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Different life-histories of native and invasive *Neogobius melanostomus* and the possible role of phenotypic plasticity in the species' invasion success

K. Hôrková(1), V. Kováč(1),*

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ABSTRACT

Key-words: *round goby, biological invasions, epigenesis, alternative ontogenies, reproductive parameters*

One of the most successful invasive fish species with negative impacts is round goby *Neogobius melanostomus* that has spread from its original Ponto-Caspian area to west and central Europe and even to North America. Previous studies focused on invasive fishes have revealed that these species have the capability to generate forms with life-history traits that differ between native and non-native populations. As a contribution to explain their invasion success, the theory of alternative ontogenies and invasive potential has been developed. The main aim of the present study was to test the hypothesis derived from this theory, which predicts that females of the non-native population of *N. melanostomus* (from Slovakia) will have significantly smaller oocytes, higher fecundity and smaller body size at maturity than those of the native population (from Bulgaria). All the three quantitative parameters of life-history traits examined in this study were found to be consistent with the predictions tested. Variations in reproductive parameters observed in non-native *N. melanostomus* demonstrate the species' phenotypic plasticity, which appears to be an important attribute that helps potential invaders to establish new populations in unknown environments. However, further experimental studies are necessary to verify this theory by testing hypotheses derived from it.

RÉSUMÉ

Différentes histoires de vie de *Neogobius melanostomus* indigène et invasif et le rôle possible de la plasticité phénotypique dans le succès de l'invasion de l'espèce

Mots-clés : *gobie à taches noires, invasions biologiques, épigenèse, ontogenèses alternatives, paramètres de reproduction*

Une des espèces les plus envahissantes de poissons aux impacts négatifs est le gobie à taches noires *Neogobius melanostomus* qui s'est propagé à partir de sa zone ponto-caspienne native vers l'ouest et le centre de l'Europe et même en Amérique du Nord. Des études antérieures sur les poissons invasifs ont révélé que ces espèces ont la capacité de générer des individus avec des traits d'histoire de vie qui diffèrent entre les populations autochtones et non autochtones. En guise de contribution à expliquer leur succès d'invasion, la théorie des ontogenèses alternatives et du potentiel invasif a été développée. L'objectif principal de cette étude était de tester l'hypothèse dérivée de cette théorie, qui prédit que les femelles de la population non autochtone de *N. melanostomus* (de Slovaquie) auront de plus petits ovocytes, une plus forte fécondité et une plus petite taille

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*(1) **Department of Ecology, Faculty of Natural Sciences, Comenius University Mlynská dolina, 84215 Bratislava, Slovakia***
* Corresponding author: kovac@fns.uniba.sk

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à maturité que celles de la population autochtone (de Bulgarie). Tous les trois paramètres quantitatifs des traits d'histoire de vie examinés dans cette étude ont été jugés conformes aux prédictions testées. Les variations dans les paramètres de reproduction observés chez *N. melanostomus* non indigènes démontrent la plasticité phénotypique de l'espèce, qui semble être un attribut important qui aide les envahisseurs potentiels à établir de nouvelles populations dans des environnements inconnus. Toutefois, d'autres études expérimentales sont nécessaires pour vérifier cette théorie en testant des hypothèses qui en découlent.

INTRODUCTION

Biological invasions of fishes, which are widely recognized as a significant component of human-caused environmental change (Copp *et al*., 2005) have become a serious issue in the last decades because of threats to global biodiversity. Their impacts vary from local environmental disturbances (competition for food and habitat, predation, introduction of parasites, replacing native species), over the extinction of endemic species, to large economic losses (aquaculture) and serious threats to human health, such as allergies, introduction of parasites and disease (Janssen and Jude, 2001; Lauer *et al*., 2004; Hogan *et al*., 2007; Karlson *et al*., 2007; Kornis *et al*., 2012).

One of the most successful invasive fish species with negative impacts is round goby *Neogobius melanostomus* (Pallas 1814) that has spread from its original Ponto-Caspian area to west and central Europe and even to North America (Jude *et al*., 1992; Skóra and Stolarski, 1993; Copp *et al*., 2005; Verreycken *et al*., 2011). It has colonized not only many European rivers (such as Danube, Sava, Morava, Dyje, Lek and Scheldt) but also coastal areas in the Baltic and North Seas (Balážová-L'avrinčíková and Kováč, 2007; Verreycken *et al*., 2011). It appears that the initial introduction of *N. melanostomus* to new areas was promoted by human activities, especially by international transport, both continental (through the Volga, Danube and Rhine rivers) and trans-continental (through Atlantic ocean; Corkum *et al*., 2004; Wiesner, 2005; van Beek, 2006; Brown and Stepien, 2009, Roche *et al*., 2013). Currently, *N. melanostomus* is reported from 16 countries in Europe but its spreading is still continuing. One of the latest occurrences of the species in new areas comes from Switzerland, River Rhine, the harbor of Kleinhüningen (Kalchhauser *et al*., 2013).

Such an expansive dispersion of *N. melanostomus* is associated with the species' tolerance of various range of environmental conditions (Moskal'kova, 1996; Charlebois *et al*., 1997; Young *et al*., 2010), a wide range of diet and flexibility in feeding behaviour (Shemonaev and Kirilenko, 2009; Števove and Kováč, 2013), aggressive behaviour during reproduction period, high reproduction rate and parental care, larger body size compared with other benthic species (Charlebois *et al*., 1997; Jude, 1997), as well as flexibility in life-history traits (Gutowsky and Fox, 2012).

Indeed, previous studies focused on invasive *N. melanostomus* have revealed that this species has the capability to generate forms with life-history traits that are different between its native populations and its non-native populations (MacInnis and Corkum, 2000; L'avrinčíková and Kováč, 2007; Kováč *et al*., 2009). Changes in life-history traits, however, have not only been observed in *N. melanostomus* but in several other invasive fish species, too (Feiner *et al*., 2012; Záhorská and Kováč, 2013; Záhorská *et al*., 2013). Such observations, made on a range of species, pose the question whether the flexibility in life-history traits, associated with successful invasions, follows some rules with more general implications. To examine this question, the theory of alternative ontogenies and invasive potential has been developed (Kováč, 2010). This theory derives from developmental biology, namely from the concept of alternative ontogenies (Balon, 2004). Central to this concept is that phenotypic plasticity of organisms results from epigenesis, the process that shapes the developing individuals and has the potential to generate alternative ontogenetic trajectories and life-histories. As a result, both generalized and specialized phenotypes (a continuum of discrete phenotypes) are formed within and/or among populations. Epigenesis thus generates a wide range of phenotypes in response to variation in the environment. Generalized phenotypes result from unpredictable or unfavourable conditions, whereas specialized forms, adapted for particular conditions, prevail in stable and favourable conditions (Balon, 2004; Kováč, 2011).

Indeed, the theory of alternative ontogenies has important implications for ecological and evolutionary studies (Vilizzi and Kováč, 2013). When applied to biological invasions, the concept of alternative ontogenies provides the hypothesis which predicts that successful invaders will produce more specialized forms in their native areas (*i.e.* under stable organism-to-environment interactions that have resulted from evolution), however, in unknown environment of the areas they have invaded, they will shift toward more generalized forms and life-histories. And, the theory of alternative ontogenies and invasive potential develops this idea further as it postulates that the wider is the range between the most generalized and the most specialized phenotype a species can generate, the wider is its invasive potential (Kováč, 2010; Záhorská *et al*., 2013). Indeed, the existence of alternative ontogenies has been observed in our previous studies devoted to invasive populations of *N. melanostomus* and bighead goby *Neogobius kessleri* (Günther 1861) (Balážová-L'avrinčíková and Kováč, 2007; Kováč *et al*., 2009), as well as topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel, 1842), where the predictions derived from the above hypothesis were tested statistically for the first time (Záhorská *et al*., 2013).

In the latter study, two of three quantitative parameters of life-history traits examined in three invasive populations of topmouth gudgeon supported the hypothesis, whereas the third one remained questionable but not sufficient to reject it. To verify the theory of alternative ontogenies and invasive potential by testing the hypotheses, another model species – round goby – was selected in the present study.

Studies of phenotypic plasticity and/or biological flexibility, especially if based on a theory and/or a hypothesis, require data collected and processed using the same methods in all the samples examined, because analyses based on comparisons between new and literature data are often biased due to differences in the methods used, evaluation of obtained data, etc., and cannot therefore deliver reliable conclusions. In fact, the best way to evaluate the range of variation in life-history traits is to analyse quantitative parameters in both native and non-native populations with proper statistical tests. Therefore, the main aim of the present study was to test the hypothesis that originates from the theory of alternative ontogenies and invasive potential. For the samples examined in the present study this hypothesis predicts that females of the non-native population of *N. melanostomus* will have significantly smaller oocytes, higher fecundity and smaller body size at maturity than those of the native population. Underlying objectives were to analyse variability in reproductive parameters of the two populations, such as duration of their spawning season, gonadosomatic index, fecundity, size of oocytes, and the size at maturity.

MATERIALS AND METHODS

Females of *N. melanostomus* were collected from the River Danube, using electrofishing and fishing rods. Samples of the native population (denoted below as BG, $n = 166$) were collected in Bulgaria (Koshava, 44°04′49″N; 23°01′49″E, river km 810 and Tutrakan, 44°03′14″N; 26°37′03″E, river km 429), whereas non-native samples (denoted below as SK, $n = 414$) in Slovakia (Karlova Ves parapotamal side-arm, 48°08′43″N; 17°4′10″E, river km 1872 and Čunovo, 48°2′1″N; 17°13′50″E, Bratislava, river km 1852; Figure 1). Sampling was carried out from March to October 2010 and the material thus includes all periods of the *N. melanostomus*' spawning cycle. Females of *N. melanostomus* were killed with an overdose of 2-phenoxyethanol and subsequently preserved in 4% formaldehyde solution for further analyses.

Standard length (SL) was measured to the nearest 1 mm using vernier caliper. Mass, eviscerated mass and gonad mass were taken to the nearest 1 mg, using the KERN ABJ balance.

Figure 1
Sampling sites of the native (Koshava and Tutrakan, Bulgaria) and non-native (Bratislava Karlova Ves side-arm and Bratislava Čunovo, Slovakia) populations of Neogobius melanostomus.

The gonadosomatic index (GSI) was defined as gonad mass /eviscerated body mass percentage. The diameters of 50 randomly chosen oocytes per individual were measured using an ocular micrometer to the nearest 0.0025 mm, and/or from photographs using the AxioVision 4.8.2 software, Carl Zeiss MicroImaging GmbH. Oocyte size groups were determined based on the oocyte diameter frequency distribution.

Traditionally, absolute fecundity of fish females is expressed as the total number of oocytes present in ovaries (Halačka *et al*., 2000; Grabowska, 2005; Valladolid and Przybylski, 2008). However, fishes with asynchronous oocyte development and protracted spawning do not release all of their oocytes within one spawning season (year). In fact, majority of these oocytes will mature later, to be spent in subsequent years (Hunter and Goldberg, 1980; Hunter *et al*., 1985) and therefore, the real number of eggs that enter the process of reproduction in a particular year differs considerably from the total number of oocytes present in ovaries. Thus, in this study, both the absolute number of oocytes (ANO) and real absolute fecundity (RAF; *i.e.* the real number of eggs spent within a season), have been examined.

During the post-spawning period, the ovaries of the native females contained almost no oocytes >0.49 mm diameter, whereas non-native females contained almost no oocytes >0.59 mm. Therefore, the real absolute fecundity was determined based on the number of oocytes >0.49 mm diameter for native females, and >0.59 mm diameter for non-native females, respectively, present in their ovaries during the pre-spawning and spawning periods. Analyzing the size distribution of oocytes (Figure 2), two or three spawning batches per season were identified in *N. melanostomus* females. Thus, the RAF was calculated using the formula:

$$RAF = n_o \times n_b$$

where n_o is the number of oocytes >0.49 mm diameter (native) and >0.59 mm (non-native), and n_b is the number of spawning batches per season.

ANO, RAF, as well as the relative fecundity (number of oocytes per 1g of eviscerated body mass) were determined gravimetrically (Holčík and Hensel, 1972). However, to calculate ANO and RAF, different sub-samples were used. ANO was calculated in specimens from the

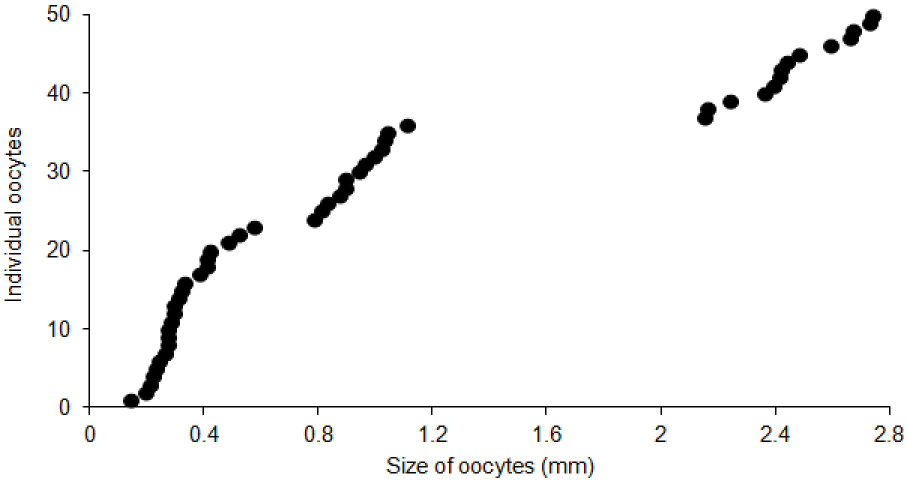

Figure 2
An example of egg size distribution in Neogobius melanostomus. Gaps between the diameters of oocytes (n = 50*) demonstrate that three size groups of oocytes were present in ovaria of this female from Bulgaria.*

pre-spawning and post-spawning periods, whereas RAF in specimens from the pre-spawning and spawning periods (see above). Depending on the results of *F*-test (homogeneity of variance) and Kolmogorov-Smirnov test, either Mann-Whitney *U*-test or *t*-test was used to evaluate the differences between BG and SK populations. All statistical analyses were performed using Past (version 2.15, Hammer and Harper, 2012) and Statistica (version 7.0, StatSoft, 2004). Mean size at maturity for specimens from the pre-spawning and spawning periods was calculated from the percentage of mature females in each size-class (in 10 mm *SL* intervals; Trippel and Harvey, 1987) using the following formula:

$$\alpha = \sum_{x=0}^{w} (x)\,[f(x) - f(x-1)]$$

where α is the mean *SL* at maturity, x is the size in mm, *f*(*x*) is the proportion of fish mature at size x, and w is the maximum size in the sample (DeMaster, 1978; Fox, 1994).

RESULTS

In the samples examined, the SL of BG and SK females ranged from 38 to 87 mm (mean 64.08 mm) and from 23 to 113 mm (mean 63.88 mm), respectively. Body mass ranged from 1.29 to 19.89 g (mean 7.58 g) in BG females and from 0.75 to 45.18 g (mean 8.35 g) in SK females. The eviscerated body mass of BG females varied between 1.10 to 15.51 g (mean 6.44 g), and in SK females between 0.66 to 40.13 g (mean 7.11 g). The mass of ovaries ranged from 0.003 to 2.402 g (mean 0.39 g) in BG females and from 0.001 to 3.194 g (mean 0.33 g) in SK females. No significant differences between the samples of BG and SK females in any of the above parameters were found (Mann-Whitney*U*-test: $U = 32729.50$, $Z = -0.915$, $P = 0.360$; $U = 33395.50$, $Z = 0.373$, $P = 0.709$; $U = 33\,365$, $Z = 0.390$, $P = 0.696$; $U = 31415$, $Z = -1.445$, $P = 0.148$, respectively).

Two or three groups of oocytes were determined in both populations during pre-spawning and spawning periods. In BG, two size-groups of oocytes were clearly distinguished in 47.9% females. The oocyte diameter in size-group I ranged from 0.06 to 1.15 mm (mean 0.36 mm), whereas in size-group II it ranged between 0.61 and 2.72 mm (mean 1.75 mm). Three size-groups of oocytes were clearly distinguished in 7.6% of females. In these females, the oocyte diameter in size group I ranged from 0.1 to 0.57 mm (mean 0.27 mm), in size group II between 0.49 and 1.11 mm (mean 0.81 mm), and in size group III between 1.92 and 2.75 mm

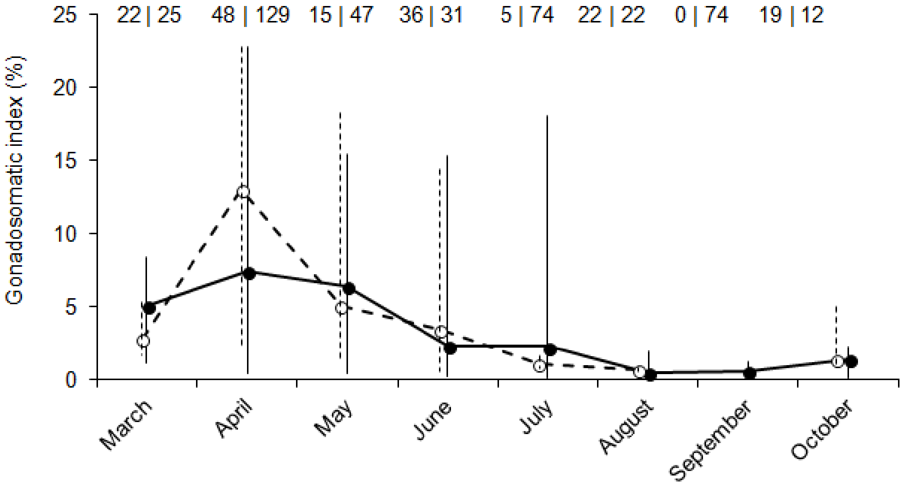

Figure 3
Monthly variation of gonadosomatic index (GSI) in native (dashed line) and non-native (solid line) populations of Neogobius melanostomus females during 2010. Dots indicate mean values, vertical lines indicate the range. Figures above the vertical lines denote the number of females from the native and non-native populations, respectively.

(mean 2.31 mm). In the rest of females (44.5%), the largest group of oocytes was absent (either because these females were juvenile or collected just after they spent their ripe batch of eggs) and/or the next batch was just under development, *i.e.* not distinguishable from the size group I. In SK, two size-groups of oocytes occurred in 48.9% females. The oocyte diameter in size group I ranged from 0.05 to 1.27 mm (mean 0.33 mm), and in size group II between 0.53 and 2.62 mm (mean 1.59 mm). Three size-groups of oocytes were formed in 4.2% of females. The oocyte diameter in size group I ranged from 0.06 to 0.54 mm (mean 0.20 mm), in size group II between 0.45 and 1.46 mm (mean 0.72 mm), and in size group III between 1.57 and 2.73 mm (mean 2.06 mm). In the rest of females (46.9%), the largest group of oocytes was absent (for the same reason as in BG population).

The size of oocytes from the entire reproductive cycle varied between 0.05 and 2.75 mm (mean 0.50 mm) in BG and between 0.04 and 2.73 mm (mean 0.48 mm) in SK. However, for the hypothesis tested, size of oocytes at the onset of ontogeny is more important (smaller oocytes at the onset of ontogeny indicate a development towards more generalized phenotypes, whereas larger oocytes at the onset of ontogeny indicate a development towards more specialized phenotypes). Egg diameters in the last phase of maturation (mature oocytes, which will be spawned soon) varied between 1.72 and 2.75 mm (mean 2.25 mm) in BG and between 1.50 to 2.73 mm (mean 2.03 mm) in SK (Mann-Whitney U-test: $U = 103928$, $Z = -17.773$, $P < 0.001$).

During the entire reproductive cycle, values of *GSI* varied from 0.14 to 22.70% (mean 5.34%) in BG females, and from 0.10 to 22.84% (mean 4.87 %) in SK females (Mann-Whitney U-test: $U = 28052$, $Z = -0.109$, $P > 0.05$). The seasonal variation in *GSI* indicates that BG females spawned from early April to June, whereas in SK females, the spawning season was protracted, as it lasted from March to July (Figure 3).

The values of ANO were found to vary from 419 to 7865 oocytes (mean 3512 oocytes) in BG females, and from 1578 to 10605 oocytes (mean 4413 oocytes) in SK females (t-test: $t = 3.264$, $d.f. = 175$, $P < 0.01$). The RAF calculated for two batches per season ranged between 508 and 3664 oocytes (mean 1718 oocytes) in BG females, and between 665 and 7572 oocytes (mean 2140 oocytes) in SK females. Alternatively, RAF calculated for three batches per season was found to range between 762 and 5496 oocytes (mean 2577 oocytes) in BG females, and between 998 and 11359 oocytes (mean 3210 oocytes) in SK females (for both alternatives Mann-Whitney U-test: $U = 7868$, $Z = 2.881$, $P < 0.01$). Finally, relative fecundity varied from 101.5 to 3158.5 oocytes·g^{-1} (652.7 oocytes·g^{-1}) in BG females, and

Table I
Length distribution of juvenile (J) and mature females (F), and the proportion of mature females in the native and non native populations of Neogobius melanostomus. SL = standard length.

	Native population					Non-native population			
Size class	**J**	**F**		**Mature**	**Size class**	**J**	**F**		**Mature**
(mm, SL)	**number**		**Σ**	**females (%)**	**(mm, SL)**	**number**		**Σ**	**females (%)**
30–39	1		1	0	30–39	2		2	0
40-49	2	1	3	33.3	40-49	4	6	10	60
50–59		36	36	100	50–59	4	59	63	93.7
60-69		35	35	100	60-69		60	60	100
70–79		41	41	100	70–79		31	31	100
80–89		9	9	100	80–89		23	23	100
90–99			–	–	90–99		7	7	100
100–109			–	–	100–109		2	2	100
110–119			–	–	110–119		2	2	100
Σ	3	122	125		Σ	10	190	200	

from 224.7 to 3 568.9 oocytes·g^{-1} (748.3 oocytes·g^{-1}) in SK females (Mann-Whitney U-test: $U = 21249$, $Z = 2.981$, $P < 0.01$).

The smallest mature female from BG was 49 mm SL, and, at the same time, all females >49 mm SL were found to be mature. In contrast, the smallest mature female from SK measured 46 mm SL, and the size class 50–59 mm contained 93.7% of mature females. All females >59 mm SL were found to be mature (Table I). The mean size at maturity of females was calculated to be 46.67 mm SL in BG and 44.63 mm SL in SK.

DISCUSSION

Samples of the two *N. melanostomus* populations did not exhibit significant differences in the basic parameters as body length, body mass and ovarian mass (all U-tests, $P > 0.05$), which allows to test for the differences in reproductive parameters without the risk of possible bias related to body size and or sampling methods. Based on the theory of alternative ontogenies and invasive potential, SK females (non-native population) were predicted to have 1) significantly smaller oocytes, 2) higher fecundity and 3) smaller body size at maturity than BG females (native population).

With regard of the size of oocytes, the prediction met the expectations, because SK females were really found to have significantly smaller oocytes of the size-groups 2 and/or 3, *i.e.* the oocytes in the final stage of maturation (U-test, $P < 0.001$). Given the higher ANO (see below), this indicates that females of the non-native population distributed the portion of acquired resources devoted to reproduction into a higher number of less capable offspring (less yolk = poorer endogenous nutrition). This is consistent with the typical features of generalized forms, which are characterized by the production of a large number of small oocytes with thin yolk, *i.e.* by higher reproductive frequency and lower investment into offspring (Balon, 1989; Flegler-Balon, 1989). Lower fitness of offspring from the non-native population was probably compensated by prolonged spawning period (indicated by *GSI*, Figure 3), in order to generate a higher number of individuals, and to enhance thus the probability that the next generation will survive in the unpredictable conditions of the invaded (*i.e.* "yet unknown") environment.

In contrast, the native population, that is considered to live in a stable environment (in terms of stable organism-to-environment interactions that have resulted from evolution), distributed the portion of acquired resources devoted to reproduction into a fewer number of more capable offspring, which is consistent with lower fecundity and larger size of oocytes in the last stage of maturation. Such allocation of acquired resources is typical for specialized forms that produce a small number of large oocytes with dense yolk. Their reproduction rate is lower but investment into offspring is higher (Balon, 1989; Flegler-Balon, 1989). Larger oocytes produce more capable offspring, because more yolk in the oocytes provides better endogenous nutrition for embryos, and such offspring thus grow faster. Faster growing provides effective protection against predators and better predispositions in competition for food, space, etc. (Wootton, 1994; MacInnis and Corkum, 2000). Native population can afford to produce less numerous offspring, since these are more specialized to the stable environment, which provides them a selective advantage and enhances their survival. This life-history strategy of the native *N. melanostomus* population appears to have been associated with a shorter spawning period (all of the five females from July were spent, see also Figure 3). Such a production of a lower number of fitter offspring allows the individuals to allocate more sources to somatic growth, which increases the potential for further dispersal of the population (Geist, 1978).

Concerning the second parameter tested, *i.e.* fecundity, the non-native population differed significantly from the native population in absolute number of oocytes (t-test, $P < 0.01$), real absolute fecundity (U-test, $P < 0.01$), as well as in relative fecundity (U-test, $P < 0.01$), with higher values in the non-native population, as predicted. Within the context of the theory of alternative ontogenies and invasive potential, the values of absolute number of oocytes and relative fecundity are more important than those of real absolute fecundity. This is because this theory assumes that individuals from a population exposed to frequent disturbances develop into the generalized phenotypes that tend to increase their production of offspring, not only diverting allocation of their sources towards reproduction rather than somatic growth (Copp and Fox, 2007) but also redistributing them into a higher number of offspring (Balon, 2004). However, what is finally the real number of successfully spawned oocytes depends on particular local conditions during the particular spawning season. In June 2010, a sudden extreme increase (plus 4 m) in water level of the Danube occurred, accompanied with highly increased current velocities and sudden temperature decline (data provided by the Slovak Hydro-meteorological Institute, Bratislava, 2011). Such a strong disturbance was likely to interrupt the spawning season of *N. melanostomus*, and to decrease thus the real number of eggs spent within a season of the non-native population. Nevertheless, despite of this disturbance, the differences in real absolute fecundity predicted by the hypothesis were observed.

Finally, females of the non-native population were found to mature at a smaller body size than those of the native population. Not only the minimum standard length of mature females but also the mean size at maturity was consistent with the prediction, though the latter must be taken with caution due to low number of specimens from the size group 40–49 mm SL (see Table I for details).

Thus, being aware that the data tested had some limitations typical for field studies, all the three quantitative parameters of life-history traits examined in this study have supported the theory of alternative ontogenies and invasive potential. Due to a pronounced founder / bottleneck effect in the population of *N. melanostomus* from Slovakia, the genetic diversity (allele frequencies) in this invasive population was found to be strongly limited compared to native populations (Brown and Stepien, 2008). Therefore, variations in the life-history described in non-native *N. melanostomus* from the Danube appear to be a demonstration of the species' phenotypic plasticity.

Life-history plasticity has been reported as "an important advantage to invasive species, allowing them to adapt for successful transitions throughout the invasion process, as well as to local conditions within the invaded system once they become fully integrated into established communities" (Feiner *et al*., 2012). Indeed, the theory of alternative ontogenies and invasive potential also postulates that a life-history that is advantageous at the beginning of the invasion, *i.e.* during the establishment of a new population, may turn into disadvantage once the population has established and achieved high density (Kováč, 2010). Thus, after several generations a shift back to specialized life-history, typical for native populations, is expected to be observed in the invasive populations of *N. melanostomus*.

In conclusion, the results presented in this study suggest that phenotypic plasticity (resulting from epigenesis) may play an important role in succesful invasions, and that this role can be tested using the hypothesis derived from the theory of alternative ontogenies and invasive potential. However, this conclusion comes with some caveats. Various environmental factors can have strong impact on attributes of each population. Unfortunately, in field based studies it is never possible to ensure that all the ecological factors that can potentially affect the results, are considered. The approach used in this study is thus based on the theoretical background which postulates that regardless any concrete environmental factors, the non-native population has to cope with unknown environment never experienced in the species' evolutionary history. And, the theory predicts that in such a case the population will generate phenotypes with life-history traits significantly different from those of the native population. Of course, this approach has limitations and experimental studies are necessary to verify this theory by testing further hypotheses derived from it.

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