



Fish predation on sympatric and allopatric prey—A case study of Ponto-Caspian gobies, European bullhead and amphipods



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ABSTRACT

Due to the increasing number of biological invasions, more and more non-native species become components of already existing food chains and new interactions develop within communities. In our study, we checked whether (1) the predation preferences depended on sympatric or allopatric occurrence of predator and prey (a predator may choose the well-known prey or rather benefit from the naïvety of the novel one) and (2) fish preferences depended on prey susceptibility to fish predation (ability to hide, active predator avoidance) and/or on its palatability. We studied foraging efficiency of two species of Ponto-Caspian gobies (the round goby *Neogobius melanostomus* and tubenose goby *Proterorhinus semilunaris*) and the European bullhead *Cottus gobio* on two species of amphipods—Ponto-Caspian *Dikerogammarus villosus* and non-invasive *Gammarus fossarum*, occurring in Central and Western Europe. The gammarids were offered to fish with or without shelters and as mobile individuals or immobilized to test the effect of their hiding ability, mobility and palatability on fish predation. Fish selectivity was exhibited only in trials with motile prey, where all tested predators preferred *G. fossarum* over *D. villosus*, showing that their selectivity was independent of prey origin. No selectivity was observed for immobilized amphipods. When shelters were present, the predation was lowest. Thus, predator preferences depended on prey behavioural traits (effective shelter utilization and/or activity reduction) rather than on their palatability. Effective predator preference of *G. fossarum* over *D. villosus* may be one of the reasons of the successful invasion of the latter to the European inland waters.

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1. Introduction

Species remaining in trophic relations, e.g. predator and prey, after a long coexistence learn how to recognize one another and develop appropriate survival strategies. Nowadays, due to the increasing number of biological invasions (Vitousek et al., 1997; Gherardi, 2007), both predator and prey encounter not only familiar species but also novel organisms. When established and then integrated, exotic species become components of already existing food chains and new interactions develop within the community (Vermeij, 1996; Gherardi, 2006). Particularly non-native predators are known to have a significant impact on native assemblages and may contribute to species extinction (e.g. Williamson and Fitter,

1996; Cox and Lima, 2006; Salo et al., 2007). The “naïve prey” hypothesis suggests that the establishment of an alien predator and its substantial impact on local communities is promoted by the lack of a common evolutionary history shared between the predator and prey (Cox and Lima, 2006; Sih et al., 2010). Naïve prey may be incapable of recognizing an alien predator, which will result in the lack of antipredator behaviour or ineffective reactions. On the other hand, a non-native predator may turn out to be inefficient in foraging on novel prey due to the lack of an appropriate hunting strategy, or because of its similarity to native predators resulting in competition and/or efficient antipredator behaviour of prey (summarized in Sih et al., 2010). In such situation, the predator might benefit from the presence of sympatric prey, simultaneously expanding their range to the same novel area.

Moreover, alien species can also become a prey for native predators, which can benefit from the introduction of invasive species (Eckmann et al., 2008). In such situation invasive prey, which often dominates the community, becomes a major food item for

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predators, thus reducing the predatory pressure on native species (Rodríguez, 2006). However, Pintor and Byers (2015) showed that a native predator benefited most from the arrival of new prey when native food sources were still available and both prey sources could be utilised. On the other hand, such predators may also prefer to feed on native, sympatric prey due to their easier recognition and evolved foraging strategies.

A community consisting of benthic fish predators and gammarids is a suitable model to study reciprocal predator-prey interactions between organisms of different origin. Ponto-Caspian gobies are among most successful invasive benthic predators spreading in the European inland waters (Copp et al., 2005; Roche et al., 2013) as well as in the Laurentian Great Lakes (Ricciardi and MacIsaac, 2000; Ricciardi, 2001). Two of them, the round goby *Neogobius melanostomus* (Pallas, 1814) and the western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837) are regarded as the most expansive species among them (Roche et al., 2013). Expansion of alien gobies in Europe is accompanied by the invasion of amphipods of the same Ponto-Caspian origin, e.g. particularly widespread and invasive *Dikerogammarus villosus* (Sovinsky, 1894) (DAISIE, 2009; Rewicz et al., 2014). These crustaceans have dominated benthic communities in many major rivers and outnumbered native macroinvertebrates including local gammarids (e.g. Rewicz et al., 2015 and references cited therein), becoming valuable food resources for both indigenous (e.g. Rezsú and Specziár, 2006; Eckmann et al., 2008; own unpublished data) and alien fish species. The Ponto-Caspian gobies are a prominent example, often reported to forage on these amphipods in their non-native area (Grabowska and Grabowski, 2005; Borza et al., 2009; Schiphouwer, 2011; Borcharding et al., 2013; Brandner et al., 2013; Števo and Kováč, 2013). In smaller tributaries, where invasive amphipods are not present, but which have been successfully colonized by gobies, native amphipods such as *Gammarus fossarum* Koch in Panzer 1836, widespread in European lowlands (Goedmakers, 1972; Jazdzewski, 1975), may become their common prey. As we showed in our previous experimental study, the invasive racer goby *Babka gymnotrachelus* exhibited a strong preference for this native gammarid over the Ponto-Caspian amphipods, perhaps due to its softer cuticle (Błońska et al., 2015). These results are in contrast to the suggestions that the invasion of gobies was facilitated by the previous arrival of amphipods of the same origin (Schiphouwer, 2011; Brandner et al., 2013).

Though invasion routes and dispersal vectors of Ponto-Caspian goby species are similar, some of them differ in their habitat and ecological demands (Kakareko, 2011; Van Kessel et al., 2011). These differences may result in different exploitation of available resources e.g. variable food preferences (e.g. Grabowska and Grabowski, 2005; Schiphouwer, 2011; Brandner et al., 2013; Vašek et al., 2014). For the round goby, *D. villosus* constitutes a very important prey item in the Danube River, but it is not clear if this is caused by the effective hunting strategy of the fish because of the common evolution of these species, or is simply driven by the high abundance and availability of this particular amphipod in the local food resources. The selectivity of the round goby for native gammarids vs. alien species is not known. Also, the relationships of the western tubenose goby with amphipod prey of different origin were not studied. Furthermore, many local fish species, such as European cottids, may also feed on amphipods to a large extent (Kobler et al., 2012). The cottids resemble gobies in their foraging behaviour (Grabowska and Grabowski, 2005; Kakareko et al., 2013) and occasionally may co-occur with them (Jurajda et al., 2005; Von Landwüst, 2006; Kakareko et al., 2016). Again, it is not known which responses of these native predators to alien amphipod prey might be expected in the case of their co-occurrence and whether they would benefit or lose in the case of the replacement of native gammarids by the aliens. Nevertheless, the number of places where the

mentioned species coexist is still increasing in Europe. The upper part of the Vistula River, still inhabited by native *G. fossarum*, is under pressure of invasive *D. villosus* and tubenose goby, which may easily expand their range upstream the river. Both species are already present in the middle course of the river, where European bullhead also occur (own unpublished data). A similar situation can be observed in the Skrwa Prawa River (the right tributary of the Vistula River), where tubenose goby and bullhead are accompanied by *G. fossarum* (Jazdzewski et al., 2012; own unpublished data), and where the invasion of *D. villosus*, entering upstream this affluent from the Vistula River, is also possible.

In this study, we compared dietary behaviour between non-native and native species. Ponto-Caspian round and tubenose gobies (predators) and the amphipod *D. villosus* (prey) were compared with native European bullhead (*Cottus gobio*; predator) and the amphipod *G. fossarum* (prey). We aimed at answering the following questions: (1) Does the predation intensity depend on sympatric or allopatric origin of predator and prey, i.e. would the predator choose the well-known food source or rather benefit from the naïvety of the novel prey? (2) Do fish preferences depend on prey susceptibility to fish predation (ability to hide, active predator avoidance) and/or its palatability?

2. Materials and methods

2.1. Sampling and stock of studied animals

Experiments were conducted in the summer and early autumn of 2015. All the fish specimens were collected with electrofishing (IUP-12, Poznań, Poland and type EFGI 650, BSE Bretschneider Spezialelektornik, Germany). Round goby were sampled in the Radunia River (a left tributary of the Motława River, 18°38'E; 54°16'N), tubenose goby were caught from the Włocławski Reservoir (the lower Vistula River, 19°28'E; 52°35'N) and bullhead were captured from the Pilica River (the Vistula River tributary, 20°04'E; 51°53'N). The European bullhead is protected by law in Poland and all actions were carried out under permission of the local water tenants and Regional Directorate for Environmental Protection (L.dz. D/959/2015; WPN-II.6401.288.2015.KW2, respectively). The kick-sweep sampling technique with a hand D-net of 0.5 mm mesh size was used to collect amphipods: *D. villosus* from the Włocławski Reservoir (the same location as above) and *G. fossarum* from the Bzura River (a left tributary of the Vistula River, 19°27'E; 51°49'N). All animals were transported in aerated containers to the laboratory.

In the laboratory, the fish were segregated by species and stocked in 70-L aquaria (7–10 individuals per aquarium) with water exchanged via a circulating water system and aerated constantly, without any substrate, at a temperature of 22–24°C. Amphipods were also divided by species and held at 15°C in aerated 20-L containers equipped with pebbles and stones for *D. villosus* or decaying leaves for *G. fossarum*. The fish and *D. villosus* were fed every second day with living chironomid larvae, whereas *G. fossarum* was fed with decaying leaves. All animals were acclimated for at least one week to the same room temperature (22–24°C) before each experimental trial.

2.2. Experimental protocol

All experimental trials were conducted in aerated 10-L tanks (29 × 19 × 17 cm) at a room temperature (22–24°C) during daylight. Three different treatments were run for each fish species. In the first treatment (1), fish selection depending on the hiding abilities of gammarids was examined. The aquaria were equipped with a 1-cm layer of sand (grain diameter 0.5–1 mm), an artificial plant

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