Open Access

Age, Growth, and Sex Ratios of the Giant Mottled eel, *Anguilla marmorata*, in Freshwater Habitats Near Its Northern Geographic Limit: A Comparison to Tropical Regions

Ryoshiro Wakiya^{1,*}, Hikaru Itakura², and Kenzo Kaifu³

¹Research and Development Initiative, Chuo University, 1-13-27 Kasuga, Bunkyo-ku, Tokyo 112-8551, Japan. *Correspondence: Tel: +818056758725. E-mail: ryoshiro.wakiya@gmail.com

²Graduate School of Sciences, Kobe University, 1-1 Rokkoudaichou, Nadaku, Kobe, Hyogo 657-8501 Japan, E-mail: itakurahikaru@gmail.com ³Faculty of Law, Chuo University, 742-1 Higashinakano, Hachioji-shi, Tokyo 192-0393 Japan, E-mail: kaifu@tamacc.chuo-u.ac.jp

Received 19 March 2019 / Accepted 18 September 2019 / Published 12 November 2019 Communicated by Benny K.K. Chan

To understand the latitudinal difference in the basic ecology of the giant mottled eel *Anguilla marmorata*, we measured its age, growth, and sex ratios in freshwater areas of Amami-Oshima Island, Japan (28.223°N–28.332°N and 129.329°E–129.439°E), near the northern geographic limit of its range and compared these biological characteristics with those observed in the tropical regions of Indonesia. A total of 109 *A. marmorata* were captured from three rivers on Amami-Oshima Island. The total length (TL) and age of sampled individuals varied across an order of magnitude (TL range: 119–1320 mm, mean: 385.5 ± 172.6; age range: 3–30 years, mean: 12.8 ± 4.9 years). Neither TL nor age differed among rivers. Male *A. marmorata* accounted for 88.5% of sexually differentiated individuals, which it contrary to previous results for males living in Indonesian watersheds where males were only found in small rivers and areas close to estuaries. Moreover, we found no males larger than 700 mm in TL and few males that were older than 20 years. The growth rates of male *A. marmorata* were significantly lower than those of females, and growth rates of sexually undifferentiated fish were significantly lower than those of males. The mean growth rate of all individuals was 25.9 ± 6.6 mm/y, which is considerably lower than what has been found at lower latitudes, suggesting that growth differences occur along a latitudinal cline.

Key words: Age, Anguilla marmorata, Freshwater, Growth rate, Sex ratio.

BACKGROUND

Species in the genus *Anguilla* consist of catadromous fish that contain leaf-like leptocephalus larvae that migrate from open oceans to freshwater and estuarine habitats (Han et al. 2016; Chen et al. 2018; Higuchi et al. 2018). After metamorphosing into yellow eels, the fish spend most of their life in continental waters until they begin their downstream migration toward spawning grounds in open ocean. The anguillid eel consists of 19 species and subspecies distributed

globally, with the exception of polar regions and the west coast of North and South America (Ege 1939; Aoyama 2003; Watanabe et al. 2004). The giant mottled eel *A. marmorata* is the most broadly distributed species in the genus, with a range from the south-east African coast to Asia and Polynesia (Ege 1939; Marquet and Galzin 1991; Marquet 1996). It is also one of the largest species in the genus, growing up to 2 m and 21 kg (Castle 1984). Despite this prominent ecology, to date, little basic biological information is available on the giant mottled eel, likely because compared with the Japanese

Citation: Wakiya R, Itakura H, Kaifu K. 2019. Age, growth, and sex ratios of the giant mottled eel, *Anguilla marmorata*, in freshwater habitats near its northern geographic limit: a comparison to tropical regions. Zool Stud **58**:34. doi:10.6620/ZS.2019.58-34.

eel *A. japonica* (Lee and Lou 2019) and the European eel *A. anguilla*, the mottled eel is not a major species in the aquaculture industry.

Previous studies on the ecology of A. marmorata have focused on its population structure (Ishikawa et al. 2004; Minegishi et al. 2008; Watanabe et al. 2008 2009; Gagnaire et al. 2009 2011; Donovan et al. 2012), spawning and recruitment (Arai et al. 1999a b 2001a b 2002a b; Sugeha et al. 2001; Robinet et al. 2003a b c 2007 2008; Kuroki et al. 2005 2009; Aoyama et al. 2007; Réveillac et al. 2008; Han et al. 2012; Leander et al. 2012; Aoyama et al. 2018). These studies found that there are multiple spawning populations in A. marmorata. Moreover, one of their spawning areas is located in the North Equatorial Current region of the western North Pacific Ocean, which is also the spawning area of the Japanese eel A. japonica. In addition, there has been some work on its migratory history, habitat use (Shiao et al. 2003; Chino and Arai 2010; Lin et al. 2012; Arai et al. 2013), and sexual maturation (Robinet et al. 2003c; Hagihara et al. 2012 2018a). To understand the ecology of this widespread species, it is important to examine its basic biological characteristics in not only the central part of its distribution in the tropics but also in the marginal areas in the subtropical and temperate zones. However, its biological characteristics have been studied only in tropical areas at low latitude (Hagihara et al. 2012 2018a b c).

Some studies reported that there are negative correlations between growth rates and latitudes in *A. anguilla* (Vøllestad 1992) and *A. rostrata* (Oliveira 1999; Jessop 2010). The wide latitudinal distribution range of *A. marmorata* suggests differences in the basic ecology of their life histories, such as age and growth, between low and high latitudes that cover different climatic zones. To understand the changes in the basic ecology of *A. marmorata* induced by differences in latitudes, we investigated the age, growth, and sex ratio of this species in freshwater habitats near the northern geographic limit of its range, and compared the results with those obtained in the lower latitude areas.

MATERIALS AND METHODS

Study area and sampling

This study was conducted in the Yakugachi, Sumiyo, and Kawauchi Rivers on Amami-Oshima Island, Kagoshima Prefecture, Japan (Fig. 1). This island is located approximately 380 km south of the southern tip of the Kyushu mainland and 250 km north of Okinawa. The average annual temperature of this island (1981–2010) is 21.6°C, which is 3.0°C higher than that of the mainland of Kagoshima, and the annual fluctuation is small. The annual precipitation is 2837.7 mm, with the monthly precipitation exceeding 150 mm even in winters; moreover, it is a particularly rainy part of Japan (statistics from Japan Meteorological Agency). The island is thought to be near the northern distribution limit of *A. marmorata* (Jacoby and Gollock 2014).

The lengths of the Yakugachi, Sumiyo, and Kawauchi Rivers are 15.1 km, 16.8 km, and 10.6 km, respectively. They are largest rivers on this island. Nine sampling sites were set up across freshwater areas of each river (27 sites in total). All sampling sites were less than 20 m long and 15 m wide. To avoid sampling bias among study sites, sampling was conducted using a consistent protocol across all sampling sites. Anguillid eels were collected using an electroshocker (LR-20B; Smith-Root, Inc., Vancouver, WA, USA) and hand nets during the daytime, from August to September 2015. Captured fish were exposed to a subzero temperature of approximately -20°C to euthanize them as per previous studies using low temperature anesthesia on eels (Barbin 1998; Han et al. 2003; Fukuda et al. 2009; Itakura et al. 2015) to satisfy both national and institutional standards. Fish were maintained under this low temperature anesthesia until they died and were kept frozen until internal and external measurements were made.

Morphological observation

Each specimen was identified morphologically according to Watanabe et al. (2004). In this study, 5 *A. japonica* were captured in the Yakugachi River, and they were excluded from data analysis. The total length (TL) was measured to the nearest 1 mm. Sex was categorized as male, female, or undifferentiated (UD) based on visual inspection of gonadal morphology.

Age determination

The extracted sagittal otoliths were embedded in epoxy resin (EpoFix Kit, Struers; www.struers.com) and ground with a grinding machine (Discoplan-TS, Struers) to expose the core along the anterior-posterior direction in the frontal plane. Samples were polished further as described by ICES (2009). The otoliths were etched using 1% HCl for 1 min and stained with 1% Toluidine blue for 1–2 h to define the rings of the otolith (ICES 2009). Age was determined by counting the number of annual rings on the otoliths, according to Hagihara et al. (2018a). The first distinct transition check outside the nucleus (elver mark), which is thought to be associated with inshore recruitment to low salinity areas, was assigned age = 0.



Fig. 1. Maps of the study area on Amami-Oshima Island, Kagoshima Prefecture, Japan. (a) Location of the Amami-Oshima Island in Japan. (b) Location of the study area on Amami-Oshima Island. (c) Map of the study area. Open circles indicate sampling sites for *Anguilla marmorata*.

Statistical analysis

All statistical analyses were performed with the R statistical package 3.3.2. To compare TL and age of A. marmorata between sex and rivers, we used a generalized linear model (GLM), which included TL and age as response variables (Gaussian distribution and log-link function) and sex and river as explanatory variables. To evaluate the relationship between growth rate and sex, age, and rivers, we used a GLM that included growth rate as the response variable (gamma distribution and log-link function) and sex, age, and river as the explanatory variables. When the effect of sex was statistically significant, we conducted pairwise multiple comparisons using the Tukey-Kramer method (glht in the package multcomp). To assess the relationship between TL and sex differentiation, we also used a GLM that included sex-differentiated (i.e., male or female) or UD as the response variable (binomial distribution and logit-link function) and TL as the explanatory variable.

RESULTS

A total of 109 Anguilla marmorata were captured in the three rivers on Amami-Oshima Island: 36 individuals from the Yakugachi River, 24 individuals from the Sumiyo River, and 49 individuals from the Kawauchi River. The total length of captured A. marmorata ranged from 119 to 1320 mm across rivers, with mean \pm SD = 385.5 \pm 172.6 mm. Age ranged from 3 to 30 years old after recruitment, with mean \pm SD = 12.8 \pm 4.9 years old (Fig. 2; Table 1).

Male A. marmorata were more abundant in our

samples than females (female: 5.5%; male: 42.2%; UD: 52.3%), with 88.5% of the sexually differentiated individuals being male (Fig. 3B). This trend was consistent across all three rivers. The percent of females, males, and UD in our samples for the Yakugachi River were 0.0%, 41.7%, and 58.3%, respectively. For the Sumiyo River, percentages were 12.5%, 50.0%, and 37.5%, respectively, and for the Kawauchi River, they were 6.1%, 38.8%, and 55.1%, respectively (Table 1).

Because both TL and age were not significantly different among rivers (TL: $\chi^2 = 4.37$, *d.f.* = 2, p > 0.05; age: $\chi^2 = 1.43$, *d.f.* = 2, p > 0.05), data obtained from the three rivers were combined. After combining, TL was significantly different among sex classifications (GLM: $\chi^2 = 164.34$, *d.f.* = 2, p < 0.001), with the TL of female *A. marmorata* being significantly larger than that of male *A. marmorata* (Tukey multiple comparisons test, p < 0.001). The ages also differed significantly among sex classifications (GLM: $\chi^2 = 112.61$, *d.f.* = 2, p < 0.001), with females being older than males of UD (Tukey multiple comparisons test, p < 0.001).

The probability of sex-differentiated *A. marmorata* was positively related to TL (GLM: coefficient \pm SE = 0.024 \pm 0.005, *z* = 4.96, *p* < 0.01). We found that 50% of individuals were sexually differentiated at 374 mm TL and 95% were differentiated when they attained a length of 494 mm.

The growth rate of *A. marmorata* was $25.9 \pm 6.6 \text{ mm/y}$ (mean \pm SD), and they were significantly differentiated by sex (GLM: $\chi^2 = 26.45$, *d.f.* = 2, p < 0.001); the growth rate of male *A. marmorata* was significantly slower than in females, whereas the growth rates of UD were significantly slower than those of others (Tukey multiple comparisons test, p < 0.001) (Fig. 3A). In addition, the mean growth rate decreased

Table 1. Total length (TL), age, and growth rate of *A. marmorata* analyzed from each river in the Amami-Oshima Island, Japan. UD = sexually undifferentiated

River name	Sex	п	LT (mm)		Age (years)		Growth rate (mm year ⁻¹)	
			$Mean \pm SD$	Range	$Mean \pm SD$	Range	$Mean \pm SD$	Range
Yakugachi	Female	0	_	-	-	-	_	-
	Male	15	439.1 ± 102.0	280-615	15.8 ± 2.7	11-20	$24.7\pm5.5a$	17.7-35.3
	UD	21	249.9 ± 63.0	148-381	8.5 ± 2.7	4–14	$23.9\pm4.1a$	15.9-32.9
Sumiyo	Female	3	862.0 ± 420.6	493-1320	20.3 ± 8.4	15-30	$39.0 \pm \mathbf{8.3a}$	29.5-45.2
	Male	12	451.2 ± 87.2	355-655	14.4 ± 2.2	10-18	$28.6 \pm \mathbf{8.5a}$	17.9-50.2
	UD	9	349.4 ± 96.8	200-521	12.7 ± 3.5	7-18	$24.0\pm5.8a$	17.2-36.1
Kawauchi	Female	3	738.7 ± 43.9	688–766	23.0 ± 4.0	19–27	$30.6\pm 6.2 ab$	26.4-37.7
	Male	19	499.6 ± 89.9	342-655	16.0 ± 3.4	11–23	$28.7\pm6.0a$	19.6-40.4
	UD	27	271.5 ± 84.1	119-435	9.4 ± 3.3	3-16	$23.7\pm 6.2b$	15.8-47.3
Total	Female	6	800.3 ± 275.9	493-1320	21.7 ± 6.1	15-30	$34.8\pm8.0a$	26 4-45.2
	Male	46	467.2 ± 95.4	280-655	15.5 ± 2.9	10-23	$27.4\pm6.7b$	17.7-50.2
	UD	57	275.8 ± 84.7	119–521	9.6 ± 3.4	3–18	$23.8\pm5.3\text{c}$	15.8-47.3



Fig. 2. Frequency distributions of total length and age of *A. marmorata* collected from three rivers in Amami-Oshima Island, Japan. UD = sexually undifferentiated.

page 6 of 10

significantly with age ($\chi^2 = 9.13$, *d.f.* = 1, *p* < 0.01), but they were not different among rivers (*p* > 0.05).

DISCUSSION

Growth rate

As expected, the estimated growth rates of *A.* marmorata in this study (Female: $34.8 \pm 8.0 \text{ mm/y}$, Male: $27.4 \pm 6.7 \text{ mm/y}$, UD: $23.8 \pm 5.3 \text{ mm/y}$) were approximately one third lower than those of the same species from Sulawesi Island, Indonesia (Female: $94.2 \pm 18.9 \text{ mm/y}$, Male: $82.2 \pm 12.2 \text{ mm/y}$, UD: $74.1 \pm 17.1 \text{ mm/y}$; Hagihara et al. 2018a) (Fig. 3A). A potential explanation for this pattern is that growth rates vary along a latitudinal cline, a results of differences in annual water temperatures and productivity of rivers. In fact, because Sulawesi Island is located on and near the equator, the average annual temperature is around 27° C (JICA 2008), much higher than 21.6° C on Amami-Oshima Island, although there are seasonal temperature differences. In particular, since the Central Sulawesi



Fig. 3. Difference between Amami-Oshima Island and Sulawesi Island (Hagihara et al. 2018a) in growth rate and sex ratio of A. marmorata. A, Mean growth rate and SD of female, male, and UD in Amami-Oshima Island and Sulawesi Island. B, Sex ratio of sexually differentiated individuals in Amami-Oshima Island and Sulawesi Island.

region, which was the main study area of Hagihara et al. (2018a), has an annual precipitation of 2500 mm or more, similar to Amami-Oshima Island. The difference in growth rates between the two regions is considered to be due to the difference in temperature. Some studies also show that there is a negative correlation between the latitude of habitats during the growth stage and growth rate in anguillid eels (A. anguilla: Vøllestad 1992; A. rostrata: Oliveira 1999; Jessop 2010). Physiological activity tends to increase with higher water temperatures at lower latitudes (Clarke 2003), suggesting that productivity may be higher at lower latitudes than in temperate rivers (Gross et al. 1988). This might explain the differences in growth rate of A. marmorata at lower latitudes compared with results in this study from the northern geographic limit.

On the other hand, the mean growth rate of female A. marmorata in this study was greater than that of males, consistent with previous reports on the same species inhabiting lower latitudes (Hagihara et al. 2018a), as well as other anguillid species (A. anguilla: Panfili et al. 1994; Svedäng 1999; A. rostrata: Oliveira 1999; Oliveira and McCleave 2002; Jessop et al. 2004; A. japonica: Tzeng et al. 2003). Furthermore, the mean growth rate of A. marmorata with undetermined sexual anatomy was lower than that in the other groups, indicating that growth rates are higher following sexual differentiation than during the few years after recruitment but before sexual differentiation. Another possible explanation for these findings is that individuals with lower growth rates in the UD group may not survive until sexual differentiation, indicating that only individuals with relatively greater growth survive long enough to differentiate into male or female.

Sex ratio

Although more than half of the collected *A. marmorata* were sexually undifferentiated, males accounted for 88.5% of the sexually differentiated individuals we sampled. This pattern differs substantially from what was found in multiple watersheds in the Central Sulawesi Island, Indonesia, where 22.8% of collected specimens were male (Hagihara et al. 2018a) (Fig. 3B).

This may be due to differences in river size rather than differences in latitude because Hagihara et al. (2018a b) found that the proportion of males was negatively correlated with increasing distance between the river mouth and the sampling area, and that high proportions of males were also observed at low latitudes. In a study by Hagihara et al. (2018a), the length of Poso River is approximately 100 km, whereas the length of each river conducted in this study is less than 20 km, which may explain the higher ratio of males. Consistent with this conclusion, studies in other anguillid eels also reported higher ratios of females at sites located at greater distances from the river mouth (*A. anguilla*: Sinha and Jones 1967; *A. rostrata*: Oliveira 1999).

Size at sex differentiation

Size at the time of sexual differentiation appears to differ among anguillid eel species. Based on the visual inspection of gonadal morphology, the results of GLM showed that by, the time the TL of Anguilla marmorata reached 494 mm, 95% of individuals were sexually differentiated (Fig. 4). In a study that visually inspected gonadal morphology of 413 individuals of A. *japonica*, 95% of fish were sexually differentiated at a TL of 406 mm (Ministry of Environment 2015 2016). A. marmorata becomes sexually differentiated at a body size relatively larger than the temperate species, A. japonica. Moreover, Oliveira and McCleave (2000) reported that the sexual differentiation of A. rostrata was complete at a TL of 270 mm based on histological analysis. Although the method for sex determination used in Oliveira and McCleave (2000) was slightly different from that used in the present study, the results of these studies suggest that A. marmorata is sexually differentiated at a larger body size than A. rostrata. Because data on the size at which sexual differentiation



Fig. 4. Probability of sexual differentiation related to total length of *A. marmorata* collected from three rivers on Amami-Oshima Island, Japan. The black lines and shaded areas indicate the regression lines and 95% confidential intervals, respectively.

occurs in *A. marmorata* in different regions is limited, the latitudinal variation in the size at sexual differentiation should be investigated in future studies.

Size and age at downstream migration of male

The male *A. marmorata* collected in this study were less than 700 mm long, and the majority of them were less than 20 years old (range 10–23 years old). This finding, at least in terms of TL, is consistent with the results of previous studies, in which downstream migrating male *A. marmorata* were captured on Réunion Island, France (708 mm and 10 years; Robinet et al. 2003c) and Sulawesi Island, Indonesia (683 mm and 7 years; Hagihara et al. 2018a). This pattern suggests that many of the *A. marmorata* collected on Amami-Oshima Island may represent individuals migrating downstream. Given that downstream migration of anguillid eels is thought to be related to size rather than age (Aoyama and Miller 2003), downstream migration of *A. marmorata* may also be related to body size.

The biggest male *A. marmorata* captured on Amami-Oshima Island was 655 mm, which was smaller than 5 of the 6 females, including the largest individual (1320 mm). There have been many reports of other anguillid eels that also found females grew to larger sizes than males (*A. anguilla*: Vøllestad 1992; Poole and Reynolds 1996; *A. rostrata*: Oliveira 1999; Jessop 1987; *A. japonica*: Lin and Tzeng 2009). Therefore, the results from this study may represent a general pattern of sexual dimorphism in anguillid eels.

CONCLUSIONS

The present study is the first to provide information on the size, age, sex ratio, and growth rate of Anguilla marmorata from Amami-Oshima Island, Japan, which is close to the northern limit of its distribution, and to compare these biological characteristics with those previously obtained at a lower latitude. A. marmorata collected in Japan showed slower growth rate and longer longevity in males than those collected in Indonesia. Despite the widespread distribution of A. *marmorata*, regions where studies on this species were conducted are still limited. Further studies should investigate the basic biological characteristics of A. marmorata from different regions, which will provide a more comprehensive understanding of the ecology of this species, as well as anguillid eels in general. This type of comparison of life history studies based on latitudes is especially important to provide baseline data for predicting changes in the ecology of angullid eels under the effects of global climatic changes.

Acknowledgments: We thank T. Shiosaki for the useful information of the rivers and the fisheries cooperative association of Naze in Amami-Oshima Island for storing our samples. We also thank K. Yonekubo and T. Yoshinaga for the otolith preparation and helpful comments on earlier drafts of the manuscript.

Authors' contributions: All authors conceived the ideas, designed the methodology, and collected the data; RW analyzed the otolith samples; RW and HI analyzed the data; RW led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests: The authors declare no competing interests.

Availability of data and materials: Relevant data are not currently available because we are drafting another manuscript using some parts of these data.

Consent for publication: Not applicable.

Ethics approval consent to participate: Captured fish were exposed to a subzero temperature of approximately -20°C to euthanize them, as per previous studies using low temperature anesthesia on eels, to satisfy both national and institutional standards.

REFERENCES

- Aoyama J. 2003. Origin and evolution of the freshwater eels, genus Anguilla. In: Aida K, Tsukamoto K, Yamauchi K (eds) Eel Biology. Springer-Verlag, Tokyo.
- Aoyama J, Miller MJ. 2003. The silver eel. *In*: Aida K, Tsukamoto K, Yamauchi K (eds) Eel Biology. Springer-Verlag, Tokyo.
- Aoyama J, Wouthuyzen S, Miller MJ, Minegishi Y, Kuroki M, Suharti SR, Kawakami T, Sumardiharga KO, Tsukamoto K. 2007. Distribution of leptocephali of the freshwater eels, genus *Anguilla*, in the waters off west Sumatra in the Indian Ocean. Environ Biol Fish 80:445–452. doi:10.1007/s10641-006-9143-z.
- Aoyama J, Wouthuyzen S, Miller MJ, Sugeha HY, Kuroki M, Watanabe S, Syahailatua A, Tantu FY, Hagihara S, Triyanto, Otake T, Tsukamoto K. 2018. Reproductive ecology and biodiversity of freshwater eels around Sulawesi Island Indonesia. Zool Stud 57:30. doi:10.6620/ZS.2018.57-30.
- Arai T, Aoyama J, Ishikawa S, Miller MJ, Otake T, Inagaki T, Tsukamoto K. 2001b. Early life history of tropical *Anguilla* leptocephali in the western Pacific Ocean. Mar Biol **138(5)**:887– 895. doi:10.1007/s002270000532.
- Arai T, Aoyama J, Limbong D, Tsukamoto K. 1999b. Species composition and inshore migration of the tropical eels *Anguilla* spp. recruiting to the estuary of the Poigar River, Sulawesi Island. Mar Ecol Prog Ser 188:299–303. doi:10.3354/ meps188299.
- Arai T, Chino N, Le DQ. 2013. Migration and habitat use of the

tropical eels *Anguilla marmorata* and *A. bicolor pacifica* in Vietnam. Aquat Ecol **47(1):57–65**. doi:10.1007/s10452-012-9424-x.

- Arai T, Limbong D, Otake T, Tsukamoto K. 1999a. Metamorphosis and inshore migration of tropical eels *Anguilla* spp. in the Indo-Pacific. Mar Ecol Prog Ser **182**:283–293.
- Arai T, Limbong D, Otake T, Tsukamoto K. 2001a. Recruitment mechanisms of tropical eels *Anguilla* spp. and implications for the evolution of oceanic migration in the genus *Anguilla*. Mar Ecol Prog Ser 216:253–264. doi:10.3354/meps216253.
- Arai T, Marui M, Miller MJ, Tsukamoto K. 2002a. Growth history and inshore migration of the tropical eel, *Anguilla marmorata*, in the Pacific. Mar Biol **140**:309–316. doi:10.1007/s002270100699.
- Arai T, Marui M, Otake T, Tsukamoto K. 2002b. Inshore migration of a tropical eel, *Anguilla marmorata*, from Taiwanese and Japanese coasts. Fish Sci 68:152–157. doi:10.1046/j.1444-2906.2002.00401.x.
- Barbin GP. 1998. The role of olfaction in homing and estuarine migratory behavior of yellow phase American eels. Can J Fish Aquat Sci **55**:564–575.
- Castle PHJ. 1984. Anguillidae. *In*: Daget J, Grosse JP, Thys van den Audenaerde DFE (eds) Checklist of the freshwater fishes of Africa (CLOFFA), vol. 1. ORSTOM, Bruxelles, pp. 34–37.
- Chen SC, Chang CR, Han YS. 2018. Seaward migration routes of Indigenous Eels, Anguilla japonica, A. marmorata, and A. bicolor pacifica, via satellite tags. Zool Stud 57:21. doi:10.6620/ ZS.2018.57-21.
- Chino N, Arai T. 2010. Migratory history of the giant mottled eel (Anguilla marmorata) in the Bonin Islands of Japan. Ecol Freshw Fish 19:19–25. doi:10.1111/j.1600-0633.2009.00385.x.
- Clarke A. 2003. Costs and consequences of evolutionary temperature adaptation. Trends Ecol Evol **18:**573–581. doi:10.1016/j.tree.2003.08.007.
- Donovan S, Pezold F, Chen Y, Lynch B. 2012. Phylogeography of Anguilla marmorata (Teleostei: Anguilliformes) from the eastern Caroline Islands. Ichthyol Res 59:70–76. doi:10.1007/s10228-011-0245-z.
- Ege V. 1939. A revision of the genus *Anguilla* Shaw: a systematic, phylogenetic and geographical study. Dana Report, vol. 16. Oxford University Press, London, pp. 1–256.
- Fukuda N, Kuroki M, Shinoda A, Yamada Y, Okamura A, Aoyama J, Tsukamoto K. 2009. Influence of water temperature and feeding regime on otolith growth in *Anguilla japonica* glass eels and elvers: does otolith growth cease at low temperatures? J Fish Biol 74:1915–1933. doi:10.1111/j.1095-8649.2009.02287.x.
- Gagnaire PA, Minegishi Y, Aoyama J, Reveillac E, Robinet T, Bosc P, Tsukamoto K, Feunteun E, Berrebi P. 2009. Ocean currents drive secondary contact between *Anguilla marmorata* populations in the Indian Ocean. Mar Ecol Prog Ser **379:**267–278. doi:10.3354/ meps07895.
- Gagnaire PA, Minegishi Y, Zenboudji S, Valade P, Aoyama J, Berrebi P. 2011. Within-population structure highlighted by differential introgression across semipermeable barriers to gene flow in *Anguilla marmorata*. Evolution **65**:3413–3427. doi:10.1111/j.1558-5646.2011.01404.x.
- Gross MR, Coleman RM, McDowall RM. 1988. Aquatic of diadromous fish migration. Science 239:1291–1293.
- Hagihara S, Aoyama J, Limbong D, Tsukamoto K. 2012. Morphological and physiological changes of female tropical eels, *Anguilla celebesensis* and *Anguilla marmorata*, in relation to downstream migration. J Fish Biol 81:408–426. doi:10.1111/ j.1095-8649.2012.03332.x.
- Hagihara S, Aoyama J, Limbong D, Tsukamoto K. 2018a. Age and growth of migrating tropical eels, *Anguilla celebesensis* and

Anguilla marmorata. J Fish Biol **92:**1526–1544. doi:10.1111/ jfb.13608.

- Hagihara S, Aoyama J, Limbong D, Tsukamoto K. 2018b. Interspecific and sexual differences in riverine distribution of tropical eels *Anguilla* spp. J Fish Biol **93:**21–29. doi:10.1111/jfb.13666.
- Hagihara S, Aoyama J, Limbong D, Tsukamoto K. 2018c. Interspecific difference in downstream migratory season between two tropical eels, *Anguilla celebesensis* and *Anguilla marmorata*. J Fish Biol 93:729–732. doi:10.1111/jfb.13750.
- Han YS, Liao IC, Tzeng WN, Huang YS, Yu JYL. 2003. Serum estradiol-17β and testosterone levels during silvering in wild Japanese eel Anguilla japonica. Comp Biochem Physiol Biochem Mol Biol 136:913–920. doi:10.1016/j.cbpc.2003.09.002.
- Han YS, Wu CR, Iizuka Y. 2016. Batch-like Arrival Waves of Glass Eels of *Anguilla japonica* in Offshore Waters of Taiwan. Zool Stud 55:36. doi:10.6620/ZS.2016.55-36.
- Han YS, Yambot AV, Zhang H, Hung CL. 2012. Sympatric spawning but allopatric distribution of *Anguilla japonica* and *Anguilla marmorata*: temperature-and oceanic current-dependent sieving. PLoS ONE 7(6):e37484. doi:10.1371/journal.pone.0037484.
- Higuchi T, Watanabe S, Manabe R, Kaku T, Okamura A, Yamada Y, Miller MJ, Tsukamoto K. 2018. Tracking *Anguilla japonica* silver eels along the West Marina Ridge using pop-up archival transmitting tags. Zool Stud **57:**24. doi:10.6620/ZS.2018.57-24.
- ICES. 2009. Workshop on Age Reading of European and American Eel (WKAREA), Bordeaux, 20–24 April 2009.
- Ishikawa S, Tsukamoto K, Nishida M. 2004. Genetic evidence for multiple geographic populations of the giant mottled eel *Anguilla marmorata* in the Pacific and Indian oceans. Ichthyol Res 51(4):343–353. doi:10.1007/s10228-004-0241-7.
- Itakura H, Kaino T, Miyake Y, Kitagawa T, Kimura S. 2015. Feeding, condition, and abundance of Japanese eels from natural and revetment habitats in the Tone River, Japan. Environ Biol Fishes 98(8):1871–1888. doi:10.1007/s10641-015-0404-6.
- Jacoby D, Gollock M. 2014. Anguilla marmorata. The IUCN Red List of Threatened Species2014. doi:10.2305/IUCN.UK.2014-1. RLTS.T166189A45832585.en.
- Japan International Cooperation Agency Makassar Field Office (JICA). 2008. Sulawesi Island Development Framework and Strategy.
- Jessop BM. 1987. Migrating American eels in Nova Scotia. Trans Am Fish Soc **116**:161–170.
- Jessop BM. 2010. Geographic effects on American eel (*Anguilla rostrata*) life history characteristics and strategies. Can J Fish Aquat Sci **67(2)**:326–346. doi:10.1139/F09-189.
- Jessop BM, Shiao JC, Iizuka Y, Tzeng WN. 2004. Variation in the annual growth, by sex and migratory history, of silver American eels *Anguilla rostrata*. Mar Ecol Prog Ser **272**:231–244. doi:10.3354/meps272231.
- Kuroki M, Aoyama J, Miller MJ, Arai T, Sugeha HY, Minagawa G, Wouthuyzen S, Tsukamoto K. 2005. Correspondence between otolith microstructural changes and early life history events in *Anguilla marmorata* leptocephali and glass eels. Coast Mar Sci 29:154–161.
- Kuroki M, Aoyama J, Miller MJ, Yoshinaga T, Shinoda A, Hagihara S, Tsukamoto K. 2009. Sympatric spawning of *Anguilla marmorata* and *Anguilla japonica* in the western North Pacific Ocean. J Fish Biol 74:1853–1865. doi:10.1111/j.1095-8649.2009.02299.x.
- Leander NJ, Shen KN, Chen RT, Tzeng WN. 2012. Species Composition and Seasonal Occurrence of Recruiting Glass Eels (*Anguilla* spp.) in the Hsiukuluan River, Eastern Taiwan. Zool Stud 51:59–71.
- Lee SC, Lou SW. 2019. Androgenic modulation in the primary ovarian growth of the Japanese eel, *Anguilla japonica*. Zool Stud **58:**2. doi:10.6620/ZS.2019.58-02.

- Lin YJ, Jessop BM, Weyl OL, Iizuka Y, Lin SH, Tzeng WN, Sun CL. 2012. Regional variation in otolith Sr: Ca ratios of African longfinned eel Anguilla mossambica and mottled eel Anguilla marmorata: a challenge to the classic tool for reconstructing migratory histories of fishes. J Fish Biol 81:427–441. doi:10.1111/j.1095-8649.2012.03357.x.
- Lin YJ, Tzeng WN. 2009. Validation of annulus in otolith and estimation of growth rate for Japanese eel *Anguilla japonica* in tropical southern Taiwan. Environ Biol Fishes **84:**79–87. doi:10.1007/s10641-008-9391-1.
- Marquet G. 1996. The freshwater eels (Anguillidae) of New Caledonia: taxonomy and distribution. Vie Milieu **46**:65–71.
- Marquet G, Galzin R. 1991. The eels of French Polynesia: taxonomy, distribution and biomass. Mer 29:8–17.
- Minegishi Y, Aoyama J, Tsukamoto K. 2008. Multiple population structure of the giant mottled eel, *Anguilla marmorata*. Mol Ecol 17:3109–3122. doi:10.1111/j.1365-294X.2008.03822.x.
- Ministry of Environment. 2015. Report of Consultation Business for Conservation Policy of the Japanese Eel.
- Ministry of Environment. 2016. Report of Consultation Business for Conservation Policy of the Japanese Eel.
- Oliveira K. 1999. Life history characteristics and strategies of the American eel, *Anguilla rostrata*. Can J Fish Aquat Sci 56:795– 802.
- Oliveira K, McCleave JD. 2000. Variation in population and life history traits of the American eel, *Anguilla rostrata*, in four rivers in Maine. Environ Biol Fishes 59:141–151. doi:10.1023/ A:1007631108201.
- Oliveira K, McCleave JD. 2002. Sexually different growth histories of the American eel in four rivers in Maine. Trans Am Fish Soc 131:203–211. doi:10.1577/1548-8659(2002)131<0203:SDGHO T>2.0.CO;2.
- Panfili J, Ximénès MC, Crivelli AJ. 1994. Sources of variation in growth of the European eel (*Anguilla anguilla*) estimated from otoliths. Can J Fish Aquat Sci 51:506–515.
- Poole WR, Reynolds JD. 1996. Growth rate and age at migration of *Anguilla anguilla*. J Fish Biol **48**:633–642.
- Réveillac E, Feunteun E, Berrebi P, Gagnaire PA, Lecomte-Finiger R, Bosc P, Robinet T. 2008. *Anguilla marmorata* larval migration plasticity as revealed by otolith microstructural analysis. Can J Fish Aquat Sci 65:2127–2137. doi:10.1139/F08-122.
- Robinet T, Feunteun E, Keith P, Marquet G, Olivier JM, Réveillac E, Valade P. 2007. Eel community structure, fluvial recruitment of *Anguilla marmorata* and indication for a weak local production of spawners from rivers of Réunion and Mauritius islands. Environ Biol Fishes **78:**93–105. doi:10.1007/s10641-006-9042-3.
- Robinet T, Guyet S, Marquet G, Mounaix B, Olivier JM, Tsukamoto K, Valade P, Feunteun E. 2003b. Elver invasion, population structure and growth of marbled eels *Anguilla marmorata* in a tropical river on Réunion Island in the Indian Ocean. Environ Biol Fishes 68:339–348. doi:10.1023/B:EBFI.0000005761.51686.f7.
- Robinet T, Lecomte-Finiger R, Escoubeyrou K, Feunteun E. 2003a. Tropical eels *Anguilla* spp. recruiting to Réunion Island in the Indian Ocean: taxonomy, patterns of recruitment and early life histories. Mar Ecol Prog Ser 259:263–272. doi:10.3354/ meps259263.
- Robinet T, Réveillac E, Kuroki M, Aoyama J, Tsukamoto K, Rabenevanana MW, Valade P, Gagnaire PA, Berrebi P, Feunteun E. 2008. New clues for freshwater eels (*Anguilla* spp.) migration routes to eastern Madagascar and surrounding islands. Mar Biol 154:453–463. doi:10.1007/s00227-008-0938-7.
- Robinet T, Sbaihi M, Guyet S, Mounaix B, Dufour S, Feunteun E. 2003c. Advanced sexual maturation before marine migration

of Anguilla bicolor bicolor and Anguilla marmorata at Réunion Island. J Fish Biol **63:**538–542. doi:10.1046/j.1095-8649.2003.00165.x.

- Shiao JC, Iizuka Y, Chang CW, Tzeng WN. 2003. Disparities in habitat use and migratory behavior between tropical eel Anguilla marmorata and temperate eel A. japonica in four Taiwanese rivers. Mar Ecol Prog Ser 261:233–242. doi:10.3354/ meps261233.
- Sinha VRP, Jones JW. 1967. On the age and growth of the freshwater eel (*Anguilla anguilla*). J Zool **153:**99–117.
- Sugeha HY, Shinoda A, Marui M, Arai T, Tsukamoto K. 2001. Validation of otolith daily increments in the tropical eel Anguilla marmorata. Mar Ecol Prog Ser 220:291–294. doi:10.3354/ meps220291.
- Svedäng H. 1999. Vital population statistics of the exploited eel stock on the Swedish west coast. Fish Res 40:251–165.
- Tzeng WN, Iizuka Y, Shiao JC, Yamada Y, Oka HP. 2003.

Identification and growth rates comparison of divergent migratory contingents of Japanese eel (*Anguilla japonica*). Aquaculture **216:**77–86. doi:10.1016/S0044-8486(02)00053-4.

- Vøllestad LA. 1992. Geographic variation in age and length at metamorphosis of maturing European eel: environmental effects and phenotypic plasticity. J Anim Ecol **61**:41–48.
- Watanabe S, Miller MJ, Aoyama J, Ishikawa S, Feunteun E, Tsukamoto K. 2008. Evidence of population structure in the giant mottled eel, *Anguilla marmorata*, using total number of vertebrae. Copeia **2008**:680–688. doi:10.1643/CG-07-080.
- Watanabe S, Aoyama J, Tsukamoto K. 2004. Reexamination of Ege's (1939) use of taxonomic characters of the genus *Anguilla*. B Mar Sci 74:337–351.
- Watanabe S, Miller MJ, Aoyama J, Tsukamoto K. 2009. Morphological and meristic evaluation of the population structure of *Anguilla marmorata* across its range. J Fish Biol 74:2069–2093. doi:10.1111/j.1095-8649.2009.02297.x.