Research Article

Forecasting impact of existing and emerging invasive gobiids under temperature change using comparative functional responses

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Abstract

Round goby *Neogobius melanostomus* (Pallas, 1814) and western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) have recently expanded substantially beyond their native ranges, posing a threat to freshwater and brackish ecosystems. Both species exert a detrimental effect on fish community structure directly via predation on fish eggs and indirectly via alterations of food webs. While the impact of *N. melanostomus* is widely documented, *P. semilunaris* receives little attention and its effect on aquatic communities has not yet been quantified. We compared aspects of their predation on common carp *Cyprinus carpio* Linnaeus, 1758 larvae at 20 °C and 25 °C using the functional response (FR) approach, which has been developed and applied to forecast invader impact. Intra-specific comparison showed no significant temperature dependency on assessed FR parameters, attack rate and handling time, suggesting broad temperature tolerance of both tested predators. *Proterorhinus semilunaris* demonstrated a marginally higher attack rate at 20 °C compared to *N. melanostomus*. The handling times did not differ between predators. *Proterorhinus semilunaris* showed a lower maximum feeding rate at 25 °C compared to the rest of treatments suggesting lower temperature optima compared to *N. melanostomus*. Both predators showed substantial maximum feeding rates, which may impact recruitment of native fish species.

Key words: biological invasion, ecological impact, maximum feeding rate, round goby, western tubenose goby

Introduction

With continuing growth of international commerce, travel, and transport, ecosystems are under increasing threat from invasions of non-indigenous organisms, which show no signs of saturation (Hulme 2009; Seebens et al. 2017). Biological invasions seriously impact global biodiversity (Blackburn et al. 2004) and ecosystem processes (Ehrenfeld 2010), causing major social and economic problems (Pimentel et al. 2001; Mazza et al. 2014). Global homogenization of previously separated biota has especially pronounced consequences for aquatic environments (Moorhouse and Macdonald 2015).

In Europe and North America, the invasive benthic fishes round goby *Neogobius melanostomus* (Pallas, 1814) and western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) have recently expanded substantially beyond their native ranges, *i.e.* the Ponto-Caspian region (Kocovsky et al. 2011; Kornis et al. 2012). Their tolerance to wide-ranging environmental conditions, including human-modified rivers (Ray and Corkum 2001; Janáč et al. 2012) along with their effective reproductive strategy (MacInnis and Corkum 2000; Valová et al. 2015), aggressive behavior (Balshine et al. 2005; Błońska et al. 2016), and physiological plasticity (Hôrková and Kováč 2014), facilitate their expansion in invaded ecosystems.

Neogobius melanostomus causes major alterations in newly invaded areas. In addition to critical food web disruptions and shifts in trophic levels (Krakowiak and Pennuto 2008; Almqvist et al. 2010), there may

be habitat and diet overlap with native ichthyofauna (Skóra and Rzeznik 2001), causing a significant decrease in, or extermination of, native fishes (Janssen and Jude 2001). Impact of *P. semilunaris*, on the other hand, has not yet been quantified and only potential threats and indirect effects are mentioned (Kocovsky et al. 2011). Both *N. melanostomus* and *P. semilunaris* are opportunistic feeders capable of adapting to locally abundant food sources (Brandner et al. 2013; Všetičková et al. 2014). Although low consumption of fish eggs and juveniles by *P. semilunaris* and *N. melanostomus* have been reported (French and Jude 2001; Vašek et al. 2014), direct predation by non-indigenous gobies on fish eggs and/or larvae in both laboratory and field conditions have also been observed (Thompson and Simon 2014; Všetičková et al. 2014) indicating these resources can form a substantial part of the diet during specific events (*e.g.* spawning season). Therefore, it is crucial to understand the interactions of these species with potential prey.

Predation is a key process in the population dynamics of lower trophic levels that influences the entire food web regardless of ecosystem type (Holling 1959; Bax 1998). Resource availability (prey density) is a crucial determinant of feeding rate and has been characterized by the use of the functional response curve (FRs; Solomon 1949; Holling 1959). The form and magnitude of FRs are important aspects of consumer-resource interactions and community dynamics, respectively (Murdoch and Oaten 1975; Juliano 2001). Invasive species often display elevated FRs compared to native or low-impact non-native ecologically analogous species and therefore comparative FR is a useful tool for comparison and assessment of the impact of newly introduced species (Dick et al. 2013; Alexander et al. 2014; Dick et al. 2014; Xu et al. 2016; Laverty et al. 2017).

Temperature is considered an important driver of nearly all biological processes, encapsulating individual and population growth rates as well as development rates and lifespans (Brown et al. 2004). Based on the current progression of climate change, we can expect a substantial alteration in consumer-resource relationships worldwide (Clavero and Garcia-Berthou 2005; Pereira et al. 2010; Schulte et al. 2011). Petchey et al. (1999) documented a decline in numbers of top predators and herbivores in warmed ecosystems. Changes in this structure may drive cascading effects at population and community levels (Brown et al. 2004; Petchey et al. 2010). Warming may also substantially alter primary and secondary production in aquatic ecosystems (Richardson and Schoeman 2004). While *N. melanostomus* has a wide temperature tolerance, ranging from −1 to 30 °C (Moskal'kova 1996), maximum consumption is estimated to be within the range of 23 and 26 °C, after which consumption rates decline abruptly (Lee and Johnson 2005). Studies on *P. semilunaris* thermal requirements are scarce but O'Neil (2013) suggests the thermal optima is lower than that of *N. melanostomus*.

In the present study, FRs were applied to compare and forecast the impacts and foraging capacity of both established and emerging invaders, *N. melanostomus* and *P. semilunaris*, upon soft-bodied pelagic prey. The impact of both predators was tested at two temperature levels to explore the relative effects at 20 °C, representing the likely spawning temperature of cyprinid fish prey, and 25 °C, representing the temperature of estimated maximum consumption in *N. melanostomus*. It was hypothesized that *N. melanostomus* would exhibit elevated FR at 25 °C compared to *P. semilunaris* due to higher temperature optima of the former species (Lee and Johnson 2005; O'Neil 2013).

Methods

Predator acquisition and acclimatization

Western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) and round goby *Neogobius melanostomus* (Pallas, 1814), were collected using a backpack pulsed-DC electrofishing unit (FEG 1500, EFKO, Leutkirch, Germany) in late April 2016 from recent colonized localities: *P. semilunaris* from the Jevišovka River (48º49′27″N; 16º27′59″E) and *N. melanostomus* from the Elbe River (50º39′7″N; 14º2′41″E). Fish were transported to the experimental facility of the Institute of Aquaculture and Protection of Waters, Faculty of Fisheries and Protection of Waters, University of South Bohemia in České Budějovice, Czech Republic. Each of these predator species was distributed between two identical recirculating aquaculture systems (RAS) filled with dechlorinated tap water (20.3 ± 0.1 °C, pH 7.4–7.6, oxygen level > 95% saturation). Size classes of both species were not matched (Table 1). During the 30-day acclimatization period, the temperature was maintained at two levels for both species, 20 °C (20.4 ± 0.3 °C) and 25 °C (24.9 ± 0.3 °C). The latter temperature was reached raising the temperature by 0.1 °C h^{-1} over the first 2 days of the acclimatization period to minimize stress caused by rapid heat change. The oxygen level was > 95% saturation and pH was 7.0–8.0 in both temperature treatments. Temperature, dissolved oxygen, and pH were measured twice daily during the acclimatization period with an HQ40d digital multi-meter (Hach Lange

Table 1. Biometric data of *Neogobius melanostomus* and *Proterorhinus semilunaris* used in experiments at two temperatures. Total length (TL), standard length (SL), and weight (W). Data are presented as mean ± SE. Different letters in particular columns denote significant differences among groups (Kruskal-Wallis, Multiple comparison of mean ranks) at α = 0.05.

Species	Temperature (°C)	n	TL (mm)	SL (mm)	W (g)
Proterorhinus semilunaris	20	48	53.1±1.2 [a]	44.4±1.1 [a]	1.9±0.1 [a]
	25	48	53.0±1.1 [a]	43.4±1.0 [a]	1.9±0.2 [a]
Neogobius melanostomus	20	48	57.3±0.7 [b]	47.8±0.6 [b]	2.1±0.1 [b]
	25	48	57.6±0.7 [b]	48.0±0.6 [b]	2.1±0.1 [ab]

GmbH, Germany). Predators were fed twice daily to satiation with frozen chironomid larvae during acclimatization. Predators were deprived of food for 24 h prior to the start of the experiment to standardize hunger levels.

Prey

Common carp *Cyprinus carpio* Linnaeus, 1758 at the early protopterygiolarval stage (3–4 days post hatching: Balon 1975) were used as prey. This stage was chosen as it represents larva size and behavior of cyprinids (see Osse and van den Boogaart 1995; Çalta 2000), representatives of the major fish communities in many European reservoirs, as well as regulated lowland rivers (Kubečka 1993; Jurajda and Peňáz 1994). Common carp larvae were obtained from artificial reproduction and incubation at the Genetic Fisheries Center, Faculty of Fisheries and Protection of Waters, University of South Bohemia. Newly hatched larvae were distributed into two separate 400 L rectangular tanks filled with dechlorinated tap water (20.2 °C, pH 7.55, oxygen level > 95% saturation). In one tank, temperature level was maintained at 20 °C, whereas in the second one, temperature was gradually increased to 25 °C over 2 days as before. The prey remained unfed to standardize weight. Wet weight of larvae thoroughly wiped with blotting paper was assessed using an XPR10 micro-balance (Mettler-Toledo, LLC, Columbus, US). Thirty groups of 10 specimens were weighed, with mean specimen weight ± SE of 1.89 mg ± 0.29 mg.

Experimental design

Transparent plastic boxes (28.5 × 19 × 7.5 cm; volume 2500 mL) were filled with 2000 mL aged tap water and 200 mL of fine aquarium sand (particle size < 0.3 mm). Two temperature levels were tested, 20 °C and 25 °C. The former represented the temperature of natural reproduction of common carp (Horváth et al. 1984), while the latter is within the reported range in which *N. melanostomus* exhibits maximum consumption rate (23–26 °C; Lee and Johnson 2005). Light was supplied by

overhead LEDs with 12 h light:12 h dark regime and intensity of 500 lux m^{-2}.

Eight prey densities (8, 20, 45, 100, 180, 290, 420, 550 larvae per box) were used. Carp larvae were placed into each box 1 h prior to introduction of predators to allow recovery from handling stress. Each combination of temperature, prey density, and predator treatment was replicated six times (192 boxes with predators). Five control replicates, with no predator, at each combination of prey density and temperature were included to assess background mortality of prey (80 control boxes). Predators were individually and randomly released into boxes with prey. After 24 h predators were removed and placed in a marked box to allow matching to preyed larvae, and the remaining prey were counted to derive those killed during the experiment. Each predator was used only once to avoid bias caused by experience. Total and standard lengths of predators, measured by digital caliper to the nearest 0.01 mm, and weight to the nearest 0.1 g (Kern 572-35, Kern and Sohn, Germany) were recorded after the feeding experiment (Table 1).

Statistical analysis

We employed logistic regression to examine predation rate as a function of prey density and decipher the form of the functional response (FR) in each temperature regime:

$$\frac{N_e}{N_0} = \frac{exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)} \quad (1)$$

where N_e is the number of prey consumed per gram of predator, N_0 is the initial prey density and P_0, P_1, P_2, and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively, estimated by maximum likelihood (Juliano 2001). If $P_1 < 0$, the proportion of prey killed declined monotonically with the initial prey density, indicating a type II FR. If $P_1 > 0$ and $P_2 < 0$, the proportion of prey killed is a unimodal function of prey density, corresponding to a type III FR (Juliano 2001). We used type II Rogers' random

predator equation (Rogers 1972), which accounts for prey depletion, to model all functional responses:

$$N_e = N_0\{1 - exp\,[a\,(N_e h - t)]\} \qquad (2)$$

where N_e is the number of prey consumed per gram of predator, N_0 is the initial prey density, a is predator attack rate classically defined as searching efficiency, h is predator handling time defined as time spent pursuing, subduing, and consuming each prey item plus the time spent preparing to search for the next prey item, and t is the duration of the experiment in days. Owing to the implicit nature of the random predator equation, we used the Lambert W function to solve Equation (2) (for further details see Bolker 2008):

$$N_e = N_0 - \frac{W\{ahN_0\,exp\,[-a\,(t - hN_0)]\}}{ah} \qquad (3)$$

We also tested whether predator a and h values were influenced by temperature and whether a and h values differ among predators within a temperature level. For each test we evaluated four FR models covering all possible combinations of temperature dependence and predator comparison in both FR parameters (Sentis et al. 2015) using the maximum likelihood method implemented in the "bbmle" package (Bolker 2008) and selected the most parsimonious model based on the lowest AICc values (Burnham and Anderson 2002).

Weight-specific maximum feeding rate was derived from the FR models (Dick et al. 2013; Alexander et al. 2014). Bootstrapping was used to generate multiple estimates ($n = 30$) of the parameter of the maximum consumption rate:

$$C_{max} = \frac{1}{hT} \qquad (4)$$

followed by full factorial comparison (*i.e.* "temperature" and "predator species" as explanatory variables) using GLM (due to non-normal data distribution) with quasi-Poisson error distribution and simplification via step-deletion process. Tukey HSD post-hoc tests were employed to assess significant differences among treatment means. All analyses were implemented in R version 3.2.5 (R Core Team 2016).

Results

In all controls, prey survival was > 98% after 24 h, thus mortality was attributed to predation, and data were not corrected for natural mortality.

Functional response

Based on the results of logistic regression, both predators showed type II FR at both temperatures (Linear parameters were negative, and the proportion of fish larvae eaten decreased with increasing prey density, Figure 1, Supplementary material Table S1). Weight-specific predator intake rate increased with prey density, reaching an asymptote corresponding with the maximum number of prey eaten in 24 h.

Attack rate and handling time

Estimates of FR parameters relative to temperature regime and predator species are provided in Table S2. Based on the most parsimonious model, we found neither attack rate (a) nor handling time (h) to significantly differ with temperature within either species (Table 2). In inter-specific comparison, a was found to be marginally higher in *P. semilunaris* at 20 °C (Table 3). Handling time did not differ between species in either temperature regime (Table 3).

Maximum feeding rate

Model selection revealed significant positive interactions among temperature and predators species (Table 4). Weight-specific maximum consumption of *N. melanostomus* at 20 °C and 25 °C and *P. semilunaris* at 20 °C showed no significant difference (mean ± SE: 84.5 ± 1.2; 85.1 ± 1.2 and 82.0 ± 1.1 fish larvae per gram of predator, respectively). At 25 °C, however, *P. semilunaris* maximum feeding rate was significantly lower compared to the other treatments (70.7 ± 1.0 fish larvae per gram of predator; Tukey HSD; Table 5).

Discussion

Many studies have been devoted to the negative impact of *N. melanostomus* (Kornis et al. 2012), whereas *P. semilunaris* has received little attention and only indirect effects are mentioned (Kocovsky et al. 2011). Calculation of Functional Response allows effective assessment and comparison of impacts of invader/native and invader/invader pairings (Dick et al. 2014; Xu et al. 2016). The FR defines the relationship between resource availability (prey density) and consumption pattern (Solomon 1949; Holling 1966) and is an essential component of ecosystem modeling (Petchey et al. 2008). In our study, both predators showed type II FR. The shape of the FR curve corroborated previous findings for *N. melanostomus* (Dubs and Corkum 1996; Fitzsimons et al. 2006) and for other piscine predators (e.g. Alexander et al. 2014); hence type II FR is a common foraging
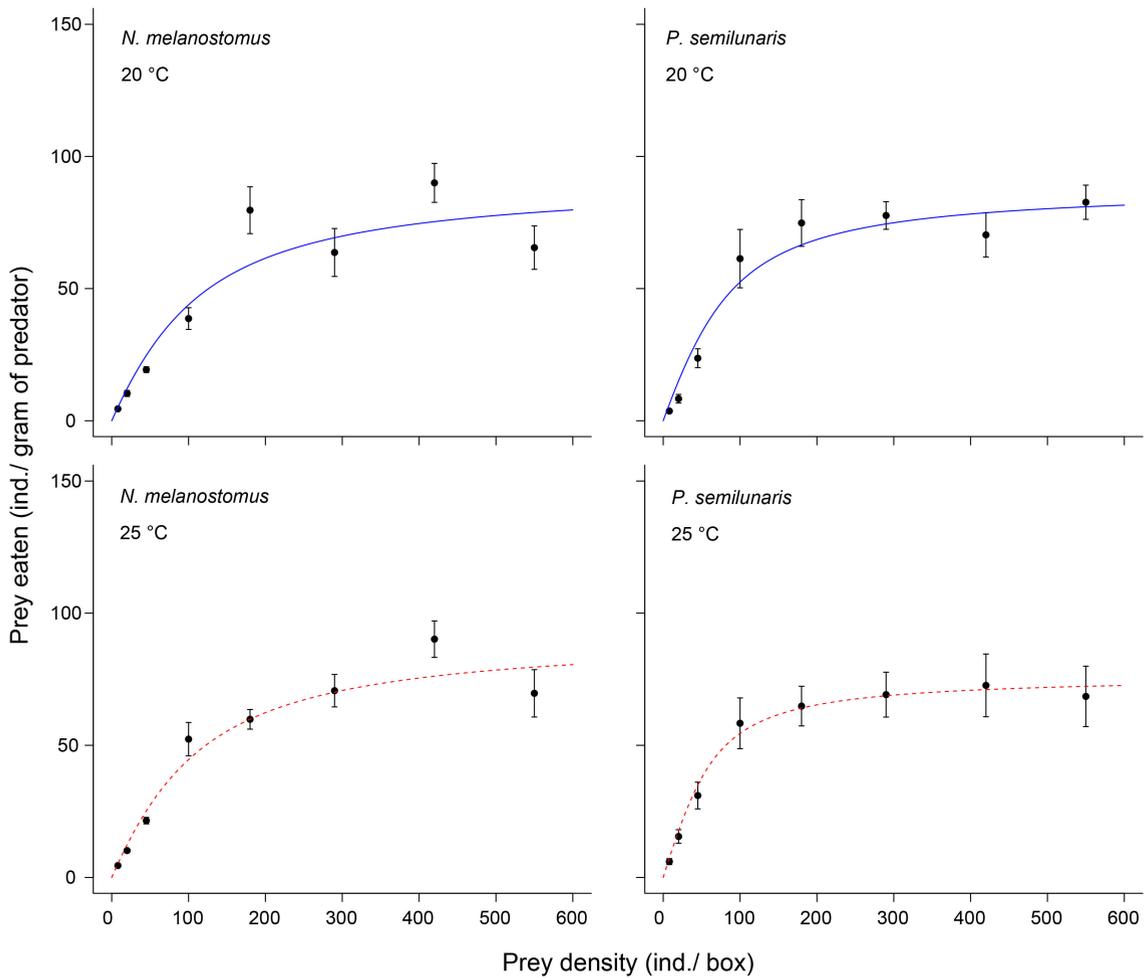
Figure 1. Relationship between prey density and number of prey eaten per gram of predator for *Neogobius melanostomus* and *Proterorhinus semilunaris*. Data are shown as mean ± SE overlaid by the model prediction (blue solid line = 20 °C, red dashed line = 25 °C).

Table 2. Temperature dependency of attack rate (*a*) and handling time (*h*) in *Neogobius melanostomus* and *Proterorhinus semilunaris*; dAICc = difference in AICc value from the most parsimonious model (in bold); *df* = degrees of freedom; weight = Akaike weight.

Model/Species	*Neogobius melanostomus*			*Proterorhinus semilunaris*		
	dAICc	*df*	weight	dAICc	*df*	weight
temperature-independent *a* and *h*	**0.0**	**3**	**0.56**	**0.0**	**3**	**0.37**
h temperature-dependent	2.1	4	0.19	0.1	4	0.35
a temperature-dependent	2.1	4	0.19	1.8	4	0.15
temperature-dependent *a* and *h*	4.4	5	0.06	2.1	5	0.13

Table 3. Comparison of the functional response models of *Neogobius melanostomus* and *Proterorhinus semilunaris* at two temperatures; dAICc = difference in AICc value from the most parsimonious model (in bold); *df* = degrees of freedom; weight = Akaike weight.

Model/Temperature	20 °C			25 °C		
	dAICc	*df*	weight	dAICc	*df*	weight
a and *h* indifferent	0.1	3	0.35	**0.0**	**3**	**0.42**
h different	1.5	4	0.17	1.6	4	0.18
a different	**0.0**	**4**	**0.36**	1.8	4	0.17
a and *h* different	2.2	5	0.12	1.2	5	0.23

pattern for this ecological group. Consequently, both predators may have a destabilizing effect on population dynamics of cyprinids through high prey exploitation at low prey densities, typical for type II FR (Murdoch and Oaten 1975). Although the *P. semilunaris* FR curve showed a steeper gradient, *N. melanostomus* curves reached slightly higher asymptotes at both temperatures.

Temperature is believed to be one of the most important environmental factors influencing predator-prey interactions (Petchey et al. 1999; Brown et al. 2004). Although published data suggest the maximum consumption rate of *N. melanostomus* falls within 23–26 °C, alteration from 20 to 26°C produced only a slight increase (Lee and Johnson 2005). This is consistent with our results, where *N. melanostomus* showed no significant differences between 20 °C and 25 °C in either attack rate or handling time. A similar conclusion is drawn for *P. semilunaris*. Attack and maximum feeding rates of ectotherms are typically characterized by hump-shaped temperature dependency and, while sharing the same temperature optima, attack rate is dynamically affected, both above and below the optimal temperature (Englund et al. 2011). Our results therefore imply that tested temperatures fall within the optima of both predator species, as we observed no significant intraspecific difference in attack rate between 20 °C and 25 °C. On the other hand, South et al. (2017) recorded higher FR curves of invasive lionfish *Pterois volitans* (Linnaeus, 1758) at 26 °C compared to 22 °C, whilst attack rates were similar.

Invasive species are often characterized by a higher maximum feeding rate, higher attack rate, and shorter handling time compared to native or low-impact non-indigenous species (Xu et al. 2016). These trends are apparent in fishes (e.g. Dubs and Corkum 1996) as well as in other aquatic organisms including amphipods (Bollache et al. 2008), crayfish (Renai and Gherardi 2004), and mysids (Dick et al. 2013). Within invader/native comparisons, Alexander et al. (2014) found similar attack rates in benthic dwelling fish species attributed to similar predatory strategies, whereas in pelagic fishes, the native showed an even higher attack rate. In our study, *P. semilunaris* showed a marginally higher attack rate at 20 °C compared to *N. melanostomus* (owing to the slightly higher AICc value), while no difference was observed at 25 °C. In a comparison between non-indigenous *N. melanostomus* and the analogous native predator European bullhead (*Cottus gobio* Linnaeus, 1758), Laverty et al. (2017) found higher FR asymptotes in *N. melanostomus*, indicating lower handling times. In comparing two alien predators, we observed no significant differences in handling time at either tested

Table 4. F and *p* values of the analysis of deviance for effects of temperature and predator species on maximum feeding rate. Bold values represent significant explanatory variables.

	df	F	*p*-value
temperature	1	23.14	**< 0.0001**
predator species	1	58.54	**< 0.0001**
temperature x predator species	1	31.36	**< 0.0001**

Table 5. Weight-specific maximum feeding rate $1/hT$ of *Neogobius melanostomus* (Nm) and *Proterorhinus semilunaris* (Ps) at 20 °C and 25 °C derived from bootstrapping ($n = 30$) and expressed as mean ± SE.

Species	Temperature (°C)	Maximum feeding rate (number of prey eaten/gram of predator) Mean ± SE
Nm	20	84.5 ± 1.2
Ps	20	82.0 ± 1.1
Nm	25	85.1 ± 1.2
Ps	25	70.7 ± 1.0

temperature, suggesting that the *per capita* impact on native communities posed by both predator species is similar, although little attention has yet been given to the impact of *P. semilunaris*. However, introducing Relative Impact Potential (RIP), Dick et al. (2017) suggested that both *per capita* effect (FR) and numerical response (abundance) should be included when estimating invader ecological impact. In general, *P. semilunaris* do not reach as high an abundance as *N. melanostomus* in invaded ecosystems (Dopazo et al. 2008; van Kessel et al. 2016; Janáč et al. 2018), and consequently the former species is no longer considered an important threat to native communities (Borcherding et al. 2011). On the other hand, *P. semilunaris* reaches high densities in shallow macrophyte-rich habitats (Kocovsky et al. 2011), where it can pose serious threat for phytophilic fauna, including cyprind larvae. Interestingly, *N. melanostomus* abundance in nearshore areas is positively correlated with temperature up to 24 °C (Dopazo et al. 2008) and hence, the RIP can be higher under such conditions.

Compared to an analogous native predator *C. gobio*, *N. melanostomus* consumes significantly more prey (Laverty et al. 2017). In laboratory conditions, Ray and Corkum (1997) documented *N. melanostomus* average consumption of 1.02 g of zebra mussel, *Dreissena polymorpha* (Pallas, 1771), wet weight per 24 h in larger specimens (SL 70–84 mm), whereas smaller fish (SL 55–69 mm) consumed ~20% that amount. This finding suggests that juveniles may depend on other food sources, possibly fish larvae or other soft-bodied organisms, rather than hard-shelled mollusks. In our study, the weight-specific maximum feeding rate of fish larvae by *N. melanostomus*

(SL 35–59 mm) showed no difference between the tested temperature regimes. Similar maximum feeding rate was reached by *P. semilunaris* (SL 35–58 mm) at 20 °C. However, at 25 °C, *P. semilunaris* maximum feeding rate was significantly lower compared to the other treatments. These results correspond with the modeled weight-maximum consumption curve of *N. melanostomus*, in which smaller specimens showed a higher weight-specific consumption rate (Lee and Johnson 2005). The model for maximum consumption rate in *P. semilunaris* has not been developed, but, based on our results, we can expect a lower temperature optima of this species, corroborating O'Neil (2013). Based on the seasonal temperature course in a Central European lowland river (River Elbe Board, State Enterprise, unpublished data), the investigated species can potentially reach maximum feeding rate from late May/early June through early October.

Conclusions

Both *N. melanostomus* and *P. semilunaris*, readily consumed cyprinid fish larvae in laboratory conditions. No significant differences in handling time relative to temperature were recorded suggesting a similar *per capita* impact on native communities. Considering the large numbers of fish larvae consumed by both studied species, the pelagic lifestyle of juveniles (Jůza et al. 2015), and abundance in invaded water bodies (van Kessel et al. 2016), the impact on native fish populations by their direct predation may be considerable. The higher maximum feeding rate of *N. melanostomus* at 25 °C compared to *P. semilunaris* indicates higher temperature optima of the former species. Further studies are needed to investigate multiple predator effects of *N. melanostomus* and *P. semilunaris*, as they are often recorded sympatrically (van Kessel et al. 2016) and thus interact with one another (Johnson et al. 2009; Wasserman et al. 2016). Despite significant differences in predator sizes between treatments, we believe that such minor differences are not biologically relevant. Yet, size-matching of tested species should be considered in future experiments to avoid these biases.

Acknowledgements

References

Alexander ME, Dick JTA, Weyl OLF, Robinson TB, Richardson DM (2014) Existing and emerging high impact invasive species are characterized by higher functional responses than natives. *Biology Letters* 10: 20130946, https://doi.org/10.1098/rsbl.2013.0946

Almqvist G, Strandmark AK, Appelberg M (2010) Has the invasive round goby caused new links in Baltic food webs? *Environmental Biology of Fishes* 89: 79–93, https://doi.org/10.1007/s10641-010-9692-z

Balon EK (1975) Terminology of intervals in fish development. *Journal of the Fisheries Research Board of Canada* 32: 1663–1670, https://doi.org/10.1139/f75-196

Balshine S, Verma A, Chant V, Theysmeyer T (2005) Competitive interactions between round gobies and logperch. *Journal of Great Lakes Research* 31: 68–77, https://doi.org/10.1016/S0380-1330(05)70238-0

Bax N (1998) The significance and prediction of predation in marine fisheries. *ICES Journal of Marine Science* 55: 997–1030, https://doi.org/10.1006/jmsc.1998.0350

Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinction and mammalian introductions on oceanic islands. *Science* 305: 1955–1958, https://doi.org/10.1126/science.1101617

Błońska D, Kobak J, Grabowska J (2016) Shelter competition between the invasive western tubenose goby and the native stone loach is mediated by sex. *Journal of Limnology* 76: 221–229, https://doi.org/10.4081/jlimnol.2016.1557

Bolker BM (2008) Ecological Models and Data in R. Princeton University Press, Princeton, USA, 396 pp

Bollache L, Dick JTA, Farnsworth KD, Montgomery WI (2008) Comparison of the functional responses of invasive and native amphipods. *Biology Letters* 4: 166–169, https://doi.org/10.1098/rsbl.2007.0554

Borcherding J, Staas S, Krüger S, Ondračková M, Šlapanský L, Jurajda P (2011) Non-native Gobiid species in the lower River Rhine (Germany): Recent range extensions and densities. *Journal of Applied Ichthyology* 27: 153–155, https://doi.org/10.1111/j.1439-0426.2010.01662.x

Brandner J, Auerswald K, Cerwenka AF, Schliewen UK, Geist J (2013) Comparative feeding ecology of invasive Ponto-Caspian gobies. *Hydrobiologia* 703: 113–131, https://doi.org/10.1007/s10750-012-1349-9

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789, https://doi.org/10.1890/03-9000

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, USA, 488 pp

Çalta M (2000) Morphological development and growth of chub, *Leuciscus cephalus* (L.), larvae. *Journal of Applied Ichthyology* 16: 83–85, https://doi.org/10.1046/j.1439-0426.2000.00164.x

Clavero M, Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution* 20: 110–110, https://doi.org/10.1016/j.tree.2005.01.003

Dick JTA, Gallagher K, Avlijas S, Clarke HC, Lewis SE, Leung S, Minchin D, Caffrey J, Alexander ME, Maguire C, Harrod C, Reid N, Haddaway NR, Farnsworth KD, Penk M, Ricciardi A (2013) Ecological impacts of an invasive predator explained and predicted by comparative functional responses. *Biological Invasions* 15: 837–846, https://doi.org/10.1007/s10530-012-0332-8

Dick JTA, Alexander ME, Jeschke JM, Ricciardi A, MacIsaac HJ, Robinson TB, Kumschick S, Weyl OLF, Dunn AM, Hatcher MJ, Paterson RA, Farnsworth KD, Richardson DM (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions* 16: 735–753, https://doi.org/10.1007/s10530-013-0550-8

Dick JTA, Laverty C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Robert Britton J, Medoc V, Boets P, Alexander ME, Taylor NG,

Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OLF, Lucy FE, Banks PB, Dodd JA, MacNeil C, Penk MR, Aldridge DC, Caffrey JM (2017) Invader Relative Impact Potential: A new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *Journal of Applied Ecology* 54: 1259–1267, https://doi.org/10.1111/1365-2664.12849

Dopazo SN, Corkum LD, Mandrak NE (2008) Fish assemblages and environmental variables associated with gobiids in nearshore areas of the lower Great Lakes. *Journal of Great Lakes Research* 34: 450–460, https://doi.org/10.3394/0380-1330(2008)34[450:FAAEVA]2.0.CO;2

Dubs DOL, Corkum LD (1996) Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). *Journal of Great Lakes Research* 22: 838–844, https://doi.org/10.1016/S0380-1330(96)71005-5

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 41: 59–80, https://doi.org/10.1146/annurev-ecolsys-102209-144650

Englund G, Öhlund G, Hein CL, Diehl S (2011) Temperature dependence of the functional response. *Ecology Letters* 14: 914–921, https://doi.org/10.1111/j.1461-0248.2011.01661.x

Fitzsimons J, Williston B, Williston G, Bravener G, Jonas JL, Claramunt RM, Marsden JE, Ellrott BJ (2006) Laboratory estimates of salmonine egg predation by round gobies (*Neogobius melanostomus*), sculpins (*Cottus cognatus* and *C. bairdi*), and crayfish (*Orconectes propinquus*). *Journal of Great Lakes Research* 32: 227–241, https://doi.org/10.3394/0380-1330(2006)32[227:LEOSEP]2.0.CO;2

French JRP, Jude DJ (2001) Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. *Journal of Great Lakes Research* 27: 300–311, https://doi.org/10.1016/S0380-1330(01)70645-4

Holling CS (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist* 91: 293–320, https://doi.org/10.4039/Ent91293-5

Holling CS (1966) The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* 98: 5–86, https://doi.org/10.4039/entm9848fv

Hôrková K, Kováč V (2014) Different life-histories of native and invasive *Neogobius melanostomus* and the possible role of phenotypic plasticity in the species' invasion success. *Knowledge and Management of Aquatic Ecosystems* 412: 01, https://doi.org/10.1051/kmae/2013081

Horváth L, Tamás G, Tölg I, Halver JE (1984) Special Methods in Pond Fish Husbandry. Akadémiai Kiadó, Budapest, Hungary, 147 pp

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalisation. *Journal of Applied Ecology* 46: 10–18, https://doi.org/10.1111/j.1365-2664.2008.01600.x

Janáč M, Valová Z, Jurajda P (2012) Range expansion and habitat preferences of non-native 0+tubenose goby (*Proterorhinus semilunaris*) in two lowland rivers in the Danube basin. *Fundamental and Applied Limnology* 181: 73–85, https://doi.org/10.1127/1863-9135/2012/0321

Janáč M, Roche K, Šlapanský L, Polačik M, Jurajda P (2018) Long-term monitoring of native bullhead and invasive gobiids in the Danubian rip-rap zone. *Hydrobiologia* 807: 263–275, https://doi.org/10.1007/s10750-017-3398-6

Janssen J, Jude DJ (2001) Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. *Journal of Great Lakes Research* 27: 319–328, https://doi.org/10.1016/S0380-1330(01)70647-8

Johnson PTJ, Olden JD, Solomon CT, Vander Zanden MJ (2009) Interactions among invaders: Community and ecosystem effects of multiple invasive species in an experimental aquatic system. *Oecologia* 159: 161–170, https://doi.org/10.1007/s00442-008-1176-x

Juliano SA (2001) Nonlinear curve fitting: Predation and functional response curve. In: Scheiner SM, Gurevitch J (eds), Design and Analysis of Ecological Experiments, 2nd edn. Oxford University Press, New York, USA, pp 178–196

Jurajda P, Peňáz M (1994) Fish community of the lower regulated stretch of the River Morava, Czech Republic. *Folia Zoologica* 43: 57–64

Jůza T, Zemanová J, Tušer M, Sajdlová Z, Baran R, Vašek M, Ricard D, Blabolil P, Wagenvoort AJ, Ketelaars HAM, Kubečka J (2015) Pelagic occurrence and diet of invasive round goby *Neogobius melanostomus* (Actinopterygii, Gobiidae) juveniles in deep well-mixed European reservoirs. *Hydrobiologia* 768: 197–209, https://doi.org/10.1007/s10750-015-2548-y

Kocovsky PM, Tallman JA, Jude DJ, Murphy DM, Brown JE, Stepien CA (2011) Expansion of tubenose gobies *Proterorhinus semilunaris* into western Lake Erie and potential effects on native species. *Biological Invasions* 13: 2775–2784, https://doi.org/10.1007/s10530-011-9962-5

Kornis MS, Mercado-Silva N, Vander Zanden MJ (2012) Twenty years of invasion: A review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology* 80: 235–285, https://doi.org/10.1111/j.1095-8649.2011.03157.x

Krakowiak PJ, Pennuto CM (2008) Fish and macroinvertebrate communities in tributary streams of eastern Lake Erie with and without round gobies (*Neogobius melanostomus*, Pallas 1814). *Journal of Great Lakes Research* 34: 675–689, https://doi.org/10.1016/S0380-1330(08)71610-1

Kubečka J (1993) Succession of fish communities in reservoirs of Central and Eastern Europe. In: Straškraba M, Tundisi JG, Duncan A (eds), Comparative Reservoir Limnology and Water Quality Management. Springer, Dordrecht, Netherland, pp 153–168, https://doi.org/10.1007/978-94-017-1096-1_11

Laverty C, Green KD, Dick JTA, Barrios-O'Neill D, Mensink PJ, Médoc V, Spataro T, Caffrey JM, Lucy FE, Boets P, Britton JR, Pegg J, Gallagher C (2017) Assessing the ecological impacts of invasive species based on their functional responses and abundances. *Biological Invasions* 19: 1653–1665, https://doi.org/10.1007/s10530-017-1378-4

Lee VA, Johnson TB (2005) Development of a bioenergetics model for the round goby (*Neogobius melanostomus*). *Journal of Great Lakes Research* 31: 125–134, https://doi.org/10.1016/S0380-1330(05)70244-6

MacInnis AJ, Corkum LD (2000) Age and growth of round goby *Neogobius melanostomus* in the Upper Detroit River. *Transactions of the American Fisheries Society* 129: 852–858, https://doi.org/10.1577/1548-8659(2000)129<0852:AAGORG>2.3.CO;2

Mazza G, Tricarico E, Genovesi P, Gherardi F (2014) Biological invaders are threats to human health: An overview. *Ethology, Ecology and Evolution* 26: 112–129, https://doi.org/10.1080/03949370.2013.863225

Moorhouse TP, Macdonald DW (2015) Are invasives worse in freshwater than terrestrial ecosystems? *Wiley Interdisciplinary Reviews: Water* 2: 1–8, https://doi.org/10.1002/wat2.1059

Moskal'kova KI (1996) Ecological and morphophysiological prerequisites to range extension in the round goby *Neogobius melanostomus* under conditions of anthropogenic pollution. *Journal of Ichthyology* 36: 584–590

Murdoch WW, Oaten A (1975) Predation and population stability. *Advances in Ecological Research* 9: 1–131, https://doi.org/10.1016/S0065-2504(08)60288-3

O'Neil JA (2013) Determination of standard and field metabolic rates in two Great Lakes invading fish species: Round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus semilunaris*). M.Sc. Thesis, Universty of Windsor, Windsor, Ontario, Canada, 109 pp

Osse JWM, van den Boogaart JGM (1995) Fish larvae, development, allometric growth, and the aquatic environment. *ICES Marine Science Symposia* 201: 21–34

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, David Cooper H, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for global biodiversity in the 21st century. *Science* 330: 1496–1501, https://doi.org/10.1126/science.1196624

Petchey OL, Beckerman AP, Riede JO, Warren PH (2008) Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences* 105: 4191–4196, https://doi.org/10.1073/pnas.0710672105

Petchey OL, Brose U, Rall BC (2010) Predicting the effects of temperature on food web connectance. *Philosophical Transactions of the Royal Society B-Biological Sciences* 365: 2081–2091, https://doi.org/10.1098/rstb.2010.0011

Petchey OL, McPhearson PT, Casey TM, Morin PJ (1999) Environmental warming alters food-web structure and ecosystem function. *Nature* 402: 69–72, https://doi.org/10.1038/47023

Pimentel D, McNair S, Janecka J, Wightman J, Simmonds C, O'Connell C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems & Environment* 84: 1–20, https://doi.org/10.1016/S0167-8809(00)00178-X

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria. http://www.R-project.org

Ray WJ, Corkum LD (1997) Predation of zebra mussels by round gobies, *Neogobius melanostomus*. *Environmental Biology of Fishes* 50: 267–273, https://doi.org/10.1023/A:1007379220052

Ray WJ, Corkum LD (2001) Habitat and site affinity of the round goby. *Journal of Great Lakes Research* 27: 329–334, https://doi.org/10.1016/S0380-1330(01)70648-X

Renai B, Gherardi F (2004) Predatory efficiency of crayfish: Comparison between indigenous and non-indigenous species. *Biological Invasions* 6: 89–99, https://doi.org/10.1023/B:BINV.0000010126.94675.50

Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305: 1609–1612, https://doi.org/10.1126/science.1100958

Rogers D (1972) Random search and insect population models. *Journal of Animal Ecology* 41: 369–383, https://doi.org/10.2307/3474

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435, https://doi.org/10.1038/ncomms14435

Sentis A, Ramon-Portugal F, Brodeur J, Hemptinne J-L (2015) The smell of change: Warming affects species interactions mediated by chemical information. *Global Change Biology* 21: 3586–3594, https://doi.org/10.1111/gcb.12932

Schulte PM, Healy TM, Fangue NA (2011) Thermal performance curves, phenotypic plasticity and the time scales of temperature exposure. *Integrative and comparative biology* 51: 691–702, https://doi.org/10.1093/icb/icr097

Skóra KE, Rzeznik J (2001) Observations on diet composition of *Neogobius melanostomus* Pallas 1811 (Gobiidae, Pisces) in the Gulf of Gdansk (Baltic Sea). *Journal of Great Lakes Research* 27: 290–299, https://doi.org/10.1016/S0380-1330(01)70644-2

Solomon ME (1949) The natural control of animal populations. *Journal of Animal Ecology* 18: 1–35, https://doi.org/10.2307/1578

South J, Dick JTA., McCard M, Barrios-O'Neill D, Anton A (2017) Predicting predatory impact of juvenile invasive lionfish (*Pterois volitans*) on a crustacean prey using functional response analysis: Effects of temperature, habitat complexity and light regimes. *Environmental Biology of Fishes* 100: 1155–1165, https://doi.org/10.1007/s10641-017-0633-y

Thompson HA, Simon TP (2014) Diet shift response in round goby, *Neogobius melanostomus*, based on size, sex, depth, and habitat in the western basin of Lake Erie. *Journal of Applied Ichthyology* 30: 955–961, https://doi.org/10.1111/jai.12441

Valová Z, Konečná M, Janáč M, Jurajda P (2015) Population and reproductive characteristics of a non-native western tubenose goby (*Proterorhinus semilunaris*) population unaffected by gobiid competitors. *Aquatic Invasions* 10: 57–68, https://doi.org/10.3391/ai.2015.10.1.06

van Kessel N, Dorenbosch M, Kranenbarg J, van der Velde G, Leuven RSEW (2016) Invasive Ponto-Caspian gobies rapidly reduce the abundance of protected native bullhead. *Aquatic Invasions* 11: 179–188, https://doi.org/10.3391/ai.2016.11.2.07

Vašek M, Všetičková L, Roche K, Jurajda P (2014) Diet of two invading gobiid species (*Proterorhinus semilunaris* and *Neogobius melanostomus*) during the breeding and hatching season: No field evidence of extensive predation on fish eggs and fry. *Limnologica* 46: 31–36, https://doi.org/10.1016/j.limno.2013.11.003

Všetičková L, Janáč M, Vašek M, Roche K, Jurajda P (2014) Non-native western tubenose gobies *Proterorhinus semilunaris* show distinct site, sex and age-related differences in diet. *Knowledge and Management of Aquatic Ecosystems* 414: 10, https://doi.org/10.1051/kmae/2014022

Wasserman RJ, Alexander ME, Dalu T, Ellender BR, Kaiser H, Weyl OLF (2016) Using functional responses to quantify interaction effects among predators. *Functional Ecology* 30: 1988–1998, https://doi.org/10.1111/1365-2435.12682

Xu M, Mu X, Dick JTA, Fang M, Gu D, Luo D, Zhang J, Luo J, Hu Y (2016) Comparative functional responses predict the invasiveness and ecological impacts of alien herbivorous snails. *PLoS ONE* 11: e0147017, https://doi.org/10.1371/journal.pone.0147017

Supplementary material

The following supplementary material is available for this article:

Table S1. Logistic regression parameters of the proportion of prey eaten per gram of predator in *Neogobius melanostomus* and *Proterorhinus semilunaris* at 20 and 25 °C.

Table S2. *Neogobius melanostomus* and *Proterorhinus semilunaris* weight-specific attack rate and handling time at 20 and 25 °C.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Gebauer_etal_SupplementaryTables.xlsx