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Life history traits of the Chinese minnow *Rhynchocypris oxycephalus* in the upper branch of Yangtze River, China

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Abstract

Background: Study of the life history traits of any species plays an essential role for understanding their relationship with the surrounding environment and scientific management. The Chinese minnow *Rhynchocypris oxycephalus*, an ecologically and economically important species which was widely distributed in East Asia, is currently diminishing. In the present study, we depicted the main life history traits of *R. oxycephalus* for the first time.

Results: A total of 442 individuals were collected from April 2012 to March 2013, with total length (TL) ranging from 32.2 to 158.0 mm. The otolith (lapillus) was proved suitable for age determination. Moreover, the results from marginal increment ratio (MIR) analyses demonstrated its unusual growth pattern: two pairs of opaque and transparent bands were formed each year, which might provide some implications for the age determination of other species. The maximum age for females (4 years) was higher than for males (3 years), while 1- and 2-year-old individuals dominated the population. Both females and males reached maturity at 1 year, and the TL at first maturity was 78.8 mm for females and 60.3 mm for males. Obvious sexual dimorphism was observed as females growing faster and larger than males after maturity. As a multiple spawner, *R. oxycephalus* releases batches of eggs from April to August. The fecundity of *R. oxycephalus* was higher, and the size of eggs was larger than that of its closely related species.

Conclusions: *R. oxycephalus* is a short-lived, fast-growing, highly fecund, and early-maturing species; therefore, even a short recovery time after overexploitation or disturbance would be of great use for their restoration. Some life history traits of *R. oxycephalus* demonstrate obvious differences with its closely related species, indicating that latitude and local environment conditions are important selective forces for this species.

Keywords: Annuli; Otolith; Age determination; Growth pattern; Reproduction

Background

The *Rhynchocypris* minnows are typical small cold water fish, mainly distributed in Asia (Chen 1998). The Chinese minnow *Rhynchocypris oxycephalus* (Sauvage et Dabry, 1874) is an endemic species of East Asia, widely distributed from southern China to most parts of the Korean Peninsula and western Japan (Chen 1998; Park et al. 2001; Ito et al. 2002; Sakai et al. 2006; Bogutskaya et al. 2008; Takai et al. 2012). In China, *R. oxycephalus* is mainly

distributed in well-oxygenated montane stream headwaters of Yangtze River Basin (Chen 1998; Zhang and Chen 1997), at the southern-distribution boundary of *Rhynchocypris* minnows. In its inhabited streams, *R. oxycephalus* often has a large population, acting as the dominant species and playing a crucial role in maintaining the balance of stream ecosystem. Besides, as an important component of local fishery, *R. oxycephalus* also has economic importance. However, with the development of agriculture and industry, most river ecosystems are experiencing severe ecological degradation in China (Chen 2005), making the fish habitats more vulnerable. As indicated by Maxent models, 78.1% of the most suitable habitats for *R. oxycephalus* would disappear by 2080, and most range contractions would occur in southeastern China (Yu et al. 2012).

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Worsened by overfishing and water pollution, the population of *R. oxycephalus* is diminishing in recent years.

The life history traits of fish display geographical variations, which are considered as responses to local environment (Vinyoles et al. 2010; Grabowska et al. 2012), and explaining those variations is a central objective of evolutionary biology. Latitude is one of the most important factors that influence several life history traits of freshwater fish (Blanck and Lamouroux 2007). Compared with its closely related species (*Rhynchocypris*, *Phoxinus*, and *Chrosomus* minnows), *R. oxycephalus* in China is distributed in the lowest latitude regions. The life history traits of many populations of *Rhynchocypris*, *Phoxinus*, and *Chrosomus* minnows have been reported (Starnes and Starnes 1981; Mills and Eloranta 1985; Mills 1987, 1988; Hamed et al. 2008; Wang et al. 2012). However, for *R. oxycephalus*, this information is very limited. There have been only a few publications about its reproductive characteristics and distributions (Xiong 1984; Chen 1998; Yu et al. 2012). Knowing the life history traits of this species may contribute to better understanding of the influence latitude has on the life history traits of freshwater fish. In addition, it is also indispensable for their effective conservation and scientific management, for fundamental links existing between the individual life history and increasing rate of population (Hutchings 2002; Foster and Vincent 2004; Jia and Chen 2011). Both theoretical and empirical analyses showed that certain life history traits made the species more vulnerable to anthropogenic threats (Jennings et al. 1999; Sadovy 2001; Denney et al. 2002; Foster and Vincent 2004).

The objectives of the current study were to (1) present the key life history traits of *R. oxycephalus* under natural conditions, including its age, growth development, and reproduction, to provide essential information for their effective protection and scientific management and (2) compare those traits with its closely related species for better understanding of the influences of latitude and local environment on the stream fish community.

Methods

Study area

This study was carried out in the Laohegou Stream (E 104° 40′, N 32° 31′), a montane stream located in the upper Yangtze River drainage, south of China (Figure 1). This stream, with an elevation span of 763 to 1,948 m, drains a surface area of 110 km^2 over its 52-km length. It has a typical subtropical monsoon climate, characterized by rainfall mainly occurring in spring and summer. The mean water temperature ranges from 3.78°C (in December) to 19.8°C (in August), and annual mean water temperature is 11.04°C. Its 20-km upper reaches and surrounding areas have been established as the
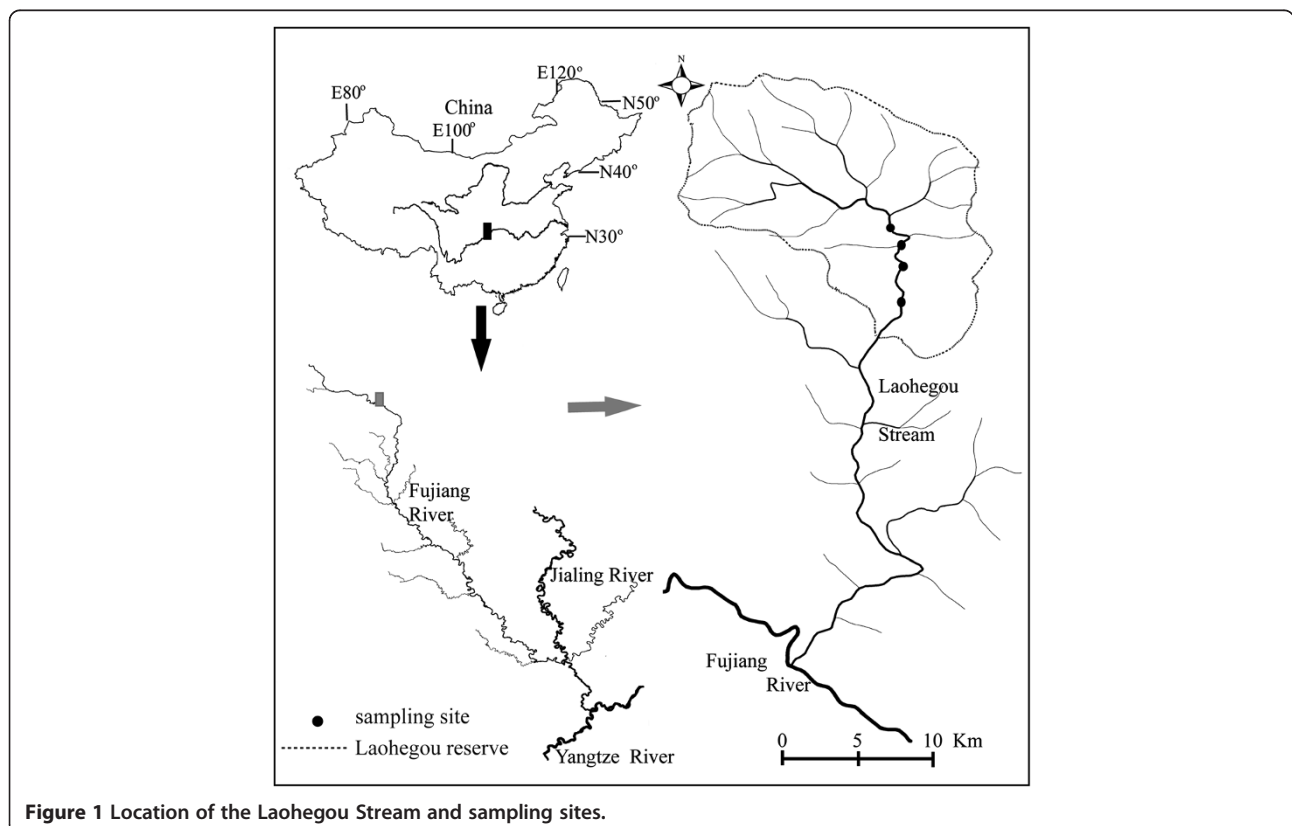
Figure 1 Location of the Laohegou Stream and sampling sites.

Laohegou Social Welfare Reserve, within which a large amount of *R. oxycephalus* is distributed.

Sample collection and procedures

From April 2012 to March 2013, 442 individuals were collected by electrofishing at monthly intervals (samplings of January and February 2013 were prevented by bad weather) from four sampling sites (Figure 1). The specimens were individually measured for total length (TL, 0.1 mm), standard length (SL, 0.1 mm), and weighted body weight (BW, 0.01 g) and dissected. Gonad of each specimen was weighted (gonad weight, GW, 0.01 g), inspected to determine the sex, and classified into six maturity stages (I-VI) based on the visual traits including profile, size, color, and vascularization, following Yin (1993). Somatic weight (SW, 0.01 g) of each specimen has also been recorded. Scales, vertebrae, opercula, dorsal fin spine, and three couples of otolith (asteriscus, lapillus, and sagitta) of each specimen were extracted to determine the age. All processed specimens and mature ovaries at stage IV were preserved in 8% neutralized formaldehyde solution. Besides, eight environmental variables were recorded during each sampling: longitude, latitude, elevation, dissolved oxygen, wetted width, water depth, water temperature, and current velocity.

Age

To determine age, every aging material was prepared following Chen et al. (2002). We chose the lapillus for age determination after analyzing and comparing the materials above. For the lapillus, respective distance from the nucleus to the edge (radius, R) and to the distal edge of each opaque band (r) along the reading zone was measured to the nearest 1 μm. The periodicity of annulus formation was determined by monthly changes of marginal increment ratio (MIR), using the following equation: $MIR = (R - r_n) / (r_n - r_{n-1})$, where r_n is the distance between the nucleus and the outer margin of the last opaque mark (Casselman 1987). Age estimation was performed independently by two readers without information of size. Samples with identical readings were used in further age and growth analysis. Ages were also verified using length frequency distribution. Identification of the first annulus in lapillus was confirmed by comparing the total length back-calculated from the first annual to the first peak of total length distribution (Mills 1987).

Growth

The relationship between TL and BW was described by the exponential equation: $BW = aTL^b$, where a is the intercept and b is the slope of the regression curve. Difference between sexes for the TL-BW relationship (LWR) was tested using analysis of covariance (ANCOVA) (Sokal and Rohlf 1995). The relative condition factor (K_N) was used to describe seasonal fluctuations of fish plumpness (Le Cren 1951), which was calculated as $K_N = SW/PW$, where PW is the predicted somatic weight at its total length by the TL-SW relationship, and SW is the measured somatic weight. To back-calculate the TL at age, the relationship between TL and radius was described by linear regression: $TL = a + bR$, where R is the radius of lapillus, and a and b are both constants. TL at age was obtained using the Fraser-Lee equation (Duncan 1980): $TL_n = a + (TL - a)r_n / R$, where TL is the measured total length, TL_n is the back-calculated total length (BCL) at age n, a is the intercept in TL-R linear function, and r_n is the distance between core and the nth annulus. The von Bertalanffy growth formula (VBGF) (von Bertalanffy 1938) was used to describe the growth curve that fitted to back-calculated data: $TL_t = L_\infty[1 - e^{-k(t - t0)}]$, where TL_t is the predicted TL at age t (year), L_∞ is the theoretical maximum TL, k is the growth rate parameter (year^{-1}) describing the rate that fish reach L_∞, and t_0 is theoretical initial age (year) when TL is zero. All those parameters were estimated by the least square method. Back-calculation of the VBGF was fitted to males and females, respectively. The growth performance index (φ') was calculated as $\varphi' = 2\log_{10}L_\infty + \log_{10}k$ (Munro and Pauly 1983). The growth inflexion age t_i (year) was calculated as $t_i = (\ln b) / k + t_0$ (Yin 1993), where b is the one in the equation of BW-TL, and k and t_0 were estimated from the VBGF.

Reproduction

To calculate the TL at first maturation (TL$_m$, TL at 50% maturity), the proportion of mature individuals per 5-mm TL intervals was fitted to a logistic function $Pi = 100(1 + e^{-(a + bTL)})^{-1}$, where Pi is the proportion of mature individuals in TL class i, and a and b are both constants. The TL$_m$ was calculated as $TL_m = -ab^{-1}$ (King 1995). To describe the reproductive effort and gonadal annual cycle, the monthly gonado-somatic index (GSI) was calculated (Yin 1993): $GSI = 100(GW/SW)$, where GW is gonad weight and SW is somatic weight. The annual fecundity (F) was estimated as the total number of ripening and ripe oocytes from mature ovaries before spawning (Yin 1993), and relative fecundity (RF) was calculated as (Bagenal 1978) $RF = F/SW$. To analyze size frequency distribution of egg diameter in ripened gonads, the diameters of 80 to 100 randomly sampled oocytes were measured during breeding season. Sex ratio was calculated, and its difference from 1:1 was tested by χ^2 test (Zar 1999). The present study was carried out following permission issued from the Hubei Province Association for Laboratory Animal Sciences.
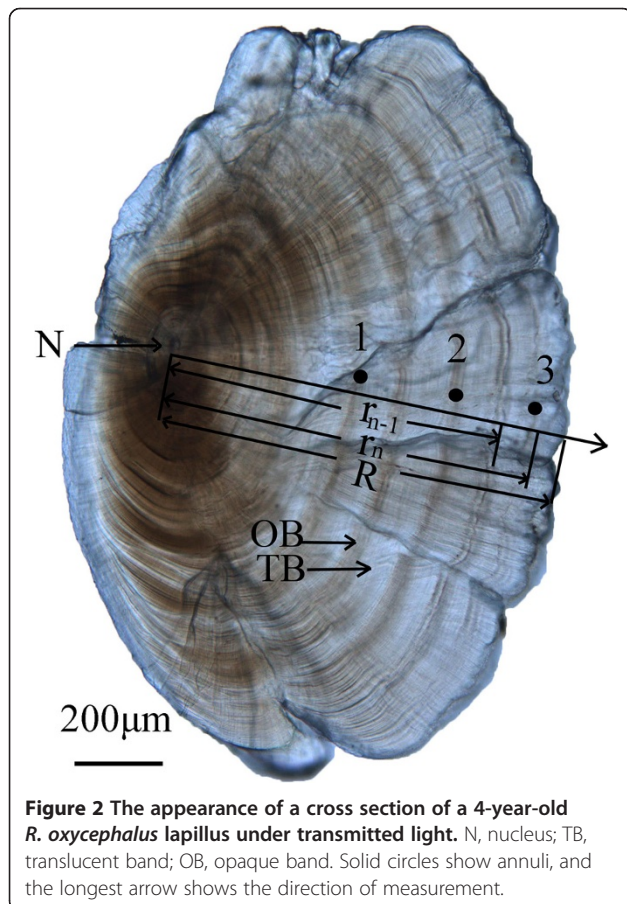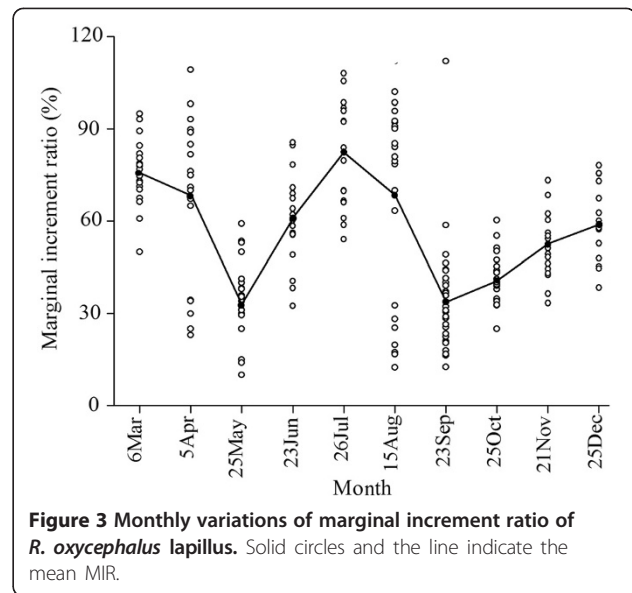
Results

Age

The sectioned lapillus showed clear nucleus and alternating opaque and translucent bands under transmitted

light (Figure 2). Monthly variations of MIR showed double cyclical trend of increment within 1 year (Figure 3). In April and August, the mean MIR decreased while the range of MIR increased, indicating that the opaque band was completed and a new translucent band began to form. Most lapilli taken from specimens in the first peak of total length frequency distribution (70 to 90 mm) (Figure 4) were forming (36.8%) or just formed (46.6%) their first opaque band. Thus, we considered the first opaque band as their first annulus. We concluded that the lapillus formed one pair of opaque and translucent bands in its first year and then two pairs every year. Consequently, *R. oxycephalus* in this study was aged as follows: individuals with none or one just-formed opaque band were in age 1 group, individuals with one or two opaque bands or having its third opaque band just formed were in age 2 group, individuals with three or four opaque bands or having its fifth opaque band just formed were in age 3 group, and so on for other individuals. The percent agreement among two readers was 94.1%, and the coefficient of variation (CV) was 9.5%.

For all collected individuals, 153 were identified as females (52.9 to 158 mm, TL), 258 males (46.8 to 123.6 mm, TL), and 31 juveniles (32.2 to 84.3 mm, TL) too young for
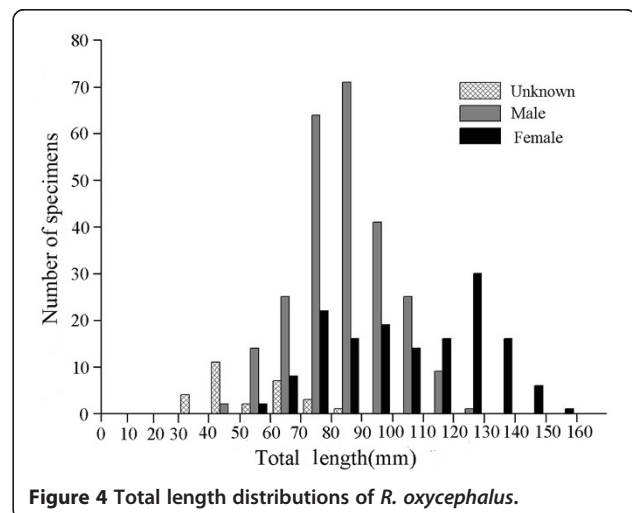

Figure 3 Monthly variations of marginal increment ratio of *R. oxycephalus* lapillus. Solid circles and the line indicate the mean MIR.

sex identification. The sex ratio (females/males) was 1:1.69, which is significantly different from 1:1 ($\chi^2 = 26.4$, $df = 1$, $P < 0.05$). Using the sectioned otolith, 416 specimens were successfully aged, and three age groups for males and four age groups for females were observed. Individuals of age 1 (63.7%) and age 2 (25.5%) groups dominated the population; only 2.7% males were in age 3 group and 5.2% females in age 4 group.

Growth

The TL-BW equations were as follows: $BW = 1.3 \times 10^{-5} TL^{2.9298}$ ($r^2 = 0.9578$, $n = 258$, $P < 0.05$) for males and $BW = 4.9 \times 10^{-6} TL^{3.1543}$ ($r^2 = 0.9665$, $n = 153$, $P < 0.05$) for females. These equations were significantly different between sexes (ANCOVA, $df = 409$, $P < 0.05$). The value of K_N showed two peaks, in March and August, throughout the year. The females and males presented similar

Figure 2 The appearance of a cross section of a 4-year-old *R. oxycephalus* lapillus under transmitted light. N, nucleus; TB, translucent band; OB, opaque band. Solid circles show annuli, and the longest arrow shows the direction of measurement.


Figure 4 Total length distributions of *R. oxycephalus*.

fluctuating patterns of K_N (Figure 5). The relationship between TL and R was calculated as TL = 33.907 + 129.1R ($r^2 = 0.8357$, $n = 140$, $P < 0.05$) for females and TL = 44.46 + 93.1R ($r^2 = 0.6702$, $n = 210$, $P < 0.05$) for males. The difference between the two equations was significant (ANCOVA, $df = 348$, $P < 0.05$). The back-calculated TLs at ages (TLs at 3 years for males and at 4 years for females were acquired by measuring the full age individuals) are presented in Table 1. The body size of males was slightly larger than that of females at age 1 year (t test, $df = 154$, $P < 0.05$) but was smaller at age 2 years (t test, $df = 81$, $P < 0.05$) and age 3 years (t test, $df = 18$, $P < 0.05$). The length and weight at age for females were described by the VBGF (Figure 6) as TL = 220.56[1 − e$^{-0.251(t\ +\ 0.80)}$] and BW = 120.89[1 − e$^{-0.251(t\ +\ 0.80)}$]$^{3.1543}$. The VBGF for males was not calculated as their age structure was too simple. Based on L_∞ and k values in VBGF, the growth performance index (φ') was 4.09 years and the growth inflexion (t_i) was 3.78 years for females. The relationship between TL and SL was described by SL = 0.8279TL − 0.3439 ($r^2 = 0.9963$, $n = 422$, $P < 0.05$).

Reproduction

Both females and males reached 50% maturity at 1 year. The TL_m was 60.3 mm for males and 78.8 mm for females (Figure 7). Among sampled mature individuals, the minimum TLs were 53.6 and 60.0 mm for males and females, respectively. The monthly variations of GSI presented similar seasonal patterns for females and males (Figure 8). In August, only 9.8% individuals have mature gonad at stage V, and no mature gonad was found in September. Therefore, the breeding season for *R. oxycephalus* in the Laohegou Stream was carried out from April to August.
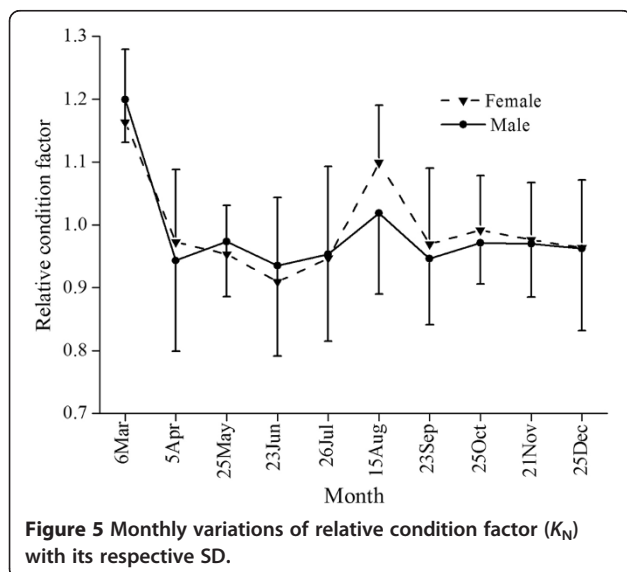
Table 1 Back-calculated total length at age of *R. oxycephalus*

Age (years)	Female	Male
1	80.11 ± 7.06 ($n = 81$)	82.75 ± 4.76 ($n = 75$)
2	111.21 ± 9.87 ($n = 54$)	98.92 ± 6.45 ($n = 29$)
3	135.81 ± 8.15 ($n = 15$)	110.42 ± 1.42 ($n = 5$)
4	154.5 ± 2.89 ($n = 4$)	

Mean ± SD (n = number of individuals measured).

The ripened ovaries of *R. oxycephalus* contained groups of oocytes of different sizes, especially at the beginning of the spawning season (Figure 9). In April, ripened oocytes (opaque) constituted about 50% of all oocytes in ripened ovaries (Figure 9A), and ripening oocytes (semi-transparent) constituted about 35%; from late June to August, the ripened oocytes constituted about 85% of all oocytes in ripened ovaries, while few ripening oocytes were found (Figure 9D,E). It can be concluded that the *R. oxycephalus* is a multiple spawner that releases at least two groups of oocytes during breeding season.
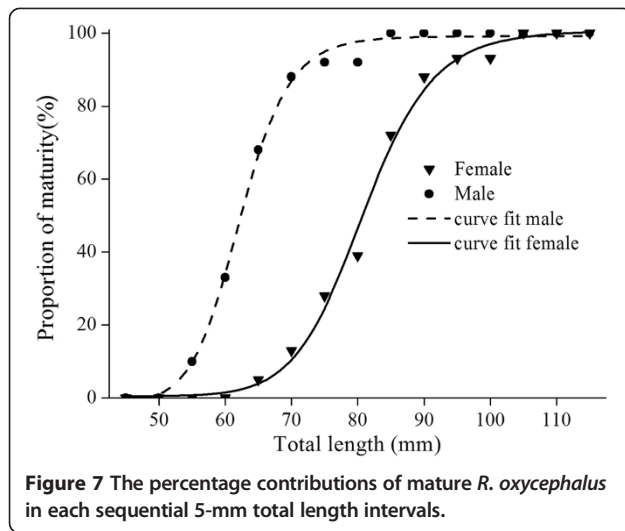
In April and May, 27 mature ovaries (at gonadal stage IV) were collected to estimate the annual fecundity (F). The mean F of *R. oxycephalus* was 2,457 oocytes, ranging from 751 (TL at 78.1 mm) to 5,189 (TL at 154.2 mm). The fecundity was correlated with TL, specified by $F = 0.1848TL^{2.0073}$ ($r^2 = 0.7319$, $n = 27$, $P < 0.05$). Mean relative fecundity was 150 oocytes/g, ranging from 88 oocytes/g to 220 oocytes/g.

Discussion

Otolith growth pattern

Otolith is one of the most frequently used aging structures (Campana 2001; Campana and Thorrold 2001). Its sequence of increment is interrupted by checks or discontinuities that mark the occurrence of stressful

Figure 5 Monthly variations of relative condition factor (K_N) with its respective SD.

Figure 6 Growth curves of total length in VBGF derived from the back-calculated data.

Figure 7 The percentage contributions of mature *R. oxycephalus* in each sequential 5-mm total length intervals.
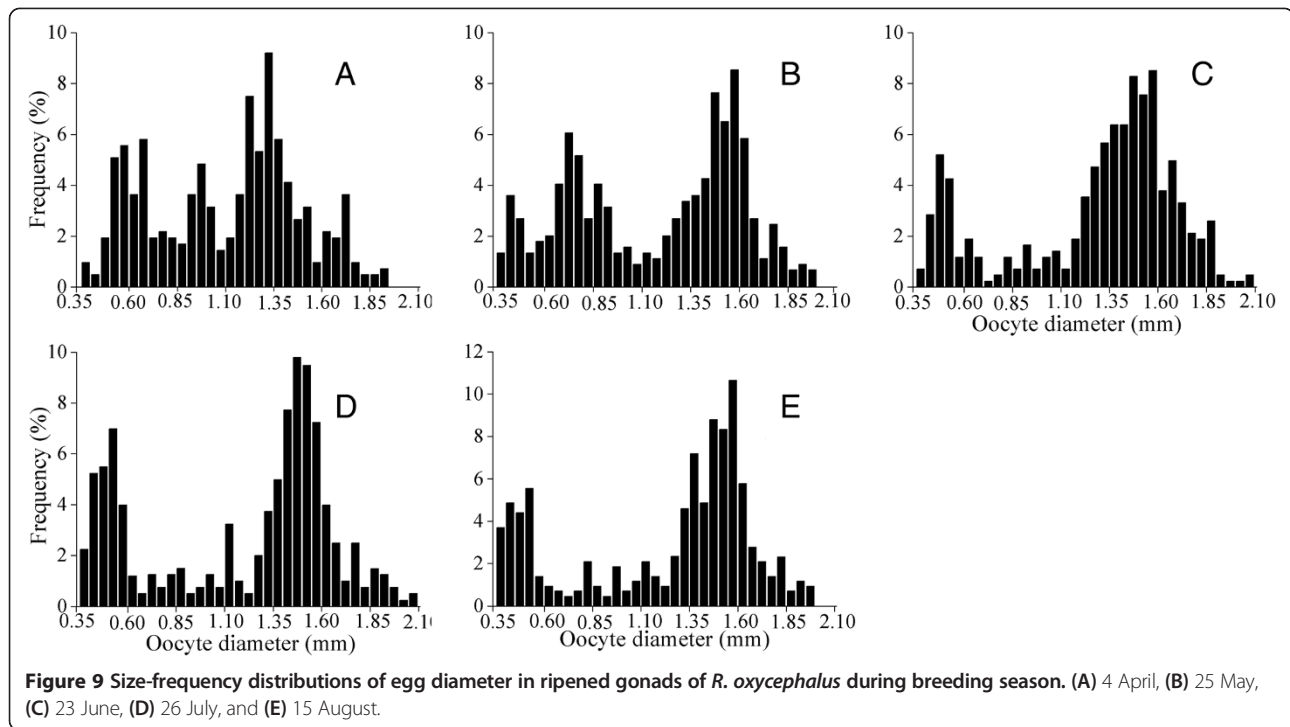
periods in the life of the fish (Pannella 1974, 1980; Campana 1983; Chen et al. 2002). For riverine fishes, the formation of increments and discontinuities of otolith is mainly influenced by water temperature, water level, and reproductive activity (Welcomme 1979; Mills 1987). In our study, the monthly variations of MIR showed that the otolith of *R. oxycephalus* formed two translucent discontinuous bands during May to early July and September to February, and two opaque incremental bands during March to April and late July to August, separately. We speculated that the first discontinuity (formed during May to July) was mainly caused by the reproductive activity, while the second one (formed during September to February) was mainly caused by the low water temperature and decreased water level. Due to energetic trade-off between somatic growth and reproduction,

Figure 8 Monthly variations of gonado-somatic index with its respective SD.
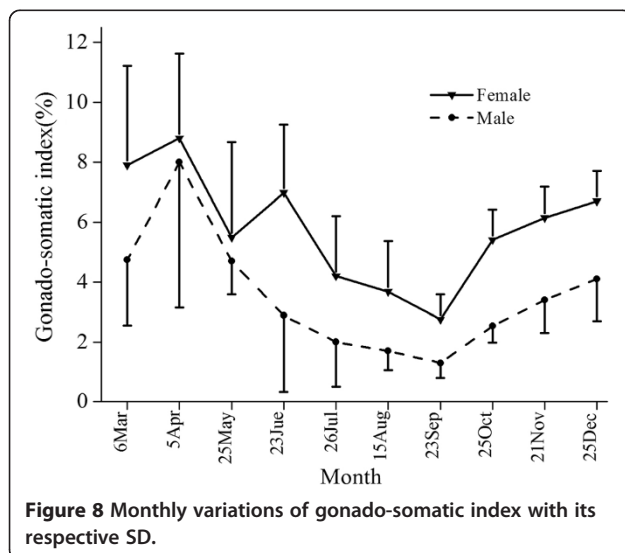
increasing reproductive effort can lead to decreasing somatic growth rate (Kozlowski 1996; Joanna et al. 2011). During breeding season, the feeding rate of *R. oxycephalus* decreased (unpublished data) while the reproductive effort sharply increased, which, as a result, would put stress on somatic growth. Results from our survey indicated that the rainfall in Laohegou Stream drainage mainly occurred from April to early September, and the water level and the abundance of bait shrunk sharply since mid-September. Along with increasing GSI, large amount of energy would be devoted to the development of gonad. Therefore, the stress of somatic growth of *R. oxycephalus* increased since then. This provides a possible explanation to why the winter in Laohegou Stream drainage began in November, but the forming of the second discontinuity on otolith began in September. The monthly variations of K_N, a useful index for assessing the condition of fish independent of fish size (Baigun et al. 2009; Llompart et al. 2013), coincided with our speculation. The K_N of *R. oxycephalus* showed two peak values in March and August, just when the two opaque bands were forming; when the two translucent bands were forming, the value of K_N was low. Mills (1987) suggested that two translucent bands formed on the otolith of *Phoxinus phoxinus* during summer and winter in southern England; a similar growth pattern was also suggested for the vertebrae of sharks (Pratt and Casey 1983; Branstetter and Musick 1994; Natanson et al. 2002).

Growth
R. oxycephalus in our study presented larger maximum observed TL and faster growth rate than most of its closely related species (Table 2), especially in the early life stage (Figure 10). Results from BCL showed that a large part of individuals had already attained 50% of the maximum observed TL by age 1 year (Figure 6). The fast growth in the early life stage is a common life history trait adopted by fish living in fluctuating environments like Laohegou Stream (Herrera and Fernandezdelgado 1994; Aparicio and de Sostoa 1998; Ribeiro et al. 2000; Vinyoles et al. 2010), as a bigger body attributes to survive their first harsh season (Baras and Philippart 1999; Duponchelle et al. 2007), i.e., winter. As proved, the growth rate of fish usually varies along the latitudinal gradient (Heibo et al. 2005; Blanck and Lamouroux 2007). The fast growth of *R. oxycephalus* in this study might relate to its lowest latitude distribution. TL distribution and BCL at each age indicated that females grow faster than males and dominated the larger size groups. Larger body could induce females to contribute more energy to reproduction and producing more offspring (Parker 1992), which is significant for the *R. oxycephalus* to maintain its population in the fluctuating environment. The WLR of *R. oxycephalus* was similar to that of its closely related species (Table 2).
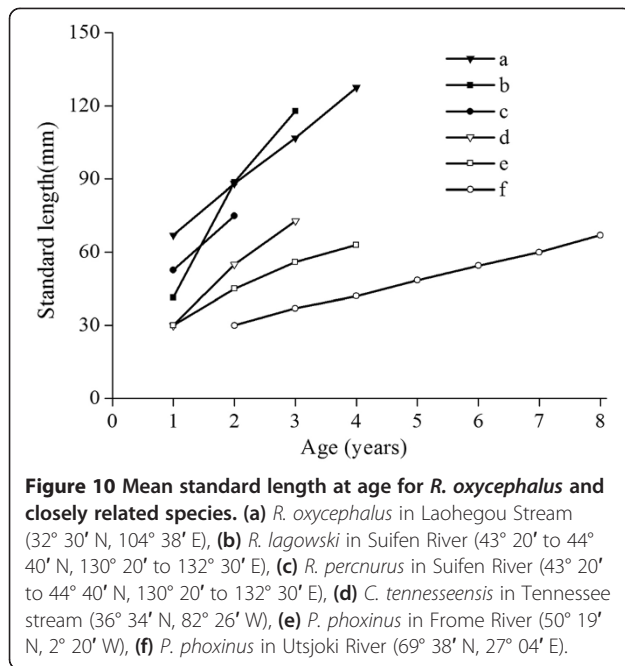
Figure 9 Size-frequency distributions of egg diameter in ripened gonads of *R. oxycephalus* during breeding season. (A) 4 April, **(B)** 25 May, **(C)** 23 June, **(D)** 26 July, and **(E)** 15 August.

Reproduction

The logistic model indicated that 50% sexual maturity of *R. oxycephalus* occurred at 1 year when they reached an SL of 64.9 mm for females and 49.6 mm for males. The age at maturity of its closely related species showed gradual changes along the latitudinal gradient, from 1 to 2 years and up to 6 years, while their SLs at maturity were similar (Table 3). Commonly, the age at maturity would be affected by environmental determinants of growth; populations in lower latitude regions often need less time to reach size for maturation (Clarke et al. 2007). The size and age at sexual maturity are important life history traits, which have profound influence on other life history characteristics such as ultimate body size, mortality, and reproductive success (Stearns 1992; Bernardo 1993; Roff 2002; Barthel et al. 2008). For example, early maturity has side effect on longevity, somatic growth, and fecundity (Heino et al. 2002). The results from the back-calculation of the only four full 4-year aged individuals showed that their SLs at 1 year were 53.53, 56.78, 57.2, and 57.61 mm, respectively, and their mean SLs at each age were 56.3 mm (1 year), 89.4 mm (2 years), and 120.2 mm (3 years). Those results indicated that none of these four individuals reached maturity at 1 year and their mean growth rate after 1 year was higher than the average of the whole population. So we speculated that early maturity has side effect on the longevity and somatic growth of *R. oxycephalus*.

Table 2 Length-weight relationship parameters of *R. oxycephalus* and closely related species

Species	Location	Coordinates	n	a	b	Length range (mm)	r^2	Source
R. oxycephalus	Laohegou Stream	32° 31′ N, 104° 40′ E	258	1.3×10^{-5} (♂)	2.930	46.8 to 123.6 (TL)	0.9578	Present study
			153	4.9×10^{-6} (♀)	3.154	52.9 to 158.1 (TL)	0.9665	
R. lagowskii	Suifen River	43° 20′ N, 130° 20′ E	193	3.67×10^{-5}	2.81	24 to 138 (SL)	0.93	Wang et al. (2012)
R. percnurus	Suifen River	43° 20′ N, 130° 20′ E	37	7.91×10^{-5}	2.65	32 to 88(SL)	0.92	Wang et al. (2012)
C. cumberlandensis	Young's Creek	37° 15′ N, 76° 43′ W	50	1.88×10^{-5} (♂)	3.52	20 to 67.5 (SL)	0.98	Starnes and Starnes (1981)
				1.86×10^{-5} (♀)	2.90		0.94	
P. phoxinus	Atares River	42° 45′ N, 0° 14′ W	27	9.1×10^{-6}	3.085	31.0 to 74.0 (TL)	0.942	Leunda et al. (2006)
P. phoxinus	Middle Gallego	42° 32 N′, 0° 19′ W	224	5.4×10^{-6}	3.349	50.0 to 94.0(TL)	0.929	Leunda et al. (2006)
P. phoxinus	Larraun River	42° 57′ N to 1° 50′ W	336	4.2×10^{-6}	3.421	22.0 to 84.0 (TL)	0.97	Oscoz et al. (2005)
P. phoxinus	France	-	-	1.07×10^{-5}	3.118	-	-	Oscoz et al. (2005)

Figure 10 Mean standard length at age for *R. oxycephalus* and closely related species. (a) *R. oxycephalus* in Laohegou Stream (32° 30′ N, 104° 38′ E), **(b)** *R. lagowski* in Suifen River (43° 20′ to 44° 40′ N, 130° 20′ to 132° 30′ E), **(c)** *R. percnurus* in Suifen River (43° 20′ to 44° 40′ N, 130° 20′ to 132° 30′ E), **(d)** *C. tennesseensis* in Tennessee stream (36° 34′ N, 82° 26′ W), **(e)** *P. phoxinus* in Frome River (50° 19′ N, 2° 20′ W), **(f)** *P. phoxinus* in Utsjoki River (69° 38′ N, 27° 04′ E).

Our study showed that in Laohegou Stream, *R. oxyce-phalus* spawned from April to mid-August, which was similar with *P. phoxinus* in Frome River and Utsjoki River (Mills 1987, 1988). For *Chrosomus tennesseensis* in Tennessee Stream and *Chrosomus cumberlandensis* in Young's Creek, spawning occurred from April to July (Starnes and Starnes 1981; Hamed et al. 2008). *P. phoxinus* in Konnevesi Lake showed delayed and shortened spawning period, from May to July (Mills and Eloranta 1985). Spawning at an appropriate time plays a crucial role for successful reproduction of fish (Lowe-McConnell 1987; Wootton 1990). For fishes living in fluctuating waters, the spawning season often coincides with local annual flood (Welcomme 1979; Goulding 1980), because flood brings abundant organics from the terrestrial ecosystem into the river ecosystem, increasing the food availability and providing more suitable breeding habitats (Goulding 1980; Lowe-McConnell 1987; Alkins-Koo 2000). The spawning season of *R. oxycephalus* in Laohegou Stream was almost simultaneous with local main rainfall period (from April to early September).

The size frequency distribution of oocytes during the spawning season indicated that *R. oxycephalus* produced batches of oocytes at different times. Repeated spawning over a long breeding period could help avoid a very high density of juveniles at one time, making better use of the diets and thus improving the survival rate of juveniles (Cambray and Bruton 1984; Burt et al. 1988; Vinyoles et al. 2010). This is an important life history trait especially for the fish living in fluctuating environments since it contributes to the recruitment of the populations (Nikolsky 1963). Commonly, the fecundity was positively associated with body size (Wootton 1990). The *R. oxycephalus* in Laohegou Stream presented the highest fecundity and the largest oocyte among its closely related species that have been reported (Table 3). This is possibly attributable to its large body size. It is well known that larvae hatched from larger oocytes tend to survive better (Ware 1975; Mann and Mills 1979). Early maturity, added by long breeding period and high GSI, indicated a high reproductive effort of *R. oxycephalus*.

Conclusions

In conclusion, *R. oxycephalus* is a short-lived, fast-growing, early-maturing, and highly fecund species. Therefore, even a short recovery time after overexploitation or disturbance would be of great use for their restoration. Many life history traits of *R. oxycephalus* are typical traits for species inhabiting fluctuating waters, indicating its great fitness to local environment. Compared with its closely related species that are distributed in higher latitude regions, *R. oxycephalus* grows faster and matures earlier, which may be responses to lower latitude distribution and local environmental conditions.

Table 3 Reproduction parameters of *R. oxycephalus* and closely related species

Species	Location	Coordinates	Ripe egg diameter (mm)	SL_m for female (mm)	SL_m for male (mm)	Mature age (year)	Spawn season	Fecundity (mean ± SD)
R. oxycephalus	Laohegou Stream	32° 31′ N, 104° 40′ E	1.52	64.9	49.6	1	April to August	2,457 ± 1,056
C. tennesseensis	Tennessee Stream[a]	36° 34′ N, 82° 26′ W	1.2	48.1	48.1	2	April to July	556 ± 46
C. cumberlandensis	Young's Creek[b]	37° 15′ N, 76° 43′ W	0.82 to 1.36	-	-	1	April to July	1,540
R. lagowskii	Suifen River[c]	43° 20′ N, 130° 20′ E	-	73.0	66.0	2	-	2,142 ± 467
R. percnurus	Suifen River[c]	43° 20′ N, 130° 20′ E	-	68.0	67.0	2	-	2,567 ± 303
P. phoxinus	Frome River[d]	50° 19′ N, 2° 20′ W	1.3	50	50	2	April to August	380
P. phoxinus	Lake Konnevesi[e]	62° 36′ N, 26° 31′ E	1.2	50.9	50.9	2	May to July	632.6 ± 112
P. phoxinus	Utsjoki River[f]	69° 41′ N, 27° 06′ E	1.2	56.2	57	6	April to August	824

[a]Hamed et al. (2008); [b]Starnes and Starnes (1981); [c]Wang et al. (2012); [d]Mills (1987); [e]Mills and Eloranta (1985); [f]Mills (1988).

Abbreviations

ANCOVA: analysis of covariance; BCL: back-calculated total length; BW: body weight; CV: coefficient of variation; F: annual fecundity; GSI: gonado-somatic index; GW: gonad weight; LWR: total length-body weight relationship; MIR: marginal increment ratio; PW: predicted somatic weight; R: radius; RF: relative fecundity; SL: standard length; SW: somatic weight; TL: total length; TL_m: TL at 50% maturity; VBGF: von Bertalanffy growth formula.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

YL carried out the experiments and drafted the manuscript. XS and YC participated in the design and coordination of the study. YJ and DH participated in sample collection and data analysis and revised the manuscript. XS finalized the manuscript. All authors read and approved the final manuscript.

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