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RESEARCH PAPER

Morphological variability in a successful invasive species originating from habitats experiencing different levels of disturbance

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Abstract. Biological invasions are part of processes connected with human activities, which threaten biodiversity and all ecosystems, including freshwaters. Many research studies aim to discover the main traits responsible for invasive success. The topmouth gudgeon is one of the most successful invasive fish species; thus, this study aimed to analyse morphological variability and sexual dimorphism of two topmouth gudgeon populations coming from different sites in Bulgaria (n = 150 in both cases) and to evaluate its morphological variability in connection to differently disturbed habitats of occurrence. For this, we measured thirty morphometric characters, which were subsequently statistically analysed. The species is characterised by high morphological variability between the populations from different sites and also within populations. We showed that populations from Bulgaria differed mainly in traits connected with specific body dimensions. The population from the Kolarovo channel showed a significantly deeper head, bigger mouth and longer body in the front part. On the other hand, the population from Lake Zafirovo had a significantly longer caudal peduncle and caudal and anal fins. Differences between males and females were found between traits connected to the head and fins, which made males more robust with longer fins. At the same time, females were characterised by deeper bodies, which is essential for their investment in reproduction.

Key words: *Pseudorasbora parva*, invasive fish species, phenotypic plasticity, morphology, sexual dimorphism

Introduction

Biological invasions are considered a major threat to global biodiversity, impacting all ecosystems, including freshwaters (Mooney et al. 2005, Pauchard et al. 2018). Fish are among the most introduced groups of aquatic animals worldwide and, simultaneously, the most threatened (Gozlan 2008). Non-native fish species can change receiving ecosystems through, e.g. increased predation pressure and competition for resources that can lead to shifts in ecosystem function and alteration of food webs (Gozlan et al. 2010, Davies & Britton 2021). However, not all newcomers impose such changes, therefore, it is important to determine the traits that predict them to become successful invaders. Thus the analyses of life-history traits and morphology represent the best source of information (Feiner et al. 2012, Záhorská et al. 2013b, 2017, Jia et al. 2019). Successful invasive species can modify their life history strategies to adapt to new areas, or they will

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be excluded/replaced. The main characteristic which allows them to do so is phenotypic plasticity induced by epigenetic mechanisms that can help with their successful establishment and distribution (Hawes et al. 2018). Phenotypic plasticity encompasses all types of environmentally induced changes, e.g. morphological, physiological, behavioural or life histories (Kelly et al. 2012). At the same time, morphology is a phenotypic aspect that often reflects deeper functional changes in the species' life history traits and thus undergoes rapid changes among an invasive population (Gutowsky & Fox 2012).

Morphological traits in fish are used to differentiate a single population and are assigned among the most easily examining mechanisms of species adaptation to new environmental elements (e.g. Torres et al. 2010, Mojekwu & Anumudu 2015) or as a result of founder effects and artificial selection (Yavno et al. 2013). Morphological differences between populations will likely result from fitness gained through adaptive phenotypic plasticity, which generates new phenotypic optima in novel environments (Ghalambor et al. 2007).

Because of a confirmed high phenotypic plasticity, we researched topmouth gudgeon (*Pseudorasbora parva*, Temminck & Schlegel, 1846), which is one of the most invasive fish species in recent times and has passed through a pan-continental invasion in the last fifty years (Gozlan et al. 2010). At the same time, it is evident that *P. parva* is a species with great morphological variability, which can be expressed in the formation of different adult phenotypes and how the phenotypes are achieved (Záhorská et al. 2009). Phenotypic plasticity can also prove important when considering sexual dimorphism, which plays a vital function because males and females have different reproductive roles (Bănărescu 1999). Females select a clear area, and breeding males clean the surface of stones and the surrounding sediment. Each male tries to attract several females that lay eggs on the stones. After fertilising them, the male actively guards the primitive nests using tubercules around its mouth (Bănărescu 1999). Few morphological studies about this species have been done (Záhorská et al. 2009, 2013a), but there is still little knowledge about the morphology connected to habitats with different levels of disturbance. Thus, the main aim of this study was to 1) analyse morphological variability and sexual dimorphism of two populations of topmouth gudgeon coming from different sites in Bulgaria; 2) evaluate the morphological variability in topmouth gudgeon populations coming from disturbed and undisturbed habitats.

Material and Methods

Specimens of two populations of topmouth gudgeon were collected by electrofishing from April to July

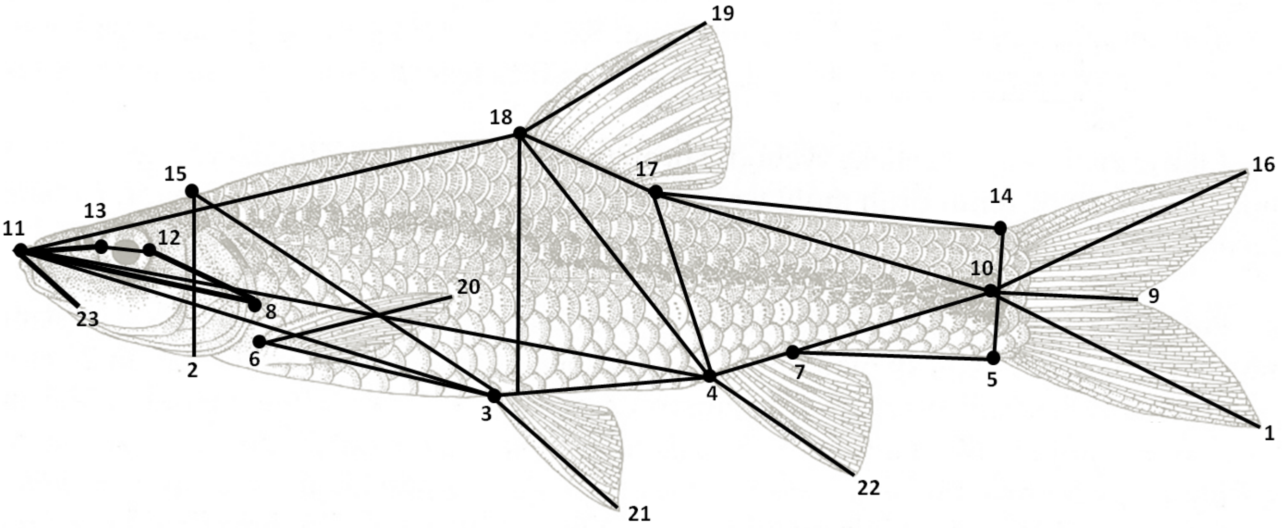

Fig. 1. Scheme of morphometric characters for distance-based measurements taken from *Pseudorasbora parva* population: head length (11-8); preorbital distance (11-13); eye diameter (13-12); postorbital distance (12-8); head depth (15-2); predorsal distance (11-18); prepelvic distance (11-3); preanal distance (11-4); pectoral fin-pelvic fin (P-V) distance (6-3); pelvic fin-anal fin (V-A) distance (3-4); body depth (18 perpendicular); dorsal fin (anterior end)-anal fin distance (Da-A) (18-4); dorsal fin (posterior end)-anal fin distance (Dp-A) (17-4); postdorsal distance (17-10); postanal distance (7-10); caudal (C) peduncle length (dorsal) (17-14); caudal peduncle length (ventral) (7-5); caudal peduncle depth (14-5); dorsal fin (D) base length (18-17); anal fin (A) base fin length (4-7); pectoral fin (P) length (6-20); pelvic (V) fin length (3-21); caudal upper lobe length (10-16); caudal fork length (10-9); caudal lower lobe length (10-1); dorsal fin length (18-19); anal fin length (4-22); gape (11-23).

Table 1. Mean values, minimum (Min), maximum (Max), and standard deviations (SD) of particular characters (see Fig. 1) of topmouth gudgeon (*Pseudorasbora parva*) from Kolarovo channel in Bulgaria with regard to sexes (TL – total length, FL – fork length, SL – standard length, P – pectoral fin, V – ventral fin, A – anal fin, C – caudal fin, D – dorsal fin, Da – anterior end of dorsal fin, Dp – posterior end of dorsal fin).

	Kolarovo channel females					Kolarovo channel males				
	n	Mean	Min	Max	SD	n	Mean	Min	Max	SD
TL	102	38.46	27.71	60.09	6.90	48	46.32	30.78	79.07	9.20
FL	102	35.68	25.91	56.36	6.52	48	43.02	28.69	74.39	8.73
SL	102	31.97	22.79	50.91	5.88	48	38.58	25.67	67.59	7.93
In % of SL										
Head length	102	26.51	23.19	30.81	1.40	48	26.87	23.75	29.91	1.35
Preorbital distance	102	7.21	5.78	9.12	0.71	48	7.68	6.39	9.07	0.71
Eye diameter	102	7.52	6.05	9.13	0.67	48	7.10	4.73	9.17	0.85
Postorbital distance	101	12.64	9.52	14.63	0.83	48	13.00	11.11	14.69	0.88
Head depth	102	19.02	17.34	21.31	0.90	48	19.36	17.45	21.03	0.91
Predorsal distance	102	51.67	47.79	55.23	1.38	48	52.10	49.44	54.14	1.11
Pre-ventral distance	102	51.05	47.26	55.14	1.49	48	51.21	48.23	53.62	1.39
Preanal distance	102	71.05	67.17	76.63	1.56	48	70.60	67.85	74.61	1.41
P-V distance	102	26.23	20.01	30.62	1.81	48	25.93	23.35	28.54	1.16
V-A distance	102	22.30	17.79	25.60	1.61	48	22.01	17.91	25.07	1.48
Body depth	102	22.92	19.47	27.07	1.33	48	23.05	19.38	26.34	1.60
Da-A distance	102	29.03	25.15	31.86	1.33	48	29.41	25.81	32.52	1.68
Dp-A distance	102	19.38	16.54	23.58	1.41	48	19.60	16.21	22.33	1.54
C peduncle (dorsal)	102	38.51	34.79	43.55	2.01	48	38.03	33.67	42.47	1.95
C peduncle (ventral)	102	21.53	17.47	25.65	1.64	48	21.88	18.82	24.59	1.21
Postdorsal distance	102	39.72	35.74	44.10	1.90	48	39.79	35.28	44.35	1.78
Postanal distance	102	22.52	13.14	25.74	1.75	48	23.13	21.11	25.56	1.18
D fin base length	102	13.21	9.14	15.86	1.23	48	13.17	9.77	15.96	1.38
A fin base length	102	9.67	6.62	12.93	1.20	48	9.76	7.47	11.09	0.91
P fin length	101	16.05	12.35	35.95	2.58	48	16.86	13.35	19.66	1.63
V fin length	101	13.67	8.14	64.69	5.44	48	14.06	10.76	17.47	1.52
C upper lobe length	102	23.38	19.19	27.61	1.61	48	23.38	19.58	26.86	1.68
C lower lobe length	102	23.65	16.24	29.59	2.10	48	23.78	18.77	29.72	1.75
D fin length	102	19.19	8.49	24.69	2.12	48	20.51	16.48	23.66	1.86
A fin length	102	10.09	6.87	14.90	1.72	48	11.28	7.37	14.18	1.82
C peduncle depth	102	12.20	10.72	14.70	0.71	48	12.58	10.12	13.93	0.85
Gape	102	7.89	5.84	10.29	0.89	48	8.00	6.20	10.02	0.84

2011 from two sites in Bulgaria (the Danube drainage) exposed to different levels of disturbances (Fig. S1). Disturbance was evaluated following the approach of pressure assessment developed for the process of inter-calibration within the implementation of the Water Framework Directive in European Union, where a pressure is defined as a physical expression of human activities that change the status of the environment, such as discharge, abstraction, environmental changes, etc. (van de Bund 2008). Habitats of the two sites examined in this study were thus characterised using the following eight criteria of pressures: water level fluctuation, character of banks (regulation), alteration in natural character of riparian vegetation, alteration in aquatic vegetation, overall habitat alteration, water quality alteration, predation pressure, and stocking/aquaculture activities. Each pressure was assessed based on a four-scale modality

Table 2. Discriminant function analysis of intraspecific sexual structure of topmouth gudgeon (*Pseudorasbora parva*) from two sites in Bulgaria. Factor structure matrix (FSM) predicates of biological importance of the trait. Significantly different traits are in bold face. (P – pectoral fin, V – ventral fin, A – anal fin, C – caudal fin, D – dorsal fin, Da – anterior end of dorsal fin, Dp – posterior end of dorsal fin).

	Lake Zafirovo				Kolarovo channel			
	Wilks λ	F test	*P*	FSM	Wilks λ	F test	*P*	FSM
Head length	0.6555	1.0245	0.3135	0.0325	0.6028	0.0721	0.7887	0.1493
Preorbital distance	0.6618	2.1980	0.1408	0.1787	**0.6288**	**5.2693**	**0.0234**	**0.3848**
Eye diameter	**0.6878**	**7.0829**	**0.0088**	–0.1819	**0.6219**	**3.8892**	**0.0509**	**–0.3262**
Postorbital distance	0.6502	0.0131	0.9091	–0.0203	0.6038	0.2724	0.6027	0.2433
Head depth	0.6659	2.9598	0.0879	0.0276	0.6035	0.2180	0.6414	0.2149
Predorsal distance	**0.6953**	**8.4774**	**0.0043**	–0.2648	0.6130	2.1066	0.1493	0.1840
Pre-ventral distance	0.6501	0.0109	0.9169	–0.1025	0.6026	0.0326	0.8571	0.0580
Preanal distance	0.6502	0.0155	0.9011	–0.0869	0.6118	1.8758	0.1734	–0.1931
P-V distance	0.6502	0.0269	0.8699	–0.1543	0.6068	0.8838	0.3491	–0.1134
V-A distance	0.6677	3.2981	0.0718	0.1359	0.6040	0.3228	0.5710	–0.1244
Body depth	**0.7454**	**17.8887**	**0.0000**	–0.1716	**0.6441**	**8.3037**	**0.0047**	0.0545
Da-A distance	0.6513	0.2231	0.6375	0.0600	0.6106	1.6332	0.2037	0.1444
Dp-A distance	0.6576	1.4127	0.2369	0.0327	0.6033	0.1899	0.6638	0.0963
C peduncle (dorsal)	0.6531	0.5706	0.4515	0.0194	0.6092	1.3494	0.2477	–0.1356
C peduncle (ventral)	0.6528	0.5070	0.4778	–0.0012	0.6069	0.8973	0.3454	0.1386
Postdorsal distance	0.6532	0.5832	0.4465	–0.0368	0.6041	0.3337	0.5646	0.0266
Postanal distance	0.6545	0.8222	0.3663	–0.0275	0.6033	0.1868	0.6664	0.2271
D fin base length	0.6540	0.7412	0.3910	0.0709	0.6031	0.1500	0.6992	–0.0318
A fin base length	0.6504	0.0592	0.8082	0.0471	0.6025	0.0319	0.8585	0.0488
P fin length	0.6514	0.2407	0.6246	0.1034	0.6035	0.2306	0.6319	**0.3465**
V fin length	0.6502	0.0275	0.8686	0.1362	0.6081	1.1291	0.2901	0.2841
C upper lobe length	0.6509	0.1564	0.6932	0.1159	0.6080	1.1126	0.2936	–0.0091
C lower lobe length	0.6503	0.0311	0.8604	0.1305	0.6027	0.0527	0.8189	0.0300
D fin length	**0.7014**	**9.6279**	**0.0024**	**0.3920**	0.6094	1.4051	0.2382	**0.3607**
A fin length	0.6621	2.2570	0.1356	0.2856	0.6198	3.4682	0.0650	**0.4131**
C peduncle depth	0.6505	0.0865	0.7691	0.0460	0.6171	2.9359	0.0892	0.2829
Gape	0.6502	0.0175	0.8949	0.0197	0.6024	0.0002	0.9883	0.0766

(no, low, medium, high) expressed numerically as 1, 2, 3, and 4, respectively. The final pressure index, considered to reflect the intensity of disturbances, was then calculated as a sum of all eight criteria values, providing a possible range from 8 (minimum disturbance) to 32 (maximum disturbance).

The Kolarovo channel (44°00′01′′ N, 26°51′54′′ E, n = 150) comprises a small stream flowing out of a fishpond where the water level fluctuates significantly. In summer, it dries up and is maintained only in the form of a few ponds. Because of this, the presence of aquatic vegetation and water quality also changes. The topmouth gudgeon population occurs here for a relatively short time, approximately ten years. Frequent manipulation of the water level causes heavy disturbances to the local habitat, and thus, this population has to cope with permanent stress (pressure index 28; Table S1) and has never been established safely.

Lake Zafirovo (43°59′23′′ N, 26°48′50′′ E, n = 150) was created in the 1970s and is used for large-scale fish farming. There are no fluctuations in the water level or water quality. The banks of the pond are stably covered with aquatic vegetation. The first documented occurrence of the topmouth gudgeon is from the late 1970s and early 1980s. Thus, it was characterised as a stable environment with a pressure index of 10 (Table S1).

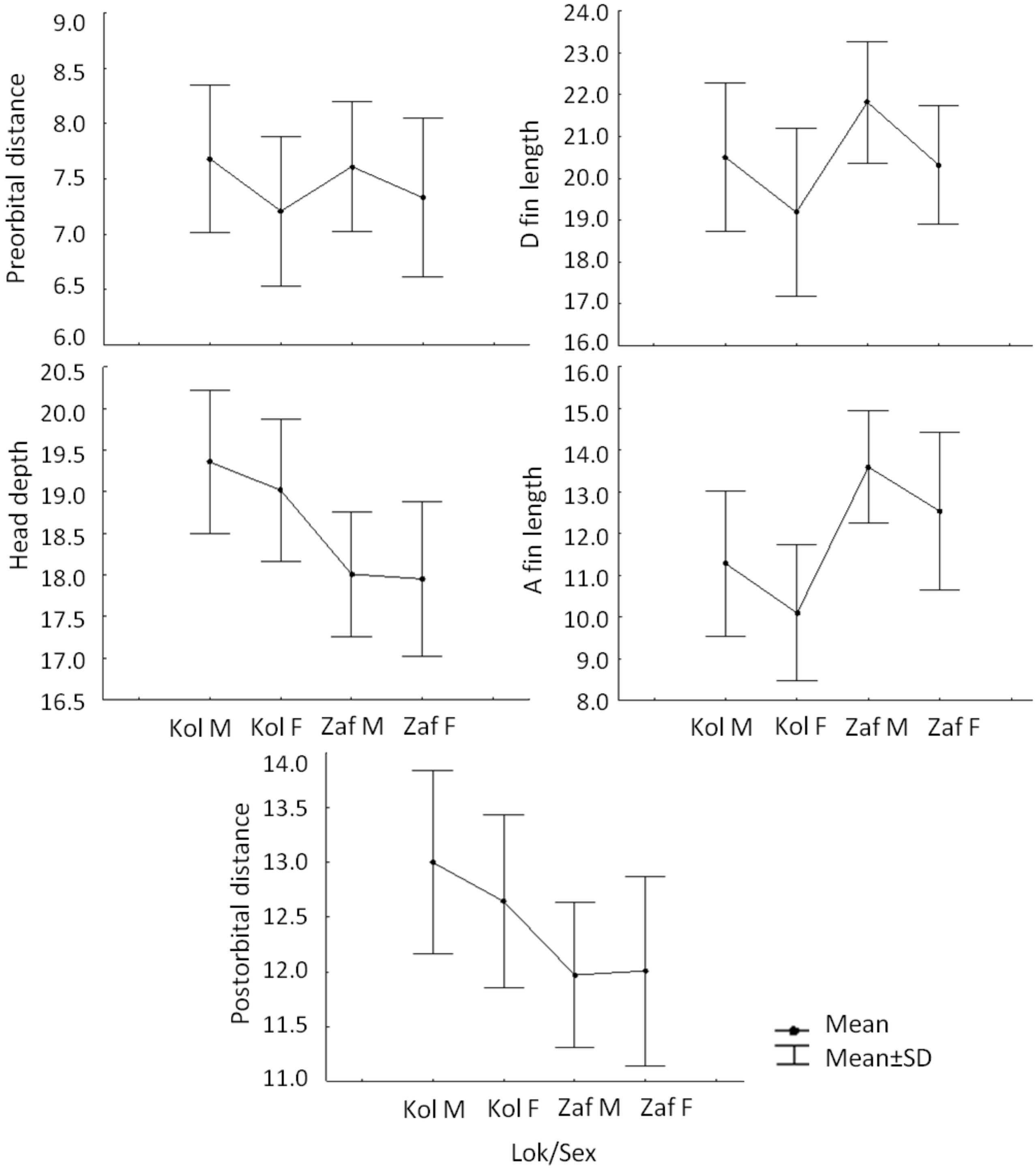

Fig. 2. Differences in biologically important traits between populations of topmouth gudgeon (*Pseudorasbora parva*) from two different sites in Bulgaria with regard to sexes (Kol M – Kolarovo channel males, Kol F – Kolarovo channel females, Zaf M – Lake Zafirovo males, Zaf F – Lake Zafirovo females).

Specimens were euthanised with an overdose of 2-phenoxyethanol and preserved in a 4% formaldehyde solution (10% neutral buffered formalin). All samples were stored in airtight plastic containers in a dark place at room temperature (approximately 20 °C). The samples were measured and processed within 5-9 months after preservation, which is a period that should not affect the somatic parameters by more than 2-3% (Paradis et al. 2007). Thirty morphometric characters, including total length (TL), standard length (SL) and fork length (FL; Fig. 1, Table S2), were measured from digital photographs taken by a Pentax camera and using the Impor 2.31E software. To allow future inter-population comparisons, 27 mensural characters were expressed in % SL and evaluated subsequently using variation analysis (Snedecor 1946). Traits were thereafter evaluated in STATISTICA 8. Factorial ANOVA was used to test the

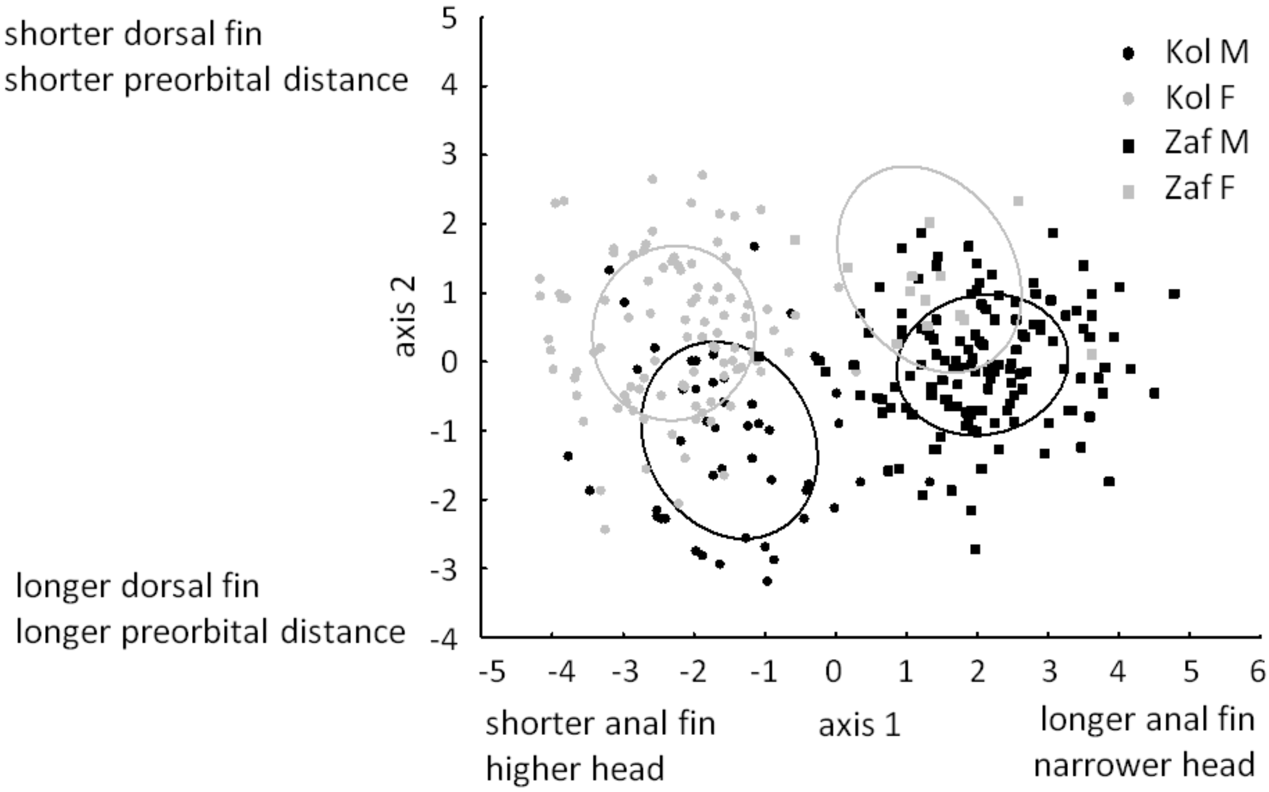

Fig. 3. Discriminant functional analysis scatter plot (DFA) with means of canonical variables and 50% ellipsoids about the centroid of each population of topmouth gudgeon from two different sites in Bulgaria, with discrimination based on morphological variability of characters. (Kol M – Kolarovo channel males, Kol F – Kolarovo channel females, Zaf M – Lake Zafirovo males, Zaf F – Lake Zafirovo females).

differences between populations as well as between males and females of topmouth gudgeon for each of the 30 mensural characters. Discriminant analysis (DCA) was performed on the same variable set. Differentiation of specimens with regard to sex and locality in multidimensional space was determined with Wilk's λ, F and P statistics.

To determine the traits affecting the total biology of the species, we used the rule defined by McGarigal (McGarigal et al. 2000), which is not based on mathematical principles but on practical observations. Therefore, traits analysed by DCA that are equal to an absolute value of 0.3 are biologically important, and traits greater than or equal to an absolute value of 0.4 are considered to have biologically significant relationships.

Results

The standard length of the population from the Kolarovo channel (n = 150) ranged from 22.8 to 67.6 mm (mean = 34.1 mm, Table S2). In this population, we analysed 48 males and 102 females (Table 1). Significant differences were found in only three traits (preorbital, eye diameter and body depth) between males and females, but five traits (preorbital distance, eye diameter, pectoral fin length, dorsal fin length and anal fin length) were biologically important (Table 2).

The SL of the population from Lake Zafirovo (n = 150) ranged from 27.5 to 74.5 mm (mean = 47.8 mm, Table 2), and we analysed 136 males and 14 females (Table 3). There were significant differences between males and females in four traits (eye diameter, predorsal distance, body depth and dorsal fin length), with only one trait (dorsal fin length) having biological importance (Table 2).

By the comparison of the two populations regardless the sexes, ten traits were determined to be significantly different (postorbital distance, head depth, pre-ventral distance, pectoral and ventral fin distance, caudal peduncle length (ventral), caudal peduncle length (dorsal), caudal upper lobe length, caudal lower lobe length, anal fin length, gape), but only two traits had biological importance (head depth and anal fin length; Table 4). By the comparison of the populations with regard to sexes, we found 14 characters significantly different (Table 5) and five having biological importance (preorbital, postorbital distance, head depth, dorsal fin length and anal fin length, Fig. 2). Table 4 was also transported to a graph, where the x-axis shows traits, which are different

Table 3. Mean values, minimum (Min), maximum (Max), and standard deviations (SD) of particular characters (see Fig. 1) of topmouth gudgeon (*Pseudorasbora parva*) from Lake Zafirovo in Bulgaria with regard to sexes (TL – total length, FL – fork length, SL – standard length, P – pectoral fin, V – ventral fin, A – anal fin, C – caudal fin, D – dorsal fin, Da – anterior end of dorsal fin, Dp – posterior end of dorsal fin).

	Lake Zafirovo females					Lake Zafirovo males				
	n	Mean	Min	Max	SD	n	Mean	Min	Max	SD
TL	14	54.38	34.11	65.53	8.51	136	58.44	34.31	88.67	11.89
FL	14	50.04	31.64	61.69	7.96	136	53.70	31.75	82.81	11.09
SL	14	44.56	27.54	54.50	7.23	136	48.14	28.72	74.55	10.13
In % of SL										
Head length	14	25.64	23.08	28.53	1.74	136	25.74	22.03	29.42	1.17
Preorbital distance	14	7.33	6.00	8.57	0.75	136	7.61	5.64	9.89	0.62
Eye diameter	14	7.19	5.90	8.55	0.82	136	6.84	5.19	8.86	0.76
Postorbital distance	14	12.01	10.28	13.60	0.91	136	11.97	10.14	14.60	0.70
Head depth	14	17.95	16.68	19.60	0.98	136	18.01	15.37	19.97	0.79
Predorsal distance	14	52.15	49.02	54.46	1.78	136	51.24	44.32	54.61	1.31
Pre-ventral distance	14	51.47	48.90	55.71	2.14	136	50.85	28.90	54.87	2.43
Preanal distance	14	70.59	68.36	74.32	1.72	136	69.64	19.74	72.87	4.54
P-V distance	14	25.83	22.83	29.10	1.61	136	25.31	22.12	29.54	1.32
V-A distance	14	20.75	17.95	24.18	1.63	136	21.22	17.95	24.23	1.34
Body depth	14	22.64	19.84	26.31	2.01	136	21.94	18.32	26.52	1.60
Da-A distance	14	28.25	25.16	30.04	1.55	136	28.55	24.60	39.79	2.07
Dp-A distance	14	18.74	15.99	21.65	1.89	136	18.87	15.89	22.85	1.56
C peduncle (dorsal)	14	38.56	34.65	40.86	1.60	136	38.63	34.48	42.67	1.42
C peduncle (ventral)	14	22.27	19.90	24.44	1.18	136	22.27	19.63	25.70	1.19
Postdorsal distance	14	40.44	35.61	42.70	1.86	136	40.32	36.90	43.39	1.29
Postanal distance	14	23.77	20.84	26.30	1.49	136	23.69	20.24	27.12	1.07
D fin base length	14	12.58	11.24	14.35	0.91	136	12.75	9.26	15.04	0.96
A fin base length	14	9.80	8.14	11.86	0.97	136	9.91	7.17	12.63	0.94
P fin length	14	16.72	13.48	18.62	1.56	136	17.15	10.55	22.26	1.69
V fin length	14	14.32	11.69	17.41	1.50	136	14.96	7.45	18.70	1.91
C upper lobe length	14	24.72	22.51	26.62	1.16	136	25.12	20.69	27.52	1.36
C lower lobe length	14	24.86	22.61	27.01	1.28	136	25.32	20.70	29.04	1.43
D fin length	14	20.32	17.73	23.43	1.49	136	21.82	13.34	24.78	1.53
A fin length	14	12.54	10.09	16.84	2.00	136	13.59	9.78	16.38	1.42
C peduncle depth	14	12.23	11.17	13.94	0.84	136	12.32	10.91	15.27	0.71
Gape	14	7.01	5.36	8.59	0.87	136	7.05	5.59	9.89	0.74

between the populations, while the y-axis captures the traits, which represent sex differences within the populations (Fig. 3). The postorbital distance is a trait with specific meaning because it is bigger in males in population from Kolarovo channel and in females in population from Lake Zafirovo (Table 1, 2).

Discussion

Studies dedicated to biological invasions usually focus on differences between successful and unsuccessful species (Peterson & Fausch 2003). A few traits determine whether a species will be a successful invasive, and morphology is one of them.

Our study shows variable differences in morphological traits in populations from different sites in Bulgaria. The morphotype from Lake Zafirovo is more slender with a longer posterior part of the head, deeper and longer caudal peduncle and longer fins. These

Table 4. Discriminant function analysis of topmouth gudgeon (*Pseudorasbora parva*) from two sites in Bulgaria regardless the sexes. Factor structure matrix (FSM) predicates biological importance of the trait. Significantly different traits are in bold face. (P – pectoral fin, V – ventral fin, A – anal fin, C – caudal fin, D – dorsal fin, Da – anterior end of dorsal fin, Dp – posterior end of dorsal fin).

	Wilks λ	F test	*P*	FSM
Head length	0.2049	1.6210	0.2040	–0.1726
Preorbital distance	0.2049	1.5655	0.2120	0.0820
Eye diameter	0.2037	0.0001	0.9910	–0.1653
Postorbital distance	**0.2131**	**12.4899**	**0.0005**	–0.2487
Head depth	**0.2315**	**36.8442**	**0.0000**	**–0.3292**
Predorsal distance	0.2040	0.4547	0.5007	–0.0925
Pre-ventral distance	**0.2095**	**7.7378**	**0.0058**	–0.0263
Preanal distance	0.2053	2.0804	0.1504	–0.0931
P-V distance	**0.2160**	**16.3137**	**0.0001**	–0.1341
V-A distance	0.2065	3.6869	0.0559	–0.1833
Body depth	0.2041	0.5301	0.4672	–0.1574
Da-A distance	0.2038	0.1660	0.6840	–0.0929
Dp-A distance	0.2038	0.2089	0.6480	–0.0968
C peduncle (dorsal)	**0.2077**	**5.3436**	**0.0216**	0.0399
C peduncle (ventral)	**0.2087**	**6.6475**	**0.0105**	0.1178
Postdorsal distance	0.2050	1.7915	0.1819	0.0929
Postanal distance	0.2037	0.0025	0.9598	0.1817
D fin base length	0.2055	2.4373	0.1197	–0.1093
A fin base length	0.2037	0.0718	0.7889	0.0493
P fin length	0.2047	1.3991	0.2379	0.1385
V fin length	0.2045	1.0420	0.3083	0.1953
C upper lobe length	**0.2163**	**16.7243**	**0.0001**	0.2875
C lower lobe length	0.2078	5.4923	**0.0198**	0.2298
D fin length	0.2040	0.4258	0.5146	0.2768
A fin length	**0.2482**	**59.0112**	**0.0000**	**0.4652**
C peduncle depth	0.2037	0.0192	0.8899	–0.0048
Gape	**0.2245**	**27.5533**	**0.0000**	–0.2740

traits may allow the fish to manoeuvre among the plants and other physical structures used for feeding and protection from predators (e.g. Pflieger 2004). Specifically, we identified three traits connected with the head region of the body (head depth, postorbital distance, and gape) that were significantly different. Differences in the proportion of head depth and postorbital distance make the head more/less robust. This outcome can result from different habitat types and water flow, where flattened or sloping heads minimise energy usage and allow the fish to remain near the substrate while moving through the water or remaining stationary in flowing water (e.g. Webb et al. 1996). Another important trait with a significant difference between the populations was the gape size. Topmouth gudgeon is known for its variability in diet, not just based on the age of an individual and the area of its occurrence, but qualitative differences in diet composition can be dependent on the sex as well (Olufemi 2007). Smaller individuals feed on a variety of prey organisms, particularly zooplankton, such as copepods, cladocerans, and rotifers, and are thereby able to avoid the negative effects of intra-specific competition (Svanbäck & Bolnick 2007). Individuals reaching sizes over 32 mm feed mainly on chironomid larvae and especially epiphytic species (Wolfram-Wais et al. 1999). However, a high degree of overlap among the size groups indicates that there might be an intra-specific competition among the consecutive size classes when resources are limited (Şükran et al. 2013). Based on the different diet sources, the gape size can also be variable, as our research confirmed.

Table 5. Discriminant function analysis of topmouth gudgeon (*Pseudorasbora parva*) from two sites in Bulgaria with regard to sexes. Factor structure matrix (FSM) predicates biological importance of the trait. Significantly different traits are in bold face. (P – pectoral fin, V – ventral fin, A – anal fin, C – caudal fin, D – dorsal fin, Da – anterior end of dorsal fin, Dp – posterior end of dorsal fin).

Trait	Wilks λ	F test	*P*	FSM	
Head length	0.1276	0.7491	0.5237	–0.1589	–0.2290
Preorbital distance	**0.1310**	**3.1412**	**0.0258**	0.0982	**–0.3665**
Eye diameter	**0.1321**	**3.9212**	**0.0092**	–0.1756	0.2583
Postorbital distance	**0.1328**	**4.4037**	**0.0048**	–0.2306	**–0.3330**
Head depth	**0.1453**	**13.2219**	**0.0000**	**–0.3077**	**–0.3616**
Predorsal distance	**0.1329**	**4.4798**	**0.0043**	–0.0883	–0.0816
Pre-ventral distance	**0.1307**	**2.8820**	**0.0363**	–0.0260	0.0038
Preanal distance	0.1283	1.1922	0.3131	–0.0943	0.0760
P-V distance	**0.1350**	**5.9647**	**0.0006**	–0.1354	0.0946
V-A distance	0.1288	1.5798	0.1946	–0.1777	–0.0347
Body depth	**0.1380**	**8.0435**	**0.0000**	–0.1524	–0.0428
Da-A distance	0.1273	0.4983	0.6838	–0.0832	–0.1727
Dp-A distance	0.1276	0.7079	0.5480	–0.0885	–0.1379
C peduncle (dorsal)	**0.1306**	**2.8297**	**0.0389**	0.0329	0.1421
C peduncle (ventral)	**0.1306**	**2.8575**	**0.0375**	0.1181	–0.0699
Postdorsal distance	0.1284	1.2985	0.2753	0.0899	0.0329
Postanal distance	0.1280	0.9879	0.3990	0.1840	–0.1192
D fin base length	0.1281	1.0527	0.3697	–0.1043	–0.0489
A fin base length	0.1269	0.2251	0.8789	0.0497	–0.0376
P fin length	0.1279	0.9335	0.4249	0.1488	–0.2594
V fin length	0.1286	1.4375	0.2322	0.2013	–0.1903
C upper lobe length	**0.1360**	**6.6748**	**0.0002**	0.2759	0.1051
C lower lobe length	0.1292	1.8561	0.1374	0.2225	0.0392
D fin length	**0.1321**	**3.8981**	**0.0094**	0.2955	**–0.3361**
A fin length	**0.1576**	**21.8899**	**0.0000**	**0.4819**	–0.2401
C peduncle depth	0.1278	0.8978	0.4428	0.0066	–0.2623
Gape	**0.1395**	**9.1310**	**0.0000**	–0.2580	–0.2096

When the species occurs in different water bodies, the mode and speed of swimming can be modified, which is connected with the modifications in body shape (Webb & Weihs 1986). Nevertheless, not only the body shape but also the shape of the fins are important determinants of swim mode, and variations in fin configuration might be responsible for different movement specialisations (Feilich 2016). Fin shape and its configuration show a wide range of variations, which are realised in multiple functions, from swimming through stabilisation to manoeuvring (Lauder & Drucker 2004). Understanding single-fin functions is crucial due to movement biomechanics because the fish body is statically unstable (Eidietis et al. 2003). In general, our study suggests that two Bulgarian populations differ in the length of all fins; in Lake Zafirovo, all fins were found to be longer. Long fins are hypothesised to be an adaptation to high manoeuvrability and efficient foraging in the vegetated littoral habitat (e.g. Webb 1984). In general, the development of various fin shapes in response to ecological variables depends on the fish's specific behaviour (Aguilar-Medrano et al. 2013). The length of the anal fin appears to have the strongest influence, which was confirmed both statistically and biologically. On the other hand, the length of the caudal fin only showed a statistically significant difference. Fins are movement organs whose morphology is particularly important because of their many functions with a direct effect on the fitness of an individual. The anal and caudal fins function in manoeuvring and stability (Standen & Lauder 2005).

A shorter anal fin is associated with a higher critical speed of swimming (Rouleau et al. 2010). It is not typically used for locomotion, as it is less powerful than the caudal fin. However, it can be used to help the fish to stop or slow down when swimming. Other traits that showed consistent differences between the two habitats were caudal peduncle length dorsal and caudal peduncle length ventral, which were longer in Lake Zafirovo. A longer caudal peduncle is better adapted for pelagic foraging, as it minimises energy loss and provides maximal thrust for sustained swimming (Robinson & Parsons 2002). Pelagic fishes usually show a fusiform body shape to reduce drag in open waters (Webb 1975). Pre-ventral distance and the distance between the pectoral and ventral fin also showed significant differences. Such body shapes are better adapted for searching for widely dispersed prey (Webb & Weihs 1986).

In addition to the divergent reproductive roles of the sexes, particular morphological structures, such as body size, are important for male and female mate choice, suggesting that sexual selection may contribute to the evolution of sexual dimorphism in these morphological cues (Wootton 1984, Schluter 2001). Several authors have attempted to describe sexual dimorphism in *P. parva*. For example, males from the River Amur differ from females by their larger size, longer fins (both paired and unpaired) and slightly reduced body depth (Nikolskij 1956). In contrast, males from a fish farm in Nucet (Romania) had much deeper bodies than females (Bănărescu 1999). In an invasive population in Poland, males differ with larger body size and higher values of minimal body depth, depth of dorsal and anal fins, and length of pectoral fins (Kotusz & Witkowski 1998). A possible explanation for such variability between the populations is the reaction to stress due to a drastic change in the ecological conditions in which a given species evolved and by following the necessity to adapt to a new environment (Holčík 1972). In our study, males were longer and more robust in general. All fins were found to be bigger in males, and the anal and dorsal fin lengths were identified as statistically significant and traits with biological importance. Longer fins (anal and dorsal) seem important in swimming modes necessitating coordination and manoeuvring alone (Standen & Lauder 2005). The dorsal fin is also considered a fundamental element in the movement anatomy of fish (Lauder et al. 2002), with a function in swimming manoeuvres at slow speed (Drucker & Lauder 2005). Simultaneously, both these fins are used in the spawning season when the males attract females and guard the nests (Robinson et al. 2011). Besides the bigger size and shape of the fins, statistically significant differences were confirmed in the majority of traits associated with the head. In nature, males can benefit from a more robust size and shape of the head, which may function in inter-sexual mate choice and in intra-sexual conflicts with rivals. The other role of a more robust head is the protection of the offspring (Katano & Maekawa 1997). On the other hand, body depth and distance between pectoral and ventral fins were found to be bigger in females, which is connected with their contribution to reproduction through elevated fecundity. Indeed, both populations from Bulgaria were characterised by the highest ever reported fecundity of the species (Švolíková et al. 2016).

Many species are exposed to changing conditions (Galis 1993), which can directly affect progressive, adaptive modifications of their morphological traits (Holzman et al. 2008). The characteristics of some morphotypes are derived from the functional selective pressure of the environment on their internal and external anatomy. Such environmental factors can stimulate gene expression and plastic answers in the morphology of an individual, and the change in trophy can lead to a change in morphology (Santos-Santos et al. 2015). The increased plasticity in forming variable phenotypes is well known for topmouth gudgeon (e.g. Záhorská et al. 2009). Different pressures of the environment can be responsible for such quick adaptations. If environments were unchanging, then fixed phenotypes would be preferred. But, because environments are constantly changing, plasticity is often favoured. There were large differences between the analysed habitats. First, the disturbed habitat (Kolarovo channel) was strongly influenced by variable factors, while the second, undisturbed (Lake Zafirovo), was represented by stable conditions. This situation can be one of the leading mechanisms for the evolution of variable adaptations. It is difficult to answer the question of the morphological variability based on different levels of selective pressure, but it is clear that such variation directly affects the fecundity of the species (Švolíková et al. 2016). However, any introduced species would be expected to adapt and pass on morphological changes to future generations that would be adaptive in the novel environment. The Kolarovo channel can be considered a novel environment because the habitat conditions are changing perpetually (fluctuations of water level, formation of a few ponds during summer dry, and changes in water quality due to the presence of aquatic vegetation). This situation can lead to the evolution of variable morphotypes, which would be appropriate in changing conditions. However, it has been shown that morphological differences can result from phenotypic plasticity, where habitat variables directly influence the phenotype of an organism (Pigliucci 2005). In general, environmental pressures have been thought to be a factor in morphological differentiation and speciation among aquatic animals (Brown 2000), and thus identifying the influence of habitats, along with selection, is paramount in understanding the invasive success of the species.

Conclusion

We identified traits responsible for morphological variability between two populations from two habitats with different selective regimes. The morphotype coming from Lake Zafirovo was more slender with a longer posterior part of the head, deeper and longer caudal peduncle and longer fins. Significant differences were connected with traits such as head depth, postorbital distance, gape, anal fin and caudal fin length, caudal peduncle length dorsal and ventral, pre-ventral distance, and distance between pectoral and ventral fins. At the same time, we evaluated traits which differentiate males from females. Males were longer and more robust in general. All fins were bigger in males, and the anal and dorsal fin lengths were identified as statistically significant. Significant differences were also confirmed in the majority of traits associated with the head. Finally, our study showed that the topmouth gudgeon is a very flexible species in the environments in which it occurred and thus expresses variable morphotypes. Even when problematic to demonstrate how the different levels of disturbance affect overall morphological variability, we can assume that increased variability in morphotype functions to facilitate establishment in disturbed and/or undisturbed conditions.

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Author Contributions

E. Záhorská: conceptualisation, methodology, formal analysis, investigation, writing – original draft, writing – review and editing, supervision. M. Šúrová: formal analysis, writing – review and editing. M. Balážová: methodology, visualisation, formal analysis.

Data Availability Statement

The data and RScript supporting this study's findings are available in the FigShare Digital Repository: https://doi. org /10.6084/m9.figshare.23523249.

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Supplementary online material

Fig. S1. Map of the sites in Bulgaria where topmouth gudgeon (*Pseudorasbora parva*) populations were sampled in 2011.

Table S1. Evaluation of selection pressure in two habitats in Bulgaria with different levels of disturbance. Pressure is assessed based on a four-scale modality (no, low, medium, high) expressed numerically as 1, 2, 3, and 4, respectively.

Table S2. Mean values, minimum (Min), maximum (Max), and standard deviations (SD) of particular characters (see Fig. 1) of topmouth gudgeon (*Pseudorasbora parva*) from two Bulgarian sites (TL – total length, FL – fork length, SL – standard length, P – pectoral fin, V – ventral fin, A – anal fin, C – caudal fin, D – dorsal fin, Da – anterior end of dorsal fin, Dp – posterior end of dorsal fin).

(https://www.ivb.cz/wp-content/uploads/JVB-vol.-72-2023-Zahorska-et-al.-Fig.-S1-Table-S1-S2.pdf)