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Fecundity of the tropical catadromous eels *Anguilla bicolor bicolor*, *A. bengalensis bengalensis* and *A. marmorata*

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Abstract Maturation is one of the most important ontogenetic transitions in an individual's life. However, the reproductive ecology of the tropical anguillid eel genus *Anguilla* at the onset of oceanic spawning migration is poorly understood. To understand the reproductive ecology, the fecundity of the tropical eels *Anguilla bicolor bicolor*, *A. bengalensis bengalensis* and *A. marmorata* was examined using advanced migrating silver eels (Stage IV and V). A close linear relationship was found between total length and fecundity in *A. bengalensis bengalensis*. The fecundities of *A. bicolor bicolor* (0.55 to 4.96 × 10^6), *A. bengalensis bengalensis* (0.33–1.72 × 10^6) and *A. marmorata* (0.99 × 10^6) were within the range of those observed in temperate eels.

Keywords *Anguilla* · Fecundity · Reproductive ecology · Silver eel · Tropical eel

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Introduction

Research on reproductive strategies and the assessment of fecundity are fundamental topics in the study of the biology and population dynamics of fish species (Hunter et al. 1992). Understanding reproductive behaviour of fish is not only important for elucidating the basic biology of the fishes but it can also help in their management and conservation. Within a given species, fecundity varies as a result of different adaptations to the environment (Witthames et al. 1995; MacNamara et al. 2014, 2016).

The freshwater eels of genus *Anguilla* are mysterious animals, and despite the huge number of scientific studies conducted with eels, crucial aspects of their biology remain a mystery. No one has yet observed eel spawning in nature, as spawning areas are located in the open ocean. Of the 19 species of freshwater eels reported worldwide, 13 are from tropical regions (Ege 1939; Arai 2016). Of the latter, seven species occur in the western Pacific around Indonesia and Malaysia (Ege 1939; Castle and Williamson 1974; Arai et al. 1999).

Freshwater eels are the most important of the eel families from a conservation standpoint because they have a unique catadromous life history and are used as food resources. Recently, however, juvenile abundance has declined dramatically: by 99% for the European eel and by 80% for the Japanese eel (Dekker 2003). The catch of the wild European eel juveniles has linearly decreased from over 200 t in the early 1960s to 20 t currently. Likewise, in Japanese eels, a shortage of fry

has become a serious problem for fish culture in recent years (Arai 2014a).

Species other than the Japanese eel, including several tropical species, seem to have replaced the European eel on the international market (Arai 2014b). The tropical eels *Anguilla bicolor bicolor* and *A. bicolor pacifica* are the most targeted species for eel trading (Pethiyagoda 1991; Arai 2014b). It is suggested that tropical eels are following the same trends in decline as European and Japanese eels (Arai 2014b). However, fewer studies are available on tropical eels than temperate eels. The lack of knowledge about basic life history, stock and population size of tropical eels could preclude us from preventing further serious declines.

Fecundity estimates are available for temperate eels such as the European eel *A. anguilla* (MacNamara and McCarthy 2012; MacNamara et al. 2014, 2016), the American eel *A. rostrata* (Wenner and Musick 1974; Barbin and McCleave 1997; Tremblay 2009), *A. japonica* (Matsui 1952) and the New Zealand eels *A. australis* and *A. dieffenbachii* (Todd 1981). However, such information on fecundity is not available for tropical eels.

In the present study, we examined the fecundity of three tropical eels, the Indonesian short fin eel *A. bicolor bicolor*, the Indian mottled eel *A. bengalensis bengalensis* and the giant mottled eel *A. marmorata,* in the wild silver stage. Our aim was to obtain baseline information on the reproductive biology of tropical anguillid eels. Fecundity was also compared with that of temperate eels to understand how the reproductive characteristics of temperate and tropical eels compare.

Materials and methods

A total of 435 tropical eels were collected by hook and line and fish traps on Penang Island of Peninsular Malaysia (between 4°45′N and 5°10′N and between 100°11′E and 100^{0}57′E) between February 2014 and Jun 2015 (Fig. 1). Water temperature and salinity levels were measured infrequently and ranged from 23.6 °C (upstream area) to 35.7 °C (downstream area) and from 0.01 ppt (upstream area) to 32.9 ppt (downstream area), respectively (Arai and Abdul Kadir 2017). For each examined specimen, the maturation stage was determined based on their histology (Arai and Abdul Kadir 2017). The maturation stage was defined following Arai and Abdul Kadir (2017). Among 435 specimens, 23 specimens were advanced silver stage female eels (either stage IV or V) and were further examined to determine fecundity. A total of 15 *Anguilla bicolor bicolor*, seven *A. bengalensis bengalensis* and one *A. marmorata* were used in this study. In 23 specimens, a total of 20 external morphometric characteristics were measured following the methods of Ege (1939) and Arai (2014c, 2016), where after molecular genetic analyses were applied for species identification of each specimen (Abdul Kadir et al. 2015, 2017; Arai et al. 2015; Arai and Wong 2016). These eels were subjected to identification using mitochondrial cytochrome oxidase subunit I (COI) and 16S ribosomal RNA (16S rRNA) sequence analysis from dorsal finclips.

Both sides of the gonads were dissected. For each specimen, total gonad weight was measured, and the gonadosomatic index (relative gonad weight to body weight) was subsequently calculated. In each specimen, 1 g of gonad was placed into each of the five containers. Two percent acetic acid was added to each container, which was shaken for 30 min and the samples were shaken for 7 days. All eggs were separated from the gonadal tissue and were examined between 7 and 9 days after they had been digested in 2% acetic acid (Barbin and McCleave 1997; Macnamara et al. 2014). Before counting the number of eggs, each container was diluted to 100 ml with 15% NaCl as an isotonic solution (Tremblay 2009). The 100 ml dilution was added to a glass container, which sat for a few minutes until it became a uniform suspension solution (Tremblay 2009). Thereafter, 0.1 ml of the sample was taken from the middle part of the container and was placed in a haematocytometer grid (LaborOptik). The vittellogenic eggs (Arai and Abdul Kadir 2017) were counted at 40× magnification, and the counts were repeated three times on the same 0.1 ml sample for each container. The number of eggs in the sub-sample was counted using the formula (D x N)/(S x K), where D is the dilution factor, N is the number of cells counted, S is the number of squares counted on the haematocytometer grid and K is the volume for each small square. The fecundity of each specimen was determined using the following formula: Fecundity = (number of eggs in the sub-sample x gonad weight)/the weight of the sub-sample. The fecundity of each specimen was examined in five replicates, and the average was calculated.

Differences in morphological parameters such as TL and BW at maturation timing and fecundities between species were analysed using the Mann–Whitney *U*-test

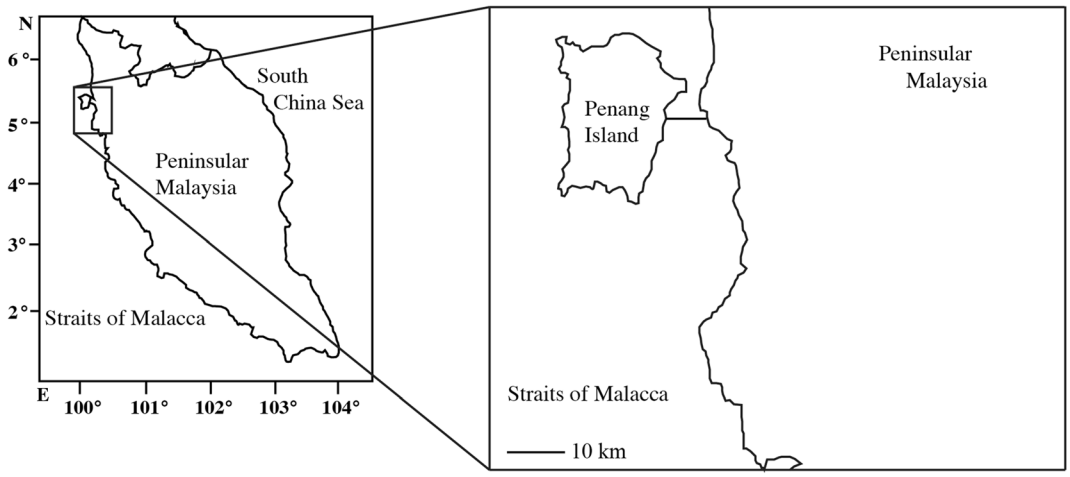

Fig. 1 Eel sampling area in Penang Island of Peninsular Malaysia, Malaysia

due to the small sample size. The significance of the correlation coefficient and the regression slope between total length and fecundity were determined using a t-test (Sokal and Rohlf 1995).

Results

The average total length (TL) and body weight (BW) of the migrating silver eels of *A. bicolor bicolor*, *A. bengalensis bengalensis* and *A. marmorata* were 651 mm, 1048 mm and 904 mm and 593 g, 2889 g and 2335 g, respectively (Table 1). These sizes were within the normal range for silver-phase individuals of these species (Arai and Abdul Kadir 2017). The morphological parameters such as TL and BW at maturation timing were significantly different between *A. bicolor bicolor* and *A. bengalensis bengalensis* ($p < 0.005$–0.0005). We could not include *A. marmorata* because only one sample was available. The results suggest that the size at the time of downstream migration differs among species.

The average fecundities of *A. bicolor bicolor*, *A. bengalensis bengalensis* and *A. marmorata* were 1.84×10^6, 0.98×10^6 and 0.99×10^6, respectively (Table 1). No significant difference in fecundity between *A. bicolor bicolor* and *A. bengalensis bengalensis* was found ($p > 0.05$). The relative fecundities (eggs kg^{-1}) of *A. bicolor bicolor*, *A. bengalensis bengalensis* and *A. marmorata* was estimated to be 3.12×10^6, 0.34×10^6 and 0.42×10^6, respectively (Table 1).

A close linear relationship was found between TL and fecundity in *A. bengalensis bengalensis* ($p < 0.0001$), while no relationship was found between these parameters in *A. bicolor bicolor* ($p > 0.05$) (Fig. 2).

Discussion

This study is the first to estimate the fecundity of three species of tropical eels found in the Western Pacific around Indonesia and Malaysia. Although more than 400 eels were captured from the wild, only 23 were in the migrating silver stage just before the downstream migration to the open ocean. Fecundity estimates from a number of other anguillid eel species were obtained from the literature (Table 2). Among the fecundity estimates, *A. japonica* had the highest fecundity compared among all eels (Table 2). However, *A. rostrata* had a highly variable fecundity (0.5 to 22.0 million eggs) depending on geographical location and time (Table 2). The fecundity of the tropical eels *Anguilla bicolor bicolor*, *A. bengalensis bengalensis* and *A. marmorata* was in the range and overlapped with those observed in temperate eels, including *A. anguilla*, *A. rostrata*, *A. australis* and *A. dieffenbachii* (Table 2). Thus, the fecundity of the anguillid eel might be generally similar among tropical and temperate species.

Tropical eels have spawning ecological characteristics that differ markedly from those of temperate eels (Arai 2014d). Analyses of the otolith microstructure have shown that the age at recruitment (to fresh waters) of tropical eels was constant throughout the year (Arai

Table 1 Fecundity, gonadosomatic indexes (GSIs) and morphological characteristics of three species tropical anguillid eels

Species	Number of specimens	Fecundity (millions)		GSI		Total length (mm)		Body weight (g)		Relative fecundity
		range	mean ± SD	range	mean ± SD	range	mean ± SD	range	mean ± SD	(millions of eggs kg-1)
A. bicolor bicolor	15	0.55–4.96	1.84 ± 1.18	1.57–4.17	2.59 ± 0.66	567–810	651 ± 63.0	308–1267	593 ± 267	3.12
A. bengalensis bengalensis	7	0.33–1.72	0.98 ± 0.62	1.17–2.06	1.67 ± 0.31	899–1295	1048 ± 140	1579–5100	2889 ± 1365	0.34
A. marmorata	1	0.99		2.64		904		2335		0.42

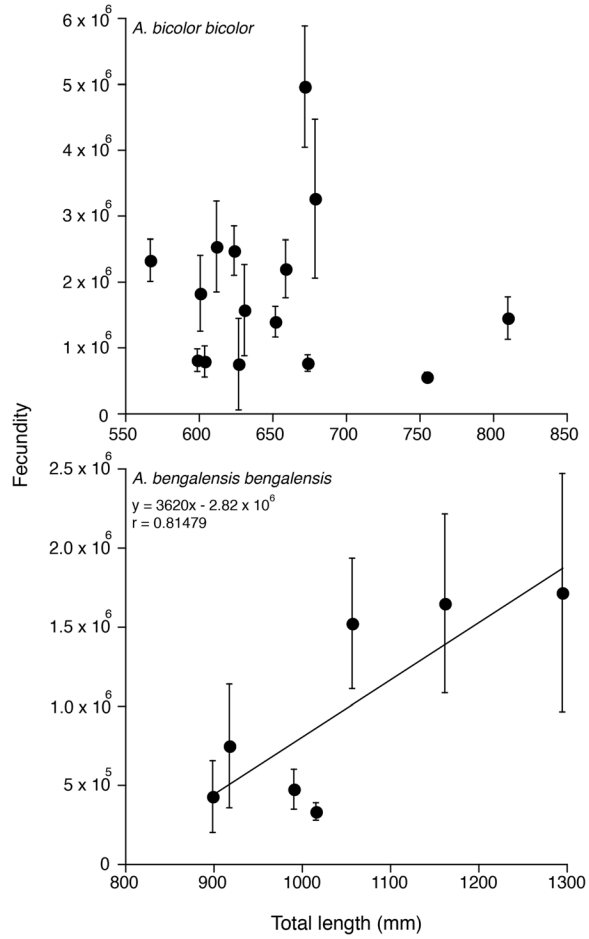

Fig. 2 Relationships between total length and fecundity of *Anguilla bicolor bicolor* (top) and *A. bengalensis bengalensis* (bottom). Error bars represent standard deviation from the mean

et al. 2001). The year-round spawning migration and a constant larval growth throughout the year extends the period of estuarine habitat recruitment to year-round in tropical eels. Recently, Arai et al. (2016) and Arai and Abdul Kadir (2017) also found a year-round spawning period, as evidenced by monthly occurrence of matured eels in *A. bicolor bicolor*. This non-seasonal spawning ecology is notably different from that of temperate eels in which silver eels make their spawning migration during the fall and winter. Judging from the similarity in fecundity between tropical and temperate eels and the year-round spawning ecology in the tropical eels, the biomass of the tropical eels might be higher than the temperate eels.

There is a widespread trend that fecundity in fish is positively correlated with fish size (length and weight)

Table 2 Fecundities of anguillid eels collected in the wild

Species	Range (millions of eggs)	Relative fecundity (millions of eggs kg-1)	Reference
Temperate eels			
A. anguilla	0.6–8.0	3.6	MacNamara and McCarthy (2012)
	3.3–11	3.9	MacNamara et al. (2014)
	1.0–6.3	2.4	Dębowska et al. (2015)
	0.8–3.6	3.9–4.4	MacNamara et al. (2016)
A. rostrata	0.5–2.6	3.8*	Wenner and Musick (1974)
	1.7–20.7	8.1*	Barbin and McCleave (1997)
	3.4–22.0	6.5–10.0	Tremblay (2009)
A. japonica	7.2–12.7	n/a	Matsui (1952)
A. australis	0.5–3.1	1.9	Todd (1981)
A. dieffenbachii	1.1–20.8	2	Todd (1981)
Tropical eels			
A. bicolor bicolor	0.6–5.0	3.1	This study
A. bengalensis bengalensis	0.3–1.7	0.34	This study
A. marmorata	1.0	0.42	This study

n/a: not applicable

*: estimated by MacNamara and McCarthy (2012)

(Peters 1983). The fecundity of the temperate eels *A. anguilla* (MacNamara and McCarthy 2012; MacNamara et al. 2014, 2016; Dębowska et al. 2015), *A. rostrata* (Wenner and Musick 1974; Barbin and McCleave 1997; Tremblay 2009), *A. australis* and *A. dieffenbachii* (Todd 1981) increases with increasing body size. In the present study, the fecundity of *A. bengalensis bengalensis* also was size-related, although no such relationship was observed between fecundity and size in *A. bicolor bicolor* probably due to the limited sample size. Fecundity is affected by many factors, such as body size, age, life history strategy, food supply and temperature. The present study provided the first fecundity estimates for three tropical eel species. Further studies regarding fecundity estimation are needed to understand the size-related fecundity in tropical eels.

During the migration to the oceanic spawning grounds, eels do not feed but instead rely upon stores of body fat to sustain them during the spawning migration (Tesch 1977; Pankhurst and Sorensen 1984). Barbin and McCleave (1997) hypothesized that the increased migration distances in eels from the northern parts of their range would result in decreased fecundity with latitude in *A. rostrata*. European eels are triggered to migrate toward the spawning area when their percentage of body lipid exceeds a certain threshold (Larsson et al. 1990), which is presumably the amount necessary to accomplish the migration and the development of the eggs (Barbin and McCleave 1997). Recently, Arai (2014d) found that, in contrast to the migrations made by the Atlantic and Japanese eels (approximately 3000 km–8000 km), the tropical eel *A. celebesensis* originally migrated only short distances of less than 100 km to local spawning areas adjacent to their freshwater growth habitats. Although spawning grounds have not been thoroughly investigated yet in *A. bicolor bicolor*, *A. bengalensis bengalensis* and *A. marmorata*, the migration distances of eels might not have an effect on interspecies variations of fecundity because the present study found few differences in fecundity between tropical and temperate eels.

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