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Foraging behavior of non-indigenous gobiid fish species

Potravní chování nepůvodních druhů hlaváčovitých ryb

Radek Gebauer

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CHAPTER 1

GENERAL INTRODUCTION

1.1. ALIEN SPECIES

Biogeographic dispersal barriers formed by natural forces over billions of years have been substantially weakened or disrupted by human activity, particularly in recent centuries (Blackburn et al., 2011; Capinha et al., 2015). As a consequence, global homogenization of previously isolated biota have been observed at an ever-increasing rate (Hulme, 2009; Meyerson and Mooney, 2007; Seebens et al., 2017b) showing no sign of saturation (Seebens et al., 2017a).

Global scale of alien species invasions is becoming more and more evident in the beginning of the new millennium being invoked as one of the major elements of human-induced global environmental change (Vitousek et al., 1997), which are responsible for biodiversity decline at global, regional and local scales (Hooper et al., 2012; Mokany et al., 2012; Sala et al., 2000). Furthermore, newly introduced species are causing severe alterations in ecosystem functioning (Simberloff et al., 2013) accompanied by ecosystem services losses (Pejchar and Mooney, 2009). Biological invasions, however, are of great concern not only for biologists, but also for the whole society, as they generate substantial economic cost associated with commodity losses as well as with eradication and mitigation of alien species (Pimentel et al., 2000; Pimentel et al., 2005; Vilà et al., 2010). Finally, serious human and animal disease risks have emerged along with new introductions (Crowl et al., 2008; Juliano and Philip Lounibos, 2005; Mazza et al., 2014).

Although biological invasions became a rapidly growing research area with large body of literature, there are still gaps in predicting future invaders as well as their impact on native communities.

1.1.1. Terminology in the field of invasion biology

The terminology used in the field of invasion biology has been discussed at least since the middle of the 19th century (see Chew, 2006) and despite the number of recent attempts to standardize the terminology (Colautti and MacIsaac, 2004; Occhipinti-Ambrogi and Galil, 2004; Richardson et al., 2000), the scientists have not reached the consensus yet. In fact, the variety of terms has multiplied (Davis, 2009) owing to the increasing number of scientific articles in the field of invasion biology (Puth and Post, 2005; Ricciardi and MacIsaac, 2008). For example, searching the invasion literature Colautti and MacIsaac (2004) listed more than 30 terms to describe a species dispersing to new areas. Nevertheless, the unification of terminology is of particular importance, otherwise the communication among different parties involved, *e.g.* ecologists, biologists, management, political authorities, public entities *etc.*, can easily end up with misunderstandings. Here, I adapted the terminology used by Richardson et al. (2000) originally proposed for plant invasions.

1.1.2.Stages of the invasion process

The invasion process is characterized by a series of continuous stages (Richardson et al., 2000; Williamson and Fitter, 1996). Three elemental stages have been proposed: arrival, establishment and spread (Williamson, 1996), but some authors have proposed additional ones (Henderson et al., 2006). Within each stage, the organism is facing number of abiotic and biotic barriers (Richardson et al., 2000), where it can get stuck. *The tens rule* implies, that one of ten arriving organisms appear in the wild (Williamson, 1993). One of ten of those introduced become established and one of ten of those established become invasive (Williamson and Brown, 1986; Williamson and Fitter, 1996). This rule, however, is not applicable for vertebrates of which the probability of establishment and becoming invasive is much higher (Cassey, 2002; Jeschke and Strayer, 2005).

1.1.2.1. Dispersal and arrival

The first challenge faced by any alien species is surviving the trip (Davis, 2009). That means the geographical barrier is the first obstacle experienced by an organism before entering novel environment (Richardson et al., 2000). In a simplified classification scheme, Hulme et al. (2008) proposed three general ways that alien species enter a new area: importation of commodity, arrival of a transport vector, and natural spread. The dispersal capacity of alien species is an important attribute determining the ability to diffuse over certain distances (Hill et al., 1999; Lee, 2002). Nevertheless, recent studies have shown that even organisms with low dispersal capacity such as pathogens (Brown and Hovmøller, 2002), pollen and spores (Kellogg and Griffin, 2006), plant seeds (Muñoz et al., 2004; Nathan et al., 2008) or even small animals (van Leeuwen et al., 2013) can be transported by wind, water currents or migratory birds within as well as among continents. Indeed, Wyatt and Carlton (2002) pointed out the passive dispersal over long distance is more common in small organisms compared to larger ones. The dispersal capacity of organisms is, however, no longer the crucial characteristic of successful invader, as a vast majority of organisms is recently transported with human assistance both, intentionally and by accident (Grigorovich et al., 2003; Keller et al., 2007) reflecting the increase in global trade, transport and tourism (Bradley et al., 2012; Hulme, 2009; Westphal et al., 2008). This is apparent especially for alien marine, euryhaline and freshwater species, as shipping is considered a dominant global vector for their translocation (Molnar et al., 2008; Ricciardi, 2006).

Immediately after arrival, alien organisms face another barrier due to environmental and climatic conditions. Three scenarios are thus possible. Firstly, the environmental and/or climatic barrier prevents the arriving organism from surviving (Richardson et al., 2000). Secondly, the introduced taxon survives, but fails to maintain population over longer periods and therefore must rely on repeated introductions for its persistence (Richardson et al., 2000). And thirdly, if the environmental and climatic conditions fit the niche requirements of an alien species, the introduced species might spread with or even without acquiring new adaptations (Facon et al., 2006).

1.1.2.2. Establishment

Aliens that successfully arrived in a new, suitable, environment, *i.e.* in a locality with environmental and climatic conditions which they can tolerate, need to establish themselves, *i.e.* persist until they are able to reproduce. In this stage, they are referred to as organisms with casual or occasional distribution (Richardson et al., 2000). Outcome of the establishment process depends on several conditions. Features of receiving environment and so called propagule pressure are determined as the most important ones (Davis, 2009).

Propagule pressure, characterized as a number of introduced individuals at a new site and a number of introduction events, has been widely recognized as a primary indicator of the outcome of an establishment process (Lockwood et al., 2005; Lockwood et al., 2009). Indeed, many studies have found propagule pressure to be proportionally related to the success of alien species (Colautti et al., 2006; Kolar and Lodge, 2001; Lockwood et al., 2005). This is related to the concept of minimum viable population size used in conservation biology (Traill et al., 2007). That means the more individuals are released, the higher is the probability of surviving either environmental or demographic stochasticity, of overcoming Alee effect or of having sufficient genetic variability to adapt to the local conditions (Lockwood et al., 2005). However, several studies showed that the success may not be enhanced by releasing more individuals above the threshold, what suggests a sigmoidal relationship between propagule pressure and establishment success (Blackburn et al., 2009b). Cassey et al. (2004) and Blackburn et al. (2009a) observed variation in relationship between propagule pressure and establishment success among different bird families depending on the alien species traits.

Specific traits possessed by alien species favor the establishment rate. The likelihood of population establishment in novel environment is proportionally related to the breadth of habitat, and of dietary requirements of novel organism (Blackburn and Duncan, 2001; Blackburn et al., 2009a; Ficetola et al., 2009; Marchetti et al., 2004b). Another species traits enhancing the establishment chance are related to growth performance, *e.g.* growth rate, body size, brain size (Kolar and Lodge, 2002; Marchetti et al., 2004b; Sol et al., 2005), and life-history traits, *e.g.* parental care, egg size (Marchetti et al., 2004b; Olden et al., 2006). Phenotypic plasticity, *e.g.* changes in growth patterns (Losos et al., 2000), behavior (Cassey, 2002; Sol and Lefebvre, 2000) and energy allocation, is also referred to as a trait needed for successful colonization of new areas, because colonists must be able to cope with a range of environmental conditions (Mack et al., 1986). Indeed, compared to evolutionary adaptations, phenotypic adjustments can be made right away after arrival into the novel environment and therefore enhance the establishment chance (Davis, 2009).

Another factor influencing the establishment success are the features of receiving environment, *i.e.* invasibility, or invasion resistance (Davis et al., 2000; Levine and D'antonio, 1999). According to Williamson (1996) all communities are more or less invasible. Researchers have focused on several hypotheses to account for invasibility, such as diversity-invasibility hypothesis, fluctuating resources hypothesis, enemy released hypothesis *etc*.

The most reliable predictor of invasibility is resource availability (Davis, 2009). Temporal and spatial fluctuations in available resources and severe habitat disturbances create open ecological niches suitable for alien species (Marvier et al., 2004; Pyšek et al., 2010). Another feature of the locality influencing rate of invasibility is based on species and functional diversity, assuming that the species-rich environments hold fewer empty niches and hence fewer resources would be available for introduced species (Maron and Marler, 2007; Shea and Chesson, 2002). Nevertheless, this relationship may be reversed at more environmentally heterogeneous sites with low productivity because of providing a greater range of available niches (Davies et al., 2005; Tanentzap et al., 2010). Therefore Davis (2009) concluded the species and functional diversity have not been shown to be reliable predictors of invasibility. Biological interactions can limit the establishment and spread of alien species through predation on novel species (Keane and Crawley, 2002), *i.e.* biotic resistance of receiving environment. Biotic resistance can stem from community diversity (*e.g.*, Case, 1990; Stachowicz et al., 1999) or from abundant native predators or strong competitors independent of diversity (Crawley et al., 1999). Nevertheless, researchers have reached various results when evaluating the relationship of invasibility and biotic conditions of receiving environments and hence Davis (2009) concluded biotic resistance itself is not reliable predictors of invasibility.

1.1.2.3. Spread

After establishing a self-sustaining viable population that means overcoming reproductive barriers and creation of sufficiently numerous population, the alien becomes naturalized (Richardson et al., 2000). The main challenge for naturalized species is to persist and spread. In other words, this stage is characterized by repeated dispersal and establishment episodes of individual organisms (Davis, 2009).

The dispersal within new environment can be mediated by dispersal capacity of alien organism, human activity or mutualism (Havel and Medley, 2006; Lonsdale, 1999). Likewise in establishment process, the spread of alien organism is influenced by specific species traits, such as reproduction strategies (Kolar and Lodge, 2001; Rejmánek and Richardson, 1996), growth rate (van Kleunen et al., 2010), tolerance to wide-ranging environmental conditions (Kolar and Lodge, 2001) and phenotypic plasticity (Davidson et al., 2011), although exceptions are not rare (Davis, 2009).

Some alien species are capable of rapid spread within new environments. These species are often referred to as invasive, despite the non-fulfilment of actual term invasive (Davis, 2009; Richardson et al., 2000).

1.1.3. Ecological impacts of alien aquatic species

The introduction of alien species in the novel environment generates ecological impacts that can be classified as direct biotic interactions with the resident community (*e.g.* predation, competition, pathogens) or indirect effects on habitat conditions (*e.g.* alteration in habitat structure, turbidity; Crooks, 2002). Both, direct and indirect effects trigger changes in food webs and trophic cascades (Strayer, 2010) altering biodiversity, resident communities and biogeochemical processes in recipient ecosystems (Parker et al., 1999; Vitousek, 1990).

The direct effects of alien aquatic species are amplified by strong trophic links in aquatic environments. Alien species trigger distinct changes depending on their trophic position either by top-down (alien predators) or bottom-up (alien primary producers) control (Heath et al., 2014; Pace et al., 1999). For example, Ordóñez et al. (2010) documented decrease in abundance and richness of large-bodied zooplankton following the introduction of roach *Rutilus rutilus* (Linnaeus, 1758) and bleak *Alburnus alburnus* (Linnaeus, 1758). Ward and Ricciardi (2007), on the other hand, observed significant reduction in phytoplankton in ecosystems invaded by zebra mussel *Dreissena polymorpha* (Pallas, 1771). Indeed, these effects can be complex in ecosystems with multiple invaders. The invasion by round goby *Neogobius melanostomus* (Pallas, 1814) and dreissenids have resulted in several indirect effects altering nutrient and contaminant pathways (Hogan et al., 2008; Ng et al., 2008). Introduced predatory fish have also been found to elicit phenotypic changes among its prey including body shape changes, earlier ontogenetic diet shifts from zooplankton to benthos and poorer growth during their first growing season (Lippert et al., 2007).

Resources, spawning site and optimal habitat represent main subjects of competition among organisms (Davis, 2003; Sax and Gaines, 2008). Alien gobies have been often documented to outcompete natives (Bergstrom and Mensinger, 2009; van Kessel et al., 2011) displacing them into sub-optimal conditions, which may lead even to local extinction (Janssen and Jude, 2001; Lauer et al., 2004).

Indirect ecological impacts of aliens in aquatic ecosystems include habitat changes mediated by species which are able to substantially alter conditions in recipient ecosystem, *e.g.* water clarity, nutrients cycling, organic matter concentration (Jones et al., 1996). Matsuzaki et al. (2007) documented shifts in primary production from macrophytes- to phytoplankton-dominated turbid state following the introduction of common carp (*Cyprinus carpio*, Linnaeus, 1758).

1.1.4. Management of biological invasions

Management of biological invasions is a fundamental discipline in invasions biology fueled by substantial threats to ecology, economy and health risks (Davis, 2009). Management actions can be applied throughout the invasion process, *i.e.* from the initial dispersal to the naturalization and spread (Fowler et al., 2007). Successful management depends on an ability to model potential spread of alien species in various climatic and geographical ranges. This ability, however, depends largely upon knowledge of prior invasion history (Seebens et al., 2018). Important elements of species distribution models are based on climate ranges and climate shifts (Wilson et al., 2007), niche requirements (Herborg et al., 2007; Thuiller et al., 2005), species traits (Kolar and Lodge, 2001) and dispersal dynamics (Guisan and Thuiller, 2005). Incorporating more factors into the comprehensive model gives greater predictive power (Ficetola et al., 2007; Gallien et al., 2010; Stohlgren et al., 2010).

Carlton and Ruiz (2005) stated that preventing the introduction of alien species is more effective and cheaper than eradication or mitigation, which is often even impossible (Mack et al., 2000). Keller et al. (2008), however, added that the costs of comprehensive preventive efforts should not be underestimated given the variety of vectors and pathways. Therefore identifying alien species pools (Keller et al., 2011; Seebens et al., 2018) and destinations, *i.e.* invasion hotspots (Stohlgren et al., 2006), are among the most cost-effective practices. Another effective approach for managing biological invasions includes denoting of high-risk alien species (Jeschke and Strayer, 2005) with particular focus on such organisms. Recent studies have shown that application of the comparative functional response method to identify high-risk alien species is a rapid, reliable and effective method with wide taxonomic and environmental applicability (Alexander et al., 2014; Dick et al., 2013; Xu et al., 2016).

1.2. ALIEN AQUATIC SPECIES IN EUROPE

Europe is considered more as a frequent donor than a recipient of alien species (Lambdon et al., 2008), though several studies proved that Central Europe possesses crucial historical, biogeographical, and anthropogenic predispositions for successful biological invasions (Hulme, 2007; Pyšek et al., 2002). Indeed, Genovesi et al. (2015) reported that one of five threatened species in Europe is directly affected by alien species. Moreover, the growth of the global economy and international trade reflects accelerating trend in aquatic invasions (Hulme, 2009) as the shipping is prominent vector of alien species introductions (Molnar et al., 2008). The estimate is alarming: 10,000 different species are being transported worldwide in the ballast water of ocean vessels during any 24-hour period (Carlton, 2001). The exchange of aquatic biota is further supported by construction of waterways connecting virtually all European navigable rivers (Bij de Vaate et al., 2002; Galil et al., 2008). Consequences of global exchange of biota are evident in most of inland waters of Europe. In some heavily invaded aquatic ecosystems, the diversity of alien species tends to reach or even exceed native biodiversity, and strongly affects the rate of ecosystem functions (Leppäkoski et al., 2002). Indeed, Vilà et al. (2009) listed 16 aquatic species in *One hundred of the most invasive alien species in Europe*, including organisms across all trophic levels. Recetly, great attention is risen by alien fish species, and particularly by alien gobiids in last decades.

1.2.1. Alien gobiids in European waters

Currently, five alien gobies are present in European freshwater ecosystems: round goby *Neogobius melanostomus* (Pallas, 1814), western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837), monkey goby *Neogobius fluviatilis* (Pallas, 1814), racer goby *Babka gymnotrachelus* (Kessler, 1857) and bighead goby *Ponticola kessleri* (Günther, 1861) (Harka and Bíró, 2007; Roche et al., 2013). Their historical distributions in freshwaters were restricted to Ponto-Caspian region including the lower reach of Danube River (Ahnelt et al., 1998). In the 1990s, however, all alien gobies were recorded far upstream their known historical distributions and have established abundant populations (Copp et al., 2005; Grabowska et al., 2010; Sapota and Skóra, 2005; Wiesner, 2005).

Success of establishment and spread of alien gobies is enhanced by a high tolerance to wide-ranging environmental conditions (Charlebois et al., 2001; Erős et al., 2005), including human-modified rivers (Janáč et al., 2012; Ray and Corkum, 2001) along with an effective reproductive strategy (Grabowska, 2005; MacInnis and Corkum, 2000; Valová et al., 2015), aggressive behavior (Balshine et al., 2005; Błońska et al., 2016; Kakareko et al., 2013), and physiological plasticity (Čápová et al., 2008; Grabowska et al., 2009; Hôrková and Kováč, 2014).

The subjects of the present Ph.D. thesis, however, are only two of the aforementioned gobies: *N. melanostomus* and *P. semilunaris*, as they are often considered more successful invaders compared to the other ones due to their ability to establish viable populations not only in Europe but also on the other side of the Atlantic – in North America (Kocovsky et al., 2011; Kornis et al., 2012).

1.2.1.1. Round goby

Round goby *Neogobius melanostomus* (Pallas, 1814) is a member of the Gobiidae family. The native range of *N. melanostomus* includes Ponto-Caspian region, where two sub-species are recognized: *N. melanostomus affinis* in the Caspian Sea basin and *N. melanostomus melanostomus* from the Black Sea basin (Berg, 1965). The latter one is found throughout European and North American water bodies (Brown and Stepien, 2008). Despite earlier classification within genus *Apollonia* (Stepien and Tumeo, 2006), recent phylogenetic studies corroborate that *Neogobius* is the correct genus (Neilson and Stepien, 2009a).

A typical identifying feature of *N. melanostomus* is a black round spot among rays on the first dorsal fin. This spot does not occur in other gobies (Stráňai and Andreji, 2004). In contrast to the other bottom-dwelling fish group – bullheads (genus *Cottus*), pelvic fins of all Ponto-Caspian gobies are fused to form a suctorial disc. The species displays marked sexual dimorphisms. Both sexes have an erectile urogenital papilla, while male papilla is longer and pointed, as compared to broad and blunt papilla of females (Kornis et al., 2012).

Invasion history

With growth of international trade and travel, *N. melanostomus* was transported to the Europe and North American Great Lakes in ballast tanks of transoceanic vessels. The primary source population for both continents is most likely the Black Sea port of Kerson, Ukraine (Brown and Stepien, 2008; Sapota and Skóra, 2005). Shortly after the initial introduction in both, Europe and North America (Jude et al., 1992; Sapota and Skóra, 2005), *N. melanostomus* has established self-sustaining populations and spread through combination of natural dispersal and commercial shipping within invaded waterbodies (Charlebois et al., 2001; Kornis et al., 2012).

The rate of spread was enhanced by a rapid adaptation to new habitats (Björklund and Almqvist, 2010), human-induced changes in rivers (Copp et al., 2005) and effective reproduction (Charlebois et al., 2001). Recent distribution of *N. melanostomus* in Europe includes nearly all navigable rivers, *e.g.* the Dnieper, Dniester and Don Rivers, the Moscow River (see Kornis et al., 2012), the Vistula River (Sapota, 2004), the Oder River (Czugała and Woźniczka, 2010), the Rhine (Borcherding et al., 2011), the Elbe River (Buřič et al., 2015; Roche et al., 2015), the Danube (Erős et al., 2005; Simonović et al., 2001) as well as some of their tributaries *e.g.* the Morava and Dyje Rivers (Prášek and Jurajda, 2005), what corroborates also a strong natural dispersal potential of *N. melanostomus*.

Diet

Neogobius melanostomus is a generalist benthic feeder with a broad diet spectrum including zooplankton (mainly in juveniles specimens), benthic invertebrates (*e.g.* amphipods, chironomids, cladocerans, crayfishes, dragonflies, dreissenids, isopods, mayflies) as well as eggs and larvae of fish (reviewed in Kornis et al., 2012).

The diet composition of *N. melanostomus* is largely influenced by habitat, time of day and year and also body size (Diggins et al., 2002; Janssen and Jude, 2001). Though, a prominent determinant of diet composition is rather the availability (abundance and accessibility) of food items (Vašek et al., 2014) with preference for soft-bodied prey over hard-shelled molluscs (Coulter et al., 2011; Polačik et al., 2009). A frequency of molluscs in the diet of *N. melanostomus* is highly variable. Molluscs are primarily consumed in localities with high abundance of *N. melanostomus* (Barton et al., 2005; Johnson et al., 2005b; Taraborelli et al., 2010), where preferred prey items are likely exploited as compared to sites with lower *N. melanostomus* abundance, where even preferred prey can still hold viable populations (Vašek et al., 2014). Similarly, the preference for molluscs in shallower habitats compared to deeper ones reflects an availability of this prey item due to later colonization event of deeper localities by dreissenids (Schaeffer et al., 2005) and also by higher densities of *N. melanostomus* nearshore (Johnson et al., 2005a). The preference of soft-bodied prey items over hard-shelled ones is also confirmed by the morphology of *N. melanostomus* teeth, where robust pharyngeal teeth for effective crushing of molluscs shells are developed only in localities with the presence of prey with these structures, while no changes in teeth morphology were observed in absence of hard-shelled food sources (Andraso et al., 2017).

Neogobius melanostomus is capable of rapid adaptation to locally abundant food sources as documented by Carman et al. (2006) who observed increased predation of chironomid pupae during their emergent ascent in the evening. This highlights the possible fish eggs and larvae predation during specific events, *e.g.* fish spawning season with subsequent substantially reduced recruitment as shown in both, laboratory experiments (Chotkowski and Marsden, 1999; Fitzsimons et al., 2006) and the field studies (Nichols et al., 2003). Such diet diversity, rapid adaptation to alternative food sources and morphological adaptability are, indeed, the right traits enhancing a high species' invasion potential.

Habitat preferences

In general, *N. melanostomus* prefers hard substrata and is usually most abundant in rocky habitats with numerous interstitial spaces (Ray and Corkum, 2001; Young et al., 2010). Indeed, such environments provide structures that are crucial for reproduction (Meunier et al., 2009) as well as for hiding from predators (Belanger and Corkum, 2003). Nevertheless, it does not necessarily mean that soft and mud substrata are resistant to invasion by *N. melanostomus* as documented in studies of Johnson et al. (2005a) and Taraborelli et al. (2009) who observed similar abundances on both, hard and soft substrata. Similarly, the variations in vegetation density also does not predict the abundance of *N. melanostomus* (Taraborelli et al., 2009). Though, reproduction, recruitment and survival in non-sheltered localities remain unclear.

During the spawning season, *N. melanostomus* prefers shallower waters over greater depths (Kornis et al., 2012). But concurrently, it appears to avoid shallow surf zones (Cooper et al., 2009). As documented by Johnson et al. (2005a), a density of *N. melanostomus* was almost four times greater in nearshore habitats compared to offshore localities during spawning season. During winter, however, *N. melanostomus* migrates offshore and has been recorded in depths, exceeding 100 m (Walsh et al., 2007). A broad habitat tolerance is behind the invasion success of N. melanostomus (Marchetti et al., 2004a).

1.2.1.2. Western tubenose goby

A native distribution range of *Proterorhinus* sp. is Ponto-Caspian region, where three separate species are present: freshwater species inhabiting the Caspian Sea basin *Proterorhinus semipellucidus* (Kessler, 1877), marine and estuarine species within the Black Sea *Proterorhinus marmoratus* (Pallas, 1814) and freshwater goby in the Black Sea basin originally described as *Proterorhinus semilunaris* (Heckel, 1837). Western tubenose goby *P. semilunaris* was later placed in synonymy with *P. marmoratus*, but recent studies confirmed *P. semilunaris* is a separate valid taxon (Neilson and Stepien, 2009b; Stepien and Tumeo, 2006). *Proterorhinus semilunaris* has had the farthest native range up the Danube of all Ponto-Caspian gobies, being found as far as Vienna (Ahnelt et al., 1998). In early 1990s, however, this species has expanded substantially beyond its native ranges into Europe and North America.

Similarly to other Ponto-Caspian gobies, *P. semilunaris* has fused pelvic fins with laterally flattened body. *Proterorhinus semilunaris* has extended nostrils in the barbel-shaped tubes being the reliable identifying feture. Male urogenital papilla is narrow and pointed, while females have broad and blunt papilla. Though, these sexual differences are less visible outside the reproductive season (Pinchuk et al., 2004).

Invasion history

In early 1990s, *P. semilunaris* was introduced together with *N. melanostomus* via ballast water into the North American Great Lakes and scientists expected rapid establishment and spread (Jude et al., 1992). However, only the latter species fulfilled the original expectancies. *Proterorhinus semilunaris* has remained within short distances of areas of original introduction (Vanderploeg et al., 2002), *i.e.* harbors with frequent vessel traffic. It implies, that the expansion of *P. semilunaris* is more gradual in comparison with *N. melanostomus* as documented in several studies (Dopazo et al., 2008; Kocovsky et al., 2011; Leslie et al., 2002).

Given the historical distribution in Danube, the natural expansion of *P. semilunaris* in Europe took place even before the end of the Cold War (reviewed in Roche et al., 2013), after which the exchange of biota between two major political and socio-economic blocks was boosted (Chiron et al., 2010). The rapid dispersal capacity both, down- and upstream is apparent in studies from the Czech Republic, where *P. semilunaris* was firstly observed in 1994 in the Mušov reservoir (Lusk and Halačka, 1995) on the non-navigable River Dyje (Danube basin) and colonized lower stretches in Dyje and Morava Rivers ever since (Janáč et al., 2012; Janáč et al., 2013; Prášek and Jurajda, 2005). Recent distribution of *P. semilunaris* in Europe includes the Danube with several tributaries (Jurajda et al., 2005), the Rhine (Manné and Poulet, 2008;

van Kessel et al., 2009; von Landwüst, 2006), the Meuse River (Cammaerts et al., 2012), the Vistula River (Grabowska et al., 2008), the Pripyat River (Rizevsky et al., 2007), the Scheldt River (Mombaerts et al., 2014) and the Dnieper and Volga River basins (Naseka et al., 2005).

Diet

Proterorhinus semilunaris is a benthic omnivorous species with broad diet spectrum, which includes chironomids, crustaceans, ostracods, trichopterans, ephemeropterans, dipterans, and occasionally fish eggs and larvae (Adámek et al., 2007; French and Jude, 2001). The diet composition is largely influenced by prey availability, which results in local and seasonal variations (Adámek et al., 2010; French and Jude, 2001; Vašek et al., 2014). In contrast to *N. melanostomus*, molluscs are regularly avoided in *P. semilunaris* diet, even if no other prey items are available (Všetičková et al., 2014), which may suggest lower morphological adaptability of *P. semilunaris* as compared to *N. melanostomus.*

Rapid adaptation to locally abundant food sources is apparent from the study of Všetičková et al. (2014), who documented an increased predation of conspecific larvae during larval drift. This observation highlights the possible depredation of native fish eggs and larvae despite no evidences from the field studies are available (Vašek et al., 2014; Všetičková et al., 2014).

Habitat preferences

Within invaded ecosystems, *P. semilunaris* shows broad habitat plasticity including rocky and sandy substrates as well as areas with aquatic macrophytes (Erős et al., 2005; Jude and DeBoe, 1996; Kocovsky et al., 2011). However, it is more abundant in rocky habitats (Jude and DeBoe, 1996; Manné and Poulet, 2008). Similarly, Janáč et al. (2012) observed clear preference of 0+ *P. semilunaris* towards rocks and dense aquatic vegetation as compared to fine substrates.

It is generally assumed, that *P. semilunaris* typically prefers shallow waters with depth less than 3 m and slow or no water current and avoids deeper habitats (Kocovsky et al., 2011; Naseka et al., 2005). This assumption was confirmed also in several field studies (Dopazo et al., 2008; Jude and DeBoe, 1996; von Landwüst, 2006).

1.2.2. Impacts of *N. melanostomus* and *P. semilunaris*

Introduced alien species in novel ecosystem often cause serious ecological disturbances influencing ecosystem functions (Vitousek et al., 1997). It also concerns environments invaded by alien gobiids. In many European rivers, alien gobiids have built up high densities often forming the majority of fish diversity in nearshore habitats (Borcherding et al., 2011; Brandner et al., 2013). In heavily invaded localities, gobiids can cause severe disruptions in food chains and impair nutrient and contaminant cycles (see Kornis et al., 2012). In addition, their invasion represents a high potential for competition with native species.

In comparison with native fish species, *N. melanostomus* is more effective in food acquisition (Bergstrom and Mensinger, 2009) as well as in shelter competition (Balshine et al., 2005; Dubs and Corkum, 1996) as it was found out in several laboratory experiments. These findings likely explain a decline in abundance and species diversity of native ichthyofauna (Lauer et al., 2004). Janssen and Jude (2001) documented a local extinction of mottled sculpins (*Cottus bairdii*, Girard, 1850) in several parts of Lake Michigan after only four years of *N. melanostomus* invasion. Similarly, van Kessel et al. (2016) detected a rapid decline in the densities of native river bullhead (*Cottus perifretum* Freyhof, Kottelat and Nolte,

2005) after appearance of *N. melanostomus*. However, at sites where only *P. kessleri* and *P. semilunaris* were present, *C. perifretum* density remained relatively high. Nevertheless, Krakowiak and Pennuto (2008), observed no difference in ichthyofauna diversity between *N. melanostomus* invaded sites and localities where *N. melanostomus* was absent. It suggests that the resulting impact depends on several factors such as native fish abundance, water temperature, food resources or suitable habitat. In this context, Karlson et al. (2007) reported in the Baltic Sea a remarkable dietary overlap between commercially important fish - European flounder *Platichthys flesus* (Linnaeus, 1758) and *N. melanostomus* causing a displacement of former species to suboptimal habitat as densities in flat nearshore areas have declined since *N. melanostomus* establishment.

Besides competition for food and habitat, *N. melanostomus* can cause a recruitment failure of native fishes via direct predation of their eggs and larvae. This fact was confirmed in the laboratory settings (Chotkowski and Marsden, 1999; Fitzsimons et al., 2006) as well as in the field studies (Nichols et al., 2003; Steinhart et al., 2004).

Although van Kessel (2016) detected relatively low impact of *P. semilunaris* upon native *C. perifretum*, several other studies recorded a substantial abundance decrease, or even extermination in related species - common bullhead (*Cottus gobio*, Linnaeus, 1758) after establishment of *P. semilunaris* (Jurajda et al., 2005; von Landwüst, 2006). It is reasonable as both, *P. semilunaris* and sculpins *Cottus* sp. share the same ecological niche by means of diet composition and spawning habitat (Adámek et al., 2010; Gosselin et al., 2010; Pinchuk et al., 2004). In laboratory conditions, *P. semilunaris* outcompetes sculpins to less preferred habitat types (van Kessel et al., 2011). In North America, French and Jude (2001) observed a substantial overlap in diets between *P. semilunaris* and several native fish species including rainbow darter (*Etheostoma caeruleum*, Storer, 1845) and northern madtom (*Noturus stigmosus*, Taylor, 1969). Moreover, given similar habitat preferences, there is a high potential for competition of *P. semilunaris* with *E. caeruleum* and *E. nigrum* (Rafinesque, 1820), as well (Jude et al., 1992).

Albeit several studies did not confirm a direct fish eggs and larvae depredation (Kocovsky et al., 2011; Vašek et al., 2014), French and Jude (2001) found *N. melanostomus* eggs in the guts of *P. semilunaris*. Moreover, Všetičková et al. (2014) observed an increased conspecific larvae predation during the larval drift. Therefore, the predation on native fish eggs and early ontogenetic stages cannot be excluded.

1.3. PREDATION, FORAGING BEHAVIOR

Predation is a key biological interaction in the population dynamics that influences the entire food web regardless of ecosystem type (Bax, 1998; Holling, 1959b). Predators tend to lower the survival and fecundity rates of prey. However, at the same time, predators depend on prey for their survival. That means predator populations are mutually affected by changes in prey populations and vice versa (Genovart et al., 2010; Horning and Mellish, 2012). Predators may also increase the biodiversity of communities by preventing a single species from becoming to be dominant (Huston, 1979). Knowledge of predatory interactions is therefore crucial for ecosystem management.

Inter- and intraspecific interaction through predation is a key source of potential change in the communities. The change is direct when a predator kills a prey, and indirect in several ways, including predation on shared prey resources, effects involving intermediate predators, and predation influencing prey behavior and resource availability (Bax, 1998).

Resource availability (prey density) is a crucial determinant of feeding rate and has been characterized by the use of the functional response curve (FRs; Holling, 1959a; Solomon, 1949). The form and magnitude of FRs are important aspects of consumer-resource interactions and community dynamics, respectively (Juliano, 2001; Murdoch and Oaten, 1975). Both parameters denote the foraging behavior by means of predators' searching and feeding efficiencies at different prey densities.

Integral components of FR calculation are parameters of attack rate and handling time. The attack rate characterizes the slope of the FR curve at low prey densities and hence indicates the predator efficiency at these densities. Handling time, on the other hand, is classically defined as the time spent pursuing, subduing, and consuming each prey item plus the time spent preparing to search for the next prey item and hence denotes the asymptote of the FR curve (Jeschke et al., 2002).

Three general responses (curve types) are described. Type I response is characterized by linear increase in predator consumption with prey availability until a threshold density plateau is reached. Type II, inversely density-dependent response, can return increase in mortality risk to prey with decreasing density (Hassell, 1978). This is in contrast to Type III response characterized by reduction in mortality risk when prey density declines (Hassell, 1978). The latter response is characteristic either for the prey shift or changes in habitat structure that result in alterations of the functional response Type and hence prey population viability (Alexander et al., 2012; Buckel and Stoner, 2000).

1.3.1. Comparative FR

One of the main challenges in ecology is an ability to predict how drivers of global change, such as biological invasions, may impact ecosystems (Dick et al., 2014; Parker et al., 1999; Ricciardi et al., 2013). Concurrently, prediction of ecological impacts and identification of high risk alien species are crucial points for successful and effective management of biological invasions (Ricciardi and Rasmussen, 1998). A promising methodology that provides both, understanding of predator-prey interactions and predictions of invasive species impact is to examine the FR.

Indeed, invasive species often display elevated FRs compared to native or low-impact non-native ecologically analogous species. For that reason the comparative FR is considered a valuable tool for a comparison as well as an assessment of an impact of newly introduced species (Alexander et al., 2014; Dick et al., 2013; Xu et al., 2016).

Although FRs are an important tool for ecology, the use of comparative FR in invasion biology has been recently subjected to controversial discussion about the proper use of this approach (Dick et al., 2017a; Dick et al., 2017b; Vonesh et al., 2017a; Vonesh et al., 2017b). Vonesh et al. (2017a) criticized omitting important factors and complexities in the calculation of FRs, including conversion efficiency, background mortality *etc.*). Indeed, the predicting power of FR method can still be improved by incorporating additional factors, *e.g.* numerical response (Dick et al., 2017c) and others.

1.3.2. Variables influencing FR

In the freshwater ecosystems, organisms are exposed to a variety of environmental conditions which may affect the interactions among species. Consequently, foraging behavior and predation are influenced by both, biotic and abiotic ecosystem parameters.

The main biotic factors affecting the resulting functional response include predator and prey size (Thorp et al., 2018), antipredator mechanisms adopted by prey (Ives and Dobson, 1987) and also interactions among predators, that share the food sources (Sih et al., 1998; Wasserman et al., 2016). The prominent abiotic drivers of foraging behavior are believed to be mainly light conditions (Koski and Johnson, 2002; Townsend and Risebrow, 1982), temperature and habitat structure (see below).

Temperature is generally considered an important driver of nearly all biological processes, encapsulating the individual and population growth rates as well as the development rates and lifespans (Brown et al., 2004) and consequently also predator-prey interactions (Petchey et al., 1999; Vucic-Pestic et al., 2011). Foraging behavior of ectotherms is typically characterized by hump-shaped temperature dependency (Englund et al., 2011). This knowledge is of paramount importance for ecology management, as the expected future temperature deviations driven by climate change can substantially alter consumer-resource relationships worldwide (Pereira et al., 2010; Schulte et al., 2011).

Habitat structure and/or complexity have been shown to significantly interfere the impact of predatory fishes (Almany, 2004; Savino and Stein, 1982; Swisher et al., 1998) and may result in differences in the magnitude and direction of predator-prey interactions (Abrams, 1990). The response is, however, widely variable depending on the predators' habitat preferences and foraging strategy as well as on an ability of prey to utilize the refuges (Alexander et al., 2012; Alexander et al., 2015; Baber and Babbitt, 2004).

1.4. OBJECTIVES OF THE PH.D. THESIS

The present Ph.D. thesis is devoted to an identification of the invasion hotspots in the Czech Republic and to a comprehensive investigation of the ecological impacts of alien gobiid species with special emphasis to elucidate the following objectives:

1. Identification of factors that are considered to be important for explaining alien species richness in the Czech Republic.
2. Development of the maps of invasion hotspots in the Czech Republic documenting the extent of biological invasions in the Czech Republic.
3. Clarification of the effect of temperature upon foraging behaviour of *N. melanostomus* and *P. semilunaris.*
4. Comparison of the foraging behaviour of *N. melanostomus* and *P. semilunaris* in different habitat structures.

REFERENCES

Abrams, P.A., 1990. The effects of adaptive behavior on the type-2 functional response. Ecology 71, 877–885.

Adámek, Z., Andreji, J., Gallardo, J.M., 2007. Food habits of four bottom-dwelling gobiid species at the confluence of the Danube and Hron Rivers (South Slovakia). International Review of Hydrobiology 92, 554–563.

Adámek, Z., Jurajda, P., Prášek, V., Sukop, I., 2010. Seasonal diet pattern of non-native tubenose goby (*Proterorhinus semilunaris*) in a lowland reservoir (Mušov, Czech Republic). Knowledge and Management of Aquatic Ecosystems 397, 02.

Ahnelt, H., Bănărescu, P., Spolwind, R., Harka, A., Waidbacher, H., 1998. Occurrence and distribution of three gobiid species (Pisces, Gobiidae) in the middle and upper Danube region-examples of different dispersal patterns? Biologia 53, 665–678.

Alexander, M.E., Dick, J.T.A., O'Connor, N.E., Haddaway, N.R., Farnsworth, K.D., 2012. Functional responses of the intertidal amphipod *Echinogammarus marinus*: effects of prey supply, model selection and habitat complexity. Marine Ecology Progress Series 468, 191–202.

Alexander, M.E., Dick, J.T.A., Weyl, O.L.F., Robinson, T.B., Richardson, D.M., 2014. Existing and emerging high impact invasive species are characterized by higher functional responses than natives. Biology Letters 10, 20130946.

Alexander, M.E., Kaiser, H., Weyl, O.L.F., Dick, J.T.A., 2015. Habitat simplification increases the impact of a freshwater invasive fish. Environmental Biology of Fishes 98, 477–486.

Almany, G.R., 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos 106, 275–284.

Andraso, G., Blank, N., Shadle, M.J., DeDionisio, J.L., Ganger, M.T., 2017. Associations between food habits and pharyngeal morphology in the round goby (*Neogobius melanostomus*). Environmental Biology of Fishes 100, 1069–1083.

Baber, M.J., Babbitt, K.J., 2004. Influence of habitat complexity on predator–prey interactions between the fish (*Gambusia holbrooki*) and tadpoles of *Hyla squirella* and *Gastrophryne carolinensis*. Copeia 104, 173–177.

Balshine, S., Verma, A., Chant, V., Theysmeyer, T., 2005. Competitive interactions between round gobies and logperch. Journal of Great Lakes Research 31, 68–77.

Barton, D.R., Johnson, R.A., Campbell, L., Petruniak, J., Patterson, M., 2005. Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in eastern Lake Erie, 2002–2004. Journal of Great Lakes Research 31, 252–261.

Bax, N.J., 1998. The significance and prediction of predation in marine fisheries. ICES Journal of Marine Science 55, 997–1030.

Belanger, R.M., Corkum, L.D., 2003. Susceptibility of tethered round gobies (*Neogobius melanostomus*) to predation in habitats with and without shelters. Journal of Great Lakes Research 29, 588–593.

Berg, L.S., 1965. Freshwater Fishes of the U.S.S.R. and Adjacent Countries. Jerusalem: Israel Program for Scientific Translations Ltd.

Bergstrom, M.A., Mensinger, A.F., 2009. Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. Transactions of the American Fisheries Society 138, 1009–1017.

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H.A.M., Gollasch, S., Van der Velde, G., 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Canadian Journal of Fisheries and Aquatic Sciences 59, 1159–1174.

Björklund, M., Almqvist, G., 2010. Rapid spatial genetic differentiation in an invasive species, the round goby *Neogobius melanostomus* in the Baltic Sea. Biological Invasions 12, 2609–2618.

Blackburn, T.M., Duncan, R.P., 2001. Determinants of establishment success in introduced birds. Nature 414, 195–197.

Blackburn, T.M., Cassey, P., Lockwood, J.L., 2009a. The role of species traits in the establishment success of exotic birds. Global Change Biology 15, 2852–2860.

Blackburn, T.M., Lockwood, J.L., Cassey, P., 2009b. Avian invasions: the ecology and evolution of exotic birds. Oxford University Press, Oxford, UK, 305 pp.

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U., Richardson, D.M., 2011. A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26, 333–339.

Błońska, D., Kobak, J., Grabowska, J., 2016. Shelter competition between the invasive western tubenose goby and the native stone loach is mediated by sex. Journal of Limnology 76, 221-229.

Borcherding, J., Staas, S., Krüger, S., Ondračková, M., Šlapanský, L., Jurajda, P., 2011. Non-native gobiid species in the lower River Rhine (Germany): recent range extensions and densities. Journal of Applied Ichthyology 27, 153–155.

Bradley, B.A., Blumenthal, D.M., Early, R., Grosholz, E.D., Lawler, J.J., Miller, L.P., Sorte, C.J.B., D'Antonio, C.M., Diez, J.M., Dukes, J.S., 2012. Global change, global trade, and the next wave of plant invasions. Frontiers in Ecology and the Environment 10, 20–28.

Brandner, J., Cerwenka, A.F., Schliewen, U.K., Geist, J., 2013. Bigger is better: characteristics of round gobies forming an invasion front in the Danube River. PLoS ONE 8, e73036.

Brown, J.E., Stepien, C.A., 2008. Ancient divisions, recent expansions: phylogeography and population genetics of the round goby *Apollonia melanostoma*. Molecular Ecology 17, 2598–2615.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Brown, J.K., Hovmøller, M.S., 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. Science 297, 537–541.

Buckel, J.A., Stoner, A.W., 2000. Functional response and switching behavior of young-of-the-year piscivorous bluefish. Journal of Experimental Marine Biology and Ecology 245, 25–41.

Buřič, M., Bláha, M., Kouba, A., Drozd, B., 2015. Upstream expansion of round goby (*Neogobius melanostomus*)–first record in the upper reaches of the Elbe river. Knowledge and Management of Aquatic Ecosystems 416, 32.

Cammaerts, R., Spikmans, F., van Kessel, N., Verreycken, H., Chérot, F., Demol, T., Richez, S., 2012. Colonization of the Border Meuse area (The Netherlands and Belgium) by the non-native western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837)(Teleostei, Gobiidae). Aquatic Invasions 7, 251–258.

Capinha, C., Essl, F., Seebens, H., Moser, D., Pereira, H.M., 2015. The dispersal of alien species redefines biogeography in the Anthropocene. Science 348, 1248–1251.

Carlton, J.T., 2001. The scale and ecological consequences of biological invasions in the World's oceans. In: Sandlund, O.T., Schei, P.J., Viken, A. (eds.), Invasive species and biodiversity management. Springer Science and Business Media, Drodrecht, The Netherlands, pp. 195-212.

Carlton, J.T., Ruiz, G.M., 2005. Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. In: Mooney, H.A. (ed.), Invasive alien species: a new synthesis. Island Press, Washington, D.C., USA, pp. 36–58.

Carman, S.M., Janssen, J., Jude, D.J., Berg, M.B., 2006. Diel interactions between prey behaviour and feeding in an invasive fish, the round goby, in a North American river. Freshwater Biology 51, 742–755.

Case, T.J., 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. Proceedings of the National Academy of Sciences of the United States of America 87, 9610–9614.

Cassey, P., 2002. Life history and ecology influences establishment success of introduced land birds. Biological Journal of the Linnean Society 76, 465–480.

Cassey, P., Blackburn, T.M., Sol, D., Duncan, R.P., Lockwood, J.L., 2004. Global patterns of introduction effort and establishment success in birds. Proceedings of the Royal Society of London B: Biological Sciences 271, S405–S408.

Charlebois, P.M., Corkum, L.D., Jude, D.J., Knight, C., 2001. The round goby (*Neogobius melanostomus*) invasion: current research and future needs. Journal of Great Lakes Research 27, 263–266.

Chew, M.K., 2006. Ending with Elton: preludes to invasion biology. Ph.D. thesis. Arizona State University Tempe, USA, 311 pp.

Chiron, F., Shirley, S.M., Kark, S., 2010. Behind the Iron Curtain: socio-economic and political factors shaped exotic bird introductions into Europe. Biological Conservation 143, 351–356.

Chotkowski, M.A., Marsden, J.E., 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. Journal of Great Lakes Research 25, 26–35.

Colautti, R.I., MacIsaac, H.J., 2004. A neutral terminology to define invasive species. Diversity and Distributions 10, 135–141.

Colautti, R.I., Grigorovich, I.A., MacIsaac, H.J., 2006. Propagule pressure: a null model for biological invasions. Biological Invasions 8, 1023–1037.

Cooper, M.J., Ruetz, C.R., Uzarski, D.G., Shafer, B.M., 2009. Habitat use and diet of the round goby (*Neogobius melanostomus*) in coastal areas of Lake Michigan and Lake Huron. Journal of Freshwater Ecology 24, 477–488.

Copp, G., Bianco, P., Bogutskaya, N., Erős, T., Falka, I., Ferreira, M., Fox, M., Freyhof, J., Gozlan, R., Grabowska, J., 2005. To be, or not to be, a non-native freshwater fish? Journal of Applied Ichthyology 21, 242–262.

Coulter, D.P., Murry, B.A., Webster, W.C., Uzarski, D.G., 2011. Effects of dreissenid mussels, chironomids, fishes, and zooplankton on growth of round goby in experimental aquaria. Journal of Freshwater Ecology 26, 155–162.

Crawley, M.J., Brown, S.L., Heard, M.S., Edwards, G.R., 1999. Invasion resistance in experimental grassland: species richness or species identity. Ecology Letters 2, 140–148.

Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97, 153–166.

Crowl, T.A., Crist, T.O., Parmenter, R.R., Belovsky, G., Lugo, A.E., 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. Frontiers in Ecology and the Environment 6, 238–246.

Czugała, A., Woźniczka, A., 2010. The River Odra estuary—another Baltic Sea area colonized by the round goby *Neogobius melanostomus* Pallas, 1811. Aquatic Invasions 5, S61–S65.

Čápová, M., Zlatnická, I., Kováč, V., Katina, S., 2008. Ontogenetic variability in the external morphology of monkey goby, *Neogobius fluviatilis* (Pallas, 1814) and its relevance to invasion potential. Hydrobiologia 607, 17–26.

Davidson, A.M., Jennions, M., Nicotra, A.B., 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14, 419–431.

Davies, K.F., Chesson, P., Harrison, S., Inouye, B.D., Melbourne, B.A., Rice, K.J., 2005. Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. Ecology 86, 1602–1610.

Davis, M.A., 2003. Biotic globalization: does competition from introduced species threaten biodiversity? Bioscience 53, 481–489.

Davis, M.A., 2009. Invasion Biology. Oxford University Press, Oxford, UK, 288 pp.

Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88, 528–534.

Dick, J.T.A., Gallagher, K., Avlijas, S., Clarke, H.C., Lewis, S.E., Leung, S., Minchin, D., Caffrey, J., Alexander, M.E., Maguire, C., Harrod, C., Reid, N., Haddaway, N.R., Farnsworth, K.D., Penk, M., Ricciardi, A., 2013. Ecological impacts of an invasive predator explained and predicted by comparative functional responses. Biological Invasions 15, 837–846.

Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B., Kumschick, S., Weyl, O.L.F., Dunn, A.M., Hatcher, M.J., Paterson, R.A., Farnsworth, K.D., Richardson, D.M., 2014. Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biological Invasions 16, 735–753.

Dick, J.T.A., Alexander, M.E., Ricciardi, A., Laverty, C., Downey, P.O., Xu, M., Jeschke, J.M., Saul, W.C., Hill, M.P., Wasserman, R., Barrios-O'Neill, D., Weyl, O.L.F., Shaw, R.H., 2017a. Fictional responses from Vonesh et al. Biological Invasions 19, 1677–1678.

Dick, J.T.A., Alexander, M.E., Ricciardi, A., Laverty, C., Downey, P.O., Xu, M., Jeschke, J.M., Saul, W.C., Hill, M.P., Wasserman, R., Barrios-O'Neill, D., Weyl, O.L.F., Shaw, R.H., 2017b. Functional responses can unify invasion ecology. Biological Invasions 19, 1667–1672.

Dick, J.T.A., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., Britton, R.J., Medoc, V., Boets, P., Alexander, M.E., Taylor, N.G., Dunn, A.M., Hatcher, M.J., Rosewarne, P.J., Crookes, S., MacIsaac, H.J., Xu, M., Ricciardi, A., Wasserman, R.J., Ellender, B.R., Weyl, O.L.F., Lucy, F.E., Banks, P.B., Dodd, J.A., MacNeil, C., Penk, M.R., Aldridge, D.C., Caffrey, J.M., 2017c. Invader relative impact potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. Journal of Applied Ecology 54, 1259–1267.

Diggins, T.P., Kaur, J., Chakraborti, R.K., DePinto, J.V., 2002. Diet choice by the exotic round goby (*Neogobius melanostomus*) as influenced by prey motility and environmental complexity. Journal of Great Lakes Research 28, 411–420.

Dopazo, S.N., Corkum, L.D., Mandrak, N.E., 2008. Fish assemblages and environmental variables associated with gobiids in nearshore areas of the lower Great Lakes. Journal of Great Lakes Research 34, 450–460.

Dubs, D.O.L., Corkum, L.D., 1996. Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). Journal of Great Lakes Research 22, 838–844.

Englund, G., Öhlund, G., Hein, C.L., Diehl, S., 2011. Temperature dependence of the functional response. Ecology Letters 14, 914–921.

Erős, T., Sevcsik, A., Tóth, B., 2005. Abundance and night-time habitat use patterns of Ponto-Caspian gobiid species (Pisces, Gobiidae) in the littoral zone of the River Danube, Hungary. Journal of Applied Ichthyology 21, 350–357.

Facon, B., Genton, B.J., Shykoff, J., Jarne, P., Estoup, A., David, P., 2006. A general eco-evolutionary framework for understanding bioinvasions. Trends in Ecology and Evolution 21, 130–135.

Ficetola, G.F., Thuiller, W., Miaud, C., 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species—the American bullfrog. Diversity and Distributions 13, 476–485.

Ficetola, G.F., Thuiller, W., Padoa-Schioppa, E., 2009. From introduction to the establishment of alien species: bioclimatic differences between presence and reproduction localities in the slider turtle. Diversity and Distributions 15, 108–116.

Fitzsimons, J., Williston, B., Williston, G., Bravener, G., Jonas, J.L., Claramunt, R.M., Marsden, J.E., Ellrott, B.J., 2006. Laboratory estimates of salmonine egg predation by round gobies (*Neogobius melanostomus*), sculpins (*Cottus cognatus* and *C. bairdi*), and crayfish (*Orconectes propinquus*). Journal of Great Lakes Research 32, 227–241.

Fowler, A.J., Lodge, D.M., Hsia, J.F., 2007. Failure of the Lacey Act to protect US ecosystems against animal invasions. Frontiers in Ecology and the Environment 5, 353–359.

French, J.R.P., Jude, D.J., 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. Journal of Great Lakes Research 27, 300–311.

Galil, B.S., Nehring, S., Panov, V., 2008. Waterways as invasion highways–Impact of climate change and globalization. In: Nentwig, W. (ed.), Biological Invasions. Springer-Verlag, Berlin Heidelberg, Germany pp. 59–74.

Gallien, L., Münkemüller, T., Albert, C.H., Boulangeat, I., Thuiller, W., 2010. Predicting potential distributions of invasive species: where to go from here? Diversity and Distributions 16, 331–342.

Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., Oro, D., 2010. The young, the weak and the sick: evidence of natural selection by predation. PLoS ONE 5, e9774.

Genovesi, P., Carnevali, L., Scalera, R., 2015. The impact of invasive alien species on nature threatened species in Europe (Technical report for the European Commision). ISPRA, Rome, Italy 18 pp.

Gosselin, M.-P., Petts, G.E., Maddock, I.P., 2010. Mesohabitat use by bullhead (*Cottus gobio*). Hydrobiologia 652, 299–310.

Grabowska, J., 2005. Reproductive biology of racer goby *Neogobius gymnotrachelus* in the Włocławski Reservoir (Vistula River, Poland). Journal of Applied Ichthyology 21, 296–299.

Grabowska, J., Pietraszewski, D., Ondračková, M., 2008. Tubenose goby *Proterorhinus marmoratus* (Pallas, 1814) has joined three other Ponto-Caspian gobies in the Vistula River (Poland). Aquatic Invasions 3, 261–265.

Grabowska, J., Grabowski, M., Kostecka, A., 2009. Diet and feeding habits of monkey goby (*Neogobius fluviatilis*) in a newly invaded area. Biological Invasions 11, 2161–2170.

Grabowska, J., Kotusz, J., Witkowski, A., 2010. Alien invasive fish species in Polish waters: an overview. Folia Zoologica 59, 73–85.

Grigorovich, I.A., Colautti, R.I., Mills, E.L., Holeck, K., Ballert, A.G., MacIsaac, H.J., 2003. Ballast-mediated animal introductions in the Laurentian Great Lakes: retrospective and prospective analyses. Canadian Journal of Fisheries and Aquatic Sciences 60, 740–756.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8, 993–1009.

Harka, Á., Bíró, P., 2007. New patterns in Danubian distribution of Ponto-Caspian gobies–a result of global climatic change and/or canalization. Electronic Journal of Ichthyology 1, 1–14.

Hassell, M.P., 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, New Jersey, USA, 237 pp.

Havel, J.E., Medley, K.A., 2006. Biological invasions across spatial scales: intercontinental, regional, and local dispersal of cladoceran zooplankton. Biological Invasions 8, 459–473.

Heath, M.R., Speirs, D.C., Steele, J.H., 2014. Understanding patterns and processes in models of trophic cascades. Ecology Letters 17, 101–114.

Henderson, S., Dawson, T.P., Whittaker, R.J., 2006. Progress in invasive plants research. Progress in Physical Geography 30, 25–46.

Herborg, L.-M., Jerde, C.L., Lodge, D.M., Ruiz, G.M., MacIsaac, H.J., 2007. Predicting invasion risk using measures of introduction effort and environmental niche models. Ecological Applications 17, 663–674.

Hill, J.K., Thomas, C.D., Blakeley, D.S., 1999. Evolution of flight morphology in a butterfly that has recently expanded its geographic range. Oecologia 121, 165–170.

Hogan, L.S., Marschall, E., Folt, C. Stein, R.A., 2007. How non-native species in Lake Erie influence trophic transfer of mercury and lead to top predators. Journal of Great Lakes Research 33, 46–61.

Holling, C.S., 1959a. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist 91, 293–320.

Holling, C.S., 1959b. Some characteristics of simple types of predation and parasitism. The Canadian Entomologist 91, 385–398.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., O'Connor, M.I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486, 105.

Hôrková, K., Kováč, V., 2014. Different life-histories of native and invasive *Neogobius melanostomus* and the possible role of phenotypic plasticity in the species' invasion success. Knowledge and Management of Aquatic Ecosystems 412, 01.

Horning, M., Mellish, J.-A.E., 2012. Predation on an upper trophic marine predator, the steller sea lion: evaluating high juvenile mortality in a density dependent conceptual framework. PLoS ONE 7, e30173.

Hulme, P.E., 2007. Biological invasions in Europe: drivers, pressures, states, impacts and responses. In: Hester, R., Harrison, R.M. (eds.), Biodiversity under threat. Cambridge University Press, Cambridge, UK, pp. 56–80.

Hulme, P.E., 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46, 10–18.

Hulme, P.E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. Journal of Applied Ecology 45, 403–414.

Huston, M., 1979. A general hypothesis of species diversity. The American Naturalist 113, 81–101.

Ives, A.R., Dobson, A.P., 1987. Antipredator behavior and the population dynamics of simple predator-prey systems. The American Naturalist 130, 431–447.

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

Janáč, M., Šlapanský, L., Valová, Z., Jurajda, P., 2013. Downstream drift of round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus semilunaris*) in their non-native area. Ecology of Freshwater Fish 22, 430–438.

Janssen, J., Jude, D.J., 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. Journal of Great Lakes Research 27, 319–328.

Jeschke, J.M., Strayer, D.L., 2005. Invasion success of vertebrates in Europe and North America. Proceedings of the National Academy of Sciences of the United States of America 102, 7198–7202.

Jeschke, J.M., Kopp, M., Tollrian, R., 2002. Predator functional responses: discriminating between handling and digesting prey. Ecological Monographs 72, 95–112.

Johnson, T.B., Allen, M., Corkum, L.D., Lee, V.A., 2005a. Comparison of methods needed to estimate population size of round gobies (*Neogobius melanostomus*) in western Lake Erie. Journal of Great Lakes Research 31, 78–86.

Johnson, T.B., Bunnell, D.B., Knight, C.T., 2005b. A potential new energy pathway in central Lake Erie: the round goby connection. Journal of Great Lakes Research 31, 238–251.

Jones, C.G., Lawton, J.H., Shachak, M., 1996. Organisms as ecosystem engineers. In: Lawson, F.B. (ed.), Ecosystem Management. Springer, New York, NY, USA, pp. 130–147.

Jude, D.J., DeBoe, S.F., 1996. Possible impact of gobies and other introduced species on habitat restoration efforts. Canadian Journal of Fisheries and Aquatic Sciences 53, 136–141.

Jude, D.J., Reider, R.H., Smith, G.R., 1992. Establishment of Gobiidae in the Great Lakes basin. Canadian Journal of Fisheries and Aquatic Sciences 49, 416–421.

Juliano, S.A., 2001. Non-linear curve fitting: predation and functional response curve. In: Scheiner, S.M., Gurevitch, J. (eds.), Design and analysis of ecological experiment. Oxford University Press, Oxford, UK, pp. 178–196.

Juliano, S.A., Philip Lounibos, L., 2005. Ecology of invasive mosquitoes: effects on resident species and on human health. Ecology Letters 8, 558–574.

Jurajda, P., Černý, J., Polačik, M., Valová, Z., Janáč, M., Blažek, R., Ondračková, M., 2005. The recent distribution and abundance of non-native *Neogobius* fishes in the Slovak section of the River Danube. Journal of Applied Ichthyology 21, 319–323.

Kakareko, T., Kobak, J., Grabowska, J., Jermacz, Ł., Przybylski, M., Poznańska, M., Pietraszewski, D., Copp, G.H., 2013. Competitive interactions for food resources between invasive racer goby *Babka gymnotrachelus* and native European bullhead *Cottus gobio*. Biological Invasions 15, 2519–2530.

Karlson, A.M., Almqvist, G., Skóra, K.E., Appelberg, M., 2007. Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. ICES Journal of Marine Science 64, 479–486.

Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17, 164–170.

Keller, R.P., Lodge, D.M., Finnoff, D.C., 2007. Risk assessment for invasive species produces net bioeconomic benefits. Proceedings of the National Academy of Sciences of the United States of America 104, 203–207.

Keller, R.P., Frang, K., Lodge, D.M., 2008. Preventing the spread of invasive species: economic benefits of intervention guided by ecological predictions. Conservation Biology 22, 80–88.

Keller, R.P., Drake, J.M., Drew, M.B., Lodge, D.M., 2011. Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. Diversity and Distributions 17, 93–102.

Kellogg, C.A., Griffin, D.W., 2006. Aerobiology and the global transport of desert dust. Trends in Ecology and Evolution 21, 638–644.

Kocovsky, P.M., Tallman, J.A., Jude, D.J., Murphy, D.M., Brown, J.E., Stepien, C.A., 2011. Expansion of tubenose gobies *Proterorhinus semilunaris* into western Lake Erie and potential effects on native species. Biological Invasions 13, 2775–2784.

Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16, 199–204.

Kolar, C.S., Lodge, D.M., 2002. Ecological predictions and risk assessment for alien fishes in North America. Science 298, 1233–1236.

Kornis, M.S., Mercado-Silva, N., Vander Zanden, M.J., 2012. Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. Journal of Fish Biology 80, 235–285.

Koski, M.L., Johnson, B.M., 2002. Functional response of kokanee salmon (*Oncorhynchus nerka*) to *Daphnia* at different light levels. Canadian Journal of Fisheries and Aquatic Sciences 59, 707–716.

Krakowiak, P.J., Pennuto, C.M., 2008. Fish and macroinvertebrate communities in tributary streams of eastern Lake Erie with and without round gobies (*Neogobius melanostomus*, Pallas 1814). Journal of Great Lakes Research 34, 675–689.

Lambdon, P.W., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., Jarošík, V., Pergl, J., Winter, M., Anastasiu, P., 2008. Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. Preslia 80, 101–149.

Lauer, T.E., Allen, P.J., McComish, T.S., 2004. Changes in mottled sculpin and johnny darter trawl catches after the appearance of round gobies in the Indiana waters of Lake Michigan. Transactions of the American Fisheries Society 133, 185–189.

Lee, C.E., 2002. Evolutionary genetics of invasive species. Trends in Ecology and Evolution 17, 386–391.

Leppäkoski, E., Gollasch, S., Olenin, S., 2002. Alien species in European waters. In: Leppäkoski, E., Gollasch, S., Olenin, S. (eds.), Invasive aquatic species of Europe. Distribution, impacts and management. Springer Science and Business Media, Dordrecht, The Netherlands, pp. 1–6.

Leslie, J.K., Timmins, C.A., Bonnell, R.G., 2002. Postembryonic development of the tubenose goby *Proterorhinus marmoratus* Pallas (Gobiidae) in the St. Clair River/Lake system, Ontario. Archiv für Hydrobiologie 154, 341–352.

Levine, J.M., D'antonio, C.M., 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 99, 15–26.

Lippert, K.A., Gunn, J.M., Morgan, G.E., 2007. Effects of colonizing predators on yellow perch (*Perca flavescens*) populations in lakes recovering from acidification and metal stress. Canadian Journal of Fisheries and Aquatic Sciences 64, 1413–1428.

Lockwood, J.L., Cassey, P., Blackburn, T.M., 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20, 223–228.

Lockwood, J.L., Cassey, P., Blackburn, T.M., 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Diversity and Distributions 15, 904–910.

Lonsdale, W.M., 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80, 1522–1536.

Losos, J.B., Creer, D.A., Glossip, D., Goellner, R., Hampton, A., Roberts, G., Haskell, N., Taylor, P., Ettling, J., 2000. Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. Evolution 54, 301–305.

Lusk, S., Halačka, K., 1995. The first finding of the tubenose goby, *Proterorhinus marmoratus*, in the Czech Republic. Folia Zoologica 44, 90–92.

MacInnis, A.J., Corkum, L.D., 2000. Age and growth of round goby *Neogobius melanostomus* in the Upper Detroit River. Transactions of the American Fisheries Society 129, 852–858.

Mack, R.N., Gray, A.J., Harper, J.L., Usher, M.B., Joysey, K., Kornberg, H., 1986. Do invading species have definable genetic characteristics? Philosophical Transactions of the Royal Society of London B: Biological Sciences 314, 673–674.

Mack, R.N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10, 689–710.

Manné, S., Poulet, N., 2008. First record of the western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) in France. Knowledge and Management of Aquatic Ecosystems 389, 03.

Marchetti, M.P., Moyle, P.B., Levine, R., 2004a. Alien fishes in California watersheds: characteristics of successful and failed invaders. Ecological Applications 14, 587–596.

Marchetti, M.P., Moyle, P.B., Levine, R., 2004b. Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. Freshwater Biology 49, 646–661.

Maron, J., Marler, M., 2007. Native plant diversity resists invasion at both low and high resource levels. Ecology 88, 2651–2661.

Marvier, M., Kareiva, P., Neubert, M.G., 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Analysis 24, 869–878.

Matsuzaki, S.S., Usio, N., Takamura, N., Washitani, I., 2007. Effects of common carp on nutrient dynamics and littoral community composition: roles of excretion and bioturbation. Fundamental and Applied Limnology 168, 27–38.

Mazza, G., Tricarico, E., Genovesi, P., Gherardi, F., 2014. Biological invaders are threats to human health: an overview. Ethology Ecology and Evolution 26, 112–129.

Meunier, B., Yavno, S., Ahmed, S., Corkum, L.D., 2009. First documentation of spawning and nest guarding in the laboratory by the invasive fish, the round goby (*Neogobius melanostomus*). Journal of Great Lakes Research 35, 608–612.

Meyerson, L.A., Mooney, H.A., 2007. Invasive alien species in an era of globalization. Frontiers in Ecology and the Environment 5, 199–208.

Mokany, K., Harwood, T.D., Williams, K.J., Ferrier, S., 2012. Dynamic macroecology and the future for biodiversity. Global Change Biology 18, 3149–3159.

Molnar, J.L., Gamboa, R.L., Revenga, C., Spalding, M.D., 2008. Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment 6, 485–492.

Mombaerts, M., Verreycken, H., Volckaert, F., Huyse, T., 2014. The invasive round goby *Neogobius melanostomus* and tubenose goby *Proterorhinus semilunaris*: two introduction routes into Belgium. Aquatic Invasions 9, 305–314.

Muñoz, J., Felicísimo, Á.M., Cabezas, F., Burgaz, A.R., Martínez, I., 2004. Wind as a long-distance dispersal vehicle in the Southern Hemisphere. Science 304, 1144–1147.

Murdoch, W.W., Oaten, A., 1975. Predation and population stability. Advances in Ecological Research 9, 1–131.

Naseka, A.M., Boldyrev, V.S., Bogutskaya, N.G., Delitsyn, V.V., 2005. New data on the historical and expanded range of *Proterorhinus marmoratus* (Pallas, 1814)(Teleostei: Gobiidae) in eastern Europe. Journal of Applied Ichthyology 21, 300–305.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A., 2008. Mechanisms of long-distance seed dispersal. Trends in Ecology and Evolution 23, 638–647.

Neilson, M.E., Stepien, C.A., 2009a. Escape from the Ponto-Caspian: Evolution and biogeography of an endemic goby species flock (Benthophilinae: Gobiidae: Teleostei). Molecular Phylogenetics and Evolution 52, 84–102.

Neilson, M.E., Stepien, C.A., 2009b. Evolution and phylogeography of the tubenose goby genus *Proterorhinus* (Gobiidae: Teleostei): evidence for new cryptic species. Biological Journal of the Linnean Society 96, 664–684.

Ng, C., Berg, M., Jude, D.J., Janssen, J., Charlebois, P., Amara, L., Gray, K., 2008. Chemical amplification in an invaded food web: seasonality and ontogeny in a high biomass, low diversity ecosystem. Environmental Toxicology and Chemistry 27, 2186–2195.

Nichols, S.J., Kennedy, G., Crawford, E., Allen, J., French, J., Black, G., Blouin, M., Hickey, J., Chernyák, S., Haas, R., 2003. Assessment of lake sturgeon (*Acipenser fulvescens*) spawning efforts in the lower St. Clair River, Michigan. Journal of Great Lakes Research 29, 383–391.

Occhipinti-Ambrogi, A., Galil, B.S., 2004. A uniform terminology on bioinvasions: a chimera or an operative tool? Marine Pollution Bulletin 49, 688–694.

Olden, J.D., Poff, N.L., Bestgen, K.R., 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. Ecological Monographs 76, 25–40.

Ordóñez, J., Armengol, J., Moreno-Ostos, E., Caputo, L., García, J.C., Marcé, R., 2010. On non-Eltonian methods of hunting Cladocera, or impacts of the introduction of planktivorous fish on zooplankton composition and clear-water phase occurrence in a Mediterranean reservoir. Hydrobiologia 653, 119–129.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14, 483–488.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1, 3–19.

Pejchar, L., Mooney, H.A., 2009. Invasive species, ecosystem services and human well-being. Trends in Ecology and Evolution 24, 497–504.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., David Copper, H., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for global biodiversity in the 21st century. Science 330, 1496–1501.

Petchey, O.L., McPhearson, P.T., Casey, T.M., Morin, P.J., 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402, 69.

Pimentel, D., Lach, L., Zuniga, R., Morrison, D., 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50, 53–65.

Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52, 273–288.

Pinchuk, V.I., Vasil'eva, E.D., Vasil'ev, V.P., Miller, P.J., 2004. *Proterorhinus marmoratus* (Pallas 1814). In: Miller, P.J. (ed.), The Freshwater Fishes of Europe. Vol. 8/II. Gobiidae 2. AULA-Verlag, Wiebelsheim, Germany, pp. 72–93.

Polačik, M., Janáč, M., Jurajda, P., Adámek, Z., Ondračková, M., Trichkova, T., Vassilev, M., 2009. Invasive gobies in the Danube: invasion success facilitated by availability and selection of superior food resources. Ecology of Freshwater Fish 18, 640–649.

Prášek, V., Jurajda, P., 2005. Expansion of *Proterorhinus marmoratus* in the Morava River basin (Czech Republic, Danube R. watershed). Folia Zoologica 54, 189.

Puth, L.M., Post, D.M., 2005. Studying invasion: have we missed the boat? Ecology Letters 8, 715–721.

Pyšek, P., Sádlo, J., Mandák, B., 2002. Catalogue of alien plants of the Czech Republic. Preslia 74, 97–186.

Pyšek, P., Bacher, S., Chytrý, M., Jarošík, V., Wild, J., Celesti-Grapow, L., Gassó, N., Kenis, M., Lambdon, P.W., Nentwig, W., Pergl, J., Roques, A., Sádlo, J., Solarz, W., Vilà, M., Hulme, P.E., 2010. Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. Global Ecology and Biogeography 19, 317–331.

Ray, W.J., Corkum, L.D., 2001. Habitat and site affinity of the round goby. Journal of Great Lakes Research 27, 329–334.

Rejmánek, M., Richardson, D.M., 1996. What attributes make some plant species more invasive? Ecology 77, 1655–1661.

Ricciardi, A., 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Diversity and Distributions 12, 425–433.

Ricciardi, A., Rasmussen, J.B., 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences 55, 1759–1765.

Ricciardi, A., MacIsaac, H.J., 2008. The book that began invasion ecology. Charles Elton's 50-year-old text on invasion ecology is now cited more than ever. Nature 652, 34.

Ricciardi, A., Hoopes, M.F., Marchetti, M.P., Lockwood, J.L., 2013. Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs 83, 263–282.

Richardson, D.M., Pyšek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6, 93–107.

Rizevsky, V., Pluta, M., Leschenko, A., Ermolaeva, I., 2007. First record of the invasive Ponto-Caspian tubenose goby *Proterorhinus marmoratus* (Pallas, 1814) from the River Pripyat, Belarus. Aquatic Invasions 2, 275–277.

Roche, K., Janáč, M., Jurajda, P., 2013. A review of Gobiid expansion along the Danube-Rhine corridor–geopolitical change as a driver for invasion. Knowledge and Management of Aquatic Ecosystems 411, 01.

Roche, K., Janáč, M., Šlapanský, L., Mikl, L., Kopeček, L., Jurajda, P., 2015. A newly established round goby (*Neogobius melanostomus*) population in the upper stretch of the river Elbe. Knowledge and Management of Aquatic Ecosystems 416, 33.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., LeRoy Poff, N., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Sapota, M.R., 2004. The round goby (*Neogobius melanostomus*) in the Gulf of Gdańsk—a species introduction into the Baltic Sea. In: Kautsky, H., Snoeijs, P. (eds.), Biology of the Baltic Sea. Springer Science and Business Media, Dordrecht, The Netherlands, pp. 219–224.

Sapota, M.R., Skóra, K.E., 2005. Spread of alien (non-indigenous) fish species *Neogobius melanostomus* in the Gulf of Gdansk (south Baltic). Biological Invasions 7, 157–164.

Savino, J.F., Stein, R.A., 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated submersed vegetation. Transactions of the American Fisheries Society 111, 255–266.

Sax, D.F., Gaines, S.D., 2008. Species invasions and extinctions: the future of native biodiversity on islands. Proceedings of the National Academy of Sciences of the United States of America, 105, 11490–11497.

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

Seebens, H., Essl, F., Blasius, B., 2017b. The intermediate distance hypothesis of biological invasions. Ecology Letters 20, 158–165.

Seebens, H., Blackburn, T.E., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., van Kleunen, M., Winter, M., Ansong, M., Arianoutsou, M., Bacher, S., Blasius, B., Brockerhoff, E.G., Brundu, G., Capinha, C., Causton, C.E., Celesti-Grapow, L., Dawson, W., Dullinger, S., Economo, E.P., Fuentes, N., Guénard, B., Jäger, H., Kartesz, J., Kenis, M., Kühn, I., Lenzner, B., Liebhold, A.M., Mosena, A., Moser, D., Nentwig, W., Nishino, M., Pearman, D., Pergl, J., Rabitsch, W., Rojas-Sandoval, J., Roques, A., Rorke, S., Rossinelli, S., Roy, H.E., Scalera, R., Schindler, S., Štajerová, K., Tokarska-Guzik, B., Walker, K., Ward, D.F., Yamanaka, T., Essl, F., 2018. Global rise in emerging alien species results from increased accessibility of new source pools. Proceedings of the National Academy of Sciences of the United States of America 115, E2264–E2273.

Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17, 170–176.

Schaeffer, J.S., Bowen, A., Thomas, M., French, J.R.P., Curtis, G.L., 2005. Invasion history, proliferation, and offshore diet of the round goby *Neogobius melanostomus* in Western Lake Huron, USA. Journal of Great Lakes Research 31, 414–425.

Schulte, P.M., Healy, T.M., Fangue, N.A., 2011. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. Integrative and Comparative Biology 51, 691–702.

Sih, A., Englund, G., Wooster, D., 1998. Emergent impacts of multiple predators on prey. Trends in Ecology and Evolution 13, 350–355.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M., 2013. Impacts of biological invasions: what's what and the way forward. Trends in Ecology and Evolution 28, 58–66.

Simonović, P., Paunović, M., Popović, S., 2001. Morphology, feeding, and reproduction of the round goby, *Neogobius melanostomus* (Pallas), in the Danube River Basin, Yugoslavia. Journal of Great Lakes Research 27, 281–289.

Sol, D., Lefebvre, L., 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. Oikos 90, 599–605.

Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P., Lefebvre, L., 2005. Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the United States of America 102, 5460–5465.

Solomon, M.E., 1949. The natural control of animal populations. Journal of Animal Ecology 18, 1–35.

Stachowicz, J.J., Whitlatch, R.B., Osman, R.W., 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286, 1577–1579.

Steinhart, G.B., Marschall, E.A., Stein, R.A., 2004. Round goby predation on smallmouth bass offspring in nests during simulated catch-and-release angling. Transactions of the American Fisheries Society 133, 121–131.

Stepien, C.A., Tumeo, M.A., 2006. Invasion genetics of Ponto-Caspian gobies in the Great Lakes: a 'cryptic'species, absence of founder effects, and comparative risk analysis. Biological Invasions 8, 61–78.

Stohlgren, T.J., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J., Master, L.L., 2006. Species richness and patterns of invasion in plants, birds, and fishes in the United States. Biological Invasions 8, 427–447.

Stohlgren, T.J., Ma, P., Kumar, S., Rocca, M., Morisette, J.T., Jarnevich, C.S., Benson, N., 2010. Ensemble habitat mapping of invasive plant species. Risk Analysis 30, 224–235.

Stráňai, I., Andreji, J., 2004. The first report of round goby, *Neogobius melanostomus* (Pisces, Gobiidae) in the waters of Slovakia. Folia Zoologica 53, 335.

Strayer, D.L., 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55, 152–174.

Swisher, B.J., Soluk, D.A., Wahl, D.H., 1998. Non-additive predation in littoral habitats: influences of habitat complexity. Oikos 81, 30–37.

Tanentzap, A.J., Bazely, D.R., Lafortezza, R., 2010. Diversity–invasibility relationships across multiple scales in disturbed forest understoreys. Biological Invasions 12, 2105–2116.

Taraborelli, A.C., Fox, M.G., Schaner, T., Johnson, T.B., 2009. Density and habitat use by the round goby (*Apollonia melanostoma*) in the Bay of Quinte, Lake Ontario. Journal of Great Lakes Research 35, 266–271.

Taraborelli, A.C., Fox, M.G., Johnson, T.B., Schaner, T., 2010. Round goby (*Neogobius melanostomus*) population structure, biomass, prey consumption and mortality from predation in the Bay of Quinte, Lake Ontario. Journal of Great Lakes Research 36, 625–632.

Thorp, C.J., Alexander, M.E., Vonesh, J.R., Measey, J., 2018. Size-dependent functional response of *Xenopus laevis* on mosquito larvae. PeerJ Preprints doi.org/10.7287/peerj.preprints.26575v1.

Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O., Rouget, M., 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology 11, 2234–2250.

Townsend, C.R., Risebrow, A.J., 1982. The influence of light level on the functional response of a zooplanktonivorous fish. Oecologia 53, 293–295.

Traill, L.W., Bradshaw, C.J.A., Brook, B.W., 2007. Minimum viable population size: a meta-analysis of 30 years of published estimates. Biological Conservation 139, 159–166.

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

van Kessel, N., Dorenbosch, M., Spikmans, F., 2009. First record on Pontian monkey goby, *Neogobius fluviatilis* (Pallas, 1814), in the Dutch Rhine. Aquatic Invasions 4, 421–424.

van Kessel, N., Dorenbosch, M., De Boer, M.R.M., Leuven, R.S.E.W., Van Der Velde, G., 2011. Competition for shelter between four invasive gobiids and two native benthic fish species. Current Zoology 57, 844–851.

van Kessel, N., Dorenbosch, M., Kranenbarg, J., van der Velde, G., Leuven, R.S.E.W., 2016. Invasive Ponto-Caspian gobies rapidly reduce the abundance of protected native bullhead. Aquatic Invasions 11, 179–188.

van Kleunen, M., Weber, E., Fischer, M., 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13, 235–245.

van Leeuwen, C.H.A., Huig, N., van der Velde, G., van Alen, T.A., Wagemaker, C.A.M., Sherman, C.D.H., Klaassen, M., Figuerola, J., 2013. How did this snail get here? Several dispersal vectors inferred for an aquatic invasive species. Freshwater Biology 58, 88–99.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., Ojaveer, H., 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 59, 1209–1228.

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

Vilà, M., Basnou, C., Gollasch, S., Josefsson, M., Pergl, J., Scalera, R., 2009. One hundred of the most invasive alien species in Europe. In: DAISIE (eds.), Handbook of alien species in Europe. Springer Science and Business Media, Dordrecht, The Netherlands, pp. 265–268.

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E., and DAISIE partners, 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment 8, 135–144.

Vitousek, P.M., 1990. Biological invasions and ecosystem process: towards an integration of population biology and ecosystem studies. Oikos 57, 7–13.

Vitousek, P.M., D'antonio, C.M., Loope, L.L., Rejmanek, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21, 1–16.

von Landwüst, C., 2006. Expansion of *Proterorhinus marmoratus* (Teleostei, Gobiidae) into the River Moselle (Germany). Folia Zoologica 55, 107–111.

Vonesh, J., McCoy, M., Altwegg, R., Landi, P., Measey, J., 2017a. Functional responses can't unify invasion ecology. Biological Invasions 19, 1673–1676.

Vonesh, J., McCoy, M., Altwegg, R., Landi, P., Measey, J., 2017b Rather than unifying invasion biology, Dick et al.'s approach rests on subjective foundations. Biological Invasions 19, 1679–1680.

Všetičková, L., Janáč, M., Vašek, M., Roche, K., Jurajda, P., 2014. Non-native western tubenose gobies *Proterorhinus semilunaris* show distinct site, sex and age-related differences in diet. Knowledge and Management of Aquatic Ecosystems 414, 10.

Vucic-Pestic, O., Ehnes, R.B., Rall, B.C., Brose, U., 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. Global Change Biology 17, 1301–1310.

Walsh, M.G., Dittman, D.E., O'Gorman, R., 2007. Occurrence and food habits of the round goby in the profundal zone of southwestern Lake Ontario. Journal of Great Lakes Research 33, 83–92.

Ward, J.M., Ricciardi, A., 2007. Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis. Diversity and Distributions 13, 155–165.

Wasserman, R.J., Alexander, M.E., Dalu, T., Ellender, B.R., Kaiser, H., Weyl, O.L.F., 2016. Using functional responses to quantify interaction effects among predators. Functional Ecology 30, 1988–1998.

Westphal, M.I., Browne, M., MacKinnon, K., Noble, I., 2008. The link between international trade and the global distribution of invasive alien species. Biological Invasions 10, 391–398.

Wiesner, C., 2005. New records of non-indigenous gobies (*Neogobius* spp.) in the Austrian Danube. Journal of Applied Ichthyology 21, 324–327.

Williamson, M.H., 1993. Invaders, weeds and the risk from genetically modified organisms. Experientia 49, 224–232.

Williamson, M.H., 1996. Biological invasions. Springer Science and Business Media, Dordrecht, The Netherlands, 244 pp.

Williamson, M.H., Brown, K.C., 1986. The analysis and modelling of British invasions. Philosophical Transactions of the Royal Society London B 314, 505–522.

Williamson, M.H., Fitter, A., 1996. The varying success of invaders. Ecology 77, 1661–1666.

Wilson, R.J., Gutierrez, D., Gutierrez, J., Monserrat, V.J., 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. Global Change Biology 13, 1873–1887.

Wyatt, T., Carlton, J., 2002. Phytoplankton introductions in European coastal waters: why are so few invasions reported? In: CIESM (Commission Internationale pour l'Exploration Scientifique de la mer Mediterranee), Workshop Monographs no. 20, pp. 41–46. CIESM, Monaco.

Xu, M., Mu, X., Dick, J.T.A., Fang, M., Gu, D., Luo, D., Zhang, J., Luo, J., Hu, Y., 2016. Comparative functional responses predict the invasiveness and ecological impacts of alien herbivorous snails. PLoS ONE 11, e0147017.

Young, J.A.M., Marentette, J.R., Gross, C., McDonald, J.I., Verma, A., Marsh-Rollo, S.E., Macdonald, P.D.M., Earn, D.J.D., Balshine, S., 2010. Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour. Journal of Great Lakes Research 36, 115–122.

CHAPTER 2

DISTRIBUTION OF ALIEN ANIMAL SPECIES RICHNESS IN THE CZECH REPUBLIC

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ORIGINAL RESEARCH

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Distribution of alien animal species richness in the Czech Republic

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Abstract

Biogeographical barriers formed by natural forces over billions of years have been substantially disrupted by human activity, particularly in recent centuries. In response to these anthropogenic changes, global homogenization of biota is observed at an ever-increasing rate, causing environmental and economic losses as well as emerging health risks. Identifying factors underlying alien species richness is essential for prevention of future introductions and subsequent spread. In this study, we examined the effects of environmental and human-related factors on distribution of alien animal species richness in the Czech Republic (Central Europe). We compiled a set of maps showing the level of invasion of six categories of alien animal species in each of 628 grid cells (*ca.* 12.0 × 11.1 km) covering the Czech Republic. Relationships between alien species richness and 12 variables characterizing climatic conditions, topography, land cover, and human population size were calculated using the generalized least squares method. Species richness of all alien species, of invertebrates, and of terrestrial species showed the strongest positive relationship with mean annual temperature, while the number of black and grey (proposed prominent invaders) and aquatic species was most closely related to the presence of large rivers. Alien vertebrates showed a strong negative relationship with annual precipitation. The highest alien animal species richness was found in and near large population centers and in agricultural landscapes in warm and dry lowlands. The gateways for alien aquatic species are rather large rivers over sport fishing and aquaculture import. Compiled maps create a powerful visual communication tool, useful in development of programs to prevent future introductions.

KEYWORDS
alien species, animal, distribution pattern, Europe, habitat invasibility, invasion level

1 | INTRODUCTION

Biological invasions, consequential biodiversity loss, and ecosystem function alterations are major components of human-induced global change (Vitousek, D'Antonio, Loope, Rejmánek, & Westbrooks, 1997) and generate economic costs associated with commodity and service losses as well as with eradication and mitigation of alien species (Pimentel, 2011; Vilà et al., 2010). Serious human health risks

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have emerged in tandem with new introductions (Mazza, Tricarico, Genovesi, & Gherardi, 2014). Although Europe is considered to be a more frequent donor than recipient of alien species (Lambdon et al., 2008), several evidences proved that Central Europe possesses crucial historical, biogeographical, and anthropogenic predispositions for successful biological invasions (Hulme, 2007; Pyšek, Sádlo, & Mandák, 2002). Moreover, Genovesi, Carnevali, and Scalera (2015) reported that one of five threatened species in Europe is directly affected by alien species. Additionally, the accelerating growth of the global economy and international trade goes hand in hand with increase in invasion rate (Hulme, 2009; Meyerson & Mooney, 2007) with no sign of saturation (Seebens et al., 2017). Understanding the drivers and prediction of invasion processes, including determining high-risk areas, is therefore of critical importance for designing appropriate management interventions.

The level of invasion varies along environmental gradients and among habitats (Chytrý et al., 2008; Richardson & Pyšek, 2006; Vicente, Alves, Randin, Guisan, & Honrado, 2010). Human-made and/or disturbed habitats are generally considered more susceptible to colonization and spread of alien species and also play a key role as corridors for new invasions (Pyšek, Chytrý, Pergl, Sádlo, & Wild, 2012). Economic and demographic variables reflecting the intensity of human impact on species and habitats include propagule pressure, pathways of introduction, eutrophication, and intensity of anthropogenic disturbance and may directly influence the outcome of invasions (Patoka et al., 2016; Perdikaris, Kozák, Kouba, Konstantinidis, & Paschos, 2012). Alien species richness therefore often positively correlates with human density and activity (McKinney, 2001; Stohlgren et al., 2006), and these variables have been suggested to be more important than environmental conditions, climate, or native species richness (Pyšek, Jarošík, et al., 2010; Spear, Foxcroft, Bezuidenhout, & McGeoch, 2013). However, even regions of low human impact are not resistant to invasion (Deutschewitz, Lausch, Kühn, & Klotz, 2003; Pyšek, Genovesi, Pergl, Monaco, & Wild, 2013; Wu et al., 2010). Aforementioned variables are important components of predictions of future invasions and alien species distribution modeling because the establishment of an alien is driven by climate and land use match (Ficetola, Thuiller, & Miaud, 2007; Thuiller et al., 2005).

In this study, we aimed to investigate which factors are important in explaining alien species richness in the Czech Republic. We considered six categories of alien species. Specific objectives of this study were to provide country-wide maps of alien animal species richness, exploring whether the above-mentioned groups exhibit different spatial patterns, and to assess which factors best correlate with their spatial distribution.

2 | METHODS

2.1 | Species distribution data

Spatial distribution (presence/absence records) of alien animal species in the Czech Republic was derived from maps published by Mlíkovský and Stýblo (2006). As primary sources, they used published records in peer-reviewed as well as in nonpeer-reviewed journals, abstract books, books, dissertations, grey literature, web databases, and personal and correspondence communications. We extracted all alien animals with compiled map, whereas only documented recent occurrences were considered. Uncertain occurrences and those presumably vanished were excluded.

This dataset utilizes the Kartierung der Flora Mitteleuropas (KFME) mapping grid, a commonly applied mapping system in Central Europe (Buchar, 1982). The KFME is based on rectangular spatial units (grid cells). Each grid cell spans 10′ of longitude and 6′ of latitude, which represents an area of *ca.* 12.0 × 11.1 km (133.2 km^2) on the 50th parallel (Figure 1). Although the area of the Czech Republic (78,866 km^2) is covered by 678 grid cells in total, we excluded marginal ones and considered only 628 cells according to Šťastný, Bejček, and Hudec (2006).

For analyses of alien animal species richness, six alien animal groups were defined based on the mentioned dataset:

1. all alien animal species (207 species);
2. black and grey species, that is, prominent invasive alien species of high concern that are the subject of priority monitoring and management (Pergl et al., 2016) for the country (36 species);
3. vertebrates (58 species);
4. invertebrates (149 species);
5. terrestrial species (either vertebrate or invertebrate, 158 species);
6. aquatic species (either vertebrates or invertebrates, dependent on the aquatic environment at least for one phase of life history, 49 species).

For a list of species in each category, see Supplementary Information.

2.2 | Explanatory variables

We calculated 12 variables describing environmental conditions and human population in each grid cell (Table 1) using ArcGIS (v. 10.2.2, ESRI, Redlands, CA, USA). Mean altitude was based on the digital elevation model of the Czech Republic with a resolution of 50 × 50 m. Based on this model, we also estimated terrain heterogeneity using the Vector Ruggedness Measure (VRM; Sappington, Longshore, & Thompson, 2007). The VRM combines variation in slope and aspect into a single measure and provides more complete information about terrain heterogeneity than do indices based on slope or altitude only. Higher VRM value indicates the higher terrain heterogeneity.

Mean annual temperature and precipitation were extracted from maps published by Tolasz et al. (2007).

Relative area of three broad land cover types within each grid cell was calculated using CORINE 2000 Land Cover data (Bossard, Feranec, & Otahel, 2000). To obtain relative area of forests, we amalgamated the CORINE-type *broad-leaved forests* (3.1.1.), *coniferous forests* (3.1.2), and *mixed forests* (3.1.3). Relative area of open and mosaic landscape was calculated based on the following categories:

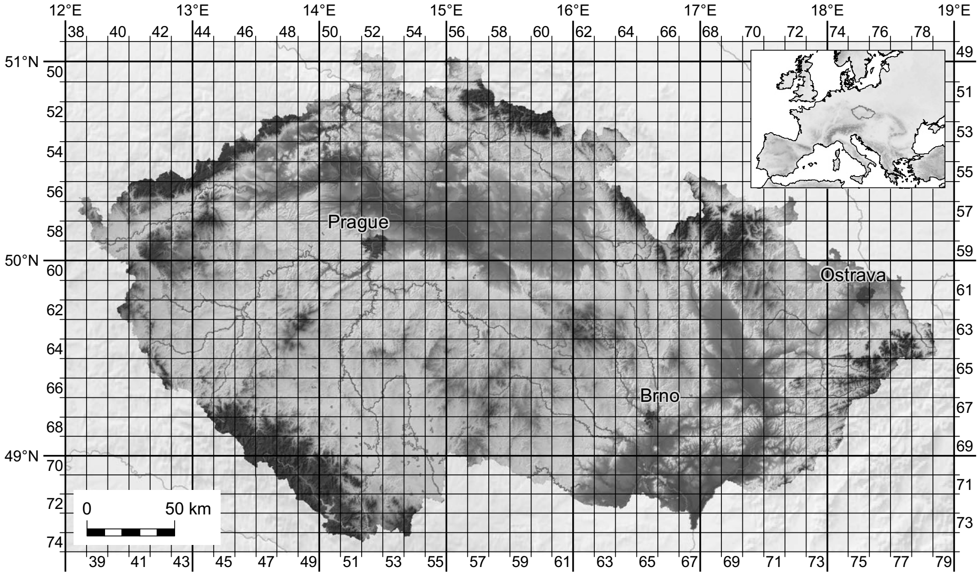

FIGURE 1 KFME grid used for mapping of the alien animal species in the Czech Republic. Three largest cities of the country are also shown

TABLE 1 Environmental variables (values per KFME mapping grid cell) used

Variable	Minimum	Mean	Maximum	*SD*
Altitude (m asl)	154	452	1,156	172
Terrain heterogeneity (VRM × 1,000)	0.0	5.3	34.3	5.4
Mean annual temperature (°C)	3.0	7.4	9.5	1.1
Annual precipitation (mm/year)	432	678	1,387	157
Proportion of forested landscape (%)	0.0	33.2	98.0	18.1
Proportion of open and mosaic landscape (%)	0.4	17.1	55.6	11.1
Proportion of arable land (%)	0.0	40.3	90.8	23.7
Number of land cover types	3	10.6	19	2.5
Proportion of (semi-)natural habitats (%)	0.3	7.0	64.2	8.0
Proportion of water bodies (%)	0.0	1.0	17.1	1.8
Size of rivers (index)	2	4.7	8	1.3
Human population (Number of inhabitants)	1	16,534	604,751	33,944

vineyards (2.2.1), *fruit tree and berry plantations* (2.2.2), *pastures* (2.3.1), *complex cultivation patterns* (2.4.2), *land principally occupied by agriculture, with significant areas of natural vegetation* (2.4.3), *natural grasslands* (3.2.1), and *moors and heathland* (3.2.2). Relative area of arable land was expressed as *nonirrigated arable land* (2.1.1). In addition to the relative area of the land cover types, we calculated the number of CORINE types per grid cell in order to quantify landscape heterogeneity. Proportion of (semi-)natural habitats was obtained from the database of natural and semi-natural habitat types of the Czech Republic, established during the extensive habitat mapping project coordinated by the Nature Conservation Agency of the Czech Republic 2001–2004 (Härtel, Lončáková, & Hošek, 2009). The database contains spatial information on 127 (semi-)natural habitat types defined by Chytrý, Kučera, Kočí, Grulich, and Lustyk (2010) and mapped at a scale of 1:10,000.

Each grid cell was also characterized by the relative proportion of water bodies (lakes, reservoirs, ponds, rivers) obtained from the digital base of water management (DIBAVOD) database (http://www.dibavod.cz/). In order to quantify the size of rivers in each grid cell, we assigned a Strahler's stream order value to each segment in a river network (Strahler, 1952). Each grid cell was then characterized by the maximum Strahler's stream order value in the grid cell.

Human population size in each grid cell was calculated based on the GEOSTAT 2011 population-grid dataset (http://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/population-distribution-demography), which contains the number of inhabitants per km^2 for the entire European Union in 2011.

2.3 | Statistical analyses

Species richness of each considered alien group was normalized using a logarithmic transformation. Where necessary, we also log-transformed explanatory variables [terrain heterogeneity, proportion of (semi-)natural habitats, proportion of water bodies, and human population]. To explore trends in alien species richness, we first plotted the number of species in each grid cell against each explanatory variable. The shape of the relationship was estimated using a locally weighted polynomial regression with a smoothing span $\alpha = 0.75$ (Cleveland, Grosse, & Shyu, 1991). Observed trends suggested that a linear model is an acceptable approximation of the relationships.

To test the effect of each variable on alien species richness, we used the normal error generalized least squares (GLS) method, appropriate in situations in which observations of the response variable are not independent, that is, significantly spatially correlated (spatial autocorrelation was tested using Moran's I statistics). The GLS fits spatial covariance among observations (*i.e.*, grid cells) to take spatial autocorrelation into account. Longitudinal and latitudinal cell centroid values were used as variables to describe spatial correlation structure within the dataset. Different models of spatial structure (spherical, Gaussian, linear and exponential; see Legendre & Legendre, 2012) were tested, and the best fitting model (exponential in all cases) was selected using the Akaike information criterion. The significance of the effect of each explanatory variable was tested using the Wald test with a critical significance level of 0.05. We use the term "effect" to indicate a statistical relationship, not proven mechanistic causation (Hawkins, 2012). All models were implemented in nlme package (Pinheiro, Bates, DebRoy, & Sarkar, 2013) in R software (R Core Team, 2016).

3 | RESULTS

Thirty-four alien species were present in more than 100 of the 628 analyzed cells. Of these, 21 species were accidentally introduced, 11 intentionally introduced, and two by spontaneous spread. Eleven species were distributed throughout the country.

In general, the highest alien animal species richness in the country was found in cities and their surroundings, floodplains of large rivers, and agricultural landscapes in warm and dry lowlands (Figure 2). Relationships among the number of all alien animal species and explanatory variables are shown in Figure 3. Using GLS, we found a significant relationship ($p < .05$) between species richness of each alien group and most explanatory variables (Table 2). The proportion of (semi-)natural habitat types in grid cells was significantly negatively related to the number of alien vertebrates and showed no relationship with other groups. All alien animal species, invertebrates, and terrestrial species showed the strongest positive relationships with mean annual temperature, while the numbers of black and grey and aquatic species were best explained by river size. For vertebrates, the strongest relationship was with decreasing annual precipitation.

4 | DISCUSSION

Rather than attempting to disentangle pure and shared effects of environmental variables on species richness patterns, we assessed the magnitude of the relationship between alien species richness and individual factors (Table 1), producing results easily accessible to policy makers and stakeholders, as well as the public, and thus more applicable in invasion ecology management. The statistical analysis was supported by the maps of alien species richness, a powerful tool for visual communication among concerned parties, as well as for identifying invasion hotspots, crucial for prevention of future introductions, which is more effective than mitigation or eradication (Figure 2). Although newly introduced species are not included in our study, as the dataset of Mlíkovský and Stýblo (2006) has not been updated, and the distribution range of aliens, particularly those highly invasive, can expand rapidly over a short time period, it is likely that our results are currently valid, reflecting successful introductions in the past decades.

4.1 | Topographical factors

Areas at high altitude and spatially heterogeneous terrain are generally considered to be more resistant to invasion, due to lower human population density and trade and more severe climate (Kumar, Stohlgren, & Chong, 2006; Zefferman et al., 2015). On the other hand, invasion by particular taxonomic groups, especially mammals, is largely shaped by intentional introductions and releases (Genovesi, Bacher, Kobelt, Pascal, & Scalera, 2009), which may counteract the altitudinal pattern.

We found both altitude and terrain heterogeneity to be negatively correlated with alien animal species richness. Altitude can be considered a primary determinant of climatic harshness, propagule

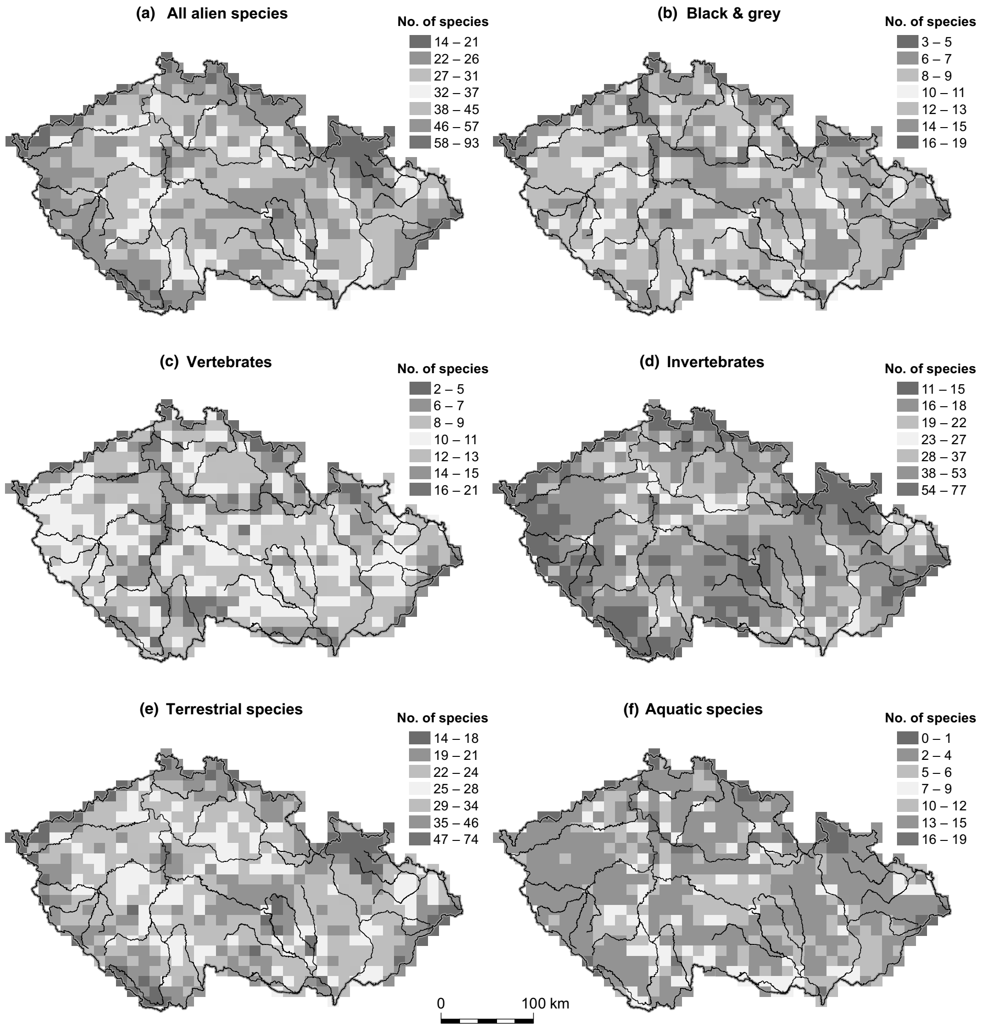

FIGURE 2 Spatial distribution of alien animal species richness in the Czech Republic. Color scale in each map was established using the Natural Breaks (Jenks) method. Thin black lines represent main river courses

pressure, and invasion history, factors reported to directly affect alien species richness along the altitude gradient (e.g., Konvicka, Maradova, Benes, Fric, & Kepka, 2003; Pyšek et al., 2012). This was reflected in our results showing the effect of altitude to be similar to that of mean annual temperature, precipitation, and human impact (population, land cover types), for the categories all alien species, terrestrial species, and invertebrates (Table 2). The effect of terrain heterogeneity on alien species richness was relatively weak compared to other variables and was consistently negative, suggesting that a rugged landscape with many topographical barriers may be more resistant to invasion (Richardson & Pyšek, 2006).

4.2 | Climatic factors

Lambdon et al. (2008) identified climate as a primary driver of invasion success of alien plants. In other taxonomic groups, the effect of climate on aliens was often outweighed by demographic and

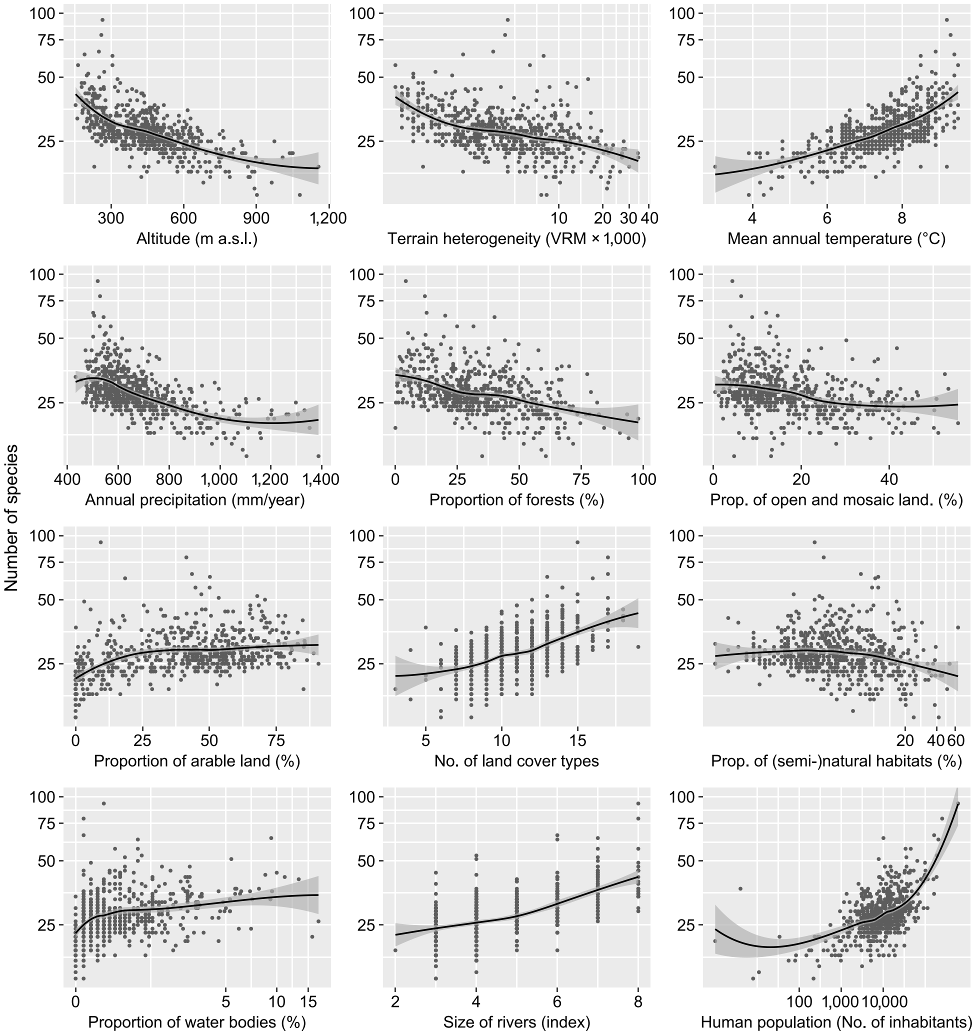

FIGURE 3 Relationships between the number of all alien animal species occurring in each grid cell (log scale) and the explanatory variables. Terrain heterogeneity, proportion of (semi-)natural habitats, proportion of water bodies, and human population were logarithmically transformed. Regression curves were fitted using locally weighted polynomial regressions. Dark grey zone either side of the regression line denotes 95% confidence interval

economic variables such as human population density and affluence (Pyšek, Jarošík, et al., 2010). However, several studies have shown that alien mammals (Winter et al., 2010) and birds (Dyer et al., 2017) are also limited by climatic conditions. In the Czech Republic, alien animal richness was strongly positively related to the mean annual temperature and negatively related to annual precipitation. This relationship was apparent in all tested animal groups (Table 2). In invertebrates, terrestrial, and all alien species, mean annual temperature showed the strongest effect among the explanatory variables. The source of this similarity among groups is probably the high proportion of invertebrate taxa within the investigated dataset, representing 72% and 83% of all species and

TABLE 2 Results of GLS models with exponential spatial structures for each considered alien animal group

	All alien species		Black & grey		Vertebrates		Invertebrates		Terrestrial species		Aquatic species	
Altitude	235.9	−−−	96.9	−−−	144.6	−−−	190.1	−−−	163.0	−−−	153.0	−−−
Terrain heterogeneity	37.9	−−−	24.5	−−−	38.5	−−−	21.3	−−−	17.8	−−−	42.0	−−−
Mean annual temperature	**278.6**	**+++**	112.5	+++	161.9	+++	**205.2**	**+++**	**188.1**	**+++**	171.7	+++
Annual precipitation	132.6	−−−	75.7	−−−	**192.1**	−−−	57.1	−−−	92.5	−−−	118.3	−−−
Proportion of forests	44.5	−−−	16.4	−−−	26.8	−−−	35.1	−−−	36.4	−−−	28.7	−−−
Proportion of open and mosaic landscape	17.9	−−−	11.1	−−−	5.5	−−	19.9	−−−	19.9	−−−	3.7	n.s.
Proportion of arable land	12.5	+++	9.6	++	25.1	+++	4.9	++	11.0	+++	9.7	++
Number of land cover types	199.5	+++	90.3	+++	66.5	+++	195.6	+++	137.3	+++	121.4	+++
Proportion of (semi-) natural habitats	0.4	n.s.	0.0	n.s.	5.3	−	0.1	n.s.	0.0	n.s.	3.3	n.s.
Proportion of water bodies	48.7	+++	39.1	+++	52.4	+++	23.4	+++	7.9	++	107.4	+++
Size of rivers	217.4	+++	**186.4**	**+++**	119.4	+++	155.2	+++	110.1	+++	**173.4**	**+++**
Human population size	233.4	+++	88.7	+++	112.0	+++	192.8	+++	181.9	+++	142.2	+++

F-values and associated significance resulting from Wald tests are shown. The highest *F*-values are in bold. Mathematical signs + and − indicate either significant positive or negative relationships, n.s. indicates nonsignificant result. The number of symbols indicates the level of significance; +++/−−− = $p < 0.001$, ++/−− = $0.001 \geq p < 0.01$, and +/− = $0.01 \geq p < 0.05$.

terrestrial species, respectively. Alien insects and invertebrates tend to occur in intensively disturbed or human-made habitats and settlements (Pyšek, Bacher, et al., 2010). Such habitats also represent important corridors, as dispersal capability of invertebrates is often limited.

Annual precipitation and mean annual temperature were found to have the strongest effect on alien vertebrate species richness (Table 2). This result is most likely driven by correlations of annual precipitation with other variables. In the Czech Republic, precipitation is generally lower in lowlands, which are in turn warmer. The richness pattern of black and grey species was affected by climate to a lesser extent than other groups, as indicated by considerably lower *F*-values of both climatic variables, although still significant. This underlines the adaptability and overall hardiness of prominent invaders included in the black and grey species list (Pergl et al., 2016).

4.3 | Landscape and habitat factors

Habitat and its heterogeneity highly influence species coexistence (Chesson, 2000) and, consequently, biological invasions (Richardson & Pyšek, 2006). A heterogeneous environment provides closely linked diverse habitats suitable for both native and alien species, and therefore, they are considered more vulnerable to invasion compared to homogeneous habitats (Davies et al., 2005). This phenomenon is also supported by a positive relationship between native and alien species richness, which often occurs in large sampling areas with high habitat variability (Melbourne et al., 2007), such as the grid cells used in our study. In this study, the number of land cover types positively correlated with the species richness of all alien groups (Table 2). Considerably lower, although significant, effects were found for both vertebrates and black and grey species, probably resulting from the high taxon diversity within these groups. Moreover, vertebrates are more evenly distributed among habitats compared to other alien taxonomic groups (Pyšek, Bacher, et al., 2010), which, in our study, was reflected by their lower correlation with both proportion of forestation and proportion of open and mosaic landscape compared to that found for invertebrates.

Habitats differ in alien species richness, what is particular in alien plants (Chytrý, Jarošík, et al., 2008). Although land cover types analyzed in our study were broad heterogeneous landscape categories, they represented a range of disturbance and habitat function. The proportion of arable land reflects the man-made cultivated habitats that are among the most invaded by plants (Chytrý, Maskell, et al., 2008). Fluctuations in available resources and severe habitat disturbance create open ecological niches suitable for aliens (Marvier, Kareiva, & Neubert, 2004). Similar trends are apparent in alien invertebrates (Pyšek, Bacher, et al., 2010; Roques et al., 2009), supported by our finding of a positive relationship of alien invertebrate richness to the proportion of arable land, although the correlation was weaker than observed for other alien species groups. The proportion of open and mosaic landscape reflected man-made as well as natural habitats with limited available resources. Their vulnerability to invasion depends primarily upon the propagule pressure (Chytrý, Jarošík, et al., 2008), and the number of species significantly decreased with the increasing proportion of open and mosaic landscape for all alien groups except aquatic species.

The proportion of forests did not accurately reflect the human disturbance pattern across the landscape, as both semi-natural forests and commercial plantations were included. However, most forests presumably comprise less disturbed habitats, with a low level of accessible resources compared to non-forest habitats. This was reflected in the significant negative correlation of proportion of forests with the number of alien animals for all groups. Considering low disturbance of (semi-)natural habitats, less invasion of these habitats might be expected. This hypothesis was confirmed only for vertebrates, other alien categories did not show significant results (Table 2). Chytrý et al. (2009) demonstrated that semi-natural habitats in lowlands, especially those located in floodplains of large rivers, are frequent recipients of alien biota.

River size showed a significant positive relationship with all alien animal groups (Table 2). Its effect was the strongest not only on aquatic species but also on black and grey species. In the latter group, river size considerably outweighed other variables, including proportion of water bodies, due to large proportion of aquatic animals, including *Mustela vison*, *Myocastor coypus*, and *Ondatra zibethicus*, which are frequently found at river banks. Alien aquatic species in the Czech Republic show clear trends in distribution toward navigable rivers influenced by ballast water exchange, such as the Elbe River, which was recently confirmed as the site of several introduction events (Buřič, Bláha, Kouba, & Drozd, 2015). Other vectors of aquatic invasions are spontaneous migration through the Danube River system, intentional and unintentional introductions into aquaculture areas, and accidental escapes from pet owners and/or vendors (Musil, Jurajda, Adámek, Horký, & Slavík, 2010; Patoka et al., 2016).

4.4 | Demographic factors

Propagule pressure substantially influences the level of biological invasion (Lockwood, Cassey, & Blackburn, 2005). Remote areas with little human intervention receive fewer alien species than densely populated trade routes or areas of intense human activity (Drake et al., 1989). Propagule pressure can be quantified using human-related data as surrogate. We used human population size as an in direct indicator of human activity related to invasions. Despite limitations, this simplification is reasonable, as human population density appears to be a reliable indicator of propagule pressure in Europe (Copp, Vilizzi, & Gozlan, 2010).

When analyzed together, economic and demographic indicators have been shown to considerably outperform climatic, geographic, and land cover factors in richness of several taxonomic groups (Dyer et al., 2017; Pyšek, Jarošík, et al., 2010). In our study, human population density showed a strong positive relationship to alien animal species richness in all assessed categories (Table 2). Its considerably higher effect on invertebrates, and consequently terrestrial and all alien animals, likely reflects a high number of alien invertebrates introduced as pests into commodity storehouses. Deliberate stocking of animals within the aquatic, black and grey, and vertebrate species categories (García-Berthou et al., 2005) into remote areas is another important factor reducing the correlation with human population density.

5 | CONCLUSIONS

Our results together with created maps contribute to better understanding and prediction of introductions of alien animals. This information is of critical importance for managers and policy makers so they can concentrate their efforts on high-risk areas. Moreover, they should also focus on raising the public awareness about alien species. Compiled maps represent a valuable communication tool for this purpose.

The distribution of introduced aliens, as well as establishment of new ones, also calls for further monitoring, as distribution ranges can change substantially due to the time-lag between introduction and spread (Roques et al., 2009) as well as changes of climate (Dukes & Mooney, 1999) and land use (Sala et al., 2000). In addition, increasing temperatures can promote the invasion and reproduction success of alien species that may subsequently become established or naturalized (Walther et al., 2009).

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTION

A.K. and M.B. conceived the original idea and developed the theory. R.G. and B.D. carried out the data acquisition. J.D. and M.V. performed the computations, analyses, and interpretation of the data. R.G. wrote the manuscript with support of all authors. All authors discussed the results and contributed to the final manuscript, revising it critically for important intellectual content.

DATA ACCESSIBILITY

Data with numbers of alien animal species in grid cells are openly available in Dryad.

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REFERENCES

Bossard, M., Feranec, J., & Otahel, J. (2000). *CORINE land cover technical guide-Addendum 2000*. Copenhagen, Denmark: European Environmental Agency.

Buchar, J. (1982). Způsob publikace lokalit živočichů z území Československa [Methods for publishing of animal distribution in the Czechoslovakia]. *Věstník Československé zoologické společnosti*, *46*, 317–318.

Buřič, M., Bláha, M., Kouba, A., & Drozd, B. (2015). Upstream expansion of round goby (*Neogobius melanostomus*)–first record in the upper reaches of the Elbe river. *Knowledge and Management of Aquatic Ecosystems*, *416*, 32.

Chesson, P. (2000). General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology*, *58*, 211–237. https://doi.org/10.1006/tpbi.2000.1486

Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L., & Danihelka, J. (2008). Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology*, *89*, 1541–1553. https://doi.org/10.1890/07-0682.1

Chytrý, M., Kučera, T., Kočí, M., Grulich, V., & Lustyk, P. (2010). *Katalog biotopů České republiky [Catalogues of habitats in the Czech Republic]*. Prague, Czech Republic: AOPK.

Chytrý, M., Maskell, L. C., Pino, J., Pyšek, P., Vilà, M., Font, X., & Smart, S. M. (2008). Habitat invasions by alien plants: A quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology*, *45*, 448–458. https://doi.org/10.1111/j.1365-2664.2007.01398.x

Chytrý, M., Wild, J., Pyšek, P., Tichý, L., Danihelka, J., & Knollová, I. (2009). Maps of the level of invasion of the Czech Republic by alien plants. *Preslia*, *81*, 187–207.

Cleveland, W. S., Grosse, E., & Shyu, W. M. (1991). Local regression models. In W. S. Chambers & T. J. Hastie (Eds.), *Statistical models in S* (pp. 309–376). Boca Raton, FL: CRC Press.

Copp, G., Vilizzi, L., & Gozlan, R. (2010). The demography of introduction pathways, propagule pressure and occurrences of non-native freshwater fish in England. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *20*, 595–601. https://doi.org/10.1002/aqc.1129

Davies, K. F., Chesson, P., Harrison, S., Inouye, B. D., Melbourne, B. A., & Rice, K. J. (2005). Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. *Ecology*, *86*, 1602–1610. https://doi.org/10.1890/04-1196

Deutschewitz, K., Lausch, A., Kühn, I., & Klotz, S. (2003). Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology and Biogeography*, *12*, 299–311. https://doi.org/10.1046/j.1466-822X.2003.00025.x

Drake, J. A., Mooney, H. A., Di Castri, F., Groves, R. H., Kruger, F. J., Rejmánek, M., & Williamson, M. (1989). *Biological invasions: A global perspective*. New York, NY: John Wiley & Sons.

Dukes, J. S., & Mooney, H. A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology & Evolution*, *14*, 135–139. https://doi.org/10.1016/S0169-5347(98)01554-7

Dyer, E. E., Cassey, P., Redding, D. W., Collen, B., Franks, V., Gaston, K. J., & Blackburn, T. M. (2017). The global distribution and drivers of alien bird species richness. *PLOS Biology*, *15*, e2000942.

Ficetola, G. F., Thuiller, W., & Miaud, C. (2007). Prediction and validation of the potential global distribution of a problematic alien invasive species—the American bullfrog. *Diversity and Distributions*, *13*, 476–485. https://doi.org/10.1111/j.1472-4642.2007.00377.x

García-Berthou, E., Alcaraz, C., Pou-Rovira, Q., Zamora, L., Coenders, G., & Feo, C. (2005). Introduction pathways and establishment rates of invasive aquatic species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 453–463. https://doi.org/10.1139/f05-017

Genovesi, P., Bacher, S., Kobelt, M., Pascal, M., & Scalera, R. (2009). Alien mammals of Europe. In Daisie (Ed.), *Handbook of alien species in Europe* (pp. 119–128). Dordrecht, The Netherlands: Springer Netherlands. https://doi.org/10.1007/978-1-4020-8280-1

Genovesi, P., Carnevali, L., & Scalera, R. (2015). *The impact of invasive alien species on nature threatened species in Europe (Technical report for the European Commision)*. Rome, Italy: ISPRA.

Härtel, H., Lončáková, J., & Hošek, M. (2009). *Mapování biotopů v České republice. Východiska, výsledky, perspektivy [Habitat mapping in the Czech Republic]*. Prague, Czech Republic: AOPK.

Hawkins, B. A. (2012). Eight (and a half) deadly sins of spatial analysis. *Journal of Biogeography*, *39*, 1–9. https://doi.org/10.1111/j.1365-2699.2011.02637.x

Hulme, P. E. (2007). Biological invasions in Europe: Drivers, pressures, states, impacts and responses. In R. E. Hester & R. M. Harrison (Eds.), *Biodiversity under threat* (pp. 56–80). Cambridge, UK: The Royal Society of Chemistry. https://doi.org/10.1039/1465-1874

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

Konvicka, M., Maradova, M., Benes, J., Fric, Z., & Kepka, P. (2003). Uphill shifts in distribution of butterflies in the Czech Republic: Effects of changing climate detected on a regional scale. *Global Ecology and Biogeography*, *12*, 403–410. https://doi.org/10.1046/j.1466-822X.2003.00053.x

Kumar, S., Stohlgren, T. J., & Chong, G. W. (2006). Spatial heterogeneity influences native and nonnative plant species richness. *Ecology*, *87*, 3186–3199. https://doi.org/10.1890/0012-9658(2006)87[3186:SHINAN]2.0.CO;2

Lambdon, P. W., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., & Hulme, P. E. (2008). Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. *Preslia*, *80*, 101–149.

Legendre, P., & Legendre, L. F. (2012). *Numerical ecology*. Amsterdam, The Netherlands: Elsevier.

Lockwood, J. L., Cassey, P., & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, *20*, 223–228. https://doi.org/10.1016/j.tree.2005.02.004

Marvier, M., Kareiva, P., & Neubert, M. G. (2004). Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis*, *24*, 869–878. https://doi.org/10.1111/j.0272-4332.2004.00485.x

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

McKinney, M. L. (2001). Effects of human population, area, and time on non-native plant and fish diversity in the United States. *Biological Conservation*, *100*, 243–252. https://doi.org/10.1016/S0006-3207(01)00027-1

Melbourne, B. A., Cornell, H. V., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A. L., & Yokomizo, H. (2007). Invasion in a heterogeneous world: Resistance, coexistence or hostile takeover? *Ecology Letters*, *10*, 77–94. https://doi.org/10.1111/j.1461-0248.2006.00987.x

Meyerson, L. A., & Mooney, H. A. (2007). Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment*, *5*, 199–208. https://doi.org/10.1890/1540-9295(2007)5[199:IASIAE]2.0.CO;2

Mlíkovský, J., & Stýblo, P. (Eds.) (2006). *Nepůvodní druhy fauny a flory České republiky [Alien species of fauna and flora in the Czech Republic]*. Prague, Czech Republic: ČSOP.

Musil, J., Jurajda, P., Adámek, Z., Horký, P., & Slavík, O. (2010). Non-native fish introductions in the Czech Republic - species inventory, facts and future perspectives. *Journal of Applied Ichthyology*, *26*, 38–45. https://doi.org/10.1111/j.1439-0426.2010.01500.x

Patoka, J., Buřič, M., Kolář, V., Bláha, M., Petrtýl, M., Franta, P., & Kouba, A. (2016). Predictions of marbled crayfish establishment in conurbations fulfilled: Evidences from the Czech Republic. *Biologia*, *71*, 1380–1385.

Perdikaris, C., Kozák, P., Kouba, A., Konstantinidis, E., & Paschos, I. (2012). Socio-economic drivers and non-indigenous freshwater crayfish species in Europe. *Knowledge and Management of Aquatic Ecosystems*, *404*, 01. https://doi.org/10.1051/kmae/2011077

Pergl, J., Sádlo, J., Petrusek, A., Laštůvka, Z., Musil, J., Perglová, I., & Pyšek, P. (2016). Black, Grey and Watch Lists of alien species in the Czech Republic based on environmental impacts and management strategy. *NeoBiota*, *28*, 1–37. https://doi.org/10.3897/neobiota.28.4824

Pimentel, D. (2011). Environmental and economic cost associated with alien invasive species in the United States. In D. Pimentel (Ed.), *Biological invasions: Economic and environmental costs of alien plant, animal, and microbe species* (pp. 411–430). Boca Raton, FL: CRC Press. https://doi.org/10.1201/b10938

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2013). nlme: Linear and nonlinear mixed effects models. R package version 3.1-113. Retrieved from https://CRAN.R-project.org/package=nlme

Pyšek, P., Bacher, S., Chytrý, M., Jarošík, V., Wild, J., Celesti-Grapow, L., & Hulme, P. E. (2010). Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. *Global Ecology and Biogeography*, *19*, 317–331.

Pyšek, P., Chytrý, M., Pergl, J., Sádlo, J., & Wild, J. (2012). Plant invasions in the Czech Republic: Current state, introduction dynamics, invasive species and invaded habitats. *Preslia*, *84*, 575–629.

Pyšek, P., Genovesi, P., Pergl, J., Monaco, A., & Wild, J. (2013). Plant invasions of protected areas in Europe: An old continent facing new problems. In L. C. Foxcroft, P. Pyšek, D. M. Richardson & P. Genovesi (Eds.), *Plant invasions in protected areas: Patterns, problems and challenges* (pp. 209–240). Dordrecht, The Netherlands: Springer Netherlands.

Pyšek, P., Jarošík, V., Hulme, P. E., Kühn, I., Wild, J., Arianoutsou, M., & Winter, M. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 12157–12162.

Pyšek, P., Sádlo, J., & Mandák, B. (2002). Catalogue of alien plants of the Czech Republic. *Preslia*, *74*, 97–186.

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Richardson, D. M., & Pyšek, P. (2006). Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, *30*, 409–431. https://doi.org/10.1191/0309133306pp490pr

Roques, A., Rabitsch, W., Rasplus, J.-Y., Lopez-Vaamonde, C., Nentwig, W., & Kenis, M. (2009). Alien terrestrial invertebrates of Europe. In. Daisie (Eds.), *Handbook of alien species in Europe* (pp. 63–79). Dordrecht, The Netherlands: Springer Netherlands. https://doi.org/10.1007/978-1-4020-8280-1

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., & Kinzig, A. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Sappington, J., Longshore, K. M., & Thompson, D. B. (2007). Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. *The Journal of Wildlife Management*, *71*, 1419–1426. https://doi.org/10.2193/2005-723

Seebens, H., Blackburn, T. M., Dyer, E., Genovesi, P., Hulme, P. E., Jeschke, J. M., & Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

Spear, D., Foxcroft, L. C., Bezuidenhout, H., & McGeoch, M. A. (2013). Human population density explains alien species richness in protected areas. *Biological Conservation*, *159*, 137–147. https://doi.org/10.1016/j.biocon.2012.11.022

Šťastný, K., Bejček, V., & Hudec, K. (2006). *Atlas hnízdního rozšíření ptáků v České republice: 2001–2003 [Atlas of breeding birds in the Czech Republic 2001–2003]*. Prague, Czech Republic: Aventinum.

Stohlgren, T. J., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J., & Master, L. L. (2006). Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biological Invasions*, *8*, 427–447. https://doi.org/10.1007/s10530-005-6422-0

Strahler, A. N. (1952). Hypsometric (area-altitude) analysis of erosional topology. *Geological Society of America Bulletin*, *63*, 1117–1142. https://doi.org/10.1130/0016-7606(1952)63[1117:HAAOET]2.0.CO;2

Thuiller, W., Richardson, D. M., Pyšek, P., Midgley, G. F., Hughes, G. O., & Rouget, M. (2005). Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, *11*, 2234–2250. https://doi.org/10.1111/j.1365-2486.2005.001018.x

Tolasz, R., Brázdil, R., Bulíř, O., Dobrovolný, P., Dubrovský, M., Hájková, L., & Žalud, Z. (2007). *Atlas podnebí Česka [Atlas of the climate of Czechia]*. Olomouc, Czech Republic: Czech Hydrometeorological Institute.

Vicente, J., Alves, P., Randin, C., Guisan, A., & Honrado, J. (2010). What drives invasibility? A multi-model inference test and spatial modelling of alien plant species richness patterns in northern Portugal. *Ecography*, *33*, 1081–1092. https://doi.org/10.1111/j.1600-0587.2010.6380.x

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., … DAISIE partners (2010). How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, *8*, 135–144. https://doi.org/10.1890/080083

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmánek, M., & Westbrooks, R. (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology*, *21*, 1–16.

Walther, G. R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., & Bugmann, H. (2009). Alien species in a warmer world: Risks and opportunities. *Trends in Ecology & Evolution*, *24*, 686–693. https://doi.org/10.1016/j.tree.2009.06.008

Winter, M., Kühn, I., La Sorte, F. A., Schweiger, O., Nentwig, W., & Klotz, S. (2010). The role of non-native plants and vertebrates in defining patterns of compositional dissimilarity within and across continents. *Global Ecology and Biogeography*, *19*, 332–342. https://doi.org/10.1111/j.1466-8238.2010.00520.x

Wu, S. H., Sun, H. T., Teng, Y. C., Rejmánek, M., Chaw, S. M., Yang, T. Y. A., & Hsieh, C. F. (2010). Patterns of plant invasions in China: Taxonomic, biogeographic, climatic approaches and anthropogenic effects. *Biological Invasions*, *12*, 2179–2206. https://doi.org/10.1007/s10530-009-9620-3

Zefferman, E., Stevens, J. T., Charles, G. K., Dunbar-Irwin, M., Emam, T., Fick, S., … Young, T. P. (2015). Plant communities in harsh sites are less invaded: A summary of observations and proposed explanations. *AoB Plants*, *7*, plv056. https://doi.org/10.1093/aobpla/plv056

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CHAPTER 3

FORECASTING IMPACT OF EXISTING AND EMERGING INVASIVE GOBIIDS UNDER TEMPERATURE CHANGE USING COMPARATIVE FUNCTIONAL RESPONSES

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Research Article

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

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Abstract

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

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

Introduction

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

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

Neogobius melanostomus causes major alterations in newly invaded areas. In addition to critical food web disruptions and shifts in trophic levels (Krakowiak and Pennuto 2008; Almqvist et al. 2010), there may be habitat and diet overlap with native ichthyofauna (Skóra and Rzeznik 2001), causing a significant decrease in, or extermination of, native fishes (Janssen and Jude 2001). Impact of *P. semilunaris*, on the other hand, has not yet been quantified and only potential threats and indirect effects are mentioned (Kocovsky et al. 2011). Both *N. melanostomus* and *P. semilunaris* are opportunistic feeders capable of adapting to locally abundant food sources (Brandner et al. 2013; Všetičková et al. 2014). Although low consumption of fish eggs and juveniles by *P. semilunaris* and *N. melanostomus* have been reported (French and Jude 2001; Vašek et al. 2014), direct predation by non-indigenous gobies on fish eggs and/or larvae in both laboratory and field conditions have also been observed (Thompson and Simon 2014; Všetičková et al. 2014) indicating these resources can form a substantial part of the diet during specific events (*e.g.* spawning season). Therefore, it is crucial to understand the interactions of these species with potential prey.

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

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

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

Methods

Predator acquisition and acclimatization

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

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

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

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

Prey

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

Experimental design

Transparent plastic boxes (28.5 × 19 × 7.5 cm; volume 2500 mL) were filled with 2000 mL aged tap water and 200 mL of fine aquarium sand (particle size < 0.3 mm). Two temperature levels were tested, 20 °C and 25 °C. The former represented the temperature of natural reproduction of common carp (Horváth et al. 1984), while the latter is within the reported range in which *N. melanostomus* exhibits maximum consumption rate (23–26 °C; Lee and Johnson 2005). Light was supplied by overhead LEDs with 12 h light:12 h dark regime and intensity of 500 lux m^{-2}.

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

Statistical analysis

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

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

where N_e is the number of prey consumed per gram of predator, N_0 is the initial prey density and P_0, P_1, P_2, and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively, estimated by maximum likelihood (Juliano 2001). If $P_1 < 0$, the proportion of prey killed declined monotonically with the initial prey density, indicating a type II FR. If $P_1 > 0$ and $P_2 < 0$, the proportion of prey killed is a unimodal function of prey density, corresponding to a type III FR (Juliano 2001). We used type II Rogers' random predator equation (Rogers 1972), which accounts for prey depletion, to model all functional responses:

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

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

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

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

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

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

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

Results

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

Functional response

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

Attack rate and handling time

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

Maximum feeding rate

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

Discussion

Many studies have been devoted to the negative impact of *N. melanostomus* (Kornis et al. 2012), whereas *P. semilunaris* has received little attention and only indirect effects are mentioned (Kocovsky et al. 2011). Calculation of Functional Response allows effective assessment and comparison of impacts of invader/native and invader/invader pairings (Dick et al. 2014; Xu et al. 2016). The FR defines the relationship between resource availability (prey density) and consumption pattern (Solomon 1949; Holling 1966) and is an essential component of ecosystem modeling (Petchey et al. 2008). In our study, both predators showed type II FR. The shape of the FR curve corroborated previous findings for *N. melanostomus* (Dubs and Corkum 1996; Fitzsimons et al. 2006) and for other piscine predators (e.g. Alexander et al. 2014); hence type II FR is a common foraging

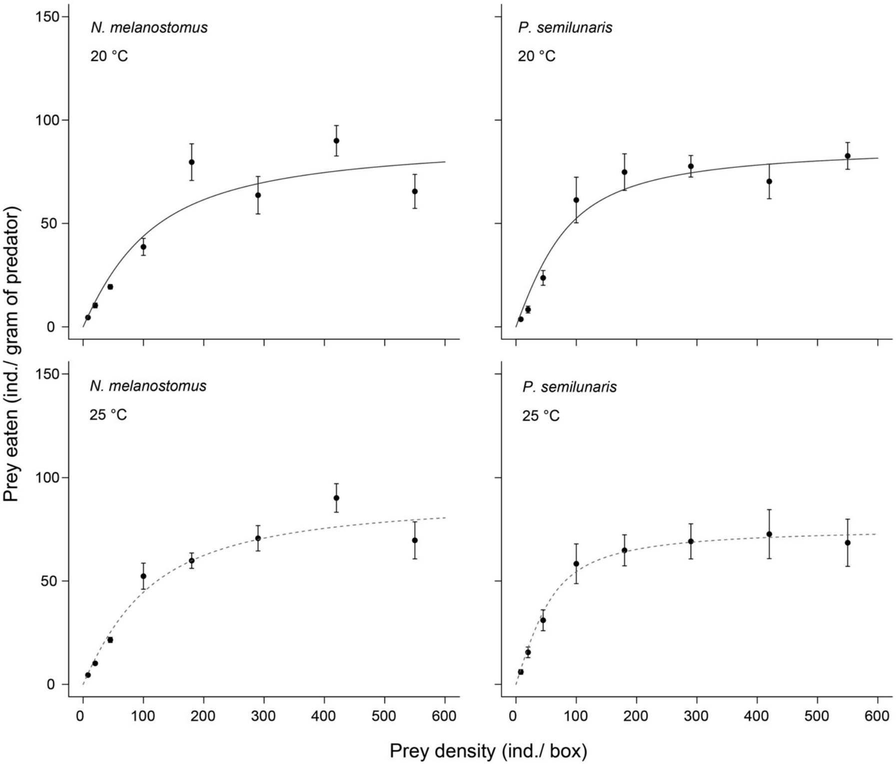

Figure 1. Relationship between prey density and number of prey eaten per gram of predator for *Neogobius melanostomus* and *Proterorhinus semilunaris*. Data are shown as mean ± SE overlaid by the model prediction (blue solid line = 20 °C, red dashed line = 25 °C).

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

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

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

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

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

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

Invasive species are often characterized by a higher maximum feeding rate, higher attack rate, and shorter handling time compared to native or low-impact non-indigenous species (Xu et al. 2016). These trends are apparent in fishes (e.g. Dubs and Corkum 1996) as well as in other aquatic organisms including amphipods (Bollache et al. 2008), crayfish (Renai and Gherardi 2004), and mysids (Dick et al. 2013). Within invader/native comparisons, Alexander et al. (2014) found similar attack rates in benthic dwelling fish species attributed to similar predatory strategies, whereas in pelagic fishes, the native showed an even higher attack rate. In our study, *P. semilunaris* showed a marginally higher attack rate at 20 °C compared to *N. melanostomus* (owing to the slightly higher AICc value), while no difference was observed at 25 °C. In a comparison between non-indigenous *N. melanostomus* and the analogous native predator European bullhead (*Cottus gobio* Linnaeus, 1758), Laverty et al. (2017) found higher FR asymptotes in *N. melanostomus*, indicating lower handling times. In comparing two alien predators, we observed no significant differences in handling time at either tested temperature, suggesting that the *per capita* impact on native communities posed by both predator species is similar, although little attention has yet been given to the impact of *P. semilunaris*. However, introducing Relative Impact Potential (RIP), Dick et al. (2017) suggested that both *per capita* effect (FR) and numerical response (abundance) should be included when estimating invader ecological impact. In general, *P. semilunaris* do not reach as high an abundance as *N. melanostomus* in invaded ecosystems (Dopazo et al. 2008; van Kessel et al. 2016; Janáč et al. 2018), and consequently the former species is no longer considered an important threat to native communities (Borcherding et al. 2011). On the other hand, *P. semilunaris* reaches high densities in shallow macrophyte-rich habitats (Kocovsky et al. 2011), where it can pose serious threat for phytophilic fauna, including cyprind larvae. Interestingly, *N. melanostomus* abundance in nearshore areas is positively correlated with temperature up to 24 °C (Dopazo et al. 2008) and hence, the RIP can be higher under such conditions.

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

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

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

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

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

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

Conclusions

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

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References

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Dick JTA, Laverty C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Robert Britton J, Medoc V, Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OLF, Lucy FE, Banks PB, Dodd JA, MacNeil C, Penk MR, Aldridge DC, Caffrey JM (2017) Invader Relative Impact Potential: A new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *Journal of Applied Ecology* 54: 1259–1267, https://doi.org/10.1111/1365-2664.12849

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Supplementary material

The following supplementary material is available for this article:

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

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

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

CHAPTER 4

ELEVATED ECOLOGICAL IMPACTS OF TWO ALIEN GOBIIDS ON HARD SUBSTRATES

Gebauer, R., Veselý, L., Vanina, T., Buřič, M., Kouba, A., Drozd, B., 2018. Elevated ecological impacts of two alien gobiids on hard substrates. Manuscript.

My share on this work was about 50 %.

ELEVATED ECOLOGICAL IMPACTS OF TWO ALIEN GOBIIDS ON HARD SUBSTRATES

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ABSTRACT

Effective management of biological invasions requires targeting towards high-impact alien species. Recent rapid expansion of round goby *Neogobius melanostomus* (Pallas, 1814) and western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) beyond their native ranges calls for urgent management actions, particularly in vulnerable localities. In several water bodies, *P. semilunaris* is no longer considered invasive due to lower abundances compared to *N. melanostomus*. Though, *P. semilunaris* can reach high abundances in macrophytes-rich habitats. Recent study documented similar *per capita* impact upon cyprinid fish larvae in laboratory settings with low structural complexity. Therefore, the resulting impact in localities with high *P. semilunaris* abundances can reach the impact posed by *N. melanostomus*. Here we used comparative functional response (FR) approach, which has been developed and applied to forecast invader impact. We quantified and compared the foraging efficiency in three different habitat structures: sand, cobbles, and cobbles with artificial plant. Both, *N. melanostomus* and *P. semilunaris* showed type II FR in all treatments. Interspecific comparison showed similar handling times in cobble substrate and cobbles with artificial plant suggesting similar *per capita* impacts. Intraspecific comparison showed significantly lower handling times of both predators in habitat with cobbles reflecting higher maximum feeding rate. Therefore, their impact in such environment could elevate. *Neogobius melanostomus* showed higher attack rate in sandy habitat compared to *P. semilunaris*, while no significant differences were observed in other habitat treatments. Our results highlight the importance of complex actions in management of biological invasions, as the elimination of invasive *N. melanostomus* can boost the population growth of alien *P. semilunaris*, which was not considered invasive until that time.

Keywords: *biological invasion, habitat structure, feeding rate, round goby, western tubenose goby*

INTRODUCTION

Freshwater ecosystems are extremely vulnerable to biological, chemical and physical alterations (Bucciarelli et al., 2014; Strayer, 2010). Invasions by alien species and habitat modifications are the main drivers of biodiversity loss in freshwater environments (Dudgeon et al., 2006; Galil et al., 2008; Strayer, 2010). Heavy encroachments in regulated rivers, including shoreline, flow regime and vegetation cover (Bunn and Arthington, 2002; Jansson et al., 2000; Nilsson and Berggren, 2000) has resulted in vanishing of intolerant native species (Wolter, 2001), which in turn increased niche opportunities for aliens (Shea and Chesson, 2002). Additionally, both phenomena provoke changes in a range of processes including predation (Griffen and Delaney, 2007; Wootton et al., 1996), which plays an essential role in organization of community ecology (Lima, 1998; Polis et al., 2000). Understanding and prediction of novel predator-prey interaction dynamics with all their consequences in invaded freshwater communities is therefore crucial for invasion management (Olden et al., 2004).

Invasive predators, being often characterized by better foraging efficiency and/or resources utilization, have higher maximum feeding rates, therefore inflicting greater ecological damage (Dick et al., 2002; Dick et al., 2013). Prominent determinant of the feeding rate is resource availability (prey density). The relationship between feeding rate and prey density can be characterized by the functional response curve (FR; Holling, 1959; Solomon, 1949). Form and magnitude of the curve are important aspects of consumer-resource interactions and community dynamics, respectively (Juliano, 2001; Murdoch and Oaten, 1975). Hence FR is an essential component of ecosystem modeling (Petchey et al., 2008). Consequently, FRs of invasive species often display elevated asymptotes compared to native or low-impact ecologically analogous alien species. Thus, comparative FR is a useful tool for assessment, comparison and prediction of the impact of newly introduced species (Alexander et al., 2014; Dick et al., 2014; Xu et al., 2016).

Two Ponto-Caspian bottom-dwellers, the round goby *Neogobius melanostomus* (Pallas, 1814) and western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) are nowadays expanding substantially beyond their native ranges (Kocovsky et al., 2011; Kornis et al., 2012). Both, *N. melanostomus* and *P. semilunaris* are opportunistic feeders. Reflecting their benthic lifestyle, the diet consists mostly of benthic invertebrates, while the consumption of fish eggs and juveniles is generally low (French and Jude, 2001; Vašek et al., 2014). On the other hand, both species are capable of adapting to temporary abundant food sources (Brandner et al., 2013; Všetičková et al., 2014) and given the preference for soft-bodied prey (Polačik et al., 2009), fish eggs and larvae can form a substantial part of the diet during specific events (*e.g.* spawning season Všetičková et al., 2014). Therefore, understanding the interactions between these predatory species and fish larvae as a potential prey is of crucial importance.

In freshwater ecosystems, organisms are exposed to a variety of factors which may affect the interactions among species. Biotic factors include the predators and prey size (Thorp et al., 2018) or multiple predator effects (Wasserman et al., 2016). Temperature and habitat structure can be considered as of the most important abiotic drivers influencing the predator-prey interactions (Alexander et al., 2012; Alexander et al., 2015; Englund et al., 2011; Vucic-Pestic et al., 2011). Recent study on comparative FR between *N. melanostomus* and *P. semilunaris* upon common carp (*Cyprinus carpio*, Linnaeus 1758) larvae demonstrated no difference in FRs on sandy substrate at 20 °C, suggesting similar impact of tested species within cyprinids spawning season (Gebauer et al., 2018). However, cyprinids are often phytophilous or lithophilous fish species and, indeed, newly hatched larvae prefer habitats occupied by submerged vegetation or cobbles (King, 2004). Concurrently, habitat structure has been shown to interfere impact of predatory fishes (Almany, 2004; Savino and Stein, 1982;

Swisher et al., 1998) and may result in differences in the magnitude and direction of predator-prey interactions (Abrams, 1990). Yet, to our knowledge, there is no study comparing the *N. melanostomus* and *P. semilunaris* predation in different habitats. Although both species show a great plasticity in habitat selection, they prefer sheltered environment due to predator avoidance (Belanger and Corkum, 2003; Janáč et al., 2012). *Neogobius melanostomus* seems to prefer hard substrates with water depths 0.7 to 3 m, though it can also be found in localities with water vegetation (reviewed in Kornis et al., 2012). Similar habitat plasticity was observed in *P. semilunaris* (French and Jude, 2001; von Landwüst, 2006), but several studies claim that *P. semilunaris* reaches high abundances in macrophyte-rich environments (Janáč et al., 2012; Jude and DeBoe, 1996; Kocovsky et al.,2011).

In the present study, foraging behavior of emerging invader *N. melanostomus* and alien *P. semilunaris* upon *C. carpio* (as a model species representing cyprinids) larvae was assessed and compared using the FR approach in three experimental set-ups with different habitat structure. We hypothesized that the impact of both predators would be lower in sandy environments compared to the other treatments. Furthermore, we hypothesized, *N. melanostomus* would exhibit elevated FR on hard substrate, while *P. semilunaris* in habitat with artificial plant, reflecting their habitat preferences. On the other hand, structured habitat can return reduced attack rate at lower prey densities due to providing refugia and shelters for fish larvae.

MATERIAL AND METHODS

Predator and prey acquisition and acclimatization

Predators were sourced in April/May 2017. Round goby *Neogobius melanostomus* (Pallas, 1814) and western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) were collected in the Elbe River (50°39′7″ N, 14°2′41″ E) and Jevišovka River (48°49′27″ N, 16°27′59″ E), respectively. Back-pack pulsed-DC electrofishing unit (FEG 1500, EFKO, Leutkirch, Germany) was used for fish collection. Afterwards, fish were transported to the experimental facility of the Institute of Aquaculture and Protection of Waters, Faculty of Fisheries and Protection of Waters, University of South Bohemia in České Budějovice, Czech Republic. Before introduction to the acclimatization tanks, predators were anaesthetized in a clove oil (0.03 mL/L) and weighed (Kern 572-35, Kern and Sohn, Germany) to ensure using restricted size classes in experiment (1–2 g). Fish out of needed weight range were omitted from further experiments.

Predators were housed species apart in 800 L holding tanks in a recirculating systems filled with dechlorinated tap water for a 30-day acclimatization. Temperature (mean±SE=20.4±0.1 °C), dissolved oxygen (> 90% saturation), and pH (7.1–8.0) were measured twice a day during the acclimatization period with the HQ40d digital multi-meter (Hach Lange GmbH, Germany). Predators were fed with frozen chironomid larvae twice a day to satiation ensuring no prior prey learning occurred in holding tanks. To standardize the hunger level, predators were deprived of food for 24 h prior to the start of the experiment.

We used common carp (*Cyprinus carpio*, Linnaeus, 1758) larvae as prey (3–4 days post hatching) as a model species representing typical larvae of cyprinid fishes. Larvae were obtained from an artificial reproduction at the Genetic Fisheries Center, Faculty of Fisheries and Protection of Waters, University of South Bohemia and housed in 400 L aerated holding tank. Larvae remained unfed to standardize their weight. For wet weight assessment, larvae were thoroughly wiped with blotting paper and ten groups of 10 specimens were weighed with mean individual weight±SE of 2.0±0.5 mg (XPR10 micro-balance, Mettler-Toledo, LLC, Columbus, US).

Experimental design

To quantify the *N. melanostomus* and *P. semilunaris* FRs towards *C. carpio* larvae, we used transparent plastic boxes (29.5 x 19.5 x 15.5 cm; volume 6400 mL) filled with 4000 mL of aged tap water. Opaque screen preventing predator disturbance by visual stimuli was placed around boxes. Both predators were tested in three different habitat structures, where they naturally occur: sand substrate (200 mL of fine aquarium sand with particle size < 0.3 mm), cobbles [8-10 pieces (1900–2000 g) of cobbles with diameter 50–65 mm on sandy substrate described above] and cobbles with artificial plant [8–10 pieces (1900–2000 g) of cobbles with diameter 50–65 mm and one piece artificial plant on sandy substrate described above]. The artificial plant was mimicked with strip of green bird netting (30 cm long and 4 cm wide) weight to the bottom of the tank with a pebble (diameter 20–30 mm) and placed in the middle of the experimental box. This allowed upward floating of the artificial plant, occupying the entire water column. Concurrently, these habitat structures simulate low, moderate and high complexity. Temperature level was maintained at 20 °C. The light was supplied by overhead LEDs with 12 h light:12 h dark regime and intensity of 500 lux/m^2.

Predators were provided with eight densities of *C. carpio* larvae (8, 20, 45, 100, 180, 290, 420, 550 larvae per box). To allow recovery from handling stress and utilizing provided habitats, prey was placed into each box 1 h prior to introduction of predators. Afterwards, predators were individually released into boxes with prey. Prey consumption was examined after 24 hours. Remaining prey individuals (alive and partially consumed) were counted to derive those killed during the experiment. Each predator was used only once to avoid bias caused by experience. Each combination of habitat complexity, prey density, and predator treatment was replicated at least five times. Control treatments (with absence of predator) were replicated seven times at each combination of prey density and habitat structure to assess background mortality of prey. Total and standard lengths of predators, measured by digital caliper to the nearest 0.01 mm, and weight to the nearest 0.1 g (Kern 572-35, Kern and Sohn, Germany) was recorded after the experiment (Table S1).

Statistical analysis

We firstly determined FR types in all habitat and predator treatments using logistic regression of the proportion of prey consumed as a function of initial prey density:

$$\frac{N_e}{N_0}=\frac{\exp(P_0+P_1N_0+P_2N^2{}_{0+}P_3N^3{}_0}{1+\exp(P_0+P_1N_0+P_2N^2{}_{0+}P_3N^3{}_0}$$

where N_e is the number of prey consumed per gram of predator, N_0 is the initial prey density and P_0, P_1, P_2, and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively, estimated by maximum likelihood. A significant negative first order term represents a Type II FR, whereas a significant positive first order term, followed by a significant negative second order term, indicates a Type III FR (see Juliano, 2001 for further details). FRs were than modelled using the Rogers' random predator equation for a Type II response, which accounts for non-replacement of consumed prey (Rogers, 1972):

$$N_e=N_0 1-\exp a(N_e h-t)$$

where N_e is the number of prey consumed per gram of predator, N_0 is the initial prey density, a is predator attack rate, h is predator handling time, and t is the duration of the experiment in days. This recursive function can be resolved using the *Lambert* W function (for further details see Bolker, 2008):

$$N_e = N_0 - \frac{WahN_0 \exp -a(t-hN_0)}{ah}$$

For each predator-habitat combination we estimated the parameters *a* (attack rate; classically interpreted as the search efficiency) and *h* (handling time; defined as the time spent pursuing, subduing, and consuming each prey item plus the time spent preparing to search for the next prey item) using non-linear least squares regression and *Lambert* W function implemented in the "emdbook" package. We assumed, that a model prediction is valid if empirical observations are within the 95% confidence interval (CI) of the predictions. Following the law of propagation of uncertainty, 95% CI of the model predictions were calculated using the standard errors associated with the values of each of the model parameters (Sentis et al., 2013).

The weight-specific maximum feeding rate was calculated from FR models:

$$C_{max} = \frac{1}{ht}$$

where *h* is predator handling time, and *t* is the duration of the experiment in days. Bootstrapping was used to generate multiple estimates (n = 30) of the parameter of the maximum consumption rate. Differences among maximum consumption rate were compared using GLMs with quasi-Poisson error distribution and simplification via step-deletion process with "habitat" and "predator species" as explanatory variables. Tukey HSD post-hoc tests were employed to assess significant differences among treatments. Non-consumptive mortality (NCM) was less than 1 % in all experimental boxes, therefore we did not correct the results for NCM. Control prey survival was greater than 98% in all treatments after 24 h, thus experimental deaths were attributed to fish predation and data were not corrected for natural mortality. All analyses were implemented in R version 3.2.5 (R Core Team, 2016).

RESULTS

Functional response

We observed type II FR in all predator-habitat treatments. The linear parameters of the logistic regression were negative with decreasing proportion of fish larvae eaten per gram of predator towards increasing prey (Figure 1, Table S2).

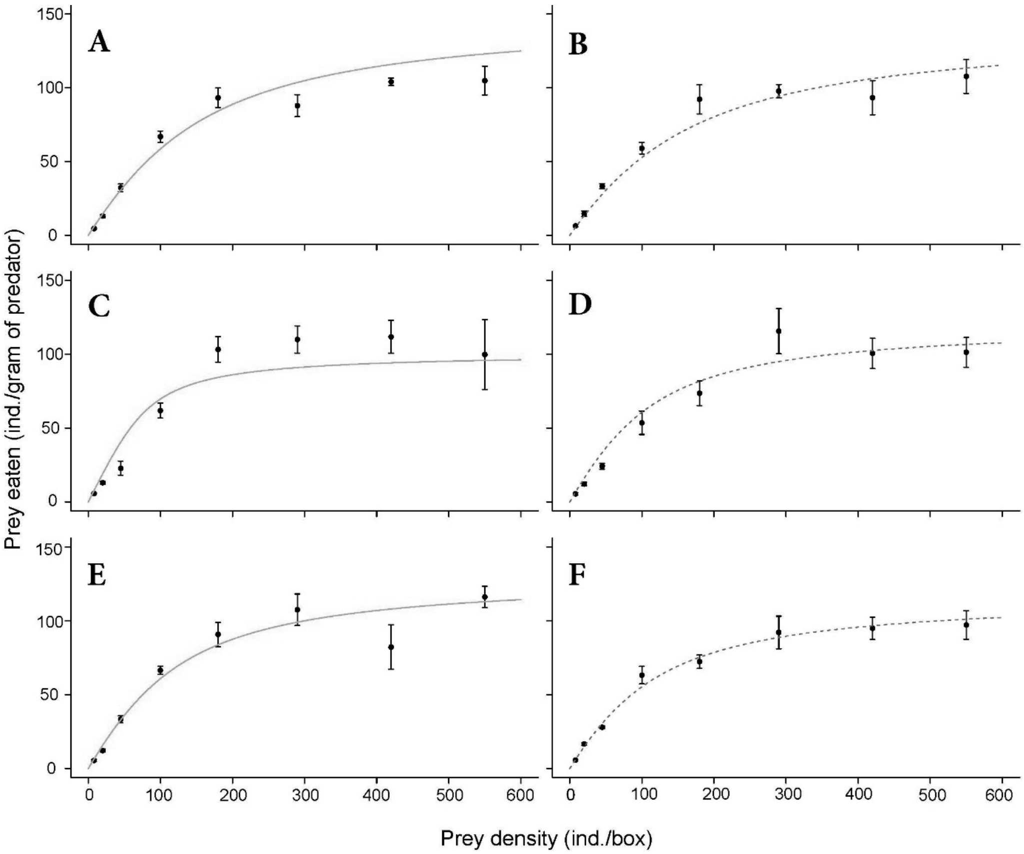

Figure 1. *Relationship between prey density and number of prey eaten per gram of predator for Neogobius melanostomus (solid line) and Proterorhinus semilunaris (dashed line) in three habitat structures: A, B – sand; C, D – cobbles; E, F – cobbles with artificial plant. Data are presented as mean±SE overlaid by the model prediction.*

Attack rate, handling time and maximum feeding rate

Based on the interspecific comparison of 95% CI of FR parameters, *N. melanostomus* showed higher values of both, attack rate (*a*) and handling time (*h*) on sandy substrate (Figure 2, Tables 1 and 2). No significant differences were found in *a* on cobbles with artificial plant and in *h* on cobble substrate between *N. melanostomus* and *P. semilunaris*. Owing to the tight overlap in 95 % CI, *N. melanostomus* showed marginally higher *a* on cobble substrate (1.066-1.336 and 1.324–1.581 for *P. semilunaris* and *N. melanostomus*, respectively), while *P. semilunaris* displayed marginally higher *h* in habitat with cobbles with artificial plant (0.007–0.008 and 0.008–0.009 for *N. melanostomus* and *P. semilunaris*, respectively).

Within intraspecific comparison of *N. melanostomus*, both, *a* and *h* were found to be significantly different among all treatments with highest values in sandy habitat, while lowest values were observed on cobble substrate (Tables 1 and 2). Similarly, *P. semilunaris* showed significantly lower *a* and *h* on cobbles, whereas no difference was found between sand and cobbles with artificial plant habitats (Tables 1 and 2).

Model selection revealed no significant interactions between predators and habitat treatment in maximum consumption ($F=_{1,299}$ 0.05, P=0.83). We found that only the habitat treatment affected maximum consumption ($F=_{1,299}$ 65.9, P<0.0001) regardless of predator species ($F_{1,299}$ 0.23, P=0.63). The weight-specific consumption was significantly different among all habitats with mean±SE: 134.3±1.4, 114.7±1.2 and 103.1±1.3 fish larvae per gram of predator in cobbles, cobbles with artificial plant and sand habitat, respectively (Tukey HSD; Figure 3).

Table 1. *Weight-specific values of attack rate for Neogobius melanostomus (Nm)and Proterorhinus semilunaris (Ps) in three habitat treatments: sand, cobbles, cobbles with artificial plant. Data expressed as low (mean-CI), mean and high (mean+CI).*

Species	**Habitat**	**Attack rate**			
		low	**mean**	**high**	**p-value**
Nm	sand	3.197	3.866	4.535	< 0.0001
Ps	sand	1.685	1.882	2.080	< 0.0001
Nm	cobbles	1.324	1.453	1.581	< 0.0001
Ps	cobbles	1.066	1.201	1.336	< 0.0001
Nm	cobbles with a. plant	1.590	1.764	1.938	< 0.0001
Ps	cobbles with a. plant	1.356	1.533	1.710	< 0.0001

Table 2. *Weight-specific values of handling time for Neogobius melanostomus (Nm) and Proterorhinus semilunaris (Ps) in three habitat treatments: sand, cobbles and cobbles with artificial plant. Data expressed as low (mean-CI), mean and high (mean+CI).*

Species	**Habitat**	**Handling time**			
		low	**mean**	**high**	**p-value**
Nm	sand	0.0094	0.010	0.0105	< 0.0001
Ps	sand	0.0079	0.008	0.0087	< 0.0001
Nm	cobbles	0.0063	0.007	0.0071	< 0.0001
Ps	cobbles	0.0066	0.007	0.0076	< 0.0001
Nm	cobbles with a. plant	0.0073	0.008	0.0081	< 0.0001
Ps	cobbles with a. plant	0.0081	0.009	0.0091	< 0.0001

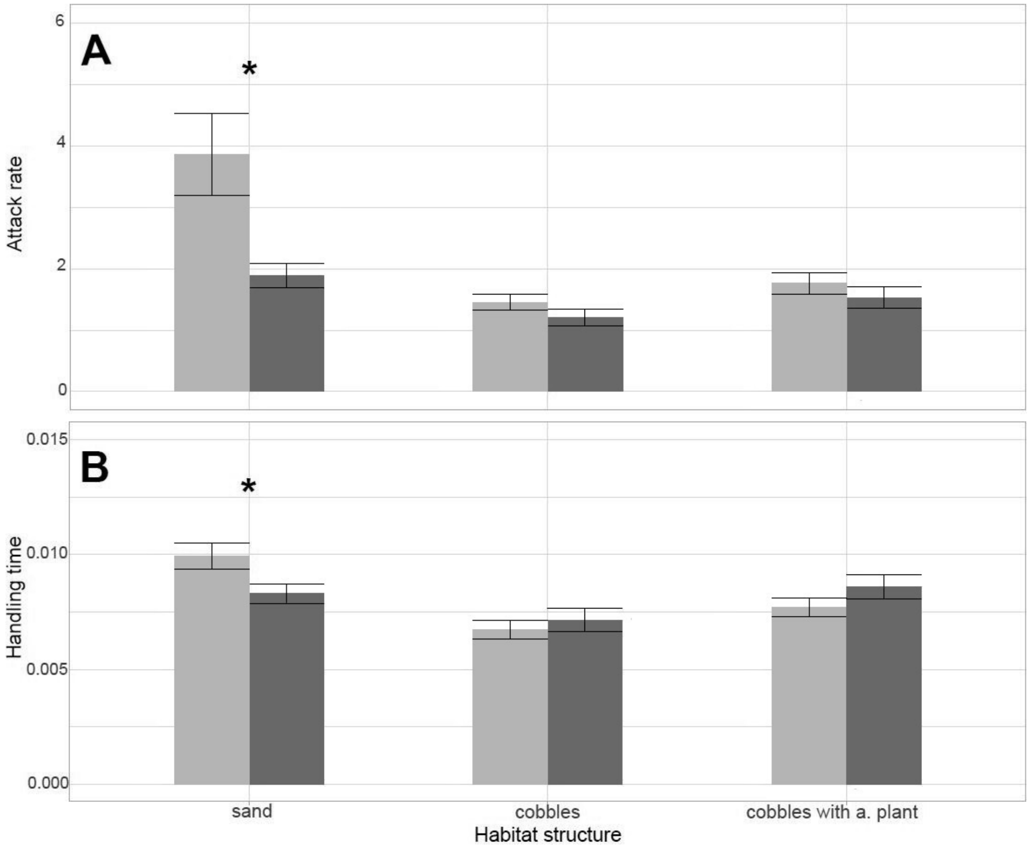

Figure 2. *Functional response parameters (A-attack rate and B-handling time) for Neogobius melanostomus (light grey column) and Proterorhinus semilunaris (dark grey column) in three habitat structures: sand; cobbles; cobbles with artificial plant. Data are presented as mean±SE. Asterisks denote significant differences between predators in particular parameter/habitat.*

DISCUSSION

Prediction of ecological impact and denoting high-risk alien species is fundamental discipline needed for successful and effective management of biological invasions (Ricciardi and Rasmussen, 1998). Recent studies have proved FR to be a rapid and reliable method for assessment and comparison of alien species ecological impact or biocontrol potential of natives with wide taxonomical applicability under a range of environmental conditions (Cuthbert et al., 2018; Dick et al., 2014; Xu et al., 2016). Although impact of *P. semilunaris* has had little attention (Kocovsky et al., 2011) compared to *N. melanostomus* (Kornis et al., 2012), Gebauer et al. (2018) showed similar *per capita* impact of both species at 20 °C. In predatory fish species, type II FR, *i.e.* inversely density dependent predation, is a common foraging pattern. Though variations in environment may return shifts in FR types (Koski and Johnson, 2002). In our study, we found that both, *N. melanostomus* and *P. semilunaris* showed type II FR towards the fish larvae prey in all habitat treatments. This corroborates previous findings of Alexander et al. (2015) in invasive largemouth bass *Micropterus salmoides* (Lacépède, 1802), implying that invasive predators may have destabilizing effect on population dynamics typical for type II FR (Murdoch and Oaten, 1975) in a range of environments as their predation behavior is not influenced in various conditions. In natural conditions, the prey population could be stabilized after becoming rare due to predator switching to alternative prey resulting in type III FR (Elliott, 2004; Murdoch, 1969).

Attack rate

Despite no differences in FR types among habitats, we found differences in model parameters. Intraspecific comparison of *N. melanostomus* attack rates (*a*) displayed significant differences among all treatments with the highest value in sandy habitats. However, in *P. semilunaris* the higher values were found on sandy substrate and cobbles with artificial plant compared to cobble substrate. The attack rate characterizes the slope of the FR curve at low prey densities and hence indicates the predator efficiency at low densities (Alexander et al., 2014; Jeschke et al., 2002). This implies that both tested predators are efficient at low prey densities in simple habitats which is in line of South et al. (2017). In addition, *P. semilunaris* is more efficient on cobbles with artificial plants in comparison to *N. melanostomus*. This is in contrast with Alexander et al. (2015), who observed *a* to be lowest in zero complexity habitat, what could be attributed to different foraging behavior of *M. salmoides* (ambush predator; Savino and Stein, 1982) compared to *N. melanostomus* and *P. semilunaris*. We observed significantly lower *a* of both, *N. melanostomus* and *P. semilunaris* on cobble substrate compared to the other treatments, which can be attributed to the larvae predator avoidance or behavioral difference in such environments. Our results suggest that *C. carpio* larvae could have utilized interstitial space among cobbles. In cobbles with artificial plant habitats, however, the phytophilous prey could have been attracted by the floating artificial plant making the searching success higher in these treatments at low prey densities. This may result in reduced ecological impact of both, *N. melanostomus* and *P. semilunaris* at low prey densities on cobble substrate (*e.g.* in regulated rivers).

In interspecific comparison of *a*, the only significant difference was found in sandy habitat with higher values for *N. melanostomus* compared to *P. semilunaris*. In cobble habitat, *N. melanostomus* displayed marginally higher *a* reflecting preference for these habitat types, while no difference was observed in artificial plant habitat between predators.

Handling time

Handling time *h* is classically defined as the time spent pursuing, subduing, and consuming each prey item plus the time spent preparing to search for the next prey item (Jeschke et al., 2002). Therefore lower *h* reflects greater predatory efficiency at higher prey densities. In our study, intraspecific comparison of handling time in *N. melanostomus* showed significant differences among all habitat structures with highest *h* on sand, followed by cobbles with artificial plant and cobble substrate. Similarly, *P. semilunaris* showed significantly lower *h* in cobble habitat, but no difference as found between the remaining two. This is in contrast with Alexander et al. (2015) who observed lower *h* of *M. salmoides* in low to zero habitat complexities possibly caused by different predator strategy in comparison with predators used in our study. Although several researchers observed *N. melanostomus* in plant environments (Cooper et al., 2009; Taraborelli et al., 2009), there are clear evidences for preferences towards hard substrate (Ray and Corkum, 2001; Young et al., 2010). It reflects lower *h* on cobble substrate compared to cobbles with artificial plant in our study. Open sandy habitat without shelter were shown to pose a higher risk of predation for *N. melanostomus* (Belanger and Corkum, 2003). Indeed, higher *h* on sandy substrate in our study can be attributed to induced stress despite reduced refuge space for prey compared to other treatments. *Proterorhinus* *semilunaris* showed significantly lower *h* in cobble habitat compared to the other treatments. This results does not confirm general hypothesis about higher impact of this species in plant environment deduced from documented higher abundances in these habitats (Kocovsky et al., 2011). This may be caused by sparse vegetation in our experimental arena. Indeed, most studies invoke *P. semilunaris* preference for macrophyte-rich environments (Cammaerts et al., 2012; Janáč et al., 2012). Another reason could be the preference of *P. semilunaris* for hard substrates (Jude and DeBoe, 1996) as well as *N. melanostomus*, while being displaced to sub-optimal conditions through some force, possibly the aggression of the latter species.

Interspecific comparison of *N. melanostomus* and *P. semilunaris* showed that only sandy habitat differ significantly in *h* with lower values in latter species. On cobble substrate and on cobbles with artificial plant, both predators displayed none and marginally difference, respectively, suggesting similar *per capita* impact of both gobies at high prey densities in these environments.

Maximum feeding rate

Based on the studies of Laverty et al. (2017) and Gebauer et al. (2018) it can be assumed that both, *N. melanostomus* and *P. semilunaris* outperform analogous native species *Cottus gobio* L. due to similar maximum feeding rates of both aliens. In our study we observed no interactions between predator species and habitat treatment in weight-specific maximum feeding rate (GLM). However, we observed significant differences among habitat treatments with highest weight-specific maximum feeding rate on cobble substrate followed by cobble with artificial plant and sandy habitats. This reflects the habitat preference of both alien predators and induced stress in non-sheltered habitats (Belanger and Corkum, 2003; Kocovsky et al., 2011; Kornis et al., 2012). This implies that both predators forage efficiently in structured habitats, that might otherwise serve as a prey refugia as previously documented in *Gambusia holbrooki* Girard, 1859 (Baber and Babbitt, 2004).

Compared to Gebauer et al. (2018) we found substantially higher weight-specific amount of fish larvae eaten by both, *N. melanostomus* and *P. semilunaris*. This is explained by lower predator sizes used in the current study. Indeed, Lee and Johnson (2005) documented in *N. melanostomus* higher weight-specific consumption rate showed by smaller specimens. According to Gebauer et al. (2018) similar trend can be expected also in *P. semilunaris* though the modeled weight-maximum consumption curve for this species is not developed so far.

CONCLUSION

Our results highlight that *N. melanostomus* and *P. semilunaris* can have the detrimental impact on fish larvae populations. Although *P. semilunaris* is not usually considered invasive due to lower abundance compared to *N. melanostomus* (Borcherding et al., 2011), we observed similar handling times on cobble substrate and cobbles with artificial plant habitat upon *C. carpio* larvae suggesting similar *per capita* impacts. Hence, the invasive potential of *P. semilunaris* would be elevated in localities with high abundances, *e.g.* habitats with submerged macrophytes (Cammaerts et al., 2012), as both, *per capita* and numerical responses are important (Dick et al., 2017). Our results also underline the importance of complex actions when managing invasive species, as the empty niche created by elimination of invasive species can boost the population growth of another alien, which was not considered invasive previously.

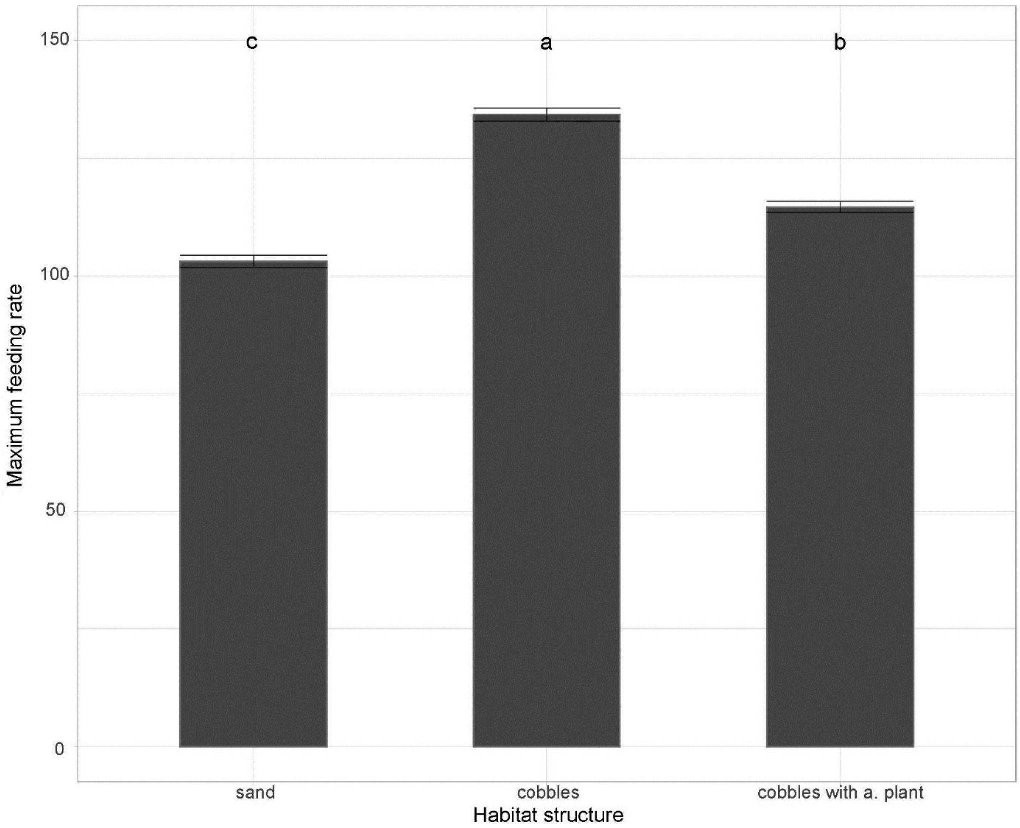

Figure 3. *Weight-specific maximum feeding rate for Proterorhinus semilunaris and Neogobius melanostomus derived from functional response models in three habitat structures: sand; –cobbles; cobbles with artificial plant. Data for both predators are pooled due to no significant interactions between predator and habitat treatments. Data are presented as mean±SE. Different letters denote statistical significance.*

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REFERENCES

Abrams, P.A., 1990. The effects of adaptive behavior on the type-2 functional response. Ecology 71, 877–885.

Alexander, M.E., Dick, J.T.A., O'Connor, N.E., Haddaway, N.R., Farnsworth, K.D., 2012. Functional responses of the intertidal amphipod *Echinogammarus marinus*: effects of prey supply, model selection and habitat complexity. Marine Ecology Progress Series 468, 191–202.

Alexander, M.E., Dick, J.T.A., Weyl, O.L.F., Robinson, T.B., Richardson, D.M., 2014. Existing and emerging high impact invasive species are characterized by higher functional responses than natives. Biology Letters 10, 20130946.

Alexander, M.E., Kaiser, H., Weyl, O.L.F., Dick, J.T.A., 2015. Habitat simplification increases the impact of a freshwater invasive fish. Environmental Biology of Fishes 98, 477–486.

Almany, G.R., 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos 106, 275–284.

Baber, M.J., Babbitt, K.J., 2004. Influence of habitat complexity on predator-prey interactions between the fish (*Gambusia holbrooki*) and tadpoles of *Hyla squirella* and *Gastrophryne carolinensis*. Copeia 2004, 173–177.

Belanger, R.M., Corkum, L.D., 2003. Susceptibility of tethered round gobies (*Neogobius melanostomus*) to predation in habitats with and without shelters. Journal of Great Lakes Research 29, 588–593.

Bolker, B., 2008. Ecological models and data in R. Princeton University Press, Princeton, New Jersey, USA, 408 pp.

Borcherding, J., Staas, S., Krüger, S., Ondračková, M., Šlapanský, L., Jurajda, P., 2011. Non-native gobiid species in the lower River Rhine (Germany): recent range extensions and densities. Journal of Applied Ichthyology 27, 153–155.

Brandner, J., Auerswald, K., Cerwenka, A.F., Schliewen, U.K., Geist, J., 2013. Comparative feeding ecology of invasive Ponto-Caspian gobies. Hydrobiologia 703, 113–131.

Bucciarelli, G.M., Blaustein, A.R., Garcia, T.S., Kats, L.B., 2014. Invasion complexities: the diverse impacts of nonnative species on amphibians. Copeia 2014, 611–632.

Bunn, S.E., Arthington, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30, 492–507.

Cammaerts, R., Spikmans, F., van Kessel, N., Verreycken, H., Chérot, F., Demol, T., Richez, S., 2012. Colonization of the Border Meuse area (The Netherlands and Belgium) by the non-native western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837)(Teleostei, Gobiidae). Aquatic Invasions 7, 251–258.

Cooper, M.J., Ruetz, C.R., Uzarski, D.G., Shafer, B.M., 2009. Habitat use and diet of the round goby (*Neogobius melanostomus*) in coastal areas of Lake Michigan and Lake Huron. Journal of Freshwater Ecology 24, 477–488.

Cuthbert, R.N., Dick, J.T.A., Callaghan, A., Dickey, J.W.E., 2018. Biological control agent selection under environmental change using functional responses, abundances and fecundities; the Relative Control Potential (RCP) metric. Biological Control 121, 50–57.

Dick, J.T.A., Platvoet, D., Kelly, D.W., 2002. Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). Canadian Journal of Fisheries and Aquatic Sciences 59, 1078–1084.

Dick, J.T.A., Gallagher, K., Avlijas, S., Clarke, H.C., Lewis, S.E., Leung, S., Minchin, D., Caffrey, J., Alexander, M.E., Maguire, C., Harrod, C., Reid, N., Haddaway, N.R., Farnsworth, K.D., Penk, M., Ricciardi, A., 2013. Ecological impacts of an invasive predator explained and predicted by comparative functional responses. Biological Invasions 15, 837–846.

Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B., Kumschick, S., Weyl, O.L.F., Dunn, A.M., Hatcher, M.J., Paterson, R.A., Farnsworth, K.D., Richardson, D.M., 2014. Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biological Invasions 16, 735–753.

Dick, J.T.A., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., Britton, R.J., Medoc, V., Boets, P., Alexander, M.E., Taylor, N.G., Dunn, A.M., Hatcher, M.J., Rosewarne, P.J., Crookes, S., MacIsaac, H.J., Xu, M., Ricciardi, A., Wasserman, R.J., Ellender, B.R., Weyl, O.L.F., Lucy, F.E., Banks, P.B., Dodd, J.A., MacNeil, C., Penk, M.R., Aldridge, D.C., Caffrey, J.M., 2017. Invader relative impact potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. Journal of Applied Ecology 54, 1259–1267.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81, 163–182.

Elliott, J.M., 2004. Prey switching in four species of carnivorous stoneflies. Freshwater Biology 49, 709–720.

Englund, G., Öhlund, G., Hein, C.L., Diehl, S., 2011. Temperature dependence of the functional response. Ecology Letters 14, 914–921.

French, J.R.P., Jude, D.J., 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. Journal of Great Lakes Research 27, 300–311.

Galil, B.S., Nehring, S., Panov, V., 2008. Waterways as invasion highways-Impact of climate change and globalization. In: Nentwig, W. (ed.), Biological Invasions. Springer-Verlag, Berlin Heidelberg, Germany, pp. 59–74.

Gebauer, R., Veselý, L., Kouba, A., Buřič, M., Drozd, B., 2018. Forecasting impact of existing and emerging invasive gobiids under temperature change using comparative functional responses Aquatic Invasions 13, 289–297.

Griffen, B.D., Delaney, D.G., 2007. Species invasion shifts the importance of predator dependence. Ecology 88, 3012–3021.

Holling, C.S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist 91, 293–320.

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

Jansson, R., Nilsson, C., Dynesius, M., Andersson, E., 2000. Effects of river regulation on river-margin vegetation: a comparison of eight boreal rivers. Ecological Applications 10, 203–224.

Jeschke, J.M., Kopp, M., Tollrian, R., 2002. Predator functional responses: discriminating between handling and digesting prey. Ecological Monographs 72, 95–112.

Jude, D.J., DeBoe, S.F., 1996. Possible impact of gobies and other introduced species on habitat restoration efforts. Canadian Journal of Fisheries and Aquatic Sciences 53, 136–141.

Juliano, S.A., 2001. Non-linear curve fitting: predation and functional response curve. In: Scheiner, S.M., Gurevitch, J. (eds.), Design and analysis of ecological experiment. Oxford University Press, Oxford, UK, pp. 178–196.

King, A.J., 2004. Ontogenetic patterns of habitat use by fishes within the main channel of an Australian floodplain river. Journal of Fish Biology 65, 1582–1603.

Kocovsky, P.M., Tallman, J.A., Jude, D.J., Murphy, D.M., Brown, J.E., Stepien, C.A., 2011. Expansion of tubenose gobies *Proterorhinus semilunaris* into western Lake Erie and potential effects on native species. Biological Invasions 13, 2775–2784.

Kornis, M.S., Mercado-Silva, N., Vander Zanden, M.J., 2012. Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. Journal of Fish Biology 80, 235–285.

Koski, M.L., Johnson, B.M., 2002. Functional response of kokanee salmon (*Oncorhynchus nerka*) to *Daphnia* at different light levels. Canadian Journal of Fisheries and Aquatic Sciences 59, 707–716.

Laverty, C., Green, K.D., Dick, J.T.A., Barrios-O'Neill, D., Mensink, P.J., Médoc, V., Spataro, T., Caffrey, J.M., Lucy, F.E., Boets, P., Britton, J.R., Pegg, J., Gallagher, C., 2017. Assessing the ecological impacts of invasive species based on their functional responses and abundances. Biological Invasions 19, 1653–1665.

Lee, V.A., Johnson, T.B., 2005. Development of a bioenergetics model for the round goby (*Neogobius melanostomus*). Journal of Great Lakes Research 31, 125–134.

Lima, S.L., 1998. Nonlethal effects in the ecology of predator-prey interactions. BioScience 48, 25–34.

Murdoch, W.W., 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs 39, 335–354.

Murdoch, W.W., Oaten, A., 1975. Predation and population stability. Advances in Ecological Research 9, 1–131.

Nilsson, C., Berggren, K., 2000. Alterations of riparian ecosystems caused by river regulation: ram operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our time. BioScience 50, 783–792.

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., Fausch, K.D., 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19, 18–24.

Petchey, O.L., Beckerman, A.P., Riede, J.O., Warren, P.H., 2008. Size, foraging, and food web structure. Proceedings of the National Academy of Sciences of the United States of America 105, 4191–4196.

Polačik, M., Janáč, M., Jurajda, P., Adámek, Z., Ondračková, M., Trichkova, T., Vassilev, M., 2009. Invasive gobies in the Danube: invasion success facilitated by availability and selection of superior food resources. Ecology of Freshwater Fish 18, 640–649.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R., Maron, J., 2000. When is a trophic cascade a trophic cascade? Trends in Ecology and Evolution 15, 473–475.

R Core Team, 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Ray, W.J., Corkum, L.D., 2001. Habitat and site affinity of the round goby. Journal of Great Lakes Research 27, 329–334.

Ricciardi, A., Rasmussen, J.B., 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences 55, 1759–1765.

Rogers, D., 1972. Random search and insect population models. Journal of Animal Ecology 41, 369–383.

Savino, J.F., Stein, R.A., 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated submersed vegetation. Transactions of the American Fisheries Society 111, 255–266.

Sentis, A., Hemptinne, J.L., Brodeur, J., 2013. How functional response and productivity modulate intraguild predation. Ecosphere 4, 1–14.

Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17, 170–176.

Solomon, M.E., 1949. The natural control of animal populations. Journal of Animal Ecology 18, 1–35.

South, J., Dick, J.T.A., McCard, M., Barrios-O'Neill, D., Anton, A., 2017. Predicting predatory impact of juvenile invasive lionfish (*Pterois volitans*) on a crustacean prey using functional response analysis: effects of temperature, habitat complexity and light regimes. Environmental Biology of Fishes 100, 1155–1165.

Strayer, D.L., 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. Freshwater Biology 55, 152–174.

Swisher, B.J., Soluk, D.A., Wahl, D.H., 1998. Non-additive predation in littoral habitats: influences of habitat complexity. Oikos 81, 30–37.

Taraborelli, A.C., Fox, M.G., Schaner, T., Johnson, T.B., 2009. Density and habitat use by the round goby (*Apollonia melanostoma*) in the Bay of Quinte, Lake Ontario. Journal of Great Lakes Research 35, 266–271.

Thorp, C.J., Alexander, M.E., Vonesh, J.R., Measey, J., 2018. Size-dependent functional response of *Xenopus laevis* on mosquito larvae. PeerJ Preprints doi.org/10.7287/peerj.preprints.26575v1.

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

von Landwüst, C., 2006. Expansion of *Proterorhinus marmoratus* (Teleostei, Gobiidae) into the River Moselle (Germany). Folia Zoologica 55, 107–111.

Všetičková, L., Janáč, M., Vašek, M., Roche, K., Jurajda, P., 2014. Non-native western tubenose gobies *Proterorhinus semilunaris* show distinct site, sex and age-related differences in diet. Knowledge and Management of Aquatic Ecosystems 414, 10.

Vucic-Pestic, O., Ehnes, R.B., Rall, B.C., Brose, U., 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. Global Change Biology 17, 1301–1310.

Wasserman, R.J., Alexander, M.E., Dalu, T., Ellender, B.R., Kaiser, H., Weyl, O.L.F., 2016. Using functional responses to quantify interaction effects among predators. Functional Ecology 30, 1988–1998.

Wolter, C., 2001. Conservation of fish species diversity in navigable waterways. Landscape and Urban Planning 53, 135–144.

Wootton, J.T., Parker, M.S., Power, M.E., 1996. Effects of disturbance on river food webs. Science 273, 1558–1561.

Xu, M., Mu, X., Dick, J.T.A., Fang, M., Gu, D., Luo, D., Zhang, J., Luo, J., Hu, Y., 2016. Comparative functional responses predict the invasiveness and ecological impacts of alien herbivorous snails. PLoS ONE 11, e0147017.

Young, J.A.M., Marentette, J.R., Gross, C., McDonald, J.I., Verma, A., Marsh-Rollo, S.E., Macdonald, P.D.M., Earn, D.J.D., Balshine, S., 2010. Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour. Journal of Great Lakes Research 36, 115–122.

Supplement

Table S1. *Biometric data of Neogobius melanostomus and Proterorhinus semilunaris used in experiments in three habitat treatments: sand, cobbles and cobbles with artificial plant. Total length (TL), standard length (SL), and weight (W). Data are presented as mean±SD.*

Species	Habitat	n	TL (mm)	SL (mm)	W (g)
Neogobius melanostomus	sand	49	53.2±3.3	44.3±3.2	1.6±0.3
	cobbles	52	51.9±3.0	43.0±2.5	1.5±0.3
	cobbles with a. plant	49	52.1±3.7	43.2±3.3	1.5±0.3
Proterorhinus semilunaris	sand	52	50.6±3.7	41.8±2.7	1.4±0.3
	cobbles	43	51.5±4.3	42.7±3.8	1.4±0.3
	cobbles with a. plant	45	50.4±3.7	41.5±3.4	1.3±0.3

Table S2. *Logistic regression parameters of the proportion of prey eaten per gram of predator in Neogobius melanostomus (Nm) and Proterorhinus semilunaris (Ps) in three habitat treatments: sand, cobbles and cobbles with artificial plant. Value±SE of the linear coefficient P1.*

Species	sand			cobbles			cobbles with a. plant		
	P1	SE	p-value	P1	SE	p-value	P1	SE	p-value
Nm	-3.51	0.21	< 0.0001	-2.80	0.22	< 0.0001	-3.26	0.21	< 0.0001
Ps	-3.63	0.21	< 0.0001	-2.66	0.23	< 0.0001	-3.57	0.23	< 0.0001

CHAPTER 5

GENERAL DISCUSSION
ENGLISH SUMMARY
CZECH SUMMARY
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TRAINING AND SUPERVISION PLAN DURING THE STUDY
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GENERAL DISCUSSION

Almost all countries in the world nowadays have thousands of alien, introduced plant and animal species inhabiting their ecosystems. Some alien species were intentionally introduced because native plants and livestock could not provide sufficient food sources for a country's needs, while other species were introduced by accident (Pimentel, 2014). The invasion of alien species into new environments is accelerating as the world's human population grows and goods are transported ever more rapidly on a global scale (Hulme, 2009).

Biological invasions and consequential biodiversity losses are major components of human-induced global change (Vitousek et al., 1997). Besides detrimental ecological alterations in invaded ecosystems (Pejchar and Mooney, 2009), they generate substantial economic costs associated with commodity and service losses as well as with eradication and mitigation of alien species (Pimentel et al., 2001; Vilà et al., 2010). The invasions of alien organisms in the United States, the British Isles, Australia, Europe, South Africa, India, and Brazil inflict more than $300 billion per year in damage and control costs in those key regions (Pimentel, 2014). In addition, serious human health risks have emerged in tandem with new introductions (Mazza et al., 2014).

Problems connected with biological invasions fuel a need for an urgent and cost-effective management. Given the number of alien species, their vectors and pathways of introduction, the most effective actions include an exhaustive prevention in the invasion hotspots (Ibáñez et al., 2009) as well as targeting high-risk alien species (Ricciardi and Rasmussen, 1998).

Invasion hotspots in the Czech Republic

Inference on where to target early control and eradication efforts has become the critical point in the management of alien species. Identifying of invasion hotspots, *i.e.* particular areas, which may likely host large numbers of alien species is one of the prominent goals for ecologists and natural resources managers (Ibáñez et al., 2009). Theory indicates that the invasion of an alien is a function of propagule pressure, abiotic characteristics of a receiving environment as well as biological characteristics of invaders and recipient community (Catford et al., 2009; Richardson and Pyšek, 2006).

In Chapter 2, we used twelve selected parameters characterizing propagule pressure and environmental conditions in order to predict areas vulnerable to invasion by alien species in the Czech Republic. This knowledge provides information about locations deserving control efforts, as they are likely prone to future invasions. Rather than predicting areas at risk of invasion by individual species, we present a more general approach where the invasion patterns by multiple species may be used to infer key drivers of invasion (Ibáñez et al., 2009). In addition, we mapped landscape susceptibility to invasion. Predicting invasion hotspots may be an extremely valuable tool for ecologists, land managers and regulators given the threat posed by increasing numbers of invaders. The specific question we aimed to answer in Chapter 2 is how geographical, climate and human-related attributes are associated with the species richness in six categories of alien animals in the Czech Republic. Moreover, we aimed at providing country-wide maps of alien animal species richness, a powerful tool for visual communication among concerned parties, as well as for identification of the invasion hotspots.

Altitude and terrain heterogeneity are among the main topographical factors influencing the alien species richness. We found both variables to be negatively correlated with alien richness. Indeed, areas at high altitude and spatially heterogeneous terrain are generally considered to be more resistant to invasion, due to lower human population density and trade and more severe climate. These factors were reported to be directly affecting the alien species richness along the altitude gradient (Kumar et al., 2006; Pyšek et al., 2012; Zefferman et al., 2015). This finding was reflected in our results showing the effect of altitude to be similar to that of mean annual temperature, precipitation and human impact (population, land cover types), for the categories of all alien species, terrestrial species, and invertebrates. The effect of terrain heterogeneity on alien species richness was relatively weak compared to other variables and was consistently negative, suggesting that a rugged landscape with many topographical barriers may be more resistant to invasion (Richardson and Pyšek, 2006).

Climatic factors were identified as a primary driver of invasion success of alien plants (Lambdon et al., 2008). In other taxonomic groups, however, the effect of climate on aliens was often outweighed by demographic and economic variables such as human population density (Pyšek et al., 2010). Though, several studies have shown that even alien mammals (Winter et al., 2010) and birds (Dyer et al., 2017) are also limited by climatic condition. We found that alien animal richness in the Czech Republic is strongly positively related to the mean annual temperature, while the opposite is true (observed negative correlation) in case of annual precipitation. In invertebrates, terrestrial, and all alien species, mean annual temperature showed the strongest effect among the explanatory variables.

Habitat and its heterogeneity highly influence species coexistence (Chesson, 2000) and, consequently, the spatial distribution of biological invasions (Richardson and Pyšek, 2006). A heterogeneous environment provides closely linked diverse habitats suitable for both, native and alien species, and hence, they are considered more vulnerable to invasion compared to homogeneous habitats (Davies et al., 2005). Indeed, we found a positive correlation between the alien species richness and the number of land cover types, which we used as a surrogate for habitat heterogeneity. River size showed a significant positive relationship with all alien animal categories, though its effect was the strongest not only on in aquatic species but also in black and grey species, *i.e.* prominent invasive alien species of high concern (Pergl et al., 2016). Alien aquatic species in the Czech Republic showed clear trend in distribution towards navigable rivers influenced by ballast water exchange, such as the Elbe River, which was recently confirmed as the site of several introduction events (Buřič et al., 2015). Other vectors of aquatic invasions are spontaneous migration through the Danube River system, intentional and unintentional introductions into aquaculture areas, and accidental escapes from pet owners and/or vendors (Musil et al., 2010; Patoka et al., 2016).

The spatial distribution of biological invasions is largely shaped by demographic and socio-economic factors (Perdikaris et al., 2012; Pyšek et al., 2010). Remote areas with little human intervention generally receive fewer alien species compared to densely populated trade routes or areas of intense human activity (Drake et al., 1989). Lockwood et al. (2005) reported that propagule pressure, *i.e.* combination of a number of introduced individuals at a site and the number of introduction events, is a primary driver of alien species distribution. In Europe, human population density appears to be a reliable surrogate of propagule pressure (Copp et al., 2010). In the Czech Republic, human population density showed a strong positive relationship to alien animal species richness in all assessed categories (Chapter 2). Considerably higher effect of human population density on alien invertebrates compared to other alien categories likely reflects a high number of invertebrates introduced as pests into commodity storehouses.

Based on the results of Chapter 2, several measures for protecting introduction and spread of alien animals can be recommended including strict controls of imported commodities into storehouses (main introduction gateway for alien invertebrates), development and application of effective ballast water management for inland vessels (alien aquatic species) and raising public and pet vendor awareness about alien species risks. In case of alien gobiids, raising public awareness and particularly game fishermen is very important as gobiids can be spread as a bait beyond the introduction sites.

Foraging behavior and ecological impact of *N. melanostomus* and *P. semilunaris*

Crucial factor influencing the feeding rate is resource availability (prey density). The relationship between feeding rate and prey density can be characterized by the functional response (FR; Holling, 1959; Solomon, 1949). FR describes the foraging behavior of a predator by means of searching and feeding efficiencies at different prey densities, which have essential implications for consumer-resource interactions, community dynamics and hence for ecosystem modeling (Juliano, 2001; Murdoch and Oaten, 1975; Petchey et al., 2008).

Recent studies have proved FR to be a rapid and reliable method for an assessment and comparison of alien species ecological impact with wide taxonomical applicability under a wide range of environmental conditions (Alexander et al., 2014; Dick et al., 2014; Xu et al., 2016). It is induced by better foraging efficiency and/or resources utilization, and higher maximum feeding rates, which was frequently documented in invasive predators (Dick et al., 2002; Dick et al., 2013). Consequently, FRs of invasive species often display elevated asymptotes compared to native or low-impact ecologically analogous alien species. This is of paramount importance for the management of biological invasions as reliable predictions of alien's ecological impact is crucial for a successful implementation of control and eradication management plans. The method has been subjected to a controversial debate among invasion biologist (Dick et al., 2017a; Dick et al., 2017b; Vonesh et al., 2017a; Vonesh et al., 2017b) for omitting important factors in predicting invasive species. Indeed, the predicting power can be improved by including additional factors into analyses, *e.g.* numerical response (Dick et al., 2017c).

Attack rate and handling time are important parameters of FR calculations and should be interpreted with caution in invasion ecology. The attack rate characterize the slope of the FR curve at low prey densities and hence indicates the predator efficiency at these densities (Alexander et al., 2014; Jeschke et al., 2002). The attack rate of native species with lower ecological impact can be even higher compared to high-impact alien species (Alexander et al., 2014) suggesting the necessity for the native species to be an effective consumer at low prey densities. On the other hand, handling time is classically defined as the time spent pursuing, subduing, and consuming each prey item plus the time spent preparing to search for the next prey item (Jeschke et al., 2002). Therefore lower handling time reflects greater predatory efficiency at higher prey densities.

In freshwater ecosystems, organisms are exposed to a variety of factors which may affect consumer-resource interactions. Biotic factors include the predator and prey size (Thorp et al., 2018) or multiple predator effects (Wasserman et al., 2016). Temperature and habitat structure can be considered as of the most important abiotic drivers influencing the predator-prey interactions (Alexander et al., 2012; Alexander et al., 2015; Englund et al., 2011; Vucic-Pestic et al., 2011). In Chapters 3 and 4, we quantified and compared the foraging behavior and ecological impact of emergent invasive round goby *Neogobius melanostomus* (Pallas, 1814) and alien western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) under two temperature regimes (20 and 25 °C; Chapter 3) and three habitat structures (sand, cobbles and cobbles with artificial plant; Chapter 4).

In predatory fish species, type II FR, *i.e.* inversely density dependent predation, is a common foraging behavior. Though, variations in environment may return shifts in FR types (Koski and Johnson, 2002). We observed type II FR in both predators and both temperature (Chapter 3) and habitat treatments (Chapter 4). The shape of the FR curve corroborated previous findings for *N. melanostomus* (Dubs and Corkum, 1996; Fitzsimons et al., 2006). Similarly, Alexander et al. (2015) found type II FR in invasive largemouth bass *Micropterus salmoides* (Lacépède, 1802) under different habitat complexities. This implies that invasive predators may have destabilizing effect on population dynamics through high prey exploitation at low prey densities (Murdoch and Oaten, 1975) under various environmental conditions.

Although published data suggest that the maximum consumption rate of *N. melanostomus* falls within 23–26 °C, alteration from 20 to 26°C produced only a slight increase (Lee and Johnson, 2005). This was corroborated in Chapter 3, where *N. melanostomus* showed no significant differences between 20 °C and 25 °C in both FR parameters, i.e. attack rate and handling time. Similar results were documented also for *P. semilunaris*. In general, attack and feeding rates of ectotherm organisms are characterized by hump-shaped temperature dependency and, while sharing the same temperature optima, attack rate is dynamically affected, both, above and below the optimal temperature (Englund et al., 2011). No significant intraspecific difference in attack rate between 20 °C and 25 °C was found in Chapter 3. It implies that tested temperatures fall within the thermal optima of both predator species.

In Chapter 4, however, *N. melanostomus* attack rates and handling times displayed significant differences among all habitat treatments with the highest value in sandy habitats. *Proterorhinus semilunaris* displayed higher FR parameters on sandy substrate and cobbles with artificial plant compared to cobble substrate. This implies that both tested predators are efficient at low prey densities in simple habitats, while *P. semilunaris* is more efficient on cobbles with artificial plants in comparison to *N. melanostomus*. At high prey densities, on the other hand, both predators are more effective on cobble substrate compared to other treatments. Alexander et al. (2015) observed lower attack rate in zero complexity habitat, what could be most probably attributed to different foraging behavior of *M. salmoides* (ambush predator; Savino and Stein, 1982) as compared to *N. melanostomus* and *P. semilunaris* that are rather actively searching for prey (Barton et al., 2005; Jude at al., 1995). Although several researchers observed *N. melanostomus* in plant environments (Cooper et al., 2009; Taraborelli et al., 2009), there are clear evidences for preferences towards hard substrate (Ray and Corkum, 2001; Young et al., 2010). This corresponds with lower handling time on cobble substrate compared to cobbles with artificial plant observed in Chapter 4. Open sandy habitat without shelter were shown to pose a higher risk of predation for *N. melanostomus* (Belanger and Corkum, 2003). Indeed, higher handling time on sandy substrate found in Chapter 4 may be attributed to induced stress despite reduced refuge space for prey. The general hypothesis about higher impact of *P. semilunaris* in plant environment deduced from documented higher abundances in these habitats (Kocovsky et al., 2011) was apparent only at low densities (higher attack rate compared to *N. melanostomus*), while at high densities *P. semilunaris* displayed significantly lower handling time in cobble habitat compared to the other treatments, suggesting higher *per capita* ecological impact.

Interspecific comparison between *N. melanostomus* and *P. semilunaris* showed no significant differences in handling time at any tested temperature (Chapter 3) and on hard substrates (cobbles and cobbles with artificial plant; Chapter 4). This implies that the per capita ecological impact on native communities posed by both predator species is similar, though little attention has been given to the impact of P. semilunaris. However, Dick et al. (2017c) suggested that both, per capita effect (FR) and numerical response (abundance) should be implemented in invader ecological impact assessment. In general, *P. semilunaris* does not reach as high abundance as *N. melanostomus* in invaded ecosystems as documented in several studies (Dopazo et al., 2008; Janáč et al., 2018; van Kessel et al., 2016). Consequently, the former species is no longer considered an important threat to native communities in some regions (Borcherding et al., 2011). On the other hand, high densities of *P. semilunaris* were documented in shallow macrophyte-rich habitats (Janáč et al., 2012; Kocovsky et al., 2011), where it can pose a serious threat for phytophilic fauna, including cyprinid larvae.

Based on the study of Laverty et al. (2017) and our results (Chapters 3 and 4), it can be assumed that both alien predators, *N. melanostomus* and *P. semilunaris* can outperform ecologicaly analogous native species *Cottus gobio* Linnaeus, 1758 due to a high maximum feeding rate, that reaches the similar values in both aliens at 20 °C in a range of habitats. At 25 °C, however, *N. melanostomus* displayed even higher maximum consumption rate as compared to *P. semilunaris*. In Chapter 4, we observed significant differences among habitat treatments with highest maximum feeding rate on cobble substrate followed by cobble with artificial plant and sandy habitats. This finding reflects the habitat preference of both alien predators and likely induced stress in non-sheltered habitats (Belanger and Corkum, 2003; Kocovsky et al., 2011; Kornis et al., 2012). It implies that both predators forage efficiently in structured habitats that might otherwise serve as the prey refugia (Baber and Babbitt, 2004).

We found substantially higher weight-specific amount of fish larvae eaten by both, *N. melanostomus* and *P. semilunaris* in Chapter 4 compared to Chapter 3. This phenomenon could be most probably explained by lower predator size used in Chapter 4. Indeed, Lee and Johnson (2005) documented in *N. melanostomus* higher weight-specific consumption rate showed by smaller specimens. Based on findings in Chapters 3 and 4, similar trend can be expected also in *P. semilunaris*, though the modeled weight-maximum consumption curve for this species is not developed so far.

Conclusion

- The results of Chapter 2 together with created maps contribute to better understanding and prediction of introductions of alien animals. This information is of crucial importance for managers and policy makers, *i.e.* they can concentrate their efforts predominantly in high-risk areas.
- The highest alien animal species richness was found in as well as near large human population centers and also in agricultural landscapes in warm and dry lowlands.
- The gateways for alien aquatic species are rather large rivers over sport fishing and aquaculture import.
- The compiled maps create a powerful visual communication tool, valuable for development of programs to prevent the future introductions.
- Regardless of temperature no significant differences in handling time between *N. melanostomus* and *P. semilunaris* suggesting a similar foraging behavior and *per capita* ecological impact of both species upon native communities (Chapter 3).
- The higher maximum feeding rate of *N. melanostomus* at 25 °C compared to *P. semilunaris* indicates higher temperature optima of the former species (Chapter 3).
- Similar handling time in both, *N. melanostomus* and *P. semilunaris* on cobble substrate and cobbles with artificial plant habitat upon *C. carpio* larvae suggesting similar *per capita* impacts in the environment with hard substrate (Chapter 4).
- Significantly higher maximum consumption rate of both, *N. melanostomus* and *P. semilunaris* on hard substrates reflects the habitat preferences of both alien predators and likely induced stress in non-sheltered habitats (Chapter 4).
- Given the similar *per capita* ecological impact, the invasive potential of *P. semilunaris* would elevate in localities with high abundances, *e.g.* in habitats with submerged macrophytes (Chapter 4).
- Results of Chapters 3 and 4 underline the importance of complex actions when managing ecosystems with multiple alien species (see Zavaleta et al., 2001), as an empty or loosen

niche created by elimination of one invasive species (*N. melanostomus*) can boost a population growth of another alien, which originally was not considered invasive (*P. semilunaris*).

REFERENCES

Alexander, M.E., Dick, J.T.A., O'Connor, N.E., Haddaway, N.R., Farnsworth, K.D., 2012. Functional responses of the intertidal amphipod *Echinogammarus marinus*: effects of prey supply, model selection and habitat complexity. Marine Ecology Progress Series 468, 191–202.

Alexander, M.E., Dick, J.T.A., Weyl, O.L.F., Robinson, T.B., Richardson, D.M., 2014. Existing and emerging high impact invasive species are characterized by higher functional responses than natives. Biology Letters 10, 20130946.

Alexander, M.E., Kaiser, H., Weyl, O.L.F., Dick, J.T.A., 2015. Habitat simplification increases the impact of a freshwater invasive fish. Environmental Biology of Fishes 98, 477–486.

Baber, M.J., Babbitt, K.J., 2004. Influence of habitat complexity on predator–prey interactions between the fish (*Gambusia holbrooki*) and tadpoles of *Hyla squirella* and *Gastrophryne carolinensis*. Copeia 2004, 173–177.

Barton. D.R., Johnson. R.A., Campbell. L., Petruniak, J., Patterson, M., 2005. Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in eastern Lake Erie, 2002–2004. Journal of Great Lakes Research 31, 252–261.

Belanger, R.M., Corkum, L.D., 2003. Susceptibility of tethered round gobies (*Neogobius melanostomus*) to predation in habitats with and without shelters. Journal of Great Lakes Research 29, 588–593.

Borcherding, J., Staas, S., Krüger, S., Ondračková, M., Šlapanský, L., Jurajda, P., 2011. Non-native gobiid species in the lower River Rhine (Germany): recent range extensions and densities. Journal of Applied Ichthyology 27, 153–155.

Buřič, M., Bláha, M., Kouba, A., Drozd, B., 2015. Upstream expansion of round goby (*Neogobius melanostomus*)–first record in the upper reaches of the Elbe river. Knowledge and Management of Aquatic Ecosystems 416, 32.

Catford, J.A., Jansson, R., Nilsson, C., 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and Distributions 15, 22–40.

Chesson, P., 2000. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology 58, 211–237.

Cooper, M.J., Ruetz, C.R., Uzarski, D.G., Shafer, B.M., 2009. Habitat use and diet of the round goby (*Neogobius melanostomus*) in coastal areas of Lake Michigan and Lake Huron. Journal of Freshwater Ecology 24, 477–488.

Copp, G., Vilizzi, L., Gozlan, R., 2010. The demography of introduction pathways, propagule pressure and occurrences of non-native freshwater fish in England. Aquatic Conservation: Marine and Freshwater Ecosystems 20, 595–601.

Davies, K.F., Chesson, P., Harrison, S., Inouye, B.D., Melbourne, B.A., Rice, K.J., 2005. Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. Ecology 86, 1602–1610.

Dick, J.T.A., Platvoet, D., Kelly, D.W., 2002. Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). Canadian Journal of Fisheries and Aquatic Sciences 59, 1078–1084.

Dick, J.T.A., Gallagher, K., Avlijas, S., Clarke, H.C., Lewis, S.E., Leung, S., Minchin, D., Caffrey, J., Alexander, M.E., Maguire, C., Harrod, C., Reid, N., Haddaway, N.R., Farnsworth, K.D., Penk, M., Ricciardi, A., 2013. Ecological impacts of an invasive predator explained and predicted by comparative functional responses. Biological Invasions 15, 837–846.

Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B., Kumschick, S., Weyl, O.L.F., Dunn, A.M., Hatcher, M.J., Paterson, R.A., Farnsworth, K.D., Richardson, D.M., 2014. Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biological Invasions 16, 735–753.

Dick, J.T.A., Alexander, M.E., Ricciardi, A., Laverty, C., Downey, P.O., Xu, M., Jeschke, J.M., Saul, W.C., Hill, M.P., Wasserman, R., Barrios-O'Neill, D., Weyl, O.L.F., Shaw, R.H., 2017a. Fictional responses from Vonesh et al. Biological Invasions 19, 1677–1678.

Dick, J.T.A., Alexander, M.E., Ricciardi, A., Laverty, C., Downey, P.O., Xu, M., Jeschke, J.M., Saul, W.C., Hill, M.P., Wasserman, R., Barrios-O'Neill, D., Weyl, O.L.F., Shaw, R.H., 2017b. Functional responses can unify invasion ecology. Biological Invasions 19, 1667–1672.

Dick, J.T.A., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., Britton, R.J., Medoc, V., Boets, P., Alexander, M.E., Taylor, N.G., Dunn, A.M., Hatcher, M.J., Rosewarne, P.J., Crookes, S., MacIsaac, H.J., Xu, M., Ricciardi, A., Wasserman, R.J., Ellender, B.R., Weyl, O.L.F., Lucy, F.E., Banks, P.B., Dodd, J.A., MacNeil, C., Penk, M.R., Aldridge, D.C., Caffrey, J.M., 2017c. Invader relative impact potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. Journal of Applied Ecology 54, 1259–1267.

Dopazo, S.N., Corkum, L.D., Mandrak, N.E., 2008. Fish assemblages and environmental variables associated with gobiids in nearshore areas of the lower Great Lakes. Journal of Great Lakes Research 34, 450–460.

Drake, J.A., Mooney, H.A., Di Castri, F., Groves, R.H., Kruger, F.J., Williamson, M. H., 1989. Biological invasions: a global perspective. John Wiley and Sons, New York, USA, 525 pp.

Dubs, D.O.L., Corkum, L.D., 1996. Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). Journal of Great Lakes Research 22, 838–844.

Dyer, E.E., Cassey, P., Redding, D.W., Collen, B., Franks, V., Gaston, K.J., Jones, K.E., Kark, S., Orme, C.D.L., Blackburn, T.M., 2017. The global distribution and drivers of alien bird species richness. PLoS biology 15, e2000942.

Englund, G., Öhlund, G., Hein, C.L., Diehl, S., 2011. Temperature dependence of the functional response. Ecology Letters 14, 914–921.

Fitzsimons, J., Williston, B., Williston, G., Bravener, G., Jonas, J.L., Claramunt, R.M., Marsden, J.E., Ellrott, B.J., 2006. Laboratory estimates of salmonine egg predation by round gobies (*Neogobius melanostomus*), sculpins (*Cottus cognatus* and *C. bairdi*), and crayfish (*Orconectes propinquus*). Journal of Great Lakes Research 32, 227–241.

Holling, C.S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist 91, 293–320.

Hulme, P.E., 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology 46, 10–18.

Ibáñez, I., Silander Jr, J., Allen, J.M., Treanor, S.A., Wilson, A., 2009. Identifying hotspots for plant invasions and forecasting focal points of further spread. Journal of Applied Ecology 46, 1219–1228.

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

Janáč, M., Roche, K., Šlapanský, L., Polačik, M., Jurajda, P., 2018. Long-term monitoring of native bullhead and invasive gobiids in the Danubian rip-rap zone. Hydrobiologia 807, 263–275.

Jeschke, J.M., Kopp, M., Tollrian, R., 2002. Predator functional responses: discriminating between handling and digesting prey. Ecological Monographs 72, 95–112.

Jude, D.J., Janssen, J., Crawford, G., 1995. Ecology, distribution, and impact of the newly introduced round and tubenose gobies in the biota of the St. Clair and Detroit Rivers. In: Munawar, M., Edsall, T., Leach, J. (Eds.), The Lake Huron ecosystem: ecology, fisheries, and management. Ecovision World Monograph Series, S.B.P. Academic Publishing, Amsterdam, The Netherlands, pp. 447–460.

Juliano, S.A., 2001. Non-linear curve fitting: predation and functional response curve. In: Scheiner, S.M., Gurevitch, J. (eds.), Design and analysis of ecological experiment. Oxford University Press, Oxford, UK, pp. 178–196.

Kocovsky, P.M., Tallman, J.A., Jude, D.J., Murphy, D.M., Brown, J.E., Stepien, C.A., 2011. Expansion of tubenose gobies *Proterorhinus semilunaris* into western Lake Erie and potential effects on native species. Biological Invasions 13, 2775–2784.

Kornis, M.S., Mercado-Silva, N., Vander Zanden, M.J., 2012. Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. Journal of Fish Biology 80, 235–285.

Koski, M.L., Johnson, B.M., 2002. Functional response of kokanee salmon (*Oncorhynchus nerka*) to *Daphnia* at different light levels. Canadian Journal of Fisheries and Aquatic Sciences 59, 707–716.

Kumar, S., Stohlgren, T.J., Chong, G.W., 2006. Spatial heterogeneity influences native and nonnative plant species richness. Ecology 87, 3186–3199.

Lambdon, P.W., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., Jarošík, V., Pergl, J., Winter, M., Anastasiu, P., 2008. Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. Preslia 80, 101–149.

Laverty, C., Green, K.D., Dick, J.T.A., Barrios-O'Neill, D., Mensink, P.J., Médoc, V., Spataro, T., Caffrey, J.M., Lucy, F.E., Boets, P., Britton, J.R., Pegg, J., Gallagher, C., 2017. Assessing the ecological impacts of invasive species based on their functional responses and abundances. Biological Invasions 19, 1653–1665.

Lee, V.A., Johnson, T.B., 2005. Development of a bioenergetics model for the round goby (*Neogobius melanostomus*). Journal of Great Lakes Research 31, 125–134.

Lockwood, J.L., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20, 223–228.

Mazza, G., Tricarico, E., Genovesi, P., Gherardi, F., 2014. Biological invaders are threats to human health: an overview. Ethology Ecology and Evolution 26, 112–129.

Murdoch, W.W., Oaten, A., 1975. Predation and population stability. Advances in Ecological Research 9, 1–131.

Musil, J., Jurajda, P., Adámek, Z., Horký, P., Slavík, O., 2010. Non-native fish introductions in the Czech Republic–species inventory, facts and future perspectives. Journal of Applied Ichthyology 26, 38–45.

Patoka, J., Bláha, M., Devetter, M., Rylková, K., Čadková, Z., Kalous, L., 2016. Aquarium hitchhikers: attached commensals imported with freshwater shrimps via the pet trade. Biological Invasions 18, 457–461.

Pejchar, L., Mooney, H.A., 2009. Invasive species, ecosystem services and human well-being. Trends in Ecology and Evolution 24, 497–504.

Perdikaris, C., Kozák, P., Kouba, A., Konstantinidis, E., Paschos, I., 2012. Socio-economic drivers and non-indigenous freshwater crayfish species in Europe. Knowledge and Management of Aquatic Ecosystems 404, 01.

Pergl, J., Sádlo, J., Petrusek, A., Laštůvka, Z., Musil, J., Perglová, I., Šanda, R., Šefrová, H., Šíma, J., Vohralík, V., 2016. Black, Grey and Watch Lists of alien species in the Czech Republic based on environmental impacts and management strategy. NeoBiota 28, 1–37.

Petchey, O.L., Beckerman, A.P., Riede, J.O., Warren, P.H., 2008. Size, foraging, and food web structure. Proceedings of the National Academy of Sciences of the United States of America 105, 4191–4196.

Pimentel, D., 2014. Introduction: nonnative species in the world. In: Pimentel, D. (ed.), Biological invasions: economic and environmental costs of alien plant, animal, and microbe species. CRC Press, Boca Raton, Florida, USA, pp. 11–17.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agriculture, Ecosystems and Environment 84, 1–20.

Pyšek, P., Jarošík, V., Hulme, P.E., Kühn, I., Wild, J., Arianoutsou, M., Bacher, S., Chiron, F., Didžiulis, V., Essl, F., Genovesi, P., Gherardi, F., Hejda, M., Kark, S., Lambdon, P.W., Desprez-Loustau, M.-L., Nentwig, W., Pergl, J., Poboljšaj, K., Rabitsch, W., Roques, A., Roy, D.B., Shirley, S., Solarz, W., Vilà, M., Winter, M., 2010. Disentangling the role of environmental and human pressures on biological invasions across Europe. Proceedings of the National Academy of Sciences of the United States of America 107, 12157–12162.

Pyšek, P., Chytrý, M., Pergl, J., Sadlo, J., Wild, J., 2012. Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. Preslia 84, 575–629.

Ray, W.J., Corkum, L.D., 2001. Habitat and site affinity of the round goby. Journal of Great Lakes Research 27, 329–334.

Ricciardi, A., Rasmussen, J.B., 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences 55, 1759–1765.

Richardson, D.M., Pyšek, P., 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30, 409–431.

Savino, J.F., Stein, R.A., 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated submersed vegetation. Transactions of the American Fisheries Society 111, 255–266.

Solomon, M.E., 1949. The natural control of animal populations. Journal of Animal Ecology 18, 1–35.

Taraborelli, A.C., Fox, M.G., Schaner, T., Johnson, T.B., 2009. Density and habitat use by the round goby (*Apollonia melanostoma*) in the Bay of Quinte, Lake Ontario. Journal of Great Lakes Research 35, 266–271.

Thorp, C.J., Alexander, M.E., Vonesh, J.R., Measey, J., 2018. Size-dependent functional response of *Xenopus laevis* on mosquito larvae. PeerJ Preprints doi.org/10.7287/peerj.preprints.26575v1

van Kessel, N., Dorenbosch, M., Kranenbarg, J., van der Velde, G., Leuven, R.S.E.W., 2016. Invasive Ponto-Caspian gobies rapidly reduce the abundance of protected native bullhead. Aquatic Invasions 11, 179–188.

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E., and DAISIE partners, 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment 8, 135–144.

Vitousek, P.M., D'antonio, C.M., Loope, L.L., Rejmanek, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21, 1–16.

Vonesh, J., McCoy, M., Altwegg, R., Landi, P., Measey, J., 2017a. Functional responses can't unify invasion ecology. Biological Invasions 19, 1673–1676.

Vonesh, J., McCoy, M., Altwegg, R., Landi, P., Measey, J., 2017b Rather than unifying invasion biology, Dick et al.'s approach rests on subjective foundations. Biological Invasions 19, 1679–1680.

Vucic-Pestic, O., Ehnes, R.B., Rall, B.C., Brose, U., 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. Global Change Biology 17, 1301–1310.

Wasserman, R.J., Alexander, M.E., Dalu, T., Ellender, B.R., Kaiser, H., Weyl, O.L.F., 2016. Using functional responses to quantify interaction effects among predators. Functional Ecology 30, 1988–1998.

Winter, M., Kühn, I., La Sorte, F.A., Schweiger, O., Nentwig, W., Klotz, S., 2010. The role of non native plants and vertebrates in defining patterns of compositional dissimilarity within and across continents. Global Ecology and Biogeography 19, 332–342.

Xu, M., Mu, X., Dick, J.T.A., Fang, M., Gu, D., Luo, D., Zhang, J., Luo, J., Hu, Y., 2016. Comparative functional responses predict the invasiveness and ecological impacts of alien herbivorous snails. PLoS ONE 11, e0147017.

Young, J.A.M., Marentette, J.R., Gross, C., McDonald, J.I., Verma, A., Marsh-Rollo, S.E., Macdonald, P.D.M., Earn, D.J.D., Balshine, S., 2010. Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour. Journal of Great Lakes Research 36, 115–122.

Zavaleta, E.S., Hobbs, R.J., Mooney, H.A., 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution 16, 454–459.

Zefferman, E., Stevens, J.T., Charles, G.K., Dunbar-Irwin, M., Emam, T., Fick, S., Morales, L.V., Wolf, K.M., Young, D.J.N., Young, T.P., 2015. Plant communities in harsh sites are less invaded: a summary of observations and proposed explanations. AoB Plants 7, plv056.

ENGLISH SUMMARY

Foraging behavior of non-indigenous gobiid fish species

Radek Gebauer

Biogeographical barriers formed by natural forces over billions of years have been substantially disrupted by human activities, particularly in recent centuries. In response to these anthropogenic changes, global homogenisation of biota is observed at an ever-increasing rate, causing environmental and economic losses as well as emerging health risks. Ecological and economic consequences of biological invasions fuel the need for an urgent targeted and cost-effective management given the amount of invaders, vectors and pathways. It lies in identification of factors underlying alien species richness, being crucial for prevention of future introductions and subsequent spread. For invaders that have already established, however, the effective management requires targeting high-impact aliens. For assessment and comparison of alien impact, recent studies have applied functional response (FR) approach, *i.e.* quantification of the foraging behavior and efficiency at different prey densities.

In Chapter 2, we examined the effects of environmental and human-related factors on distribution of alien animal species richness in the Czech Republic (Central Europe). We compiled a set of maps showing the level of invasion of six categories of alien animal species in each of 628 grid cells (ca. 12.0 × 11.1 km) covering the Czech Republic. Relationships between alien species richness and 12 variables characterizing climatic conditions, topography, land cover, and human population size were calculated using the generalized least squares method. Species richness of all aliens, of invertebrates, and of terrestrial species showed the strongest positive relationship with mean annual temperature, while the number of black and grey (proposed prominent invaders) and aquatic species was most closely related to the presence of large rivers. The highest alien animal species richness was found in and near large population centres and in agricultural landscapes in warm and dry lowlands. The gateways for alien aquatic species are rather large rivers over sport fishing and aquaculture import.

Round goby *Neogobius melanostomus* (Pallas, 1814) and western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) have recently expanded beyond their native ranges, posing a threat to freshwater and brackish ecosystems. In the Czech Republic, both species have established abundant populations and form a substantial part of nearshore ichthyofauna. Both species exert a detrimental effect on fish communities' structure directly via predation on fish eggs and indirectly via alterations of food webs. While the impact of *N. melanostomus* is widely documented, *P. semilunaris* received little attention and its effect on aquatic communities has not yet been quantified. We quantified and compared the foraging behavior and efficiency of invasive *N. melanostomus* and alien *P. semilunaris* upon common carp (*Cyprinus carpio*, Linnaeus), 1758 larvae at two temperature levels (20 and 25 °C, Chapter 3) and in three different habitat structures (sand, cobbles, cobbles with artificial plant; Chapter 4).

Both alien predators showed type II FR in both temperature and habitat treatments. In Chapter 3, intra-specific comparison showed no significant temperature dependency on assessed FR parameters, attack rate and handling time. *Proterorhinus semilunaris* demonstrated a marginally higher attack rate at 20 °C compared to *N. melanostomus*. The handling times did not differ between predators suggesting similar *per capita* ecological impact at high prey densities. *Proterorhinus semilunaris* showed a lower maximum feeding rate at 25 °C compared to the rest of treatments suggesting a lower temperature optima compared to *N. melanostomus*.

In Chapter 4, interspecific comparison showed similar values of handling time in cobble substrate and cobbles with artificial plant suggesting similar *per capita* ecological impacts of both aliens. Intraspecific comparison showed significantly lower values of handling time in both predators in habitat with cobbles reflecting higher maximum feeding rate. Therefore, impact of both invaders in such environment could elevate. *Neogobius melanostomus* showed higher attack rate in sandy habitat compared to *P. semilunaris*, while no significant differences were observed in other habitat treatments.

In conclusion, both predators showed substantial values of maximum feeding rate, which may impact recruitment success of native fish species. In addition, our results highlight the importance of complex actions in management of biological invasions, as the elimination of invasive *N. melanostomus* can boost a population growth of alien *P. semilunaris*, which was not considered invasive until that time.

CZECH SUMMARY

Potravní chování nepůvodních hlaváčovitých ryb

Radek Gebauer

V posledních několika dekádách byly lidskou činností oslabeny, nebo výrazně narušeny biogeografické bariéry, které byly po dobu miliard let formovány přírodními silami. Jedním z důsledků těchto antropogenních změn je globální homogenizace bioty prostřednictvím tzv. biologických invazí nepůvodními organismy. Biologické invaze způsobují environmentální a ekonomické škody, ale také závažná zdravotní rizika. Vzhledem k množství nepůvodních druhů, jejich vektorů a způsobů transportu vyvolávají důsledky biologických invazí potřebu naléhavého cíleného a finančně efektivního managementu. To spočívá v identifikaci faktorů, které určují druhovou pestrost nepůvodních druhů. To je pak klíčové pro budoucí prevenci. U nepůvodních druhů, které se již na určitém území etablovaly, však vyžaduje efektivní management v prvé řadě zaměření se na druhy s vysokým ekologickým vlivem na původní společenstva. Pro posouzení a porovnání ekologického vlivu nepůvodních druhů byla v recentních studiích využita metoda založená na funkční odpovědi (FR), což je kvantifikace potravního chování a jeho efektivity při různých hustotách kořisti.

V kapitole 2 jsme zkoumali vliv environmentálních a demografických faktorů na distribuci druhového bohatství nepůvodní fauny v České republice. Zároveň jsme sestavili soubor map znázorňujících úroveň invaze nepůvodními druhy u šesti kategorií fauny v každém z 628 mapovacích kvadrátů (cca 12,0 × 11,1 km) pokrývajících Českou republiku. Vztahy mezi druhovou pestrostí a 12 faktory popisujícími klimatické podmínky, topografii, půdní pokryv a hustotu zalidnění byly vyhodnoceny pomocí metody GLM (zobecněné lineární modely). Druhové bohatství v kategoriích „všechny nepůvodní druhy“, „nepůvodní bezobratlí“ a „terestrické nepůvodní druhy“ bylo nejsilněji korelováno se vzrůstající průměrnou teplotou. Kategorie „nepůvodní druhy uvedené na černém a šedém seznamu (významné nepůvodní druhy)“ a „akvatické nepůvodní druhy“ byly nejčastěji dokumentovány ve velkých řekách nebo jejich okolí. Nejvyšší druhová pestrost nepůvodní fauny byla dokumentována ve velkých populačních centrech a v jejich okolí a také v zemědělsky obdělávané krajině v teplých a suchých nížinných oblastech. Vstupní bránu pro nepůvodní akvatické druhy představují především velké řeky.

Hlaváč černoústý *Neogobius melanostomus* (Pallas, 1814) a hlavačka poloměsíčitá *Proterorhinus semilunaris* (Heckel, 1837) jsou dva druhy bentické ichtyofauny, které se v posledních dekádách významně rozšířily mimo své původní areály. Oba druhy osídlily i několik řek v České republice, v nichž tvoří podstatnou část příbřežní ichtyofauny. Hlaváč černoústý i hlavačka poloměsíčitá představují závažnou hrozbu pro sladkovodní i brakické ekosystémy. Zároveň mají oba druhy škodlivý vliv na původní rybí společenstva, a to buď přímo predací jiker a plůdku, nebo nepřímo vlivem kompetice o potravní zdroje. Zatímco ekologický vliv hlaváče černoústého je dokumentován v řadě studií, vliv hlavačky poloměsíčité zatím není patřičně prozkoumán. V kapitolách 3 a 4 jsme kvantifikovali a porovnali potravní chování a efektivitu predace invazního hlaváče černoústého a nepůvodní hlavačky poloměsíčité při dvou teplotních režimech (20 a 25 °C; kapitola 3) a ve třech různých habitatech (písek, kameny, kameny s umělou rostlinou; kapitola 4). Jako kořist byl použit plůdek kapra obecného *Cyprinus carpio*, Linnaeus, 1758.

Oba nepůvodní predátoři vykazovali funkční odpověď potravního chování II. typu. Při vnitrodruhovém srovnání nebyl u hlaváče černoústého ani hlavačky poloměsíčité prokázán žádný signifikantní rozdíl mezi teplotními režimy u obou sledovaných parametrů funkční odpovědi, tj. u efektivity při vyhledávání kořisti a u doby zpracování kořisti. To naznačuje široké teplotní optimum obou druhů. Hlavačka poloměsíčitá projevila mírně vyšší efektivitu vyhledávání kořisti při 20 °C v porovnání s hlaváčem černoústým. Doba zpracování kořisti se však mezi predátory nelišila. To ukazuje na stejný ekologický vliv *per capita* při vysokých hustotách kořisti. Hlavačka poloměsíčitá také prokázala nižší hodnoty maximálního příjmu potravy při 25 °C v porovnání s 20 °C a s hlaváčem černoústým při obou teplotních režimech. To svědčí o nižším teplotním optimu hlavačky v porovnání s hlaváčem.

V kapitole 4 byla zjištěna stejná doba zpracování kořisti na kamenitém substrátu a na kamenech s umělou rostlinou. To naznačuje stejný ekologický vliv *per capita* na tvrdých substrátech jak u hlaváče černoústého, tak u hlavačky poloměsíčité. Při vnitrodruhovém srovnání projevili oba predátoři nejnižší dobu zpracování kořisti na kamenitém substrátu. To se pak odráželo také ve větším maximálním příjmu potravy v tomto habitatu. Z toho vyplývá, že ekologický vliv obou predátorů v kamenitém prostředí je vyšší. Hlaváč černoústý prokázal vyšší efektivitu při vyhledávání kořisti v písečném habitatu v porovnání s hlavačkou poloměsíčitou, zatímco v ostatních habitatech nebyly dokumentovány žádné významné rozdíly.

V souhrnu, oba studovaní nepůvodní predátoři prokázali značnou žravost (díky zdokumentovaným vysokým hodnotám maximálního příjmu potravy) a reálný potenciál negativního ovlivnění početních stavů původních rybích společenstev. Naše výsledky také ukazují na nutnost komplexních akcí při managementu biologických invazí, protože eliminace jednoho invazního druhu (hlaváče černoústého) může zcela reálně nastartovat populační růst jiného nepůvodního druhu (hlavačky poloměsíčité), který nebyl do té doby považován za invazní.

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- MoBI-aqua: Cross border monitoring of biological invasions as a tool for freshwater biodiversity conservation (100314623, program of cross-border cooperation with Free State of Saxony; Interreg VA/2014–2020) (project coordinator at FFPW USB: Miloš Buřič, Ph.D.)

LIST OF PUBLICATIONS

Peer-reviewed journals with IF

Gebauer, R., Divíšek, J., Buřič, M., Večeřa, M., Kouba, A., Drozd, B., 2018. Distribution of alien animal species richness in the Czech Republic. Ecology and Evolution 8 (9): 4455–4464. DOI:10.1002/ece3.4008. (IF 2016 = 2.440)

Gebauer, R., Veselý, L., Kouba, A., Buřič, M., Drozd, B., 2018. Forecasting impact of existing and emerging invasive gobiids under temperature change using comparative functional responses. Aquatic Invasions 13 (2): 289–297. https://doi.org/10.3391/ai.2018.13.2.09. (IF 2016 = 2.069)

Abstracts and conference proceedings

Gebauer, R., Divíšek, J., Buřič, M., Večeřa, M., Kouba, A., Drozd, B., 2017. Aquaculture industry as an important vector of alien aquatic species richness in the Czech Republic. In: EAS (eds.), Aquaculture Europe 2017 Abstracts, Dubrovnik, Croatia, October 17–20, 2017, pp. 1289–1290 (Poster)

Gebauer, R., Veselý, L., Kouba, A., Buřič, M., Drozd, B., 2017. Inconspicuous threat: Comparison of foraging pattern of two non-indigenous gobiid fishes in a simple predator-prey system. In: EFFS (eds.), 10th Symposium for European Freshwater Sciences Abstract book, Olomouc, Czech Republic, July 2–7, 2017, p. 41 (Poster)

Gebauer, R., Dvořák, P., 2014. Monitoring plůdkových společenstev ve vybraných tocích na Moravě. In: Kouřil, J., Podhorec, P., Dvořáková, Z. (Eds.), XIV. česká rybářská a ichtyologická konference, Sborník abstraktů, Vodňany, Česká republika, October 1–3, 2014, p. 45 (Poster)

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Basic of scientific communication	2015
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Seminar days of FFPW	2015 2016 2017 2018
International conferences	**Year**
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Gebauer, R., Veselý, L., Kouba, A., Buřič, M., Drozd, B., 2017. Inconspicuous threat: Comparison of foraging pattern of two non-indigenous gobiid fishes in a simple predator-prey system. In: EFFS (eds.), 10th Symposium for European Freshwater Sciences Abstract book, Olomouc, Czech Republic, July 2–7, 2017, 41.	2017
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Dr. Susanne Worischka, Institute of Hydrobiology, Technical University Dresden, Germany (1 month, population genetics of round goby *Neogobius melanostomus* from different basins)	2017

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Lecturing of students of bachelor study, Ecology, FFPW USB, in range of 32 teaching hours	2015–2017
Lecturing of students of bachelor study, Zoology, FFPW USB, in range of 32 teaching hours	2015–2017
Lecturing of field excursion with student from Yspertal in range of 26 teaching hours	2015–2018
Supervision of one B.Sc. thesis	2017
Concultancy of three B.Sc. theses	2017–2018
Leading of student project entitled Shelter competition in two non-indigenous benthic fish species	2017
Announcing the project entitled Interactions and foraging behavior of *Neogobius melanostomus* and *Proterorhinus semilunaris* in multiple predator system within International fishery summer school	2018

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COMPLETED COURSES

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12/11 2015	Manipulation with hazardous chemical substances and compounds, Prague, Czech Republic
12/02–16/02 2015	Basics of scientific comunicatiion Faculty of Fisheries and Protection of Waters, University of South Bohemia, Vodňany, Czech Republic

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