

## Research Article

**Fecundity, growth and body condition of invasive black bullhead (*Ameiurus melas*) in eutrophic oxbow lakes of River-Körös (Hungary)**Július Varga<sup>1</sup>, Dorottya Lilla Fazekas<sup>2</sup>, Béla Halasi-Kovács<sup>2</sup>, Vilmos Józsa<sup>2</sup>, Flórián Tóth<sup>2</sup>, Krisztián Nyeste<sup>3</sup> and Attila Mozsár<sup>4,5</sup><sup>1</sup>Department of Ecology, Faculty of Humanities and Natural Sciences, University of Presov, 080 01 Prešov, Ul. 17. novembra č.15, Slovakia<sup>2</sup>Research Centre for Aquaculture and Fisheries, Institute of Aquaculture and Environmental Safety, Hungarian University of Agriculture and Life Sciences, 5540 Szarvas, Anna-liget utca 35, Hungary<sup>3</sup>Department of Hydrobiology, Faculty of Science and Technology, University of Debrecen, 4032 Debrecen, Egyetem square 1, Hungary<sup>4</sup>HUN-REN Balaton Limnological Research Institute, 8237 Tihany, Klebelsberg Kuno 3, Hungary<sup>5</sup>National Laboratory for Water Science and Water Security, HUN-REN Balaton Limnological Research Institute, 8237 Tihany, Klebelsberg Kuno 3, HungaryCorresponding author: Július Varga ([julius.varga@smail.unipo.sk](mailto:julius.varga@smail.unipo.sk))

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**Abstract**

Black bullhead *Ameiurus melas* is a widespread invasive fish in Europe and is considered an ecological and economic threat. Yet, sporadic data are available on its life-history traits. This study assessed the fecundity, growth, and body condition of black bullhead in three oxbows in Hungary. Samples were collected in the resting (October) and pre-spawning (April) periods. Considerable negative allometric growth was observed (b slope ranged between 1.64 and 1.67). The Fulton's condition factor was lower than any previously reported data (mean = 1.01; SD = 0.09). The mean male : female ratio of the three populations was 1.18:1. Mean absolute fecundity was 3,319 eggs (SD = 1521; range = 1,111–12,727), and mean relative fecundity was 78.8 eggs g<sup>-1</sup> (SD = 21.8; range = 34.8–146.0). The mean oocyte diameter was 0.39 mm in autumn and 0.41 mm in spring. Oocyte size positively correlated with body length. The mean standard length at age was 76.5–81.00 mm at 1+, 126.23–134.35 at 2+, 153–154.5 mm at 3+, and 180–181 mm at 4+. Our results confirmed the phenotypic plasticity of black bullhead out of its native range.

**Key words:** Ictaluridae, length-weight relationship, Fulton's condition factor, oocyte size, life-history**Introduction**

The success of invasive species is associated with numerous environmental factors and species traits (Hamilton et al. 2005; Bomford et al. 2010). Besides wider physiological tolerance (Marchetti et al. 2004; Cucherousset et al. 2007), opportunistic habitat occupation (Cucherousset et al. 2008; Van Kessel et al. 2011; Grabowska et al. 2016) and feeding habits (Adámek et al. 2007; van Kleef et al. 2008; Neuhaus et al. 2016), breeding-related phenotypic plasticity (i.e. the capability of species to shift from K-selected to r-selected breeding strategy at the beginning of the invasion) is a cornerstone of the successful invasion (Sakai et al. 2001; Geburzi and McCarthy 2018). Greater reproductive investment, i.e. higher fecundity of

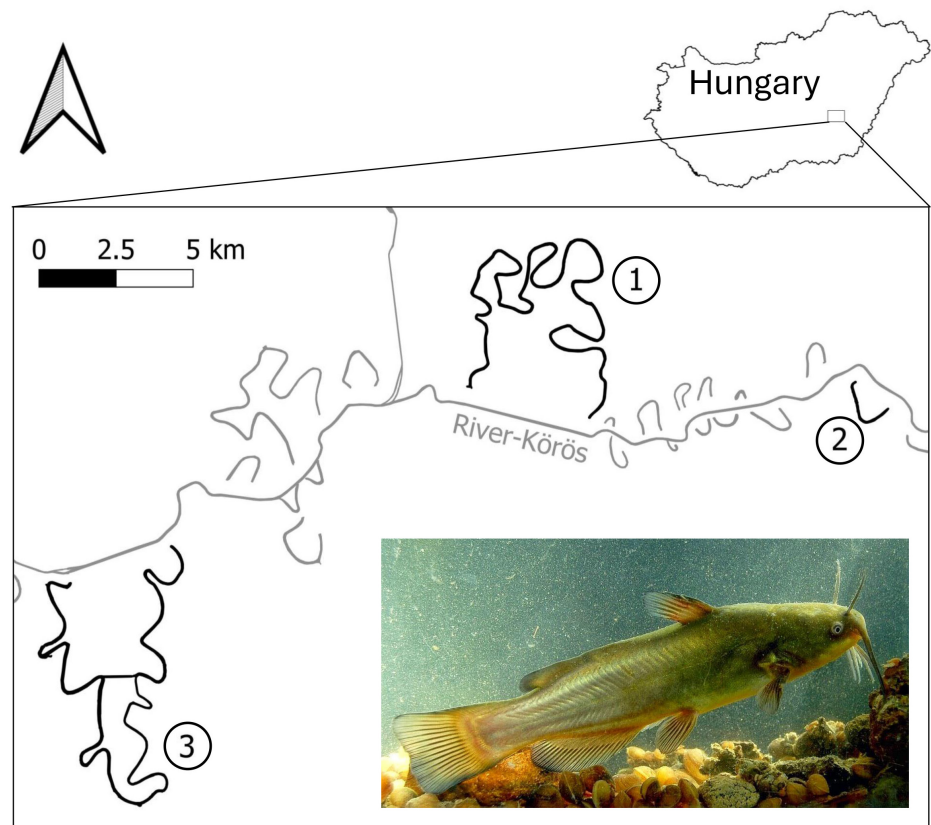
females, earlier and/or smaller size at maturity, and longer spawning period, is common in invasive species in the newly occupied areas during establishment (Bohn et al. 2004). Due to the energetic trade-off between reproduction and somatic growth, greater reproductive investment results in slower growth (Grabowska et al. 2011; Nyeste et al. 2017).

The black bullhead *Ameiurus melas* (Rafinesque, 1820) is among the most frequent invasive species in Central Europe (Koščo et al. 2004; Jarić et al. 2015; Takács et al. 2017). It is often dominant in lentic ecosystems (Carpentier et al. 2004; Cucherousset et al. 2007, 2008) and creates dense populations mainly dominated by small individuals (Rutkayová et al. 2013) challenging the recreational fisheries management (e.g. Sikora et al. 2021). The invasion success of black bullhead is associated with its broad environmental tolerance (Scott and Crossman 1973; Stuber 1982; Ribeiro et al. 2008), nest-guarding behavior (Stuber 1982), opportunistic feeding habits (Leunda et al. 2008; Jaćimović et al. 2021) and breeding-related phenotypic plasticity (Copp et al. 2016).

Life-history characteristics fundamentally determine the resilience of the population to harvest (Winemiller 2005). In species which exhibit high breeding-related phenotypic plasticity, mass removal can induce an increase in reproductive effort (density-dependent phenotypic response), decreasing the efficiency of eradication measures (e.g. Ruiz-Navarro et al. 2013; Mintram et al. 2021). In practice, eradication efforts and methods should be adjusted to increased recruitment and altered size distribution of the population. Therefore, understanding the life-history of invasive species is crucial for reliable risk assessment and feasible removal actions (Ricciardi and Rasmussen 1998). Despite the substantial negative ecological (Kreutzenberger et al. 2008; Leunda et al. 2008) and economic effects of black bullhead and high eradication efforts (Cucherousset et al. 2006; Lenhardt et al. 2011), sporadic data are available on its life-history traits, especially fecundity. Although black bullhead has invaded more than twenty European countries (Copp et al. 2016; Piria et al. 2016; Ristovska et al. 2017; Vancheva et al. 2020), data on fecundity of invasive populations is available only from five countries (England, France, Italy, Slovakia, Serbia), involving merely eleven populations (Copp et al. 2016; Jaćimović et al. 2019). We aimed to evaluate the fecundity, growth and body condition of the invasive black bullhead in typically occupied habitats in Hungary.

## Materials and methods

Black bullhead was collected in three eutrophic lowland oxbows of River-Körös (Southeast Hungary; Figure 1): Peresi-Holt-Körös (PHK; 46.984167; 20.723117), Hantoskerti Holt-Körös (HKH; 46.940350; 20.833883) and Szarvas-Békésszentandrás Holt-Körös (SHK; 46.859000; 20.514167) in resting (18, 22 October 2019) and pre-spawning (22, 24 April 2020) periods.



**Figure 1.** Map of sampling sites and a photo about black bullhead *Ameiurus melas*. Site 1: Peresi-Holt-Körös, site 2: Hantostkerti Holt-Körös, site 3: Szarvas-Békésszentandrás Holt-Körös.

Samples were collected with crayfish/fish traps (Hanchin et al. 2002; Cucherousset et al. 2006; Ruiz-Navarro et al. 2014). Traps were 70 cm long and 30 cm wide, with a 15 cm throat and 1 cm mesh size. Fifteen unbaited traps were deployed in each oxbow for 24 hours. Fish were euthanized with an overdose of 2-phenoxyethanol. Standard (SL) and total length (TL) were measured to the nearest 1 mm. The body weight (W) of all specimens and the gonad weight of females were recorded to the nearest 0.1 g and 0.0001 g, respectively. The gonads were preserved in Gilson's solution. The reproductive characteristic is hypothesized to change among different environments and along with wide a geographical range. Therefore, we avoid using formerly applied threshold diameters (e.g. Novomeská and Kováč 2009) for immature oocytes. To obtain this trait, the specimens were examined in descending order by total length during the measurement of oocyte diameter. If we noted the absence of larger oocytes in subsequent smaller individuals, the measurement was stopped. The threshold diameter was assessed based on the oocyte sizes of these individuals.

Length-weight regression analyses were calculated on log-transformed data according to the equation:  $\log(W) = \log(a) + b \log(TL)$ , where W is body weight (g), TL total length (cm), a the intercept and b the slope (Froese et al. 2011) on the data of the first sampling (October 2019). Fulton's condition factor (FCF) was calculated as:  $FCF = 10^5 W / TL^3$ , where

**Table 1.** Length-weight regression parameters for male and female black bullhead sampled in autumn (T: total, M: male, F: female).

Sampling site	Sex	n	a	CI 95% (a)	b	CI 95% (b)	r <sup>2</sup>
PHK	T	129	0.34	0.33–0.34	1.67	1.66–1.68	0.99
	M	71	0.34	0.33–0.35	1.67	1.66–1.68	0.99
	F	58	0.33	0.33–0.34	1.67	1.66–1.68	0.99
HKH	T	99	0.35	0.33–0.36	1.65	1.63–1.67	0.99
	M	49	0.34	0.32–0.35	1.66	1.64–1.68	0.98
	F	50	0.35	0.33–0.37	1.64	1.61–1.67	0.97
SHK	T	99	0.34	0.33–0.35	1.66	1.65–1.66	0.99
	M	57	0.34	0.33–0.35	1.66	1.65–1.67	0.99
	F	42	0.34	0.33–0.36	1.65	1.63–1.66	0.98

W is total body weight (g), and TL is the total length (mm). Despite using b slope from length-weight regression, we use exponent 3 to obtain data comparable to previous studies (e.g. Copp et al. 2016). General linear model (GLM) was fitted to reveal the effect of sampling site, season, sex, and TL on Fulton's condition factor (Statsoft Statistica Version 12.0). We tested the main effects; interactions were not included in the model.

The sex ratio was calculated by dividing the number of males by the number of females sampled in autumn. Chi-square test was used to reveal the significant deviation of sex ratio from the hypothesized 1:1 ratio. Small individuals with oocyte diameters below 0.3 mm were excluded from fecundity assessment, hence 0.3 mm diameter was used as a threshold. Absolute fecundity (AF) was estimated by counting the number of oocytes with a diameter greater than 0.3 mm. The relative fecundity was determined by using the  $RF = AF/W$  formula. Pearson correlation was used to assess the relationship between fecundity, mean oocyte size and body size (TL) using Statsoft Statistica Version 12.0.

The age groups were determined using the Petersen (Tesch 1968) method based on the length-frequency distribution with each high peak representing a separate age group (Tesch 1968). Descriptive statistics of age groups were calculated by the Bhattacharya method (Bhattacharya 1967) using FiSAT software (Gayanilo et al. 2005). The von Bertalanffy growth model  $L_t = L_\infty (1 - \exp(-k(t - t_0)))$  was applied for mathematical description of growth (von Bertalanffy 1934; Ricker 1975) using FiSat software (Gayanilo et al. 2005).

## Results

### *Length-weight relationship, condition factor*

The slopes *b* ranged between 1.64 and 1.67 indicating negative allometric growth (Table 1). The mean Fulton's condition factor was 1.01 (SD = 0.09). Significant differences in Fulton's condition factor were not observed between sampling site, season and sex, but FCF was negatively related to TL (GLM, TL:  $F_{1,568} = 93.22$ ,  $p < 0.0001$ ; adj.  $R^2 = 0.1826$ ).

### Reproduction

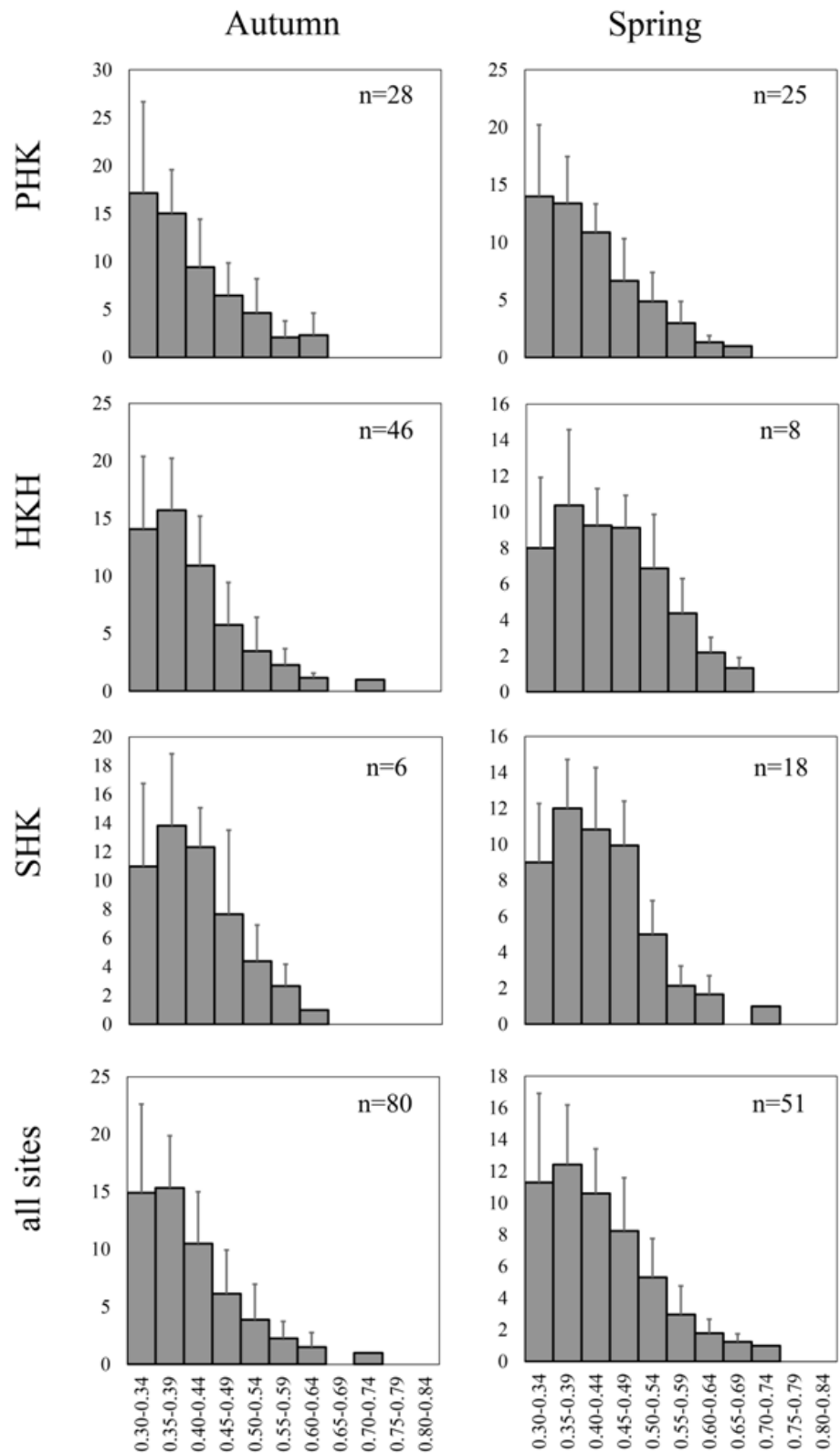
The sex ratio (male:female) was 1.22:1 in PHK, 0.98:1 in HKH and 1.35:1 in SHK. The average value for three sampling sites (1.18:1) did not differ significantly from the expected 1:1 ratio (Chi-square: 0.02;  $p = 0.86$ ). The mean absolute fecundity of the three populations in autumn (i.e. resting period) was 3,251 eggs (SD = 1,734; range = 1,111–12,727 eggs) and mean relative fecundity was 76.4 eggs  $g^{-1}$  (SD = 20.9; range = 34.8–134.7 eggs  $g^{-1}$ ). In spring, the mean absolute fecundity was 3,427 eggs (SD = 1,117; range = 1,557–7,135 eggs) while the mean relative fecundity was 82.7 eggs  $g^{-1}$  (SD = 22.8; range = 39.9–146.0 eggs  $g^{-1}$ ). The body size positively correlated absolute fecundity with  $r = 0.71$ ,  $p < 0.0001$ ; but not with relative fecundity  $r = 0.03$ ,  $p = 0.7431$ . Positive association occurred between body size and mean oocyte diameter ( $r = 0.44$ ,  $p < 0.0001$ ). The mean oocyte diameter of mature females was 0.39 mm, SD = 0.03 (PHK 0.38 mm, SD = 0.04; HKH 0.39 mm, SD = 0.03; SHK 0.40, SD = 0.03) in autumn and was 0.41 mm, SD = 0.03 (PHK 0.40 mm, SD = 0.03; HKH 0.44 mm, SD = 0.02; SHK 0.42, SD = 0.02) in spring, respectively (Figure 2).

### Growth

Four age groups were identified by the Bhattacharya method (Figure 3; Tables 2, 3). The mean standard lengths of the age groups were similar in the three sampled oxbows (Figure 3). The overlaps in older age groups (2+ and 3+) were more emphasized in females, and the mean standard length was slightly lower than in males (Figure 3). The von Bertalanffy growth curves were fitted to the SL at age data for sexes separately. The estimated parameters of the von Bertalanffy equations were:  $L_{\infty} = 224.41$  mm ( $\pm 30.83$ ),  $k = 0.39$  ( $\pm 0.17$ ),  $t_0 = -0.86$  ( $\pm .36$ ) for males,  $L_{\infty} = 192.32$  mm ( $\pm 45.44$ ),  $k = 0.50$  ( $\pm 0.39$ ),  $t_0 = -0.90$  ( $\pm 0.52$ ) for females,  $L_{\infty} = 219.65$  mm ( $\pm 25.50$ ),  $k = 0.39$  ( $\pm 0.12$ ),  $t_0 = -0.86$  ( $\pm 0.21$ ) for PHK,  $L_{\infty} = 213.13$  mm ( $\pm 17.39$ ),  $k = 0.44$  ( $\pm 0.10$ ),  $t_0 = -0.99$  ( $\pm 0.17$ ) for HKH,  $L_{\infty} = 201.39$  mm ( $\pm 25.84$ ),  $k = 0.52$  ( $\pm 0.21$ ),  $t_0 = -1.00$  ( $\pm 0.28$ ) for SHK.

### Discussion

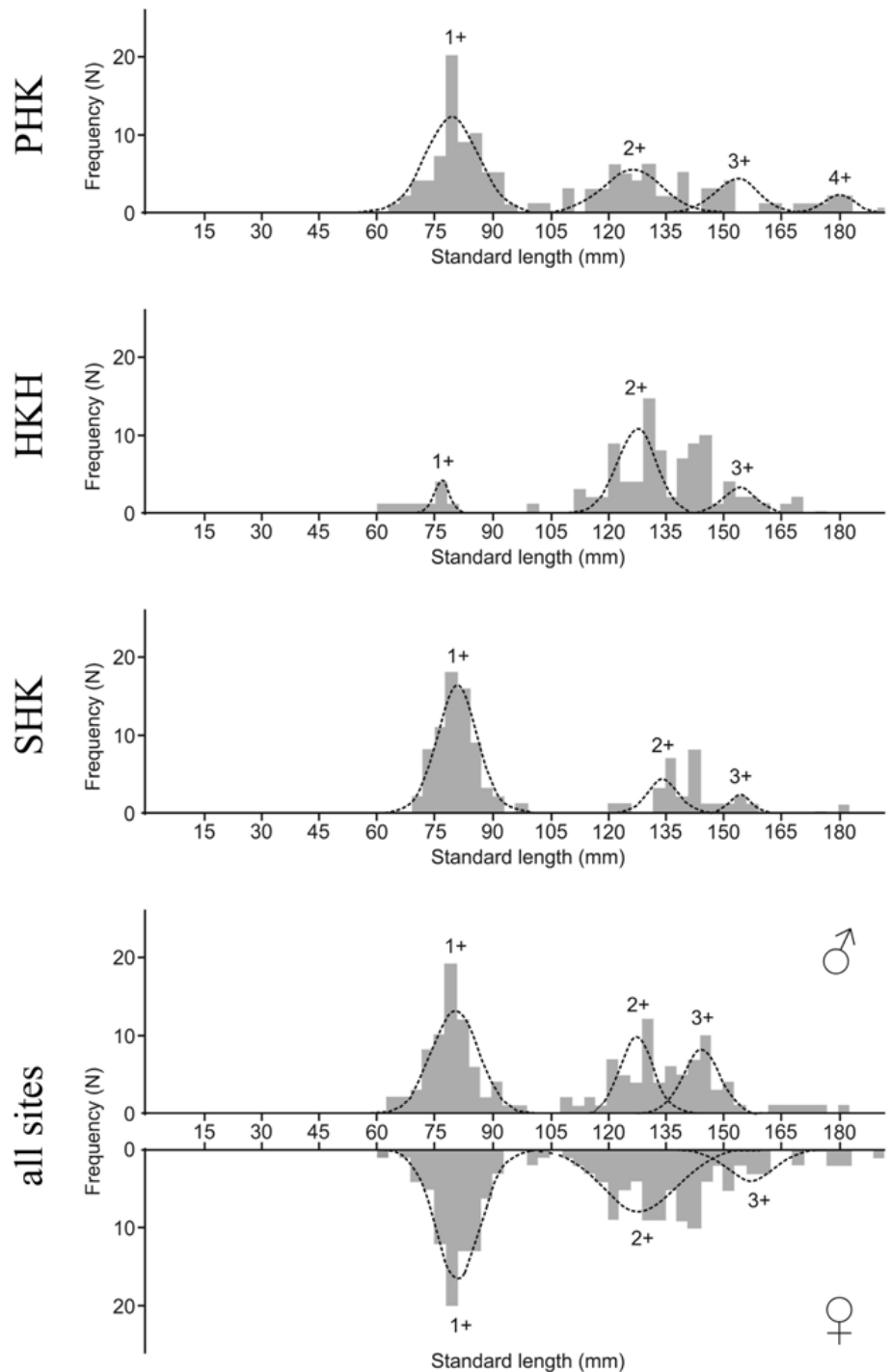
Although black bullhead is widely established in Europe and is considered an ecological and economic threat, merely sporadic data are available on the life-history traits out of its native range. Similarly to other non-native populations, we observed that black bullhead invest more energy in reproduction (i.e. higher relative fecundity) than in growth, supporting the phenotypic plasticity of this species (Copp et al. 2016). The black bullhead population in our study systems exhibited slower growth rate than in native populations. The absolute fecundity was similar to the native populations; however, the relative fecundity was higher than in natives but similar to other non-native populations. Furthermore, our study revealed



**Figure 2.** Mean size-frequency distribution of oocytes of black bullhead in the sampled Hungarian oxbows.

negative allometric growth and poor body condition of black bullhead populations.

In the sampled populations, the body length increased more rapidly than body weight during the ontogeny, irrespective of sex. Such negative allometric



**Figure 3.** Frequency distribution of standard length of black bullhead sampled in autumn. Cells are left-opened and right-closed intervals; Dotted line represents the fitted normal distribution estimated by the Bhattacharya method.

growth was not reported previously in the case of black bullhead (Copp et al. 2016, and references therein). Further, in other European populations the mean of slope  $b$  is 3.03 (Copp et al. 2016), which ranged between 1.64–1.67 in our study. This low body condition and negative allometric trend were also confirmed by Fulton’s condition factor values. Mean Fulton’s condition factor of European populations is 1.37, while it was 1.01 in our study systems. The slope  $b$  and body condition usually increase with increasing

**Table 2.** Descriptive statistics of age groups of different black bullhead populations identified by the Bhattacharya method. The analysis is based on the samples taken in autumn.

Location	Age group	Rate (%)	Standard length (mm)	Separation index
PHK	2 (1+)	53.81	79.50; SE = 6.79	–
	3 (2+)	26.32	126.23; SE = 7.51	2.75
	4 (3+)	14.7	153.00; SE = 5.42	2.21
	5 (4+)	5.16	180.00; SE = 3.60	2.23
HKH	2 (1+)	16.62	76.50; SE = 1.80	–
	3 (2+)	46.17	127.50; SE = 5.00	3.13
	4 (3+)	37.21	154.50; SE = 4.03	2.27
SHK	2 (1+)	79.12	81.00; SE = 5.21	–
	3 (2+)	14.85	134.35; SE = 3.79	3.03
	4 (3+)	4.91	154.50; SE = 2.55	2.2
	5 (4+)	1.12	181.00; SE = 0.00	4.05

Note: Standard length values are mean and standard error (SE). CI = confidence interval. Rate = relative frequency of individuals found in each age group.

**Table 3.** Descriptive statistics of age groups of males and females of black bullhead identified by the Bhattacharya method. The analysis is based on the samples taken in autumn.

Sex	Age group	Rate (%)	Standard length (mm)	Separation index
♂	2 (1+)	48.30	81.00; SE = 5.72	–
	3 (2+)	37.15	128.09; SE = 9.24	2.74
	4 (3+)	11.49	157.07; SE = 6.10	2.20
	5 (4+)	3.06	182.80; SE = 4.21	3.07
♀	2 (1+)	48.37	80.74; SE = 6.20	–
	3 (2+)	25.19	127.79; SE = 4.40	2.75
	4 (3+)	23.58	144.63; SE = 4.90	2.21
	5 (4+)	2.86	175.00; SE = 5.72	3.45

Note: Standard length values are mean and standard error (SE). CI = confidence interval. Rate = relative frequency of individuals found in each age group by sexes.

habitat suitability (Oliva-Paterna et al. 2003) and reach the highest values in less vegetated habitats (Thiero Yatabary 1981). The sampled oxbows are eutrophic and are in turbid water state with low macrophytes density; therefore, we expected higher values for slope  $b$  and Fulton's condition factor. Based on the available data, this contradiction cannot be explained without speculations, hence it should be the focus of further studies. Collapses of black bullhead population—caused mostly by viral infection—frequently occur (Pozet et al. 1992; Jaćimović et al. 2019). Although it is assumed to be a consequence of overpopulation, direct association between density and mass mortality has not been revealed (Jaćimović et al. 2019). Substantial decrease in somatic condition—instead of changes in density—can be the first sign of drifting to population collapse. Revealing the drivers of changes in somatic condition can contribute to understanding the mechanisms of natural mass mortality events.

Copp et al. (2016) reported considerably wide range of both absolute (seven-fold differences between min and max) and relative fecundity (almost ten-fold differences) in non-native populations. Conversely, Jaćimović et al. (2019) reveal high and abrupt intrapopulation change in fecundity (both absolute and relative) suggesting the crucial role of population dynamics and environmental conditions in reproductive effort

(i.e. fecundity) of black bullhead. Our values were slightly under the means of non-native populations (Copp et al. 2016), while relative fecundity was considerably higher than in native populations (Copp et al. 2016), suggesting that the non-native black bullhead population invests more energy in reproduction than in growth (Kozłowski 1996, 2006; Grabowska et al. 2011). The absolute fecundity and oocyte size was a function of body size as it was described in previous studies (DeMartini and Fountain 1981; Thorpe et al. 1984; L'Abée-Lund and Hindar 1990); however, the relative fecundity can decrease (Docker and Beamish 1991) or increase (DeMartini and Fountain 1981) with body and can be even independent form that (Ali 1993). Although the fecundity was as high as in other non-native populations, the mean oocyte size was slightly smaller (Copp et al. 2016). Oocyte size—assessed in the same periods, i.e. autumn and spring—in Slovakian populations (Novomeská and Kováč 2009) was slightly higher than in the present study. Because oocyte size determines the viability and survival of offspring (Hórková and Kováč 2014), further data and comparative studies on oocyte size (reproductive allocation) among the non-native population would be essential to understand the phenotypic plasticity of black bullhead.

The growth and the length at age depend on environmental conditions (Rypel 2011; Copp et al. 2016). But in general, the growth of non-native populations is slower than that of natives (Copp et al. 2016) which is more pronounced after maturity. After maturity, similar slowdown in growth has been reported also in native populations (Sikora et al. 2022). Juvenile growth (length at 2<sup>nd</sup> year) was as low as recoded in Slovakian and English populations (see Copp et al. 2016). The high proportion of this age cohort in our samples suggested high survival rate and potentially high level of intraspecific competition in juveniles which could be the cause of decreased growth rate in younger cohorts. In older age cohorts, the length at age was similar to the mean of other non-native populations (Copp et al. 2016). The high length overlaps in 3<sup>rd</sup> and 4<sup>th</sup> age cohorts presumably led to bias in length at age estimations; thus, evaluation should be done with cautions in this regard. Applicability of length-frequency based estimation on length at age in slow growing species like black bullhead can be questionable, primarily due to the overlap in age cohorts. But Jaćimović et al. (2019) highlight the reliability of Bhattacharya method in length at age estimations in black bullhead. The high degree of variability in length within an age cohort challenges the assessment of differences in growth rate between sexes. In species with biparental care, like bullhead, both sexes invest energy in reproduction (Wallace 1967); hence, substantial differences in length at age between sexes are not assumable.

In conclusion, non-native black bullhead populations exhibit lower growth rate and—as a side effect—higher (Copp et al. 2016; present study) but

remarkably variable fecundity (Copp et al. 2016; Jaćimović et al. 2019). The data on fecundity of black bullhead is available merely from eleven European populations but shows almost ten-fold interpopulation difference (Copp et al. 2016; Jaćimović et al. 2019). Drivers behind this high variability are still unknown. Jaćimović et al. (2019) documented a considerable increase in fecundity of black bullhead after a mass mortality event. It suggests that fecundity can change along with density, as a compensatory mechanism which ensures the resiliency of population. In contrast, targeted removal actions did not result in increases in the ratio of YOYs (Cucherousset et al. 2006), but data on fecundity was not available. Because the compensatory mechanisms can highly decrease the success of eradication measures, they should be in focus of the studies of highly invasive species like black bullhead. High eradication efforts—using fyke nets, for example—and continuous monitoring of life-history traits of the populations could reveal potential compensatory mechanisms and density-dependent changes in fecundity.

### Authors' contribution

JV: research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, funding provision, roles/writing – original draft. DLF: investigation and data collection. BH-K: investigation and data collection. JV: investigation and data collection. FT: investigation and data collection. KNY: data analysis and interpretation. AM: research conceptualization; sample design and methodology, investigation and data collection, data analysis and interpretation, ethics approval, funding provision, writing – review and editing.

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### Ethics and permits

The collection was approved by the Agricultural, Public Administration Office of Hungary. Permission number: HaGF/300/2019.

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