FULL PAPER



Life history of Pike Gudgeon, *Pseudogobio esocinus* (Cypriniformes, Cyprinidae): differences between the upper and lower reaches in a single river

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Abstract The variability of life history traits in *Pseudo*gobio esocinus was investigated in a single river (Nakagawa River, Kyushu Island, Japan) by comparing two subpopulations inhabiting river reaches with different thermal characteristics. A total of 689 individuals in the upper reach (St. A) and 705 individuals in the lower reach (St. B) were collected from April 2004 to March 2006 at monthly intervals. Water temperatures of both stations were measured by a logger during the period of survey, and these dates clearly showed that St. A was colder than St. B. The sub-population of St. A consisted of six age groups, and the age at maturity was 2 or 3 years. Spawning occurred between April and July, and peaked in May. The subpopulation of St. B consisted of four age groups, the age at maturity was 1 or 2 years and spawning occurred between March and July, peaking in April. The length-weight relationship and body condition were also different between the two sub-populations. In conclusion, the sub-population in the colder reach was characterised as longer lived, slower growing and later maturing, with larger body size and higher fecundity compared with the sub-population of the warmer reach. These results showed that the life history

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traits of *P. esocinus* were variable under the influence of water temperature, even in a single small river.

Keywords Intraspecific variation · Phenotypic plasticity · Gobioninae · GSI · Condition factor

Introduction

Variation in life history traits, such as variability of growth or age structure, is considered as phenotypic responses to variability of the environment (Fox 1978; Mills 1988; Goto 1998; Blanck and Lamouroux 2007; Vinyoles et al. 2010; Joanna et al. 2011). Explaining phenotypic plasticity of organisms, including variability of life history traits, is one of the goals of evolutionary biology (Price et al. 2003; Blanck and Lamouroux 2007). Intraspecific variation in life history traits of freshwater fishes has often been related to latitudinal clines, due to the direct effect of water temperature (Abdoli et al. 2007; Blanck and Lamouroux 2007; Reyjol et al. 2009). It is known that populations at higher latitudes (= lower temperature) grow more slowly, mature later and have a longer life span and higher maximal length than populations at lower latitudes (= warmer temperature) (Blanck and Lamouroux 2007).

Pike Gudgeon, *Pseudogobio esocinus*, belonging to the cyprinid subfamily Gobioninae, is a benthic freshwater fish widely distributed in the rivers of northeast China, the Korean Peninsula and western Japan (Uchida 1939; Bănărescu and Nalbant 1965; Nakamura 1969; Bănărescu 1992). A number of studies have investigated the life history and ecological features of this species (Uchida 1939; Nakamura 1969; Ueno et al. 1998, 2000; Ueno 2001, 2002; Nakajima 2006; Nakajima et al. 2006, 2008; Nagata 2014; Nakajima 2015; Nakajima and Onikura 2015). Uchida



(1939) stated that the size-age relationships of P. esocinus of the Korean Peninsula vary according to the river environment they inhabit. In Japan, it is known that this species is widely distributed from the upper to lower reaches in a single river, and the longitudinal distribution pattern is unusual compared with any other Japanese river fishes (Kamohara 1949; Ito and Nikaido 1959; Niwa 1954, 1967). Thus, such a wide population distribution is likely to be caused by variability of life history traits. However, Hayashi et al. (2013) have previously pointed out that interspecific variation in life history traits of species of Japanese Gobioninae, including P. esocinus, and the intraspecific variation in life history traits of Gobioninae between different temperature zones have not been researched. The aim of this study was to provide basic information on the life history of *P. esocinus* and to compare the life history traits of the sub-populations between the upper and lower reaches exposed to different temperature regimes in a single river.

Materials and methods

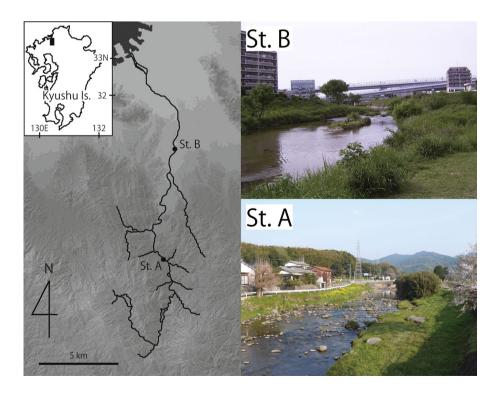
Study site. This study was conducted in the upper and lower reaches of the Nakagawa River, Fukuoka Prefecture, Kyushu Island, Japan (Fig. 1). The Nakagawa River originates on Sefuri Mountain (alt. 1,054 m), flows through Nakagawa Town and Fukuoka City and drains into the Hakata Bay, Sea of Japan. The main river length is 35 km,

Fig. 1 Location and geographical landscapes of St. A (upper reach) and St. B

(lower reach) in the Nakagawa River, northern Kyushu, Japan and the river catchment area is 124 km². The catchment has a typical humid temperate climate characteristic of the East Asian Monsoon area and has high rainfall during early summer and autumn. The average temperature and precipitation during a 20 year interval from 1981 to 2010 in the Fukuoka Prefecture were 17.0 °C and 1,612.3 mm, respectively (Japan Meteorological Agency 2014).

Two study stations, St. A (33.465348N, 130.425424E) and St. B (33.539576N, 130.431612E), were established along the river course (Fig. 1). The distance between the two stations along the river course is approximately 10 km. The upper reach station, St. A, was established at an altitude of 67 m, in a reach of approximately 300 m long and 10–15 m wide. The lower reach station, St. B, was established at an altitude of 13 m and was approximately 300 m long and 15–20 m wide. Both stations were characterised by some riffles and pools, and the maximum water depth was approximately 60–100 cm. The bottom material mainly consisted of sand and gravel. Water temperatures of St. A and St. B were measured once every hour by data loggers (StowAway TidbiT; Onset Computer Corporation, Bourne, Massachusetts) from April 2004 to March 2006.

Fish sampling and procedure. From April 2004 to March 2006, 689 individuals at St. A and 705 individuals at St. B were collected using cast nets (mesh size, 5–9 mm; circumference, 17–19 m) and hand nets (mesh size, 2–10 mm; diameter, 40–60 cm) at monthly intervals. However, sampling during September 2004 was prevented due to bad weather. Collected specimens were fixed in





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10 % neutral formalin following sedation using a narcotic (MS-222) and transported to the laboratory. The specimens were measured for standard length (SL) to 0.1 mm resolution. These were then dissected, and the gonad weight (GW) and somatic weight (SW) were measured to a resolution of 0.01 g. Sex and maturity were determined by visual inspection of the gonadal tissue in the dissections. Tominaga et al. (2009) reported that *Pseudogobio esocinus* includes two highly differentiated mitochondrial DNA lineages called Group 1 and Group 2, and the population in St. A and St. B has been confirmed to be of Group 1 only (Tominaga and Nakajima, unpublished data).

Age and growth. The relationship between SL and SW examined using the exponential equation: $SW = aSL^b$, where a is the intercept and b is the slope of the regression curve. Differences between stations and sexes for the SL-SW relationship were tested using analysis of covariance (ANCOVA). A previous study has reported that the age of P. esocinus could be confirmed by growth rings on the scales, and one annulus is formed every winter (Ueno 2002). The three lowest temperature months were January, February and December during 20 years from 1981 to 2010 in the Fukuoka Prefecture (Japan Meteorological Agency 2014). Thus, the age of individuals collected from March to November was determined by annuli on the scales. The scales in three parts of the body, namely the dorsal fin front, the lateral body and the pelvic fin base, were removed, and the number of annuli on the scales was counted using a stereoscopic microscope. Ages were also verified using the length frequency distribution. The von Bertalanffy growth formula (VBGF; von Bertalanffy 1938) was used to describe the growth curve: $SL_t = L_{\infty}[1 - e^{-k(t - t0)}]$, where SL_t is the predicted SLat age t (year), L_{∞} is the theoretical maximum SL, k is the growth rate parameter (year⁻¹) describing the rate that fish reach L_{∞} , and t0 is a theoretical initial age (year) when SL is zero. The age and length data were used to calculate the parameters of VBGF by analysing length-at-age data, using the FiSAT software package (Gayanilo et al. 2005). Back calculation of the VBGF was fitted to sub-populations of St. A and St. B. The seasonal growth pattern was assessed using the monthly SL for each cohort and VBGF. The Fulton's condition factor (K) (Blackwell et al. 2000) was used to describe seasonal fluctuations of body condition, which was calculated as $K = (SW/SL^3) \times 10^5$.

Reproduction. The spawning month was presumed on the basis of seasonal changes of the gonadosomatic index (GSI) and appearance of gonads. The monthly GSI was calculated as $GSI = (GW/SW) \times 100$. Females whose ovaries occupied almost the whole abdominal cavity, who had clearly visible ova and who had the maximum size of ova ≥ 1.0 mm were judged to be mature. Males whose testes were white, long and thickened were judged to be

mature. To calculate the SL at first maturation (SL_m, SL at 50 % maturity), the proportion of mature individuals was fitted to a logistic function $P = (1 + e^{-(a + bSL)})^{-1}$, where P is the proportion of mature individuals in a spawning month, and a and b are both constants. After determining an approximate formula by logistic regression analysis, SL_m was calculated for females and males at St. A and St. B based on individuals that were collected during spawning months.

All statistical analyses were performed using R version 3.0.3 (R Development Core Team 2014).

Results

Seasonal change of water temperature. The seasonal changes of water temperature at St. A and St. B from April 2004 to March 2006 are shown in Fig. 2. The average water temperatures (mean \pm SD) during the survey period were 14.9 \pm 6.5 °C at St. A and 17.1 \pm 7.0 °C at St. B and were significantly different between the stations (Student's t test; t = -31.3, df = 34806, P < 0.01). The average water temperatures during spring (March to May), summer (June to August), autumn (September to November) and winter (December to February) were also significantly different between stations (Student's t test; spring, t = -28.5, df = 8613, P < 0.01; summer, t = -60.9, df = 8832, P < 0.01; autumn, t = -23.0, df = 8738, P < 0.01; winter, t = -30.4, df = 8633, P < 0.01). The maximum water temperature of St. A and St. B was 28.4 °C and 31.2 °C respectively. The minimum water temperature of St. A and St. B was 2.2 °C and 3.9 °C, respectively.

Age and growth. A total of 202 females and 195 males were collected from St. A, and 252 females and 297 males from St. B. The sex ratio (female:male) at St. A (202:195)

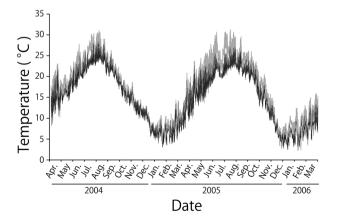


Fig. 2 Seasonal pattern of water temperature in St. A (black line) and St. B (grey line) from April 2004 to March 2006



and St. B (252:297) was not significantly different from 1:1 (Pearson's chi-square test; St. A, $\chi^2 = 0.03$, df = 1, P = 0.86; St. B, $\chi^2 = 1.68$, df = 1, P = 0.19). The SL-SW equations at St. A were as follows: SW = 9×10^{-6} $SL^{3.1184}$ $(r^2 = 0.9960, n = 202)$ for females and $SW = 7 \times 10^{-6} SL^{3.1662}$ $(r^2 = 0.9955, n = 195)$ for males. These equations were not significantly different between sexes (ANCOVA: df = 394, P = 0.861). The equations at St. B were as follows: $SW = 9 \times 10^{-6} SL^{3.11}$ $(r^2 = 0.9942, n = 252)$ for females and SW = 8×10^{-6} $SL^{3.1492}$ ($r^2 = 0.9921$, n = 297) for males. These equations were also not significantly different between sexes (ANCOVA; df = 546, P = 0.154). The SL–SW equations for all individuals were as follows: $SW = 1 \times 10^{-5} SL^{3.097}$ $(r^2 = 0.9966, n = 689)$ for St. A and SW = 1×10^{-5} $SL^{3.0958}$ ($r^2 = 0.9951$, n = 705) for St. B. These equations were significantly different between stations (ANCOVA; df = 943, P = 0.049).

The ages of 483 individuals in St. A and 522 individuals in St. B were determined. The sub-population of St. A consisted of six age groups, whereas St. B consisted of four age groups (Fig. 3). As will become apparent later, the peak spawning month was suggested as May in St. A and April in St. B. Appropriately then, the approximate date of

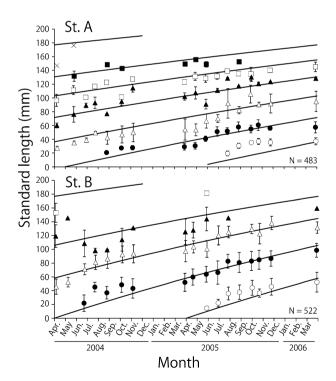


Fig. 3 Seasonal growth pattern for 2005 (open circles), 2004 (closed circles), 2003 (open triangles), 2002 (closed triangles), 2001 (open squares), 2000 (closed squares) and 1999 (crossed bars) cohorts and growth curves of Pseudogobio esocinus in St. A and St. B, Nakagawa River. Each cohort was determined from the annulus number of scales. Values are given in mean \pm SD. Growth curves are von Bertalanffy growth formula derived from the back-calculated data

birth was designated as 1 May in St. A and 1 April in St. B, and the SL-age data in each month was used to calculate VBGF. The length at age was described by the VBGF as SL = $348.27[1 - e^{-0.12(t - 0.00)}]$ for St. A and as SL = $321.20 [1 - e^{-0.20(t - 0.00)}]$ for St. B (Fig. 3). Seasonal change of condition factor showed an analogous pattern between St. A and St. B, the peak occurring during spring and summer (from March to August) and the dip occurring during autumn and winter (from September to February) (Fig. 4). Average condition factor values (mean \pm SD) during the survey period were 1.52 ± 0.16 at St. A and 1.49 ± 0.17 at St. B. These were significantly different between stations (Student's t test; t = 2.88, df = 1292, P < 0.01).

Reproduction. By visual identification, GSI over 4.0 in females and over 0.6 in males was judged to be mature. The SL of matured individuals was all over 80 mm (Table 1); thus, analysis of GSI was performed using individuals over 80 mm SL. Monthly variations of GSI presented similar seasonal patterns for females and males at each station, but the peak of females at St. B was 1 month earlier than that of St. A (Fig. 5). The seasonal change of GSI and the monthly ratio (%) of the number of mature individuals demonstrated that the spawning season was between April and July, peaking during May in St. A, and between March and July, peaking during April in St. B

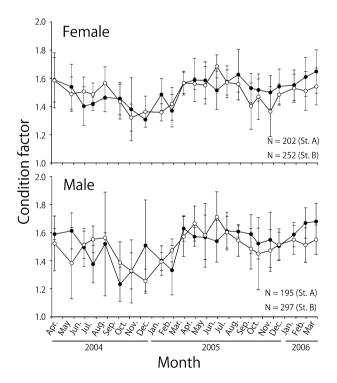


Fig. 4 Monthly variations of condition factor at St. A (*closed circles*) and St. B (*open circles*) of *Pseudogobio esocinus* in females and males. Values are given as mean \pm SD



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Table 1 Standard length (mm) and age of mature individuals (gonadosomatic index over 4.0 in females, over 0.6 in males) in each station

	St. A		St. B	
	Female $(n = 24)$	Male $(n = 30)$	Female $(n = 19)$	Male $(n = 38)$
Standard length				
Mean \pm SD	123.0 ± 23.6	117.2 ± 19.2	134.2 ± 23.4	116.3 ± 19.1
Range	80.3-176.3	82.2-152.1	102.1-181.5	83.9-153.9
Age				
Mean \pm SD	3.6 ± 1.1	3.4 ± 0.7	2.6 ± 0.7	2.3 ± 0.6
Range	2–5	2–5	1–4	1–3

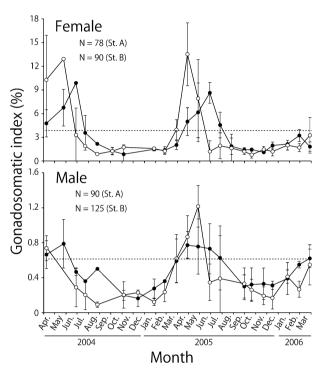


Fig. 5 Monthly variations of gonadosomatic index at St. A (closed circles) and St. B (open circles) of Pseudogobio esocinus in females and males (> 80.0 mm SL). Values are given as mean \pm SD. The dotted line shows the gonadosomatic index 4.0 in females and 0.6 in males

(Fig. 5; Table 2). The SL and age of mature females and males in both stations are shown in Table 1. The size at maturity was not significantly different between stations (Student's t test; t = -0.56, df = 109, P = 0.58). In contrast, the average age of maturity was significantly different between stations (Student's t-test; t = 7.31, df = 109, P < 0.01). SL_m was calculated based on individuals that were collected in April to July in St. A and March to July in St. B. SL_m of females and males was 104.3 and 104.1 mm, respectively, in St. A (logistic regression analysis; female, n = 80, P < 0.01; male, n = 78, P < 0.01) and 119.8 and 110.4 mm, respectively, in St. B (logistic regression analysis; female, n = 113, P < 0.01; male, n = 155, P < 0.01).

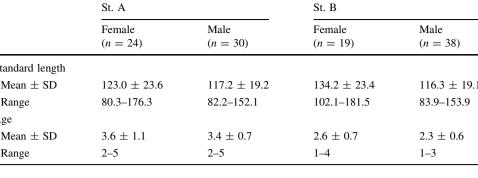


Table 2 Ratio (%) of mature females and males in each month (April 2004 to March 2006). Figures in parentheses indicate all individuals. Bold font indicates the highest ratio month

	St. A		St. B	
	Female	Male	Female	Male
March	0.0 (16)	29.4 (17)	13.8 (29)	18.2 (22)
April	33.3 (21)	46.7 (15)	33.3 (21)	47.1 (51)
May	48.0 (25)	47.8 (23)	18.2 (22)	23.1 (26)
June	20.0 (15)	23.8 (21)	15.8 (19)	7.1 (28)
July	10.5 (19)	10.5 (19)	4.5 (22)	7.1 (28)
August	0.0 (11)	0.0 (7)	0.0 (15)	0.0 (15)
September	0.0 (7)	0.0 (10)	0.0 (15)	0.0 (15)
October	0.0 (24)	0.0 (14)	0.0 (18)	0.0 (20)
November	0.0 (19)	0.0 (13)	0.0 (27)	0.0 (16)
December	0.0 (19)	0.0 (21)	0.0 (19)	0.0 (21)
January	0.0 (11)	0.0 (20)	0.0 (15)	0.0 (26)
February	0.0 (15)	0.0 (15)	0.0 (30)	0.0 (29)

Discussion

General features of life history. The current study described some life history traits of Pseudogobio esocinus at the upper (St. A) and lower (St. B) reaches exposed to different temperature conditions in a single river.

The sex ratio (females:males) at each station was 1:1, confirming observations by Nakamura (1969). The SL-SW relationships, growing speed and life span were not significantly different between males and females at each station. The logistic model indicated that 50 % sexual maturity was attained when individuals reached approximately 100–110 mm SL in both sexes. These results indicated that the basic growth pattern was not different between sexes in P. esocinus. Although it is reported that females grow for longer periods than males (Nakamura 1969; Ueno 2002), the present results disagreed with the previous descriptions.

The sub-population of St. A consisted of six age groups: the age at maturity was 2 or 3 years and spawning occurred between April and July, peaking during May (Figs. 3, 5; Table 2). In contrast, the sub-population of St. B consisted of



four age groups; the age at maturity was 1 or 2 years and spawning occurred between March and July, peaking during April (Figs. 3, 5; Table 2). Ueno (2002) identified four age groups, and the age at maturity was 1 or 2 years in the Yamato River system, Osaka Prefecture, Honshu, Japan. Thus, the growth pattern of the upper reach population presented a lower growth rate and longer life span than that given in a previous report by Ueno (2002). The reported spawning period of *P. esocinus* varies as follows according to past studies: between April and July (Yamato River system, Osaka Prefecture, Honshu, Ueno et al. 2000), May and July (Lake Biwa, Kawabata 1931) and May and June (Korean Peninsula, Uchida 1939). In view of these past results, the spawning period of *P. esocinus* occurs roughly during spring, but the peak varies from one region to another.

The SL at 50 % maturity in the upper reach was not different from that of the lower reach, but the age was different between the two stations and the smallest mature size was approximately 80 mm SL for both sexes (Table 1). Ueno (2002) previously reported that the sexual maturity of P. esocinus was related to the body size, and not to the age, and that the individuals > 80 mm SL were almost mature in both sexes. Our results confirmed the previous description by Ueno (2002).

The seasonal change of condition factor demonstrated the same tendency in both sub-populations, i.e. body condition increased from winter to summer and decreased from summer to winter (Fig. 4). This indicated that the body condition increased before the spawning season and decreased after the spawning season. A similar pattern of changing condition factor dependent on season was already recorded for other cyprinids species, such as *Abbottina rivularis* (see Nakajima and Nakagawa 2007) and *Rhynchocypris oxycephalus* (see Liang et al. 2014).

Plasticity of life history traits. In the current study, we found that the age structure, life span, growth speed, spawning season, age at maturity, length-weight relationship and body condition in P. esocinus were different between the upper and lower reaches in a single river (Table 3). It is known that water temperature is the main factor influencing intraspecific variation in the life history of fish (Blanck and Lamouroux 2007). The water temperature was clearly different between the two survey sites, and the sub-population in the colder reach is characterised as long lived, slower growing and later maturing, with larger body size and more fecundity compared with the sub-population of the warmer reach in the current study (Table 3). It is typically expected that individuals have a longer life span, grow slower, mature later and have a higher maximal body length with decreasing temperature (Colby and Nepszy 1981; Mills 1988; Abdoli et al. 2007; Blanck and Lamouroux 2007; Reyjol et al. 2009). Therefore, the results of the current study suggest strongly that

Table 3 Comparisons of ecological feature in *Pseudogobio esocinus* between two study sites

	Upper reach (St. A)	Lower reach (St. B)	
Water temperature	Lower	Higher	
Age structure	Six age groups	Four age groups	
Calculated SL (mm) in	each year of age		
One	39.4	58.2	
Two	74.3	105.9	
Three	105.3	144.9	
Four	132.8	176.9	
Five	157.1	_	
Six	178.7	_	
Growing speed	Slower	Faster	
Spawning season	April to July	March to July	
Peak of spawning	May	April	
First maturational age	Two or three	One or two	
Body size	Larger	Smaller	
Condition factor	Higher	Lower	

the variability of life history traits of *P. esocinus* is caused by the difference in water temperature.

Rivers of the Japanese archipelago are short and have a large slope, and the river environment and fish fauna change enormously along the river course (Miyadi et al. 1978; Mizuno and Gose 1993; Yamamoto 2010). However, P. esocinus is known to be widely distributed in both the upper and lower reaches in a single river, with a very unusual longitudinal distribution pattern compared with any other river fishes (Kamohara 1949; Ito and Nikaido 1959; Niwa 1954, 1967). In fact, in the Nakagawa River, the fish fauna is roughly different between St. A and St. B, and only P. esocinus is distributed in abundance in both stations [Electronic Supplementary Material (ESM) Table S1]. The current study demonstrated that age structure, growth rate, spawning season, age at maturity and some other life history traits for P. esocinus were different between the upper and lower reaches. The optimum hatching temperature for *P. esocinus* is in the range of 14–27 °C, a much broader range than is known for other fishes (Nakajima et al. 2006). In conclusion, these ecological features suggest that such a high biological plasticity for water temperature is one of the major adaptations by P. esocinus to having such a wide longitudinal distribution. While there are a number of reports for intraspecific variability of life history traits caused by water temperature, these are between different latitudinal or regional populations. The results of the current study demonstrated that even within a comparatively small area, such as a single small river *P. esocinus* is able to change life history traits.

Previous reports suggested that intraspecific variation in life history traits was also affected by food supply (e.g.



Barbatula barbatula, see Vinyoles et al 2010), existence of predators (e.g. Abbottina rivularis, see Yan and Chen 2007) and population density (e.g. Cottus nozawae, see Goto 1998). We did not investigate the difference in these factors between the upper and lower reaches. In the current study, the body condition was different between the two stations, possibly because of the difference in food supply. Further studies are needed to understand the system of intraspecific variability for *P. esocinus* in greater detail.

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