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ORIGINAL ARTICLE

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Condition status and parasite infection of *Neogobius kessleri* and *N. melanostomus* (Gobiidae) in their native and non-native area of distribution of the Danube River

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Abstract The success of introduced species is often facilitated by escape from the effects of natural predators and parasites. Introduced species can profit from this favourable situation, attaining higher population densities and greater individual sizes in novel areas. In this study, somatic condition and parasite infection were compared between native and non-native populations of *Neogobius kessleri* Günther; introduced only within the interconnected Danube and Rhine River system, and *N. melanostomus* (Pallas); widely introduced throughout several river systems in Europe and North America. Higher values of Fulton's condition factor were observed in non-native populations of both goby species. *Neogobius melanostomus* attained higher gonadosomatic index values in non-native populations, indicating potential increased investment in reproduction in its new area. A lower splenosomatic index was observed in non-native populations, especially in *N. melanostomus*. Parasite infracommunity richness and mean abundance were higher in *N. kessleri* in both native and non-native populations, suggesting higher susceptibility of *N. kessleri* to these parasites. Non-native populations of both hosts showed higher infra-community richness as a result of acquiring parasites native to the new area, but lower parasite abundance. Differences in success of the introduction and establishment in new areas between the two fish species may be associated with a relatively low parasite infection rate and a higher gonadosomatic index in non-native populations of *N. melanostomus* in comparison to *N. kessleri*.

Keywords Danube River · Fish introductions · Parasite · Ponto-Caspian gobies · *Apollonia melanostoma*

Introduction

The introduction and spread of non-native fish species into aquatic ecosystems is a worldwide problem that is increasing in frequency. Many areas have been affected by the presence of non-native species. However, most of the introductions are not successful and only a minority of introduced species establish stable populations and become invasive (Simberloff and Gibbons 2004). Aquatic introductions are known to be facilitated by a range of factors, including human activities such as river regulation, connection of contiguous basin by canals, ballast water transport (Grigorovich et al. 2003) as well as species-specific traits.

Interest in life history traits making species more invasive has received a great deal of recent attention because of the potential predictive power of this perspective. Some studies have focused on biological and ecological traits that may predispose species to rapid population expansion (Moyle 1986; Vila-Gispert et al. 2005; Devin and Beisel 2007), but no simple biological predictor of invasion success has been demonstrated, though some aspects were more common in alien species than in natives (Devin and Beisel 2007). Traits that characterise freshwater fish invaders include tolerance to a broad range of environmental conditions, rapid dispersal and colonisation, aggressive behaviour and competitiveness, and desirability to humans (Moyle 1986). Biological characteristics of the species; e.g. condition factors, are also suspected to play an important role in invasive biology. Individual condition is an important component of performance, survivorship and reproductive success in fish (Forseth et al. 1999), reflecting the amount of energy possessed by an individual. As demonstrated in several fish species, larger fish with high

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fecundity are suspected to be more successful invaders (Vila-Gispert et al. 2005).

Besides life history traits, the success of introduced species may also be facilitated by emancipation from the effects of natural predators and parasites. Decreased parasite species richness in non-native goby populations has been described in introductions within the same and also among different river systems (Pronin et al. 1997; Camp et al. 1999; Ondračková et al. 2005). According to the parasite/predator escape hypothesis, an introduced species may profit from this favourable situation, attaining higher population densities and greater individual sizes in the colonised areas compared to the conspecifics in their native range (Torchin et al. 2003). On the other hand, introduced hosts may bring with them all or a subset of their native parasite fauna into the new area or they may even acquire local parasites (Prenter et al. 2004). The importance of parasites has also been recognised in invasions when native host populations are infected by a new parasite transported with introduced host (Moravec and Taraschewski 1988).

One of the largest fish introductions during the last decades has been the introduction of Ponto-Caspian gobies within Europe. In the River Danube, water retention structures constructed to facilitate energy production and navigation have resulted in a gradual increase in mean annual and seasonal water temperatures (Copp et al. 2005). Since the early 1990s, four Ponto-Caspian gobies appeared upstream of their native Danubian distribution. *Neogobius kessleri* Günther, *N. melanostomus* (Pallas) (*Apollonia melanostoma* (Pallas, see Stepien and Tumeo 2006), *N. fluviatilis* (Pallas) and *N. gymnotrachelus* (Kessler) have been recorded in the Middle and Upper Danube since the 1990s (e.g. Jurajda et al. 2005; Wiesner 2005). Whilst the three latter species have also been introduced into the different sea-drainage areas (e.g. Baltic Sea), *N. kessleri* is the only species exclusively invading new regions within the two river-basin continuum: the middle and upper part of Danube River and Rhine River via Rhine-Main-Danube Canal (Freyhof and Huckstorf 2006). Although there are several explanations for the rapid spread of Ponto-Caspian gobies during last few decades, their introduction with ships and their subsequent spreading from harbours is presently accepted as the most probable reason for their expansion (Wiesner 2005; Polačik et al. 2008).

The differences between *N. kessleri* and *N. melanostomus* in the dynamics of range extension (*N. kessleri*, introduced within a small area, against the widely introduced *N. melanostomus*) were ideal for a comparative survey of two important factors associated with successful establishment of species introduction; fish condition status and parasite load. Because parasite loss is one of the important factors affecting invasions (Torchin et al. 2003; Prenter et al. 2004), the parasite community structure and ecological parameters of parasite infection were compared between native and non-native populations of two goby hosts in the present study. Moreover, parasites may have detrimental effects on the survival and fecundity of individuals and can regulate host population dynamics (Tompkins and Begon 1999). Therefore, the effect of the most abundant parasites on condition factors and also condition differences between both native and non-native host populations were evaluated.

Materials and methods

Host and parasite collection

Native populations of *N. kessleri* and *N. melanostomus* were sampled in the Bulgarian section of the River Danube, near the town of Vidin (N 43°57′35″, E 22°53′16″, 783–806 river km). The non-native population of *N. kessleri* was sampled in the Slovak section of the River Danube, near the town of Gabčíkovo, (N 47°52′17″, E 17°31′04″, 1,812–1,819 river km) and the non-native population of *N. melanostomus* was sampled in the Austrian section of the River Danube, near the town of Orth an der Donau (N 48°07′23″, E 16°42′46″, 1,899–1,903 river km; Fig. 1). The fish were collected by electrofishing or using a beach seine, depending on the habitat conditions during April (spring sample: all fish were caught prior to spawning) and October (autumn sample) of 2005 and 2006. The water temperature did not differ among samples in spring (10.5–11°C). In autumn, the water temperature was higher in the Bulgarian section of the Danube River (16–18°C) compared to the Slovak (14–16°C) and Austrian (11–14°C) sections of the Danube River.

A total of 113 adult individuals of *N. kessleri* and 148 adult individuals of *N. melanostomus* were sampled. Collected fish were transported alive in river water to the laboratory and individually sacrificed prior to dissection within 24 h of transport. Standard length (SL, to the nearest 1 mm), total body weight (W) and eviscerated body weight (without internal organs, WE, to the nearest 0.1 g) were measured (Table 1). Then, wet weight of gonads, liver and spleen were measured to the nearest 0.001 g.

Fish were examined under a binocular microscope for the presence of metazoan parasites according to standard methods (Ergens and Lom 1970). Collected parasites were preserved in 4% formaldehyde (Acanthocephala, Digenea, Cestoda, Bivalvia, Crustacea, Acarina), in a mixture of ammonium picrate and glycerine (Monogenea) or in a mixture of glycerine and alcohol (Nematoda). Prior to species identification, acanthocephalan were cleared with clove oil, nematodes were cleared with a glycerine–water solution. Fixed digenean and cestodes were stained in ferric acetocarmine (IAC), dehydrated in gradual alcohol series, and mounted into “Canada” balsam (Ergens and Lom 1970). Parasites were identified using a light microscope equipped with phase-contrast, differential

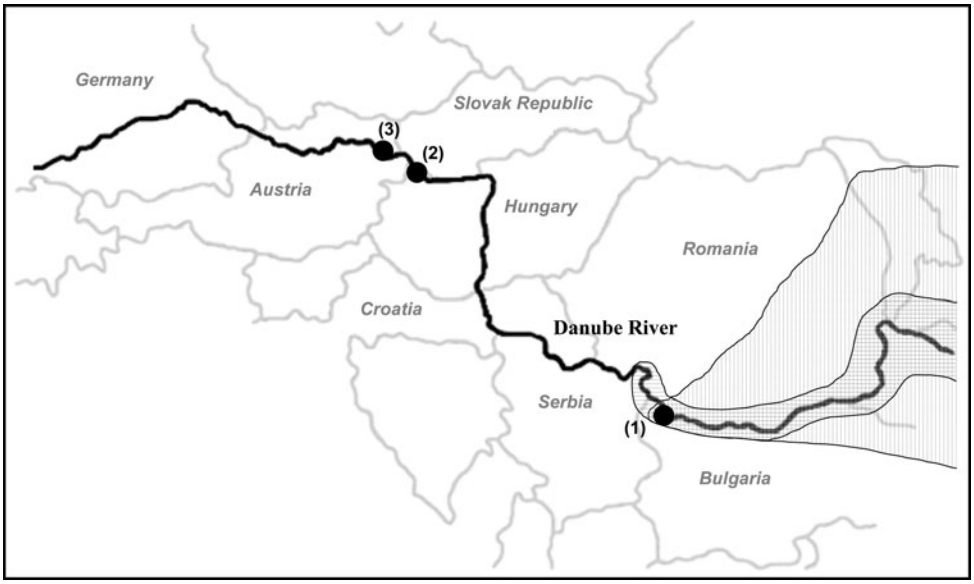

Fig. 1 Map of the study area. *1* Native range of *Neogobius kessleri* (horizontal hatching) and *Neogobius melanostomus* (vertical hatching; Bulgarian section of the Danube River); *2* non-native range of *N. kessleri* (Slovak section of the Danube River); *3* non-native range of *N. melanostomus* (Austrian section of the Danube River)

Table 1 Number of fish examined, mean ± SD of fish length and total parasite abundance, mean and range of infracommunity richness and total parasite species richness in native and non-native populations of *Neogobius kessleri* and *Neogobius melanostomus* in spring and autumn samples

	Spring sample		Autumn sample	
	Native	Non-native	Native	Non-native
N. kessleri				
N	26	29	27	31
SL ± SD	94 ± 13	108 ± 12	104 ± 8	109 ± 9
Total parasite abundance	173.6 ± 103.2	51.7 ± 27.6	109.0 ± 67.7	105.8 ± 45.8
Infracommunity richness	4.2 (2–7)	5.4 (4–8)	4.5 (2–8)	4.6 (3–7)
Total species richness	11	15	15	16
N. melanostomus				
N	28	33	43	44
SL ± SD	70 ± 10	73 ± 13	94 ± 10	102 ± 6
Total parasite abundance	63.1 ± 38.0	33.9 ± 30.2	100.7 ± 59.0	79.3 ± 36.0
Infracommunity richness	2.0 (0–4)	3.3 (2–7)	2.4 (1–5)	2.4 (1–4)
Total species richness	10	14	11	9

SL standard length (mm)

interference contrast (DIC) and Lucia 5.0 Image Analysis Systems.

Data analyses

Four indices of fish condition were calculated for each individual fish: (1) Fulton's condition factor: $K = WE \times 10^5/SL^3$; (2) hepatosomatic index: $HIS = W(liver) \times 10^2/WE$; (3) splenosomatic index: $SSI = W(spleen) \times 10^3/WE$; and (4) gonadosomatic index: $GSI = W(gonads) \times 10^2/WE$, using WE and weight of organs in grams and SL in millimetres. Not all internal organs could be reliably weighed in some individuals (due to constraints imposed by parasitological dissections), which resulted in unequal sample sizes for the four indices. Although logarithmic transformations were applied prior to parametric analyses, parametric methods were not applicable for the gonadosomatic index because data still did not meet assumptions of normality. Thus, parametric *t* tests were used for comparison of K, HSI and SSI between the native and non-native fish population and non-parametric Mann–Whitney *U* tests (MW-*U*) were used for comparisons of GSI for males and females separately.

Ecological parameters of parasite infection were used according to Bush et al. (1997). Prevalence was defined as the percentage of infected fish of a given parasite species in a sample, mean abundance as the mean number of parasites per host, infected and non-infected, in a sample and mean intensity as the mean number of parasites per infected fish. The classification of core and satellite species followed Hanski (1982), with core species as locally abundant and regionally common species (prevalence $>50\%$, mean abundance >10), satellite species as locally and regionally rare species (prevalence $<10\%$, mean abundance <1), and parasites between the two groups as intermediate species. For data analyses, all parasite abundance data were $^3\sqrt{(x)}$ transformed. The analyses of parasite infections were based on measurements of infracommunity richness, total parasite abundance, and parasite abundance of core parasite species. Generalised linear model (GLM) factorial analysis of variance (ANOVA) was applied to compare parasite infection between the fish host species (*N. kessleri* and *N. melanostomus*), the origin of the fish population (native and non-native), and between sampling seasons (spring and autumn).

GLM ANOVA was performed to examine the combined effects of factors influencing fish condition: the total parasite abundance, infracommunity richness, and abundance of two core parasite species. Because the assumption of normality was not met in GSI in all samples; only K, HSI, and SSI were included in the analysis. The relationship between the abundance of core species and GSI was analysed using Spearman rank correlation. All analyses were performed using Statistica 8 for Windows (http://www.statsoft.com/).

Results

Condition factors in gobies

Significantly higher values of K were found in spring and autumn samples of non-native populations in *N. kessleri* ($t_{51} = 3.14$, $P = 0.003$ and $t_{58} = 3.02$, $P = 0.004$, respectively) and *N. melanostomus* ($t_{69} = 2.24$, $P = 0.028$ and $t_{75} = 2.13$, $P = 0.036$, respectively; Fig. 2a) compared to native populations. No differences between populations in HSI were found in *N. melanostomus* ($t_{51} = 0.52$, $P = 0.608$ in spring and $t_{74} = 0.88$, $P = 0.383$ in autumn) and in the spring sample of *N. kessleri* ($t_{28} = 0.25$, $P = 0.804$); higher values of HSI were attained by *N. kessleri* from non-native populations in autumn sample ($t_{58} = 2.09$, $P = 0.041$; Fig. 2 b). The splenosomatic index did not differ between populations in *N. kessleri* for the spring sample ($t_{50} = 0.35$, $P = 0.725$) and was significantly higher in the native compared to the non-native population in the autumn sample ($t_{57} = 5.64$, $P < 0.001$). Significantly higher values of SSI in native population were found in both spring and autumn samples in *N. melanostomus* ($t_{61} = 5.25$, $P < 0.001$ and $t_{72} = 2.13$, $P = 0.037$, respectively; Fig. 2c).

The GSI was characterised by high variability. GSI from spring samples of *N. kessleri* was not significantly different between populations in both males and females (MW-*U* test, $P = 0.801$ and $P = 0.186$ respectively, see Fig. 3). In autumn, higher values of GSI were found in female *N. kessleri* in the non-native compared to the native population ($P < 0.001$), but no differences were found in males ($P = 0.778$). Females of non-native *N. melanostomus* attained higher GSI values in both the spring and autumn sample ($P = 0.021$ and $P < 0.001$, respectively). Despite the trend of higher GSI in non-native *N. melanostomus* males, there was a significant difference between populations in the autumn sample only ($P < 0.001$) and not in the spring sample ($P = 0.198$). However, this latter result was likely due

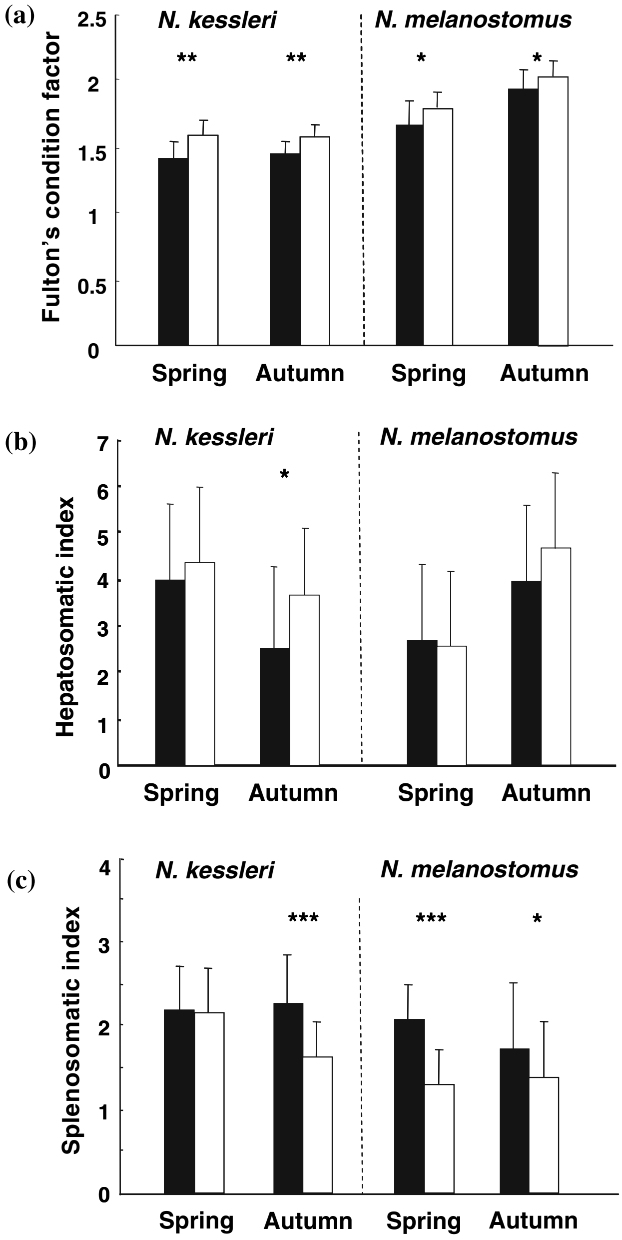

Fig. 2 Comparisons of **a** Fulton's condition factor, **b** hepatosomatic index (HSI), and **c** splenosomatic index (SSI) between native (*black bars*) and non-native (*white bars*) populations of *N. kessleri* and *N. melanostomus*. *Histograms* Mean values and associated standard deviations, *asterisks* significant differences of *t* test: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

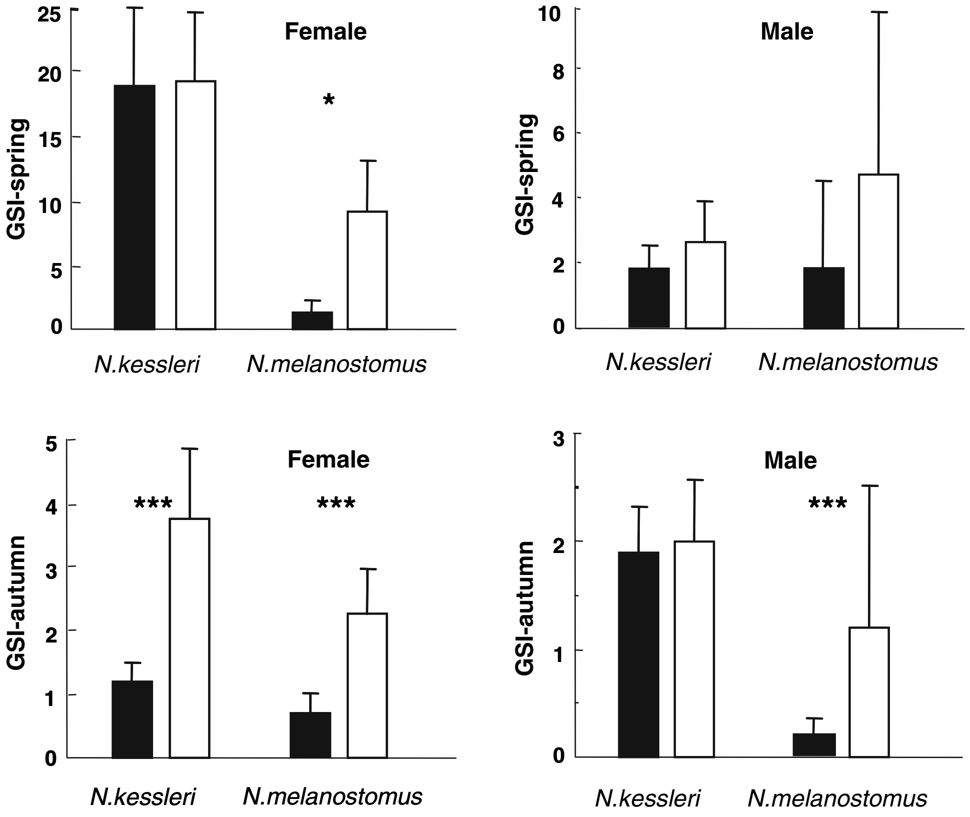

Fig. 3 Comparisons of gonadosomatic index (GSI) between native (*black bars*) and non-native (*white bars*) populations of *N. kessleri* and *N. melanostomus*, separately for males and females in both seasons. *Histograms* Mean values and associated standard deviations, *asterisks* significant differences of MW-*U* test: $^{*}P < 0.05$, $^{***}P < 0.001$

to the high variability of GSI and low number of males in the sample (Fig. 3).

Parasite infection

A total of 31 parasite species were found to parasitise gobies in the River Danube: 25 species infected *N. kessleri* (17 in native and 20 in non-native populations) and 22 species infected *N. melanostomus* (16 in native and 16 in non-native populations; see Table 5 in Appendix). The infracommunity richness ranged from 2 to 8 species per fish in *N. kessleri* and from 0 to 7 species per fish in *N. melanostomus* (Table 1). The total parasite abundance and the mean infracommunity richness were significantly higher in *N. kessleri* compared to *N. melanostomus*, and this was consistent for both native and non-native populations (details on statistics in Table 2). In both host species, the total parasite abundance was higher in native populations. However, the infracommunity richness in native populations was lower compared to the non-native populations (Table 2). In *N. kessleri*, differences in both the total abundance and infracommunity richness were driven mainly by data from the spring sample. For *N. melanostomus*, total abundance was significantly higher in native populations in both seasons and differences in infracommunity richness between populations were affected mainly by data from the spring sample (Table 2).

Most species in the parasite community belonged to the intermediate and satellite species, occurring in low prevalences and abundances. Three parasites belonged to core species in *N. kessleri*: acanthocephalan *Pomphorhynchus laevis* (Müller) in both populations, and adult trematode *Nicolla skrjabini* (Iwanitzky) and larval nematode *Raphidascaris acus* (Bloch) in non-native populations. Moreover, *Gyrodactylus proterorhini* reached prevalence over 50% in both *N. kessleri* populations during spring. Two parasites belonged to core species in *N. melanostomus*: *P. laevis* in both and *R. acus* in non-native populations (Table 3). In both fish hosts, *P. laevis* showed maximum prevalences and abundances. Species with low prevalence and abundance were represented mainly by larval helminths (metacercariae of digeneans, larval cestodes and nematodes).

Effect of parasite infection on fish condition factors

All indices in *N. melanostomus* and HSI in *N. kessleri* were affected by season; the effect of fish population origin on K was found in *N. kessleri* and the effect on SSI in *N. melanostomus*. No relationship was found with any of the core parasites in *N. melanostomus*, but

Table 2 Results of generalised linear model (GLM) factorial analysis of variance (ANOVA) showing the effects of host species and population origin (native and non-native), and population origin and season, on the total parasite abundance and parasite infracommunity richness in both host species *N. kessleri* and *N. melanostomus*

	Parasite abundance			Infracommunity richness		
	df	*F*	*P*	*df*	*F*	*P*
Host species and population origin						
Species	1	28.75	< 0.001	1	222.07	< 0.001
Origin	1	24.48	< 0.001	1	20.49	< 0.001
Species × origin	1	0.79	0.374	1	0.03	0.871
Error	257			257		
Population origin and season						
N. kessleri						
Origin	1	22.78	< 0.001	1	8.43	0.004
Season	1	0.49	0.485	1	0.79	0.376
Origin × season	1	27.73	< 0.001	1	5.01	0.027
Error	109			109		
N. melanostomus						
Origin	1	10.68	0.001	1	17.23	< 0.001
Season	1	40.84	< 0.001	1	1.90	0.170
Origin × season	1	1.84	0.177	1	15.27	< 0.001
Error	144			144		

Table 3 Prevalence (P, in %) and mean abundance (A) of core parasite species in native and introduced populations of bighead (*N. kessleri*) and round (*N. melanostomus*) gobies in spring and autumn samples

Parasite species	*N. kessleri*				*N. melanostomus*			
	Spring		Autumn		Spring		Autumn	
	Native	Introduced	Native	Introduced	Native	Introduced	Native	Introduced
Monogenea								
Gyrodactylus proterorhini								
P	84.6	77.8	20.7	29.0				
A	27.2	7.8	14.5	0.4				
Digenea								
Nicolla skrjabini								
P	57.7	48.1	93.1	100				
A	3.9	0.7	7.2	33.2				
Acanthocephala								
Pomphorhynchus laevis								
P	100	88.9	100	100	96.4	65.1	100	97.7
A	136.3	10.0	82.7	31.6	54.5	8.2	97.5	50.2
Nematoda								
Raphidascaris acus								
P	29.9	96.3	51.7	100	3.6	88.4	39.4	97.7
A	0.4	12.9	1.0	37.7	0.04	10.3	1.2	28.1

the total parasite abundance significantly affected HSI. Furthermore, GLM results showed a marginally significant ($P = 0.05$) influence of *P. laevis* abundance on SSI in *N. kessleri* (Table 4). No significant correlations between the total parasite abundance or parasite infracommunity richness and GSI were found in any sample. No relationship between the parasite abundance of core species and GSI was found in *N. melanostomus* males or females. In *N. kessleri* females, there was a negative correlation of *R. acus* and GSI ($r_s = 0.58$; $P < 0.01$) found in the spring sample of the non-native population. No correlations were detected in *N. kessleri* males.

Discussion

The success of introduced species in new environments is often explained by their escape from the effects of natural predators and parasites. An introduced species can profit from this favourable situation, attaining greater densities and larger average body size than native populations (Torchin et al. 2001). Both higher density and larger body size in non-native goby populations were confirmed for *N. kessleri* and *N. melanostomus* in the Danube River by Polačik et al. (2008), as a result of increased food availability (Polačik et al. 2009).

Table 4 Results of GLM ANOVA on factors (total parasite abundance, infracommunity richness, abundance of core parasite species *P. laevis* and *R. acus*, origin of the fish population and season of sampling) affecting the condition indices in *N. kessleri* and *N. melanostomus*

	N. kessleri			*N. melanostomus*		
	df	*F*	*P*	*df*	*F*	*P*
Fulton's condition factor						
Total abundance	1	1.54	0.218	1	0.02	0.876
Infracommunity richness	1	0.14	0.714	1	0.06	0.813
P. laevis	1	2.11	0.149	1	0.32	0.570
R. acus	1	0.05	0.821	1	0.01	0.904
Origin	1	7.41	0.008*	1	3.74	0.055
Season	1	0.05	0.816	1	21.59	<0.001*
Origin × season	1	1.12	0.293	1	0.59	0.443
Error	105			140		
Hepatosomatic index (HSI)						
Total abundance	1	0.361	0.549	1	7.370	0.008*
Infracommunity richness	1	0.103	0.749	1	0.483	0.488
P. laevis	1	0.849	0.359	1	2.767	0.099
R. acus	1	0.684	0.411	1	0.620	0.433
Origin	1	0.100	0.752	1	0.039	0.843
Season	1	7.260	0.009*	1	21.954	<0.001*
Origin × season	1	0.350	0.556	1	1.517	0.220
Error	82			121		
Splenosomatic index (SSI)						
Total abundance	1	2.691	0.104	1	0.282	0.596
Infracommunity richness	1	0.772	0.381	1	0.094	0.759
P. laevis	1	3.947	0.050*	1	0.181	0.671
R. acus	1	1.065	0.305	1	0.914	0.341
Origin	1	0.162	0.689	1	5.764	0.018*
Season	1	3.046	0.084	1	5.587	0.020*
Origin × season	1	4.583	0.035*	1	0.528	0.469
Error	103			129		

*$P \leq 0.05$

Similarly, in this study, non-native fish reached higher values of Fulton's condition factor as compared to native fish. However, no association between Fulton's condition factor and parasite infection was found. Therefore, higher values of condition factors most probably result predominantly from higher food quality and availability in the area of introduction (Polačik et al. 2009).

In general, parasite infection played a marginal role in the effect on the fish host condition in this study. Acanthocephalan *P. laevis* dominated the parasite community of all samples in both *N. kessleri* and *N. melanostomus*. This parasite was the most important species significantly affecting parasite community structure, and also influenced fish host condition. *P. laevis* was the only parasite species influencing SSI in *N. kessleri*. Spleen size has been commonly used as a measure of investment in immunological defence (Skarstein et al. 2001), demonstrating that host species that encounter more parasites have larger spleens because of greater investment in immunological defence (Møller et al. 1998), or on the intra-specific level the relationship may represent a simple response to parasite infection (Brown and Brown 2002). The decrease in spleen size in non-native populations was readily apparent, particularly in *N. melanostomus* (Fig. 2c). Parasite abundance was higher in *N. kessleri* compared to *N. melanostomus* in both native and non-native populations. The ability to resist parasite infection, together with a reduction in spleen size in non-native *N. melanostomus*, indicates lower energy costs for immune defence in comparison to *N. kessleri*, especially during spring when energy demands for reproduction are increased.

Similarly, a positive relationship between total parasite abundance and HSI in *N. melanostomus* was affected strongly by the abundance of *P. laevis* (representing 73% of all individual parasites associated with *N. melanostomus*), although the direct effect of this parasite was not confirmed (see Table 4). However, even heavy infections of acanthocephalan do not have a large pathogenic effect on their fish hosts, especially in paratenic hosts (reviewed in Taraschewski 2000) such as gobies (Ondračková et al. 2005; Kvach and Skóra 2007). Thus, a high proportion of amphipods in fish diets (Polačik et al. 2009) could lead to high infection rates of *P. laevis*, but simultaneously also to high values of lipid storage due to the nutritive value of the consumed prey (Diggins et al. 2002), resulting in higher values of HSI.

Variability in GSI values showed both interspecies and interseasonal differences. The strongest effect of origin on GSI was evident in the autumn sample of *N. melanostomus*. Fecundity has been implicated as a life-history trait that discriminates successful from unsuccessful invaders (Vila-Gispert et al. 2005). Although fecundity was not measured directly, GSI was a suitable measure for the comparison of gonad weights between native and non-native populations of both species in this study. Significantly higher GSI values in non-native populations found in almost all *N. melanostomus* samples suggested higher investment into reproduction in newly established populations (Ľavrinčíková and Kováč 2007). Furthermore, GSI in *N. melanostomus* was not affected by parasite infection. On the contrary, a decrease in GSI during spring was found in females of *N. kessleri* highly infected with the larval nematode *R. acus* (Table 3). The parasite load of this species was considerably lower in the native range of goby fishes. Unexpected similar values of GSI in non-native *N. kessleri* populations to their native conspecifics may therefore be associated with high infection rates of *R. acus* and its effect on gonad weight. Alternatively, the difference in GSI values in native populations may also be a consequence of the different timing of reproduction between the two areas of distribution. The state of gonad ripeness indicated that non-native populations of *N. melanostomus* (but not *N. kessleri*) were ready to spawn earlier in the spring than fish from the native population, as full gonad maturity was not observed in non-native fish at the time of our survey.

Although parasite loss is implicated as one reason for successful species introductions (Torchin et al. 2003), the structure of the parasite community with strong dominance of one species (*P. laevis*) was similar in native and non-native areas of distribution in both of the hosts examined in this study. Moreover, parasite infracommunity richness was higher in non-native populations of both *N. kessleri* and *N. melanostomus*. Introduced species confront three possible scenarios with respect to their parasites: (1) they bring their native parasites to the recipient area, (2) they acquire parasites native to the new area, or (3) they invade without their parasites and remain free of parasites or are colonised by only a limited number of native parasites (Prenter et al. 2004). In our study, both goby species brought their native parasites to the new area and also acquired new species in the recipient area. However, low parasite species richness was observed in *N. melanostomus* introduced into either the Baltic Sea (Rokicki and Rolbiecki 2002) or the Great Lakes (Pronin et al. 1997; Camp et al. 1999, Kvach and Stepien 2008). The non-native and native populations in the present study belonged to the same river system, the River Danube, which is the most likely reason for the high susceptibility to local parasites in both goby species. Because of low prevalences and abundances of these parasites in the new host, these new host–parasite interactions probably do not have important implications for parasite population dynamics.

Parasite infections have been recognised as one of many potential factors that may lower the resistance of hosts and their ability to adapt to changing environmental conditions (Williams and Jones 1994). In both populations, *N. melanostomus* was less parasitised than *N. kessleri*, although both species share similar habitat (Polačik et al. 2008) and diet, namely the frequent consumption of amphipods (Polačik et al. 2009). Both habitat and diet are characteristics influencing the structure of parasite communities (Sasal et al. 1997). The phenomena of a less-parasitised *N. melanostomus* as compared to *N. kessleri* was also described in a previous study of non-native populations in Slovakian sections of the Danube River (Ondračková et al. 2005). The lower susceptibility to parasite infection observed in *N. melanostomus* may be one of the important factors affecting the differences in dispersion success of the two goby species examined in this study.

In summary, the successful establishment of both goby species in the non-native area could be associated with better somatic conditions. Although a significant increase in Fulton's condition factor in non-native areas was found for both fish species, interspecies differences were found in parasite infection rate and GSI. *Neogobius melanostomus*, a fish species that has colonised successfully several drainages of the Black, Caspian, and Baltic Seas and the Great Lakes in North America (Corkum et al. 2004), was parasitised by a significantly lower species richness and abundance of parasites than *N. kessleri*, a species introduced only into some river sections of the interconnected Danube and Rhine River basins. Successful colonisation of the new areas by *N. melanostomus* could be facilitated further by their higher investment in reproduction. In contrary, the advantage of parasite loss does not apply to *N. kessleri*, due to the high susceptibility of non-native fish to local parasites (Ondračková et al. 2009). Therefore, the balanced trade-off between the investment in growth, reproduction and immune defence may be one reasons underlying the lower invasion success of this fish species.

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Appendix

See Table 5.

Table 5 List of parasite species found in native and non-native populations of *Neogobius kessleri* and *N. melanostomus*

	Parasite life stage	*N. kessleri*		*N. melanostomus*	
		Native	Non-native	Native	Non-native
Monogenea					
Gyrodactylus proterorhini		S, A	S, A	S	
Gyrodactylus sp.				S	
Digenea					
Bucephalus polymorphus	Metacercariae				S, A
Apophalus mühlingi	Metacercariae			A	
Apophalus donicus	Metacercariae	S, A			
Metagonimus yokogawai	Metacercariae			S, A	
Apatemon cobitidis proterorhini	Metacercariae	S, A	S, A	A	S
Diplostomum spp.	Metacercariae	S, A	S, A	S, A	S, A
Tylodelphys clavata	Metacercariae		S, A		S
Holostephanus cobitidis	Metacercariae	A	S	A	
Nicolla skrjabini	Subadult, adult	S, A	S, A	S, A	S, A
Pseudochetosoma salmonicola		S			
Digenea sp. 1	Metacercariae			A	
Digenea sp. 2	Metacercariae	A			
Digenea sp. 3	Metacercariae				S
Cestoda					
Caryophyllidae fam sp.	Larva		S		
Proteocephalus sp.	Larva	S, A	A		
Triaenophorus crassus	Larva	A	S		S
Nematoda					
Anguillicoloides crassus	Larva	S, A	S, A	S, A	S, A
Camallanus lacustris	Larva, adult		A		S
Camallanus truncatus	Larva, adult		A		
Eustrongylides excisus	Larva	S, A		S, A	S
Pseudocapillaria tomentosa	Larva, adult	A	S, A		S, A
Raphidascaris acus	Larva	S, A	S, A	S, A	S, A
Rhabdochona denudata	Adult		A		
Streptocara crassicauda	Larva		S, A	S	S, A
Acanthocephala					
Pomphorhynchus laevis	Subadult, adult	S, A	S, A	S, A	S, A
Mollusca					
Anodonta anatina	Glochidia	S, A	S, A	S, A	S, A
*Anodonta woodiana*a	Glochidia		S, A		
Pseudoanodonta complanata	Glochidia	S		S	S, A
Acarina					
Hydrozetes lacustris			S		

S spring samples, *A* autumn samples

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