habitats.

Introduction

Catadromous eels of the genus *Anguilla* Schrank, 1798, are semelparous fish with long spawning migrations and extended larval durations (Tesch 2003). These eels are classified into 19 species (Ege 1939; Castle and Williamson 1974; Arai et al. 1999; Watanabe et al. 2013). Among these species, 13 are tropical and six are temperate species. In general, temperate eels are distributed mainly in subtropical/temperate areas, whereas tropical eels are distributed mainly in tropical/subtropical regions. Despite the different biogeographical distributions of these two types of eels, all anguillids spawn in the tropical/subtropical ocean and have leptocephalus larvae that disperse via ocean currents from their oceanic spawning area to continental habitats, where they metamorphose into glass eels (Tesch 2003).

After growing for years in rivers, estuaries and coastal waters, eels return to their origin to spawn and subsequently die. Temperate eels mostly have well-defined spawning and recruitment seasons, long larval durations and panmictic populations. The recruitment period in tropical eels differs depending on species and/or site. *A. marmorata*, *A. bicolor bicolor* and *A. mossambica* were present 5 months in the year in Réunion Island, Mascarene Islands, western Indian Ocean (Robinet et al. 2003). In contrast, tropical eels of *A. celebesensis*, *A. marmorata* and *A. bicolor pacifica* had year-round recruitment to their habitats in North Sulawesi, Indonesia, western Pacific Ocean (Arai et al. 1999, 2001; Sugeha et al. 2001). The spawning period of tropical eels is still unknown. Additionally, several tropical eel species are composed of multiple populations, defined by their use of different spawning areas (Arai et al. 2003, 2014; Minegishi et al. 2008). These findings suggest that characteristics of both life history and ecology differ between temperate and tropical eels.

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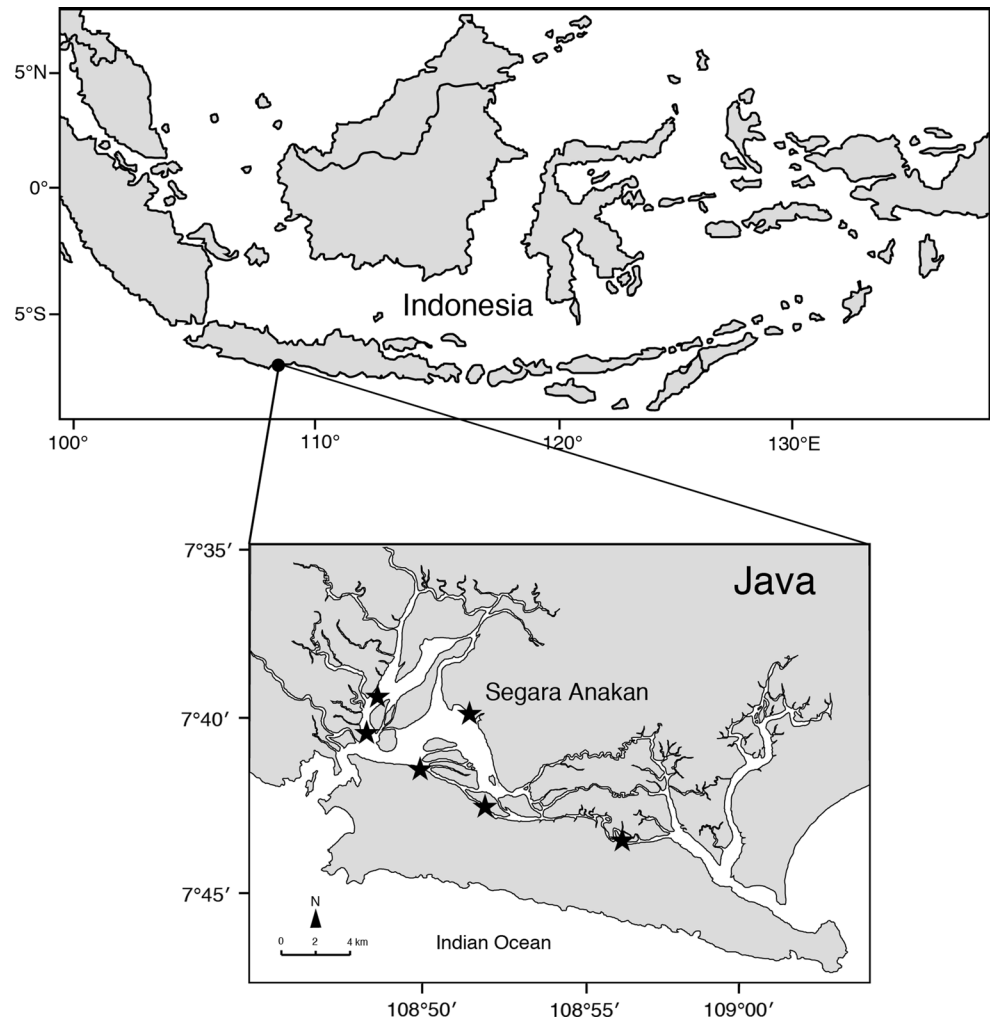
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Fig. 1 Map showing the location of Segara Anakan, central Java of Indonesia. The approximate locations where eels were collected in Segara Anakan are shown with *small stars*



Ecological studies examining the migration and early life history of anguillid eels have been conducted mainly on temperate eels due to the high demand for these species, particularly European and Japanese eels, as a fisheries resource. The spawning location and season have been described for temperate eels *Anguilla anguilla* and *A. rostrata* (Schmidt 1922) and *A. japonica* (Tsukamoto 1992), and there have been several studies investigating the early life history and recruitment of these species. The spawning migration of temperate eels generally takes place during autumn months, between August and December (Kotake et al. 2007; Acou et al. 2008; Verreault et al. 2012) in the Northern Hemisphere and between February and May in the Southern Hemisphere (Todd 1981). Further, favorable environmental conditions to start their migration are also well studied. The exact timing depends on both internal (morphological, endocrine and metabolic) and environmental factors operating across a wide range of time scales, from day (e.g., precipitation, wind, atmospheric depression and sunshine hours) to month (e.g., lunar phase) and even season (e.g., water flow and level, water temperature, turbidity and photoperiod) (Acou

et al. 2008; Breukelaar et al. 2009). However, no study to date has confirmed the timing and season of seaward migration for spawning in tropical eel species.

In this study, we aimed to understand the spawning timing and migration in a tropical catadromous eel *Anguilla bicolor bicolor* using monthly captured specimens. The timing of maturation and seaward migration for spawning was examined by investigating fluctuations in both the gonadosomatic index and gonadal histology. This study provides the first evidence of year-round spawning in a catadromous eel species.

Materials and methods

A total of 438 *Anguilla bicolor bicolor* were collected in Segara Anakan, central Java Island, Indonesia (approximately 7°35'–7°48'S, 108°46'–109°03'E), from December 2007 to July 2009 (Fig. 1). All eels were purchased, postmortem, from local fishermen. To examine temporal variability of maturation, eels were collected in December 2007 and year-round from May 2008 to July 2009. The eels were collected using

angling and bamboo traps at night. The Segara Anakan consists of a lagoon isolated from the Indian Ocean by Nusakambangan Island (Fig. 1) and comprises a mangrove forest area, a settlement area, and rice field areas. This lagoon is the only major estuarine-mangrove area in the central part of Java. This area experiences two seasons, the rainy or wet season, ranging from November to April, and the dry season, ranging from July to September. This equatorial climate experiences an average high monthly temperature between 28.0 °C (dry season) and 31.3 °C (wet season) (White et al. 1989).

After eels were collected, biological parameters, such as total length and body weight, were measured. The sex of each eel was determined by visual and histological observations of the gonads. Whole gonad weight was measured, and gonadosomatic index (GSI; percent relative gonad weight to body weight) was subsequently calculated.

Fragments from the middle region of one gonad were fixed in formalin for histological analysis. Tissue fragments were prepared for resin and routine paraffin embedding. Resin blocks were processed routinely, and paraffin blocks were sectioned at 5 µm and stained with hematoxylin-eosin for histological observation.

Results

Eels were observed to occur throughout the year, all eels were identified as *Anguilla bicolor bicolor*, and all eels were determined to be female (i.e., no male was collected).

The GSI ranged from 0.0 to 4.5, and the values were highly variable between months (Fig. 2a). Gonadal histology by transverse sections revealed that oocyte characteristics of each maturation stage also varied within months from Stage I (primary stage) to V (final stage for spawning) (Fig. 2b). During Stage I at the early stage of oogenesis, the gonads were composed of primary germ cells, oogonia, lamellae and primary oocytes. During Stage II, immature cells developed with primary oocytes and few oil droplets. The early maturation stage of Stage III exhibited oocytes with cortical alveoli and oil droplets in the cytoplasm (Fig. 3). The early vitellogenic stage of Stage IV exhibited vitellogenic oocytes, nucleus, yolk granules and central yolk platelets, and the oocyte diameter increased drastically and the cytoplasm filled with yolk granules (Fig. 3). During the final stage of maturation, Stage V, midvitellogenic oocytes developed in final preparation for spawning; disintegrated nuclei were observed and whole nuclei were no longer visible (Fig. 3). Eels in more developed stages, such as Stages IV and V, were found every month, although the frequency differed among months (Fig. 2b). These findings suggest that *A. bicolor bicolor* carries out seaward migration for spawning throughout the year.

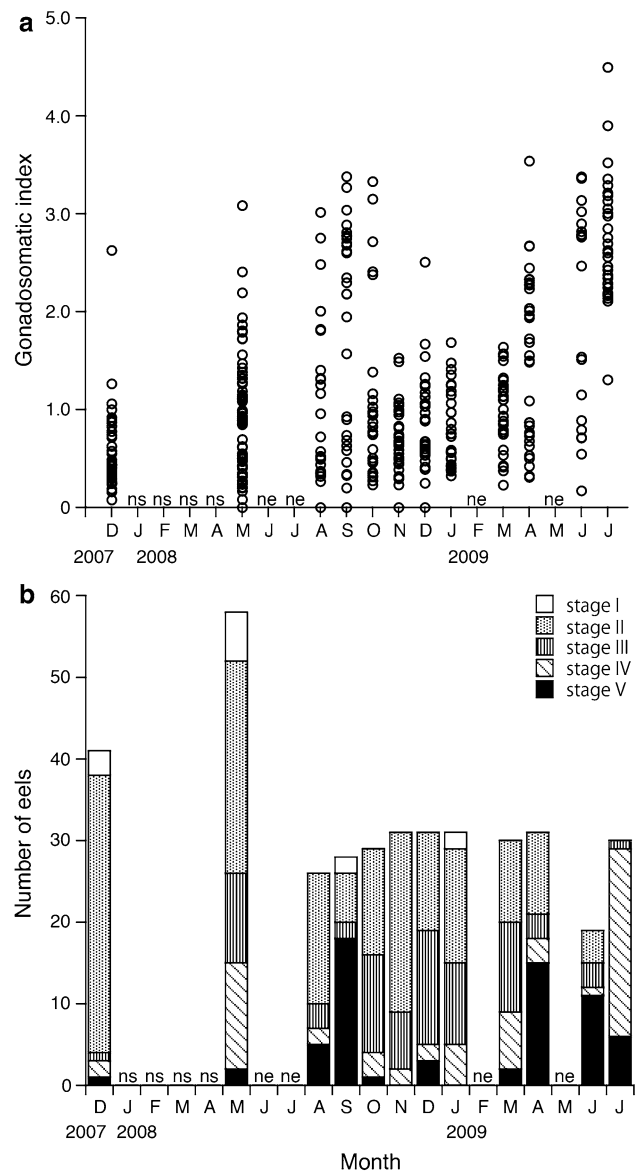


Fig. 2 Monthly fluctuation of gonadosomatic index (a) and maturation stage (b) in a tropical catadromous eel *Anguilla bicolor bicolor* collected in Segara Anakan, central Java of Indonesia, between December 2007 and July 2009. *ns* no study for eel sampling was conducted that month, *ne* study was conducted, but no eels were collected

The mean GSI values of each stage of I, II, III, IV and V were 0.40, 0.55, 1.03, 1.93 and 2.47, respectively (Table 1). Significant differences were found GSI values between the each stage in all combinations (Fig. 4) (Kruskal–Wallis test, $p < 0.05$ – 0.0001). A significant positive correlation was found between maturation stage and GSI value (Fig. 4) (Fisher's Z-Transformation, $p < 0.0001$).

Fig. 3 Gonadal histology of *Anguilla bicolor bicolor* collected in Segara Anakan, central Java of Indonesia, between December 2007 and July 2009. Stages correspond to a growth phase (Stages I and II), a pre-migrant phase (III) and two migrating phases (IV and V) in accordance with Durif et al. (2005). Each stage was modified according to Todd (1974) and Lokman et al. (1998). Each scale bar is 100 μ m

Stage I
early stage of oogenesis

Stage II
immature cells developed with primary oocytes

Stage III
oocytes with cortical alveoli

Stage IV
vitellogenic oocytes, nucleus, yolk granules and central yolk platelets

Stage V
midvitellogenic oocytes

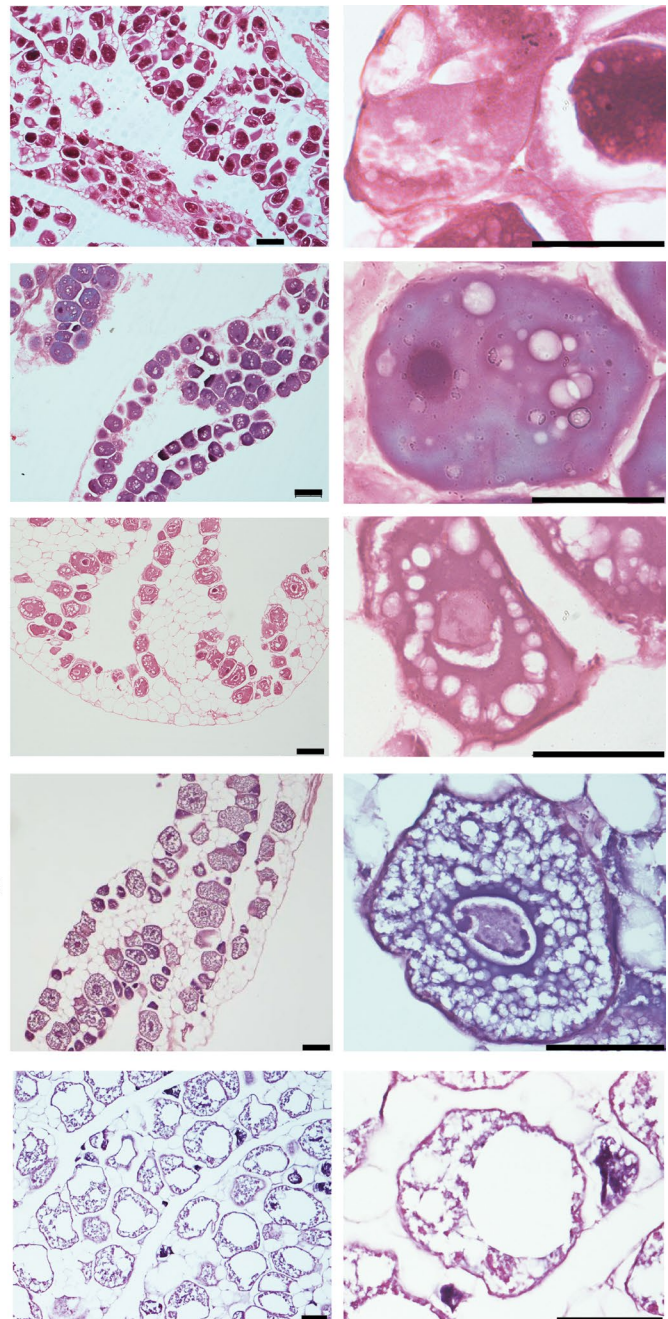


Table 1 Gonadosomatic index (GSI) in a tropical catadromous eel *Anguilla bicolor bicolor*

Stage	GSI	
	Mean \pm SD	Range
I	0.40 \pm 0.19	0.08–0.75
II	0.55 \pm 0.28	0.08–1.7
III	1.0 \pm 0.33	0.39–2.4
IV	1.9 \pm 0.76	0.71–3.9
V	2.5 \pm 0.65	1.1–4.5

Discussion

This study is the first description of a spawning period of a tropical eel that extends throughout the year, as revealed by gonadal development and histology. Until recently, considerably less research has examined the spawning migration of tropical eels in comparison with that of temperate eel species. The findings described in this report indicate that tropical eels have life history characteristics that differ markedly from those of temperate eels. Temperate anguillid

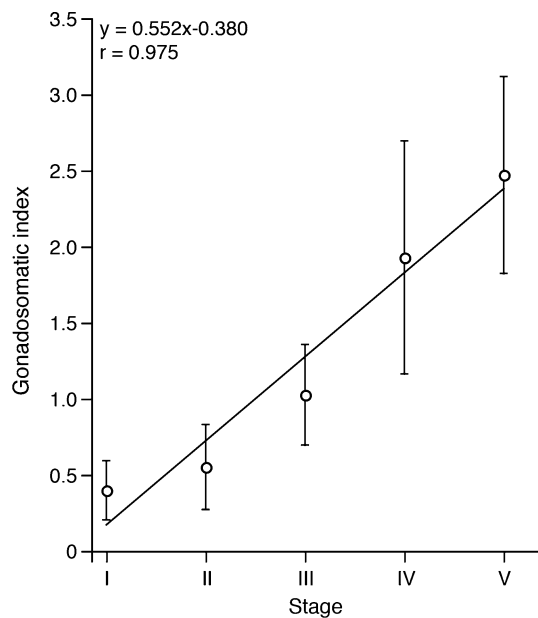


Fig. 4 Relationship between gonadosomatic index and maturation stage for a tropical eel *Anguilla bicolor bicolor* that was collected in Segara Anakan, central Java of Indonesia, between December 2007 and July 2009

species make their spawning migration as silver eels during the fall and winter. Silver eels of the Japanese eel *Anguilla japonica* (Matsui 1957, 1972), the American eel *A. rostrata* (Verreault et al. 2012), the European eel *A. anguilla* (Tesch 2003; Vøllestad et al. 1986; Durif et al. 2005, 2009), and the Australian and New Zealand eels *A. australis* and *A. dieffenbachii* (Todd 1981; Sloane 1984; Jellyman 1987) all descend freshwater rivers and streams in the fall and enter saltwater, where they begin their marine migration to the open ocean spawning areas. The difference in spawning season duration and timing between tropical and temperate species could be attributed to differences in the seaward migration seasons of maturing adult eels. Analyses of otolith microstructure showed that the age at recruitment of tropical eels was constant throughout the year in *A. celebesensis*, *A. marmorata* and *A. bicolor pacifica* (Arai et al. 2001). The year-round spawning migration of tropical species and constant larval growth extend the period of recruitment to estuarine habitats to year-round in tropical eels. The spawning seasons of tropical eels were found to extend throughout the year by back calculation of otolith daily increment in *A. celebesensis*, *A. marmorata* and *A. bicolor pacifica* in North Sulawesi of Indonesia (Arai et al. 2001) which is close to central Java Island of Indonesia. Additionally, the present results support a year-round spawning period, as evidenced by the monthly occurrence of matured eels in *A. bicolor bicolor*. However, the recruitment period in tropical eels differs depending on species and/or site. *A.*

marmorata, *A. bicolor bicolor* and *A. mossambica* were present 5 months in the year in Réunion Island of western Indian Ocean (Robinet et al. 2003). The periods of spawning in tropical eel recruits to Réunion Island were not year-round (Robinet et al. 2003). Therefore, further study is needed to accumulate more information regarding spawning period in tropical eels.

There remains only limited knowledge of the level of maturation of tropical eels as they begin their spawning migration. Downstream migrating female European eels typically have GSI values of >1.2 (Vøllestad and Jonsson 1986; Durif et al. 2005) but lower than 3.0 (Svedäng and Wickström 1997; Durif et al. 2005). The level of female maturation of Japanese eels as they begin their spawning migration in coastal areas ranged from 1.0 to 4.0 in GSI, and the levels were similar to those collected in the East China Sea and other Japanese coastal areas (Sasai et al. 2001; Kotake et al. 2007). GSI values of *Anguilla celebesensis* collected in the Poso Lake of Indonesia were greater than 9.0 (11.2 in maximum value) and in the range of GSI values characteristic of spawning conditions in *A. japonica* and *A. marmorata*, despite being collected inland in a freshwater lake far from the ocean (Arai 2014). GSI values of *A. marmorata* collected from same area were also high; all GSI values were greater than 4.0 (6.4 in maximum value). In the present study, GSI value of *A. bicolor bicolor* increased with advancing of maturation stage (Fig. 4), and it exhibited 2.5 on average with 4.5 at the maximum in Stage V (Table 1) even though the eels were collected from coastal lagoons and not from the open ocean. Thus, these results indicate that tropical eels in the silver phase at the onset of seaward spawning migration have comparatively higher maximum GSI values than those of temperate eels.

Downstream migration of tropical eels has not been properly investigated. Factors affecting downstream migration of temperate silver eels are highly variable both within localities and years and between localities (Vøllestad et al. 1994). However, it is widely recognized that water discharge greatly influences the downstream migration of European (Frost 1950; Lowe 1952; Deelder 1954, 1970; Vøllestad et al. 1986; Jonsson 1991), American (Smith and Saunders 1955) and New Zealand (Todd 1981; Boubée et al. 2001) silver eels. A long-term effect of water temperature on downstream migration based on 10 years of continuous observation in a Nordic river suggested that downstream migration started earlier in years with a lower mean temperature between 9 and 11 °C (Vøllestad et al. 1986). Water temperature might act as a trigger for downstream migration. However, these triggers might not apply to *Anguilla bicolor bicolor* in central Java Island of Indonesia. Water discharge is quite different between the dry and wet season in central Java Island of Indonesia because the average monthly rainfall ranges

from 100 to 180 mm during the dry season and from 180 to 400 mm during the wet season (White et al. 1989). However, downstream migration of *A. bicolor bicolor* was found to extend throughout the year (Fig. 2). Furthermore, the water temperature does not fluctuate dramatically throughout the year between 27.5 °C (dry season) and 35.0 °C (wet season) (White et al. 1989). This constant climate in central Java Island, Indonesia, might induce non-seasonal seaward migration for spawning in a tropical eel *A. bicolor bicolor*.

The unique year-round spawning ecology and behavior of a tropical eel *Anguilla bicolor bicolor* may facilitate mating between adult eels from different year classes (cohorts) or from different habitats. Such flexibility in the life history of *A. bicolor bicolor* might help to maintain the population.

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