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FULL PAPER

Spawning behaviour and male mating success of Pike Gudgeon, *Pseudogobio esocinus* (Cypriniformes, Cyprinidae), in an experimental tank

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Abstract The spawning behaviour of *Pseudogobio esocinus* was examined in an experimental water tank. Spawning was observed on 66 occasions in five experiments, and one female repeatedly spawned 7–18 times during one night. Four easily distinguishable behavioural phases were recognised during the spawning sequence: phase 1, male nuzzling to the female's body or face; phase 2, male pursuing a swimming female; phase 3, pair or trio trembling while swimming; and phase 4, spawning (scattering eggs and sperm) near the water surface. The spawning behaviour mainly occurred between pairs (53 times) and occasionally among a trio (13 times). A generalised linear mixed model was used to analyse the relationships between male spawning success and four fixed variables. As a result, more aggressive and larger males tended to be successful spawners. A digital video image of *P. esocinus* spawning behaviour is available at http://www.momo-p.com/index.php?movieid=momo150129pe01b.

Keywords Gobioninae · Reproductive ecology · Demersal adhesive egg · Mate choice · GLMM

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Introduction

The gudgeons, in the subfamily Gobioninae, are a group of morphologically and ecologically diverse Eurasian freshwater cyprinid fishes comprising approximately 130 species in approximately 30 genera (Bănărescu and Nalbant 1973; Bănărescu 1992, 1999; Nelson 2006). Gobioninae members are monophyletic, but composed of several lineages (Yang et al. 2006; Tang et al. 2011). Although the spawning ecology of Gobioninae species is poorly understood (Nakamura 1969; Bănărescu 1999; Kim and Park 2002; Chen and Chang 2005; Kottelat and Freyhof 2007), the known patterns vary, e.g. making a nest and guarding by the male (*Abbottina rivularis*, see Tsukahara 1954), scattering and drifting eggs with the current (*Gobio gobio*, see Mann 1980), depositing eggs in freshwater bivalves (*Sarcocheilichthys variegatus*, see Nakamura 1969), attaching eggs to the substrate and guarding by the male (*Pseudorasbora parva*, see Nakamura 1969), brood parasitised (attaching eggs on the nest of other fish) (*Pungtungia herzi*, see Baba et al. 1990), burying eggs in the bottom sand (*Hemibarbus barbus*, see Katano and Hakoyama 1997) and carrying gravels and piling it on the eggs after spawning in a hole in the riverbed (*Hemibarbus mylodon*, see Choi and Baek 1970). Thus, this subfamily is a suitable model to understand the evolution of spawning ecology in cyprinid fish.

Pike Gudgeon, *Pseudogobio esocinus*, are benthic freshwater fish distributed in northeast China, the Korean Peninsula and western Japan (Uchida 1939; Nakamura 1969; Bănărescu 1992). Some studies have investigated their ecology, including a description of their general life history (Uchida 1939; Nakamura 1969; Nagata 2014), discovery of eggs in a natural river (Ueno et al. 1998; Nakajima 2015), growth (Ueno et al. 2000), migration

(Ueno 2001), age and size at maturation (Ueno 2002), larval phototaxis (Nakajima 2006), effect of temperature on egg hatching (Nakajima et al. 2006), habitat selection (Nakajima et al. 2008), embryonic and larval development (Lee et al. 2008) and larval and juvenile morphology (Nakajima and Onikura 2015). This species is presumed to lay eggs on sandy bottoms (Nakamura 1969) or to scatter eggs on cobbles and sandy bottoms (Hosoya 2001a), but the descriptions in these studies are not based on direct observations. Recently, it was reported in brief that one female spawns with one male and that they scatter their eggs near the water surface (Nagata 2014). However, the spawning behaviour and reproductive ecology of *P. esocinus* is not completely understood. In the present study, we describe the spawning behaviour of *P. esocinus* in detail during aquarium observations and analyse male mating success.

Materials and methods

Experimental tank. The experiments were conducted in a glass-fronted concrete tank (width, 95 cm; height, 90 cm; depth, 125 cm) at the Fishery Research Laboratory, Kyushu University. The water was constantly circulated with an electric water pump (Eheim 1262 universal pump; EHEIM GmbH & Co. KG., Deizisau, Germany). The tank had sufficient area for fish to swim. A 100 W naked light bulb shielded by a clear red plastic board was hung 10 cm above the tank. Artificial algae (Kinran New Type; Tanaka Sanjiro Co., Ltd., Ogori, Japan) was placed on the water surface to make the tank environment appear similar to an inhabited river, and a 2–5 mm layer of river sand (grain diameter, approximately 1 mm) was used as a bottom substrate.

Spawning behavioural observations. The experiments were conducted five times in May 2005 and in April and May 2006 and named Exp. 1–5 in sequential order (Table 1). Live *Pseudogobio esocinus* specimens were collected using a cast net from Nakagawa River (33.539576N, 130.431612E), Fukuoka Prefecture, Kyushu Island, Japan, on each observational day. Tominaga et al. (2009) reported that *P. esocinus* includes two highly differentiated mitochondrial DNA lineages called Group 1 and Group 2, and the population in the Nakagawa River has been confirmed to be of Group 1 only (Tominaga and Nakajima, unpublished data).

Individual fish were placed in the tank approximately 1–2 h prior to observations. Previous studies have reported that *P. esocinus* spawn at night (Ueno et al. 1998; Nakajima 2015); thus, our observations were conducted for 10 h during the evening (approximately 2000 hours) until the following morning (approximately 0600 hours) using a digital video camera (TRV 30; Sony, Tokyo, Japan) and by direct observations. Based on previous observations (Nagata, personal communication; Nagata 2014), we considered that a single female spawned with more than one male. Accordingly, each experimental group consisted of one ovulating female and five mature males (Table 1). Five males were selected for each experiment on the basis of size difference to aid individual identification and analyse the spawning success of each male. A digital video image of the spawning behaviour has been registered at the Movie Archives of Animal Behavior website (http://www.momo-p.com/index-e.html).

Data analysis. After videotaping, spawning behaviour was classified into discrete phases. In addition, the generalised linear mixed model (GLMM) was used to analyse the relationships between spawning success of an individual male (SS) and four fixed variables, including standard length (SL), relative difference in SL (RDSL), absolute RDSL (ARDSL) and the number of times a male was intercepted by a female (FI). Each experiment was defined as a random effect in the GLMM. SS was defined as $1/n$, where n is the number of males spawning during a single spawning event (Kuwamura and Nakajima 1996). The RDSL between a male (C mm SL) and a female (D mm SL) was calculated from the following formula, as given by Iguchi and Maekawa (1993): $\mathrm{RDSL} = 100 \times (C - D)/(C + D)$. FI was the number of fish participating in the second to last spawning phase, but not the last phase (i.e. spawning). These analyses were

Table 1 Water temperature and standard length (mm) of females and males in each experiment

Exp. No.	Data	WT (°C)	Female (mm)	Male (mm)				
				1	2	3	4	5
1	1-2 May, 2005	21.0	155	140	135	120	114	103
2	16-17 May, 2005	20.5	145	145	136	130	120	95
3	26-27 April, 2006	14.4	146	171	147	129	114	94
4	2-3 May, 2006	18.5	161	151	141	130	113	100
5	3-4 May, 2006	18.3	143	154	141	133	118	103

WT water temperature

performed using the statistical software, R version 3.0.3 (R Development Core Team 2014), with the glmmML package (Broström 2013). Akaike's information criterion (Akaike 1974) was used to select the models.

Results

Spawning behaviour was observed 66 times in five experiments. The numbers of spawning events during each experiment were as follows: 18 (Exp. 1), 7 (Exp. 2), 14 (Exp. 3), 9 (Exp. 4) and 18 (Exp. 5) (mean ± SD, 13.4 ± 5.3; $n = 5$). Four easily distinguishable behavioural phases were recognised during spawning (Fig. 1): phase 1, male nuzzling to a female's body or face (Fig. 1a); phase 2, male pursuing a swimming female (Fig. 1b, c); phase 3, pair or trio of fish trembling while swimming (Fig. 1d); and phase 4, spawning (scattering eggs and sperm) near the water surface (Fig. 1e, f). Spawning times were between 2047 hours and 0223 hours, and durations from the first to last spawning event were as follows: 1,963 s (Exp. 1), 1,885 s (Exp. 2), 2,034 s (Exp. 3), 532 s (Exp. 4) and 5,794 s (Exp. 5) (mean ± SD, 2,441.6 ± 1,974.2 s; $n = 5$) (Fig. 2). One female spawned repeatedly with one or two males at an interval of 2–1,098 s. Spawning (phase 4) always occurred between pairs (53 times) and occasionally with one other male (13 times). Males were often rejected from spawning (phase 4), despite participating in trembling (phase 3). The ratios (%) of phase 4 to phase 3 were as follows: 51.3 (Exp. 1), 70.0 (Exp. 2), 63.6 (Exp. 3), 81.2 (Exp. 4) and 39.1 (Exp. 5) (mean ± SD, 61.2 ± 16.5; $n = 5$). Males immediately went back to phase 1 after being rejected from spawning with a female. Males occasionally pecked at other males; however, this behaviour was not sustained. Spawned eggs drifted, sunk slowly, and then attached to the artificial algae

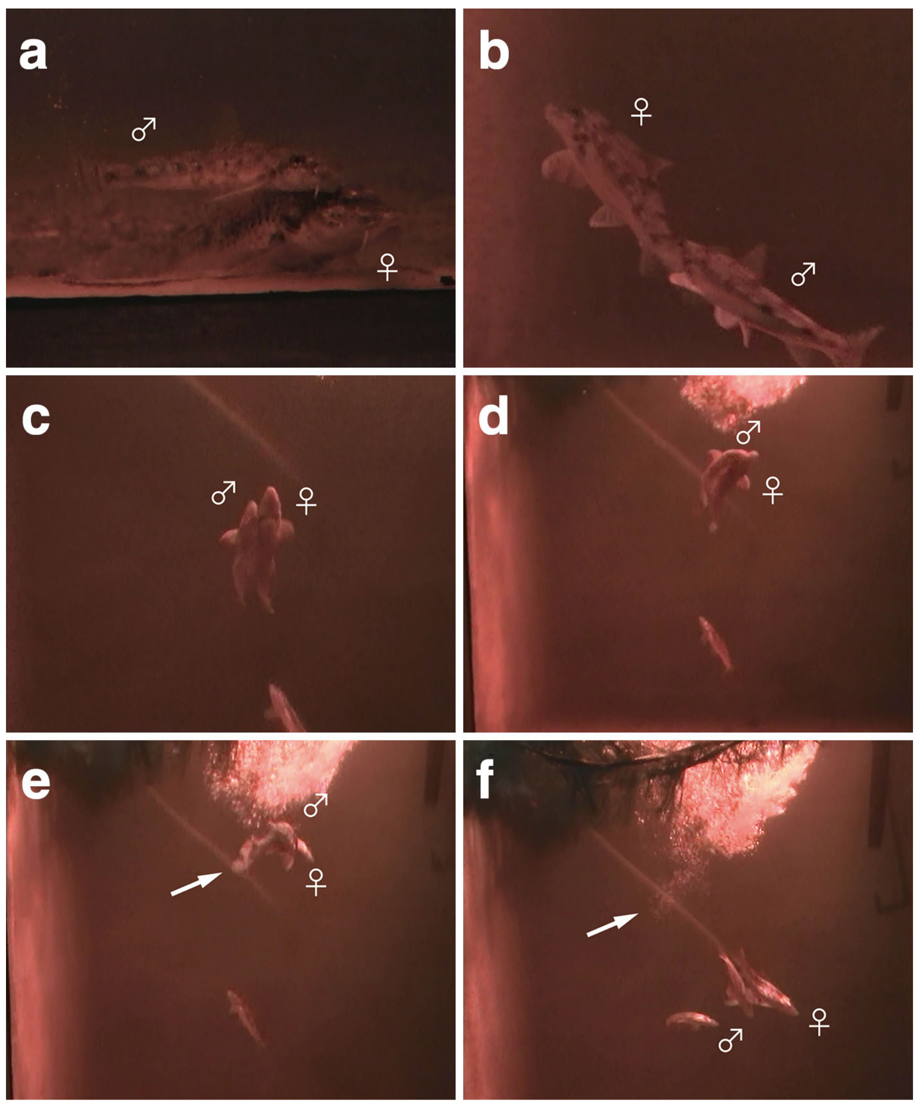

Fig. 1 Spawning behaviour of *Pseudogobio esocinus*. **a** Male nuzzling to a female's face; **b**, **c** male pursuing a swimming female; **d** pair trembling; **e** spawning; **f** after spawning. *Arrows* indicate scattered eggs and sperm. The digital video image is available at http://www.momo-p.com/index.php?movieid=momo150129pe01b

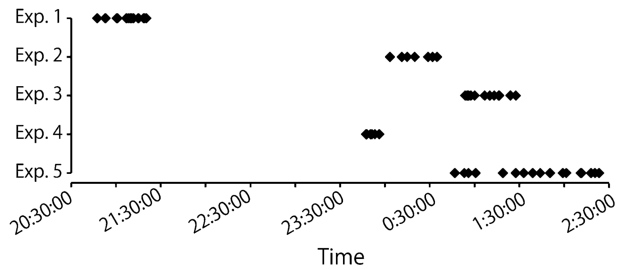

Fig. 2 Spawning numbers, times and durations in each experiment

and the bottom and walls of the tank. Both sexes of fish often ate their spawned eggs on the bottom of the tank. After the observations, we collected the artificial algae with eggs attached and confirmed that most of the eggs had been fertilised.

The GLMM showed that FI was selected in the top five models, and SL was selected in four models as a positive effect on male spawning success (Table 2).

Discussion

Spawning behaviour of *Pseudogobio esocinus* was classified previously into six phases by Nagata (2014) as follows: phase 1, male nuzzling to a female's body or head; phase 2, a male pursuing a swimming female; phase 3, female and male changing swimming direction near the water surface; phase 4, female scattering eggs; phase 5, male coming through scattered eggs; and phase 6, female and male landing on the bottom. The spawning behaviour that we observed was essentially consistent with the observations by Nagata (2014); however, trio spawning and pecking between males were described for the first time in the present study. In addition, we did not observe phase 5 (male coming through scattered eggs) described by Nagata (2014).

The results of our experiment clearly demonstrated that *P. esocinus* broadcast their eggs into the water, and that these spawned eggs drift and attach to various materials. Nakajima (2015) reported that mature females appear between 2000 hours and 0100 hours and that many free-drifting eggs can be caught using egg collecting nets between 2100 hours and 0200 hours in the Nakagawa River, Kyushu Island, Japan. *Pseudogobio esocinus* eggs have been discovered on filamentous green algae and underwater sands and gravels in the field (Nakamura 1969; Nagata 2014). Taken together, *P. esocinus* spawn as pair or trio early at night and broadcast eggs and sperm near the water surface; the fertile eggs sink, gradually disperse with the flow and then attach to various substrates. This scenario overlaps with the established view that this fish spawns eggs on sandy bottoms (Nakamura 1969) or scatters eggs on cobbles and sandy bottoms (Hosoya 2001a). Scattering demersal adhesive eggs in flowing water at night is a highly peculiar behaviour and exclusive to this Japanese freshwater fish.

The GLMM results showed that the number of female intercepts was most related to male spawning success, indicating that the males participating in the majority of the courting (phase 3) succeeded in spawning (phase 4). Large male body size was the second most related variable for spawning success. We observed pecking between males, suggesting that a large body size may be advantageous during competition between males. These results show that aggressive large males tend to succeed in spawning. Although the dimensions of the body or floridness of the body colour are important factors in sexual selection by fish (Karino 1996a, b; Andersson and Simmons 2006), no differences in average body size, body colouration or form are observed between mature male and female *P. esocinus* (see Uchida 1939; Nakamura 1969). These morphological features suggest that sexual selection due to direct phenotypic effects or sensory bias scarcely affects *P. esocinus*. In

Table 2 Coefficients of selected variables for the top five models explaining the successful spawning rate of male *Pseudogobio esocinus*

Model	AIC	ΔAIC	Coefficients (SD)				
			Intercept	SL	RDSL	ARDSL	FI
1	34.44	0	−2.985 (1.163)	0.023 (0.007)		0.017 (0.011)	0.154 (0.033)
2	34.62	0.18	−6.638 (3.518)	0.049 (0.023)	0.031 (0.021)		0.176 (0.038)
3	34.8	0.36	−1.662 (0.867)	0.016 (0.006)			0.151 (0.032)
4	35.49	1.05	−6.236 (3.572)	0.044 (0.024)	0.022 (0.023)	0.013 (0.012)	0.171 (0.038)
5	37	2.56	0.633 (0.247)		−0.012 (0.001)		0.150 (0.042)
Null model	60.48	26.04	0.948 (0.160)				

SL standard length; *RDSL* relative difference in SL; *ARDSL* absolute value of RDSL; *FI* number of times a male was intercepted by a female

Table 3 Comprehensive list of Gobioninae spawning ecology

Spawning ecology		Scientific name	Reference	Classification by Tang et al. (2011)
1	Spawning eggs on a nest made of mud and guarding by the male	*Abbottina rivularis*	Tsukahara (1954)	Gobionini
2	Spawning egg batch under vegetation and guarding by the male	*Biwia yodoensis*	Nagata (2014)	Gobionini
		Biwia zezera	Kawase et al. (2011)	Gobionini
3	Scattering and drifting adhesive eggs with the current	*Gobio gobio*	Mann (1980)	Gobionini
		Gobiobotia macrocephala	Ko et al. (2012)	–
		Pseudogobio esocinus	present study	Gobionini
		Romanogobio kesslerii	Kottelat and Freyhof (2007)	Gobionini
		Romanogobio uranoscopus	Bănărescu (1999)	Gobionini
		Sarcocheilichthys sinensis	Song and Ma (1994)	Sarcocheilichthyini
4	Scattering and drifting pelagic eggs with the current	*Coreius heterodon*	Liu et al. (1990)	Sarcocheilichthyini
		Coreius guichenoti	Liu et al. (1990)	Sarcocheilichthyini
		Rhinogobio ventralis	Zhou and He (1992)	–
		Saurogobio dabryi	Hubei Institute of Hydrobiology (1976)	Gobionini
		Saurogobio gymnocheilus	Hubei Institute of Hydrobiology (1976)	Gobionini
5	Scattering eggs to attach on underwater bush or vegetation	*Gnathopogon caerulescens*	Nakamura (1969)	–
		Gnathopogon elongatus	Nakamura (1969)	Sarcocheilichthyini
		Hemibarbus maculatus	Miao and Yin (1983)	*Hemibarbus–Squalidus* group
		Squalidus banarescui	Chen et al. (2010)	–
		Squalidus gracilis	Fujioka (1954)	*Hemibarbus–Squalidus* group
		Squalidus iijimae	Chen et al. (2012)	–
6	Attaching eggs to the substrate and guarding by the male	*Pseudorasbora parva*	Nakamura (1969)	Sarcocheilichthyini
		Pseudorasbora pugnax	Kano et al. (2010)	Sarcocheilichthyini
7	Brood parasitised (attaching eggs on the nest of another fish)	*Pseudopungtungia nigra*	Kim et al. (2004)	Sarcocheilichthyini
		Pungtungia herzi	Baba et al. (1990)	Sarcocheilichthyini
8	Burying eggs in the sandy bottom	*Hemibarbus barbus*	Katano and Hakoyama (1997)	*Hemibarbus–Squalidus* group
		Hemibarbus longirostris	Akiyama (1996)	*Hemibarbus–Squalidus* group
9	Depositing eggs in living freshwater bivalves	*Sarcocheilichthys biwaensis*	Hosoya (2001b)	–
		Sarcocheilichthys nigripinnis morii	Uchida (1939); Kang et al. (2007)	–
		Sarcocheilichthys variegatus	Nakamura (1969)	Sarcocheilichthyini
10	After spawning eggs in a hole, carrying gravels and piling these up on the eggs	*Hemibarbus mylodon*	Choi and Baek (1970)	*Hemibarbus–Squalidus* group

addition, one female repeatedly spawned 7–18 times with various males during one night, and trio spawning was observed 20 % of the time in the current study. Consequently, we presume that the sexual selection mechanism of *P. esocinus* fulfils the definition of a 'genetic compatibility mechanism' (Andersson and Simmons 2006). Our study was not designed to detect female mate preference. Another experiment needs to be designed and conducted to eliminate the effects of male–male interactions to reveal the sexual selection system of this species in more detail.

The spawning ecology of species of Gobioninae varies and can be classified into 10 patterns (Table 3). The spawning ecology of *P. esocinus* resembles that of *Gobio gobio*, *Gobiobotia macrocephala*, *Romanogobio kesslerii*, *R. uranoscopus* and *Sarcocheilichthys sinensis* (see Mann 1980; Song and Ma 1994; Bănărescu 1999; Kottelat and Freyhof 2007; Ko et al. 2012). Phylogenetic (Yang et al. 2006; Tang et al. 2011), and morphological (Bănărescu and Nalbant 1973; Hosoya 1986; Bănărescu 1992, 1999) studies indicate that the genus *Pseudogobio* is not evolutionarily close to *Gobio*, *Romanogobio* or *Sarcocheilichthys*, but *Abbottina*, *Biwia*, *Gobiobotia*, *Huigobio*, *Microphysogobio*, *Platysmacheilus*, *Rostrogobio* and *Saurogobio* are related genera. The spawning ecology of these genera is poorly understood; the spawning ecology of *Abbottina rivularis*, *Biwia zezera* and *Biwia yodoensis* differs from that of *P. esocinus*. *Abbottina rivularis* spawns eggs on a nest made by mud and the eggs are guarded by the male (Tsukahara 1954). *Biwia zezera* and *B. yodoensis* spawn egg batches under vegetation and the egg batches are guarded by the male (Kawase et al. 2011; Nagata 2014). Therefore, the spawning ecology of Gobioninae is not always congruous with phylogenetic relationships. Hayashi et al. (2013a) classified Japanese Gobioninae into two groups with different ecological traits: small-sized species with a short lifespan (SS type) and large-sized species with a long lifespan (LL type). They also classified *A. rivularis* and *B. zezera* into the SS type and *P. esocinus* into the LL type. The main habitat of *P. esocinus* is relatively stable permanent bodies of water, such as rivers or lakes (Nakamura 1969; Ueno 2001; Nakajima et al. 2008), whereas *A. rivularis* inhabit unstable temporary bodies of water, such as floodplains (Nakamura 1969; Hayashi et al. 2013a, b). Thus, they concluded that these intraspecific differences in life history traits between related species are caused by the response to environmental risk. These results suggest that the spawning ecology of Gobioninae is not always associated with phylogenetic position and may have evolved over a relatively short period in response to the inhabiting environment or life history traits.

The *P. esocinus* spawning ecology of scattering demersal adhesive eggs in flowing water is highly peculiar and exclusive to this Japanese freshwater fish. Although the adaptive significance of this spawning behaviour remains unclear, we observed that females and males often ate their spawned eggs from the bottom of the tank; thus, this spawning behaviour may be of benefit to prevent cannibalising eggs. Gobioninae fish are a suitable model to understand the evolution of cyprinid spawning ecology, but limited information is available. Further life history descriptions including the spawning ecology of Gobioninae species are required.

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