

# Influence of host habitat on the occurrence of gill monogeneans *Pseudodactylogyrus* spp. on wild Japanese eels *Anguilla japonica*

Hirotaka Katahira<sup>1,\*</sup>, Kouki Mizuno<sup>1,2</sup>, Tetsuya Umino<sup>1</sup>, Kazuya Nagasawa<sup>1</sup>

<sup>1</sup>Graduate School of Biosphere Science, Hiroshima University, 1-4-4 Kagamiyama, Higashi-Hiroshima, Hiroshima, 739-8528 Japan

<sup>2</sup>Ehime Prefectural Uwajima Fishery High School, 1-2-20 Meirin, Uwajima, Ehime, 798-0068 Japan

**ABSTRACT:** With technological improvements in otolith microchemical analysis, the flexible use of habitat from coastal marine to fresh waters has been discovered in Japanese eels *Anguilla japonica*. We examined the occurrence of 3 congeneric gill monogeneans — *Pseudodactylogyrus anguillae*, *P. bini*, and *P. kamegaitii*— on wild Japanese eels, in relation to the host's flexibility. From April 2008 to October 2009, 114 eels were collected from a brackish-water cove and 2 rivers flowing into the cove in Ehime Prefecture, western Japan. Based on otolith microchemical analysis, the eels were discriminated according to the following 4 types of habitat use: freshwater residents (Type I), individuals utilizing low-salinity habitats (Type II), downstream habitat-shifters (Type III), and cove residents (Type IV). *P. anguillae* occurred mainly on Type I and II eels, while *P. bini* was primarily found on Type I eels. In contrast, *P. kamegaitii* occurred mainly on Type III and IV eels. Thus, we conclude that species composition and infection levels of *Pseudodactylogyrus* spp. clearly differed with habitat-use patterns of Japanese eels. Also, since *P. anguillae* was scarcely found on either Type III or IV eels, this study suggests that previous identifications of monogeneans collected from European brackish-water localities as *P. anguillae* may require verification.

**KEY WORDS:** Parasites · Monogenea · *Pseudodactylogyrus* · Japanese eels · *Anguilla japonica* · Otolith · Sr:Ca ratio

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## INTRODUCTION

Anguillid eels have a unique life history, characterized by migration to distant, oceanic spawning grounds after spending a significant part of their lifetime in freshwater habitats (McDowall 1988). This dynamic migratory loop is termed 'catadromy' (McDowall 1988), and eels have long attracted a great deal of biological interest as representatives of economically important catadromous fish species (reviewed by Tesch 2003). Recently, a microchemical analysis, based on the ratio of strontium (Sr) to cal-

cium (Ca) in the otoliths of both European (*Anguilla anguilla* [Linnaeus, 1758]) and Japanese eels (*Anguilla japonica* Temminck & Schlegel, 1846), indicated that some individuals within a population are found in fresh waters, while others reside primarily in high-salinity habitats during their growth phase, without migrating into freshwater environments (Tsukamoto et al. 1998). In addition, various patterns of habitat usage, such as brackish-water residency (e.g. Tsukamoto & Arai 2001) and several types of habitat shifting (e.g. Kaifu et al. 2010), have been reported for European and Japanese eels, as well as further

\*Email: paraparparasites@gmail.com

anguillid species (see Chino & Arai 2010), by using the same microchemical technique.

Thus, eels should currently be considered a facultative catadromous fish with various habitat-use patterns called ecophenotypes (Tsukamoto et al. 2002). However, these ecophenotypes of eels have largely been ignored in parasitological investigations. As far as we know, there has only been a single study to date, by Han et al. (2009), dealing with the relationship between facultative catadromy and parasite infection. Based on otolith microchemical analysis, they detected the infection of a freshwater nematode, *Anguillicoloides crassus* (Kuwahara, Niimi & Itagaki, 1974) Moravec & Taraschewski, 1988 (Anguillicolidae), in multiple habitat-shifters that move between marine-coastal and freshwater habitats, within a population of Japanese eels in Taiwan, and concluded that facultative catadromy potentially contributes to the dispersion of this pathogenic nematode. This flexible behavior appears to be closely involved in parasite ecology from individual to community levels. Even if a parasite is well studied under natural conditions, it may need to be reinvestigated with regard to its host's flexibility.

*Pseudodactylogyrus anguillae* (Yin & Sproston, 1948) Gusev, 1965; *P. bini* (Kikuchi, 1929) Gusev, 1965; and *P. kamegaili* Iwashita, Hirata & Ogawa, 2002 (Ancyrocephalidae: Pseudodactylogyrinae) are monogenean gill parasites of Japanese eels (Ogawa & Egusa 1976, Iwashita et al. 2002). Both *P. anguillae* and *P. bini* are commonly found on Japanese eels (Ogawa & Egusa 1976, Nagasawa et al. 2007), with a history of spreading to European eels via commercial transportation of live Japanese eels from Asia to Europe (Buchmann et al. 1987b, Hayward et al. 2001, Kania et al. 2010). These monogeneans feed exclusively on the mucus and epithelial tissues of the gill surface (Buchmann et al. 1987a), but their hamuli can inflict damage to and deformation of host tissues (Chan & Wu 1984, Buchmann et al. 1987a,b). Economic losses to eel farms have sometimes been reported, due to stress induced by heavy infections with these parasites (reviewed by Kōie 1991, Kennedy 2007). Since European eels are especially prone to being heavily infected and impaired by both monogeneans (Ogawa & Egusa 1976, Egusa 1979, Fang et al. 2008), the current state of invasion is under scrutiny in European countries, where *P. anguillae* has been reported from freshwater to brackish-water environments, while *P. bini* has been found only in freshwater (reviewed by Jakob et al. 2009). In contrast, investigations of the 2 monogeneans in wild Japanese eels are quite few (see Naga-

sawa et al. 2007), because they rarely cause a problem. Thus, the host–parasite relationships in Japanese eel populations have never been completely clear. The one remaining species, *P. kamegaili*, was described by Iwashita et al. (2002) as a valid species from Japanese eels caught at the mouth of a river flowing into Tokyo Bay in Japan, but there has been no subsequent record for this species.

The aim of the present study was to examine the infection status of *Pseudodactylogyrus* spp. on wild Japanese eels, considering distinctions in the host's facultative catadromy. For this purpose, we combined a traditional parasitological survey with otolith microchemical analysis on the eels inhabiting a brackish-water cove and 2 rivers flowing into the cove in western Japan.

## MATERIALS AND METHODS

### Sample collection

The sampling was conducted in Misho Cove (salinity range: 3.6 to 30.7‰) and 2 adjacent rivers, the Renjoji and Sozu Rivers, flowing into the cove in Ehime Prefecture, western Japan (Fig. 1). In these localities, Japanese eels *Anguilla japonica* were caught with covert traps and eel pots from April 2008 to October 2009. The eels collected were kept alive in oxygenated containers with ambient waters and brought to the laboratory at Hiroshima University, where they were measured for total length (TL, in mm) and examined for parasites within a few days.

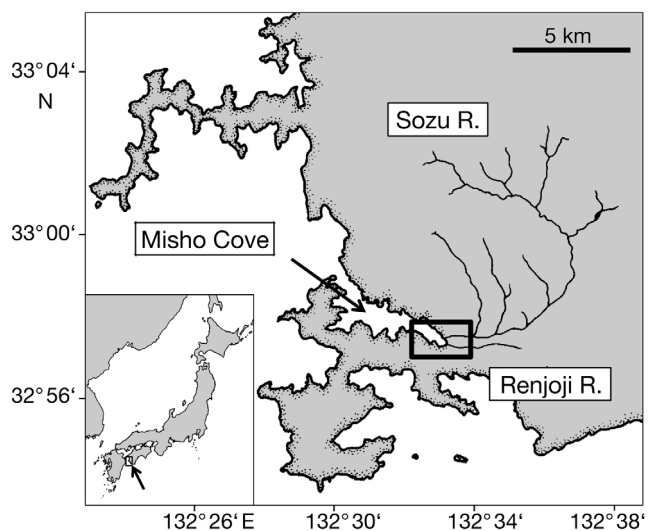


Fig. 1. Map of the study area. Japanese eels *Anguilla japonica* were collected in the boxed area

All pseudodactylogyrid monogeneans recovered from the gills of eels were fixed in 70% ethanol under slight pressure. These specimens were subsequently stained with Heidenhain's iron hematoxylin or Alum carmine, dehydrated in a series of ascending concentrations of ethanol, cleared in xylene, and mounted in Canada balsam. Identifications of *Pseudodactylogyrus* spp. were confirmed according to the descriptions by Ogawa & Egusa (1976) and Iwashita et al. (2002): *P. bini* apparently has smaller hamuli than both *P. anguillae* and *P. kamegaili* and *P. kamegaili* differs from *P. anguillae* in having a wider and sclerotized cirrus and vagina and shorter marginal hooks. Specimens of *Pseudodactylogyrus* spp., including the holotype and paratypes of *P. kamegaili*, deposited in the collections of the Meguro Parasitological Museum (MPM), Tokyo, were also used to confirm our identifications: *P. anguillae* (MPM Coll. Nos. 19139, 19140a, 19140c, 19164a, 19165a, 19166a, 19166c, 19168c, 19169a, 19171c), *P. bini* (MPM Coll. Nos. 19140b, 19141, 19165c, 19166d, 19167a, 19168a, 19170a, 19171b), and *P. kamegaili* (MPM Coll. Nos. 19767–19768).

#### Otolith preparation and Sr:Ca ratio analysis

Sagittal otoliths were extracted from each Japanese eel when the parasitological examination was carried out. All otoliths were first stored in 70% ethanol and embedded in epoxy resin after air-drying. Subsequently, they were ground using a grinding machine (Struers S5629, Marumoto Struers K.K.) to expose the core along a horizontal plane. For the finishing polish, 1  $\mu\text{m}$  diameter diamond paste with lubricant liquid was used. Each otolith polished was then coated with carbon in a high-vacuum evaporator, and Sr and Ca concentrations were measured along the line from core to edge at intervals of 10  $\mu\text{m}$  using an electron probe microanalyzer (JOEL JXA-8200; the accelerating voltage and beam current were 15 kV and 10 nA, respectively).  $\text{SrCO}_3$  and  $\text{CaCO}_3$  were used as standards. The electron beam was focused on a point 10  $\mu\text{m}$  in diameter, with 10 s of irradiation per point.

The Sr:Ca measurement values were used to interpret the habitat usage of Japanese eels, based on the criteria of Tsukamoto & Arai (2001): Sr:Ca ratios  $< 2.5 \times 10^{-3}$  correspond to freshwater living, Sr:Ca ratios ranging from  $2.5 \times 10^{-3}$  to  $6.0 \times 10^{-3}$  indicate brackish-water living, and Sr:Ca ratios  $> 6.0 \times 10^{-3}$  indicate eels living in a high-salinity environment such as seawater.

#### Data analysis

Prevalence (percentage of host individuals infected with a parasite), mean intensity (the average number of individuals of a parasite per infected host), and mean abundance (the average number of individuals of a parasite per examined host) of monogeneans were calculated for each ecophenotype of host, in accordance with the definitions of Bush et al. (1997).

Generalized linear models (GLM) were applied to examine relationships between the abundances and biological parameters of eels using R 2.8.1 (R Development Core Team 2008) with the MASS-package (Venables & Ripley 2002). In this analysis, ecophenotype and TL of eels were tested as explanatory variables. For the fitting of models to the abundances of *Pseudodactylogyrus* spp., a negative binomial error distribution and a logarithmic link function were employed, because macro-parasites often represent aggregated infection patterns, which are best described as a negative binomial distribution, in their host population (Wilson et al. 1996, Shaw et al. 1998). The candidate models were selected by a forward stepwise procedure based on Akaike's information criterion (AIC; Burnham & Anderson 2002). The difference in AIC value ( $\Delta\text{AIC}$ ) between a constructed model and a model with the lowest AIC value was also calculated: as a rule of thumb, a model with  $\Delta\text{AIC} < 2$  is substantially supported and received consideration in making data inference (see Burnham & Anderson 2002).

## RESULTS

#### Habitat-use patterns of Japanese eels

A total of 114 Japanese eels *Anguilla japonica* were collected from 3 localities during the sampling period. The eels ranged from 204 to 684 mm TL, with a mean ( $\pm\text{SD}$ ) of  $382 \pm 74.5$  mm TL. Based on their otolith Sr:Ca ratios, the eels were divided into 4 categories of ecophenotype (i.e. habitat-use patterns) (Fig. 2): freshwater residents (designated hereafter as Type I,  $n = 22$ ), individuals moving between freshwater and low-salinity habitats (Type II,  $n = 19$ ), downstream habitat-shifters which reside in the cove after migrating down from freshwater habitats (Type III,  $n = 51$ ), and cove residents without any migration into freshwater (Type IV,  $n = 22$ ).

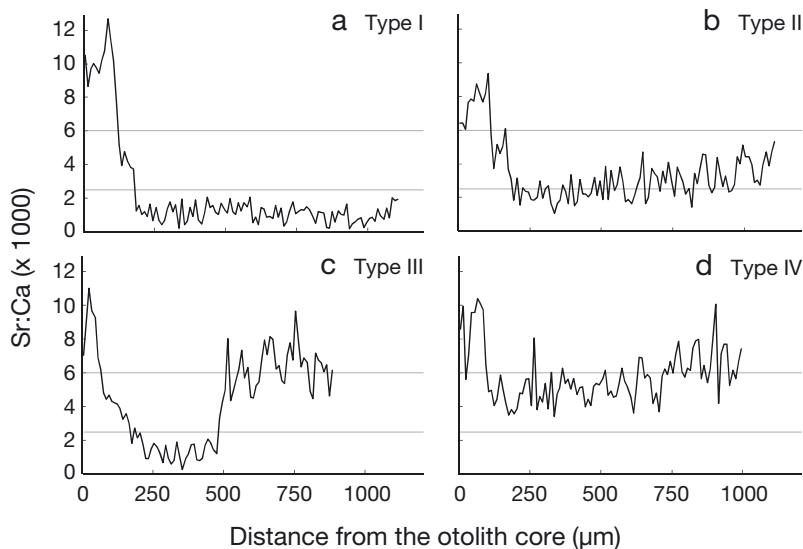


Fig. 2. *Anguilla japonica*. Typical changes in otolith Sr:Ca ratios along a transect line from the core (0  $\mu\text{m}$ ) to the edge of the otolith in Japanese eels, collected from Misho Cove and the Renjoji and Sozu Rivers. (a) Type I: freshwater resident, (b) Type II: individual utilizing low-salinity habitats, (c) Type III: downstream habitat-shifter, and (d) Type IV: cove resident. Horizontal lines indicate Sr:Ca ratios of  $2.5 \times 10^{-3}$  and  $6.0 \times 10^{-3}$

### Parasite occurrence

All 4 ecophenotypes of Japanese eels were infected with at least 1 species of *Pseudodactylogyrus* (Table 1). Type I eels were infected by *P. anguillae* and *P. bini*. Type II eels harbored 3 species of *Pseudodactylogyrus*. Type III eels were infected with *P. anguillae* and *P. kamegaili*. In Type IV, only *P. kamegaili* occurred.

As a result of the model selections, the abundances of *Pseudodactylogyrus bini* and *P. kamegaili* were confirmed to significantly vary with host ecophenotypes and TL (Table 2). For *P. anguillae* abundance, the multivariate model composed of 2 explanatory variables (ecophenotype and TL) represented no improvement over the AIC value from the univariate model consisting of ecophenotype. However, due to the slight difference in AIC value ( $\Delta\text{AIC} = 0.44$ ) from the univariate

model, the multivariate model could not be eliminated. In the present study, thus, the multivariate model was tentatively accepted as the final model for *P. anguillae* abundance, according to the models for *P. bini* and *P. kamegaili* abundances.

In all final models, *Pseudodactylogyrus* spp. abundances were positively, yet only slightly, associated with host TL (Table 3). The abundances of *P. anguillae* and *P. bini* also increased with the ranking of the 4 types of eel habitats from saline to freshwater. In contrast, *P. kamegaili* severely infected the 2 host groups (Type III and IV) inhabiting brackish-water areas.

### DISCUSSION

Anguillid eels are thought to be derived from a marine ancestor that completed its migration loop within the ocean (Tsukamoto et al. 2002, Inoue et al. 2010). The genus *Pseudodactylogyrus* is also assumed to be of marine origin (Ogawa 1984), and Iwashita et al. (2002) speculated that the freshwater congeners *P. anguillae* and *P. bini* diverged from their marine ancestor as their host went through evolutionary adaptation from marine to freshwater environments, whereas *P. kamegaili* originates from the ancestor remaining in coastal marine and brackish-water environments. No occurrence of *P. kamegaili* was found in freshwater residents, designated as Type I in the present study, thus indicating that this monogenean has maintained the original marine distribution by parasitizing non-catadromous eel individuals since divergence. If all eel individuals had a catadromous life-history, migrating up to freshwater habitats, *P. kamegaili* might not have survived or might have been forced to adapt to freshwater habitats.

Table 1. *Anguilla japonica*. Infection levels of *Pseudodactylogyrus* spp. on Japanese eels from Ehime Prefecture, western Japan, with distinction of 4 habitat-use patterns in eels. N: sample size; TL: mean total length ( $\pm\text{SD}$ ); P: prevalence; MI: mean intensity ( $\pm\text{SD}$ ); MA: mean abundance ( $\pm\text{SD}$ ); for type descriptions, see Fig. 2

<i>A. japonica</i> ecophenotype	N	TL (mm)	<i>P. anguillae</i>			<i>P. bini</i>			<i>P. kamegaili</i>		
			P (%)	MI	MA	P (%)	MI	MA	P (%)	MI	MA
Type I	22	407.1 $\pm$ 117.8	63.6	4.00 $\pm$ 4.07	2.55 $\pm$ 3.76	54.6	14.00 $\pm$ 18.02	7.64 $\pm$ 14.86	0	–	–
Type II	19	346.2 $\pm$ 89.1	36.8	4.43 $\pm$ 4.54	1.63 $\pm$ 3.42	15.8	1.33 $\pm$ 0.58	0.21 $\pm$ 0.54	31.6	5.00 $\pm$ 4.47	1.58 $\pm$ 3.36
Type III	51	380.2 $\pm$ 50.8	3.9	1.50 $\pm$ 0.71	0.06 $\pm$ 0.31	0	–	–	82.4	4.98 $\pm$ 4.58	4.10 $\pm$ 4.57
Type IV	22	378.1 $\pm$ 35.1	0	–	–	0	–	–	81.8	11.17 $\pm$ 11.49	9.14 $\pm$ 11.24

Table 2. Forward stepwise generalized linear model constructions for explanatory variables affecting *Pseudodactylogyrus* spp. abundances on Japanese eels *Anguilla japonica*. AIC: Akaike's information criterion; null: a model with no explanatory variable; TL: total length

Model	Residual df	Residual deviance	AIC	$\Delta$ AIC
<b><i>P. anguillae</i></b>				
Null	91	51.48	206.70	26.22
+ Ecophenotype	89	50.45	180.47	0
+ Ecophenotype + TL	88	50.91	180.92	0.44
<b><i>P. bini</i></b>				
Null	40	29.42	153.71	14.81
+ Ecophenotype	39	29.71	142.65	3.76
+ Ecophenotype + TL	38	31.95	138.90	0
<b><i>P. kamegaili</i></b>				
Null	91	100.6	481.13	13.47
+ Ecophenotype	89	100.8	469.94	2.29
+ Ecophenotype + TL	88	100.1	467.66	0

Table 3. Estimated effects of explanatory variables selected in the final models. TL: total length; for type descriptions, see Fig. 2

Parameter		Estimate	SE	z-value	p
<b><i>P. anguillae</i></b>					
Intercept		-0.777	0.998	-0.778	0.437
Ecophenotype	Type I	0.218	0.581	0.376	0.707
	Type II	0			
	Type III	-3.392	0.752	-4.510	<0.001
TL		0.003	0.003	1.351	0.177
<b><i>P. bini</i></b>					
Intercept		-4.571	1.283	-3.564	<0.001
Ecophenotype	Type I	2.537	0.737	3.442	<0.001
	Type II	0			
TL		0.009	0.003	2.944	0.003
<b><i>P. kamegaili</i></b>					
Intercept		-1.641	0.952	-1.724	0.085
Ecophenotype	Type II	0			
	Type III	1.001	0.391	2.560	0.011
	Type IV	1.723	0.435	3.961	<0.001
TL		0.005	0.002	2.212	0.027

Conversely, the presence of *P. kamegaili* probably indicates the resource stability of non-catadromous individuals that primarily inhabit coastal and brackish-water areas.

In European countries, *Pseudodactylogyrus anguillae* or unidentified species of *Pseudodactylogyrus* have sometimes been reported from European eels in brackish-water localities, with relatively high prevalence and intensity: for example, 2 fjords (salinity: 15 to 20‰ and about 10‰, respectively) adjoining the Baltic and North Seas and a strait (4 to 8‰) within the Baltic Sea, Denmark (Køie 1988); a lagoon (10 to

40‰) in the North Tyrrhenian Sea (Kennedy et al. 1997) and 2 lagoons (15 to 35‰ and 30 to 42‰, respectively) in the North Adriatic Sea, Italy (Di Cave et al. 2001); 3 lagoons (3 to 30‰, 8 to 36‰, and 8 to 30‰, respectively) in the Balearic Sea, Spain (Maillo et al. 2005); lagoons (no salinity data) in the Gulf of Lion, Mediterranean Sea, France (Fazio et al. 2008); and a lagoon, a fjord, and a strait (overall salinity range: 15 to 26‰) in northwestern Germany (Jakob et al. 2008). However, it is noteworthy that *P. anguillae* was scarce on the Japanese eels inhabiting Misho Cove (3.6 to 30.7‰) in the present study, with a low intensity if present at all. Instead, these cove eels were exclusively infected with *P. kamegaili*, even if the eels were identified as Type III, i.e. having migrated down from the freshwater habitats where *P. anguillae* is mainly distributed. Therefore, our findings in the present study suggest that some of the monogenean specimens from brackish-water localities in Europe previously reported to be *P. anguillae* may actually have been *P. kamegaili*.

*Pseudodactylogyrus kamegaili* and *P. anguillae* are easily confused because their morphologies are very similar (see Iwashita et al. 2002), but *P. kamegaili* can be distinguished from *P. anguillae* by its wider and sclerotized cirrus and vagina and shorter marginal hooks (Iwashita et al. 2002). To date, no information on occurrence of *P. kamegaili* is available, except for that provided in the present study and that from the first record by Iwashita et al. (2002) based on specimens from Japanese eels. Unfortunately, there are no reports on the current status of *P. kamegaili* in European countries. However, in view of recent reports that European eels are also facultatively catadromous (Tsukamoto et al. 1998, Arai et al. 2006, Daverat et al. 2006), *P. kamegaili* appears to be able to survive and sustain its population by utilizing coastal marine and brackish-water residents of European eels, just like the present case in Japanese eels. Further investigations are therefore needed in European countries, not only of *P. anguillae* and *P. bini*, but also of *P. kamegaili*, to examine its existence there.

If *Pseudodactylogyrus kamegaili* does not exist in Europe, the discrepancy in the occurrence of *P. anguillae* between the current findings in European countries and our data in Japan suggest another explanation. According to Køie (1991), *P. anguillae* is capable of reproducing in brackish-water salinities up to 20‰. Even though this species can occur in relatively high-salinity environments, its distribution is possibly restricted to freshwater environments because it rarely co-occurred with *P. kamegaili*: only 3 cases of coexistence on the same eel individual were

observed in the present study (Table 1). On the other hand, as reported in European countries (Buchmann 1988, Dzika 1999, Fang et al. 2008), the coexistence of *P. anguillae* and *P. bini* was confirmed in our study. In either case, salinity tolerance of each monogenean species needs to be reinvestigated under experimental conditions, especially with regard to a possible revision of the range of *P. anguillae*.

The present study also detected slight positive relationships between the host's body size and the infection level of each species of *Pseudodactylogyrus*. A similar positive relationship has also been documented for cultured and wild European eels (Buchmann 1989, Nie & Kennedy 1991, but see K oe 1988), and it is presumed that higher infection levels in larger eels are attributable to a higher probability of infection of the gill due to more space for parasite attachment and greater flows of water (Buchmann 1989, Nie & Kennedy 1991). The size-related principle, as previously suggested, may work for all 3 *Pseudodactylogyrus* spp.

In conclusion, the present study showed among that species composition and infection levels of *Pseudodactylogyrus* spp. clearly differ among the habitat-use patterns of Japanese eels. The concomitant use of microchemical analysis can reveal the relationship between the host's ecophenotypes and the infection status of the gill monogeneans, and eventually afford a useful baseline to determine the distributional ranges of the monogeneans from coastal marine to freshwater environments. This technique could also help to investigate other eel parasites. Further applications could, therefore, enable a greater understanding of the patterns and processes of parasite assemblages in the facultative catadromy of eels. Other fish species undertaking regular, seasonal, or ontogenetic migration between marine and freshwater environments also represent flexible migratory diversity (see Yang et al. 2011), as well as the cases of anguillid eels. In cases where these fishes are examined for parasites, otolith microchemical data are needed to corroborate the host's mobility.

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