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Age, growth and mortality of invasive sharpbelly, *Hemiculter leucisculus* (Basilewski, 1855) in Erhai Lake, China

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Summary

The sharpbelly *Hemiculter leucisculus*, an invasive species, has expanded its range throughout much of Asia and into the Middle East. However, little is known of its adaptive changes regarding life history traits such as age, growth and mortality that could possibly explain its success as an invasive species. A detailed study of the invasive sharpbelly was conducted based on 4539 samples collected from July 2009 to June 2011 in Erhai Lake, China. Standard length ranged from 4.3–19.1 cm for females and 4.6–12.3 cm for males. Length–weight relationships for females and males were significantly different and described as $W = 0.0076SL^{3.2608}$ and $W = 0.0084SL^{3.1901}$, respectively. Otoliths are ideal for age determination because of the single annulus formed each year. Based on marginal increment analysis, the total mean CV for age estimate between two readings was 3.55%. The von Bertalanffy growth curves computed by observed length-at-age data were expressed as $L_t = 25.6\ (1 - e^{-0.176\ (t\ +\ 1.347)})$ for females and $L_t = 16.4\ (1 - e^{-0.354\ (t\ +\ 0.819)})$ for males. According to the age, growth and mortality data, there are three possible reasons for *H. leucisculus* attaining such dominance within a short time in Erhai Lake. First, because of the simple age structure of this species: 97.58% of males were 1–2 years old with a maximum age of only 3 years; 93.14% of females were 1–3 years old, with a maximum age of 6 years. Second, females grew larger than males at any age. Third, instantaneous mortality rates were much higher for males (4.22 $year^{-1}$) than for females (1.17 $year^{-1}$).

Introduction

Sharpbelly *Hemiculter leucisculus* (Basilewski, 1855) is a small cyprinid fish with an original distribution extending from China, Korea, Vietnam, to the far-eastern region of Russia (Dai and Yang, 2003; Nelson, 2006) and is the dominant species in many of the water bodies in those regions (Gao et al., 2010; Tan et al., 2010). Apparently through the associated movement of aquaculture fish species, the sharpbelly has invaded many other countries including Iran (Holcik and Razavi, 1992; Patimar, 2008; Esmaeili and Gholamifard, 2011), Iraq (Coad and Hussain, 2007), Kazakhstan (Petr and Mitrofanov, 1998), Afghanistan (Coad, 1981), Uzbekistan (Borisova, 1972), Turkmenistan (Sal'nikov, 1998), and Russian Federation (Kolpakov et al., 2010). In Erhai Lake, the largest fault lake in the western Yunnan Plateau, *H. leucisculus* was first identified in 2004. It has now become the dominant species and one of the important commercial fishing species in Erhai Lake according to our 2009–2010 investigation.

By analyzing how *H. leucisculus* became the dominant species within a short time in Erhai Lake, we can improve our understanding of its adaptation to the new habitat and its invasive ability. Age and growth are important to elucidate these mechanisms because they can reveal the life history strategy of this fish, which is part of understanding the invasion. There are many studies on the age and growth of *H. leucisculus* in its native ecosystems (Xie et al., 1986; Sun, 1987; Cao and Wen, 1996; Li et al., 2009). In the invaded ecosystems, however, only Patimar (2008) did research in three lakes of Iran. These studies are all based on age assessment from scales, a less precise method than using otoliths. The object of the present article was to describe the age, growth and mortality of invasive *H. leucisculus* in a new habitat by using otoliths, and to compare the calcified structure method with the length–frequency analysis method in the evaluation of age and growth. Another study objective was to analyze the mechanisms influencing the species enabling it to become a successful invasive species in Erhai Lake.

Materials and methods

Study site

Erhai Lake (100°05′-17′E, 25°35′-58′N, altitude: 1974 asl) is located north of Dali City in Yunnan Province, southwestern China (Fig. 1). The lake is 42 km in length and 8.4 km in maximum width with a surface area of 249.8 km^2, an average water depth of 10.5 m and a maximum depth of 20.9 m. Annual average temperature is 15°C and precipitation 1.060 mm, with a potential evaporation of 1.970 mm $year^{-1}$ in this subtropical monsoon climate zone.

In Erhai Lake, there were 17 indigenous fish species, including eight endemic species. As of 1960, many small fish, such as *Pseudorasbora parva* and *Ctenogobius giurinus*, were accidentally introduced into Erhai Lake in association with the introduction of the four major Chinese carps used for aquaculture. Consequently, indigenous fish gradually declined to just eight species by 1998 (Du and Li, 2001); by 2010, there were only five species remaining, two of which are maintained by stocking.

Collection of samples

All 4539 specimens of *H. leucisculus* were obtained from 10 sites in Erhai Lake, southwestern China (Fig. 1) either monthly or bimonthly from July 2009 to June 2011. They were caught by gill nets with an inner mesh of 30 mm and an outer mesh of 110 mm. In addition, juvenile *H. leucisculus* samples were collected by purse-seine with a mesh size of

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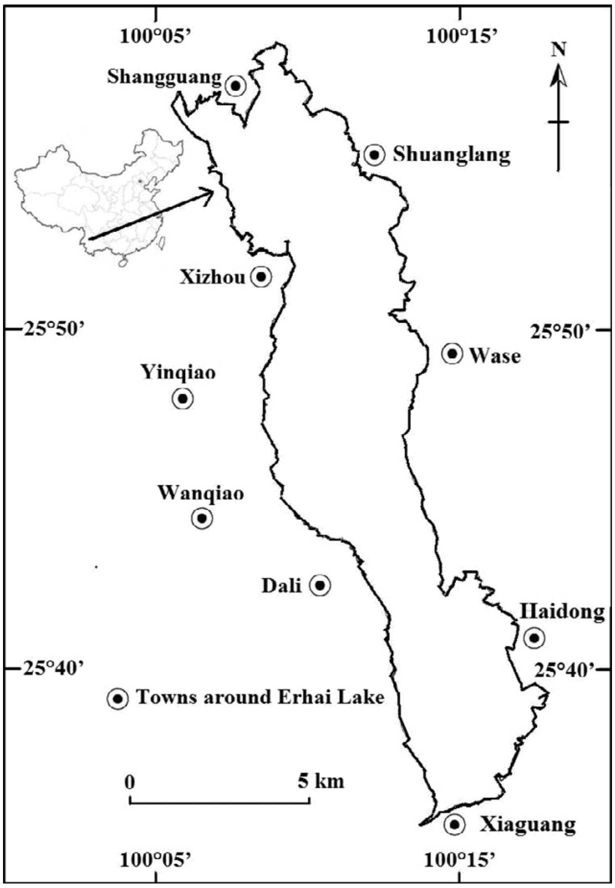

Fig. 1. Study area of *Hemiculter leucisculus* in Erhai Lake. All samples collected near the towns of Dali, Xizhou, Shuanglang, Wase and Haidong

3 mm, as well as by trap nets. Standard length (SL, 0.1 cm) and weight (W, 0.1 g) were recorded and the sex determined by macroscopic inspection of the gonads. Because sagittal otoliths are acicular and fragile, and asteriscus otoliths are flaky, only the lapillus otoliths were extracted, cleaned, and stored dry in labeled tubes.

Length–weight relationship

We used the Kolmogorov–Smirnov test (K–S test) to examine the difference in SL distributions between sexes. The relationship between standard length and weight ($W = \mathrm{aSL}^{\mathrm{b}}$) was converted into its logarithmic expression: $\ln W = \ln a + b \ln L$ (Ricker, 1975). Parameters a and b were calculated by least-squares regression. An analysis of covariance (ANCOVA) was used to compare SL–W relationships between sexes. Student's *t*-test was applied to verify if the b value was significantly different from the isometric expected value of 3 (Pauly, 1984).

Age estimate

Opaque zones in the otoliths were interpreted twice by one reader with no prior information on the sex, length, or capture time. The first and second counts were made with an interval of at least 2 weeks. Counts were accepted only when both counts by the same reader were in agreement. If the estimated numbers of bands differed, the otolith was recounted and the final count was accepted as the agreed number. If the third count did not match either of the previous two counts, the specimen was discarded (Joung et al., 2008). Otoliths were placed in xylene and examined under a binocular microscope (10×) with reflected or transmitted light. The number of opaque bands was recorded (Fig. 2).

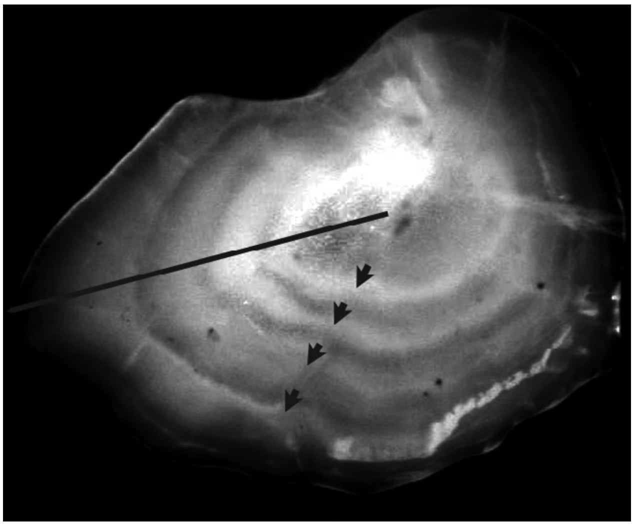

Fig. 2. Lapillus under a compound microscope with reflected light, from an age 4 (14.8 cm SL) *Hemiculter leucisculus*. Line = axis for measuring the radius; arrows = annuli

To validate the first growth increment, the radius of young-of-year otoliths at the time of annulus formation was measured (Campana, 2001). Otoliths were obtained from 32 fish (<7 cm) captured in the spring surveys, presumably when the first annulus is laid down.

The marginal increment ratio (MIR) was used to examine the periodicity of opaque zone formation in otoliths. The monthly MIR changes were estimated with the formula:

$$\mathrm{MIR} = (R - R_n)/(R_n - R_{n-1}),$$

where R is the otolith radius, R_n is the radius of the last complete zone, and R_{n-1} is the radius of the penultimate complete zone (Haas and Recksiek, 1995). Measurements were made along the axis (Fig. 2) using FishBC 3.0. Photographs were taken using the Leica Application Suite (version 15) with a CCD (charge coupled device) connected to the dissecting microscope and the computer.

A birth date of 1 July was assigned to individuals in the age groups. The index of the coefficient of variation (CV) (Campana et al., 1995; Campana, 2001) was calculated to assess the level of precision of age interpretations. Systematic differences in estimated age (bias) within readings were assessed by age bias plot.

Growth

von Bertalanffy growth curves, based on length-at-age from all age readings, were fitted separately for males and females by non-linear regression: $L_t = L_\infty(1 - e^{-k(t-t_0)})$, where L_t is the length at age t, L_∞ is the asymptotic length, k is the growth coefficient, and t_0 is the age at length 0. The growth performance index (Ø) was calculated based on the growth parameter estimates by the equation of Munro and Pauly (1983):

$$\emptyset = \log_{10} k + 2\log_{10} L_\infty.$$

The index was used to compare growth parameters obtained in this study with those reported by other authors.

Length–frequency analysis

All fish specimens were grouped into length classes at 1 cm intervals. Length frequency distributions were analyzed using the FiSAT (FAO-ICLARM Stock Assessment Tools) software (Gayanilo et al., 2002). The Powell-Wetherall plot program in FiSAT II was applied to estimate the asymptotic length (L_∞). According to the L_∞, the growth coefficient (k) was then estimated by the ELEFAN I program in FiSAT II.

Mortality

To calculate the total instantaneous annual mortality rate (Z), the length-converted catch curve (Pauly, 1983; Munro, 1984) was applied to the pooled length frequency data using the estimated growth parameter. The calculation was done using the FiSAT program (Gayanilo and Pauly, 1997).

Natural mortality was calculated by Pauly's empirical equation:

$$\log M = -0.2107 - 0.0824 \log W_\infty + 0.6757 \log k + 0.4267 \log T$$

where W_∞ (in g) = asymptotic weight; T = the mean annual temperature (in°C), which is assumed to reflect the local lake surface temperature (Pauly, 1980) (in the present study, T = 17.6°C); M = natural mortality.

Results

Length–weight relationships

A total of 3733 specimens (2443/1290 females/males) were used for length–weight relationship analyses.

Standard length range of the total samples was 2.3–19.1 cm (mean ± SD = 9.8 ± 2.1 cm). The ranges for identified females and males were 4.3–19.1 cm (mean ± SD = 10.6 ± 2.0 cm) and 4.6–12.3 cm (mean ± SD = 9.2 ± 1.5 cm), respectively (Fig. 3). The K–S test found significant differences between SL distributions of females and males (H = 8.584, $P < 0.001$).

Length–weight relationships were calculated separately for females and males. The regression equations were described as

$$W = 0.0076\mathrm{SL}^{3.261} (R^2 = 0.965, \mathrm{n} = 2443)$$

and

$$W = 0.0084\mathrm{SL}^{3.190} (R^2 = 0.971, \mathrm{n} = 1290)$$

for females and males, respectively (Fig. 4). The WLRs for females and males were significantly different based on analysis of covariance (n = 3733, $P < 0.001$). Therefore, the female and male data cannot be pooled. The allometric index value (b) for females ($P < 0.05$) and males ($P < 0.05$) were significantly different from 3, and both indicated positive allometric growth of *H. leucisculus*.

Age estimate

Microscopically, the ageing structures of the *H. leucisculus* otoliths showed the typical pattern of teleost fishes, with alternating opaque and translucent zones attributed to slow and fast growth periods (Fig. 2).

To determine the first annulus, young-of-the-year (YOY) fish were taken in April (n = 19) and June (n = 13). In the transmitted light, the otoliths of YOY in April (<6 cm) all showed absence of an opaque zone, but in June (<7 cm) all showed presence of an opaque zone. Otolith radius ranges of YOY were 0.35–0.47 mm (mean ± SD = 0.42 ± 0.04 mm) in April and 0.43–0.61 mm (mean ± SD = 0.51 ± 0.06 mm) in June.

Both the lapillus otoliths with 1–2 annuli and total marginal increment ratio (MIR) fell sharply in July, and then increased gradually to a peak the next April (Fig. 5). Thus, the marginal increment analysis revealed that a single annulus was formed during the early summer months.

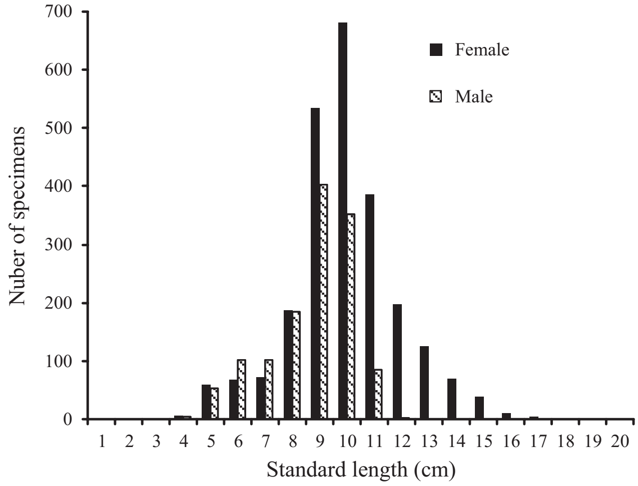

Fig. 3. Standard length-frequency distributions of *Hemiculter leucisculus* in Erhai Lake

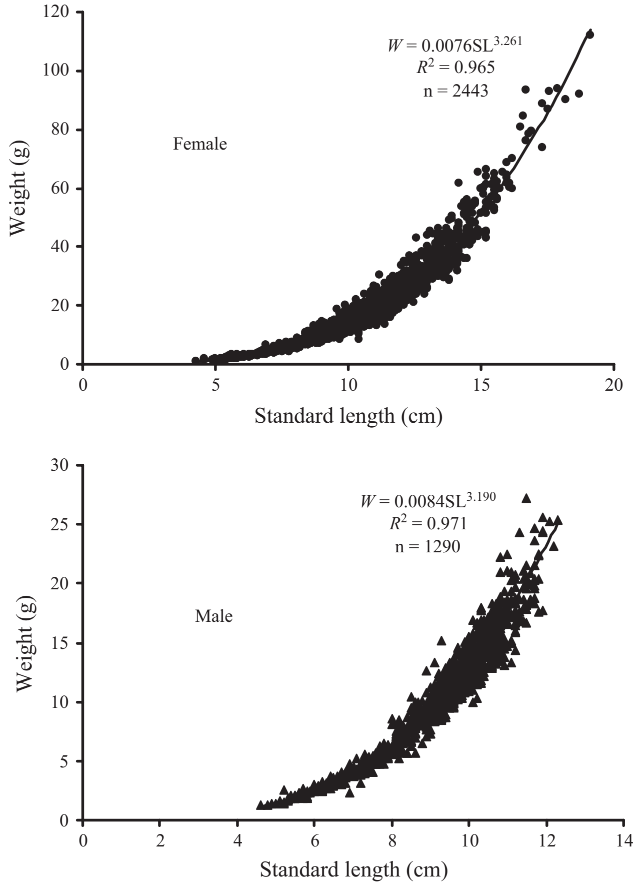

Fig. 4. Length–weight relationships of *Hemiculter leucisculus* in Erhai Lake

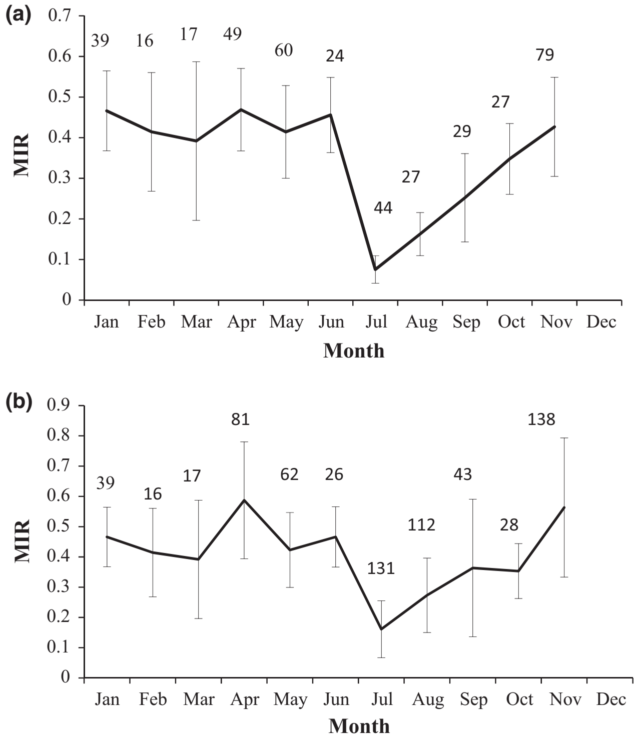

Fig. 5. Mean monthly marginal increment ratio (MIR) for (a) *Hemiculter leuciscuslus* lapillus otoliths with 1–2 annuli and (b) mean monthly MIR of total of *H. leuciscuslus* lapillus otoliths. Error bars = SD. All samples collected in Erhai Lake, July 2009 to June 2010. Sample sizes indicated above the data points.

In the 776 otoliths counted twice, 673 otoliths (88.01%) showed complete agreement; the other 93 otoliths (11.99%) had only a 1-year difference between the two counts. On the third counting of the 93 otoliths, all were in agreement on the first or second count. Total mean CV was 3.55%, and the mean CVs of ages 1–6 were 1.55, 2.47, 7.87, 5.48, 4.28 and 0%, respectively. The age-bias plot showed no systematic bias between the two counts at ages 1, 2 and 6, whereas the first count was larger in ages 3 and 4, but to the contrary in age 5 (Fig. 6).

Age structure

Age structure of the *H. leuciscuslus* population in Erhai Lake was simple, with 1 (0+) to 6 (5+) years, and 93.14% thereof being 1- to 3-year-old females; that of males was even simpler, only 1–3 years, with 97.58% being 1–2 years old (Fig. 7).

Growth

As there were significant differences in growth between sexes, the VBGFs fitted to length-at-age data were described as $L_t = 25.6\ (1 - e^{-0.176(t + 1.347)})$ for females (n = 495) and $L_t = 16.4\ (1 - e^{-0.354(t + 0.819)})$ for males (n = 165), respectively. Females were of much greater length than males in all age groups as well as in asymptotic length (Fig. 8). Growth performances (Ø) of *H. leuciscuslus* were 2.063 for females and 1.978 for males.

Length–frequency analysis

A total of 3820 specimens (2491 females, 1329 males) were used for length frequency analyses. A preliminary estimate of asymptotic length (L_∞) of *H. leuciscuslus* was obtained with

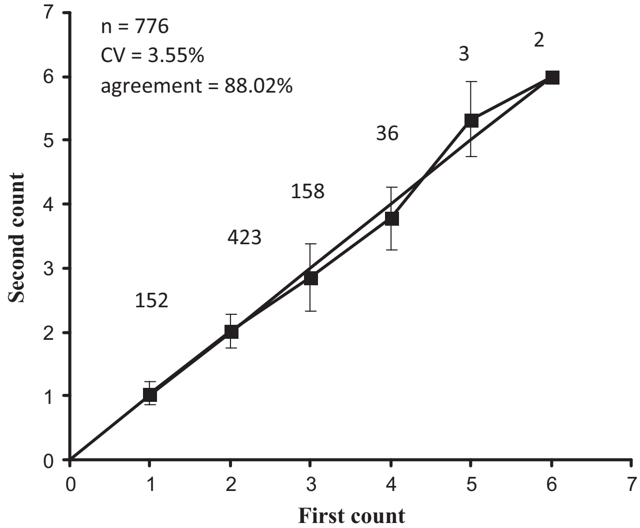

Fig. 6. Age-bias plot of two opaque zone counts, *Hemiculter leuciscuslus* in Erhai Lake. Each error bar = 95% confidence interval about the mean age. The 1 : 1 equivalence is also indicated. Sample sizes indicated above the data points

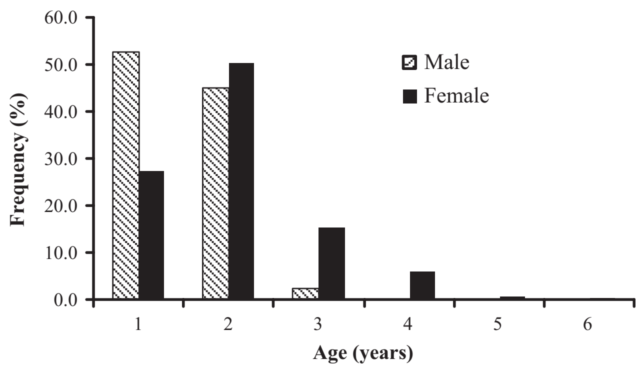

Fig. 7. Age frequency composition of *Hemiculter leuciscuslus* in Erhai Lake

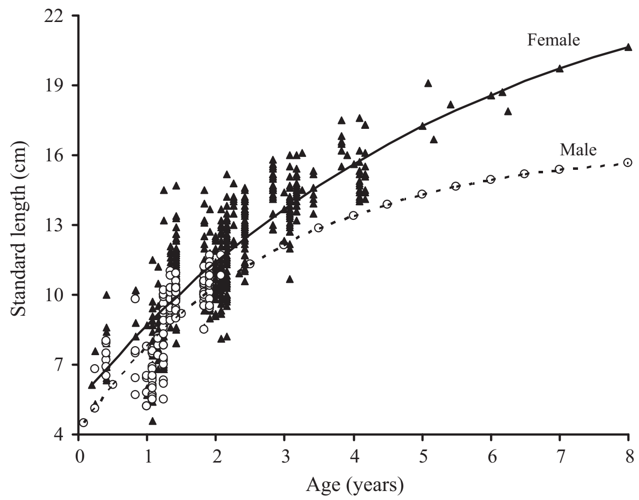

Fig. 8. Von Bertalanffy growth curve of *Hemiculter leuciscuslus* in Erhai Lake with observed standard length at age estimated from otolith readings

the Powell and Wetherall method, which gave the parameters: L_∞ = 24.11 cm (r^2 = 0.970) and L_∞ = 14.56 cm (r^2 = 0.989) for females and males, respectively. The *K* (growth coefficient) was estimated by ELEFAN I with the above L_∞. The ELEFAN I programme produced the growth parameters: $L_\infty = 24.11$ cm, $K = 0.23$, with $R_n = 0.232$ for females and $L_\infty = 14.56$ cm, $K = 2.2$ with $R_n = 0.261$ for males.

Mortality

The length converted catch curve analysis is presented in Fig. 9. Estimated instantaneous total mortality rates (Z) were 1.17 (with a 95% confidence interval of 0.36–2.70) year^{-1} for females and 4.22 (with a 95% confidence interval of 3.11–11.56) year^{-1} for males. Instantaneous natural mortality rates (M) using the equation of Pauly (1980) were 0.48 year^{-1} for females and 2.53 year^{-1} for males.

Discussion

All previous studies on the age and growth of sharpbelly, *H. leucisculus* used only the scales (Sun, 1987; Cao and Wen, 1996; Patimar et al., 2008; Li et al., 2009). Scales have been widely used for ageing because they are easy to collect and process, causing little harm to the sampled fish. However, otoliths have been considered as rendering more accurate age determinations than the scales (Carlander, 1987; Casselman, 1990), and so are most of the materials used for estimating age and growth (Campana and Thorrold, 2001). In this study, by thoroughly analyzing the MIR for both 1–2 annuli and their total, we demonstrated that the annuli on the otoliths were formed once a year. Furthermore, the CV of two age readings of otoliths was 3.55%, lower than the threshold precision levels of CV (5%) recommended by Campana (2001), with an agreement of 88.01% between the two-time age readings and suggesting high precision for sharpbelly age assessment using otoliths.

Both our study and other research showed that the asymptotic length of sharpbelly (L_∞) was lager in females than in males (Table 1). In our study, however, the L_∞ for females (25.6 cm) was much larger than that for males (16.4 cm) estimated from the observed length-at-age; the same resulted from length frequency analysis (females: 24.11 cm; males: 14.56 cm). The larger asymptotic length for females could be attributed to their relatively longer longevity and greater absolute growth rate. Maximum age in females was 6 years in contrast with 3 years for males. Females were also significantly larger than males at any age. The longer lifespan and larger size of females could be considered a life history strategy for supporting increasing egg production (Roff, 1983; Beckman et al., 1988), and leading directly to higher survival of offspring in Erhai Lake. Hence, these are most likely the two attributes that make this exotic species a successful colonizer in Erhai Lake.

By comparison, the estimated L_∞ of sharpbelly in Erhai Lake is similar to those in three lakes of Iran [as inferred from

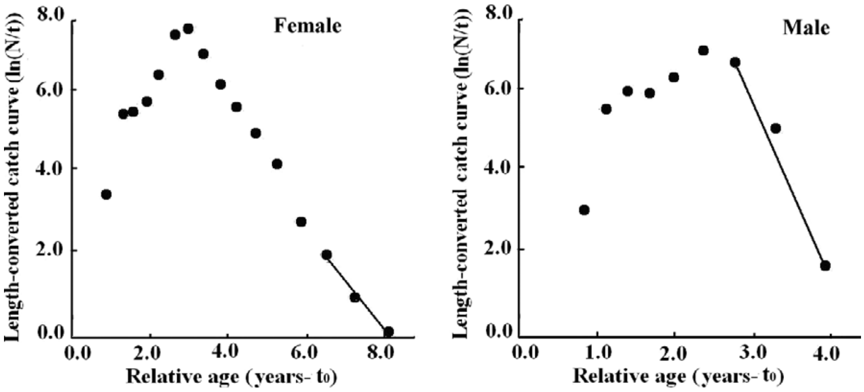

Fig. 9. Length-converted catch curve of *Hemiculter leuciscul*us in Erhai Lake

Table 1
Summary of parameters of von Bertalanffy growth equation for *Hemiculter leucisculus* from different studies

Study area	Aging structure	Sex	n	L_∞	K	t_0	Ø	Age range	First author, year
Alma-Gol, Iran	Scales	♀	233	27.5	0.27	−0.348	2.31	1–6	Patimar (2008)
		♂	202	23.8	0.29	−0.478	2.22	1–6	Patimar (2008)
Adji-Gol, Iran	Scales	♀	54	29.8	0.23	−0.547	2.31	1–6	Patimar (2008)
		♂	41	23.6	0.3	−0.523	2.22	1–6	Patimar (2008)
Ala-Gol, Iran	Scales	♀	214	30.8	0.21	−0.580	2.30	1–6	Patimar (2008)
		♂	210	25.5	0.26	−0.539	2.23	1–6	Patimar (2008)
Fenhe, China	Scales	♀	426	22.2	0.26	−0.028	2.11	1–6	Xie (1986)
		♂	388	21.5	0.24	−0.171	2.05	1–6	Xie (1986)
Baiyangdian Lake, China	Scales	♀+♂	69					1–4	Cao and Wen (1996)
Erlongshan, China	Scales	♀+♂	106					1–5	Sun (1987)
Beijiang River, China	Scales	♀+♂	321	28.4	0.178	−1.350	2.16	1–6	Li (2009)
Erhai Lake, this study	Otoliths	♀	495	25.6	0.176	−1.347	2.06	1–6	This study
		♂	165	16.4	0.354	−0.819	1.98	1–3	This study
Erhai Lake, this study	LF	♀	2491	24.11	0.23		2.13		This study
		♂	1329	14.56	2.2		2.67		This study

LF, length frequency analysis; n, sample size; L_∞, asymptotic length; k, growth coefficient; t_0, age at length 0; Ø, growth performance index.

the length–length relationship of sharpbelly: TL = 1.222 × SL according to FishBase (Patimar, 2008; Froese and Pauly, 2013)]. However, it is larger than in Fenhe Reservoir and smaller than in Beijiang River (Table 1). Beijiang River is located in Guangzhou, Guangdong Province, in southern China; the Fenhe Reservoir is in Taiyuan, Shanxi Province, northwestern China. The temperature and other physiochemical, biological factors characteristic of geographic surroundings may contribute to the differences in growth and the ultimate asymptotic length among the different populations.

Growth parameter estimates (Ø) were similar in all studies (Table 1), except for that of Patimar (2008) and the length frequency analyses of the males in the present study, the former as result of using total length for estimation, the latter resulting in the particularly large value of the growth coefficient (*K*). The overall growth performance has minimum variance within the same species because it is independent of growth rates (Lopez Cazorla and Sidorkewic, 2011). The similar values confirm the accuracy of our growth estimation from otoliths.

Previous works as well as the present study indicate that the maximum age of sharpbelly is no more than 6 years: 4 in Bai Yangdian Lake (Cao and Wen, 1996), 5 in Erlongshan Reservoir (Sun, 1987), and 6 years in other studies (Xie et al., 1986; Patimar et al., 2008; Li et al., 2009) (Table 1). The brief generation of *H. leucisculus* is very similar to *Pseudorasbora parva*, where the maximum age is no more than 5 years (Gozlan et al., 2010). *P. parva* is one of the most compelling invasive fishes in the world (Gozlan et al., 2010), and classified as an international pest species (Welcomme, 1992). This very brief generational period is one of the principal reasons for the invasive success of *P. parva* (Gozlan et al., 2010; Záhorská et al., 2010). The very simple age structure of *H. leucisculus* aids in its high degree of invasive vigor, leading it to becoming the dominant species and one of the important commercial fishing species in Erhai Lake within a very short time.

In contrast to both sexes having the same maximum age in previous studies (Table 1), maximum age for the sharpbelly in Erhai Lake was markedly different (6 years in females, 3 years in males). The much shorter lifespan and higher instantaneous total mortality rates for males (4.22 year^{-1} vs 1.17 year^{-1} for females) may be an adaptive variation in the life-history traits. This would prompt the survival of larger females, beneficial for more energy for growth and reproduction. This is likely a third reason that makes the species a successful colonizer in Erhai Lake.

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