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Doctoral thesis

Foraging efficiency and capacity of non-native round goby (*Neogobius melanostomus*) under various biotic conditions

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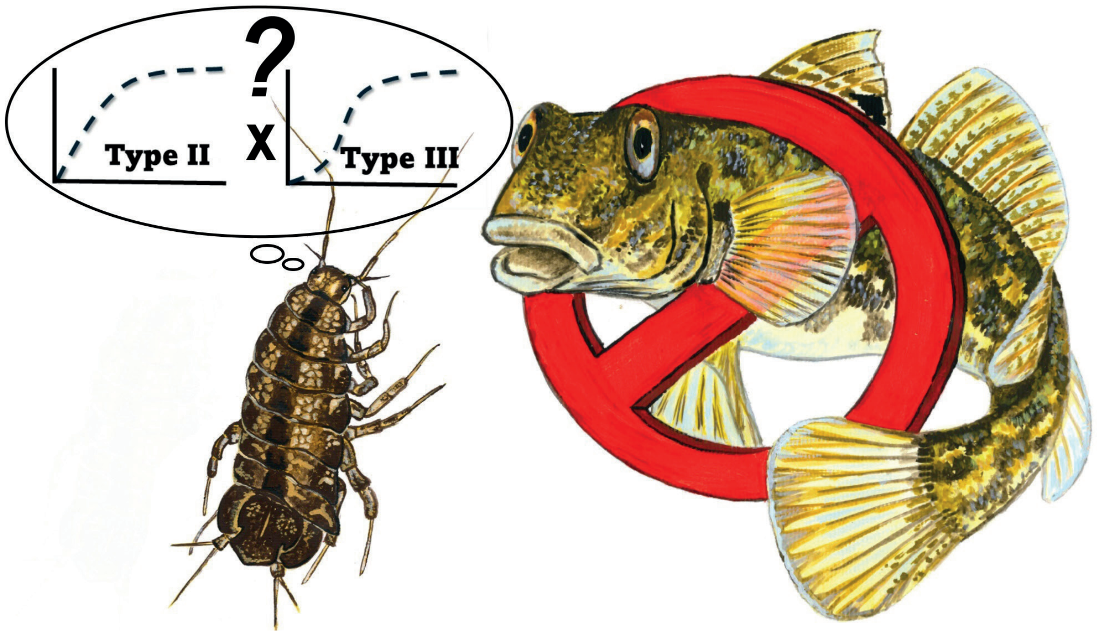

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CONTENT

CHAPTER 1

GENERAL INTRODUCTION

1.1. The issues of invasions

Although global climatic changes and biological invasions are considered one of the major drivers of ecological degradation (Sorte et al., 2013), the biological invasions themselves are often key drivers of changes, and interaction with other drivers of global changes aggravates current biological invasions and facilitates new ones (Pyšek et al., 2020). Indeed, all regions have shown the highest rates of first records of non-native species in recent years (Seebens et al., 2017). Moreover, the anthropogenic alternation of abiotic factors (Crooks et al., 2011), degradation and homogenization of habitats (Alexander et al., 2015), and disruption of natural barriers formed for centuries (Rahel, 2007) together with continually increasing international trade of goods and pets (Westphal et al., 2008) accelerated invasive success. Although only a small percentage of introduced species can be qualified as invasive (Seebens et al., 2018), they exhibit a huge impact such as biodiversity loss, i.e. extinction of native species, trophic cascade alteration, increased hybridization rate (Aloo et al., 2017); and a significant impact on the human population through the loss of more than 20% of the world's food production (Nentwing, 2007) and other socio-economic aspects (Aloo et al., 2017). The total economic cost of invasive alien species effect in the European Union is estimated to be US$ 140.2 billion (Haubrock et al., 2021), while the cumulative total cost worldwide is estimated to be US$ 2,168 billion (Leroy et al., 2021), with the highest share for alien animals followed by plants and fungi (Cuthbert et al., 2021).

Once established, non-native species are hard to eradicate or prevent their subsequent spread from colonized regions, especially from interconnected ecosystems like streams, rivers, and coastal seas. Additionally, eradication efforts require substantial financial and human resources (Dextrase and Mandrak, 2006). Several case studies on eradicating vertebrates were published (Siefkes, 2017; Huntley, 2023), while the success of cases is mainly predetermined by the isolation of colonized regions. The successful eradication was achieved with a combination of several methods and long-term financial support. Additionally, even eradication must be done cautiously. Excluding one invader from the community of invasive species can lead to a higher impact of another invader, especially in an environment without apex predators (Bergstrom et al., 2009; Wallach et al., 2010; Huntley, 2023). For instance, the eradication of invasive cats from Marion Island triggered a subsequent increase in rat population and its impact on bird assemblages (Huntley, 2023). Therefore, prevention and fast detection of the introduction, together with the limitation of the spread of already established populations are crucial in the stabilization of accelerated invasions (Harris, 1988; Dextrase and Mandrak, 2006). These approaches are especially crucial in aquatic ecosystems where invasions are even more detrimental (Ricciardi and MacIsaac, 2011).

1.2. Freshwater invasions

Freshwater ecosystems (rivers, lakes, groundwater, etc.) constitute only 0.8% of the Earth's surface and fresh water alone creates only 0.01% of global water reserves (Dudgeon et al., 2006). However, this minor surface fraction hosts approximately 126,000 animal species and 2,600 macrophytes, representing 9.5% and 1% of total animal and plant species, respectively (Balian et al., 2008) and many others, including human, rely on fresh water. Additionally, freshwater inland systems constitute a valuable natural resource in economic, cultural, aesthetic, scientific, and educational terms (Dudgeon et al., 2006). Despite such an important function, fresh-water ecosystems face high anthropogenic pressure due to habitat alteration, fragmentation, pollution, overexploitation, global climatic changes, and the introduction of alien species. Alien species pose a primary threat to native species (Dextrase and Mandrak, 2006; Dudgeon et al., 2006; Arya, 2021), but at the same time, they cause a secondary threat due to the enhanced invasibility of freshwater ecosystems, which are highly sensitive to alien invasions because of high connectivity and strong trophic links (Bij de Vaate et al., 2002; Gallardo et al., 2016).

Several notoriously known introductions confirm the high connectivity and vulnerability of aquatic ecosystems. For example, introducing the Nile perch (*Lates niloticus*) into Lake Victoria aiming to improve fish production led to decreased populations or even extinction of some native species with subsequent changes in habitat structure and trophic cascade associated with crucial socio-economic impact (Aloo et al., 2017). A similar collapse of native communities is associated with the introduction of the sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes (Siefkes, 2017) and red swamp crayfish (*Procambarus clarkii*) in Europe (Souty-Grosset et al., 2016). Introducing the bighead carp (*Hypophthalmichthys nobilis*), mosquito fishes (*Gambusia affinis* or *G. holbrooki*) (Pyke, 2008), or dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) (Vanderploeg et al., 2002; Soto et al., 2023) change ecosystem functions. Indeed, dreissenids are usually established first and subsequently followed by other non-native species from the Ponto-Caspian region, one of the main European and North American donors of invasive species (Paiva et al., 2018; Soto et al., 2023). Generally, other 28 non-native species from this region usually followed dreissenids (Soto et al., 2023), which often facilitated invasive success in some of them including the round goby (*Neogobius melanostomus*) or benthic amphipod *Echinogammarus isthmus*, so called invasional meltdown (Vanderploeg et al., 2002).

Illegal introductions of fish to improve recreational angling and/or fisheries production (Aloo et al., 2017; Cucherousset et al., 2018), intentional and non-intentional release of pets (Patoka et al., 2018) but especially international long-distance shipping associated with ballast water exchange with „hitchhikers" are considered the main vectors of non-native species introduction in aquatic systems (Bij de Vaate et al., 2002; Sapota, 2004). The latter vector has the main role in spreading of Ponto-Caspian species due to their higher tolerance to fresh or brackish water than most marine species (Paiva et al., 2018; Adrian-Kalchhauser et al., 2020). A wide range of species was detected in ballast water (Gollasch and David, 2012), and although still not confirmed, the ballast water is probably considered the main vector for one of the most invasive fish species – the round goby (Kotta et al., 2016; Florin et al. 2018) which is listed among one hundred of the most invasive alien species in Europe (Vilà et al., 2009).

1.3. The round goby

Generally, five gobies from the Ponto-Caspian region, i.e. the round goby, bighead goby (*Ponticola kessleri*), monkey goby (*Neogobius fluviatilis*), racer goby (*Babka gymnotrachelus*), the western tubenose goby (*Proterorhinus semilunaris*), spread to the main European and Asian basins and some of them even to Laurentian Great Lakes. Nevertheless, none reached abundance and colonized areas as the round goby (Figure 1). It shows higher aggressiveness than bighead goby (Kakareko et al., 2013) or western tubenose goby (Cartwright et al., 2019). Although its diet overlaps with that of the western tubenose goby (Vašek et al., 2014) and monkey goby (Piria et al., 2016), the round goby shows higher plasticity in diet and niche than the western tubenose goby (Pettitt-Wade et al., 2015). Generally, among others, the round goby shows higher flexibility toward general feeding strategy (Števove and Kováč, 2013) with lower morphological specialization and thus can colonize various habitats (Jakubčinová et al., 2017). Round goby was found in habitats ranging from rocky substrates, like rip-rap that fulfill demands for shelter and spawning places, to sand and even mud (Florin et al., 2018) with or without macrophytes (Taraborelli et al., 2009). Nevertheless, a rock habitat with moderate flow is usually preferred (Phillips et al., 2003; George et al., 2021) as a suitable spawning site (Sapota, 2004). However, even in the sandy substrate, the round goby expresses high spawning substrate plasticity (Sapota et al., 2014).

This small bottom-dwelling fish spawns multiple times within a season and possesses different reproduction strategies, including sneakers and nests guarding males (Marentette et al., 2009). Guarding males take care of the brood until larvae leave the nest. Moreover, at hatching, the individuals are already highly developed (Moskal'kova, 2007).

Additionally, the round goby disposes a high thermal resilience (Walsh et al., 2007; Christensen et al., 2021), a high tolerance to salinity (Behrens et al., 2017), and dispersal ability (Janáč et al., 2013; Pennuto and Rupprecht, 2016). All the above-mentioned features can play an essential role in the establishment and spread of round goby and make it one of the most invasive fish species in the world.

Figure 1. *The round goby (Neogobius melanostomus; photo Pavel Franta).*

1.3.1. Distribution and proliferation ability

The round goby is native to the Ponto-Caspian region, including coastal waters of the Black, Caspian, and the whole Azov Sea and lower stretches of tributaries, including River Danube, Dniester, Dnieper and Don (Moskal´kova, 1996; Kottelat and Freyhof, 2007). In those rivers, round goby has been spreading upstream since the 1970s (Moskal´kova, 1996; Copp et al., 2005; Shemonaev and Kirilenko, 2011), when the round goby populations in the Black, Caspian and Azov Sea dramatically declined because of anthropogenic activities, i.e. overfishing, pollution, eutrophication, and salinity changes (Moskal´kova, 1996). Nevertheless, lately, it was almost simultaneously detected in the Baltic Sea (Skora and Stoarski, 1993) and in the North American St Clair River in 1990 (Jude et al., 1992), in both cases, far away from the region of natural origin.

During the last three decades, it colonized the Hron River, the Slovakian (Stránai and Andreji, 2004) and Yugoslavian (Simonović and Paunović, 1998) stretch of the Danube, Elbe (Hempel and Thiel, 2013), Scheldt (Verreycken et al., 2011), Lek (Van Beek, 2006), Rhine and Moselle River (Manné et al., 2013) in Europe. Moreover, the round goby continues to spread upstream and enter the Elbe River in the Czech Republic (Buřič et al., 2015). A similar trend is in the Laurentian Great Lakes basin, where the round goby first colonized Lake Michigan in 1994 and subsequently, within five years, other remaining Great Lakes (Charlebois et al., 1997).

Moreover, shortly after the invasion, the round goby reaches high abundance and usually becomes a dominant fish species in the colonized regions. In the Danube River, the round goby has formed 73% of fish abundance and 58% of the fish biomass in the artificial shore-line zone in only two years after the first record (Brandner et al., 2013a). Five years after the first detection of the round goby in Lake Erie, its population reached an abundance of 4.2±1.5 billion individuals (Johnson et al., 2005) and 40 kg per hectare in Lake Ontario (Pennuto et al., 2012). Although there is a handful evidences of the round goby abundance decline (Johnson et al., 2005; Jůza et al., 2021; Astorg et al., 2022), it continually spreads, and populations in many places still grow (Uspenskiy et al., 2021; George et al., 2021). However, its population has shown significant changes since its introduction. The individuals in the pioneering population at the invasive front reached a larger size and condition due to less limited resources (Brandner et al., 2013a; Azour et al., 2015) and showed higher resting metabolism rate (Myles-Gonzalez et al., 2015) probably correlated with a higher proportion of bold individuals (Myles-Gonzalez et al., 2015; Behrens et al., 2020). With increasing population growth, the round goby reached ecosystem capacity and high intraspecific competition, leading to decreased conditions and reproduction rates (Masson et al., 2018). Nevertheless, compared to its regions of origin, the invasive populations mature early at a smaller body size with a lower fecundity (MacInnis and Corkum 2000; L'avrinčíková and Kováč, 2007; Gutowsky and Fox, 2012).

It was generally assumed that the round goby has a low dispersal ability corresponding to approximately 380 m per 22 days (Blair et al., 2019) or a range of 1.2–3.2 km a year (Šlapanský et al., 2017) closely related to the low capacity to face velocity higher than 0.35 $m.s^{-1}$ (Tierney et al., 2011). However, recent data from telemetric observation pointed to more active migration of the round goby than was expected (Christoffersen et al., 2019). During the last decade, several cases of its proliferation to smaller rivers or even salmonid streams were published (Krakowiak and Pennuto, 2008; Verliin et al., 2017), including seasonal migration to these valuable ecosystems (Christoffersen et al., 2019; Glenn and Pennuto, 2023). That is supposed to be another threat to highly valued macrozoobenthic communities that inhabit those ecosystems (Meyer et al., 2007). Additionally, fused pelvic fins probably allow the round goby to overcome even stream barriers (Pennuto and Rupprecht, 2016). On the contrary, in downstream migration, the round goby has a high dispersal mechanism in the form of the passive downstream drift of larvae estimated to be 5.2–10.4 km a night (Janáč et al., 2013). Nevertheless, international trade, especially ship traffic, probably plays a crucial role in the round goby introduction and spreading over a longer distance (Kotta et al., 2016; Florin et al., 2018). Once present on a new site round goby possesses several qualities denoting its establishment advantage including multiple spawning events within one season and nest guarding (Vivó-Pons et al., 2023).

1.3.2. The round goby foraging habits as a key invasion advantage

The gobies are usually generalists preying mainly on the most dominant organisms to reduce energy associated with searching (Zander, 2011), and the round goby is not an exception (Brandner et al., 2013b; Kihlberg et al., 2023; Glenn and Pennuto, 2023). That is supported by studies on the round goby diet composition in Danube River where the percentage of any eaten prey component does not exceed 40% across a wide spectrum of consumed prey (Brandner et al., 2013b). Other studies reported round goby dietary preferences for molluscs (Simonović et al., 2001; Barton et al., 2005). Mussels, although low energetically valuable, probably represent the most abundant and easily caught alternative prey that supplement its diet in resource-limited areas (Bauer et al., 2007; Polačik et al., 2009). On the other hand, the round goby mainly avoids mussels' consumption in the Sava River (Piria et al., 2016). The preference for soft-bodied and most abundant (available) prey documented in many studies (Diggins et al., 2002; Polačik et al., 2009; Henseler et al., 2021) point out that the round goby follows optimal foraging theory, i.e., maximizing energy intake against energy output (Townsend and Winfield, 1985). For instance, in the Danube River, chironomids are dominant at the beginning of the season (Borza et al., 2009; Brandner et al., 2013b), with their decrease in late summer, the amphipods become essential prey items compensated by the decrease of chironomids' abundance (Brandner et al., 2013b). Although round goby is mainly active at night (Christoffersen et al., 2019), its larvae and juveniles undertake vertical migration from near-shore water rich in benthic invertebrates to pelagic areas where foraging mainly on pelagic prey (Hensler and Jude, 2007; Jůza et al., 2016). That foraging behavior in some localities remains even in adult individuals (Carman et al., 2006; Perello et al., 2015).

This leads to various conclusions of round goby diet preferences reflecting the actual composition of available prey in an ecosystem or short-term availability of energetically rich sources such as fish eggs during spawning season (Steinhart et al., 2004a; Ng et al., 2008). The non-selective foraging is another advantage in its continual proliferation to various freshwater and brackish ecosystems (Pettitt-Wade et al., 2015; Nurkse et al., 2016).

1.3.3. Ecological impact of the round goby

Across all colonized regions, the round goby exhibits a negative impact through the diet overlap/ competition for prey with native fish, predator pressure on invertebrates and eggs of native fish, trophic cascade, new energetic, pollutants and parasites pathway (Lauer et al., 2004; Steinhart et al., 2004a; Ng et al., 2008; Kipp and Ricciardi, 2012; Emde et al., 2014; Mikl et al., 2017a). Additionally, it competes with native fish species for shelter and spawning places (Dubs and Corkum, 1996; Janssen and Jude, 2001). That can result in native invertebrates and/or vertebrate species decline (Brandner et al., 2013a; Mikl et al., 2017a; Jůza et al., 2018), followed by changes in ecosystem functionality and stability (Kuhns and Berg, 1999; Kipp and Ricciardi, 2012).

1.3.3.1. The impact caused by the round goby consumption and non-consumptive effect

The round goby has a broad diet spectrum, up to 51 prey taxa (Števove and Kováč, 2013), and can adapt to various food resources (Pettitt-Wade et al., 2015; Nurkse et al., 2016). Although three main components usually prevailed in its diet across colonized regions, i.e. crustaceans (mainly amphipods), molluscs, and dipterans (mainly chironomids larvae) (Borza et al., 2009; Mikl et al., 2017a) the round goby affects various macroinvertebrates directly or indirectly through the consumption rate (Krakowiak and Pennuto, 2008).

1.3.3.1.1. The round goby impact on macroinvertebrates

Cumulative predator pressure of the round goby and western tubenose goby show a significant decrease in annelids, crustaceans, and ephemeropterans (Mikl et al., 2017a), or dreissenids, isopods, amphipods, trichopterans and gastropods in case of the round goby alone (Lederer et al., 2008; Kipp and Ricciardi, 2012). The dreissenids with a high reproduction rate are likely considered less vulnerable. The highly threatened ephemeropterans and net-spinning caddisflies hardly coexist with the round goby (Krakowiak and Pennuto, 2008; Mikl et al., 2017a). Additionally, several other studies determined a decline in macroinvertebrate density, biomass and/ or large-bodied individuals' dominance with increasing round goby density (Kuhns and Berg, 1999; Barton et al., 2005; Kipp and Ricciardi, 2012).

Moreover, not only the consumption but also the presence of the round goby can modify invertebrates' behavior in response to predation risk, i.e. non-consumptive effect. The non-consumptive effect of the round goby is reflected in a decrease in the consumption rate and activity of macroinvertebrates (Richter et al., 2022; Musil et al., 2023). Lower invertebrates' consumption rate or abundance decline in the environment, especially grazers, can lead to decreased fitness or changes in trophic cascade. For instance, heavy predation on filter feeders (molluscs) or grazers (mayflies) by round goby increases algae density, thus decreasing the water transparency, which in turn affects other predators in the ecosystems (Kuhns and Berg, 1999; Kipp and Ricciardi, 2012).

1.3.3.1.2. Impact on analogous trophic levels

Although the round goby has no special sensory advantages compared to native analogous species (Bergstrom and Mensinger, 2009), it competes with native fish species and other Ponto-Caspians gobies. The round goby is more aggressive than the European bullhead (*Cottus gobio*) (Kakareko et al., 2013), the mottled sculpin (*Cottus bairdi*) (Dubs and Corkum, 1996), or other invaded gobies such as the western tubenose goby (Cartwright et al., 2019). Although all these conclusions are built on laboratory experiments, field studies of the population dynamic of native analogous species usually present their decline shortly after the round goby invasion, e.g. the johnny darter (*Etheostoma nigrum*), mottle sculpin in Laurentian Great Lakes system (Lauer et al., 2004) or ruffe (*Gymnocephalus cernua*) in Netherland (Jůza et al., 2018), probably because of the round goby more effective predation, while the suboptimal prey (energetically-wise) may remain for native fish species causing suppressing their fitness and hence population decline (Henseler et al., 2021). Despite evidence of habitat/ spawning space competition between the round goby and especially members of the Cottidae (Janssen and Jude, 2001; Kessel et al., 2011), the field investigation pointed to the food competition as a crucial driver of the decline or behavior changes of native species (Lauer et al., 2004; Jůza et al., 2018).

1.3.3.2. The round goby impact on higher trophic levels

Invasive mesopredators usually display high pressure on their prey. At the same time, however, they are often included into the diets of trophically higher native predators very soon after the establishment. The round goby has reached high abundance in many colonized regions, thus constituting a highly abundant prey source with poor swimming ability (Johnson et al., 2005; Pennuto et al., 2012; Brandner et al., 2013a). Additionally, the predator's shift to the round goby is often accompanied by benefits for their condition since it represents an energetically rich prey source (Steinhart et al., 2004b; Crane and Einhouse, 2016; Bruestle et al., 2019). The current higher predator population status has only a regulatory effect on the round goby (Madenjian et al., 2011; Hempel et al., 2016; Mikl et al., 2017b). However, increased efforts to restore and protect apex predator populations, including fisheries regulation, may lead to greater apex predator pressure on this invasive species (Hempel et al., 2016) together with non-consumptive effects of predators on the round goby that have yet to be clearly determined.

Currently, a wide range of native predators prey on the round goby. In the European aquatic regions, the round goby was detected in the diet of zander (*Sander lucioperca*) (Hempel et al., 2016), European perch (*Perca fluviatilis*), pike (*Esox lucius*), Atlantic cod (*Gadus morhua*) (Herlevi et al., 2023), European catfish (*Silurus glanis*) (Mikl et al., 2017b). Similarly, in Laurentian Great Lakes, it was incorporated into the diet of smallmouth bass (*Micropterus dolomieu*) (Crane and Einhouse, 2016), pike, sauger (*Sander canadensis*), walleye (*Sander vitreus*), yellow perch (*Perca flavescens*), brown bullhead (*Ameiurus nebulosus*), channel catfish (*Ictalurus punctatus*) (Reyjol et al., 2010), lake trout (*Salvelinus namaycush*) (Dietrich et al., 2006), lake sturgeon (*Acipenser fulvescens*) (Bruestle et al., 2019) and burbot (*Lota lota*) (Madenjian et al., 2011). Frequently, the round goby forms a dominant part of their diet (Steinhart et al., 2004b; Madenjian et al., 2011; Crane and Einhouse, 2016; Mikl et al., 2017b; Herlevi et al., 2023).

The increasing predation of the round goby builds a new pathway to transport energy and pollutants between mussels and higher trophic levels created by increasing consumption of the round goby, especially in localities poor on molluscivorous species (Hogan et al., 2007; Almqvist et al., 2010; Hares et al., 2015). Moreover, the round goby represents a transport vector of *Clostridium botulinum* into the piscivorous birds (Yule et al., 2006) or infection agens of *Anguillicoloides crassus* on European eels (*Anguilla anguilla*) (Emde et al., 2014). Additionally, the benefits of round goby predation can prevail by the round goby predation pressure on top predator eggs (Steinhart et al., 2004a; Lutz et al., 2020) or a diet overlap with juveniles of top predators.

1.4. Predator-prey interaction

Interaction between a predator and prey related to energy transfer is essential for ecosystem functioning (Miller et al., 2006; Mihalitsis et al., 2021), and it depends on the dynamics between predator and prey populations. It is ensured by the long-term coevolution of prey defenses and predator offenses in different levels of interactions, including predator searching, encounter, detection, and attack (Jeschke, 2006). In a stable ecosystem, any developed prey defense is density-dependent, i.e. with successful defense the prey abundance increases up to the level when a high availability restricts the defense to a predator which leads to regulation of prey population. Similarly, the predator switches to alternative prey at a low density of preferred prey. In those systems, the predator is regulated instead of destabilizing effect on prey (Jeschke and Tollrian, 2000). However, each prey defense decreasing the consumption rate of a predator brings trade-offs with, e.g. prey fitness. In this way, the decreased consumption rate is usually reflected by the increasing non-consumption effect of a predator (Sih et al., 2010), which includes decreasing foraging activity, increasing shelter use and ventilation rate of the prey (Rahel and Stein, 1988; Preisser et al., 2005; Mitchell and Harborne, 2020). The non-consumption rate may have an even higher impact than the consumption rate alone and play a crucial role in the trophic cascade in aquatic systems (Preisser et al., 2005). While the visual contact of predator-prey is present only in encounters, the predator odour cues can be transferred for long distances in densely weeded areas with a longer period of efficiency to prey (Brown et al., 1997).

Deviation from that predator-prey equilibrium can be observed even in stable ecosystems during uncommon events, e.g. dark nights with rain and wind, favoring a predator/prey for a short period (McKee et al., 1997). In some cases, this can lead even to non-consumptive mortality of prey (known also as surplus killing or wasteful killing), i.e. the killing of prey without their consumption (Kruuk, 1972). These events can be accompanied by a crucial consequence for prey population in vertebrate's predator-prey system (Kruuk, 1972; Jędrzejewska and

Jędrzejewski, 1989). For example, red foxes (*Vulpes vulpes*) were able to kill 230 individuals of adult birds (*Larus ridibundus*) out of a total of 8,000 nesting pairs in a single dark night, or they killed 12–16% of the nesting bird population (*Sterna sandwichensis*) in a year. This behaviour can even threaten the fox population itself (Kruuk, 1972). On the contrary, the surplus killing exhibited by invertebrate predators probably depends on predator gut fullness. The predator with an empty midgut is probably driven to kill other prey that cannot be eaten due to a full foregut (Johnson et al., 1975; Fantinou et al., 2008). That represents a common behaviour of some invertebrate predators like damselflies (Johnson et al., 1975), predatory bugs (Fantinou et al., 2008) or carabids (Lang and Gsödl, 2003), and it gets minor with decreasing prey density (Johnson et al., 1975; Lang and Gsödl, 2003; Fantinou et al., 2008; Veselý et al., 2017).

The predator-prey interactions are a complicated system driven and influenced by wide-scale biotic and abiotic factors. However, this system seems very fragile (Madin et al. 2010a,b; Atwood et al., 2018), especially when any invasive species enters the system. Invasive species are usually opportunistic feeders with a very broad diet that represents a serious threat to naïve prey because of missing co-evolution. That risk depends on the experiences of prey and invasive predators to similar counterparts. Highly experienced non-native predators and less experienced prey represent the highest risk (Saul and Jeschke, 2015). Moreover, the invasive mesopredator can profit from a low predation risk if the top predators are missing in the invaded ecosystem or cannot forage on it because of lack of co-evolution (Sih et al., 2010).

1.5. The comparative functional responses

The functional response is a consumer's response to gradually increasing prey resources. Three functional response curves that reflect the consumer's effectiveness in utilizing prey sources were described by Holling (1959). In type I, the functional response increases linearly with increasing prey sources. This type is conditioned by negligible consumer handling time, while even other sources are searched with maximal effort until consumer satiation is reached, which is typical for filter feeders (Jeschke et al., 2004). Predators usually show type II and III. Logarithmic type II pointed to a high attack rate/predator pressure to prey even in low density, thus possibly having a destabilizing effect on the prey population (Twardochleb et al., 2012; Dick et al., 2014). Contrary sigmoidal type III denotes a low predator ability to attack prey in low density (Holling, 1959; Dick et al., 2014).

Quantifying and predicting the ecological impact of invasive or potentially invasive species is always challenging. The invasive species are usually characterized by high resource utilization (Bollache et al., 2008; Barrios-O'Neill et al., 2016; Laverty et al., 2017), which simultaneously represents key parameter for the determination of their potential impact. Based on the simple comparison of per-capita functional response, existing, emergent or potential invaders with native analogous species predict higher or lower impact on lower trophic levels or potential risk (Dick et al., 2014).

Indeed, the simple principle of functional response allows the comparison of wide-scale factors at different levels, not limited only to species comparison. Factors such as body size (Thorp et al., 2018), the origin of an invader (Paton et al., 2019), light and noise pollution (Sanders et al., 2018; Fernandez-Declerck et al., 2023), habitat complexity (Alexander et al., 2015; Gebauer et al., 2019), oxygen level (Dickey et al., 2021), and different prey types (Laverty et al., 2017) were investigated in correlation with invaders' per-capita consumption rate. The comparative functional response depended on all these factors. Therefore, the comparative functional response represents a unique concept in invasive ecology in which many variables can be incorporated in controlled or natural conditions. Moreover, some studies translocated this method even to the field condition (Zimmermann et al., 2015; Soria-DÍaz et al., 2018).

Nevertheless, for comparison of the overall invader ecological impact, also other factors, not only the per-capita consumption rate determined by the functional response, must be taken into consideration – mainly abundance and reproduction rate (Parker et al., 1999). The metrics such as Impact potential (IP), Relative Impact Potential (RIP) or Relative Impact Risk (RIR) represent a valuable extension of functional response concept, including abundance as a crucial factor in the ecological impact of invaders since even the invader with a high per-capita consumption rate can have a low ecological impact if it occurs in low abundance in invaded regions (Laverty et al., 2017; Dick et al., 2017; Dickey et al., 2020). Nevertheless, other factors, i.e. life span, fecundity, propagule pressure, attack rate, and handling time, can be incorporated into Impact potential instead of the abundance or maximum feeding rate (Dickey et al., 2018, 2020) regarding the proposed hypothesis.

1.6. Objectives of Ph.D. thesis

The present Ph.D. thesis follows on previous research activities conducted within the Ph.D. thesis of Radek Gebauer focused on the foraging behavior of the round goby under different abiotic conditions, to extend and refine the knowledge of the foraging behavior of this invasive fish. The present Ph.D. thesis is aimed at experimental examination of various biotic conditions and their effect on foraging efficiency and capacity of the round goby. The particular objectives were as follows:

- To assess the potential foraging efficiency of the round goby on crustaceans, especially on crayfish as an important invertebrate freshwater predator in the simple one-to-one predator-prey and multi-prey systems (**Chapter 2**).
- To determine the role of body size on per-capita foraging efficiency and capacity in the round goby (**Chapter 3**).
- To evaluate the importance of body size structure in the round goby population for quantification of its Impact Potential (IP; **Chapter 3**).
- To identify the non-consumptive effect of the top predator on the mesopredator (round goby) foraging as a potential way to manage the round goby impact on its native prey (**Chapter 4**).

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CHAPTER 2

THE INVASIVE ROUND GOBY *NEOGOBIUS MELANOSTOMUS* AS A POTENTIAL THREAT TO NATIVE CRAYFISH POPULATIONS

Franta, P., Gebauer, R., Veselý, L., Buřič, M., Szydłowska, N.Z., Drozd, B., 2021. The invasive round goby *Neogobius melanostomus* as a potential threat to native crayfish populations. Animals 11, 2377.

My share on this work was about 40%.

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Article

The Invasive Round Goby *Neogobius melanostomus* as a Potential Threat to Native Crayfish Populations

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Simple Summary: *Neogobius melanostomus* is a highly invasive fish that has colonized most major European rivers and is dispersing into their tributaries. Its foraging behaviour does not show particular prey preferences, which makes predicting its interactions with endangered members of the macrozoobenthic community in tributaries a challenge. We observed the interaction of *N. melanostomus* and crayfish juvenile or *A. aquaticus* in single- and multiple-prey systems to better predict its ecological impact. The results suggest an impact of *N. melanostomus* on crayfish similar to that on *A. aquaticus*, potentially making it a threat to crayfish population stability. Destabilization of a keystone species such as crayfish in river tributaries may lead to a trophic cascade in the ecosystem with irreversible consequences.

Abstract: Despite the spread of round goby *Neogobius melanostomus* into freshwater streams, there is a lack of information with respect to its effect on macroinvertebrate communities, especially crustaceans. We studied foraging efficiency of *N. melanostomus* on *Procambarus virginalis* and *Asellus aquaticus*, using a functional response (FR) approach. Stocking density of the prey species was manipulated to determine its effect on consumer utilization, with prey offered separately or combined at 1:1, 3:1, and 1:3 at each tested density. For both prey species, *N. melanostomus* exhibited type II FR, occasionally with a high proportion of non-consumptive mortality. *Procambarus virginalis* suffered a significantly higher attack rate compared to *A. aquaticus*. *Neogobius melanostomus* killed significantly more of the most prevalent prey, regardless of species. In trials with prey species of equal proportions, a difference in the number of each species killed was observed only at the highest density, at which *P. virginalis* was preferred. *Neogobius melanostomus* may be an important driver of population dynamics of prey species in the wild. The non-selective prey consumption makes *N. melanostomus* a potential threat to macrozoobenthic communities of river tributaries.

Keywords: *Asellus aquaticus*; biological invasion; ecological impact; prey preferences; functional response; *Procambarus virginalis*

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1. Introduction

Crayfish have an impact at multiple trophic levels through predation, shedding, burrowing, and competition [1–3] and are considered keystone species influencing stability and functionality of ecosystems, particularly in tributaries to major streams [4–6]. Crayfish populations worldwide are threatened by multiple stressors: Climate change, water pollution, habitat modification, invasive species, and disease [5,7]. Nearly one third of crayfish species worldwide are threatened with extinction [7]. Although interventions in the EU [8] and throughout the world [9,10] aim to improve the ecological status of freshwater lotic ecosystems, the threat presented by non-indigenous species is ever-increasing [11]. In addition to interactions with non-indigenous crayfish, native crayfish interact with small benthic fishes, including non-native species [1].

The round goby *Neogobius melanostomus* (Pallas 1814), among the most invasive of freshwater fish species [12], has expanded substantially beyond its native range the Ponto-Caspian region. It poses a serious threat to freshwater and brackish ecosystems [13] causing critical food web disruptions, shifts in trophic levels, extermination of native species through direct predation and/or competition for resources and habitat, and spread of disease [14–17]. In major rivers, after establishing a viable population, *N. melanostomus* spreads both down- and up-stream [18,19]. It is increasingly found in tributaries of major rivers [20–22] that are often used as refugia for native species [23] and contain unique highly diverse macrozoobenthic communities including endangered species such as crayfish [24]. These communities may be seriously threated by *N. melanostomus* invasion and dispersion [25,26].

Macrozoobenthos represent a predominant proportion of the *N. melanostomus* diet [27,28], reflecting the community structure in a given locality [29,30]. In contrast to major rivers and lakes, which often harbour several non-native macrozoobenthos species, in small streams with highly diverse macrozoobenthic communities, *N. melanostomus* remains a generalist omnivore [30]. This can lead to a significant transformation of the community structure with severe consequences to endangered species, since even partial depletion of a single prey population can alter the predator food selectivity [31]. Nevertheless, crayfish are rarely reported in *N. melanostomus* diet in invaded regions [32,33], possibly the result of a unique flip-tail escape strategy, as observed for dragonfly nymph predation on early-stage crayfish [34].

With respect to the coexistence of small benthic fish and crayfish, due to similar body size, the primary focus has been on competition for food and shelter and on behaviour interactions in the presence of a common predator, as opposed to their mutual predation relationship [1]. However, crayfish juveniles that have become independent after leaving the female are threatened by fish predation due to their small size [35,36] and limited antipredator defences, usually restricted to the tail-flip escape movement [35–38]. The impact of small voracious benthic fish such as *N. melanostomus* on early crayfish stages may be intensified when sharing a common habitat. The ecological impact of *N. melanostomus* on crayfish populations has not been quantified.

Understanding and predicting novel predator-prey interaction dynamics and their consequences for invaded freshwater communities is a critical issue in invasion management [39]. Invasive predators, often possessing better foraging efficiency and/or resource utilization, may have higher maximum feeding rates than the analogous native predators and therefore greater ecological impact [40,41] with especially pronounced consequences in aquatic environments [42].

Resource availability represents a crucial determinant of feeding rate as illustrated by a functional response (FR) curve [43,44]. The shape and asymptote of the curve depict important parameters of consumer-resource interactions and population community dynamics [45,46]. Invasive species often display elevated FRs compared to native or low-impact non-native ecologically analogous species [47–49] making comparative FR a valuable tool for invasion biologists [48–50]. Functional response has been calculated for comparison of *N. melanostomus* foraging efficiency with native [51] as well as non-native analogous species [52] and can be employed for comparison of predator impact on prey components, since predator response to prey may be prey species–dependent [53–57]. A higher FR asymptote denotes more effective prey exploitation, possibly due to greater prey attractiveness or palatability and/or greater predator adaptation to prey antipredation behaviour. Currently, knowledge of the relationship between *N. melanostomus* and crayfishes is lacking, especially in tributaries serving as refuges for native aquatic biota and sources of genetic diversity for main stream ecosystems.

The aim of our study was to characterize *N. melanostomus* foraging efficiency on early juvenile crayfish. While natural ecosystems generally consist of multiple prey species per predator, the majority of research experiments address interaction between a single predator and prey species. We observed the predation behaviour of *N. melanostomus* in the presence of two prey species differing in escape behaviour at several densities and stocking proportions. We hypothesized that prey defence, as well as the presence of an alternative prey in various proportions, may significantly influence predator foraging efficiency.

2. Materials and Methods

2.1. Predator and Prey Acquisition and Acclimatization

Neogobius melanostomus were collected with a backpack pulsed-DC electrofishing unit (FEG 1500, EFKO, Leutkirch, Germany) in early October 2018 from a recently colonized locality in the Elbe River (50.6524583 N, 14.0441314 E). Specimens (TL = 55.9 ± 2.6 mm; W = 2.1 ± 0.3 g) were transported to the Institute of Aquaculture and Protection of Water and acclimated in a 1600 L recirculating aquaculture system for 7 days. They were fed frozen chironomid larvae to satiation twice daily. Water temperature (20.3 ± 0.3 °C), dissolved oxygen (100.6 ± 2.9%), and pH (7.7 ± 0.2) were measured twice daily with an HQ40d digital multimeter (Hach Lange GmbH, Düsseldorf, Germany).

We used two hard-bodied benthic invertebrate prey species of similar body mass differing in escape strategy: The native water louse *Asellus aquaticus* (L.) (W = 5.56 ± 1.94 mg) is representative of isopods that form a component of the *N. melanostomus* diet [58,59]. Isopod locomotion is restricted to slow crawling with no escape strategy [60]. The second species was the juvenile non-native marbled crayfish *Procambarus virginalis* (Lyko 2017) (W = 5.45 ± 0.66 mg), a common crayfish model species for laboratory research [61], which exhibits a flip-tail escape strategy as the native crayfish species [34]. Both native crayfish species in the Czech Republic (i.e., *Astacus astacus* and *Austropotamobius torretium*) are classified as critically endangered species in the Red list of threatened species of the Czech Republic with a continual populations decline [62]. Therefore, their use for experiments performance is strongly forbidden and dispensation from law is impossible.

Asellus aquaticus was collected with hand nets in late September 2018 in the Kyselá voda stream (49.0195475 N, 14.4640344 E). The *P. virginalis* were obtained from the Laboratory of Ethology of Fish and Crayfish, FFPW USB. Both prey species were housed in 200 L glass aquaria equipped with PVC trickling filter media (Hewitech GmbH, Ochtrup, Germany) that served as shelter and filter. Half the water volume was exchanged daily with dechlorinated tap water.

2.2. Experiment Design

Transparent plastic boxes (295 × 185 × 155 mm; total volume = 6000 mL) filled with 5000 mL dechlorinated tap water and 200 mL fine aquarium sand (particle size < 0.3 mm) were used as experimental arenas. Five prey exposures were tested: *A. aquaticus* and *P. virginalis* separately and combined at respective ratios of 1:1, 1:3, and 3:1. Each exposure included prey densities of 4, 8, 20, 36, 60, and 100 individuals/box with six replicates per density. Overall, 180 *N. melanostomus* specimens were used in the experiment, whereas each predator was used only once. Baseline prey mortality was assessed with control groups of the same combinations, ratios, and densities in six replications without predators. *Neogobius melanostomus* were starved for 24 h before each trial to standardize hunger level and placed individually into the experimental arenas 1 h after prey insertion. A light regime of 500 lux m^2 was maintained in a 12 L:12 D photoperiod. The predator was removed from the arena after 24 h, and the number and species of surviving prey and non-consumptive mortality (NCM) were determined. Non-consumptive mortality was calculated as in [63] including dead prey not ingested by the predator. Each predator was used once to avoid experience bias.

2.3. Data Analysis

The FR of *N. melanostomus* was fitted separately for each prey organism and ratio and calculated as a total number of killed prey (sum of NCM and eaten prey). Hence, FR quantified the overall impact of *N. melanostomus* on prey. The FRs of *N. melanostomus* on prey were compared between species and among stocking ratios. The type of FR was determined by fitting of logistic regression on the basis of the relationship between the killed prey (N_e) and the initial prey density (N_0):

$$\frac{N_e}{N_0} = \frac{\exp\left(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3\right)}{1 + \exp\left(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3\right)} \tag{1}$$

where P_0, P_1, P_2, and P_3 represent intercept, linear, quadratic, and cubic coefficients, respectively, estimated using the method of maximum likelihood. If P_1 reaches a positive value with P_2 negative, the proportion of prey killed is positively density-dependent, which is peculiar to type III FR. However, if P_1 is a negative value, the proportion of prey killed declines monotonically from initial prey density, indicating type II FR [46]. Based on logistic regression, we used Rogers's random predator equation [64] for type II FR in all prey types and ratios, which is suitable for non-replacement design:

$$N_e = N_0 - (1 - \exp(\mathrm{a}(N_eh - T))) \tag{2}$$

where T is time of prey exposure to predator (24 h), a is predator attack rate (predator relative consumption rate corresponds to search efficiency in low prey density manifested in an initial slope steepness on FR curve; L day-1), and h is predator handling time (time pursuing, subduing, and eating of prey combined with time spent prey searching and digestive pause; days prey-1) [65]. For bordering of the Rogers's random-predator equation by Ne on both sides of the equation, we used the Lambert W function for solving Equation [66]:

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

We estimated parameters a and h using non-linear least-squares regression and Lamber *W* function included in the EMDBOOK package [66]. Differences in parameters among prey species and ratios were evaluated based on an overlap of 95% confidence intervals. If no overlap was observed, the parameters significantly differed among the treatments [67].

The effects of prey species, ratio, density, and their interaction upon the number of prey eaten, NCM, and killed prey were tested using a generalized linear model (GLM) with Gaussian distribution. Tukey's HSD post-hoc test was subsequently used for determination of significant differences among exposures. Since the survival rate in all control treatments exceeded 97% (97.2–100.0%), the mortality of predator-exposed prey was attributed exclusively to the presence of *N. melanostomus*, and datasets were not adjusted for natural mortality. All analyses were conducted in R version 4.0.3 (R Development Core Team 2018).

3. Results

3.1. Functional Response Type

In all exposures, *N. melanostomus* exhibited the type II functional response (Figure 1): Significant negative linear coefficients in logistic regressions (Table 1).

Table 1. Linear coefficient P_1 of logistic regression of *Neogobius melanostomus* relative to prey species and stocking ratio.

Exposure	Linear Coefficient P_1	SE	*p*-Value
A. aquaticus	−1.145	0.364	0.002
P. virginalis	−1.107	0.360	0.002
1:1 *A. aquaticus/P. virginalis*	−1.047	0.360	0.004
3:1 for *A. aquaticus*	−1.580	0.365	$<10^{-4}$
3:1 for *P. virginalis*	−1.302	0.361	$<10^{-3}$

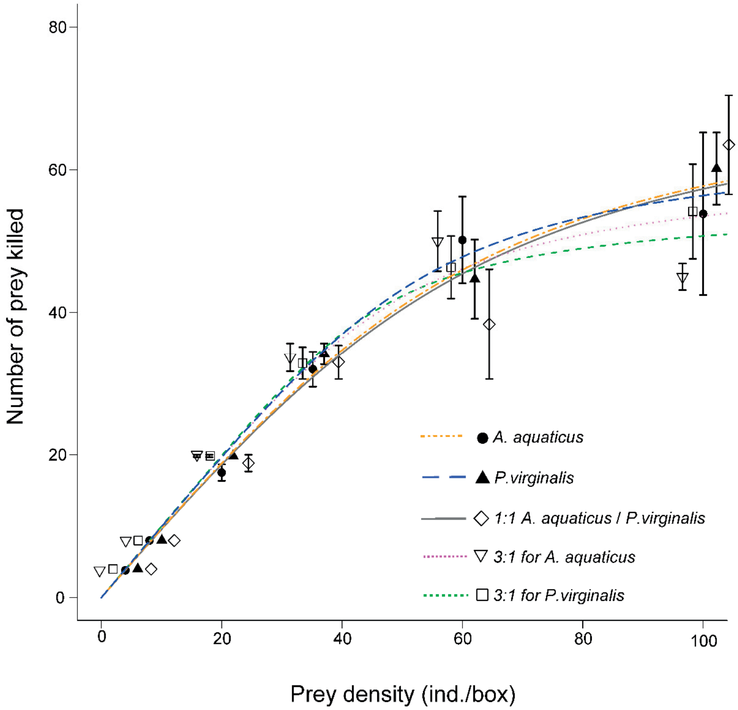

Figure 1. Functional response (mean ± SE) of *Neogobius melanostomus*. *Asellus aquaticus* is represented by the orange dot-dash line and *Procambarus virginalis* by the blue dashed line. Prey were offered separately and combined 1:1 (grey solid line), 3:1 for *A. aquaticus* (pink dotted line), and 3:1 for *P. virginalis* (green dotted line).

3.2. Attack Rate and Handling Time

Significantly higher values of attack rate were observed in the trial with *P. virginalis* offered separately as well as in both 3:1 prey combinations compared with the 1:1 combination and *A. aquaticus* offered separately. *Neogobius melanostomus* displayed the highest handling time in the 3:1 trials, with no significant differences among groups in which prey species were offered separately or at 1:1 (Table 2 and Figure 2).

Table 2. Confidence intervals (95% CI) of handling time and attack rate of *Neogobius melanostomus* relative to prey species and presentation (separately or mixed). In multiple prey trials, *Asellus aquaticus* and *Procambarus virginalis* were offered at ratios of 1:1, 3:1 or 1:3.

Parameter	Prey	Lower Limit of 95% CI	Mean	Upper Limit of 95% CI	*p*-Value
Attack rate	*A. aquaticus*	2.573	3.094	3.615	$<10^{-6}$
	P. virginalis	4.433	5.640	6.848	$<10^{-6}$
	1:1 *A. aquaticus*/*P. virginalis*	2.830	3.568	4.307	$<10^{-6}$
	3:1 for *A. aquaticus*	5.900	7.724	9.548	$<10^{-6}$
	3:1 for *P. virginalis*	4.491	5.825	7.158	$<10^{-6}$

Table 2. *Cont.*

Parameter	Prey	Lower Limit of 95% CI	Mean	Upper Limit of 95% CI	*p*-Value
Handling time	*A. aquaticus*	0.008	0.010	0.012	$<10^{-6}$
	P. virginalis	0.011	0.012	0.014	$<10^{-6}$
	1:1 *A. aquaticus*/*P. virginalis*	0.011	0.013	0.015	$<10^{-6}$
	3:1 for *A. aquaticus*	0.016	0.018	0.019	$<10^{-6}$
	3:1 for *P. virginalis*	0.014	0.016	0.018	$<10^{-6}$

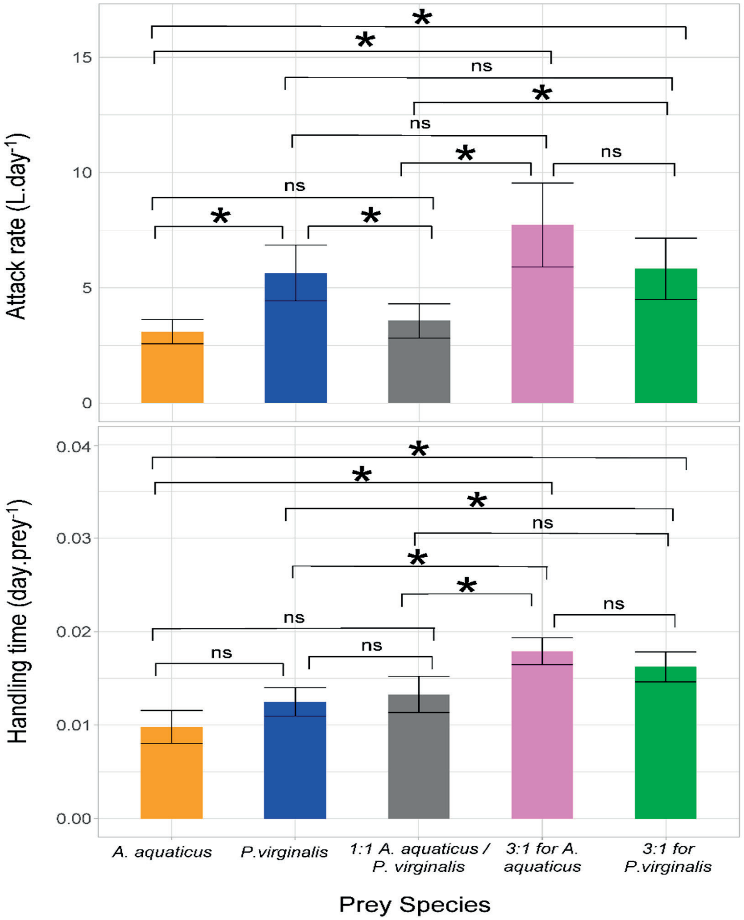

Figure 2. Attack rate and handling time (error bars denote 95% confidence intervals) of *Neogobius melanostomus* with respect to prey species separately and combined. In multiple prey trials, *Asellus aquaticus* and *Procambarus virginalis* were offered at ratios of 1:1, 3:1, and 1:3. Asterisks denote significant ($p < 0.05$) differences among trials and NS indicates non-significant difference.

3.3. Number of Killed and Eaten Prey and Non-Consumptive Mortality

The number of prey eaten by *N. melanostomus* was significantly affected by the interaction of species and ratio ($F_{2,102} = 4.71$, $p = 0.011$). This was reflected in a significantly higher number of *P. virginalis* consumed than *A. aquaticus* in the group with 3:1 for *P. virginalis*. There were no other significant differences among trials in the number of prey eaten (Figure 3).

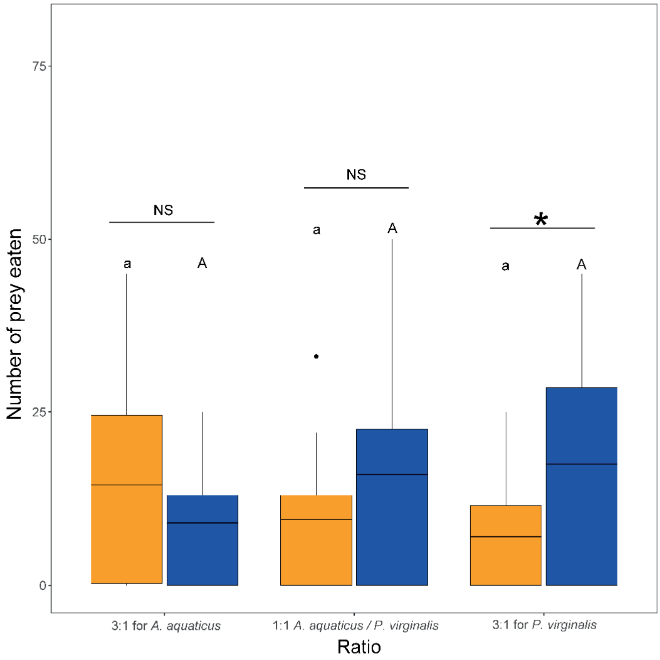

Figure 3. Number of *Asellus aquaticus* (orange) vs. *Procambarus virginalis* (blue) consumed by *Neogobius melanostomus* is prey species ratio–dependent. Exposures with the same letter do not significantly differ ($p > 0.05$). Asterisk denotes significant difference ($p < 0.05$) between species and NS indicates non-significant difference. The points denote outliers.

The NCM was affected by prey density ($F_{1,103} = 7.33$, $p = 0.008$) and the interaction between prey species and ratio ($F_{2,101} = 5.87$, $p = 0.004$). The NCM at 1:1 was significantly higher at the highest density (100 ind/box) than at densities < 60 ind/box at the same ratio (Figure 4B). There was no difference in NCM of *A. aquaticus* among the three ratios. In contrast, the NCM of *P. virginalis* at 3:1 for *P. virginalis* was significantly higher than 3:1 for *A. aquaticus*. The NCM was always significantly higher in the prevalent prey species than in the less abundant (Figure 4A). At 1:1, no significant species differences were observed in NCM (Figure 4B). In all exposures, NCM ranged from 0 to 100% of killed prey.

The number of killed prey was significantly affected by prey density ($F_{1,103} = 29.82$, $p < 0.001$), species ($F_{1,106} = 4.21$, $p = 0.042$), and interaction of prey species with prey ratio ($F_{2,101} = 40.07$, $p < 0.001$) and density ($F_{1,100} = 6.13$, $p = 0.015$). In both 3:1 trials, *N. melanostomus* killed a significantly higher number of the prevalent prey species. The number of killed *A. aquaticus* differed significantly with the proportion and reflected the number offered. In contrast, the number of killed *P. virginalis* reached similar values at

1:1 and 3:1 for *P. virginalis* only at 3:1 for *A. aquaticus* and was significantly lower than at other ratios (Figure 5A). At 1:1, there was no significant difference between species in the number of killed prey at densities <60 individuals/box. With 100 individuals/box at 1:1, *N. melanostomus* killed significantly more *P. virginalis* than *A. aquaticus* (Figure 5B).

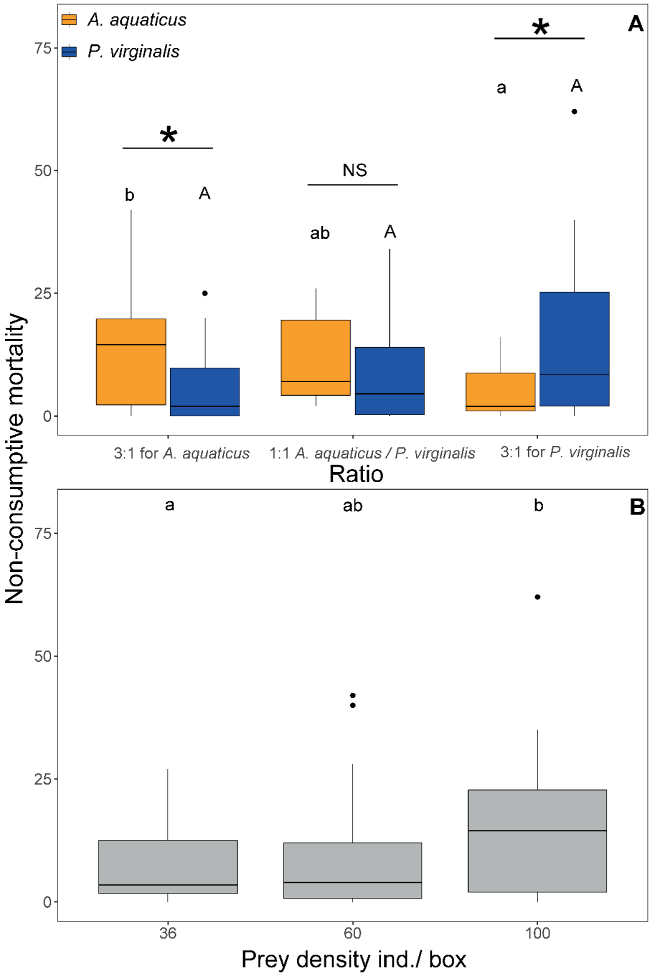

Figure 4. Number of non-consumptive mortality of *Asellus aquaticus* (orange) and *Procambarus virginalis* (blue) by *Neogobius melanostomus* relative to the prey species ratio (**A**) and density (**B**). Effect of density, regardless of prey species, is shown for 1:1 (grey colour) at the highest prey densities (36, 60, and 100 individuals/box). Treatments with the same letter did not differ significantly ($p > 0.05$). Asterisk indicates significant difference ($p < 0.05$) and NS indicates non-significant difference. The points denote outliers.

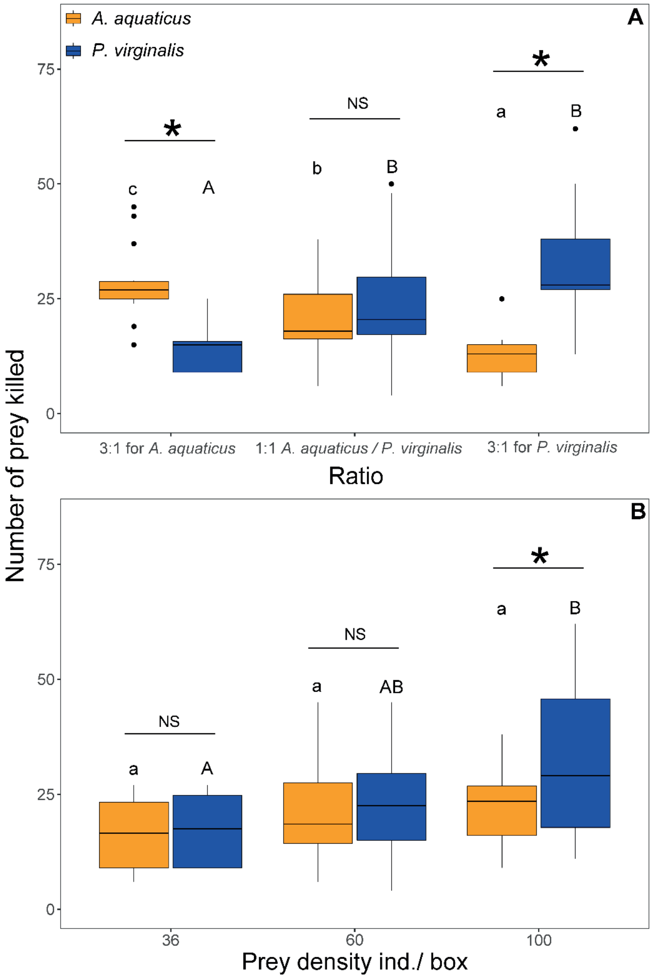

Figure 5. Number of killed *Asellus aquaticus* (orange) and *Procambarus virginalis* (blue) by *Neogobius melanostomus* relative to prey species ratio (**A**) and density (**B**). Effect of density is shown only for 1:1 at 36, 60, and 100 individuals/box. Exposures with the same letter did not significantly differ ($p > 0.05$). Asterisk indicates significant difference ($p < 0.05$) between groups and NS indicates non-significant difference. The points denote outliers.

4. Discussion

The ability to utilize different prey sources and to switch among prey species as required is an attribute of successful invasive predators that can negatively affect not only prey species populations but also coenoses stability [31,68]. *Neogobius melanostomus* significantly changes composition of the macrozoobenthic communities in the invaded freshwater ecosystems [25,69]. Tributaries of major rivers serve as refuges for native aquatic biota and as sources of genetic diversity for the main streams [23] that are currently heavily affected by biological invasions [70].

Neogobius melanostomus exhibited type II FR toward prey organisms differing in escape strategy regardless of presentation. This type of functional response is typical of carnivorous predators [63,71] and is usually associated with destabilization of prey organism populations [72]. Type II FR was previously observed in *N. melanostomus* towards amphipods [49,51,73], *A. aquaticus* [49], and common carp *Cyprinus carpio* L. larvae [52] under experimental conditions. With increasing habitat complexity [74], switching among prey types [45] and consumption of less preferred prey [75] or prey with a well-developed antipredator defence [76] commonly involves a shift from type II FR to type III FR. However, this expected phenomenon was not observed in our two prey–species system, although prey organisms displayed different escape abilities. This is consistent with Gebauer et al. [77] who found no shift in *N. melanostomus* FR with increased habitat complexity, suggesting that *N. melanostomus* is a highly effective predator irrespective of habitat conditions [76] and prey behaviour (this study).

Handling time, as the ability to find and process prey, determines the predator maximum feeding rate [50]. This parameter closely correlates with habitat complexity [57,77,78] and, especially, with prey morphology and behaviour [53,79]. The typical crayfish flip-tail escape is generally considered a successful antipredation strategy [34,80] that reduces predator success or at least requires higher predator energy [81,82]. Contrary to expectations, we observed no significant differences in handling time of *A. aquaticus* and *P. virginalis*, suggesting that the crayfish escape strategy is ineffective against *N. melanostomus* predation, at least in early crayfish ontogenetic stages and in sandy substrates. In the trials with a single prey species at low density, *N. melanostomus* exploited *P. virginalis* more effectively than *A. aquaticus*, reflected in its significantly higher attack rate on *P. virginalis*.

Based on these results, we can conclude that crayfish populations, including native species (e.g., genus *Astacus* and *Austropotamobius* for European regions), in freshwater ecosystems may be exposed to predation stress by *N. melanostomus* similar to that on *A. aquaticus*. Lawton et al. [83] reported that the predator attack rate decreases and handling time is elevated when alternative prey items are available [83], and Colton [53] demonstrated that, in a multi-prey system, both handling time and attack rate vary with quantity and characteristics of the second most available prey item [53]. However, our experimental design did not allow analysis of those parameters with respect to prey species separately in the multiple-prey exposures. Handling time and attack rate in our multi-prey trials reached values different from those that would be expected in single-prey exposures. Regardless of the proportion of *P. virginalis*, the prey item considered to be a driver of the *N. melanostomus* attack rate, on the overall offered prey amount, *N. melanostomus* showed a higher attack rate in both 3:1 ratios compared to 1:1 or *A. aquaticus* offered separately. At 1:1, the attack rate was similar to that in the system with only *A. aquaticus*. In both 3:1 trials at lower densities, the attack rate was positively affected, while, at higher densities, *N. melanostomus* handling time was prolonged compared to expectations based on results gained in the single-prey systems, implying ongoing predator switch to the alternative prey. The prey alternation could be more challenging when prey species occur in unequal quantities. This is in agreement with Colton [53], who stated that the addition of a prey species to a system leads to additional interactions and behaviour changes, and the food system becomes unpredictable. Lawton et al. [83] reported reduced predator pressure on individual prey in such conditions due to the increased handling time and depressed attack rate. However, our data clearly showed that addition of a second prey item led to an increase in *N. melanostomus* attack rate as well as elevated impact on the prey community. In addition, our study confirms the value of multi-species experimental design in ecological studies to gain a more realistic assessment of predator impact upon prey communities.

Several studies have documented *N. melanostomus* feed selectivity [30,84,85] that differs with locality. The optimal foraging theory states that a predator will maximize energy profit to cost with respect to prey acquisition and processing [86]. Prey selectivity in aquatic ecosystems is affected by multiple factors including prey availability [87]; predator experience [56]; prey size, morphology, and colour [87,88]; and water turbidity [89,90]. The latter is demonstrated by *N. melanostomus* diet shift to easily available prey under experimental conditions of high turbidity [89]. Therefore, it can be assumed that prey exhibiting an effective escape response and/or high mobility will be less preferred by predators [86]. However, studies of *N. melanostomus* feed selectivity have often shown contradictory results, with respect to preferences for native [91,92] or non-native [93] species. In addition, overexploitation of certain benthic species regardless of abundance has been observed [30,84,85] and confirmed by our findings of no species-differences in the number of prey killed when presented in equal numbers, while at 3:1, *N. melanostomus* killed significantly more specimens of the prevalent species. These findings support the hypothesis that *N. melanostomus* often shows indiscriminate foraging, taking the most readily available prey and easily switching to another source [30,94]. The ineffectiveness of crayfish tail-flip escape strategy against *N. melanostomus* predation was also shown. An exception was 1:1 presentation of prey at density of 100 ind/box, when *N. melanostomus* killed significantly more *P. virginalis* than *A. aquaticus*, possibly showing predator food preference after satiation [45].

Although the focus is generally on the direct consumption of prey, this is not the only means by which predator ecological impact may occur [95]. We observed that non-consumptive mortality (NCM) may have an even higher effect on prey populations than direct predation [96]. This component of predator behaviour, also known as waste or surplus killing, has been observed in invertebrates [63,97,98] and mammals [99–101]. Ignoring NCM may cause a significant underestimation of predator ecological impact [102] as well as energy transfer among trophic levels [97]. In our experimental exposures, *N. melanostomus* exhibited a high rate of NCM, indicating its potential role in the effect of this predator on prey population abundance and ecosystem function. Our observed NCM is in contrast with previous studies of *N. melanostomus* FR with fish larvae as prey [52,77] in which no NCM was observed. In mammals, NCM is usually connected either with an ineffective anti-predator response due to lack of co-evolution with the predator [101] or to lack of prey escape response as a consequence of isolated short-term events [102]. In invertebrates, it seems that the satiation level determines whether the prey is consumed. However, hunting and killing of prey are probably directed by mechanisms [97] in invertebrates that differ from that of vertebrates [103]. Johnson et al. [97] assumed that an empty midgut may stimulate predatory damselfly nymphs to capture more prey than can be processed due to filled foregut. It seems that an effect of satiation was not confirmed in our experiment, since *N. melanostomus* killed both prey species without their consumption after 24 h starvation, even at the lowest densities. Although the NCM has usually been reported to increase as prey density rises [63,97,98], we did not find a correlation of NCM rate and prey density in *N. melanostomus*, and the proportion of NCM in total prey mortality ranged from 0–100% (33.4 ± 39.2%).

Fantinou et al. [63] described NCM elevation at temperatures outside the predator thermal optimum, i.e., in stressful conditions. Similarly, Veselý et al. [98] in a study of *Aeschna cyanea* nymphs, and Jedrzejewska and Jederzejewski [100] in *Mustela nivalis*, described higher NCM at lower temperature. However, it is unclear whether the low temperature directly caused change of predator behaviour or influenced prey occurrence and/or behaviour and subsequently predator response. In our study, the temperature ranged within the optimum range reported for *N. melanostomus* [104]. We can assume that a potential reason for observed high NCM values might be the absence of shelter as a possible trigger of stress, although we have no evidence supporting this assumption or quantifying its importance in the wild in *N. melanostomus*.

Neogobius melanostomus successfully exploited both hard-bodied prey species differing in escape strategy without showing a distinct preference. The simultaneous effects of high *N. melanostomus* foraging efficiency on *P. virginalis* and previously documented successful competition of *N. melanostomus* for shelter with crayfish [105] may demonstrate a potential to regulate *P. virginalis* populations in the wild. Bovy et al. [106] pointed out that a destabilization effect of predator presence on prey populations is negatively correlated with prey reproduction and dispersal abilities. Therefore, despite a strong interaction between *P. virginalis* and *N. melanostomus* as invasive non-native species, an eradication effect is less likely in established *P. virginalis* populations due to its high fertility rate and overall reproduction ability [107]. However, for native crustaceans, including indigenous European crayfishes that are threatened for many reasons [7,62] and exhibit lower fecundity [108], *N. melanostomus* may pose a serious risk. Particularly with regards to increasing records of *N. melanostomus* in smaller tributaries [30,109,110] inhabited by native crayfish, this can be crucial for continuing crayfish existence. More attention should be focused on identifying and clarifying non-consumptive mortality in the wild as a potential element of *N. melanostomus* foraging behaviour. The reason for ineffective predation in *N. melanostomus* is unclear, and this is one of the first laboratory foraging studies to report non-consumptive predation in fish. Both indiscriminate foraging behaviour and non-consumptive mortality are important factors that should be taken into consideration for quantification of *N. melanostomus* impact on native crustaceans in freshwater ecosystems.

5. Conclusions

Although *N. melanostomus* shows comparable predation pressure on both preys, it can be a threat to the population stability of already endangered crustaceans such as crayfish. Effective control to limit further spreading of *N. melanostomus* to tributaries should be a priority. There is a need for more multiple-prey studies, as quantification of *N. melanostomus* impact on the macrozoobenthic community based on the single prey model may be insufficient. In addition to prey species, their density and relative proportions can significantly influence the *N. melanostomus* foraging efficiency.

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Institutional Review Board Statement: Ethical review and approval were waived for this study, due to the character of the experiment. The vertebrates were held in captivity and fed natural food under laboratory conditions for a short time with unnecessary handling. Therefore, this study was not subject to authorization under the Czech Republic legislation.

Data Availability Statement: The data presented in this study are available from the corresponding author upon request.

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CHAPTER 3

SIZE-DEPENDENT FUNCTIONAL RESPONSE OF THE ROUND GOBY *NEOGOBIUS MELANOSTOMUS*; IMPLICATIONS FOR MORE ACCURATE IMPACT POTENTIAL CALCULATION

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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 rage – 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.

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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 (Laverty 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-depending 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 zigzag wading in the near-shore water (length = 100 m, width = 4 m, area = 400 m^2) with stony bottom no 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* (Števove 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:

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

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):

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

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 rage 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:

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

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:

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

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

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

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

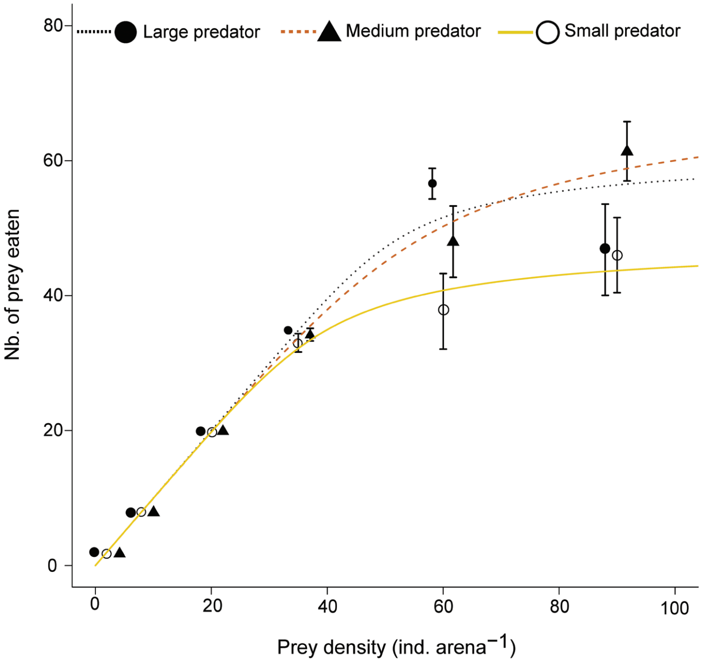

Figure 1. Functional response (mean ± SE) of three size classes of *Neogobius melanostomus* preying upon *Asellus aquaticus*.

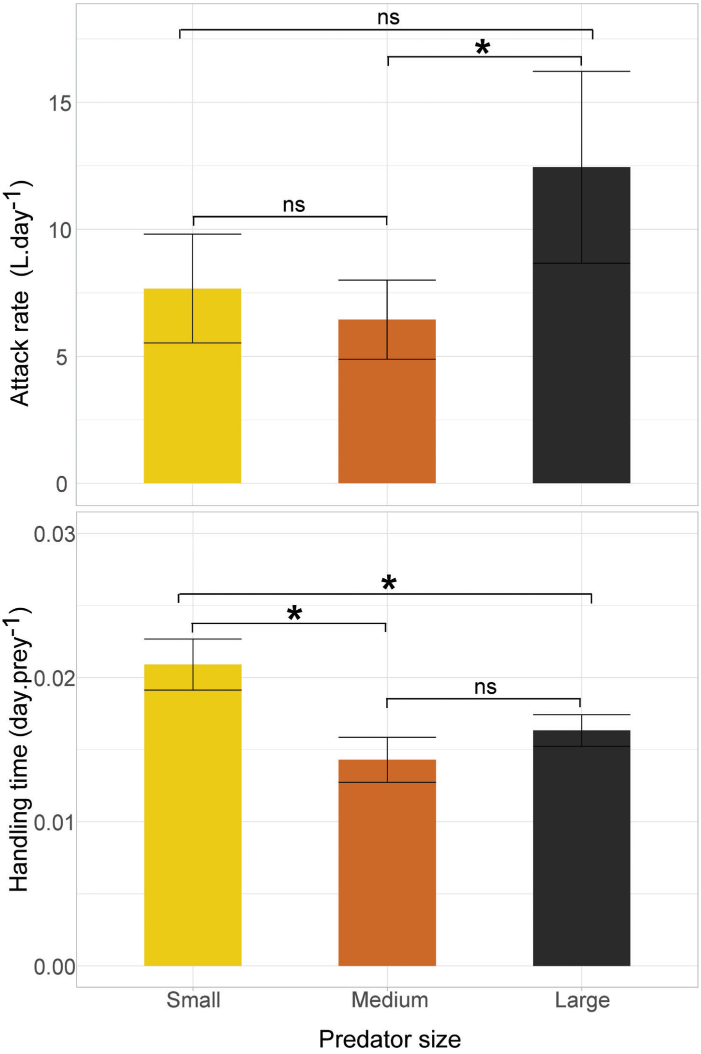

Figure 2. Attack rate and handling time (error bars denote 95% confidence intervals) of three size classes of *Neogobius melanostomus* preying upon *Asellus aquaticus*. Asterisks denote significant ($p < 0.05$) differences.

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).

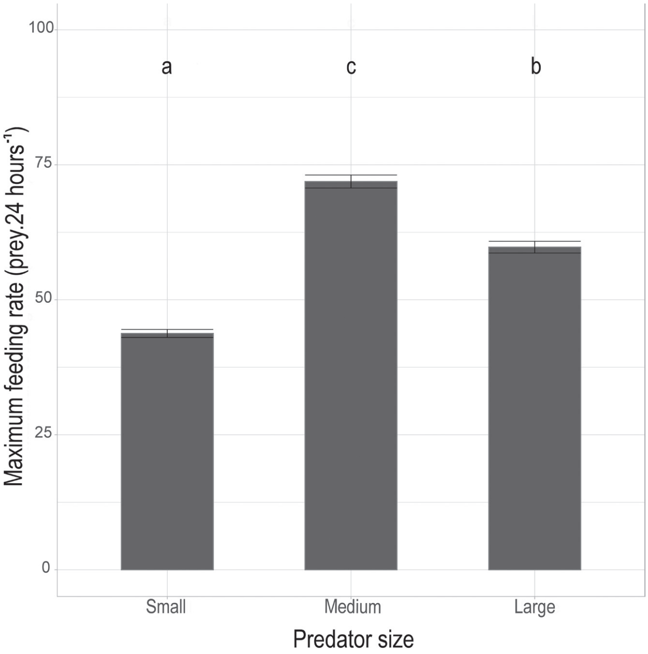

Figure 3. Maximum feeding rate (mean ± SE) of three size three size classes of *Neogobius melanostomus* preying upon *Asellus aquaticus*. Groups with the same lower case letters (a, b, c) do not significantly differ ($p < 0.05$).

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^2), with 717 individuals (1.79/m^2) fitting into the three size classes used in the experiment: small (W = 2.25–4.24 g; 434 individuals with abundance 1.09/m^2); medium (W = 4.25–6.24 g; 184, abundance 0.46/m^2); large (W = 6.25–10.25 g; 99, abundance 0.25/m^2). 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

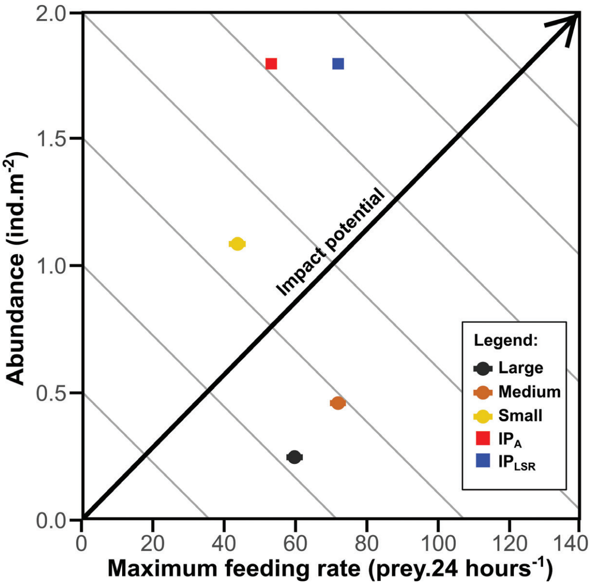

Figure 4. Biplot showing impact potential (IP) of each *N. melanostomus* size class separately; IP$_{LSR}$, calculated based on maximum feeding rate of the medium predator size class only (traditional IP calculation; Equation 3); IP$_A$, calculated as a combined IP of small, medium, and large predator size classes (Equation 4). Abundance (ind/m^2) 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 (Laverty et al. 2017). Laverty 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 (Laverty 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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CHAPTER 4

THE TRADE-OFF BETWEEN FORAGING EFFICIENCY MAXIMIZING AND PREDATOR AVOIDANCE IN THE ROUND GOBY (*NEOGOBIUS MELANOSTOMUS*): TO BE SCARED OR FINE?

Franta, P., Szydłowska, N.Z., Kolář, V., Gebauer, R., Drozd, B., 2024. The trade-off between foraging efficiency maximizing and predator avoidance in the round goby (*Neogobius melanostomus*): To be scared or fine? Manuscript.

My share on this work was about 40%.

The trade-off between foraging efficiency maximizing and predator avoidance in the round goby (*Neogobius melanostomus*): To be scared or fine?

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Abstract

After over thirty years of spreading out of its native range, invasive round goby *N. melanostomus* is affected by consumptive effect (CE) of many native predators across colonized regions. However, the non-consumptive effect (NCE) of the apex predators on CE of *N. melanostomus* remains elusive. We experimentally determined the consumption rate of *N. melanostomus* as mesopredator upon chironomid larvae via comparative functional response under predation risk represented by chemical cues of European eel (*Anguilla anguilla*) as apex predator fed by heterospecific (heterospecific treatment) or conspecific prey and alarm cues (conspecific treatment). Predator derived chemical cues negatively influenced the foraging efficiency of *N. melanostomus*. The foraging efficiency of *N.melanostomus* in lower densities was significantly reduced in conspecific treatment compared to the other two treatments. On the other hand, individuals in heterospecific treatment showed the lowest maximum feeding rate resulting in the highest handling time, while those in the other two treatments exhibited the higher rate. Our results showed the potential of apex predator *A. anguilla* to reduce the negative impact of mesopredator *N. melanostomus* through increased NCE. Hence, our results support management optimization leading to the restoration of the population of apex predators in highly human-impacted homogenized European freshwater ecosystems to decrease the ecological impact of *N. melanostomus.*

Key words: *biological invasion; gobiids; functional response; chemical cues; heterospecific, conspecific alarm cues; European eel*

Introduction

The round goby (*Neogobius melanostomus*), the fish originating in the Ponto-Caspian region, is considered one of the “100 worst” invasive species (Vilà et al., 2009) due to the successful colonization of many European and North American basins (Corkum et al., 2004; Kornis et al., 2012). It often becomes a dominant species at invaded sites (Sapota and Skóra, 2005; Kornis et al., 2013; Jůza et al., 2018). Negative impacts of *N. melanostomus* include displacement of native fishes (Lauer et al., 2004; Jůza et al., 2018) mainly via diet overlap (Dubs and Corkum, 1996; French III and Jude, 2001; Ustups et al., 2016), modification of benthos community (Lederer et al., 2008; Pagnucco et al., 2016; Henseler et al., 2021), disturbance of food webs (Kuhns and Berg, 1999; Pagnucco et al., 2016; Pennuto et al., 2018) and new energetic/pollutant pathways (Hogan et al., 2007; Almqvist et al., 2010; Hares et al., 2015). The higher consumption rate (Laverty et al., 2017), abundance correlated with multiple-spawning in season (Corkum et al., 2004) and non-selective foraging (Dashinov and Uzunova, 2020; Franta et al., 2021) represent drivers of *N. melanostomus* negative impact upon invaded environment, which often lead to collapse of ecosystem stability (Pagnucco et al., 2016; Pennuto et al., 2018). Moreover, the human-made changes of stream morphology (Winter et al., 2006; Oeberst et al., 2012), interconnectivity of inland waters by canals (Bij de Vaate et al., 2002; Panov et al., 2009) and general biodiversity loss (Olden et al., 2004) manifested in decreased abundance of apex predators (Weis, 2011), caused increasing the invasibility of an ecosystem and facilitating subsequent impact of invaders (Wallach et al., 2010; Weis, 2011).

Predation is considered the main driver of ecosystem stability and continuously shapes the community structure (Miller et al., 2006). The coexistence of a predator and its prey leads to the development of antipredator mechanisms. Indeed, a prey's ability to early detect a predator by visual or chemical cues is an elementary characteristic in the predator-prey system. The ability to detect chemical cues of predators results from a long-term co-evolution in a predator-prey system but can be developed even in a naïve prey (Ferrari et al., 2010). The antipredator behavior not only reduces direct predation, i.e., the consumptive effect (CE), however at the same time, causes the so-called non-consumptive effect (NCE, Sih et al., 2010), such as higher respiration rate (Pūtys et al., 2015), increased use of shelters or decreased foraging activity leading to lower prey fitness (Rahel and Stein, 1988; Preisser et al., 2005; Mitchell and Harborne, 2020) or higher vulnerability to other predators (Rahel and Stein, 1988; Preisser et al., 2005). Moreover, the NCE can be equal or stronger than CEs (Sih et al., 2010). Additionally, the NCEs of predators on prey may impact the whole community, leading to indirect interactions (Huang and Sih, 1990; Abrams et al., 1986). Hence, in functional ecosystems with a stable trophic pyramid, mesopredators' fear of apex predators may significantly reduce their impact on lower trophic levels. (Preisser et al., 2005; Creel and Christianson, 2008; Mitchell and Harborne, 2020). This phenomenon can lead to lower overall impact of invasive species than originally expected (Aquiloni et al., 2010; Musseau et al., 2015). However, knowledge of the NCE of native predators on *N. melanostomus* is scarce and points only to behavioral responses (Pūtys et al., 2015; Michels et al., 2021; Galli et al., 2023) without connection to CE of *N. melanostomus*. Hence, there is a missing link to conclude lowering of the ecological impact of *N. melanostomus* as mesopredator by restocking of native apex predators.

Shortly after invasion and establishment, *N. melanostomus* was recorded in diets of many native predators (Reyjol et al., 2010; Roseman et al., 2014; Mikl et al., 2017a), making a dominant dietary component in some cases (Dietrich et al., 2006; Reyjol et al., 2010; Hares et al., 2015; Crane and Einhouse, 2016; Hempel et al., 2016; Herlevi et al., 2023). Although *Lota lota* is considered a voracious predator of *N. melanostomus* (Madenjian et al., 2011; Mikl et al., 2017a) and the evidence of *N. melanostomus* in the diet of *A. anguilla* has not been published to date, several aspects predetermine *A. anguilla* as a successful apex predator of *N. melanostomus*: i) both species share benthic lifestyle (Emde et al., 2014) and similar temperature optimum (Seymour, 1989; Lee and Johnson, 2005); ii) living in sympatry as it is known in the Elbe River; iii) the *A. anguilla* morphology allows effective foraging in rip-rap habitats, frequent shelters of *N. melanostmus* (Janáč et al., 2019); iv) evidence of frequent gobiids in *A. anguilla* stomachs (Doornbos and Twisk, 1987) and unpublished records of *N. melanostomus* individuals in *A. anguilla* stomach from the Baltic Sea that are moreover supported by the evidence of sharing same parasites (Emde et al., 2014; Janáč et al., 2019).

To reveal the effect of an apex predator on the ecological impact of *N. melanostomus* as non-native mesopredator we examined the functional response of *N. melanostomus* in the presence of chemical cues of native apex predator represented by *Anguilla anguilla*. We exposed the *N. melanostomus* to conspecific and heterospecific chemical cues in the laboratory conditions. We hypothesized that the exposition of *N. melanostomus* to chemical and conspecific alarm cues can decrease its foraging efficiency, reflected by lower attack rate and/or handling time and thus the possible change of type of functional response in treatments with presence of the odour of apex predator *A. anguilla.*

Materials and Methods

Collection of experimental fish

Neogobius melanostomus as a non-native mesopredator was collected in Elbe River (Czech Republic; 50°50'33,5" N, 14°13'01,9" E) using a backpack pulsed-DC electrofishing unit (FEG 1500, EFKO, Leutkirch, Germany). Fish were transported and acclimatized in a 1,600 l recirculating aquaculture system (RAS) of the Institute of Aquaculture and Protection of Water. During the acclimatization period, they were fed by frozen chironomid larvae. Water temperature (22.06±0.75 °C), oxygen saturation (91.13±2.58%), and pH (6.90±0.34) were measured daily with an HQ40d digital multimeter (Hach Lange GmbH, Düsseldorf, Germany).

The apex predator *A. anguilla was* collected in Elbe River from the localities with sympatric occurrence with *N. melanostomus* (Czech Republic; 50.5165686N, 14.0595781E). The acclimatization of the apex predator was carried out in two RAS (2x1,600 l) separately from the *N. melanostomus* acclimatization system. In 1st RAS, *A. anguilla* was fed by individuals of *N. melanostomus* (conspecific treatment), while in the 2nd RAS, by earthworms (heterospecific treatment) from the beginning of the ten-week acclimatization period to ensure a sufficient intake of offered prey by an apex predator. The temperature (21.71±0.63 and 21.72±0.71 °C), oxygen saturation (89.05±3.29 and 85.50±4.11%) and pH (7.09±0.31 and 7.18±0.26) were measured daily. The tanks with *A. anguilla* were equipped with PVC tubes to ensure sufficient shelter availability.

Preparation of alarm cues

The alarm cues were prepared from 24 individuals of *N. melanostomus* ranged from 74 to 87 mm of total length (80.08±4.07 mm, mean ± S.D.) as previously described in Wisenden et al. (2003) with minor modifications. Fish were killed with a blow to the head. Subsequently, the skin was removed from both body sides of the fish and placed in the chilled distilled water. Then, the skin (app 211 cm^2) was homogenized by an A11 basic analytical mill (IKA-Werke GmbH & Co. KG, Staufen, Germany) with distilled water and filtered through glass wool to remove solid particles. The solution was diluted by chilled distilled water to the final concentration of 0.1 cm^2 of skin.ml^{-1} and stored in 5 ml syringes at -29 °C to ensure the alarm cues stability prior to its use in the experiment (Achtymichuk et al., 2022). To ensure similar conditions in alarm cues-free treatments, 5 ml of distilled water was applied instead of skin extract.

Experimental design

The consumption rate of *N. melanostomus* individuals with individual TL = 60.22±3.45 mm and weight 2.45±0.39 g (mean ± S.D.) fed on chironomid larvae were tested in three experimental treatments: i) conspecific treatment, i.e. mesopredator *N. melanostomus* exposed to conspecific alarm cues and chemical cues of apex predator *A. anguilla* fed by *N. melanostomus* individuals; ii) heterospecific treatment, i.e. *N. melanostomus* exposed to chemical cues of apex predator *A. anguilla* fed by earthworms; iii) control treatment, i.e. *N. melanostomus* exposed to any cues free water (no apex predator). For each treatment, the chironomid larvae were offered to *N. melanostomus* in 6 densities (20, 50, 100, 280, 450, and 650 mg chironomids.arena^{-1}) at six replications. The average individual weight of chironomid larvae was 5.61±0.13 mg. Moreover, the same prey densities, but without the presence of *N. melanostomus* in the arena, were used as a control groups (with five replications per each density) in all three experimental treatments to uncover possible natural mortality of prey. Each experimental treatment was located in a separate recirculating aquaculture system (RAS), which consisted of four tanks (V = 400 l). Seven individuals *A. anguilla* in size range from 540 to 840 mm of TL were stocked in the first tank and fed in groups by 15 individuals of *N. melanostomus* of the individual weight 5.48±0.94 g (conspecific treatment) or 12 earthworms of the individual weight 3.00±0.67 g (heterospecific treatment). In the control treatment, the first tank was without apex predator, and the whole system contained only chemical cues-free water, i.e. tap water filtered through a carbon active filter. In all treatments, water from the first tank continued to the second tank with experimental arenas with *N. melanostomus* and then through the third tank with mechanical filtration and the fourth tank with biological filter back to the first tank (see Figure 1).

The experimental arena (aquarium 23.0x19.5x20 cm) includes a 2 cm layer of sand substrate with three stones and a half-cut PVC pipe as a shelter for *N. melanostomus* with an upper located outlet covered with mesh to avoid *N. melanostomus* escape. Walls of arenas were covered with opaque foil to prevent the visual contact of experimental fish among arenas. Each experimental trial took 24 hours. The chironomid larvae were placed in arenas for acclimatization half an hour before the start of the experiment. Simultaneously, 5 ml of alarm cues (conspecific treatment) or distilled water (heterospecific and control treatment) were added to each arena and lately continually added every 4 hours till the end of the experiment. The experiment started with adding of *N. melanostomus* into the arena. The *N. melanostomus* was starved for 24 hours prior to the experiment. The temperature (22.41±0.44 °C), oxygen saturation (89.03±4.17%), and pH (7.20±0.32) were measured after each experimental run, and the number of survived and dead prey was counted. Moreover, the number of eaten individuals of *N. melanostomus* by *A. anguilla* was counted in conspecific treatment, i.e., 2 ind. (1st run); 10 ind. (2nd run); 5 ind. (3rd run); 9 ind. (4th run); 10 ind. (5th run) and 8 ind. (6th run). Earthworms were always completely eaten in heterospecific treatment at each run.

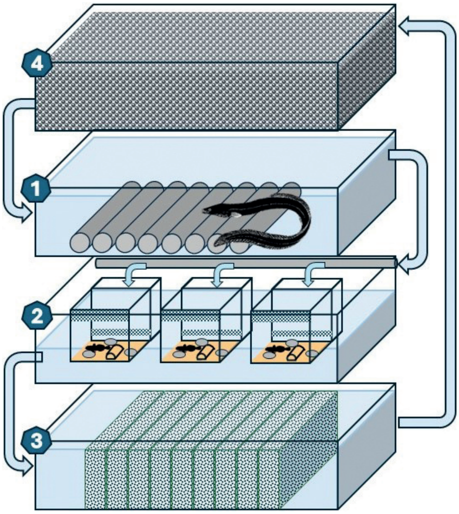

Figure 1. *Setup diagram for the experimental recirculating aquaculture system (RAS). Arrows indicate direction of the water flow through RAS.*
Tank 1 was stocked by seven individuals of the apex predator (European eel – Anguilla anguilla) in heterospecific and conspecific treatment, but no apex predator was present there in control treatment. Tank 2 was occupied by the individual experimental arenas with the mesopredator (round goby – Neogobius melanostomus; 1 individual.arena^{-1}). Tanks 3 and 4 served for mechanical or biological filtration, respectively.

Data analysis

All analyses were done using R 3.4.4 (R Development Core Team 2018). The functional responses for all treatments were fitted by package *frair*. First, the type of functional response was determined by fitting logistic regression of the proportion of eaten prey against an initial prey weight using the *frair_test* included in the package (Pritchard et al., 2017). The simultaneously, significantly positive first and negative second-order terms denote type III FR. Meanwhile, the significantly negative first-order term determines type II FR (Juliano, 2001). Regarding the results of logistic regressions, Roger's random predator equation for non-replacement design was used:

$$N_e=N_0(1\text{-exp}(a(N_eh\text{-}T)))$$

where N_e is a quantity of eaten prey, N_0 is an initial prey density, a is attack rate, h is handling time and T is the time of prey exposition to predator (24 h) (Rogers, 1972). We did not count individual prey but used total prey weight for package *frair*, rounded to the nearest mg, as a measure of prey density in the predation experiments for initial (N_0) and final eaten quantity of prey (N_e). Since N_e borders Roger's random equation on both sides, the Lambert W function was used for solving the equation (Bolker, 2008):

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

For all three treatments, the handling time and attack rate were estimated using non-linear least-squares regression and the Lamber W function in the package EMDBOOK (Bolker, 2008). The 95% confidence interval was calculated for all FR parameters from their standard error. If the 95% CIs overlap, no significant difference exists between treatments and vice versa (Sentis et al., 2013).

Results

The number of eaten individuals of *N. melanostomus* by *A. anguilla* in conspecific treatment was, on average, seven individuals per trial. *Neogobius melanostomus* shows type II functional response in all three treatments (Figure 2), i.e. significantly negative first-order terms of logistic regression (Table 1). Both functional response parameters were chemical cues-dependent. The highest average attack rate was determined in the control treatment (0.170 arena.day^{-1}), followed by heterospecific treatment (0.161 arena.day^{-1}) without significant difference between these treatments. On the contrary, the lowest average attack rate (0.130 arena.day^{-1}) was found for *N. melanostomus* individuals in conspecific treatment and it significantly ($p<0.05$) differed from other treatments (Figure 3). A different trend was determined in handling time, where the highest significantly ($p<0.05$) different from each others, average value reached *N. melanostomus* in heterospecific treatment (0.072 day.mg^{-1}). The individuals in control and conspecific treatments showed more effective prey handling, thus lower values of average handling time (0.061 and 0.060 day.mg^{-1}, respectively) which did not significantly differ (Figure 4).

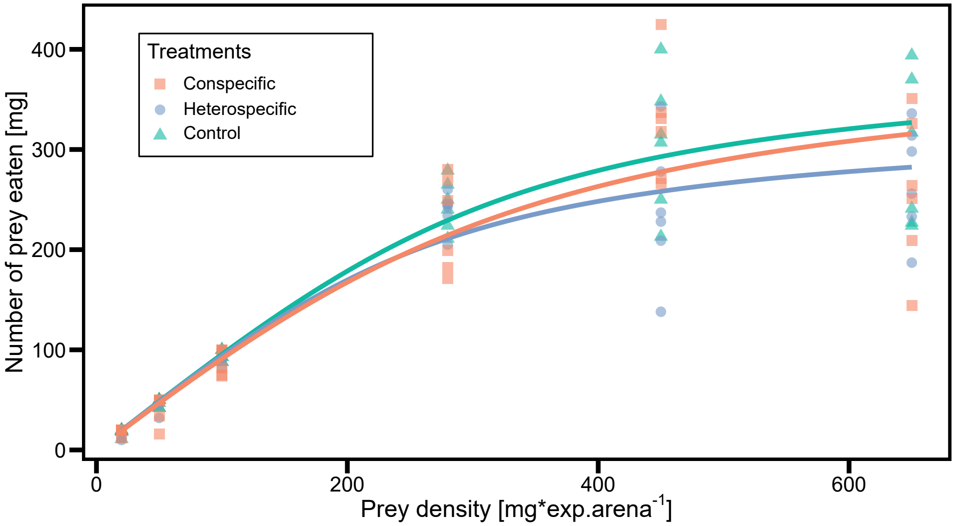

Figure 2. *Functional responses of Neogobius melanostomus as mesopredator upon chironomid larvae exposed to: i) chemical cues of apex predator A. anguilla fed on conspecific prey with added conspecific alarm cues (conspecific treatment); ii) chemical cues of apex predator A. anguilla fed on heterospecific prey (heterospecific treatment); iii) chemical cues free conditions (control treatment).*

Table 1. *Linear coefficient P_1 of logistic regression of N. melanostomus as mesopredator upon chironomid larvae, depending on the exposition to cues from apex predator A. anguilla fed by heterospecific prey (heterospecific treatment) or conspecific prey with added conspecific alarm cues (conspecific treatment). In control treatment, N. melanostomus individuals were not exposed to any chemical cues derived from apex predator or alarm cues of prey.*

Treatment	Linear coefficient P_1	SE	p-value
Control	-0.0052	0.0002	$<10^{-6}$
Conspecific	-0,0048	0,0001	$<10^{-6}$
Heterospecific	-0,0048	0,0001	$<10^{-6}$

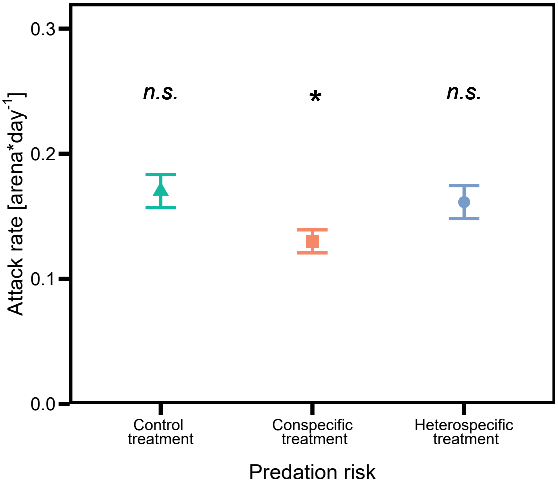

Figure 3. *Average attack rate (errors bars denote 95% confidence intervals) of Neogobius melanostomus as mesopredator upon chironomid larvae exposed to: i) chemical cues of apex predator A. anguilla fed on conspecific prey with added conspecific alarm cues (conspecific treatment); ii) chemical cues of apex predator A. anguilla fed on heterospecific prey (heterospecific treatment); iii) chemical cues free conditions (control treatment). Asterisk denotes significant (p<0.05) difference, while n.s. denotes absence of significant difference.*

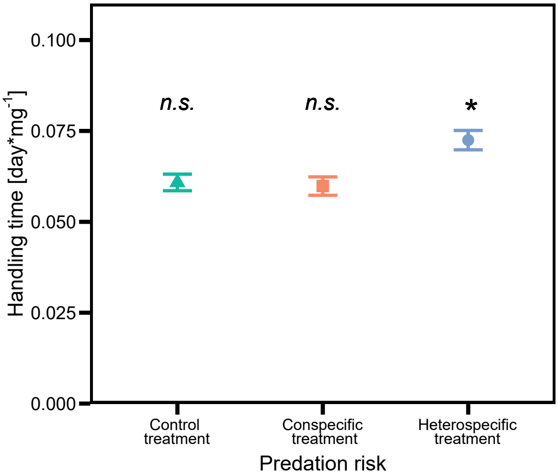

Figure 4. *Average handling time (errors bars denote 95% confidence intervals) of Neogobius melanostomus as mesopredator upon chironomid larvae exposed to: i) chemical cues of apex predator A. anguilla fed on conspecific prey with added conspecific alarm cues (conspecific treatment); ii) chemical cues of apex predator A. anguilla fed on heterospecific prey (heterospecific treatment); iii) chemical cues free conditions (control treatment). Asterisk denotes significant (p<0.05) difference, while n.s. denotes absence of significant difference.*

Discussion

Biological invasions are believed to be a major driver of ecological degradation (Pyšek et al., 2020), associated with a huge annual economic cost (Nentwing, 2007; Cuthbert et al., 2021). Moreover, once established, invasive species are almost impossible to eradicate (Harris, 1988). Restoration of aquatic ecosystems including native predator populations is considered one of the possible ways how to achieve decrease of the ecological impact of non-native hydrobionts (Wallach et al., 2010; Weis, 2011) including highly invasive fish – round goby (*N. melanostomus*) listed among one hundred worst invasive species of Europe (Vilà et al., 2009). However, the overall impact of native predators upon non-native *N. melanostomus* as mesopredator including both consumptive (CE) and non-consumptive effects (NCE) should be investigated in advance. While records of CE are relatively well described across the colonized regions by *N. melanostomus*, NCE remains ambiguous. The functional response represents a fundamental tool to analyze predator foraging efficiency and capacity (Dick et al., 2014), which is also sufficiently flexible for the incorporation of wide-scale variables (Gebauer et al., 2018, 2019; Franta et al., 2023) including the presence/absence of apex predator.

The chironomid larvae are one of the most important diet components of *N. melanostomus* (Janssen and Jude, 2001; Phillips et al., 2003; Števove and Kováč, 2016). This fact is also confirmed by the type II functional response (FR) of *N. melanostomus* upon chironomids in our study, which suggests a strong interaction between predator and prey (Dick et al., 2014). Type II FR was previously described in *N. melanostomus* with chironomids by Fernandez-Declerck et al. (2023) as well as with other prey sources like isopods, fish larvae, or amphipods (Gebauer et al., 2018, 2019; Paton et al., 2019; Franta et al., 2023). These strong interactions correspond with higher resource utilization by *N. melanostomus* compared to native analogous species (Dick et al., 2014; Laverty et al., 2017; Paton et al., 2019), resulting in substantial dietary overlap and consequent displacement of native species. The resulting effect of a predator upon prey is a sum of CE and NCE, while NCE can be even or stronger than CE (Sih et al., 2010). In the present study, we found evidence of a change of *N. melanostomus* FR towards chironomids depending on predator-born chemical cues with or without conspecific alarm cues. Functional response parameters, i.e., handling time and attack rate, show a general high sensitivity towards many environmental parameters which were tested in *N. melanostomus*, such as anthropogenic noise, body size, habitat complexity, or population origin (Gebauer et al., 2019; Paton et al., 2019; Fernandez-Declerck et al., 2023; Franta et al., 2023) and now chemical cues have been proven to be included among these parameters as well.

Fish olfaction is the most highly developed olfactory system in vertebrates and plays an important role in reproductive, parental, feeding, defensive, territorial, schooling, and migration behavior (Kasumyan, 2004). Moreover, predator-born chemical cues are transported for long distances in a lotic system as a useful alarm for prey before visual contact with a predator, evoking a non-consumptive effect. Generally, gobies respond equally to visual and chemical cues (Utne and Bacchi, 1997; McCormick and Manassa, 2008). In *N. melanostomus*, chemical cues (Gammon et al., 2005) and visual signals play an important role in reproductive strategy (Yavno and Corkum, 2010), and records of gobiids' behavioral changes in response to predator risk have already been published. Previous studies mostly focused on shelter use or other antipredator responses, such as physiological and behavioral changes (Michels et al., 2021; Augustyniak et al., 2022; Kłosiński et al., 2022; Galli et al., 2023). For instance, the operculum movement and blood cortisol level in *N. melanostomus* increased in response to conspecific alarm cues (Pūtys et al., 2015; Galli et al., 2023). Yet, despite the cortisol increase, Galli et al. (2023) found no behavioral changes in *N. melanostomus*. Moreover, another non-native Ponto-Caspian goby, *Neogobius fluviatilis*, responded less intensively to conspecific alarm cues than a native *Gobio gobio* in vertical movement, immobility time, and social distance response (Kłosiński et al., 2022). However, no study focused on predation risk to *N. melanostomus* foraging efficiency and capacity. The foraging efficiency of *N. melanostomus* in lower prey density manifested by lower attack rate, seems highly affected by predation risk, especially if it is exhibited to a combination of predator-born chemical cues and conspecific alarm cues. That probably points to *N. melanostomus* avoidance to increase efforts connected with searching for prey in habitats with lower prey availability and high predator risk. That is in line with the equal foraging capacity, i.e. comparable values of handling time, of *N. melanostomus* recorded in control and conspecific treatment in our study when the prey was in a high density and thus easy to utilize. However, the *N. melanostomus* foraging capacity time was negatively affected by chemical cues of predator-consumed heterospecific prey. Nevertheless, based on our experimental design, we cannot decide if it is an effect of alarm cues originating from heterospecific prey or chemical cues realized by *A. anguilla* consumed heterospecific prey or their mutual combination.

Indeed, the origin of *N. melanostomus* can play an important role in response to predation risk. The invasive front, which is characterized by a higher rate of bold individuals (Myles-Gonzalez et al., 2015) and probably other factors like sex and habitat type (Yeung et al., 2023), can result in lower predator NCE in *N. melanostomus*. However, generally a strong NCE of predators is usually reflected in a weaker CE and vice versa (Creel and Christianson, 2008; Sih et al., 2010). Indeed, the bold *N. melanostomus* abundant in the pioneering population (Brandner et al., 2013; Myles-Gonzalez et al., 2015) may exhibit lower sensitivity to NCE. However, their smaller body size compared to their shy siblings of the same age (Brandner et al., 2013) can make them more vulnerable to CE, regarding the hypothesis bigger-is-better (Sogard, 1997; Mittelbach, 1981). Moreover, their higher relative metabolic rate is associated with an increased need to search for food, and thus become even more susceptible to exposure to predators (Bell and Sih, 2007; Brandner et al., 2013). Therefore, it can be assumed an equal total impact of apex predators (evaluated as a sum of CE and NCE) on *N. melanostomus* originated either from invasive front or established populations, as it is reviewed by Sih et al. (2010).

Anguilla anguilla occurs sympatrically with *N. melanostomus* in its native area, though in lower densities (Apostolou, 2013). Moreover, both species have coexisted and share the same habitat at the invaded localities in the Elbe River, where our study fish originated from, at least from 2015 (Buřič et al., 2015). Although the abundance of *A. anguilla* in our experiment has overcome its current common abundance in European rivers (Prchalová et al., 2013), our results provide the first evidence of a decrease in foraging activity of *N. melanostomus* as mesopredator in response to the threat of presence of apex predator. Moreover, *N. melanostomus* represents an important diet component of piscivorous fish at the invaded localities (Dietrich et al., 2006; Reyjol et al., 2010; Hares et al., 2015; Crane and Einhouse, 2016; Mikl et al., 2017a; Herlevi et al., 2023) which may ultimately display similar NCE on *N. melanostomus* foraging activity like *A. anguilla*. Thus, the cumulative NCE of higher predators upon *N. melanostomus* could be similar or even higher in the wild compared to experiment conditions. Records of an effective control of the invasive crayfish population by *A. anguilla* (Aquiloni et al., 2010; Musseau et al., 2015) and the high CE of *L. lota* upon *N. melanostomus* (Madenjian et al., 2011; Mikl et al. 2017a) can be considered crucial findings regarding potential impact management of *N. melanostomus* in the invaded European freshwaters. However, the current abundances of both native apex predators are low there. The river modification and homogenization of freshwater ecosystems, high pressure of angling, commercial fishery and piscivorous birds are important factors in decreasing their population (Winter et al., 2006; Stapanian et al., 2010; Oeberst et al., 2012).

Even stable, pristine ecosystems cannot fully prevent the invasion of non-native species (Sih et al., 2010). However, the invasibility, as well as the impact of invasive species, can be reduced by the restoration of freshwater habitats (Stachowicz et al., 2002; Olden et al., 2004; Wallach et al., 2010) as many invasive species benefit from the absence of apex predators (Weis, 2011) and based on our results, *N. melanostomus* is not an exception. Indeed, the reduction of *N. melanostomus* consumption rate due to higher presence of apex predator could decrease its predation pressure on macrozoobenthos (Lederer et al., 2008; Mikl et al., 2017b; Henseler et al., 2021), competition with analogous fish species (Dubs and Corkum, 1996; French III and Jude, 2001; Ustups et al., 2016) and transfer of energy, nutrients and pollutants to higher trophic levels (Hogan et al., 2007; Almqvist et al., 2010; Hares et al., 2015). Although populations of higher predators are currently under high pressure (Stapanian et al., 2010; Oeberst et al., 2012), they have probably already affected *N. melanostomus* populations through NCE (proven in our study) and previously described CE (Madenjian et al., 2011; Hempel et al., 2016; Mikl et al., 2017a). Even though further research is needed to determine the actual importance of magnitude of NCE in natural conditions, our results emphasize the importance of protecting and managing apex predator populations in managing invasive *N. melanostomus*. Liversage et al. (2017) suggested manipulating management practice to increase the CE of percids upon *N. melanostomus* in the north-eastern Baltic Sea. However, the same approach can be adopted for an increase of NCE of apex predators. Indeed, stabilizing apex predator populations needed to control populations of non-native mesopredator species relies mainly on sufficient freshwater body management, including restoration of freshwater ecosystems and adequate fisheries regulation (Winter et al., 2006; Stapanian et al., 2010; Oeberst et al., 2012).

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CHAPTER 5

GENERAL DISCUSSION
ENGLISH SUMMARY
CZECH SUMMARY
ACKNOWLEDGEMENTS
LIST OF PUBLICATIONS
TRAINING AND SUPERVISION PLAN DURING THE STUDY
CURRICULUM VITAE

General discussion

Nowadays, both aquatic and terrestrial ecosystems face extraordinary pressure from biological invasions, climatic changes, and many other anthropogenic activities (Sorte et al., 2013; Pyšek et al., 2020). The functionality and biodiversity richness are crucial for the stability and resilience of natural ecosystems (Peterson et al., 1998; Oliver et al., 2015). Both non-intentional and intentional introductions to improve production or limit the spread of disease usually end up with dramatic impacts on native biota (Pyke, 2008; Aloo et al., 2017; Siefkes 2017; Soto et al., 2023). Therefore, recently, much effort has been allocated to determining the impact of invasive species and applying restrictions as well as management actions, to prevent the introduction, establishment, a decrease of impact and/or eradication of invaders (Dextrase and Mandrak, 2006). The evidence of successful eradication exists predominantly for terrestrial non-native species when successful methods include catching/trapping, poisoning, sterilization, or a combination (Siefkes, 2017; Huntley, 2023). On the other hand, these reports are rather unique and difficult to transfer aquatic ecosystems.

The round goby (*Neogobius melanostomus*) is included in the list of one hundred most invasive species in Europe (Vilà et al., 2009) and is listed as an invasive species in the Global Invasive Species Database (GISD). It colonized basins of numerous European rivers, the Baltic Sea, and all lakes belonging to the Laurentian Great Lakes system including their tributaries (Charlebois et al., 1997). In all invaded sites, round goby has rapidly reached high abundance with a dominant status in near-shore water zones and is distinguished by a wide range of negative impacts on native biota (Lee and Johnson, 2005; Pennuto et al., 2012). Since there is no evidence of possible eradication, we still depend on prevention and a precise assessment of the impact of the round goby in colonized areas without further negative anthropogenic effects to highlight its potential risk to less affected pristine ecosystems and to set regulations, restrictions, and management measures leading to at least partial reduction of its impact.

Functional response of the round goby

The results across the invaded regions showed a remarkably broad diet niche of the round goby. Indeed, in our experiments, the round goby showed a strong interaction manifested by type II functional responses rate with all tested prey species, i.e. crustaceans – waterlouse (*Asellus aquaticus*), marbled crayfish (*Procambarus virginalis*) (**Chapter 2 and 3**), and insects – chironomids larvae (**Chapter 4**). These findings suggest a strong top-down effect on native prey species. Type II functional response was also reported in other studies with gammarids (Laverty et al., 2017) or fish larvae (Gebauer et al., 2018, 2019) as prey organisms. Type II functional response is the most common for predators and is sometimes associated with the destabilization effect of a predator on prey assemblage (Dick et al., 2014). However, that must be interpreted cautiously, as type II is also associated with experimental conditions, which can limit prey defenses because of low habitat complexity (Dunn and Hovel, 2020). Nevertheless, the round goby exhibits type II FR even in highly complex conditions (Gebauer et al., 2019), including our experiments, where chironomids larvae were able to burry in sand or hide below the stones and yet type II functional response best fitted our data sets. Moreover, the comparative functional response approach (CFRA) is built up to compare different species or factors where simplification and/or restriction of other factors is crucial to reveal advantages that characterize and determine invasive species and their predominance on native analogs (Dick et al., 2014).

The foraging of the round goby in multiple prey systems

Compared to laboratory conditions, the areas colonized by the round goby usually offer a wider range of benthic prey (Pennuto et al., 2010; Števove and Kováč, 2013). Indeed, the multi-prey systems include many interactions among predators and prey (Colton, 1987). If one prey is close to depletion, the predator switches to another, more abundant prey to avoid losing time by searching for a less abundant one (Sih et al., 2010). Therefore, even in the case of strong interaction manifested by type II functional response, where the predator successfully utilizes prey in low abundance, the impact of a generalist predator may be split among other prey in multiple-prey systems (Lawton et al., 1974; Jeschke and Trollrian, 2000). Indeed, the round goby foraging is density-dependent (Diggins et al., 2002; Polačik et al., 2009; Henseler et al., 2021) thus its diet composition reflects the composition of benthic invertebrates. On the other hand, the round goby showed dietary preferences for crayfish compared to isopods in our study, which was observed only in the highest abundance (**Chapter 2**). However, such a phenomenon can hardly ever play an important role in natural conditions of functional ecosystems, usually with naturally lower prey abundance and a wider prey species spectrum. That is in line with a broad diet niche of the round goby across colonized regions (Pettitt-Wade et al., 2015; Števove and Kováč, 2016). However, the current worldwide condition of freshwater systems is alarming because of homogenization, fragmentation, and pollution (Dextrase and Mandrak, 2006; Dudgeon et al., 2006; Arya, 2021). Therefore, some vulnerable benthic invertebrates in those anthropogenically strongly affected systems can be seriously endangered if they must, in addition to that, face a higher consumption rate from invasive predators than from native analogs co-evolving with them for a long time (Bollache et al., 2008; Barrios-O'Neill et al., 2016; Laverty et al., 2017).

That can seriously threaten endangered invertebrate groups such as crayfish, which are already highly affected by crayfish plague, or presence and competition for food and space with other invasive crayfish analogs (Edwards et al., 2009; Richman et al., 2015). The round goby exhibits a higher efficiency in utilizing crayfish at low density compared to isopods. The cumulative attack rate in multi-prey systems changes depending on the prey ratio but mainly increases if one of the offered prey predominates over the other (**Chapter 2**). The addition of another prey to the predator-prey system leads to additional interactions among prey and their behavioral changes (Colton, 1987). We assume increasing vulnerability of one of the offered prey, especially isopods, in the presence of prevailing crayfish because of some hardly predicted interactions between two prey types. Similarly, the effect was described in a multi-predator system, whereas the defense of prey against one predator can make the prey vulnerable to another predator (Preisser et al., 2005). On the contrary, the round goby handling time is prolonged in multi-prey systems, thus decreasing the maximal feeding rate. While switching the round goby to another prey can decrease the consumption rate, the attack rate is influenced by more factors and interactions, which should be an object of future research (**Chapter 2**).

Moreover, the notorious tail-flip defense of crayfish does not change the foraging efficiency or capacity of the round goby towards crayfish compared with isopods (**Chapter 2**), at least in early life crayfish stages, which are more vulnerable because of small body size. Indeed, the crayfish are rather sporadically found in the round goby diet (Shemonaev and Kirilenko, 2009; Kirilenko and Shemonaev, 2012). However, this is likely to be related to the current critical status of the native crayfish populations in Europe (Richman et al., 2015) rather than to avoid this prey, as in our study the round goby showed high efficiency in utilizing crayfish. This finding is alarming, since smaller lotic ecosystems like small rivers and streams, which represent the last refuges of the native crayfish populations, are currently targets of more frequent round goby invasions or seasonal migrations from colonized main rivers or lakes (Krakowiak and Pennuto, 2008; Christoffersen et al., 2019; Glenn and Pennuto, 2023). Together with a lower reproduction rate of crayfish compared to other crustaceans usually preyed by round goby such as amphipods or isopods (Vašek et al., 2014; Števove and Kováč, 2016), the round goby can represent a serious threat to native crayfish populations.

Role of body size and population structure in the round goby consumption rate

The predator-prey system includes complex interactions, including an offensive and defensive arms race between predator and prey (Sih et al., 2010). This system can be simplified for the comparative functional response approach to determine the reason for the higher efficiency of invasive, emergent, or potentially invasive species compared to analogous ones (Dick et al., 2014). However, also other factors should be considered for a more precise estimation of invasive species impact in a real locality (Parker et al., 1999). One of these crucial factors is the abundance/ population size of invasive species incorporated into the new metric of the Impact potential (Dick et al., 2017; Laverty et al., 2017; Dickey et al., 2020). However, we assume that body size is of similar importance as another crucial factor.

Indeed, except for the smaller tributaries, the round goby spreads continually to the new localities (George et al., 2021; Uspenskiy et al., 2021). However, these pioneering populations constitute the invasive front, displaying a range of differences compared to the established populations, e.g. larger size, higher metabolism rate, higher fitness, and different size composition in populations (Brandner et al., 2013; Myles-Gonzalez et al., 2015; Azour et al., 2015). These attributes, mainly individual body size, can change many physiological as well as overall environmental processes (Weitz and Levin, 2006), resulting in significantly changed predators' per-capita foraging efficiency and capacity (Mittelbach, 1981; De Roos et al., 2003). Moreover, body size and related diet composition influence the trophic position of the round gobies (Ng et al., 2008). Previously, the predator body size dependence of functional response in frogs was determined (Thorp et al., 2018). Despite this, many experiments were conducted with only one size cohort of predator, overlooking other size cohorts and their potential different effect. Those can lead to over- or underestimation of predator foraging efficiency at the per-capita level, which can even be pronounced at the population level.

In our study, the comparison of functional response confirmed significant differences in per-capita foraging efficiency among three round goby size classes that covered the body size spectrum of the round goby preyed on isopods/amphipods in the invaded localities. The body size dependence of functional responses was previously determined in other fishes (Werner, 1974; Mittelbach, 1981). Indeed, the big and medium-sized classes of the round goby achieved higher maximum feeding rates compared to the size cohort of small individuals (**Chapter 3**). Therefore, the bigger individuals represent a higher risk for the examined isopods. However, the biggest individuals in the population usually do not reach the abundance of smaller-sized cohorts usually formed by juveniles (Šlapanský et al., 2017). Thus, the lower per-capita efficiency of smaller individuals can be compensated by their higher abundance in the wild. This trend was observed in the round goby population in the Czech section of the Elbe River close to the borders with Germany. The smaller individuals reached the highest impact potential compared to large individuals with the lowest impact potential despite the high per-capita foraging efficiency. Regardless of population size structure, only overall abundance is commonly used for impact potential calculation. Nevertheless, our results explicitly show that omitting the round goby population structure can lead to overestimating its overall ecological impact. Although, in our study, the overestimation rate is not significant (**Chapter 3**), at least two factors should be considered before calculating impact potential when omitting the round goby population structure. Firstly, a type of prey that should be consumed by the entire size spectrum or the size range for which the impact potential will be calculated. Secondly, a medium-sized cohort should be used for the experiment, not a small one, which is the most abundant class, or a large one, which is the less abundant cohort. Hence, if we calculate the per-capita consumption rate of medium-sized individuals for which the chosen prey represents the optimal prey item, then we probably underestimate the impact of the small-sized cohort and simultaneously overestimate the impact potential of the large-sized cohort. To sum up, incorrectly chosen prey or predator (out of average/ most abundant cohort) size can lead to a more noticeable misestimation of the round goby impact potential.

The non-consumptive effects in the round goby

Generally, considering the trophic position in the native area, gobies play an important role in food webs, especially in marine ecosystems (Zander, 2011). However, outside of the native areas, their incorporation into food webs depends on many factors. The long-term co-evolution between native prey and predator is lacking in interaction with new species. The native prey can be naïve towards non-native predators, and vice versa, the native predator can be unable to prey on invasive prey because of missing experience/co-evolution (Sih et al., 2010). Occasionally, the naivety of prey can lead to a significant mortality rate, mainly in areas inhabited by species that evolved in conditions without predators (Bergstrom and Mensinger, 2009; Huntley, 2023). Even in a balanced environment without non-native species, high mortality of prey by predation can occur after certain triggers favourable to predators against the defense of prey (Kruuk, 1972; Fantinou et al., 2008). Under certain, often extraordinary conditions, such as low temperatures and dark stormy nights (Kruuk, 1972; Jędrzejewska and Jędrzejewski, 1989), the high availability of prey and predators' killing instinct resulted in so-called non-consumptive mortality, when part of the caught prey is not consumed, only killed (Kruuk, 1972). Within our study, we detected this behavior in the round goby preying on isopods and the early stages of crayfish. Although non-consumptive mortality increased with the increasing density of prey, no species-specific trend was found between the two prey types (**Chapter 2**). It is probably a bias of experimental conditions that was not detected during our other experiments. However, its possible occurrence in the field during some extraordinal event cannot be overlooked.

Except for non-consumptive mortality, the non-consumptive effect (NCE), another element of the predator effect, was described in the round goby towards benthic organisms (Pennuto and Keppler, 2008; Richter et al., 2022; Musil et al., 2023). Indeed, naive prey lacking experience with the round goby is susceptible to predator consumption (Sih et al., 2010). However, experienced prey can recognize predator-based visual or chemical signals (Ferrari et al., 2010; Richter et al., 2022). Mainly chemical cues transported in rivers for a long distance with longer efficiency (Brown et al., 1997) can play an important role in effective prey defense. Although prey can avoid consumption, it pays the cost for lower activity, longer time in the shelter, etc. (Rahel and Stein 1988; Preisser et al., 2005; Mitchell and Harborne, 2020), which can negatively influence its fitness (Preisser et al., 2005). This effect can be described as NCE. Indeed, the round goby itself must face both consumptive effect (CE) (Reyjol et al., 2010; Hares et al., 2015; Hempel et al., 2016; Mikl et al., 2017) and NCE (Pūtys et al. 2015; Galli et al. 2023) in invaded regions. However, small body size, high abundance, and lower mobility related to undeveloped swim bladders usually make the round goby an easy catch for higher trophic levels. Similarly, the abundance of the round goby in fish communities shortly after introduction (Johnson et al., 2005; Pennuto et al., 2012; Brandner et al., 2013) makes the species sometimes a dominant diet item of many piscivorous species, including birds (Jakubas

2004), snakes (King et al., 2006), but predominantly fishes (Reyjol et al., 2010; Mikl et al., 2017). Fish foraging in near-shore zones, such as burbot (*Lota lota*), is an effective predator of the round goby (Madenjian et al., 2011; Mikl et al., 2017), with a high potential to control populations of this non-native fish. Six predators in the Dyje River (Danube basin) annually consumed approximately 52% of the round goby biomass, while the burbot itself consumed 42% (Mikl et al., 2017). The high CE of burbot probably contributed to the stabilization of an increasing round goby population in eastern Lake Erie (Madenjian et al., 2011). However, such reports are still rare in invaded regions.

Nevertheless, the impact of round goby as a mesopredator can be modified by native apex predators via NCE. Several studies point to an equal role of visual and olfactory stimuli in gobiids (Utne and Bacchi, 1997; McCormick and Manassa, 2008). Despite that, gobiids can effectively detect predator-born chemical or alarm cues. The round goby is considered a visual predator (Števove and Kováč, 2016), and visual contact is crucial in reproduction strategy as well (Yavno and Corkum, 2010). However, even the round goby reacts to chemical alarm cues by increasing operculum movement (Pūtys et al., 2015) or cortisol level in blood (Galli et al., 2023). Our results showed that consumption rate, which represents another crucial factor affecting the impact of the round goby in the invaded ecosystems, is also negatively influenced by apex predator odor in combination with alarm cues, mainly in low prey availability/density (Chapter 4). Our experiment included only one apex predator – European eel (*Anguilla anguilla*) but at a higher density compared to the common abundance in European rivers. On the other hand, the natural ecosystems include multiple predators. Therefore, we assume that this NCE can occur in natural ecosystems. However, populations of apex predators in freshwaters are recently under intensive stress caused by angling, commercial fisheries, and homogenization of rivers which has negative impacts on the predators' populations, manifested in their limited natural potential to control round goby (Winter et al., 2006; Stapanian et al., 2010; Oeberst et al., 2012).

Worldwide, freshwater ecosystems are under high pressure due to human activities (Dextrase and Mandrak, 2006; Dudgeon et al., 2006). Increasing global trade has accelerated the introduction and spreading of invasive species (Westphal et al., 2008). The round goby, which is under fisheries pressure in its native range of the Ponto-Caspian water systems (Moskal'kova, 1996), has spread in most of European main rivers (Verreycken et al., 2011; Hempel and Thiel, 2013; Manné et al., 2013) and Laurentian Great Lakes water system with its tributaries on the other side of the Atlantic Ocean within just three decades (Charlebois et al., 1997). Many studies show the benefits of functional and stable freshwater ecosystems regarding low rates of biological invasions (Stachowicz et al., 2002; Olden et al., 2004; Wallach et al., 2010). However, noise pollution (Fernandez-Declerck et al., 2023), free ecosystem niches, and missing apex predators can facilitate invasive species' establishment and their accelerated spread (Weis, 2011). That is in line with our results of NCE of the European eel upon CE of the round goby (**Chapter 4**). There is no evidence of possible eradication or elimination of the round goby populations in any invaded regions. However, reducing the round goby impact through CE and NCE of native predators appears to be an effective tool to regulate the negative impact of the round goby in invaded freshwater ecosystems (Madenjian et al., 2011; Hempel et al., 2016). This approach, however, relies on restoring predator populations, especially through restoring freshwater ecosystems' functionality and stability together with the regulation of angling and commercial fishery (Winter et al., 2006; Stapanian et al., 2010; Oeberst et al., 2012).

Conclusion

- The round goby shows a high interaction strength upon all tested benthic preys (**Chapter 2–4**).
- The antipredator tail-flip behavior of early ontogenetic stages of crayfish appears to be insufficient against the round goby predation pressure (**Chapter 2**).
- The round goby exhibited equal functional response towards isopods and crayfish. Regarding the insufficient antipredator behavior of crayfishes and their lower reproduction rate compared to other members of macro zoobenthos, the round goby represents a serious risk of endangering native crayfish populations (**Chapter 2**).
- Except for consumption mortality, the round goby can display non-consumptive mortality upon its prey in some circumstances in laboratory conditions (**Chapter 2**). Future research should examine its role in the field.
- The individual body size is an important factor affecting handling time and attack rate in the round goby (**Chapter 3**).
- The most abundant size cohort in the invaded localities in the Elbe R., i.e. small-sized cohort, reached the lower foraging capacity, while the large-sized individuals manifested the highest foraging capacity. Therefore, omitting the individual body size in the calculation of the impact potential of the round goby upon invaded ecosystems can lead to over- or under-estimation of its entire population impact. The significance of this deviation depends on the population size structure and chosen size cohort for the calculation of the per-capita consumption rate (**Chapter 3)**.
- The presence of native apex predators can negatively affect the foraging capacity and efficiency of the round goby as mesopredator (**Chapter 4**).
- The restoring apex predator populations can play an important role in reducing the population size and the overall negative impact of the round goby upon invaded freshwaters (**Chapter 4**).

Limitation and future studies

Our studies were built up to the versatile method of comparative functional response, which included experiments in less or more simplified conditions. This allowed us to determine some aspects of the round goby foraging behaviour without limiting a broad spectrum of variables complicating the interpretation and quantification of the role of some chosen biotic factors in the field. Based on our findings, we have been able to address the hypotheses that were previously defined. However, further research is necessary to fully understand specific issues and their application to the field conditions, which contains a broad spectrum of conditions of different habitats across the round goby colonized areas. Resolving these issues should involve a combination of experiments conducted in laboratory settings as well as in semi-natural or entirely natural conditions.

The high rate of the round goby NCM on both crayfish and isopods in **Chapter 2** was not observed in any other study. However, we assumed two main aspects contributing to the high rate of NCM based on the comparison with conditions in **Chapter 3**, where the round goby exhibited minor NCM upon isopods. Firstly, unexpected interactions in multiple-prey systems, where one prey could interact, made the second prey more vulnerable to predation. The second considered aspect should be a chosen proportion between prey size and the round goby's body size. Nevertheless, future studies should focus on both considered aspects and, thus, the possible role of the round goby NCM in natural conditions.

Additionally, our results confirmed a relevant effect of chemical cues on the foraging efficiency and capacity of the round goby as a mesopredator in the invaded ecosystems (**Chapter 4**). However, we were not able to distinguish the effects of predator-born cues and chemical stimuli originating from stressed or attacked prey from each other. Our findings also raised some unanswered questions, such as the effective concentration of chemical cues, the potential for round gobies to develop resistance to long-term exposure to chemical cues in natural conditions, and their possible synergies with visual or chemical cues of conspecific or heterospecific apex predators. Therefore, the effective management and prediction of the round goby's impact upon invaded freshwaters remain challenging tasks for future research on this highly invasive fish species.

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English summary

Foraging efficiency and capacity of non-native round goby (*Neogobius melanostomus*) under various biotic conditions

Pavel Franta

The worldwide trend of continually increasing records of non-native species has resulted in an increasing number of potentially invasive species that have a dramatic impact on native biota. In the case of a predator introduction, its impact is mainly displayed via the consumption rate of native species. The non-native fish – round goby (*Neogobius melanostomus*) poses a serious threat to native macrozoobenthos, which represents a main diet component in invaded or seasonally colonized regions. Therefore, a quantification of the consumption rate of invasive, emergent, or potentially invasive predators is a keystone step to their effective management and prevention of continuous spreading. The functional response (FR) evaluating predator-prey interaction based on predator foraging efficiency has become an effective tool in ecological modelling to determine a predator foraging efficiency. Moreover, this method allows to experimentally determine the foraging efficiency of the invasive species under various biotic factors, as in the present Ph.D. thesis, or to compare the impact of non-native species with its native analog. In the present thesis, various prey types in density gradients were offered to the round goby to determine the FR and impact potential (IP) of this species. Based on the results, the foraging efficiency, foraging capacity in multiple prey systems as well as under stress caused by presence of apex predator or regarding population size structure in the round goby were quantified.

The round goby showed a type II FR in all experiments, including different prey types, such as isopods, or chironomid larvae or early stages of crayfish. Neither the body size of the round goby as a predator nor the tail-flip antipredator strategy of the crayfish as a prey changed the type of FR. The round goby showed equal handling time and significantly lower attack rate to isopods than crayfish when both prey types were offered separately. The combination of both prey types led to prolonging the round goby handling time and increased or decreased attack rate depending on the ratio of both preys. Despite that, no prey selectivity was detected in the round goby except for the highest prey density (100 individuals.box^{-1}), where crayfish were preferred. The round goby can seriously threaten native endangered crayfish species in smaller tributaries where it continually or seasonally spreads, regarding its equal foraging towards tested prey and lower reproduction rate of crayfishes.

Our results also confirmed that the predator (round goby) body size represents an important parameter influencing its foraging efficiency towards isopods. Small individuals showed significantly lower attack rates and longer handling times than large ones. However, the lower *per capita* foraging efficiency of the small individuals is compensated by their numerical dominance in population structure. Therefore, the small-sized cohort of the round goby reached the highest overall impact potential (IP) compared to medium or large-sized cohorts with lower proportional abundance in the investigated population. Nevertheless, overlooking the body size structure of the round goby population in calculating the species IP led to only a minor overestimation of the IP in the investigated population. However, the body size cohort used to estimate the round goby IP should always be cautiously chosen reflecting body size structure of particular investigated population to prevent misestimation.

Although the round goby is a voracious predator of macrozoobenthos, our results showed that chemical cues signalizing predation risk by the apex predator (European eels) remarkably influenced both attack rate and handling time of the round goby as a mesopredator. The

chemical cues of the European eel combined with conspecific alarm cues significantly decreased the attack rate of the round goby. On the contrary, the handling time was significantly prolonged if the round goby was exposed to chemical cues of European eel fed by heterospecific prey. These findings suggest that optimized management of apex predator populations might lead to a decrease in the impact of the round goby at the invaded areas driven by its lowered consumption rate.

The round goby's non-selective foraging and effective consumption of a wide prey spectrum make this fish a serious threat to native freshwater biota. Even small round goby individuals having lower consumption rate may reach a high total impact potential upon invaded ecosystem regarding their abundance population. Despite that, it seems that native apex predators through their non-consumptive effect can noticeably decrease the overall round goby's negative impact. However, that relies on rehabilitating the native apex predator population, which depends on restoring freshwater ecosystems currently facing high anthropogenic pressures.

Czech summary

Potravní efektivita a kapacita nepůvodního hlaváče černoústého (*Neogobius melanostomus*) v různých biotických podmínkách

Pavel Franta

Celosvětový trend narůstajícího počtu introdukcí má za následek rostoucí počet potenciálně invazních druhů, které mají dramatický dopad na původní biotu. V případě introdukce predátora se jeho dopad projevuje zejména prostřednictvím predace původních druhů. Nepůvodní ryba hlaváč černoústý (*Neogobius melanostomus*) představuje zásadní riziko pro původní makrozoobentos, hlavní složku jeho potravy v kolonizovaných, sezónně obývaných oblastech. Právě proto je kvantifikace predační míry u teprve se formujících, potenciálně invazních nebo invazních predátorů klíčová pro jejich účinný management a prevenci jejich dalšího šíření. Funkční odpověď (FR – z anglického *functional response*), popisující interakci predátor-kořist na základě efektivity predátora využívat kořist v různých hustotách, se stala účinným nástrojem ekologického modelování pro stanovení efektivity predátora ve využívání potravního zdroje. Navíc tato metoda umožňuje porovnání efektivity invazních druhů využívat kořist s původními analogickými druhy nebo v závislosti na různých biotických faktorech, jako tomu bylo v předložené disertační práci. Různá kořist nabízená v početnostním gradientu byla vystavena predačnímu tlaku hlaváče černoústého pro stanovení jeho FR a potenciálního dopadu (IP – z anglického *impact potential*). Na základě těchto výsledků byla kvantifikována potravní efektivita a kapacita hlaváče černoústého využívat kořist v potravním systému s více typy kořisti, pod vlivem stresu vyvolaného přítomností vrcholového predátora nebo s přihlédnutím k velikostní struktuře jeho populace na invadovaných lokalitách.

Hlaváč černoústý vykazoval typ II FR ve všech experimentech, které zahrnovaly různé typy kořisti, jako např. stejnonožce, larvy pakomárů či raná vývojová stadia raků. Ani velikost hlaváče černoústého ani obranná úniková reakce raků tzv. *„tail-flip“* neměla vliv na typ FR. Hlaváč černoústý vykazoval srovnatelnou dobu zpracování a signifikantně nižší efektivitu vyhledávání u stejnonožců ve srovnání s raky, pokud oba typy kořisti byly nabízeny odděleně. Kombinace obou kořistí však vedla k prodloužení doby zpracování a snížení nebo zvýšení efektivity vyhledávání kořisti v závislosti na početnostním poměru zastoupení obou kořistí. Přesto nebyla u hlaváče černoústého zaznamenána žádná selektivita kořisti, až na nejvyšší hustotu (100 jedinců.experimentální aréna^{-1}), při které preferoval hlaváč raky. S ohledem na vyrovnanou potravní efektivitu hlaváče černoústého využívat oba typy kořistí a nižší reprodukční kapacitu raků, může hlaváč černoústý představovat zásadní riziko ohrožující existenci ohrožených původních druhů raků v menších přítocích velkých řek, do kterých se kontinuálně nebo sezónně šíří.

Naše výsledky také potvrzují, že velikost predátora (hlaváče černoústého) je důležitým kritériem ovlivňující jeho efektivitu využívat stejnonožce jako potravu. Malí jedinci vykazovali nižší efektivitu vyhledávání kořisti, a naopak delší dobu zpracování kořisti než velcí jedinci hlaváče černoústého. Avšak nižší *per capita* efektivita malých jedinců je kompenzována jejich početnostní převahou v populaci hlaváče na invadovaných lokalitách. Proto velikostní kohorta menších jedinců dosahuje vyšší hodnoty IP ve srovnání s velikostními kohortami středně velkých nebo velkých jedinců vykazujících nižší početnostní zastoupením ve zkoumaných populacích hlaváčů. Nicméně zanedbání velikostní distribuce jedinců v populaci hlaváče černoústého při výpočtu IP vedlo pouze k nepatrnému nadhodnocení IP zkoumané populace. Avšak velikostní kohorta by měla být pro odhad IP u hlaváče černoústého vždy vybírána s ohledem na velikostní strukturu dané populace, jako prevence chybného odhadu IP.

Ačkoli je hlaváč černoústý žravý predátor makrozoobentosu, naše výsledky ukázaly, že chemické podněty signalizující predační risk v podobě přítomnosti vyššího (vrcholového) predátora (úhoře říčního) ovlivňují u hlaváče černoústého jako mezopredátora (níže postaveného predátora) jak efektivitu vyhledávání kořisti, tak její dobu zpracování. Chemické podněty původem od vrcholového predátora (úhoře říčního) společně s konspecifickými alarmujícími podněty (signály pocházejícími ze zraněné či zabité kořisti náležící ke stejnému druhu jako stresovaný objekt) signifikantně snížily efektivitu vyhledávání kořisti u hlaváče černoústého. Naopak doba zpracování kořisti byla u hlaváče černoústého signifikantně delší, pokud byl vystaven chemickým signálům od vrcholového predátora (úhoře říčního) krmeného heterospecifickou kořistí (potravou nenáležící ke stejnému druhu jako stresovaný objekt). Tyto výsledky tak poukazují na nezbytnost zavedení udržitelného managementu pro obnovení/posílení populací vrcholových predátorů za účelem snížení celkového negativního dopadu hlaváče černoústého na invadované oblasti skrze snížení jeho početnosti i míry žravosti.

Vysoce efektivní a neselektivní využívání široké škály potravy dělá z hlaváče černoústého skutečnou hrozbu pro původní sladkovodní biotu. Dokonce i malí jedinci hlaváče černoústého mající nižší *per capita* predační kapacitu dosahují v konečném důsledku vysokého dopadu s ohledem na jejich vysokou početnost v populaci. Přesto se zdá, že původní predátoři prostřednictvím svých chemických signálů mohou signifikantně snížit celkový negativní dopad hlaváče černoústého. Avšak reálný výsledek závisí na míře obnovení populací původních predátorů, která je podmíněna znovuobnovením funkčnosti sladkovodních ekosystémů, které v současnosti čelí značnému antropogennímu tlaku.

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List of publications

Peer reviewed journals with IF

Franta, P., Gebauer, R., Veselý, L., Szydłowska, N.Z., Drozd, B., 2023. Size-dependent functional response of the round goby *Neogobius melanostomus*; implications for more accurate impact potential calculation. Aquatic Invasions 18, 507–520. (IF 2022 = 1.600)

Franta, P., Gebauer, R., Veselý, L., Buřič, M., Szydłowska, N.Z., Drozd, B., 2021. The invasive round goby *Neogobius melanostomus* as a potential threat to native crayfish populations. Animals 11, 2377. (IF 2020 = 2.752)

Patoka, J., Buřič, M., Kolář, V., Bláha, M., Petrtýl, M., **Franta, P.**, Tropek, R., Kalous, L., Petrusek, A., Kouba, A., 2016. Predictions of marbled crayfish establishment in conurbations fulfilled: evidences from the Czech Republic. Biologia 71, 1380–1385. (IF 2015 = 0.719)

Manuscripts prepared for submission to peer-reviewed journals with IF

Franta, P., Szydłowska, N.Z., Kolář, V., Gebauer, R., Drozd, B., 2024. The trade-off between foraging efficiency maximizing and predator avoidance in the round goby (*Neogobius melanostomus*): To be scared or fine? Manuscript.

Szydłowska, N.Z., **Franta, P.**, Let, M., Mikšovská, V., Buřič, M., Drozd, B., 2024. Risk perception: chemical stimuli in predator detection and feeding behaviour of the invasive round goby *Neogobius melanostomus*. Animals – submitted.

Szydłowska, N.Z., Let, M., **Franta, P.,** Buřič, M., Worischka S., Richter L., Drozd B., 2024. Gut evacuation rate as a tool for revealing feeding patterns in the invasive round goby (*Neogobius melanostomus*) under different feeding modes, food types and temperatures. Aquatic Invasions – under review.

Šindler, M., Buřič, M., Plesch, M., **Franta, P.,** Drozd, B., 2024. Effectiveness of the mass marking of sterlet (*A. ruthenus*) juveniles with alizarin red S staining and detection methods usable for field determination. Fisheries Management and Ecology – submitted.

Peer-reviewed journals without IF

Kolář, V., **Franta, P.**, Hesoun, P., 2022. Water beetles and bugs of selected protected areas in South Bohemia V. Sborník Jihočeského muzea v Českých Budějovicích 62, 49–60.

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Abstracts and conference proceedings

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Šindler, M., Plesch, M., **Franta, P.,** Drozd, B., 2020. Estimation of an effectiveness and detectabbility of the sterlet (*A. ruthenus*) juveniles mass marking using alizarin red **S** for species management in the Slovak section of the Danube River. In: Holubová, M., Blabolil, P. (Eds), Abstracts from 17. Czech Ichthyological Conference, November 4–5, 2020, České Budějovice, Czech Republic, p. 7. (oral presentation)

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Franta, P., Gebauer, R., Veselý, L., Buřič, M., Drozd, B., 2019. Ecological impact of the round goby *Neogobius melanostomus* (Pallas, 1814) towards hard-bodied benthic prey in dependence upon its type, ratio and density: functional response in lab. In: Perić, M.S., Miliša, M., Gračan, R., Ivković, M., Buj, I., Stanković, V.M. (Eds), 11th Symposium for European Freshwater Sciences Abstract book. Zagreb, Croatia, June 30 – July 5, 2019, 146 p. (oral presentation).

Franta, P., Drozd, B., Kouril, J., Stejskal, V., Prokesova, M., 2014. Effect of water temperature on early ontogeny of African sharptooth catfish (*Clarias gariepinus*) during embryonic development. In: Abstracts from 14. Czech Ichthyological Conference, October 1–3, 2014, Vodňany, Czech Republic, 47 p. (poster presentation)

Training and supervision plan during study

Name	Pavel Franta
Research department	2018–2024 Laboratory of Freshwater Ecosystems of FFPW
Supervisor	Bořek Drozd Ph.D.
Period	12th February 2018 until September 2024

Ph.D. courses	**Year**
Biostatistics	2018
Ichthyology and fish taxonomy	2018
Applied hydrobiology	2018
Basic of scientific communication	2019
Fish ecology	2020
English language	2021

Scientific seminars	**Year**
Seminar days of FFPW	2019 2020 2021 2022

International conferences	**Year**
Franta, P., Gebauer, R., Veselý, L., Buřič, M., Drozd, B., 2019. Ecological impact of the round goby *Neogobius melanostomus* (Pallas, 1814) towards hard-bodied benthic prey in dependence upon its type, ratio and density: functional response in lab. In: Perić, M.S., Miliša, M., Gračan, R., Ivković, M., Buj, I., Stanković, V. M., (Eds), 11th Symposium for European Freshwater Sciences Abstract book. Zagreb, Croatia, June 30 – July 5, 2019, 146 p. (oral presentation)	2019

Pedagogical activities	**Year**
Supervising a block of practice exercises for students of the bachelor study programme within the subject Ecology, FFPW USB, in range of 45 teaching hours	2018–2020
Assisting in practice exercises for students of the bachelor study programme within the subject, Zoology, FFPW USB, in range of 45 teaching hours	2018–2020
Leading of project entitled Experimental estimation of gut evacuation rate in the invasive fish – round goby (*Neogobius melanostomus*)	2019
Supervision of one B.Sc. thesis	2020
Consultancy of two B.Sc. theses	2019–2022

Curriculum vitae

PERSONAL INFORMATION

Name: Pavel
Surname: Franta
Title: Dipl.-Ing.
Born: 20th February 1991, Jindřichův Hradec, Czech Republic
Nationality: Czech
Languages: Czech, English (B2 level – IELTS certificate)
Contact: pfranta@frov.jcu.cz

PRESENT POSITION

2021–present	Technician in the Laboratory of Nutrition, University of South Bohemia in České Budějovice, Faculty of Fisheries and Protection of Waters, Institute of Aquaculture and Protection of Waters

EDUCATION

2018 – present	Ph.D. student in Fishery, Faculty of Fisheries and Protection of Waters, University of South Bohemia, Ceske Budejovice, Czech Republic
2014–2017	M.Sc., Fishery, Faculty of Fisheries and Protection of Waters, University of South Bohemia, Ceske Budejovice, Czech Republic
2010–2014	B.Sc., Fishery, Faculty of Fisheries and Protection of Waters, University of South Bohemia, Ceske Budejovice, Czech Republic
2006–2010	High school in Veselí and Lužnicí, specialization: Environmental protection and creation

COMPLETED COURSES

3/6/2022	Certificate of competence for drivers and attendants pursuant to Article 17(2) of Council Regulation (EC) No 1/2005
29/3 – 30/3/2022	Certificate of professional competence for the handling of substances for plant pests and disease control according to Act No 326/2004 On Phytosanitary Care
15/3/2022	Certificate of handling of dangerous chemical substances and mixtures
28/2 – 4/3/2022	Certification of acquiring the qualification and professional competence (designing experiments and experimental projects) in the field of experimental animal use according to Act No. 246/1992 On the Protection of Animals Against Cruelty
19/04 – 20/04/2018	Electrotechnical qualification, Vodňany, Czech Republic