

## Research Article

# Size-dependent functional response of the round goby *Neogobius melanostomus*; implications for more accurate impact potential calculation

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## Abstract

Abundance and per-capita foraging efficiency are essential factors for predicting and quantifying an invasive predator impact on prey, i.e., the impact potential (IP). However, population structure is not included in the calculation, and IP accuracy might be improved by incorporating predator body size. The population structure of the round goby *Neogobius melanostomus*, a highly invasive predator, was surveyed in the Elbe River. We determined the functional response (FR, per capita foraging) of the three most abundant size classes of *N. melanostomus* on the water louse *Asellus aquaticus*. We then calculated the IP for each size class and for the entire population with (the actual impact potential –  $IP_A$ ) and without (the impact potential for limit size range –  $IP_{LSR}$ ) population body size structure (based on FR of the medium size class). All three size classes of the predator showed type II FR with respect to *A. aquaticus*. The estimated FR parameters, attack rate and handling time, as well as the maximum feeding rate, were size dependent. Despite the lowest per capita foraging efficiency, small individuals displayed the highest IP among the tested size classes because of their high abundance. Conversely, medium and large individuals, although showing highest per capita foraging efficiency, displayed lower IP. Hence,  $IP_A$  showed more precise IP calculations compared to  $IP_{LSR}$ . Overestimation of the potential impact as a consequence of omitting predator population size structure was negligible at the investigated locality. The IP of the *N. melanostomus* population five years post-invasion can be accurately calculated based on the FR of medium-sized fish.

**Key words:** *Asellus aquaticus*, biological invasion, ecological impact, foraging efficiency, invasive species, risk assessment

## Introduction

The continuing homogenization of freshwater ecosystems facilitates the establishment and spread of aquatic invasive species (Baur and Schmidlin 2007), frequently cited as a major cause of biodiversity loss and disturbance of food webs (Andersen

et al. 2004; Henseler et al. 2021; Carvalho et al. 2022). The recent surge in reports of non-native species (Baur and Schmidlin 2007; Rocha et al. 2023) indicates an urgent need for quantification of the ecological impact of existing, emerging, and potentially invasive species to facilitate the focus of management efforts on the most prominent invaders (Dick et al. 2014). Invasive species are often more effective foragers than analogous native species (Dick et al. 2002; Dick et al. 2013; Dick et al. 2014). Comparative functional response (FR), i.e., predator efficiency in prey utilization (Holling 1959), represents a fundamental tool in the study of invasion ecology (Alexander et al. 2014; Xu et al. 2016; Thorp et al. 2018; Gebauer et al. 2019). Comparative FR has been used to analyse the per capita foraging efficiency among predators of different origins or characteristics (Laverly et al. 2017; Gebauer et al. 2018; Howard et al. 2018; Gebauer et al. 2019). The higher predation rate of an invader is crucial but not the only predictor of negative impact (Parker et al. 1999). In addition to the per capita effect, factors such as abundance, reproduction parameters (Parker et al. 1999; Dickey et al. 2018), and environmental variables (Dick et al. 2014) contribute to overall predator ecological impact.

Although robust comparative FR includes a range of environmental variables such as dissolved oxygen concentration (Dickey et al. 2021), temperature (Xu et al. 2016; Gebauer et al. 2018), and habitat complexity (Gebauer et al. 2018), invader abundance has been overlooked. Dick et al. (2017) recently developed an Impact Potential (IP) scale that combines abundance with the per capita impact of a predator, while Relative Impact Potential (RIP) enables comparing IP of two or more species/size classes/environmental variables. Moreover, both metrics preserve robustness to be fit for predators or plants (Dickey et al. 2020). Although abundance is a meaningful measure, the population size structure, i.e., relative abundance of size classes, might expand the informative value of the IP assessment. Fish body size influences foraging capacity (Mittelbach 1981; De Roos et al. 2003), bioenergy needs (Weitz and Levin 2006), and food preferences (Mittelbach 1981). Generally, per capita foraging efficiency increases with body size (Rudolf 2012), as large predators can ingest larger prey, for higher energy gain and can select prey from a broader diet niche (Werner 1974; Paradis et al. 1996). Smaller predators can display higher foraging efficiency towards small motile prey (Aljetlawi et al. 2004) that can be difficult to handle or provide insufficient energy for a large predator (Costa 2009). Additionally, small predators are generally more abundant (Cohen et al. 2003; Woodward and Hildrew 2005). Hence including population structure in the IP calculation might provide a more accurate prediction of novel predator-prey interaction dynamics and their consequences in freshwater communities, essential information for invasion management (Olden and Poff 2004).

The highly invasive benthic fish *Neogobius melanostomus* has proliferated in many European rivers and the Great Lakes of North America (Kornis et al. 2012). Its establishment is accompanied by competition for food (French and Jude 2001; Ustups et al. 2016; Herlevi et al. 2018) and space with native species (Greenberg et al. 1995; Dubs and Corkum 1996) and by a decrease in, or change of, entire macrozoobenthic assemblages (Lederer et al. 2008; Mikl et al. 2017; Pennuto et al. 2018). *Neogobius melanostomus* is highly fecund (Charlebois et al. 1997) and lays eggs several times a year. Hence, multiple age classes are usually present in an invaded site. Although small specimens prefer zooplankton (Števove and Kováč 2016; Olson and Janssen 2017), larger individuals are voracious and adaptable feeders, and the dietary composition usually reflects prey available in the locality (Dashinov and Uzunova 2020), with some prey overlap among size classes (Števove and Kováč 2016).

Comparing the FR of different size classes/population structure of *N. melanostomus* can enable accurate prediction of invasive predator impact on their potential prey in the colonized regions. Since we assume that both the parameters and type of functional response could be size-dependent in fish, similarly in the African clawed frog (Thorp et al. 2018). Indeed, quantifying the impact potential of an invasive species population based on the per capita consumption rate of only one size class can result in a misestimation of impact potential concerning the prey utilization and abundance of other size classes. We aim to uncover predator body size relevance in comparative functional response and regarding that more reliable calculation of an impact potential on an example of invasive fish species *N. melanostomus*.

## Materials and methods

On 14.7.2020, the field survey and *N. melanostomus* collection took place in the Elbe River (Czech Republic; 50.6540922N, 14.0439108E) using a backpack pulsed-DC electrofishing unit (FEG 1500, EFKO, Leutkirch, Germany) and zig-zag wading in the near-shore water (length = 100 m, width = 4 m, area = 400 m<sup>2</sup>) with stony bottom not blocked by any nets, which is heavily populated by *N. melanostomus*. For assessment of predator IP, the captured fish were divided into three size classes: small [wet weight (WW) = 2.25–4.24 g], medium (WW = 4.25–6.24 g), and large (WW = 6.25–10.25 g). The abundance of each predator size class per square meter of the near-shore water to a distance 4 m from the bank was calculated.

The predators were transported to the Institute of Aquaculture and Protection of Waters, Faculty of Fisheries and Protection of Waters, University of South Bohemia in České Budějovice, Czech Republic. Before the experiment, *N. melanostomus* were held in a recirculating aquaculture system (1600 l) for 28 days of acclimatization. Predators were fed *ad-libitum* with frozen *Chironomus* sp. larvae.

We used *Asellus aquaticus* as prey, a principal crustacean dietary item of *N. melanostomus* in the field (Vašek et al. 2014). Large crustaceans are a key component of diet for several size classes of *N. melanostomus* (Števoňová and Kováč 2016). *Asellus aquaticus* were collected with hand nets from submerged vegetation around banks in Kyselá voda stream (49.0195475N, 14.4640344E) and kept in a 200 l tank with aeration and organic substrate collected from the same site.

## Experimental design

Per capita foraging efficiency and capacity to utilize *A. aquaticus* were investigated in three size classes of *N. melanostomus*: small (WW = 3.0–3.5 g; SL = 59.2±2.0 mm), medium (5.0–5.5 g; 69.6±1.2 mm), and large (8.0–8.5 g; 79.1±1.9 mm). We used six prey densities, each in five replications (2, 8, 20, 35, 60, and 90 individuals per experimental arena) with an individual body weight of 6.5±2.7 mg WW. The experiment was conducted in plastic boxes (295 × 185 × 155 mm) with aeration filled with 5000 ml dechlorinated tap water and 200 ml fine aquarium sand (particle size < 0.3 mm). The temperature was maintained at 21.1±0.3 °C with a light regime of 12 h:12 h dark:light (light intensity 500 lux). *Neogobius melanostomus* were starved for 24 hours before the experiment. The prey was placed in the experimental arena 30 minutes before the predator. Control conditions with no predator were replicated five times at each prey density to assess baseline mortality. After 24 h, the number of eaten, killed, and still living *A. aquaticus* were counted, where still living and partially eaten individuals were counted to calculation consumed prey.

## Data analysis

Based on Juliano (2001), we fitted the logistic regression to proportional consumption data to determine the FR type of each size class. Type III FR is designated as a significantly positive first-order term, while a significantly negative first-order term defines type II FR. We subsequently used Rogers' random predator equation, commonly used to describe type II FR in an experimental design without replacement of consumed prey:

$$N_e = N_0 - (1 - \exp(a(N_e h - T))) \quad \text{Eq.1}$$

where  $N_e$  is the quantity of eaten prey,  $N_0$  is initial prey density,  $a$  is attack rate,  $h$  is handling time, and  $T$  is the total time of prey exposure to predator (Rogers 1972). Since Rogers' equation has eaten prey ( $N_e$ ) on both sides, the Lambert W function was necessary for solution (Bolker 2008):

$$N_e = N_0 - \frac{W\{ahN_0 \exp[-a(T-hN_0)]\}}{ah} \quad \text{Eq.2}$$

The FR parameters ( $a$  and  $h$ ) for each size class were estimated using non-linear least-squares regression and the Lambert W function of the package `emdbook` (Bolker 2008). Finally, we determined a maximum feeding rate ( $C = 1/hT$ ) for each size class. Differences in FR parameters and maximum feeding rates among size classes were determined using the 95% confidence interval (CI) overlaps. Where 95% CIs was calculated from the standard error associated with the values of each functional response parameter (Sentis et al. 2013). The results were not corrected for non-consumptive mortality since it was in range from 0 to 2.2% in all experimental arenas. With respect to survival rate higher than 98% (98.3–100.0%) in all control treatments after 24 h, the mortality in experimental arenas was attributed exclusively to the predator presence thus datasets were not adjusted for natural mortality. Statistical analyses were calculated in R v. 3.4.4 (R Development Core Team 2018).

Subsequently, we combined the maximum feeding rate and field abundance data to calculate the IP for limited size range ( $IP_{LSR}$ ) based on the following equation:

$$IP_{LSR} = C \times AB \quad \text{Eq.3}$$

where  $AB$  is the abundance of predators in the locality and  $C$  is the maximum feeding rate. Since the maximum feeding rate of only one predator size class is commonly used in IP calculation of an entire predator population (Dick et al. 2017; Laverty et al. 2017; Dickey et al. 2018), we chose the maximum feeding rate of the medium size class to calculate  $IP_{LSR}$ . We then calculated IP using maximum feeding rate and abundance of each size class obtained during the field survey ( $IP_s$ ,  $IP_M$ , and  $IP_L$ ) and, subsequently, the actual IP ( $IP_A$ ) using the following formula:

$$IP_A = (C_{small} \times AB_{small}) + (C_{medium} \times AB_{medium}) + (C_{large} \times AB_{large}) \quad \text{Eq.4}$$

We compared the two measures using the RIP (Dick et al. 2017) based on following formula:

$$RIP = \frac{IP_A}{IP_{LSR}} \quad \text{Eq.5}$$

where  $RIP = 1$  reflects an equal impact of both populations, while  $RIP < 1$  reflects a higher impact of the population with  $IP_A$ . An  $RIP > 1$  signifies a higher impact of population on prey with  $IP_{LSR}$ .

## Results

### Functional response

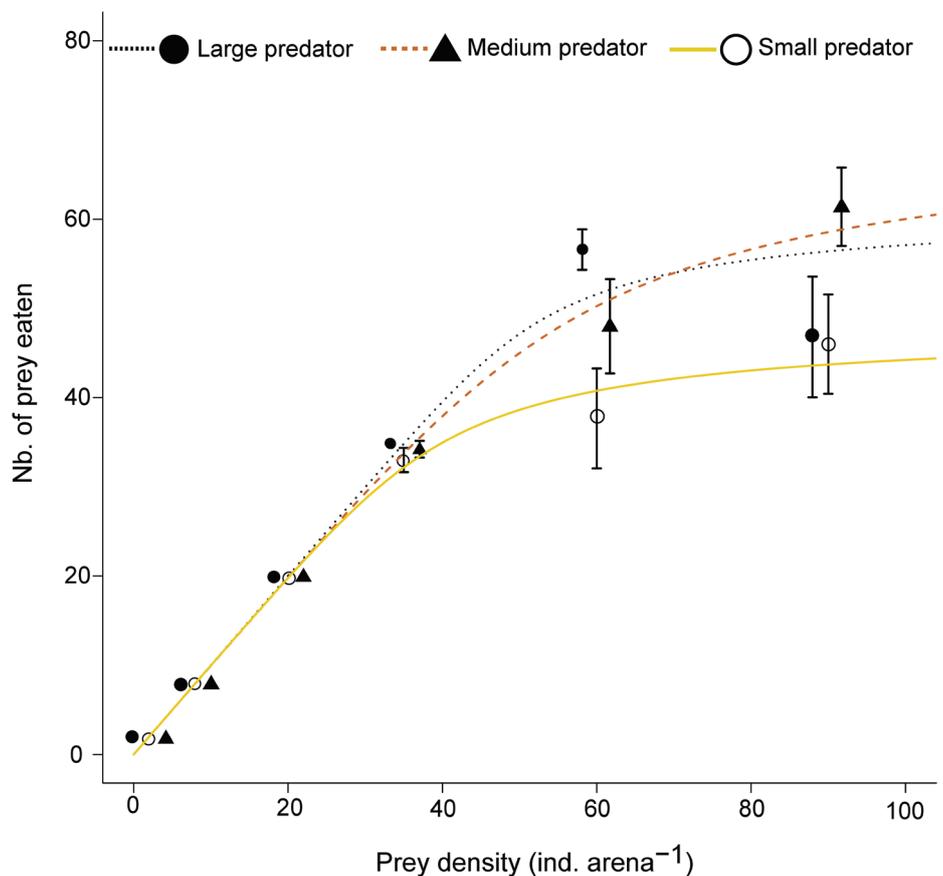
All tested size classes of *N. melanostomus* displayed negative first-order terms of logistic regression (Table 1). The proportion of consumed prey declined with increasing prey density. Thus, all size classes displayed type II FR towards *A. aquaticus*. The FR curve of small individuals showed the lowest magnitude (Fig. 1).

### Attack rate, handling time, and maximum feeding rate

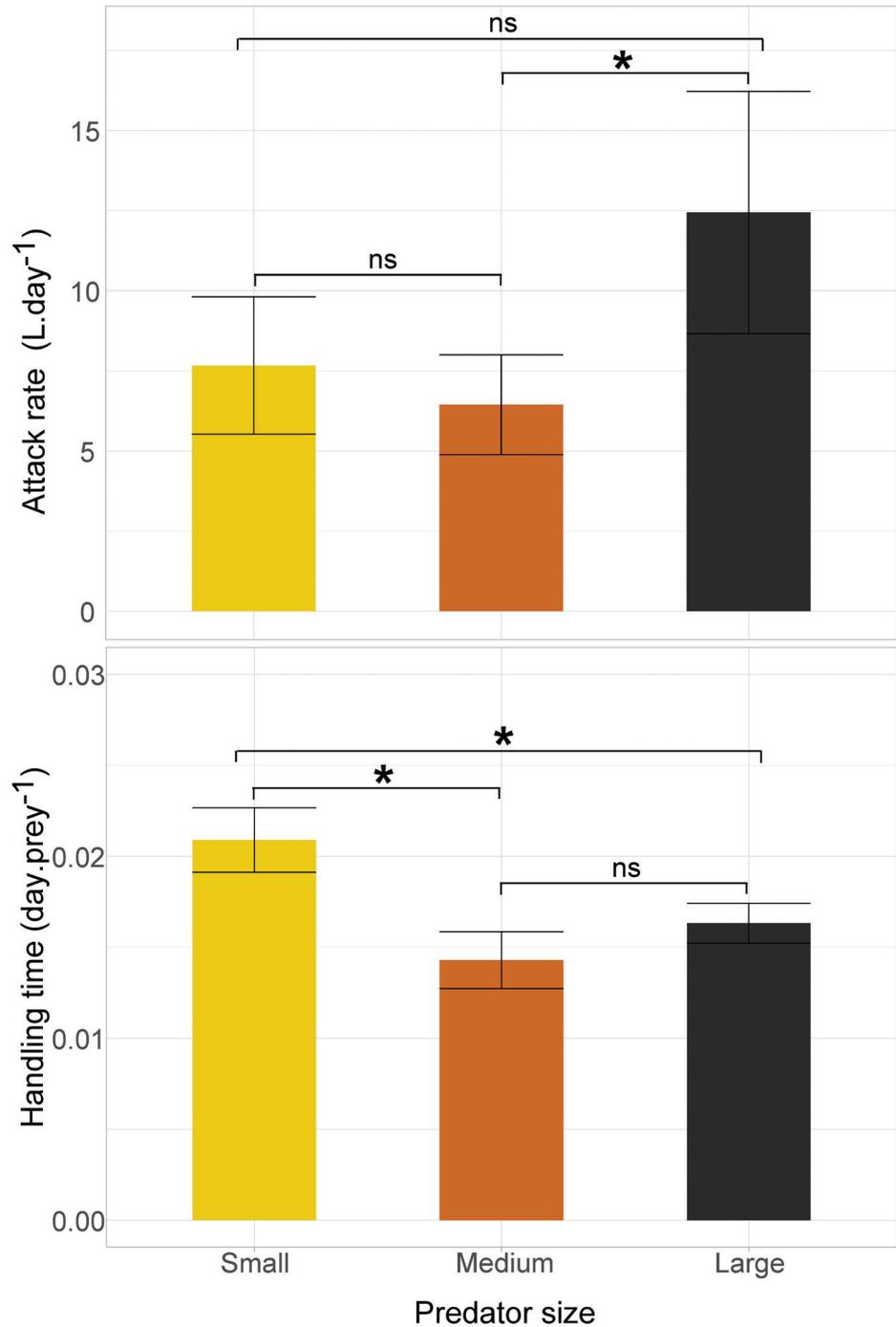
Estimated attack rates and handling time with 95% CI for each size class of *N. melanostomus* are presented in Fig. 2. Both handling time and attack rate were size-dependent. Large *N. melanostomus* individuals showed the highest attack rate, followed by that of small individuals without significant difference. The medium-sized individuals exhibited the lowest attack rate, significantly

**Table 1.** Linear coefficient  $P_1$  of logistic regression in predator *Neogobius melanostomus* relative to body size class.

Size class	Linear coefficient $P_1$	SE	p-value
Small	-1.434	0.425	$<10^{-3}$
Medium	-0.882	0.363	0.015
Large	-1.083	0.438	0.013

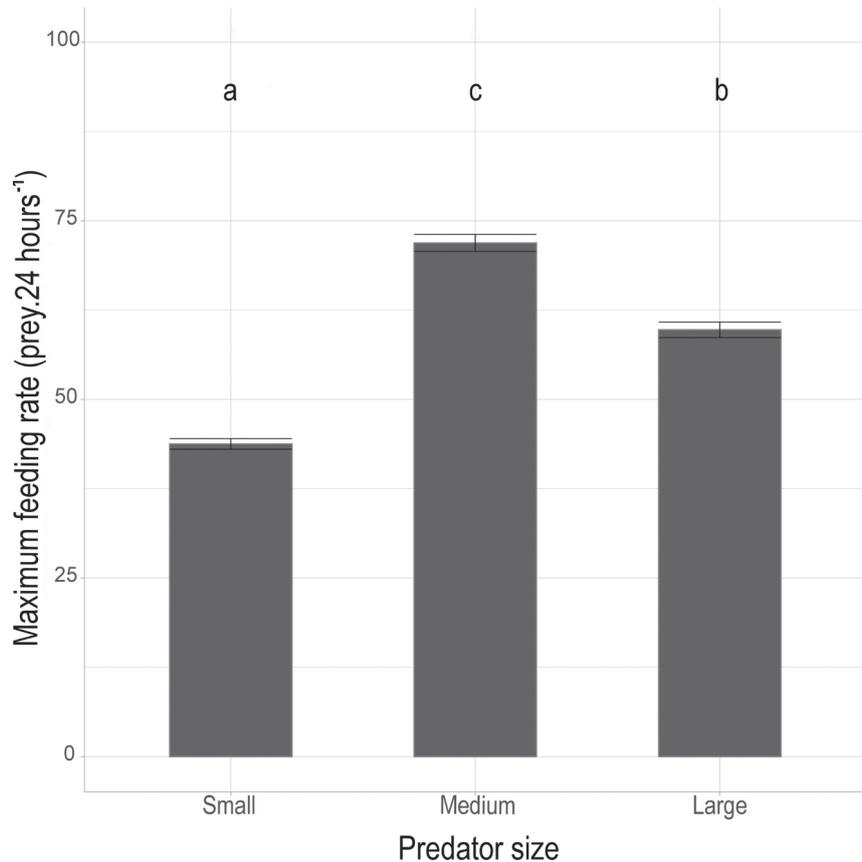


**Figure 1.** Functional response (mean  $\pm$  SE) of three size classes of *Neogobius melanostomus* preying upon *Asellus aquaticus*.



**Figure 2.** Attack rate and handling time (error bars denote 95% confidence intervals) of three size classes of *Neogobius melanostomus* preying upon *Asellus aquaticus*. Asterisks denote significant ( $p < 0.05$ ) differences.

lower than that of large individuals. The shortest handling time was observed in medium-sized *N. melanostomus*, followed by large individuals. Small individuals displayed significantly longer handling time than medium and large individuals, which did not significantly differ (Fig. 2). The maximum feeding rate followed a trend similar to that of handling time. The highest maximum feeding rate was observed in medium-sized fish, followed by large and small individuals (Fig. 3).



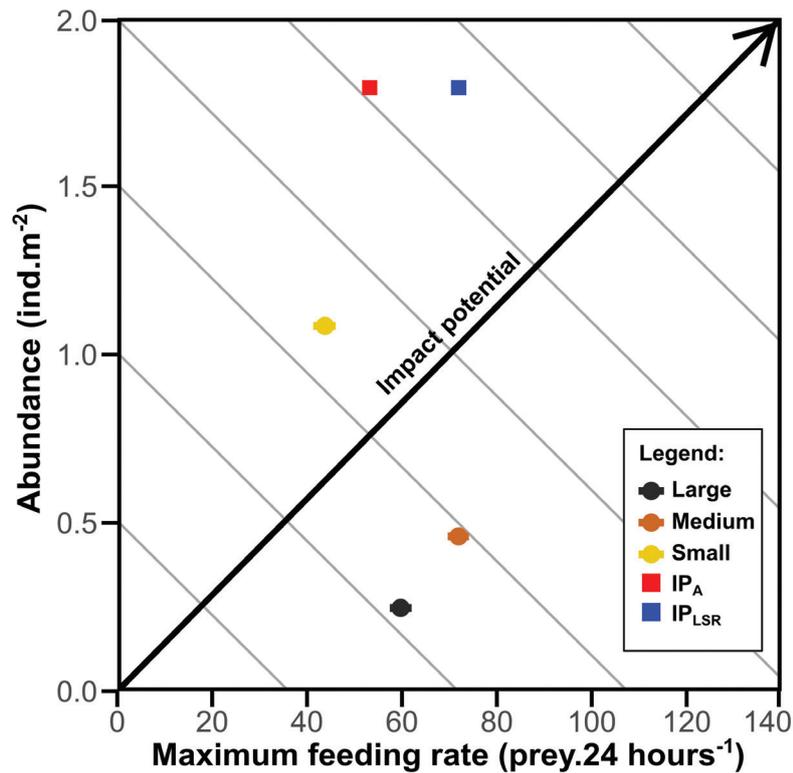
**Figure 3.** Maximum feeding rate (mean  $\pm$  SE) of three size classes of *Neogobius melanostomus* preying upon *Asellus aquaticus*. Groups with the same lower case letters (a, b, c) do not significantly differ ( $p < 0.05$ ).

### Field survey data and Impact Potential value

We captured 1032 *N. melanostomus* (weight range from 0.17 g to 26.4 g; total predator abundance 2.58/m<sup>2</sup>), with 717 individuals (1.79/m<sup>2</sup>) fitting into the three size classes used in the experiment: small ( $W = 2.25\text{--}4.24$  g; 434 individuals with abundance 1.09/m<sup>2</sup>); medium ( $W = 4.25\text{--}6.24$  g; 184, abundance 0.46/m<sup>2</sup>); large ( $W = 6.25\text{--}10.25$  g; 99, abundance 0.25/m<sup>2</sup>). The small class showed the highest IP (47.49) towards *A. aquaticus*, followed by the medium (IP = 33.09), with the large class exhibiting the lowest IP (14.78). The combined body size classes showed  $IP_A$  of 95.36, while  $IP_{LSR}$ , calculated as the maximum feeding rate of medium-sized individuals as proxy for the entire population abundance, was 128.94 (Fig. 4). The RIP was 0.74, which indicated overestimation of *N. melanostomus* total impact on *A. aquaticus* when the size composition of its population was omitted.

### Discussion

The type of predator functional response curve is one of the important predictors of the stability of a prey population utilized by a predator (Miller et al. 2006; Dick et al. 2014). As in previous research, *N. melanostomus* showed type II FR with respect to *A. aquaticus* (Laverty et al. 2017; Franta et al. 2021) and other prey types (Gebauer et al. 2018; Gebauer et al. 2019; Paton et al. 2019). In this study, all three size classes showed type II FR. Type II FR is common (Leeuwen et al. 2007) and



**Figure 4.** Biplot showing impact potential (IP) of each *N. melanostomus* size class separately;  $IP_{LSR}$ , calculated based on maximum feeding rate of the medium predator size class only (traditional IP calculation; Equation 3);  $IP_A$ , calculated as a combined IP of small, medium, and large predator size classes (Equation 4). Abundance (ind/m<sup>2</sup>) of size classes (small, medium, large) of predator obtained from invaded locality (Elbe River, CZ; 50.8431656°N, 14.2175247°E).

indicates high ability to utilize prey even at low densities and thus the potential of a predator to destabilize prey populations (Miller et al. 2006; Dick et al. 2014). Nevertheless, slight differences among FR curves were evident in the present study. Small *N. melanostomus* showed a lower magnitude of the FR curve, hence lower interaction strength with *A. aquaticus* compared to medium and large individuals. Generally, larger predators can forage for larger prey over a wider area with a low risk of predation (Mittelbach 1981; Brown and Maurer 1989; Paradis et al. 1996; Costa 2009). Therefore, they can be less cautious in prey selection (Werner 1974) and show higher interaction strength. On the other hand, larger fish may be more prey-specialized (Jacob et al. 2011) or exhibit diet shifts with ontogeny. Although *N. melanostomus* of ~60 mm can ingest bivalves (Parker et al. 1999), they constitute a small portion of the *N. melanostomus* diet when prey of higher energy value is available. *Neogobius melanostomus* diet composition reflects the prey community abundance composition (Pennuto et al. 2010; Raby et al. 2010) rather than the highest energy yield per bite.

Mouth size is an important prey-limiting factor. Predation usually follows optimal foraging theory, i.e., a trade-off of energy gain with cost of prey capture and handling (Tytler and Calow 2012). Therefore, larger predators often avoid smaller prey, as energy cost exceeds gain (Costa 2009). On the other hand, small predators exhibit higher capture rates and lower handling time when attacking small prey (Persson 1987). *Neogobius melanostomus*, however, seems to be a voracious predator able to capture large prey that is only partially consumed (Roje et al. 2021). The attack rate of small fish did not significantly differ from that of large in the present study, indicating boldness against larger prey despite the longer handling time.

Thorp et al. (2018) reported the highest observed attack rate in the smallest specimens of the frog *Xenopus laevis*, which could indicate higher efficiency of small frogs in utilizing offered prey. Larger body size can lead to a decrease in predator efficiency in catching small prey because of lower agility (Persson 1987). Also, prey that is too small (Hyatt 1979) or represents a low energy gain (Costa 2009) may be ignored by a large predator. Our assessment of attack rate did not confirm lower foraging efficacy of large *N. melanostomus* within the target size range. Thorp et al. (2018) observed lowest handling time in medium-sized frogs. The medium class of *N. melanostomus* in our study also showed the lowest handling time, but with no significant difference from that of large individuals.

Generally, handling time increases with the size of prey (Hoyle and Keast 1987) until size exceeds predator gape size (Kislalioglu and Gibson 1976; Aljetlawi et al. 2004), but handling small prey can be difficult for a large predator (Costa 2009). Our results show that the size range of offered *A. aquaticus* was suitable for both medium and large *N. melanostomus* size classes, while small fish showed longest handling time. A possible explanation is the high ratio of *A. aquaticus* size to small *N. melanostomus* gape size, as described in *Micropterus salmoides* (Kislalioglu and Gibson 1976). Factors such as digestion capacity (Brown and Maurer 1989; Aljetlawi et al. 2004; Li et al. 2017) and satiation level (Kislalioglu and Gibson 1976; Li et al. 2017) can also influence handling time. Digestion is a component of handling time (Woodward and Hildrew 2002), and high handling time can reflect the limited digestion capacity of smaller predators (Li et al. 2017). Generally, gastric evacuation rate, i.e., the quantity of food evacuated per body weight of predator per time unit, is similar among predator sizes. However, a large predator can ingest more food (Brown and Maurer 1989), reaching satiation more rapidly, and handling time declines with increasing satiation (Kislalioglu and Gibson 1976). Although *N. melanostomus* were starved to ensure sufficient time for evacuating the gut, we could not measure the speed of satiation of a particular size class. Specifying the above mentioned factors influencing handling time in *N. melanostomus* would require techniques exceeding the scope of this study.

Field abundance provides a numerical estimate of predator response (Dickey et al. 2021) and, when combined with FR data, substantially extends predictive accuracy of ecological impact (Dick et al. 2017). Although invasive species commonly reach high abundance, this alone cannot be sufficient to assess predation impact (Lavery et al. 2017). Lavery et al. (2017) presented a much lower FR (per-capita effect) of the non-native topmouth gudgeon *Pseudorasbora parva* than the native analogous European bitterling *Rhodeus amarus*. However, *P. parva* reaches several times the field abundance of *R. amarus*, which explains its high ecological impact. Moreover, IP can include various proxies for abundance, including fecundity, lifespan, or propagule pressure (Dickey et al. 2018) that are closely related to population size and fluctuation. *Neogobius melanostomus* shows different IP and RIP in response to prey type, oxygen conditions, and the commonly used field abundance data (Lavery et al. 2017; Dickey et al. 2021). In our study, the most abundant size class showed the lowest maximum feeding rate. Although IP of individual size classes differed significantly, the final comparison of RIP showed that body size plays only a minor role in assessing *N. melanostomus* total impact. However, depending on field abundance and population structure of established or recently invaded sites (Taraborelli et al. 2010; Brandner et al. 2018), predator size can be important factor in total impact.

*Neogobius melanostomus* can be considered a voracious invasive predator of *A. aquaticus* across various size classes. There are significant body-size differences in the magnitude of *N. melanostomus* interaction with prey with respect to per capita foraging efficiency, which can affect its IP. Abundance as well as the size

structure of a *N. melanostomus* population may fluctuate with time post-colonization (Rakauskas et al. 2013; Denys et al. 2015; Brandner et al. 2018), season (Blair et al. 2018), and habitat (Uspenskiy et al. 2021). Although basing analysis on a limited size range can overestimate the IP of *N. melanostomus* because of high per capita consumption rate in small individuals combined with their high abundance in the population and *vice versa* (Dick et al. 2017), the size-group comparison of IP in our study does not show a major difference. Hence, for simplicity and rapid calculation of *N. melanostomus* IP, there may be no need to consider the maximum feeding rates of individual size classes. Nevertheless, our results show size to play an important role in the per capita effect and trophic interactions in the food web.

We encourage considering population structure for future quantification of invasive predator consumption pressure. Although only a minor effect of body size was determined in *N. melanostomus* on precise calculation of impact potential. We assume that increasing numerical differences among size classes can fundamentally increase the importance of body size in IP calculation because of the size dependency of the per capita consumption rate. Additionally, the role of body size can be different in other invasive species or even higher in a predator-prey system with multiple prey species carried on in the field where not a subset, but an entire population is included in the calculation. Unfortunately, the FRs from the field are only occasionally published (Zimmermann et al. 2015; Sorial-Diaz et al. 2018). However, FR for estimating a predator consumption rate on the population level in a lab or the field brings new challenges, including the importance of many other species-specific features or behaviour which incorporation should be solved in the future.

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## Authors' contribution

P.F., R.G. and B.D. research conceptualization, P.F., R.G. sample design and methodology, P.F., R.G., N.Z.S. investigation and data collection, L.V., P.F. data analysis and interpretation, B.D. funding provision and P.F. and R.G. writing – original draft; B.D. and R.G. writing – review.

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