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Does latitude drive the phenotypic plasticity of morphological traits in non-native pumpkinseed populations from Europe?

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Abstract – Phenotypic plasticity is one of the traits often associated with successful invasive species, providing each individual with a unique ability to adapt to novel environments. The aim of the present study was to evaluate the morphological plasticity of *Lepomis gibbosus*, a successful invader outside of its native North American range, across the latitudinal extent of the species' introduced European range to determine whether or not climate, using latitude as a surrogate of thermal conditions, has an underlying influence on the species' morphology and consequently its invasiveness potential. Five characters (body depth, dorsal, ventral and pelvic fins, and eye diameter) differed significantly among the populations, and in particular the Slovakian population, with a significant effect of latitude on five other characters (maxilla length, pre-dorsal, pre-ventral, pre-orbital distances, and caudal peduncle length), which distinguished the various populations and distinguished the Portuguese population from the rest. The results suggest considerable morphological plasticity in *L. gibbosus*, with two different patterns of development that can reflect to different allocation of sources as well as different stage of invasion process.

Keywords: phenotypic plasticity / *Lepomis gibbosus* / latitudinal effect / morphology

Résumé – Est-ce que la latitude influence la plasticité phénotypique des traits morphologiques dans les populations de perche soleil non indigène d'Europe? La plasticité phénotypique est l'un des traits souvent associés à des espèces envahissantes, offrant à chaque individu une capacité unique à s'adapter à de nouveaux environnements. L'objectif de la présente étude était d'évaluer la plasticité morphologique de *Lepomis gibbosus*, un envahisseur performant en dehors de son aire nord-américaine native, dans l'étendue latitudinale de la répartition européenne de l'espèce introduite pour déterminer si le climat, en utilisant la latitude en tant que proxy des conditions thermiques, a une influence sous-jacente sur la morphologie de l'espèce et par conséquent son potentiel d'invasion. Cinq caractères (hauteur du corps, nageoires dorsale, ventrale et pelvienne et diamètre de l'œil) diffèrent significativement parmi les populations, et en particulier la population slovaque, avec un effet significatif de la latitude sur cinq autres caractères (longueur du maxillaire, distances pré-dorsale, pré-ventrale, pré-orbitale et longueur du pédoncule caudal), qui distingue les différentes populations et la population portugaise du reste. Les résultats suggèrent une plasticité morphologique considérable chez *L. gibbosus*, avec deux modèles de développement différents qui peuvent être liés à une répartition des ressources différente ainsi qu'à différents stades de processus d'invasion.

Mots-clés : plasticité phénotypique / *Lepomis gibbosus* / effet latitudinal / morphologie

1 Introduction

The ability of an introduced species to adapt and make use of the available resources in a novel environment plays an important role in determining its invasion success (Sakai *et al.*, 2001). There are several traits essential for successful invasion, and these are usually connected with phenotypic plasticity, which reflects the potential of a species to adapt to novel conditions. Successful invaders are able to switch between alternative developmental trajectories and/or react quickly

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Table 1. Country, site code, site name, latitude and longitude (in GPS coordinates), and number (*n*) of specimens of pumpkinseed *Lepomis gibbosus* from each population in European inland waters.

Country	Code	Site name	Latitude	Longitude	*n*
Netherlands	NSP	Schoapedobbe Pond	52.951944N	6.258333E	53
	NMP	Meeuwven Pond	51.391111N	5.499722E	98
England	ELC	Cottesmore Lower Pond	51.089046N	0.219408W	95
	EUC	Cottesmore Upper Pond	51.088147N	0.219443W	100
	ECS	Cottesmore School Pond	51.087248N	0.219477W	100
	E6T	Tanyard Fishery Pond No. 6	51.024187N	0.009114E	100
	EBS	Batts Bridge Stream	51.019472N	0.073074E	66
Belgium	BWP	Webbekomsbroek Pond	50.968333N	5.076667E	147
	BSS	Slangebeek Stream	50.956111N	5.302778E	74
Slovakia	SCN	Čunovo	48.031436N	17.229953E	171
France	FBM	Brière Marsh	47.366111N	2.312500W	111
	FGL	Grand-Lieu Lake	47.083333N	1.650000W	95
Portugal	**PMN**	**MonteNovo**	**38.3044N**	**7.4237W**	**172**
	PM	**Montargil**	**39.0503N**	**8.1789W**	**181**
	PF	**Fratel**	**39.3235N**	**7.4810W**	**166**
	PB	**Belver**	**39.4794N**	**7.9969W**	**129**
	PR	**Régua**	**41.1422N**	**7.7080W**	**251**

(in phenotypic terms) to local conditions, which includes the absence of (or release from) native competitors, diseases, or predators (*e.g.* Alpert, 2006; Kováč, 2011). Amongst the most important biological traits that demonstrate plasticity are: fecundity, age and length at maturity (*e.g.* Copp and Fox, 2007), and morphology (Copp *et al.*, 2002; Ľavrinčíková *et al.*, 2005; Tomeček *et al.*, 2005; Záhorská *et al.*, 2009). There are several invasive freshwater fishes that support this assumption, including pumpkinseed *Lepomis gibbosus* (Tomeček *et al.*, 2005), topmouth gudgeon *Pseudorasbora parva* (Záhorská *et al.*, 2009), and round goby *Neogobius melanastomus* (Ľavrinčíková *et al.*, 2005). Pumpkinseed, a freshwater sunfish (Centrarchidae) native to North American, was introduced intentionally or unintentionally into European inland waters during the 19th and 20th centuries (Copp and Fox, 2007). After some initial difficulties in establishing self-sustaining populations, *e.g.* in France (Künstler, 1908), the species subsequently established itself in most locations where it was introduced, spreading in many cases into adjacent waters with or without human intervention (Copp and Fox, 2007). As a consequence, it is a species with amongst the highest rates of successful establishment in Europe (García-Berthou *et al.*, 2005).

Following an initial, exploratory examination of a relationship between pumpkinseed morphological characters and latitude (Copp *et al.*, 2002), subsequent studies in Iberia demonstrated morphological differences in pumpkinseed populations that correspond to broad habitat types (Bhagat *et al.*, 2006, 2011a) rather than geographic regions (Canada *vs.* Central Europe), and this suggests that this species has a high degree of developmental plasticity in morphology under ambient (Tomeček *et al.*, 2005) as well as artificially heated conditions (Šumer *et al.*, 2005). And in its native range, the pumpkinseed's morphology varies according to its trophic position, habitat use, presence/absence of predator (Robinson and Wilson, 1996) and water flow (river *vs.* lake; Brinsmead and Fox, 2002). Differences in mouth morphology in two reservoir populations of introduced *L. gibbosus* in Greece have been linked to their different diets (Bobori *et al.*, 2006).

In Europe, Copp *et al.* (2002) provided the morphological data for *L. gibbosus* in the first study of the species in England, and using data from earlier morphological studies for elsewhere in Europe (Sedlár, 1957; Tandon, 1976, 1977) to undertake a preliminary test the hypothesis that some morphological characters (caudal-peduncle length, dorsal fin length and depth) varied with latitude. In view of the low number of populations ($n = 4$) around Europe, Copp *et al.* (2002) noted the possibility that the observed patterns may be due to growth variability rather than to different environments. Since then, these hypothesised relationships with latitude have not been further investigated. Thus, the aims of the present study were to: (1) assess the morphological characters of non-native *L. gibbosus* populations from water bodies and water courses from across the Europe (6 countries, 17 localities) and (2) to re-assess the hypotheses of Copp *et al.* (2002) that some morphological characters vary as a function of geographical location (latitude).

2 Methods

Fish were collected from 17 locations across Europe (Tab. 1). In England, fish were collected from five locations: (i) Cottesmore School Pond (ECS; $n = 100$), the headwater of the Buchan Stream system (Pease Pottage, West Sussex, England, UK), which is believed to be one of the first water bodies in England into which *L. gibbosus* were introduced in the late 1890s or early 1900s (Copp *et al.*, 2002). Originally an ornamental pond, ECS is a reservoir fed by a chalk spring located about 20 m upstream. ECS' outflow feeds a small stream, which meanders a short distance before discharging into; (ii) Cottesmore Upper

Table 2a. Mean values of morphological characters in pumpkinseed from European inland waters (see Tab. 1 for study site codes).

	Study site	NSP	NMP	ELC	EUC	ECS	E6T	EBS	BWP	BSS	SCN	FBM	FGL
	Standard length (SL)	122.7	66.6	62.2	65.2	60.4	95.0	67.7	60.6	47.9	64.67	89.5	65.3
	In % of SL												
1	Head length	34.3	35.7	35.2	34.6	33.4	35.0	36.0	34.8	34.0	36.3	37.9	35.9
2	Pre-orbital distance	5.8	6.1	6.2	6.1	6.0	6.2	7.4	6.5	6.3	7.1	7.2	6.7
3	Eye diameter	7.8	11.3	10.9	9.7	9.8	9.0	10.0	10.3	10.4	11.3	9.6	10.5
4	Post-orbital distance	21.1	18.8	18.4	18.9	17.6	20.4	18.8	18.1	17.5	18.4	21.3	19.1
5	Maxilla length	8.1	8.1	9.3	8.5	8.6	9.3	9.4	8.8	7.2	7.9	10.3	9.6
6	Head depth	37.0	34.3	34.7	31.3	33.5	36.7	36.0	32.9	32.2	32.7	39.3	37.7
7	Pre-dorsal distance	42.6	43.4	42.8	42.2	41.1	45.4	43.4	43.6	42.9	43.5	44.1	44.5
8	Pre-ventral distance	43.3	42.9	41.9	41.5	41.6	44.1	43.1	42.5	42.6	43.4	44.7	43.7
9	Pre-anal distance	67.6	65.3	63.2	63.6	63.5	66.4	63.9	64.6	63.9	64.4	67.5	66.0
10	Pectoral (P)–ventral (V) distance	17.5	15.4	14.7	14.4	13.9	17.0	16.0	15.0	13.8	15.3	17.3	16.2
11	Ventral (V)–anal (A) distance	27.7	25.3	23.7	24.5	24.4	25.4	23.6	24.7	23.9	23.0	25.3	24.7
12	Body depth	49.9	44.5	41.4	41.5	41.4	49.9	43.6	44.4	40.3	41.4	49.2	46.8
13	Caudal (C) peduncle length	20.8	22.7	22.5	22.3	22.6	21.1	22.0	22.1	22.8	21.8	20.0	21.2
14	Caudal (C) peduncle depth	20.6	19.2	18.8	19.4	19.7	20.8	19.9	20.9	19.8	19.5	21.2	21.7
15	Min body depth	14.4	13.0	13.3	13.3	13.4	14.3	14.0	14.2	13.5	14.3	14.9	14.3
16	Caudal (C) base fin length	17.1	15.3	15.9	16.0	15.5	15.4	17.3	15.8	15.2	16.3	17.1	16.9
17	Dorsal (D) fin length	50.9	45.9	46.2	46.9	46.5	49.3	47.0	47.0	44.6	45.8	51.0	48.4
18	Anal (A) fin length	21.6	19.1	20.0	19.9	20.0	21.4	20.9	20.7	19.7	20.4	22.6	21.5
19	Pectoral (P) fin length	26.6	27.0	27.1	25.0	25.6	29.9	26.3	24.1	22.8	30.4	26.7	24.5
20	Pectoral (P) base length	7.4	23.1	6.5	6.3	6.3	7.7	7.0	6.5	6.1	7.8	7.4	7.0
21	Ventral (V) fin length	22.6	15.4	22.4	21.6	21.1	24.2	22.1	21.3	19.8	20.5	22.3	20.8
22	Caudal (C) fin length	24.8	29.7	30.1	28.7	30.1	26.4	29.4	26.9	27.7	28.8	28.0	27.5
23	Dorsal (D) fin1 depth	13.6	16.4	14.8	14.0	14.1	15.8	15.5	15.7	14.4	10.7	14.9	13.9
24	Dorsal (D) fin2 depth	17.2	17.4	17.2	17.6	17.4	17.6	17.5	16.5	15.7	16.0	18.3	16.7
25	Anal (A) fin depth	15.8	16.3	17.3	17.6	17.1	17.1	17.8	15.9	14.6	15.5	17.5	17.0

Pond (EUC; $n = 100$), which itself discharges *via* a short stream into; (iii) Cottesmore Lower Pond (ELC; $n = 95$). EUC and ELC are artificial "water hazards" constructed circa 2001 on the Cottesmore Golf Course, which encircles ECS (Fox *et al.*, 2011); (iv) Cackle Street (EBS; $n = 66$) is a stretch of Batts Bridge Stream in East Sussex situated just downstream of a commercial angling lake (see Fobert *et al.*, 2013); and (v) a commercial angling pond, Tanyards Lake 6 (E6T; $n = 100$), which is situated near Danehill, East Sussex. For geographic location details, see Villeneuve *et al.* (2005).

Three locations in Western Europe were included. In the Netherlands, *L. gibbosus* were sampled in Schoapedobbe Pond (NSP; $n = 53$) and in Meeuwven Pond (NMP; $n = 98$). Two sites located in Flanders, in the northeast of Belgium, were sampled: Slangebeek Stream (BSS; $n = 74$), a small tributary of the River Demer; and Webbekomsbroek Pond (BWP; $n = 147$), an artificial water body with characteristics of near-natural floodplain ponds (Van Thuyne and Breine, 2005). In France, two sites in the River Loire drainage basin (northwest France) were sampled: Brière Marsh (FBM; $n = 111$), a freshwater wetland system composed of a complex network of permanently-flooded canals (Cucherousset *et al.*, 2006) and Grand-Lieu Lake (FGL; $n = 95$), a large, shallow, naturally turbid and eutrophic lake (Paillisson and Marion, 2006). For geographic location details of these western European sites, see Cucherousset *et al.* (2009).

Six further sites, one in Central Europe (Slovakia) and five in Southern Europe (Portugal) were also sampled. In southern Slovakia, *L. gibbosus* were collected from a densely-vegetated, former gravel-pit (area = 15 ha; maximum depth = 5 m) in the River Danube flood plain, Veľké Čunovo (SCN; $n = 171$). The Portuguese sites consisted of five artificial water bodies: (i) Belver Reservoir (PB; $n = 129$), a lowland reservoir with a "sinuous" shoreline with many small littoral areas containing a mix of emergent and submersed vegetation that is located on the main channel of the River Tejo; (ii) Montargil Reservoir (PM; $n = 181$), an off-stream water storage reservoir created primarily for irrigation that is situated adjacent to the River Tejo River; (iii) Régua Reservoir (PR; $n = 251$), situated in the main channel of the River Douro and has a relatively extensive pelagic habitat (Bhagat *et al.*, 2006); (iv) Monte Novo Reservoir (PMN), located on the River Guadiana (the southern frontier between Spain and Portugal), which is fed by three connecting tributaries and is primarily used as a source of irrigation in the region. It has a circular morphometry with gentle slope banks and a bottom dominated by fine sediments, resulting in well developed littoral areas, colonized mostly by emergent macrophytes and floating vegetation; and (v) Fratel Reservoir (PF), located in the main course of the River Tejo and has a narrow and elongated morphometry, with steep banks containing an incipient littoral zone. PF runs through constrained, V-shaped valleys and is delimited by another

Table 2b. Mean values of morphological characters in pumpkinseed from water bodies in Portugal (see Tab. 1 for study site codes).

	Study site	PB	PM	PR	PMN	PF
	Standard length (SL)	85.74	78.48	79.94	72.38	83.93
	In % of SL					
1	Head length	35.66	35.07	35.10	34.36	36.34
2	Pre-orbital distance	9.61	9.95	9.88	10.58	10.74
3	Eye diameter	10.27	10.03	10.32	–	11.22
5	Maxilla length	10.82	10.52	10.59	10.65	41.53
7	Pre-dorsal distance	40.64	41.10	40.79	40.25	40.24
8	Pre-ventral distance	40.20	40.08	39.58	39.21	43.67
12	Body depth	43.51	41.37	43.03	42.38	47.18
13	C-peduncle length	48.50	47.01	47.96	47.28	20.20
16	C-base fin length	21.16	20.60	21.09	20.91	19.70
17	D-fin length	19.78	19.71	19.71	19.33	14.22
18	A-fin length	14.35	14.15	14.45	14.23	14.22
19	P-fin length	28.18	27.95	28.79	–	30.47
20	P-base length	6.75	6.66	6.70	6.64	6.74
21	V-fin length	23.25	22.48	23.21	22.63	24.63

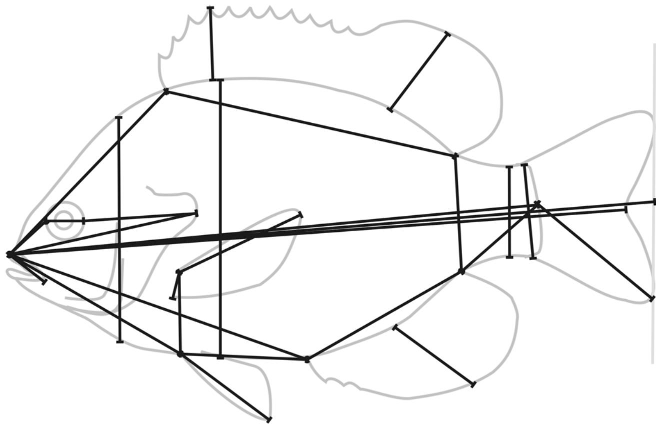

Fig. 1. Scheme of morphometric characters for distance-based measurements (Tab. 2a) taken from pumpkinseed.

reservoir located upstream. For further details on these locations, see Bhagat *et al.* (2011b).

Specimens were collected during the respective spawning periods of the populations (mainly from mid-May to early July) by various means (electrofishing, netting, funnel trapping, and angling): in Belgium, England, France and the Netherlands in 2006 (Cucherousset *et al.*, 2009); in Portugal during 2004–2007 (Bhagat *et al.*, 2011b). Captured fish were immediately killed by an overdose of anaesthetic and placed in a slurry of ice water and chilled to freezing for storage.

In the laboratory, the specimens were defrosted and 26 mensural characters (Fig. 1), including standard length (SL), were immediately measured (except for specimens from Portugal with 14 characters) from digital photographs taken by a Nikon CoolPix 5000 camera using the IMPOR 2.31E software. Specimens from Portugal were measured with Ultra-Cal Mark III digital calliper (Accuracy 40 µm; Fowler Co., Inc., Newton, MA, USA). Significant differences between the measurement methods were not observed (paired *T*-test). To examine patterns of relative growth, raw data from morphometric characters were plotted against SL as described by Kováč *et al.* (1999). Triple regression analysis (TRA) was used to test whether body proportions change abruptly rather than gradually (Kováč *et al.*, 1999) based on the three possible growth patterns (isometric, allometric and isometric with abrupt change). The analysis tests primarily the null hypothesis characterized by isometric growth with a straight line with positive slope. If the hypothesis is rejected, then the alternative hypotheses are analysed. Allometric growth is characterized by a non-linear relationship between the character and SL represented by quadratic curve (concave upwards or downwards). Growth that demonstrates abrupt change was characterized by the presence of two linear lines separated with a gap – a breakpoint. We fitted simple linear, quadratic and split-linear regression models to plots of the dependent variables against SL, and tested them for significant improvements in fit over the simple linear model. The growth with abrupt change was only accepted if the split linear fit was significantly better than both the simple linear and quadratic fits (Kováč *et al.*, 1999).

Single-factor ANOVA was used to test for differences among populations of *L. gibbosus* for 14 mensural characters (those measured in all populations examined, including Portuguese populations) as well as singular traits connected with habitat type (littoral *vs.* pelagic and riverine *vs.* lacustrine). Tukey's HSD post-hoc test was used to determine which populations were differentiated for each of the variables.

In view of the spatial proximity of five Portuguese populations established under a range of conditions, the discriminant functional analysis (DFA) was used to determine its effect on overall similarity/difference between populations in the context of different habitats. Correlation analysis with Pearson correlation coefficient was used to test for the correlation of characters with standard length (SL), latitude (LAT) and longitude (LONG).

Table 3a. Linear (L), quadratic (Q) and split linear (S) regression codes for morphometric character in pumpkinseed from European inland waters (see Tab. 1 for study site codes).

	Study site	NSP	NMP	ELC	EUC	ECS	E6T	EBS	BWP	BSS	SCN	FBM	FGL
1	Head length	L	L	L	L	S	L	S	S	L	L	L	L
2	Pre-orbital distance	Q	L	L	L	S	S	L	S	L	L	L	L
3	Eye diameter	L	L	S	L	Q	Q	Q	L	L	Q	Q	L
4	Post-orbital distance	L	L	L	Q	S	S	Q	S	L	L	Q	L
5	Maxilla length	L	L	L	Q	L	L	L	L	Q	L	L	L
6	Head depth	L	L	Q	S	Q	L	L	S	L	L	S	Q
7	Pre-dorsal distance	L	L	L	L	L	L	L	Q	L	L	Q	S
8	Pre-ventral distance	L	L	L	L	L	L	L	L	L	L	Q	L
9	Pre-anal distance	L	L	Q	L	S	S	Q	Q	L	L	S	L
10	P–V distance	L	L	Q	L	S	L	S	L	L	L	Q	L
11	V–A distance	L	L	L	S	S	S	Q	Q	L	L	Q	L
12	Body depth	L	L	L	L	S	L	L	S	L	Q	S	L
13	C-peduncle length	L	Q	Q	L	S	L	Q	S	L	L	L	L
14	C-peduncle depth	L	L	Q	L	Q	L	L	L	L	L	L	L
15	Min body depth	L	L	L	Q	Q	L	L	L	L	L	L	S
16	C-base fin length	L	Q	L	L	Q	L	Q	Q	S	S	Q	S
17	D-fin length	L	L	S	L	Q	S	L	Q	L	L	L	L
18	A-fin length	L	L	L	L	S	Q	Q	L	L	Q	L	S
19	P-fin length	L	L	L	L	L	L	L	Q	L	S	S	Q
20	P-base length	L	L	L	Q	S	L	L	L	L	Q	L	L
21	V-fin length	S	L	L	L	Q	L	S	S	L	Q	Q	L
22	C-fin length	L	L	L	L	Q	L	Q	S	L	Q	L	L
23	D-fin1 depth	S	L	L	L	Q	S	Q	L	Q	Q	L	Q
24	D-fin2 depth	L	L	L	L	Q	L	L	Q	L	L	L	L
25	A-fin depth	L	L	Q	L	L	L	S	Q	S	L	Q	S

Table 3b. Linear (L), quadratic (Q) and split linear (S) regression codes for morphometric characters in pumpkinseed from water bodies in Portugal (see Tab. 1 for study site codes).

	Character	PB	PM	PR	PMN	PF
1	Head length	S	L	L	L	L
2	Pre-orbital distance	L	Q	L	L	L
3	Eye diameter	Q	L	L	–	L
4	Post-orbital distance	–	–	–	–	–
5	Length of maxilla	Q	L	L	L	Q
6	Head depth	–	–	–	–	–
7	Pre-dorsal distance	Q	L	L	L	L
8	Pre-ventral distance	Q	Q	L	L	L
9	Pre-anal distance	–	–	–	–	–
10	P–V distance	–	–	–	–	–
11	V–A distance	–	–	–	–	–
12	Body depth	L	S	Q	L	L
13	C-peduncle length	Q	L	Q	Q	L
14	C-peduncle depth	–	–	–	–	–
15	Min body depth	–	–	–	–	–
16	C-base fin length	Q	L	L	L	Q
17	D-fin length	L	L	L	L	L
18	A-fin length	S	L	L	L	Q
19	P-fin length	S	S	L	–	L
20	P-base length	L	L	L	L	S
21	V-fin length	Q	L	L	Q	Q
22	C-fin length	–	–	–	–	–
23	D-fin1 depth	–	–	–	–	–
24	D-fin2 depth	–	–	–	–	–
25	A-fin depth	–	–	–	–	–

Table 4. Correlation based on correlation analysis of each trait toward standard length and latitude for all populations. Significant differences are in boldface.

Morphological trait	Standard length	Latitude
Head length	0.18	0.00
Pre-orbital distance	0.27	**–0.89**
Eye diameter	**–0.56**	0.05
Maxilla length	0.31	**–0.68**
Pre-dorsal distance	0.04	**0.56**
Pre-ventral distance	0.00	**0.64**
Body depth	**0.66**	0.13
D-fin length	**0.65**	–0.12
A-fin length	**0.35**	–0.16
C-peduncle length	–0.26	**0.66**
C-base fin length	0.17	**0.51**
P-fin length	**0.41**	–0.30
P-base length	0.27	0.05
V-fin length	**0.48**	–0.29

Table 5. Canonical loadings (*i.e.* correlations) for all populations between morphological traits and each canonical axis in the overall discriminant functional analysis (DFA) concerning the effect of latitude. Traits with correlations that are greater than or equal to an absolute value of 0.4 are considered to have biologically significant relationships (in boldface; McGarigal *et al.*, 2000).

	Discriminant functional analysis	
Morphometric characters	Axis 1	Axis 2
Pre-orbital distance	**0.629**	0.128
Maxilla length	0.351	**0.710**
Pre-dorsal distance	–0.276	**0.667**
Pre-ventral distance	–0.323	**0.520**
C-peduncle length	–0.266	**–0.427**
C-base fin length	–0.219	0.302
Eigen value	11.160	0.570
Cumulative % of total variance explained	89.700	94.300

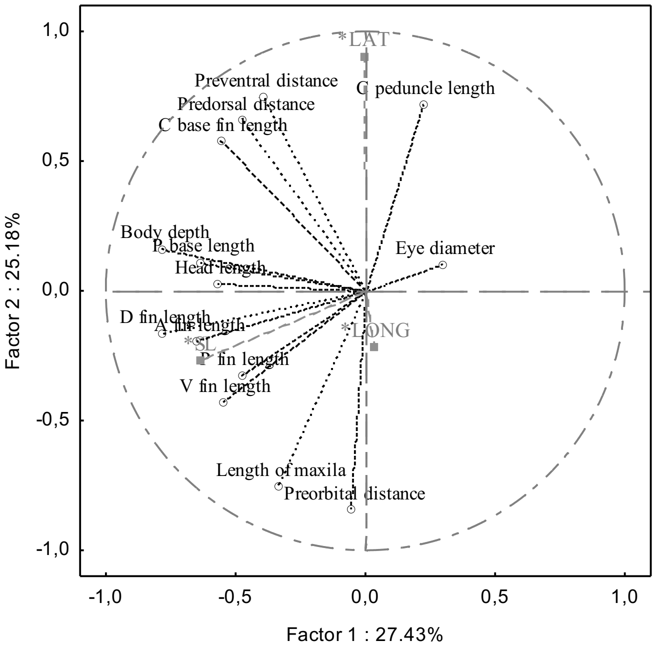

Fig. 2. Principle component analysis plot (PCA) of measured characters distribution with three additional supplementary variables (LAT – latitude, LONG – longitude, and SL – standard length) in pumpkinseed from different sites. The two dimensions of the PCA plot represent 53% of the data variability of first two factors resulted from PCA (C – caudal, P – pectoral, V – ventral, D – dorsal, and A – anal).

Principal component analysis (PCA) was used to explore the best combinations of variable groups explaining total variability among the populations. In PCA, analysis of 14 characters were used, with SL, LAT and LONG as supplementary variables. DFA was performed consequently particularly on variables significantly correlating with SL and LAT. Differentiation of populations in multidimensional space was determined with Wilk's λ and *F* and *P* statistics. Statistical analyses (ANOVA, PCA, DFA) were made with usage of STATISTICA 8 software (Statsoft).

3 Results

The morphological measurements (Tabs. 2a and 2b) subjected to TRA (Tabs. 3a and 3b) revealed that a majority of characters were best described by simple linear regression, which means isometric growth. In the populations from Belgium (BWP) and England (E6T, ECS), at least six characters were best described by split linear regression, which indicates two intervals of isometric growth interrupted by a short interval of allometric growth. In BWP specimens, four characters (head length, post-orbital distance, head depth and body depth) were in the same interval, with the breakpoints from 52.02 to 64.89 mm SL. In E6T specimens, five characters (pre-orbital distance, post-orbital distance, V–A, D-fin length and D-fin1 depth) were in the same interval, with the breakpoints from 116.50 to 118.24 mm SL. In ECS specimens, two intervals of breakpoints were clearly distinguishable – one from 30.59 to 51.32 mm SL for four characters (pre-orbital distance, pre-anal distance, V–A and body depth), and the second interval from 74.75 to 93.64 mm SL for five characters (head length, post-orbital distance, P–V, C-peduncle length and A-fin length).

Correlation analysis identified characters, such as fin lengths (D, A, P, V), eye diameter and body depth which correlated significantly with SL (Tab. 4). Characters describing body shape and the caudal peduncle (pre-orbital distance, maxilla length, pre-dorsal distance, pre-ventral distance, C-peduncle length and C-base fin length) significantly correlated with latitude (Tab. 4). Two characters (head length and P-base length) did not correlate with either SL or LAT, and none correlated with LONG.

Reliability of the dataset described by Cronbach α was 0.711. In PCA, 77% of total accumulated variance was

Table 6. Comparison of particular morphological characters in Portuguese populations based on their local conditions.

Character	Littoral/Pelagic		Lacustrine/Riverine	
	P	*F*	*P*	*F*
Head length	0.0000	29.120	0.0009	15.478
Pre-orbital distance	0.4047	0.695	0.0002	13.768
Eye diameter	0.0000	79.813	0.0334	4.538
Maxilla length	0.0000	29.080	0.0004	12.750
Pre-dorsal distance	0.0998	2.714	0.0100	6.667
Pre-ventral distance	0.0007	15.863	0.0006	11.846
Body depth	0.0000	41.217	0.6360	0.226
C-peduncle length	0.0000	62.869	0.4000	0.709
C-base fin length	0.0018	9.797	0.9511	0.004
D-fin length	0.0000	23.621	0.6701	0.182
A-fin length	0.0019	9.664	0.0037	8.450
P-fin length	0.1539	2.036	0.6237	0.241
P-base length	0.0001	20.687	0.3235	0.976
V-fin length	0.0003	13.310	0.5943	0.284

accounted by five factors, with 53% represented in first two components. The first component described the variability in characters with regard to SL (Fig. 2). The second component described morphological variability associated with latitude (characters with this direction are connected mainly with latitude; Fig. 2).

Results from correlation analysis to evaluate changes individually, as well as results from PCA analysis to evaluate total morphological variability, demonstrated that among-population variations based on geographical area of occurrence were mainly in pre-orbital distance, maxilla length, pre-dorsal distance, pre-ventral distance, C-peduncle length and C-base fin length. Only these characters were later used in DFA for population discrimination. All characters had significant effect on distribution. In this case, it indicates that on average only 68.5% of specimens were correctly classified to proper population despite the first two canonical axes (accounted for 94% of the total variation). The overall value was a result of high similarity in proper correctly classified specimens of some populations (only 7.6% in EUC, 21.1% in FGL, 28.7% in ELC and 33.1% in BWP). Whereas, the specimens from Portugal were completely separated based on the characters mentioned above (Tab. 5). Their extreme separation was along the *x*-axis, though only one mensural character was significantly correlated to it. Thus, the populations from Portugal were characterized mainly by longer pre-orbital distance in comparison with other northern populations.

The variations within Portuguese populations can be linked to a habitat type (littoral *vs.* pelagic, as well as river *vs.* lake) at the five locations (Tab. 6). The significant difference was confirmed in all measured characters among specimens altogether from different habitat types and high variability was found also between particular types of conditions (ANOVA, Tab. 6). The littoral *vs.* pelagic habitat distinction had a stronger effect, with 75.5% of specimens correctly classified to their proper group (based on DFA), *i.e.* if any individual is selected without information about its relationship to the appropriate population, the probability of correct habitat categorisation of riverine *vs.* lacustrine would be low (slightly above random distribution) based on its morphological parameters. Only 62.5% of specimens were correctly classified as to their proper habitat in comparison to lacustrine *vs.* riverine populations. Also, DFA analysis correctly classified altogether (the combination of littoral *vs.* pelagic and lacustrine *vs.* riverine) only 49% into the proper population. Despite the within-population variations with regard to habitat, these variations were not sufficiently great to warrant the distinction of habitat types in subsequent analysis.

The overall morphometric variability in individual characters between European populations of *L. gibbosus* was great (ANOVA, Tukey's HSD post-hoc test, Tab. 7). However, the definitive adult phenotypes were achieved in the same manner in majority of populations. Across the European populations, another six mensural characters correlated significantly to SL development with five of them having biologically significant relationships (Tab. 8). In this case, the 62.2% of specimens were correctly classified to their proper population with 93.1% in PT and 75.3% in SCN and 0% in ELC and EBS, respectively 4.4% in EUC. Specimens from Portugal (all specimens combined) were characterized with shorter body depth and longer P-fin length. Specimens from Slovakia, besides these same two characters, were characterized by larger eye diameter and shorter dorsal and ventral fin lengths.

4 Discussion

Studies devoted to the understanding of invasion dynamics often look for differences among the successful and the unsuccessful invaders (Miller and Alcorn, 1945; Peterson and Fausch, 2003), and a high degree of phenotypic plasticity in life-history traits and external morphology is often observed in the invading species (Balážová-Ľavrinčíková and Kováč, 2007; Tomeček *et al.*, 2007; Feiner *et al.*, 2012; Záhorská *et al.*, 2013). Owing to this plasticity, a species is able to adapt

Table 7. Comparison of differences between individual 14 traits in 13 populations observed. Tukey's *P* describes the number (*n*) of positively significant differences between individual population in given trait (maximal number is 78). The number of positive inter-population differences gives the number of significant differences in individual population from remaining 12 in given character (see Tab. 1 for study site codes).

Character	*P*	*F*	Tukey's *P* (*n*)	NSP	NMP	ELC	EUC	ECS	E6T	EBS	BWP	BSS	SCN	FBM	FGL	PT
				Number of positive interpopulation differences												
Head length	0	37.20	48	6	7	4	6	9	7	7	6	8	9	12	8	7
Pre-orbital distance	0	772.00	51	7	6	6	6	6	5	10	9	5	10	10	10	12
Eye diameter	0	74.93	56	12	10	8	9	8	12	5	8	7	10	9	7	7
Maxilla length	0	293.87	62	8	8	9	8	8	9	9	10	12	10	12	9	12
Pre-dorsal distance	0	190.42	59	8	7	8	11	11	12	6	8	7	8	10	11	11
Pre-ventral distance	0	245.07	55	6	7	8	10	10	9	6	8	7	8	11	8	12
Body depth	0	96.58	61	10	10	8	8	8	10	9	10	8	8	10	12	11
C-peduncle length	0	161.64	54	10	8	6	6	6	10	7	7	8	9	11	9	11
C-base fin length	0	140.57	56	9	9	7	8	6	7	9	8	9	10	9	9	12
D-fin length	0	77.97	56	11	7	6	6	6	11	6	7	12	9	11	11	9
A-fin length	0	50.50	58	9	11	9	8	8	9	6	9	8	8	9	12	10
P-fin length	0	94.54	57	7	7	8	8	6	11	6	10	12	11	7	9	12
P-base length	0	73.55	58	10	7	7	8	8	9	9	8	10	11	10	10	9
V-fin length	0	66.60	52	6	7	7	5	8	12	6	8	11	9	7	8	10

Table 8. Canonical loadings (*i.e.* correlations) for all populations between traits and each canonical axis in the overall discriminant functional analysis (DFA) concerning the effect of standard length. Traits with correlations that are greater than or equal to an absolute value of 0.4 are considered to have biologically significant relationships (in boldface; McGarigal *et al.*, 2000).

Discriminant function analysis		
Morphometric characters	Axis 1	Axis 2
Eye diameter	–0.1701	**–0.6134**
Body depth	**0.5526**	0.1873
D-fin length	0.2748	**0.4249**
A-fin length	0.1703	0.1854
P-fin length	**–0.6002**	–0.0735
V-fin length	–0.1688	**0.5123**
Eigen value	0.8048	0.6675
Cumulative % of total variance explained	0.3314	0.6063

to local conditions and establish a population in these novel environments. Indeed, in native populations of *L. gibbosus* as much as 53% of morphological plasticity was found to be caused phenotypically (by environmental conditions) and only 14% genetically (Robinson *et al.*, 2000). However, the selection process associated with adaptation to a novel environment can eventually lead to a reduction in plasticity. This was demonstrated in recent research that compared the progeny of indigenous *L. gibbosus* populations in Ontario, Canada, with the progeny of *L. gibbosus* stocks repatriated from the species' introduced range in Spain. Both sets of progeny were reared under identical conditions in Ontario, Canada. Progeny of the repatriated *L. gibbosus* were found to be morphologically less plastic than progeny of the indigenous *L. gibbosus* in response to sustained water velocities, habitat type, locomotion, competition (Yavno and Fox, 2013, 2014; Yavno *et al.*, 2013, 2014).

As such, the effect of environment on the morphology of *L. gibbosus* is indisputable, with geographical location playing an important role in how populations adapt to local conditions. Morphology can vary within (pelagic *vs.* littoral) and between different types of habitat (riverine *vs.* lacustrine). For example, stream-dwelling *L. gibbosus* in the species introduced range (Iberia) were found to have longer pelvic and pectoral fins than those inhabiting lakes (Naspleda *et al.*, 2012), whereas in the native range, stream-dwelling *L. gibbosus* populations had more robust caudal peduncles and more anterior fin positions than did their lake con-specifics (Brinsmead and Fox, 2002). These four characters are functionally significant for locomotion and the conditions in streams are different than in lakes (*e.g.* water velocity, macrophyte abundance). Also, *L. gibbosus* from the limnetic zone are characteristically more shallow-bodied, with smaller heads, shorter pectoral fins, longer and deeper caudal peduncles, and more anterior placement of the pectoral and pelvic fins than *L. gibbosus* occupying the littoral zone of the same lake (Robinson *et al.*, 2000; Gillespie and Fox, 2003).

These earlier results are consistent with our results for introduced European populations of *L. gibbosus*. Indeed, several differences in traits were identified in Portuguese populations within individuals from littoral and pelagic zones; as well as between individuals from rivers and lakes (Tab. 6). These results emphasize the phenotypic plasticity of the species in response to changing local conditions, not only in terms of morphology (this study) but other life-history traits (Fox and Copp, 2014). However, when examining the populations from at a larger scale, there do not appear to be broad geographical patterns in morphology. Whereas, there do appear to be broader geographical patterns in the ontogenetic trajectories that *L. gibbosus* populations follow in achieving

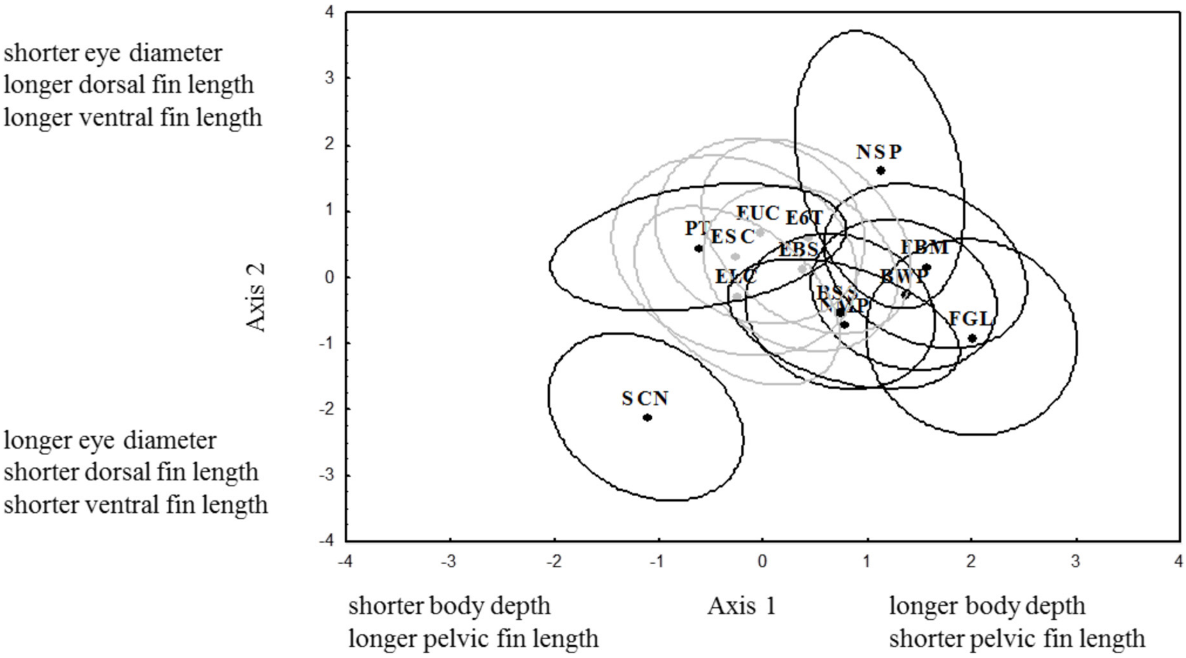

Fig. 3. Discriminant functional analysis scatter plot (DFA) with means of canonical variables and 50% ellipsoids about the centroid of each population of pumpkinseed from 12 different sites and latitudes, with discrimination based on morphological variability of 5 characters significantly correlated with SL. Abbreviations for populations are available in Table 1.

their definitive phenotype. The two different, distinguishable developmental trajectories (Kováč, 2011) reflect differences in the allocation of sources at different stage of invasion process. This resembles the differences in growth and life-history traits observed in another invasive species, round goby *Neogobius melanostomus*, at its invasion fronts in both Europe and North America (*e.g.* Brandner *et al.*, 2013; Masson *et al.*, 2016). In the majority of *L. gibbosus* populations, isometric growth predominated over non-isometric growth (*i.e.* allometric and abrupt isometric) in most morphometric characters (Tabs. 3a and 3b). That means that the external shape of these individuals developed early, when they were of small size (<60 mm SL; Tomeček *et al.*, 2005). The second type of development was apparent in specimens from Belgium (BWP) and England (ECS), where non-isometric growth predominated in most characters (Tabs. 3a and 3b). Non-isometric growth is also evident for several morphometric characters for the population from England (E6T). The high frequency of non-isometric growth with characters in these populations represents more extended, slower development. Furthermore, the presence of characters that grew isometrically until a certain size was reached, and then changed abruptly to grow isometrically again, raises the question of whether the shifts in proportions of these characters indicate one or more life-history thresholds. Such a question becomes appropriate if the majority of break points (in otherwise isometric growth) appear within a narrow interval of SL (Kováč *et al.*, 1999).

The coincidence of breakpoints may indicate developmental thresholds and/or transitions, although only if these are associated with other ecological, physiological and/or behavioural changes (Tomeček *et al.*, 2005). In Webbekomsbroek Pond, Belgium (a population with slower development), the break points were observed in narrow interval of SL (52.02–64.89 mm). All traits in this interval were connected with the changes of head and body, which appears to define the threshold between the juvenile and adult periods of development. In the Cottesmore School population (England), there were two narrow intervals of SL. One of these was at small size (30.59–51.32 mm SL) and involved traits connected with changes to the head and body; this appears to represent a life-history interval during which some remodelling of external body shape occurs. The second interval was at larger size (74.75–93.64 mm SL) and involved traits associated with changes to the head and fins. This contrasted the angling pond (E6T) which is only 25 km away from Cottesmore School, where the growth of most traits was linear, but changes of the external shape (head, fins, V–A distance) of these fish appeared at a larger SL (116.50–118.24 mm) and were probably associated with reproduction development.

The effect of SL was apparent in five characters that clearly distinguished the Slovak population (SCN; Fig. 3, which was characterized by a unique, shallower body shape, with longer eye diameter, short D- and V-fin lengths, and a longer P-fin length (Tab. 8). A similar effect of SL was observed in a French population (FGL), which was characterized by short P-fin length and wider body (Fig. 3), but with slight difference in sizes of D- and V-fin lengths and in eye diameter. Both are from the small lakes, and thus the habitat type (pelagic *vs.* littoral) should not play a major role. The possible explanation of this difference would be in character of the water bodies.

All populations analysed overlap morphologically without formation of any other significant model except for Slovakia, which was distinctly separated. However, the ellipsoid of Portuguese population overlapped on one side with others (especially the English populations), but on the other side (based on the DFA analyses) as many as 93% of individuals were correctly classified to their proper population. This suggests the existence of another unique morphological model. Despite the

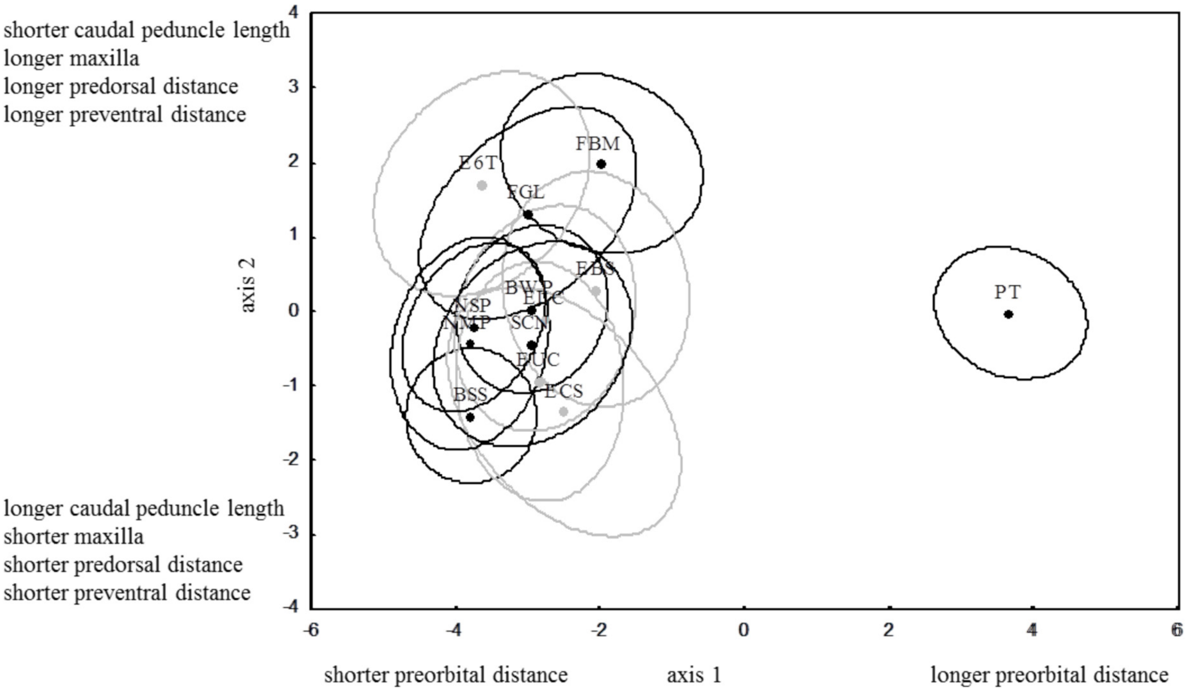

Fig. 4. Discriminant functional analysis scatter plot (DFA) with means of canonical variables and 50% ellipsoids about the centroid of each population of pumpkinseed from 12 different sites and latitudes, with discrimination based on morphological variability of 5 characters significantly correlated to latitude. Abbreviations for populations are available in Table 1.

great variability of Portuguese individuals (almost 900 individuals), most of them correspond with the morphological model localized around the determined population centroid, which is characterized by shorter body depth and longer P-fin length. At the same time, it differs from the Slovakian population, which has shorter eye diameter and longer D- and V-fin lengths.

Of the characters hypothesised by Copp *et al.* (2002) to vary with latitude (*i.e.* C-peduncle length, D-fin length and depth), only one character (C-peduncle length) demonstrated a significant relationship with latitude (Figs. 3 and 4). On the other hand, we identified four other characters (maxilla length, pre-dorsal, pre-ventral and pre-orbital distances; Tab. 4) that varied with latitude but not with LONG (*cf.* Section 3). Life-history traits are known to vary with latitude (Copp and Fox, 2007), which as such has been used as surrogate for water temperature (Cucherousset *et al.*, 2009). In the present context, this emphasizes the potential influence of geographical location on *L. gibbosus* biology. The strongest effect of latitude was visible on Portuguese populations (Fig. 4), which distinguished themselves from the other 16 populations in terms of snout size. This can be connected with the different size of the eye (even if this trait did not differ significantly). The remainder of the populations formed one cluster and differed significantly in remaining four characters (without pre-orbital distance).

This is the first known morphological study in which several non-native populations of *L. gibbosus* have been compared across a broad geographical area. The hypothesis that populations from the same region will be morphologically similar and will be morphologically distinct from the populations in other regions is corroborated, morphological variability due to latitude was identified. The geographical distinction between populations is apparent at a finer scale in the two different ontogenetic trajectories that pumpkinseed followed to achieve their definitive phenotype (Kováč, 2011). As such, the present study has demonstrated the considerable phenotypic plasticity of *L. gibbosus* in terms of morphological adaptations, such as observed in growth and life-history traits of both native and introduced populations (Fox and Copp, 2014).

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References

Alpert P. 2006. The advantages and disadvantages of being introduced. *Biol Invasions* 8: 1523–1534.

Balážová-Ľavrinčíková M, Kováč V. 2007. Epigenetical context in the life-history of round goby *Neogobius melanostomus* from Slovak stretch of the Danube. In: Gherardi F, ed. Freshwater bioinvaders: profiles, distribution, and threats. Dordrecht: Springer-Verlag, pp. 275–287.

Bhagat Y, Fox MG, Ferreira MT. 2006. Morphological differentiation in introduced pumpkinseed *Lepomis gibbosus* (L.) occupying different habitat zones in Portuguese reservoirs. *J Fish Biol* 69: 79–94.

Bhagat Y, Wilson CC, Fox MG, Ferreira MT. 2011a. Genetic relationships among pumpkinseed (*Lepomis gibbosus*) ecomorphs in freshwater reservoirs of Portugal. *Ecol Freshw Fish* 20: 287–298.

Bhagat Y, Wilson CC, Fox MG, Ferreira MT. 2011b. Trophic polymorphism in introduced pumpkinseed (*Lepomis gibbosus*) inhabiting Iberian reservoirs. *Environ Biol Fish* 91: 203–217.

Bobori DC, Tsikliras AC, Economidis NI. 2006. Some morphological and biological characteristics of fishes from Tavropos Reservoir (western Greece). *Folia Zool* 55: 199–210.

Brandner J, Cerwenka AF, Schliewen UK, Geist J. 2013. Bigger is better: characteristics of round gobies forming an invasion front in the Danube River. *PLOS ONE* 8: e73036.

Brinsmead J, Fox MG. 2002. Morphological variation between lake- and stream-dwelling rock bass and pumpkinseed populations. *J Fish Biol* 61: 1619–1638.

Copp GH, Fox MG. 2007. Growth and life history traits of introduced pumpkinseed (*Lepomis gibbosus*) in Europe, and the relevance to its potential invasiveness. In: Gherardi F, ed. Freshwater bioinvaders: profiles, distribution, and threats. Dordrecht: Springer-Verlag, pp. 289–306.

Copp GH, Fox MG, Kováč V. 2002. Growth, morphology and life history traits of a cool-water European population of pumpkinseed *Lepomis gibbosus*. *Arch Hydrobiol* 155: 585–614.

Cucherousset J, Paillisson JM, Carpentier A, Eybert MC, Olden JD. 2006. Use of an artificial wetland by the invasive catfish *Ameirus melas*. *Ecol Freshw Fish* 15: 589–596.

Cucherousset J, Copp GH, Fox MG, *et al.* 2009. Life-history traits and potential invasiveness of introduced pumpkinseed *Lepomis gibbosus* populations in northwestern Europe. *Biol Invasions* 11: 2171–2180.

Feiner ZS, Aday DD, Rice JA. 2012. Phenotypic shifts in white perch life history strategy across stages of invasion. *Biol Invasions* 14: 2315–2329.

Fobert E, Zięba G, Vilizzi L, *et al.* 2013. Predicting non-native fish dispersal under conditions of climate change: case study in England of dispersal and establishment of pumpkinseed *Lepomis gibbosus* in a floodplain pond. *Ecol Freshw Fish* 22: 106–116.

Fox MG, Copp GH. 2014. Old world *vs* new world – life history alterations in a successful invader introduced across Europe. *Oecologia* 174: 435–446.

Fox MG, Villeneuve F, Copp GH. 2011. Seasonal reproductive allocation, local-scale variation and environmental influences on life history traits of introduced pumpkinseed (*Lepomis gibbosus*) in southern England. *Fund Appl Limnol* 178: 231–243.

García-Berthou E, Alcaraz C., Pou-Rovira Q., Zamora L., Coenders G., Feo C. 2005. Introduction pathways and establishment rates of invasive aquatic species in Europe. *Can J Fish Aquat Sci* 62: 453–463.

Gillespie GJ, Fox MG. 2003. Morphological and life history differentiation between littoral and pelagic forms of pumpkinseed (*Lepomis gibbosus*). *J Fish Biol* 62: 1099–1115.

Kováč V. 2011. Genes and development. In: Hutchins M, ed. Grzimek's animal life encyclopedia. Evolution. Farmington Hills, MI: Gale, pp. 141–150.

Kováč V, Copp GH, Francis MP. 1999. Morphometry of the stone loach, *Barabatula barbatula*: do morphometric characters reflect the species' life history thresholds? *Environ Biol Fish* 56: 105–115.

Künstler J. 1908. Ameiurus nebulosus et Eupomotis gibbosus. *Bulletin de la Societé d'Acclimatation* 238–244.

Ľavrinčíková M, Kováč V, Katina S. 2005. Ontogenetic variability in external morphology of round goby *Neogobius melanostomus* from Middle Danube, Slovakia. *J Appl Ichthyol* 21: 328–334.

Masson L, Brownscombe JW, Fox MG. 2016. Fine scale spatio-temporal life history shifts in an invasive species at its expansion front. *Biol Invasions* 18: 775–792.

McGarigal K, Cushman SA, Stafford S. 2000. Multivariate statistics for wildlife and ecology research. New York: Springer-Verlag, 283 p.

Miller RR, Alcorn JR. 1945. The introduction of fishes of Nevada, with a history of their introduction. *Trans Am Fish Soc* 73: 173–193.

Naspleda J, Vila-Gispert A, Fox MG, Zamora L, Ruiz-Navarros A. 2012. Morphological variation between non-native lake- and stream-dwelling pumpkinseed *Lepomis gibbosus* in the Iberian Peninsula. *J Fish Biol* 81: 1915–1935.

Paillisson JM, Marion M. 2006. Can small water level fluctuations affect the biomass of *Nymphaea alba* in large lakes? *Aquat Bot* 84: 259–266.

Peterson DP, Fausch KD. 2003. Testing population-level mechanisms of invasion by a mobile vertebrate: a conceptual framework for salmonids in streams. *Biol Invasions* 5: 239–259.

Robinson BW, Wilson DS. 1996. Genetic variation and phenotypic plasticity in a trophically polymorphic population of pumpkinseed sunfish (*Lepomis gobbosus*). *Evol Ecol* 10: 631–652.

Robinson BW, Wilson DS, Margosian AS. 2000. A pluralistic analysis of character release in pumpkinseed sunfish (*Lepomis gibbosus*). *Ecology* 81: 2799–2812.

Sakai AK, Allendorf FW, Holt JS, *et al.* 2001. The population biology of invasive species. *Ann Rev Ecol Syst* 32: 305–332.

Sedlár J. 1957. A contribution to distribution and biometrics of pumpkinseed (Lepomis gibbosus Linne, 1758) and catfish (*Ameiurus nebulosus* Le Sueur, 1819) in southern Slovakia. *Poľnohospodárstvo* 4: 1104–1109.

Šumer S, Kováč V, Povž M, Slatner M. 2005. External morphology of a Slovenian population of pumpkinseed *Lepomis gibbosus* (L.) from a habitat with extreme thermal conditions. *J Appl Ichthyol* 21: 306–311.

Tandon KK. 1976. Note on the systematics of the pumpkinseed, *Lepomis gibbosus* (Osteichthyes, Perciformes, Centrarchidae). *Věstník Československé Zoologické Spoločnosti* 40: 307–311.

Tandon KK. 1977. Age and growth study of *Lepomis gibbosus* from Italy. *Věstník Československé Zoologické Spoločnosti* 41: 211–217.

Tomeček J, Kováč V, Katina S. 2005. Ontogenetic variability in external morphology of native (Canadian) and non-native (Slovak) populations of pumpkinseed (*Lepomis gibbosus*, Linnaeus 1758). *J Appl Ichthyol* 21: 335–344.

Tomeček J, Kováč V, Katina S. 2007. Biological flexibility of pumpkinseed, a successful coloniser throughout Europe. In: Gherardi F, ed. Freshwater bioinvaders: profiles, distribution, and threats. Dordrecht: Springer-Verlag, pp. 307–336.

Van Thuyne G, Breine J. 2005. Visbestandopnames op de hengelvijver van het Webbekomsbroekte Webbekom. Hoeilaart-Groenendaal, Belgium: Instituut voor Bosbouw en Wildbeheer.

Villeneuve F, Copp GH, Fox MG, Stakėnas S. 2005. Interpopulation variation in the growth and life history traits of the introduced sunfish, pumpkinseed *Lepomis gibbosus*, in Southern England. *J Appl Ichthyol* 21: 275–281.

Yavno S, Fox MG. 2013. Morphological change and phenotypic plasticity in native and non-native pumpkinseed sunfish in response to sustained water velocities. *J Evol Biol* 26: 2383–2395.

Yavno S, Fox MG. 2014. Morphological plasticity in native and non-native pumpkinseed sunfish in response to habitat type. *Evol Ecol Res* 16: 373–395.

Yavno S, Fox MG, Vila-Gispert A, Bhagat Y. 2013. Morphological differences between native and non-native pumpkinseed in traits associated with locomotion. *Environ Biol Fish* 96: 507–518.

Yavno S, Rooke AC, Fox MG. 2014. Morphological change and phenotypic plasticity in native and non-native pumpkinseed sunfish in response to competition. *Naturwissenschaften* 101: 479–492.

Záhorská E, Kováč V, Falka I, *et al.* 2009. Morphological variability of the Asiatic cyprinid, topmouth gudgeon *Pseudorasbora parva*, in its introduced European range. *J Fish Biol* 74: 167–185.

Záhorská E, Švolíková K, Kováč V. 2013. Do invasive populations of topmouth gudgeon (*Pseudorasbora parva*, Temminck and Schlegel) from disturbed and undisturbed habitats follow different life-histories? *Int Rev Hydrobiol* 98: 61–70.

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