A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 99: 131–147 (2025)
DOI: 10.3897/neobiota.99.154887

Research Article

Effect of the tapeworm *Ligula pavlovskii* on the life-history of the alien monkey goby (*Neogobius fluviatilis*)

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Abstract

The life-history traits of fish are influenced by numerous factors, including parasitic infections. Parasites can significantly impact host mortality, growth performance, and reproductive success. This study examines the effects of the parasite *Ligula pavlovskii* (Diphyllobothriidae) on its host, the monkey goby (*Neogobius fluviatilis*), in Lake Balaton, Hungary. Both species originated in the Ponto-Caspian region, with the fish arriving in the 1970s and the parasite following in the 2000s. Our research reveals substantial impacts of *L. pavlovskii* on the life history of the monkey goby, including differences in somatic (condition, length) and reproductive (gonadosomatic index, fecundity, egg size) investments between infected and non-infected individuals. Condition declined with higher parasite index in infected individuals. Female GSI was influenced by both parasite presence and severity of the infection, whereas male GSI was affected by the presence of the parasite. Additionally, the length frequency distributions of infected and non-infected fish showed seasonal differences, due to the bigger body size of infected individuals in summer and autumn. The high prevalence of the parasite and associated mortality resulted in a significantly reduced expected lifespan for infected fish. Our findings suggest that the competitive advantage of *N. fluviatilis* may be reduced when this fish is infected by *L. pavlovskii.* This should be considered when developing management interventions for this species.

Key words: Condition, growth, invasive species, parasite, reproduction

Academic editor: Emili García-Berthou
Received: 4 April 2025
Accepted: 18 May 2025
Published: 13 June 2025

Citation: Vitál Z, Czeglédi I, Megyeri E, Preiszner B, Takács P, Erős T, Sallai M, Boross N (2025) Effect of the tapeworm *Ligula pavlovskii* on the life-history of the alien monkey goby (*Neogobius fluviatilis*). NeoBiota 99: 131–147. https://doi.org/10.3897/neobiota.99.154887

Introduction

Numerous factors affect the life-history traits of fish. Large-scale studies of geographically widely dispersed populations of freshwater fish species have shown that latitude, which encompasses important environmental parameters like temperature, photoperiod, productivity, and the length of the growing season, is an important factor influencing traits (Blanck and Lamouroux 2007). Human impacts on ecosystems (e.g., ocean acidification, temperature fluctuations, fishing, and overfishing) also cause severe changes in the life history of fish on a global scale (Munday et al. 2009; Burt et al. 2011; Watson et al. 2018), but several local factors play an important role as well. Parasites, for example, can impact the host

population in various ways since they belong to almost all taxa and have a wide range of size, from single cells to relatively large and complex organisms, like parasitic lampreys (Petromyzontiformes). Their potential effects on host individuals include an influence on mortality through direct or indirect killing of their host (Henricson 1977; Price 1980; Krkošek et al. 2007; e.g. Fujiwara et al. 2011) or by altering behaviour, thereby increasing predatory pressure on infected individuals (e.g. Harris and Wheeler 1974; Bean and Winfield 1989; Barber et al. 2000). They can also positively or negatively affect the growth performance of fish species (e.g. Arnott et al. 2000; Ould Ruis et al. 2016; Ooue et al. 2017), while they can cause remarkable impacts on the reproduction of host species as well (e.g. Bean and Winfield 1989; Carter et al. 2005; Fogelman et al. 2009).

Invasive species often cause changes in life history, rapid population declines, or even the extinction of native species (Clavero and Garcia-Berthou 2005; Catford et al. 2018). The role of non-native species in the parasite–host relationship of native species is multifaceted. Although parasite load is often lower in new habitats than in native range ("Enemy release hypothesis"; Keane and Crawley 2002, Torchin et al. 2003), they can transmit non-native parasites to native species (parasite spillover) and harbour native parasites, which can increase parasitic pressure on natives (parasite spillback). Therefore, the lower parasite pressure on non-natives is limited and the richness of native parasites may increase over time (Gendron et al. 2012; Kołodziej-Sobocińska et al. 2018), however, the parasites left behind during the invasion of hosts may follow them later (Vitál et al. 2021).

The range expansion and invasion of Ponto-Caspian fish species is considered one of the greatest threats to indigenous aquatic species in Europe (Copp et al. 2005). Following further human-facilitated dispersal, some of these species appeared in the Laurentian Great Lakes and caused major changes to the ecosystems there (Jude et al. 1992; Kornis et al. 2012). In Europe, the area of habitats colonised by Ponto-Caspian gobies is rapidly expanding (Copp et al. 2005; Kvach et al. 2021). They are migrating via the three main large river corridors described by Bij de Vaate (2002), thus they are or will be present in the waters which are in connection with the Volga, Dniester and Danube rivers. The first newcomer of Ponto-Caspian gobiids in Hungary was the western tubenose goby (*Proterorhinus semilunaris*, Heckel, 1837), which has been known in the Middle Danube since the late 19th century (Herman 1887) followed by the monkey goby (*Neogobius fluviatilis*, Pallas, 1814), first recorded in Lake Balaton (Bíró 1971). Nowadays, monkey goby is one of the most abundant non-native fish in the riverine systems of Hungary (Takács et al. 2017), and in the littoral habitats of Lake Balaton (Czeglédi et al. 2019).

Ligula pavlovskii (Dubinina, 1959) is a large parasitic flatworm belonging to the family Diphyllobothriidae. The life cycle of the parasite requires three hosts: the first intermediate host is a copepod, the second is a fish, and the final host is a piscivorous bird. The parasite is highly specific to the host fish species which are Ponto-Caspian gobiids (stellate tadpole-goby *Benthophilus stellatus* (Sauvage, 1874), monkey goby, round goby *N. melanostomus* (Pallas, 1814), bighead goby *Ponticola kessleri* (Günther, 1861), syrman goby, *P. syrman* (Nordmann, 1840), marbled goby *Pomatoschistus marmoratus* (Risso, 1810), and an unclear species from genus Knipowitschia; Dubinina 1959; Yuryshynets et al. 2017; Kvach and Ondračková 2020). The species' native distribution range includes various saline, freshwater, and brackish waters of the Ponto-Caspian region, where it occurs in lakes, lagoons, river deltas, and reservoirs (Fig. 1) (Kvach and Ondračková 2020).

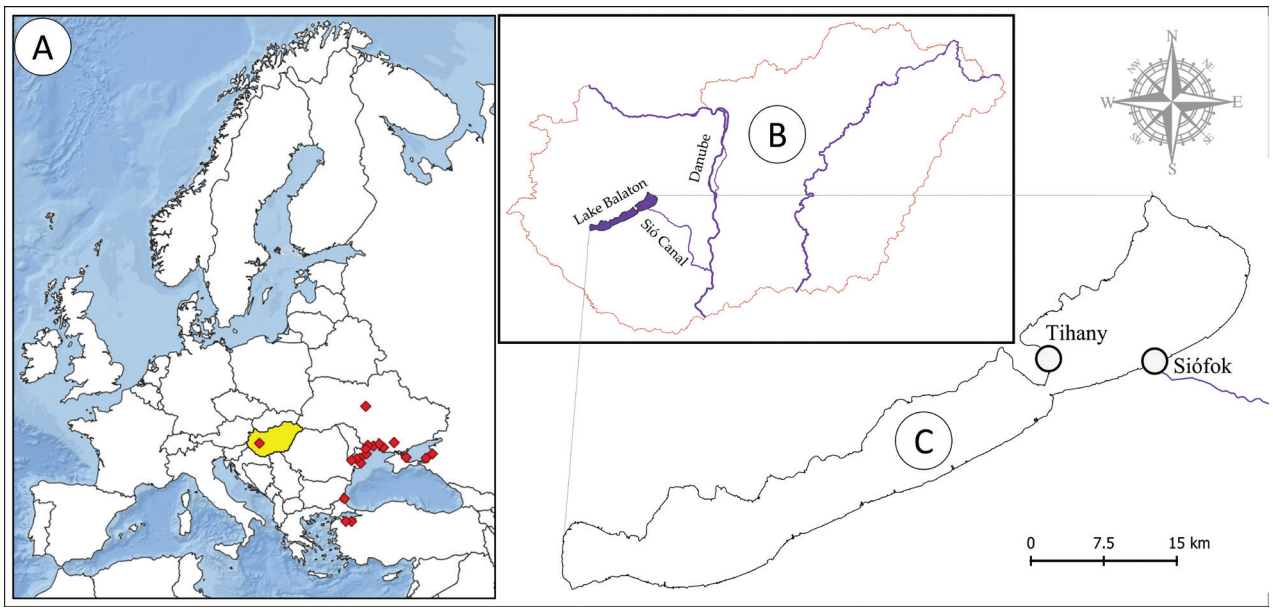

Figure 1. The sampling sites within Lake Balaton (**C**). The geographic position of Lake Balaton in Hungary, and the location of Hungary in Europe are indicated in the inserts **B** and **A**, respectively. The red diamonds indicate the occurrence of *L. pavlovskii* based on the collection of Kvach and Ondračková (2020).

Plerocercoid larvae of the tapeworm *Ligula pavlovskii* were detected for the first time in monkey goby individuals from Lake Balaton in 2004, 34 years after the first record of the fish in the lake (Vitál et al. 2021). The parasite's overall prevalence is high in Lake Balaton's monkey goby population (44%); in some sampling sites the rate of infected individuals exceeds 80% (Vitál et al. 2021).

Invasive Ponto-Caspian goby species have become widespread, significantly altering the ecosystems they invade. One critical factor that could influence their impact on native environments is the presence of their co-introduced parasite, *L. pavlovskii*, which may exert substantial pressure on goby populations. Despite its potential ecological significance, the effects of *L. pavlovskii* on its goby host remain largely unexplored. Understanding this host-parasite relationship is essential for assessing the broader ecological consequences of goby invasions. In this study, we hypothesize that *L. pavlovskii* significantly influences the life history traits of its host. Specifically, we predict and examine that parasitic infection negatively affects somatic growth and reproductive output of monkey goby, while substantially increasing host mortality.

Materials and methods

Study area

Lake Balaton is the largest shallow lake in Central Europe, with a surface area of 596 km^2 and an average depth of 3.3 m. Its outflow, the Sió Canal connects the lake with the River Danube, which serves as the primary invasion corridor of Ponto-Caspian species to Western Europe (Bij de Vaate et al. 2002). The most abundant fish species in the lake are bleak (*Alburnus alburnus*, L.), bream (*Abramis brama*, L.), roach (*Rutilus rutilus*, L.) and razor fish (*Pelecus cultratus*, L.) (Specziár et al. 2010). The zooplankton community of the lake is dominated by copepods with a great proportion of *Eudiaptomus gracilis* (Németh and G-Tóth 2003), which

is the most favourable host for *L. intestinalis* (Loot et al. 2001), that is closely related to *L. pavlovskii* (Nazarizadeh et al. 2023). There are numerous piscivorous bird species as potential definitive hosts of ligulids feeding on fish from Lake Balaton (Kovács 2017).

Sample and data collections

Altogether, 547 monkey goby individuals were collected at two sites of Lake Balaton, along the northern (Tihany: 46.913078, 17.893328; 339 individuals) and southern shores (Siófok: 46.911114, 18.044530; 208 individuals) of the eastern basin (Fig. 1). The fish were collected once per month between April and October 2018 by electrofishing. Both sites are mainly characterized by rip-rap habitats, where monkey goby is abundant (Czeglédi et al. 2019).

Monkey gobies were immediately euthanized with clove oil before being stored in 4% formaldehyde and transferred to the laboratory within a few hours. Samples were stored at 4–5 °C until processing. During the sample processing, total length (TL, to the nearest mm), total weight (W_F) and eviscerated body weight of the fish (W_{EF}) were measured individually to the nearest 0.01g. During the dissection, plerocercoid larvae were removed, counted and weighted (W_P, to the nearest 0.01g.). The gonads of the fish (W_G, to the nearest mg) were weighted. Three subsamples of the gonads were collected from all mature female fish in which the gonads were visible, to determine fecundity and egg size. Subsamples were 1.4–100% (mean 11%) of the total ovarian weight, depending on the size of the ovary. Photos were taken from each of the subsamples under binocular microscope. Absolute fecundity (AF) was estimated gravimetrically using all three subsamples of the gonad.

The diameter of all oocytes was measured with ImageJ software (Schneider et al. 2012) on a randomly chosen subsample of the ovary. To avoid measuring errors derived from non-spherical shape of the oocytes, all diameters were measured in the same direction. Immature individuals were excluded from this investigation (n = 208).

Gonadosomatic index (GSI) = $(W_G/W_F) \times 100$ (Anderson and Gutreuter 1983) and Fulton's condition factor (K) = W_{EF}/TL^3 (Nash et al. 2006) were calculated. To express the severity of infection, we used the parasite index (PI), which represents the ratio of parasite mass to eviscerated body mass: PI = $(W_P/W_{EF}) \times 100$. The following parasitological indices were used according to Bush et al. (1997): Prevalence is defined as the proportion of individuals infected at a given sampling site relative to the total number of individuals examined. Mean intensity refers to the average number of *L. pavlovskii* individuals among the infected monkey gobies. Mean abundance is defined as the total number of *L. pavlovskii* individuals in the sample divided by the total number of monkey gobies examined.

Statistical analyses

Statistical analyses were performed using R v.3.3.2. We tested the effect of the infection (being infected or not) and the PI (severity of the infection) on the K, GSI, mean egg size and AF of the fish by applying general linear models. To achieve a normal distribution, we performed log transformation on the K and arcus sinus square root transformation on the values of GSI.

Separate models were used for the above-mentioned dependent variables, while the primary interest predictor variables were either parasite infection or the parasite index. Each model also contained the following predictor variables: month, sample site, sex (when testing the effects on the condition factor), and TL (when testing the effects on mean egg size and AF of females). Backward stepwise selection was applied on the predictor variables, each initial model was reduced by omitting the variable associated with the largest P value stepwise, except that we retained the predictor of primary interest, such as parasite infection and parasite index, regardless of their significance level to estimate their effects (Table 1).

The significance of each predictor variables was based on Type II analyses of variance table using the "Anova" function from the "car" R package v.3.0-2 (Fox and Weisberg 2011). F tests were calculated. Chi-square test was used to determine the effect of sampling site and sexes on the prevalence of *L. pavlovskii* in monkey goby and to compare the length distributions between infected and non-infected groups seasonally. Some length categories were pooled to avoid expected values less than five. In total, nine groups were created in every season: seven groups with 4 mm interval and a small and a big size group (spring: <4.4 mm and ≥ 7.2 mm, summer: <5.0 mm and ≥ 7.8 mm, autumn: <5.2 mm and ≥ 8.0 mm). The "loess" function was used to fit a local regression model with PI and K variables. Smoothing value was 0.7.

Figures were created in Microsoft Excel, PAST software (v. 3.26b Hammer et al. 2001) and QGIS (v. 3.28.10, QGIS Develoment Team 2023). An alpha value of 0.05 was used to determine statistical significance of all tests.

Results

We detected *L. pavlovskii* plerocercoids in 224 individuals from 547 dissected monkey gobies (155 individuals from a total of 339 fish in Tihany and 69 individuals from a total of 208 fish in Siófok). *Ligula pavlovskii* showed a significantly higher prevalence in monkey gobies collected at Tihany (45.4%) than in those collected at Siófok (33.2%; $\chi^2_{1,\ n\ =\ 547} = 8.4$; $p = 0.004$). Parasite prevalence did not differ between sexes ($\chi^2_{1,\ n\ =\ 546} = 0.4$; $p = 0.528$). Mean intensity (± SE) of *L. pavlovskii* were 1.7 ± 0.1 in Tihany and 1.4 ± 0.1 in Siófok. Mean abundance (±SE) of *L. pavlovskii* were 0.8 ± 0.1 in Tihany and 0.5 ± 0.1 in Siófok. The summed wet weight of the tapeworms taken from each goby individual varied between 0.002 and 1.87 g (mean ± SD; 0.439 ± 0.329 g). The SL of the sampled fish ranged from 31 to 113 mm (62 ± 13 mm), their W_F varied between 0.56 and 28.78 g (4.47 ± 3.35 g).

Median PI was typically low in May and June due to an increased number of new infestations from the given year and a reduced number of fish infected in previous year. Median PI then increased steadily until October (effect of month: df = 6,216; F = 8.903; p < 0.001; Fig. 2). The highest median PI values were found in October (13.3) and April (12.9) (Fig. 2).

The K of fish ranged from 0.47 to 1.18 (0.82 ± 0.08) and was not affected by the presence of the parasite, however we found a relationship between K and PI within the infected group (Df = 1;214; $F = 20{,}906$; $p < 0.001$; Table 1). A noticable decline in K was observed at high PI values (>10%; Fig. 3). Additionally, K varied with months and sexes, but showed no significant differences between study sites (Table 1).

Table 1. Effect of *L. pavlovskii* infection and parasite index on the life history traits of the monkey goby. Final results of general linear models are shown after applying backward stepwise selection of the non-significant predictor background variables (referred to as omitted).

Dependent variables →	Condition factor			GSI (female)			GSI (male)			Mean egg size			Fecundity		
Predictor variables ↓	*F*	df	*p*	*F*	df	*p*	*F*	df	*p*	*F*	df	*p*	*F*	df	*p*
Parasite infection	0.0153	1;537	0.902	74.719	1;308	**< 0.001**	7.237	1;158	**0.008**	114.11	1;215	**< 0.001**	6.772	1;214	**0.010**
Month	24.942	6;537	**< 0.001**	37.006	6;308	**< 0.001**	4.446	6;158	**< 0.001**	18.361	6;215	**< 0.001**	8.46	6;214	**< 0.001**
Sample site	omitted			4.56	1;308	**0.034**	omitted			5.95	1;215	**0.016**	omitted		
Sex	17.271	1;537	**< 0.001**	–			–			–			–		
Month×Infection	omitted			5.324	6;308	**< 0.001**	omitted			4.434	6;215	**< 0.001**	omitted		
Sex × Infection	omitted			–			–			–			–		
Sample site × Infection	omitted			omitted			omitted			omitted			omitted		
TL (females only)	–			–			–			30.824	1;215	**< 0.001**	204.01	1;214	**< 0.001**
Parasite index	20.906	1;214	**< 0.001**	29.488	1;124	**< 0.001**	0.018	1;59	0.893	14.539	1;88	**< 0.001**	0.095	1;82	0.759
Month	10.298	6;214	**< 0.001**	2.609	6;124	**0.021**	3.360	6;59	**0.007**	3.166	6;88	**0.007**	5.008	6;82	**< 0.001**
Sample site	omitted			omitted			omitted			omitted			5.975	1;82	**0.017**
Sex	9.978	1;214	**0.002**	–			–			–			–		
Month × PI	omitted			omitted			omitted			omitted			omitted		
Sex × PI	omitted			–			–			–			–		
Sample site × PI	omitted			omitted			omitted			omitted			omitted		
TL (females only)	–			–			–			24.942	1;88	**< 0.001**	50.4	1;82	**< 0.001**

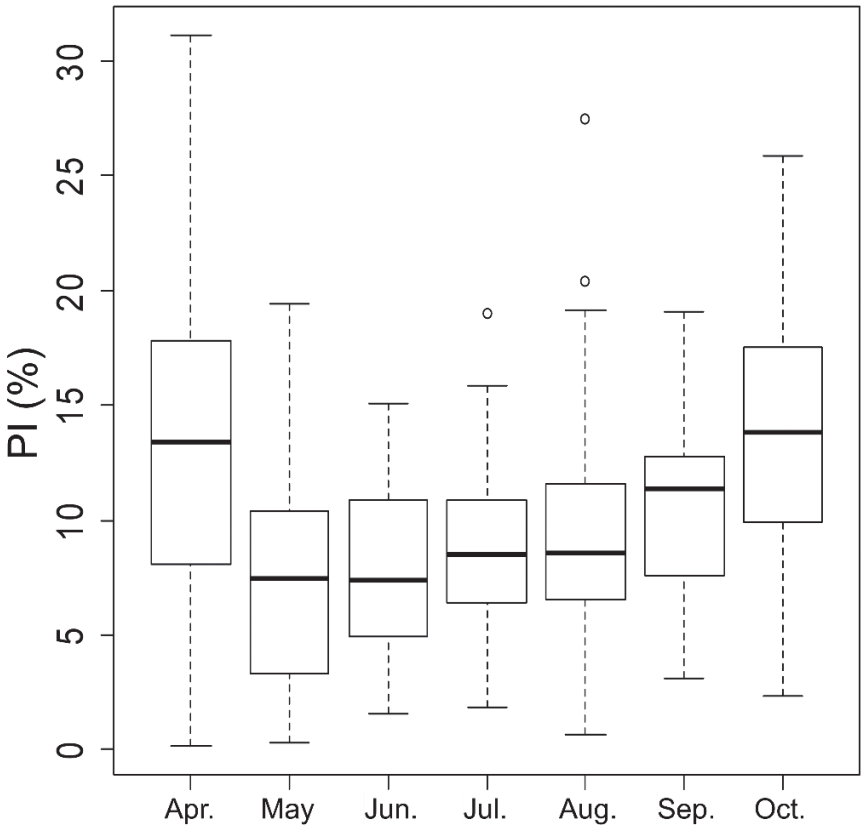

Figure 2. Monthly variation of the parasite index (PI) values in monkey goby. Black lines: median; Whiskers: minimum and maximum (excluding outliers); Dots: outliers.

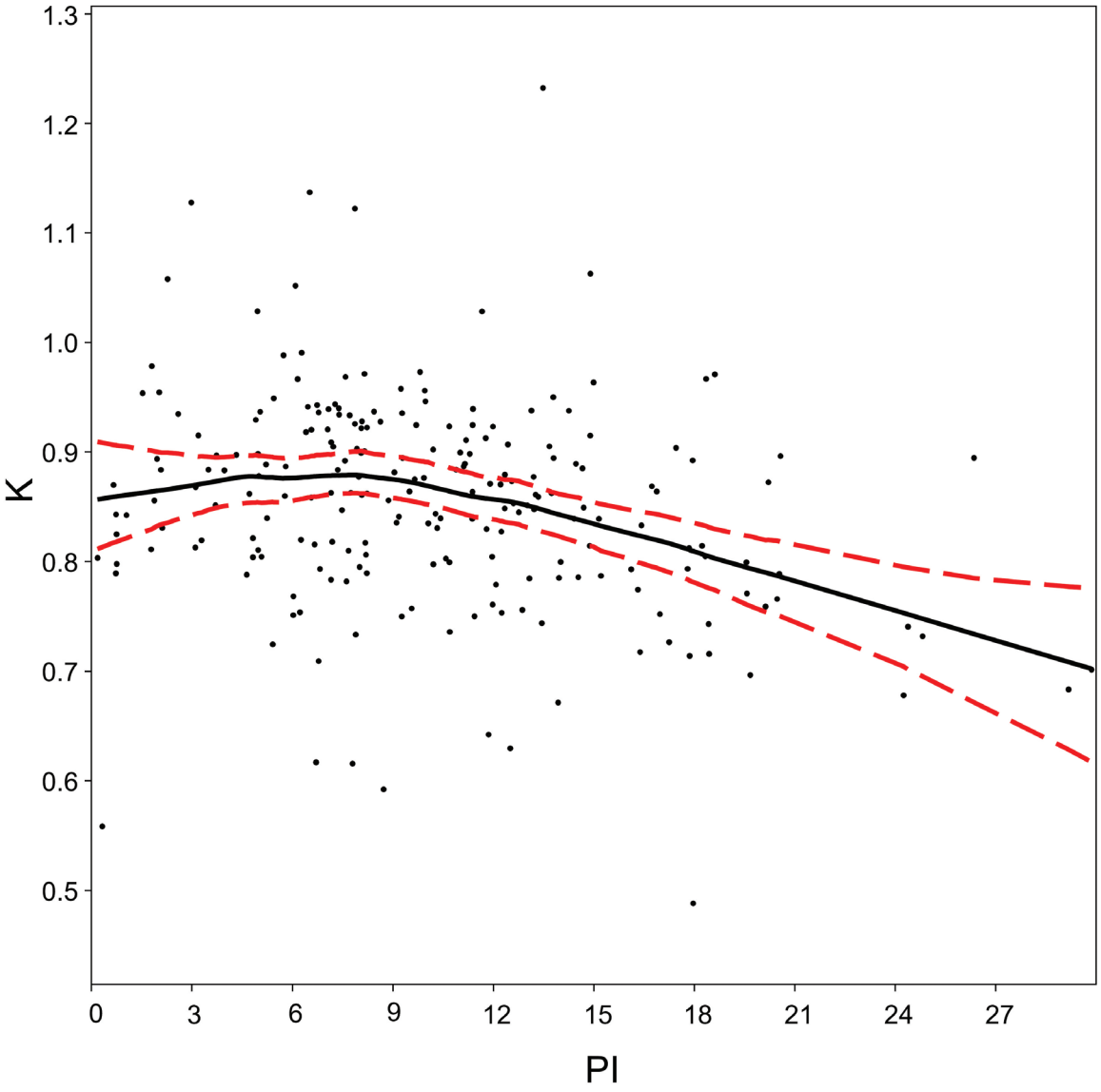

Figure 3. Scatterplot of parasite index (PI) and Fulton's condition factor (K) with locally weighted regression curve (black line) and 95% confidence band based on 999 random replicates (between red dotted lines).

The length frequency distributions of infected and non-infected monkey goby showed seasonal differences. There was no difference in spring ($\chi^2_{8,\ n\ =\ 217} = 8.3$; $p = 0.407$), but a statistically significant difference was found in summer and autumn ($\chi^2_{8,\ n\ =\ 196} = 31.91$; $p < 0.001$ and $\chi^2_{8,\ n\ =\ 152} = 42.84$; $p < 0.001$) due to the bigger body size of the infected individuals (Fig. 4).

Female monkey goby GSI ranged between 0.01 and 18.33 (2.59 ± 3.49) and was affected by both the presence of the parasite and the PI. GSI also varied according to sampling months and sampling sites. Male monkey goby GSI ranged between 0.00 and 6.82 (0.57 ± 1.10), and it was only affected by the presence of the parasite (Table 1, Fig. 5.) The monthly trend in GSI was similar in both sexes; mean values for ligula-free individuals increased in spring, reaching peak values in May (Fig. 5). Afterward, GSI values declined gradually toward summer and autumn. Mean GSI values of infected monkey goby rarely approched the values of the ligula-free group in the same month. This is particularly true for the spawning season, thus the seasonal trend is not obvious (Fig. 5).

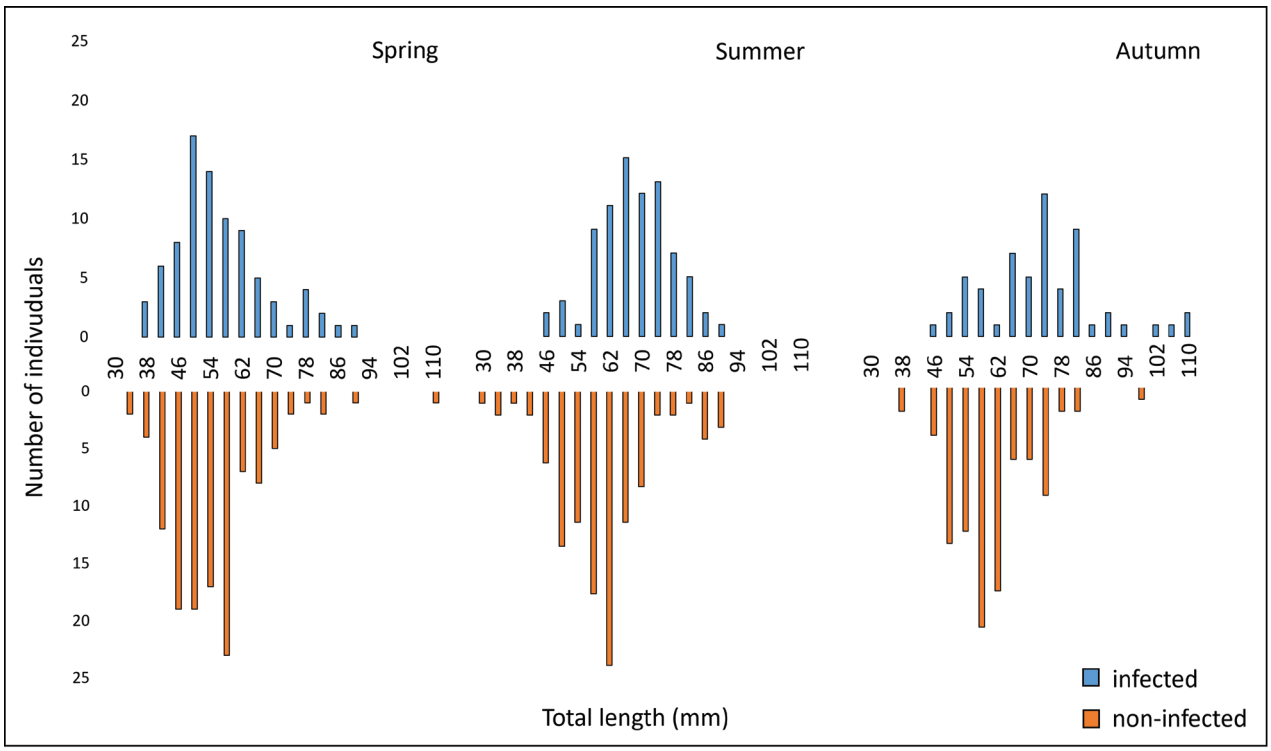

Figure 4. Seasonal variation in the size frequency distribution of infected (blue bar) and ligula-free (orange bar) monkey goby specimens in Lake Balaton.

Absolute fecundity ranged between 65 and 2726 (785 ± 375) during the sampling period. Although the presence of the tapeworm had significant effect on AF, the PI did not affect it (Table 1). Positive correlation was found between TL and AF in the case of prespawning individuals (April and May, n = 118, R^2 = 0.6031). Number of eggs and mean egg size were affected by total length of the fish (Table 1).

Size of eggs ranged between 0.1 and 1.9 mm, and was influenced by the presence of the parasite, the PI and the sampling month (Table 1). In the active months of reproduction, the ovaries of non-infected females contained bigger, matured or maturing eggs in higher frequency than in infected females (Fig. 6).

Relatively large ligula has additional physical effect on inner organs, such as gonads. The bigger the parasite, the more it compresses the organs (Fig. 7).

Discussion

Our results demonstrated a considerable effect of *L. pavlovskii* on the life history of monkey goby host. Firstly, the sampled populations of monkey goby were highly exposed to parasite infection. As a presumed consequence of the large body size of the parasite compared to its host, we found a difference in both somatic and reproductive investments. On the other hand, the high prevalence of the parasite and the inevitable mortality resulted in a much shorter expected lifespan for the fish. The individual effects observed underscore the substantial impact of the parasite's presence on the monkey goby population of the lake.

The prevalence observed in the studied populations is approximately in line with the data reported by Vitál et al. (2021). In light of the prevalence values reported for different sampling sites in Lake Balaton, the prevalence data of the present study are not extremely high. The average prevalence across 17 sites in the

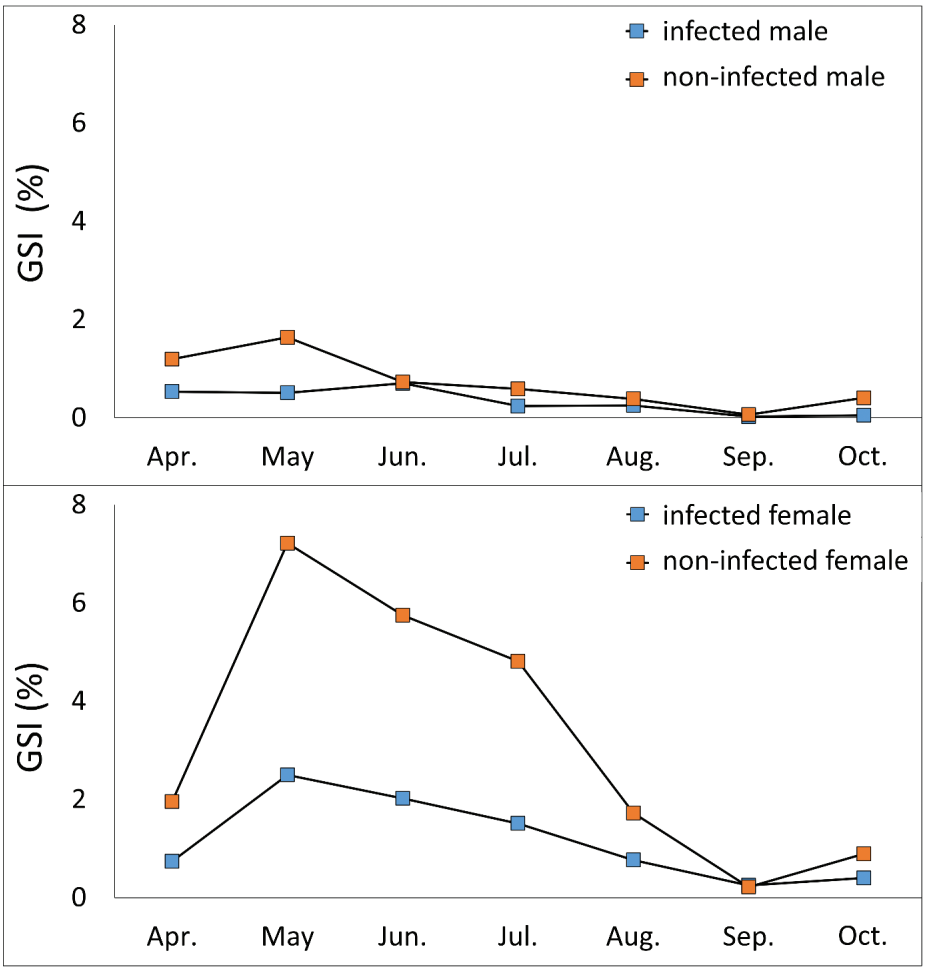

Figure 5. Mean monthly GSI values of male and female monkey goby. Blue squares represent infected, oranges represent ligula-free individuals. SD values have been omitted for clarity.

lake was 44.4%, with a maximum exceeding 84% (Vitál et al. 2021). In the native range of the monkey goby, across various populations in the Black Sea region, prevalence ranged from 0% to 22.8%, mean intensity ranged from 0 to 4, and mean abundance from 0 to 0.3 across sampling sites (Kvach 2005, 2010; Kvach et al. 2014; Yuryshynets et al. 2017). The infestation parameter values observed in the present study exceed those reported in the native range of the species.

The reproductive cycle considerably differed between infected and non-infected monkey gobies. Non-infected individuals (both sexes) showed a normal reproductive cycle. This is confirmed by the trend of GSI values (Fig. 5) and the size-frequency of the oocytes (Fig. 6). According to the within-year trend of GSI for ligula-free individuals, females increase ovary masses rapidly between April and May, after which a decline is typical. This trend indicates that the reproductive season of the monkey goby in Lake Balaton takes place from April to August. This is in accordance with the report of the species in non-native areas (Gertzen et al. 2016) and natives as well (Konečná and Jurajda 2012). By contrast, infected individuals were inhibited in reproduction; GSI values were typically low in the reproductive season (Fig. 5) as a result of the lack of oocyte maturity (Fig. 6).

Parasites have two different strategies to influence host reproduction: direct manipulation of energy allocation by 'castrators' and nutrient theft by 'consumers'. True castrators directly deactivate host reproduction using physical or chemical ways. By

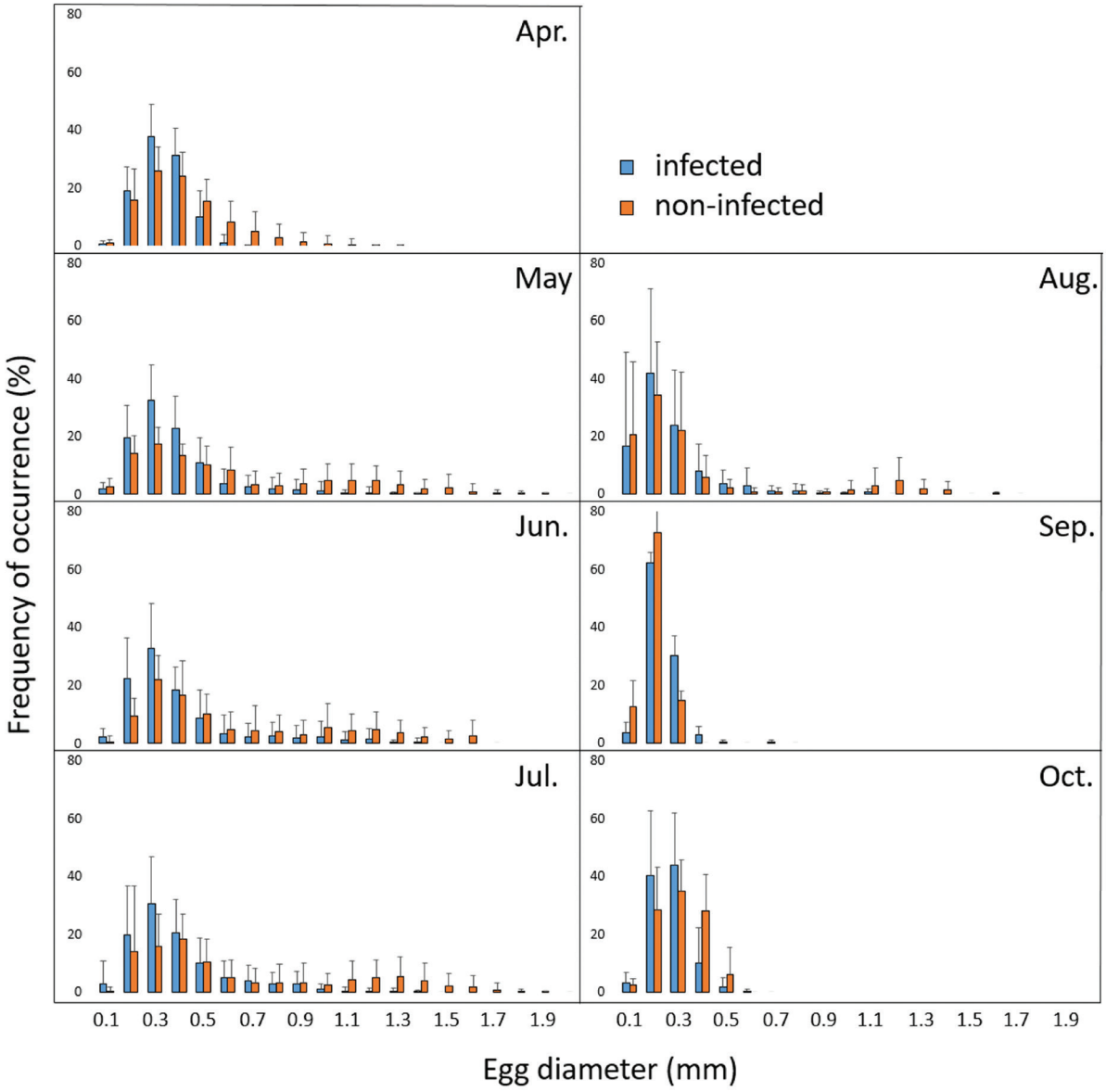

Figure 6. Mean monthly size-frequency distribution of oocytes of monkey goby. Blue columns represent infected, orange columns represent non-infected individuals.

contrast, consumers have an indirect effect on host reproduction as a side effect of stealing host energy (Baudoin 1975). Therefore, the effect of true castrators on reproduction occurs early in the infection, influencing both less and heavily infected individuals, while the effect of consumers increases with the severity of infection (PI) (Hurd 2001; Hall et al. 2007). Closely related parasite species act both as true castrators and consumers. Hormonal studies found that *L. intestinalis*, L. 1758 (Diphyllobothriidae) parasite behaves as a castrator, because it inhibits gonad development in both male and female roach by altering levels of sex hormones (Geraudie et al. 2010; Trubiroha et al. 2010, 2011). Furthermore, *Schistocephalus pungitii*, Dubinina, 1959 (Diphyllobothriidae) causes host sterility as a result of nutrient drainage (Heins 2017). The process for the caused sterility of *L. pavlovskii* in the monkey goby remains unknown and further experimental studies are needed to elucidate this.

In any case, the lack of oocyte development results energy surplus which could be used for the energy requirement of the parasite or other life history elements.

Figure 7. Physical effect of large *L. pavlovskii* on monkey goby gonads. Ligulas may fill the whole body cavity (**a, b**), and they can compress the internal organs like gonads (**c**); **d** is an ovary of a non-infected individual from the same month (October) and sampling site (Siófok).

Our results suggest, as long as the parasite does not exceed a considerable size, the energy surplus from gonadal maturation is higher than the needs of the parasite. Host individuals might be able to invest more energy in their body development which seems to be confirmed by maintained condition factor and accelerated growth of infected monkey goby in our study. Ould Ruis et al. (2016) found similar phenomena, *L. intestinalis* did not affect the condition of Algerian barb (*Luciobarbus callensis*, Valenciennes, 1842), but the infected fish were significantly longer than the uninfected, and had inhibited gonad development. In some cases, this apparent good fitness could not be explained by reduced gonad development (see: parasite induced 'gigantism'; e.g. Arnott et al. 2000). Arnott et al. (2000) found that experimentally infected three-spined sticklebacks (*Gasterosteus aculeatus*, Linnaeus, 1758) grew faster, maintained similar or better conditions compared to uninfected fish, and successfully developed an immune response, despite the energy drain of the parasite *S. solidus* (Müller, 1776) Steenstrup, 1857 (Diphyllobothriidae). In this case, the parasite fitness is directly linked to the host energy allocation. Since the parasite is large-bodied, the accelerated growth of the small-bodied host fish could assist the growth of a relatively large plerocercoid to produce eggs. The survival of the host species is critical for the parasite during development. Lower metabolic rate of larger individuals (Clarke and Johnston 1999) with good condition could prevent the overwinter mortality caused by starvation (Berg and Bremset 1998; Post et al. 1998). Nevertheless, predatory birds select the largest individuals from the population (Van der Veer et al. 1997), thereby the life cycle of the parasite in a bigger fish may be guaranteed at higher probability than in a smaller fish. This situation is similar to the case of *L. pavlovskii* and monkey goby, therefore we cannot exclude the parasite induced gigantism, but further experimental research is needed to determine the role of *L. pavlovskii* in growth and condition of monkey goby. Condition depended on the sampling month and sex of the fish as well. The effect of months evidently follows the cyclical process of the year, while the effect of sex on K factor is attributed to the parental care (guarding eggs) of male individuals, which is energetically costly because of constraint foraging opportunities (Smith and Wootton 1995).

The highest PI was found in monkey gobies collected in April, compared to the other sampling months. Those individuals were the ones that were infected in the previous year and managed to survive the winter. In May we were able to detect the new infections, resulting in small larvae in the abdominal cavity of the fish. Although we did not examine changes in monkey goby mortality, our data allow us to conclude increased mortality due to parasite infection. Based on the seasonal

variation of the parasite index, we can assume that fish can only survive infection with the parasite to a negligible extent for more than a year. This is indicated by the seasonal trend of the PI values, where the high values in early spring are followed by a decline, then a slow and gradual increase, reaching values similar to those observed in spring.

The appearance of the parasite, its high prevalence, and the strong physiological effects it causes suggest that parasitic pressure on the monkey goby can strongly affect infected populations. This may also influence populations of uninfected, competing species. Increased mortality (for example, due to higher exposure to predation; e.g. Harris and Wheeler 1974; Bean and Winfield 1989; Barber et al. 2000) and reduced reproduction success may decrease the abundance of the non-native fish species involved in competition. Parasites can reduce the host's competitive ability (Aliabadi and Juliano 2002). As a result, the parasite may slow the spread of the invasion front and lessen the impact of populations behind the front on native fish. Therefore, carefully managed infestation with *L. pavlovskii* may reduce the invasion success of the parasite-sensitive Ponto-Caspian goby species, although spill over to native taxa and the implications there of remains unconsidered.

Conclusions

In this study, we demonstrate for the first time the impact of the *L. pavlovskii* parasite on its host organism. Our results indicate that the parasite significantly affects, and can even completely suppress the reproductive capabilities of the host, influences individual growth and condition, and increases mortality. Given the observed high prevalence, this has a substantial effect on the entire population. As such, our findings may prove valuable in the future for developing various conservation intervention in the fight against invasive species.

Acknowledgments

We would like to thank Bernadett Kern for her general help during the project and Kálmán Molnár for his advice.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was supported by the GINOP-2.3.2-15-2016-00004 project. The work of IC, BP, PT and TE was supported by the Széchenyi Plan Plus Program (RRF-2.3.1-21-2022-00014) and the Sustainable Development and Technologies National Programme of the Hungarian Academy of Sciences (NP2022-II-3/2022). István Czeglédi was also supported by the OTKA PD 138296 grant (National Research, Development and Innovation Office – NKFIH).

Author contributions

Sample collections were performed by Z. Vitál, I. Czeglédi, B. Preiszner, P. Takács, and N. Boross. The laboratory work was performed by Z. Vitál E. Megyeri, and N. Boross. Study design and data analyses were conducted by Z. Vitál, N. Boross, T. Erős. The first draft of the manuscript was written by Z. Vitál. All authors made substantial contributions to the preparation of the manuscript. All authors have read and approved the final version of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Raw data of the investigated individuals

Authors: Zoltán Vitál, István Czeglédi, Eszter Megyeri, Bálint Preiszner, Péter Takács, Tibor Erős, Márton Sallai, Nóra Boross

Data type: xlsx

Explanation note: Raw data of the investigated monkey goby individuals includes sampling data, somatic and reproductive parameters, and *L. pavlovskii* informations.

Link: https://doi.org/10.3897/neobiota.99.154887.suppl1

Supplementary material 2

Egg sizes

Authors: Zoltán Vitál, István Czeglédi, Eszter Megyeri, Bálint Preiszner, Péter Takács, Tibor Erős, Márton Sallai, Nóra Boross

Data type: xlsx

Explanation note: It contains monkey goby egg diameters.

Link: https://doi.org/10.3897/neobiota.99.154887.suppl2