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Running head: Invasive species

Title: Impact of invasive species on aquatic food webs

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1. Summary

The spreading of invasive species is still fostered through increased global trade and is considered an increasing threat to native biodiversity on a global scale, particularly in aquatic systems. While dispersal and establishment of invasion processes are well investigated in many cases, understanding the ecological impacts of invasive species is not as advanced. Since species invasion may cause complex interactions to modify, they can interfere with the effects of environmental factors and habitat complexity on the abundance or diversity level of the resident benthic community. Even though mechanistic knowledge about the field situation, like changes in food web structure, is essential to understand the impact of an invasion, knowledge of species interactions is often derived from laboratory experiments. Moreover, understanding the ecological impacts of invasive species – especially with regard to relevant food web interactions modified by invasive species – is not as advanced, probably also caused by the variety of taxonomic groups and invaded aquatic systems on a global scale. Here, we focus on selected species of four important groups of invasive vertebrate and invertebrate species (i.e. fish, crayfish, mussels and amphipods), giving an insight into potential changes of invasive species on the food web level. In our view, it is essential to thoroughly consider the relevance of food web interactions under field conditions to comprehend the mechanistic effects of invasive species in a changing aquatic environment.

2. Non-indigenous species in aquatic systems

Biological invasions have received increasing attention and are, besides the impact of climate change on ecosystems, one of the most considered ecological topics within the last decades. Since Elton's book 'The ecology of invasions by animals and plants' (Elton, 1958), which is credited with starting invasion ecology (Ricciardi and MacIsaac, 2008), numerous studies, reviews and books have been published on this topic (see Fig. 1). Due to ongoing new introduction processes, invasion biology remains a relevant topic in ecology.

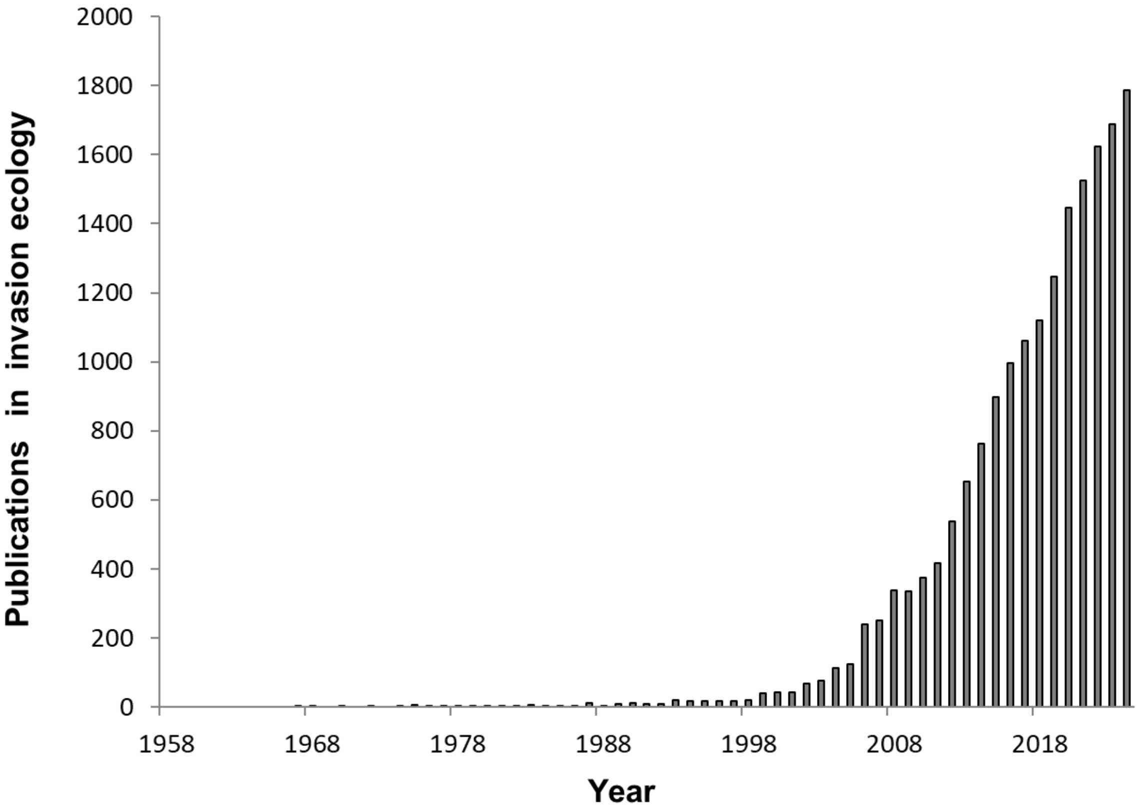

Figure 1 Number of publications per year in invasion ecology since the year of publication of the book *The ecology of invasions by animals and plants* by Charles S. Elton in 1958, which is regarded by Riccardi and MacIsaac (2008) as "The book that began invasion ecology". The literature search was done in the online research database PubMed using (invasi*) AND (ecolog*) on 2025-01-27.

Biological invasions have been described to run through different stages (e.g. Blackburn et al., 2014; Kolar and Lodge, 2001). Although the number and naming of stages differ among authors, the general process described consistently includes dispersal from one ecosystem to another, establishment in the new environment, and further spread. However, Davis (2009) stated that it is important to keep in mind that these stages are not distinct, but rather a continuous process. Hence, he suggested a concept of an ongoing series of cyclical iterations, with the two fundamental process stages dispersal and establishment. Being independent of the actual susceptibility of a new environment, the propagule pressure for the dispersal of a species is the initial and crucial step because, without the dispersal of individuals, an invasion is impossible. Even if propagules reach a new habitat, a successful invasion is not ensured, because arriving individuals need to establish themselves. In simplified terms, the establishment in a new environment can be defined as the successful reproduction and development of a stable population size over time. Theory predicts that the likelihood of a successful establishment in a new environment is high for species exhibiting fast growth and high reproduction rates as well as a great tolerance to abiotic environmental conditions as life-history traits (e.g. Grabowski et al., 2007; Kolar and Lodge, 2002). Further, Elton’s (1958) diversity-invasibility hypothesis predicted that species-rich ecosystems should have a higher resistance towards invasions because lowered resource availability decreases the probability of creating new ecological niches. However, the main drawback of this hypothesis is the prerequisites of stable and homogenous conditions, which are not fulfilled in most ecosystems in the long term (Davis, 2009).

An established founder population does not necessarily result in a stable population, as the persistence of an invasion process also requires the successful reproduction of subsequent generations. As the last step of a successful invasion, further spreading (i.e. further colonisation of new areas from a persistent population in an invaded area) of individuals to found additional (sub-)populations results from repeated successful dispersal and establishment as described above. Hence, spreading is an emerging property from the fundamental processes at the population level within an invasion process (Davis, 2009).

Furthermore, not every successful invasion of a non-indigenous species has a strong impact on the native community. Thus, only a proportion of non-indigenous species can be characterised as invasive, i.e. locally dominant and affecting the native community significantly (Colautti and MacIsaac, 2004).

Due to increased global trade, dispersal and establishment of non-indigenous species – as the fundamental processes of biological invasions – are more common, increasing the relevance of such species at a global scale (Sala et al., 2000). In river systems, for example, Schäfer et al. (2016) demonstrated that invasive species are important stressors besides habitat degradation and chemical pollution. In addition to the tremendous economic impact caused by biological invasions (e.g. Cuthbert et al., 2021; Fantle-Lepczyk et al., 2021), invasive species are an increasing threat to native biodiversity, particularly in freshwater systems (Chandra and Gerhardt, 2008; Sala et al., 2000). Within the last 200 years, freshwater systems have experienced invasions of non-indigenous species, especially in regions with intensive ocean and inland shipping, like North America and Central Europe (Bij de Vaate et al., 2002; Leuven et al., 2009; Panov et al., 2009; Ricciardi and MacIsaac, 2000). For example, the overall area of connected river catchments to the Rhine River system in Central Europe increased approximately tenfold by the year 2000, leading to its characterization as a ‘global highway’ for the dispersal of species (Leuven et al., 2009). Furthermore, ornamental trade, aquaculture or active stocking play an important role in the dispersal of species (Chucholl, 2013a; Hussner et al., 2010; Leuven et al., 2009; Nunes et al., 2015).

3. Impact of invasive animal species

While dispersal and establishment of invasive species are well investigated in many cases, understanding their ecological impacts is not as advanced, mainly because studies are more scattered based on case studies under specific local conditions (Simberloff et al., 2013). For marine systems, it has been proposed that the impact of invasive species is context-dependent in relation to the species identity, as well as species density (Thomsen et al., 2011). Gallardo et al. (2016) reviewed the impact of invasive species on freshwater ecosystems on a global scale. Independent of investigated habitat and experimental approach applied, the results of 151 screened studies demonstrated that aquatic invasive species generally have a strong negative effect on species abundance, but not on species diversity. This is probably caused by a time lag between an observed decrease in abundance and the complete displacement of native species resulting in a decrease in diversity (Gallardo et al., 2016). Despite well-known examples like the impact of the invasive Nile Perch (*Lates* sp.) in Lake Victoria, which led to the extirpation of about more than 200 species (Witte et al., 1992), proven local or even global extinction events caused by an invasion process are rare. More commonly, coexistence due to niche partitioning is observed (e.g. MacNeil, 2019; MacNeil et al., 2001; Palmer and Ricciardi, 2005; Priddis et al., 2009). Coexistence between native and invasive freshwater species might also be fostered by spatial heterogeneity of physical conditions like flow disturbances (Boddy and McIntosh, 2021). On the other hand, species invasion can also affect environmental conditions like water turbidity, nitrogen and organic matter concentration, indicating the capability of invaders to transform their new environment (Gallardo et al., 2016) and hence probably act as ecosystem engineers.

Since invasion of non-predators or omnivorous species can cause complex modifications in species interaction and food web structure (e.g. Verstijnen et al., 2019), effects on the abundance or diversity of the resident benthic community might interfere with effects of environmental factors. However, as trophic interactions are essential for structuring communities, a key factor to gain mechanistic knowledge on the impact of invasive species is the investigation of their trophic relationships and subsequent changes in the food web (Hardy et al., 2010). For marine habitats, a mechanistic understanding of how habitat attributes modify invasion impacts is just at the beginning (Thomsen et al., 2011). This also holds true for freshwater benthic habitats, which are highly patchy with large variations of structural complexity.

Here, we highlight the potential of linking invasion biology with community structure and food web analyses based on selected species from different taxonomic groups and feeding strategies. We choose representatives for invasive fish, crayfish, amphipods and mussels, which are of concern in freshwater ecosystems on several continents (see Fig. 2). The impact of an invader on different functional groups of the resident community can strongly depend on the trophic position of the respective invader (Gallardo et al., 2016). Hereby, omnivory is an important part of natural food webs and high levels of omnivory are supposed to weaken trophic interaction strength and therefore stabilise food webs (Brönmark et al., 1997; Granados et al., 2019), because classical top-down or bottom-up effects are diminished by the flexibility of food sources used. Moreover, the degree to which omnivores weaken the effects of trophic cascades may also depend on the species' impact on each trophic level. For example, the more a predator feeds across trophic levels (i.e., omnivory), the more likely trophic cascades will be diminished (Benkendorf and Whiteman, 2021). Hence, understanding food web structures plays a key role in understanding species diversity and is an important mechanism in defining community structures and patterns of energy flow (Thompson et al., 2012) and, therefore, also in understanding the mechanistic impact of invasive species.

From our point of view, investigating changes on the community or population level under field conditions is crucial to gain knowledge on the impact of stressors, which not only applies to invasive species. Furthermore, assessing the relevant biotic interactions, particularly under natural field conditions, appears to be the most realistic approach to derive hypotheses about underlying mechanisms for observed changes at the community level (e.g. Bonsall and Hassell, 2005; Carpenter et al., 1995; Lindenmayer et al., 2012). However, the complexity of biotic and abiotic environmental conditions may often reduce the validity of field studies, e.g.

due to insufficient duration and replication, and therefore their potential to highlight the relevant food web interactions for the observed effect at the community level (e.g. Bonsall and Hassell, 2005; Carpenter et al., 1995; Englund and Leonardsson, 2008).

a) *Neogobius melanostomus* (Pallas, 1814)

b) *Procambarus clarkii* (Girard, 1852)

c) *Dikerogammarus villosus* (Sowinsky, 1894)

d) *Dreissena polymorpha* (Pallas, 1771)

Figure 2 Selected invasive species of larger concern with a well-studied food web impact that represent invasive a) fish, b) crayfish, c) amphipods and d) mussels. Photographs by Karsten Grabow.

3.1 Fish

The number of introduced fish species is still growing as intentional (e.g., by releasing aquarium fish, stocking) or unintentional introductions (e.g. via ballast water) continue. The number of invasive fish species estimated to be present in Europe in 2024 is 264 (Roy et al., 2020), with diverse geographical origins. The consequences on existing food webs and trophic interactions within an ecosystem are determined by their feeding mode and, thus, their trophic position. Most of the introduced species are omnivorous and have intermediate trophic positions or are carnivorous and have top trophic positions (Cucherousset and Olden, 2011). Hence, top-down effects on native species are to be expected if predatory fish invade the food web. The exerted direct predation is the predominant mechanism by which invaders can dramatically decrease populations of indigenous species or even cause their extinction (Jackson et al., 2017b). Bottom-up effects can be expected if invasive fish occupy intermediate or low trophic positions, and native species at higher trophic levels may change their diet to exploit them. Hence, invasive species represent a new, often abundant resource to local predators or parasites (David et al., 2017).

Aside from such direct effects, indirect food web effects such as apparent competition and resource competition with native species are some of the most well-described impacts. For example, two invasive bass species (smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*)) compete with native lake trout (*Salvelinus namaycush*) for prey fish in lakes in North America, and the resources available to lake trout have declined. This caused a shift in the trophic position of lake trout as they were forced to forage on macroinvertebrates (Vander Zanden et al., 1999). Apparent competition between non-native and native fish can also have broader ecosystem effects, impacting resource subsidies across ecosystem boundaries. For example, the foraging of non-native rainbow trout (*Oncorhynchus mykiss*) on terrestrial prey that fell into the stream altered the foraging behaviour of native Dolly Varden trout (*Salvelinus malma*) in northern Japan (Baxter et al., 2007). This change in behaviour forced the Dolly Varden trout to forage alternatively on benthic macroinvertebrate grazers, which in turn reduced the number of emerging insects and the density of forest consumers like spiders that relied on these aquatic subsidies (Baxter et al., 2004). A further example of how non-native fish invasions impact food webs of adjacent ecosystems is the invasion of lake trout (*Salvelinus namaycush*) into freshwaters of the Greater Yellowstone ecosystem and the concomitant decline of native cutthroat trout (*Oncorhynchus clarkii*) (Middleton et al., 2013).

Cutthroat trout constitutes an important dietary item of grizzly bears, which shifted their diet from trout to elk calves, following declines in cutthroat trout populations.

Despite such prominent effects of fish invasions, studies on food web impacts are available for only a few invasive species. As one of the best-described examples, changes in food web structures caused by the round goby (*Neogobius melanostomus*; Fig. 2a) are well studied. The round goby is a small bottom-living fish native to the Ponto-Caspian region. The species was first discovered in the Baltic Sea in 1990 and was most likely introduced via the ballast water of ships travelling through canals connecting the Black and Caspian Seas to the Baltic Sea (Sapota and Skóra, 2005). Since then, a rapid range expansion has occurred throughout all major European waterways as well as freshwater ecosystems in North America (Barrett et al., 2017; Karatayev et al., 2022). The latest invasion in Europe has been reported from the Elbe River (Germany), where a simultaneous invasion from upstream reaches in the Czech Republic and from downstream near the mouth of the Northern Sea was found (Nogueira Tavares et al., 2020). This invasion pattern was surprising because 600 river km between the upstream and downstream populations were not colonized. Additionally, the upstream sections of the Elbe River are isolated from other waterways that would allow for the spread of round gobies. In terms of ecology, round goby prefers solid substrates (Kornis et al., 2012) and colonised engineered shore structures such as rip rap, which are abundant in European navigable waterways. Once established, adverse effects on food webs in the invaded rivers have been reported. For example, the invasion of round goby exerts strong top-down effects on native freshwater mussels, threatening mussel populations of conservation concern (Clark et al., 2022). Declining filter-feeding mussel abundance may, in turn, affect the rate of benthic-pelagic coupling, but further research is needed. Round gobies have also been documented to affect populations of other native macroinvertebrates such as Crustacea, Ephemeroptera, and Odonata (Mikl et al., 2017), but also non-native macroinvertebrates such as *Corbicula* sp., *Dreissena* sp. or *Dikerogammarus villosus* (Beggel et al., 2016; Borcherding et al., 2013). The strength of the top-down effects depends on gobies' size distribution (Hirsch et al., 2016), invasion stage (Nogueira Tavares et al., 2020) and habitat availability (Kornis et al., 2012).

Direct top-down effects on native fish are rather rarely observed due to gobies' smaller body size compared to native competitors, but round gobies have been reported to prey on egg masses or young-of-the-year populations, affecting native fish populations (Kornis et al., 2012). Conversely, gobies' small size makes them susceptible to top-down control by native predators such as zander (Hempel et al., 2016) or perch (Almqvist et al., 2010). More important is resource competition and round gobies share a diet with several native fish, such as European perch (*Perca fluviatilis*) and burbot (*Lota lota*) (Grabowska et al., 2023; Skora and Rzeznik, 2001). Moreover, diets of round gobies overlap with other non-native gobies such as tubenose goby (*Proterorhinus seminularis*), bighead goby (*Ponticola kessleri*), and monkey goby (*Neogobius fluviatilis*) (Borcherding et al., 2013) but these other goby species can adapt habitat use and foraging patterns to avoid or limit competition with round goby (Grabowska et al., 2023). Nevertheless, Borcherding et al. (2013) reported decreasing body conditions with increasing non-native goby communities and suggested that the continued invasion of the Rhine River approached or even reached the carrying capacity of the river.

3.2 Crayfish

Through various pathways, including aquaculture and aquarium trade, crayfish belong to one of the most widely introduced freshwater taxa (Gherardi, 2010). In Europe, at least seven alien crayfish species are considered to be of Union concern by the European Invasive Alien Species Regulation (Regulation (EU) 1143/2014), of which six originate from North America (*Faxonius rusticus, Procambarus clarkii, P. virginalis, Pacifastacus leniusculus, F. limosus and F. virillis*) and one from Australia (*Cherax destructor*). Although variable in detailed type (i.e. which native species are affected in which manner) or strength of their effects, all invasive crayfish can have strong negative ecological impacts on invaded ecosystems, with effects being strikingly consistent among introduced species (Twardochleb et al., 2013). As opportunistic omnivores, most invasive crayfish occupy a central position in food webs of invaded systems strongly interacting with various trophic levels (e,g, Geiger et al., 2005; Kreps et al., 2016; Linzmaier et al., 2020). Their ecological effects are documented from more than three decades of case studies and have been quantitatively synthesised by Twardochleb et al. (2013) to identify generalised effects on recipient systems. Acting as ecosystem engineers, invasive crayfish increase leaf-litter breakdown and nutrient cycling in streams (e.g. Bobeldyk and Lamberti, 2008; Charlebois and Lamberti, 1996), reduce benthic algae and macrophytes cover by their burrowing and grazing (Feminella and Resh, 1989; Matsuzaki et al., 2009) and decouple energy flows between habitats (Kreps et al., 2016). In case of direct predation, invasive crayfish reduce not only the abundance and diversity of native invertebrates (e.g. Correia and Anastácio, 2008; Jackson et al., 2016) but also amphibian populations (e.g. Cruz and Rebelo, 2005; Gamradt et al., 1997). Furthermore, invasion of crayfish can lead to declines in fish abundance due to direct predation, competition for shelter as well as indirect competition for prey (reviewed by Reynolds, 2011). In their synthesis, Twardochleb et al. (2013) found that alien crayfish had strong negative effects across the food web, exhibiting larger effects on algae, fish, and aquatic invertebrates, in particular snails, than native crayfish. Strong negative effects of invasive crayfish on macrophyte abundance and biomass, coupled with their effects on snails are suggested to potentially lead to trophic cascades and shifts from macrophyte- to algae-dominated systems (e.g. Lodge et al., 1994; Twardochleb et al., 2013).

As a case study for invasive crayfish, we focus in more detail on the red swamp crayfish, *Procambarus clarkii* (Fig. 2b), one of the most widely introduced freshwater species in the world (Souty-Grosset et al., 2016). Native to north-eastern Mexico and southern USA, *P. clarkii* is nowadays present in at least 40 countries of 4 continents (Oficialdegui et al., 2020).

While most introductions of other invertebrates were accidental (García-Berthou et al., 2007), *P. clarkii* was initially introduced intentionally for commercial reasons, either to be bred and consumed as food (Hobbs et al., 1989) or traded as a pet for aquaria (Chucholl, 2013a; Faulkes, 2015). In Europe, the species was first brought to Spain in 1973 from Louisiana (USA) for aquaculture (Habsburgo-Lorena, 1978) and has rapidly spread across Europe after escaping (Souty-Grosset et al., 2016), nowadays established in 14 European countries (Oficialdegui et al., 2020).

From their natural habitats in Louisiana, a dominant herbivorous feeding of *P. clarkii* is well documented (Geiger et al., 2005) and case studies from areas invaded by the species have shown strong negative effects of *P. clarkii* on primary producers (macrophytes) caused by direct consumption and/or by their plant clipping and uprooting (e.g. Anastácio et al., 2005; Gherardi and Acquistapace, 2007; Rodríguez et al., 2003). For example, in situ experiments detected a low amount of animal matter in gut contents of *P. clarkii* and showed that an exclusion of crayfish led to a six-fold increase in macrophytes. The results thus revealed evidence of *P. clarkii* reducing the biomass of the macrophytes *Potamogeton pectinatus* in the Coyote Hills marshes in California apparently via direct consumption of plants (Feminella and Resh, 1989). Apart from direct effects, the benthic feeding of *P. clarkii* can also indirectly affect macrophytes. For instance, resuspension of sediment by their feeding can lead to increased nutrient release resulting in increased turbidity and nutrient content reducing light availability for macrophytes (Angeler et al., 2001). Furthermore, *P. clarkii* has been shown to affect basal resources inter alia by direct consumption of leaf litter (Carvalho et al., 2016). Hence, by reducing basal resources, *P. clarkii* can also affect primary invertebrate consumers, especially grazers.

Since the red swamp crayfish is described as an omnivorous species (Carvalho et al., 2016; Chucholl, 2013b), also direct as well as indirect effects on higher trophic levels (i.e., other than primary resources and consumers) by predation or competition are indicated. In experimental settings, *P. clarkii* has also been shown to directly prey mainly on aquatic invertebrates, preferentially arthropods and gastropods (reviewed by Momot, 1995), but also on tadpoles (e.g. Cruz and Rebelo, 2005) and fish (reviewed by Reynolds, 2011), even despite high occurrences of plant material and detritus (Gutiérrez-Yurrita et al., 1998). Furthermore, stable isotope studies showed strong resource overlap between *P. clarkii* and various other native and alien invertebrates, indicating the potential for competition effects (e.g. Cicala et al., 2023; Haubrock et al., 2019; Wu et al., 2022) possibly leading to their decline. The reduction of invertebrates, however, can, in turn, have indirect cascading effects on other trophic levels. For instance, the predation on important grazers, such as snails, by crayfish may lead to increased abundance of benthic algae due to reduced grazing pressure (top-down effect) (e.g. Jackson et al., 2014) and thereby induce a trophic cascade in littoral food webs (Gherardi and Acquistapace, 2007).

Besides acting as a predator or competitor in invaded food webs, *P. clarkii* is a potential prey for fish (e.g. García-Berthou, 2002), birds and mammals (e.g. Correia, 2001), thus itself represents a new resource for higher trophic levels (bottom-up effect) in invaded systems. For example, in some invaded systems, *P. clarkii* is now the most important food source for several fish species (e.g. Elvira et al., 1996; García-Berthou, 2002). Then again, *P. clarkii*, also frequently being shown to use detritus and sediment grains with their attached microorganisms as food sources (e.g. Geiger et al., 2004), also makes the detrital energy pool directly available to higher trophic levels thereby shortening the energy pathway.

However, the trophic ecology of *P. clarkii* is not only subject to ontogenetic shifts (Chucholl, 2013b), but also appears to be influenced by inter alia seasonal variations (e.g. He et al., 2021) or population size as well as size or productivity of the inhabited system. Jackson et al. (2017a), for instance, observed that the trophic position and niche width of *P. clarkii* decreased with increasing crayfish abundance. Furthermore, in lakes with low productivity, the trophic position of *P. clarkii* was found to increase with body size, whereas, in more productive lakes, the trophic position decreased with body size (Jackson et al., 2017a). The authors emphasise the importance of characterising the diet of *P. clarkii* across its non-native distribution and across environmental gradients as variation in its diet influences which species in the food web and ecosystem processes will be affected by its invasion. Consequently, in order to gain a more comprehensive understanding of the influence of *P. clarkii* on the food webs of invaded ecosystems, future research should consider the intricate and mutually reinforcing relationships between invasion success, trophic ecology and the diverse environmental conditions that prevail in these ecosystems.

3.3 Amphipods

In general, amphipods are a major part of the benthic food web, especially in riverine ecosystems and as mostly omnivores, they play an important role in the flow of nutrients and energy to higher trophic levels (e.g. Bärlocher and Kendrick, 1973; Kelleher et al., 1998; MacNeil et al., 1997). In the last century, a high number of non-native amphipod species, mostly from North America and the Ponto-Caspian region, have been introduced to river systems, for example, in Europe, having a strong negative impact not only on native amphipods but also on the total benthic community structure (e.g. Bij de Vaate et al., 2002; Grabowski et al., 2007).

As a case study for invasive amphipods, we focus on the Ponto-Caspian amphipod *Dikerogammarus villosus* (Fig. 2c), which is one of the most impactful invasive aquatic species in Europe (e.g. Rewicz et al., 2014). After the Rhine-Danube-Canal was opened in 1992, the species colonised the Rhine River and spread rapidly into connected freshwater river systems (Bij de Vaate et al., 2002; Tittizer et al., 2000). Several field studies indicated a strong negative impact of this invader on the abundance of native invertebrates subsequent to the introduction of *D. villosus* (e.g. Dick and Platvoet, 2000; Gergs and Rothhaupt, 2015). However, indigenous gammarids often were not displaced completely, even several years after the introduction of *D. villosus*, and coexistence with the invader is facilitated along gradients of abiotic water quality parameters (Gergs et al., 2013; MacNeil, 2019) and underwater vegetation (Hesselschwerdt et al., 2008). More recent studies also provide evidence that the species' impact is not as strong in all cases or on all spatial scales (Hellmann et al., 2017; Koester et al., 2018). For example, even though there was a decline in abundance of the indigenous amphipod *Gammarus roeselii* in Lake Constance, no genetic impoverishment of the remaining population of the indigenous amphipod was detected (Gergs et al., 2019). Moreover, on a larger spatial scale of a river course, *D. villosus* was only one of nine relevant taxa that altogether reflected a large part of the variation in the benthic samples along the River Rhine system, and a combination of non-faunal environmental factors mainly structured the benthic community composition (Koester et al., 2018). Despite those studies, reviewing the variety of case studies under different environmental conditions and spatial scales is still needed for generalising this invasive species' impact (but see Rewicz et al., 2014).

A strong predatory potential (i.e. mainly intraguild predation [IGP]) of *D. villosus* found in small-scale laboratory experiments was suggested to be the responsible mechanism for the decrease in abundance of benthic invertebrates (especially of indigenous amphipods) in the field (Dick et al., 2002; e.g. Dick and Platvoet, 2000). Alternatively, in case the predatory potential is not of dominant importance under field conditions and *D. villosus* might be a strong competitor, interspecific exploitative competition with native species for a basal resource would result in an indirect negative effect of the invasive amphipod, leading to a decrease in abundance of native species. Even though laboratory experiments mentioned above provided hints for the relevance of predation in this case, only an investigation of the trophic annidation of *D. villosus* in the field enables the determination of the realised predatory potential. This would lead to detect which of the alternative interaction scenarios is most likely responsible for the observed decrease in abundance of native species. A study on the relevance of IGP towards other amphipod species at an invasion front of *D. villosus* in the Untere Lorze (Switzerland) using stable isotope and genetic gut content analyses revealed a strong overlap of the isotopic niches of *D. villosus* and native amphipods. Moreover, there was no direct evidence for intraguild predation, as DNA of native gammarid species was not detected in any gut content of the more than 60 analysed individuals of the invader (Koester and Gergs, 2014). Comparing different habitats, a trophic annidation of *D. villosus*, comparable to primary consumers, was detected at ten different sites along the River Rhine system, where the invasive amphipod had already been established for more than ten years (Koester et al., 2016). Furthermore, comparing two river food webs, *D. villosus* occupied a low trophic position in both systems indicating it likely functions as a primary consumer in the Elbe River or, at the most, as an omnivore with a high importance of herbivory, evaluated from the isotope mixing model SIAR, in the River Rhine (Hellmann et al., 2015). Based on these studies, *D. villosus* appears to exhibit a variable but mostly low predacious feeding behaviour under field conditions indicating that predation seems not to be the key factor responsible for the effect on benthic invertebrate communities and other factors might be of higher importance.

There are first indications that interspecific competition and/or apparent competition are potential mechanisms responsible for the displacement of native species (e.g. amphipod species) by *D. villosus*. The study of Beggel et al. (2016) supports the relevance of apparent competition by selective fish predation as a driver for the displacement of native species, as indicated by a higher susceptibility of the native *Gammarus pulex* compared with *D. villosus* to predation by the invasive goby *N. melanostomus*. Hence, this study provides evidence for synergistic effects of the two invasive Ponto-Caspian species as an underlying process contributing to species displacements during invasion processes. This is also supported by the preference and dominance of *D. villosus* towards stony habitats, which were also used by indigenous species (Hesselschwerdt et al., 2008; Mörtl et al., 2005). Hence, it is likely that the occurrence of *D. villosus* caused a habitat shift of native species, potentially increasing their predation risk to top predators like fish. However, further studies are needed to verify if such a case of apparent competition is also relevant under field conditions.

Studies investigating the non-predatory feeding strategy found the invasive *D. villosus* to lower leaf litter decomposition rates by reducing the shredding efficiency of resident gammarid species indirectly via non-consumptive effects, or directly by a lower feeding rate on leaf litter itself, potentially resulting in a propagating ecosystem effect by a decreased energy processing (Boeker and Geist, 2015; MacNeil et al., 2011; MacNeil and Briffa, 2019). However, other studies revealed that *D. villosus* can also exhibit a high leaf shredding efficiency, suggesting that this species may also play an important role in leaf litter decomposition (Bundschuh et al., 2013; Truhlar et al., 2014). Hence, there is increasing evidence that *D. villosus* is an omnivorous species with a flexible feeding strategy rather than solely a predator in the field, and several studies demonstrate that the species is also able to feed and grow on a variety of resources, including periphyton, leaf litter and biodeposited material of freshwater mussels (Gergs and Rothhaupt, 2008a; MacNeil et al., 2011; Platvoet et al., 2009; Worischka et al., 2018). The actual feeding strategy indicated by the measured trophic level can be highly variable in the field with regard to spatial scales, as well as to a potential ontogenetic shift (e.g. Haubrock et al., 2019; Hellmann et al., 2015; Mancini et al., 2021; Sahm et al., 2021). This opportunistic feeding behaviour of *D. villosus,* also indicated by different isotopic niche widths (Koester et al., 2016; Koester and Gergs, 2014), supports the assumption that the species is highly competitive. Moreover, *D. villosus* can also exhibit higher consumption rates than indigenous species (e.g. Truhlar et al., 2014; Worischka et al., 2018), potentially leading to the exploitation of relevant resources for native species. Hence, the potential high feeding rates, in combination with the flexibility in feeding strategy (Platvoet et al., 2009), obviously foster the success of the invader in newly invaded systems and support the assumption that omnivory can be important for structuring benthic food webs and communities as stated by Diehl (1993).

3.4 *Mussels*

Within the taxonomic group of the Bivalvia, dreissenid mussels (the zebra mussel *Dreissena polymorpha* (Fig. 2d) and the quagga mussel *Dreissena bugensis*) are the most harmful invasive species not only leading to ecological changes but also causing tremendous economic damage worldwide (e.g. Connelly et al., 2007; LePage, 1993). For the Laurentian Great Lakes in North America, the dreissenid introduction was characterised as one of the major factors for observed changes in the benthic community (Burlakova et al., 2024). Even though both species are originally located in the region of the Black Sea and the Caspian Sea, their invasion history was different. The dispersion of the zebra mussel over Europe started commonly from estuary regions in the early 19th century (Thienemann, 1950), whereas the species was first found in the Laurentian Lakes (North America) in 1988 (Hebert et al., 1989). The zebra mussel is now commonly distributed in Europe and North America often occurring in high densities (e.g. Kinzelbach, 1995; Stanczykowska, 1977; Stewart and Haynes, 1994). For the quagga mussel, the range expansion over Europe outside the Black Sea basin was documented since the early 1900s (Orlova et al., 2005, 2004), and the species was first found in the River Rhine system in Central Europe in 2007 (Martens et al., 2007; van der Velde and Platvoet, 2007). In the North American Great Lakes, the quagga mussel was already identified for the first time in 1991 (Spidle et al., 1994). Nowadays, dreissenid mussels are still a major part of the benthic community and play an important role in the food web of invaded systems (e.g. Burlakova et al., 2024; Karatayev et al., 2022; Sabel et al., 2024).

Invasive dreissenid mussels are well known to reduce phytoplankton productivity through their filtration activity, increasing water clarity but also reducing zooplankton populations indirectly (Fahnenstiel et al., 2010; Holland, 1993; Nicholls and Hopkins, 1993). Effects on the zooplankton can propagate further to planktivorous fishes shown for the pelagic feeding whitefish (*Coregonus* spp.), indicating that the species have been forced to more nearshore resource usage (e.g. Baer et al., 2022; Trumpickas et al., 2022). The increased light transmittance can further lead to the proliferation of rooted aquatic macrophytes (Skubinna et al., 1995). Filtration of zebra mussels is highly selective, mainly with particle size as a relevant factor leading to higher ingestion rates, but potentially also driven by chemical food quality (Naddafi et al., 2007; Ten Winkel and Davids, 1982). As a result, primary producers like cryptophytes and small-sized diatoms are preferentially ingested, whereas cyanobacteria and colony-forming diatoms and green algae are often expelled (Bastviken et al., 1998; Naddafi et al., 2007). The reduction of pelagic phytoplankton results in a changed nutrient cycling (Fahnenstiel et al., 2010; Li et al., 2021; Naddafi et al., 2008) and an accumulation of organic material in the benthic zone by the excretion of faeces and undigested pseudofaeces (i.e. biodeposited material) (e.g. Klerks et al., 1996; Stanczykowska et al., 1976; Stewart et al., 1998; Walz, 1978). Related to the seston concentration in the pelagic zone, biodeposition rates per mussel in the field were found to be highest during summer and can be in a magnitude comparable or even higher than benthic primary production (Gergs et al., 2011, 2009). Thus, dreissenid mussels mediate the benthic-pelagic coupling and can increase bioavailability of high-quality pelagic food particles to the benthic community (Gergs et al., 2009; Klerks et al., 1996; Roditi et al., 1997).

Several studies showed an increase in abundance of many invertebrate taxa, also leading to a higher benthic invertebrate alpha diversity after the invasion of dreissenid mussels, whereas a simultaneous decrease of beta diversity was found by increasing the evenness of the benthic habitat on the long-term (MacIsaac, 1996; Ozersky et al., 2011; Stewart and Haynes, 1994). Increased abundances of benthic invertebrates in the presence of dreissenid mussels were found to be due to two mechanisms. On the one hand, invertebrate species responded to the increased habitat structure provided by the mussel shells, but several taxa (e.g. amphipods and chironomids) additionally reacted with a preference towards living mussel suggesting a trophic relation as a response to filtration-mediated biodeposition of pelagic primary producers (e.g. Gergs and Rothhaupt, 2008b; Griffiths, 1993; Mörtl and Rothhaupt, 2003). Hence, it was assumed that the increased amount of organic material by the biodeposition activity of zebra mussels may be used as a new food source, leading to a biodeposition-based food web (Mitchell et al., 1996; Stewart and Haynes, 1994). In fact, in the laboratory chironomids and amphipods are able to grow on zebra mussel biodeposited material indicating the potential suitability of the food source (Gergs and Rothhaupt, 2008a; González and Burkart, 2004; Izvekova and Lvova-Katchanova, 1972). The contribution of this resource to the diet, at least for amphipods, was confirmed under field conditions using stable isotope analyses (Gergs et al., 2011; Limén et al., 2005; Verstijnen et al., 2019). Moreover, comparing the phases before and after the dreissenid invasion further revealed that pelagic material was, in general, of higher importance in the benthic food web of Lake Ontario in the presence of dreissenid mussels (Ozersky et al., 2012).

Besides providing food resources for benthic species via their filtration activity, dreissenid mussels can be a food resource for higher trophic levels, especially water birds and fish. Water birds like tufted duck *Aythya fuligula*, pochard *Aythya ferina* and coot *Fulica atra* are well known to feed on dreissenid mussels with a preference for larger individuals (e.g. Hamilton et al., 1994; Mitchell et al., 2000). However, predation rates can be highly variable depending on ice coverage during winter time, water depth, substrate or other factors (Mitchell et al., 2000; van Nes et al., 2008; Werner et al., 2005). For example, a reduction by predation of overwintering diving ducks of more than 90% of zebra mussel biomass in shallow areas was found in Lake Constance in Central Europe (Cleven and Frenzel, 1993; Werner et al., 2005). Thereafter zebra mussel population can recover to a comparable abundance and biomass by remaining juvenile (i.e., young of the year) mussels reproducing in the following summer (Cleven and Frenzel, 1993; Walz, 1973). Since dreissenid mussels became an important food source for overwintering water birds, their population responded to the occurrence of mussels on the one side by an increase of the total overwintering number of water birds after the invasion (e.g. by three to four times in Lake Constance; Stark et al., 1999) or on the other side in response to annual variations in mussel abundance (Hamilton et al., 1994).

Several fish species like ruffe (*Gymnocephalus cernuus*), tench (*Tinca tinca*), roach (*Rutilus rutilis*) or perch (*Perca* spp.) are known to consume dreissenid mussels, but also the round goby (*N. melanostomus*), itself an invasive species in many ecosystems invaded by dreissenid mussels. Such positive effect by the presence of dreissenid mussel can further propagate to higher trophic levels, i.e., piscivorous fish (Baer et al., 2022; Bethke et al., 2023; Vanderploeg et al., 2002; Verstijnen et al., 2019). As the round goby can be a strong competitor for food to native species (see also chapter 3.2), the altered trophic interactions were potentially linked to the decline in abundance of ruffe in Dutch reservoirs (Verstijnen et al., 2019). Such invader-invader trophic interaction might also be the case for dreissenid mussels and the invasive amphipod *D. villosus* because this species can use biodeposited material of zebra mussel as a food source (Gergs and Rothhaupt, 2008a). These are examples of the facilitation of one invasive species by another one, which is a step potentially contributing to an ‘invasional meltdown’ but does not itself constitute a meltdown (Simberloff, 2006; Simberloff and Von Holle, 1999).

Table 1 Synthesis table to summarize individual chapter information on food web effects of fish, crayfish, amphipods and mussels. Classification of the trophic impact of each species is divided into bottom-up, top-down, indirect effect or unknown. Specification of the trophic effect is described as positive (↑) or negative (↓) for native species.

Group	**Invasive taxon**	**Bottom-up**	**Top-down**	**Indirect trophic effect**	**Effect on native species**		**Reference**
Fish	*Micropterus dolomieu, Ambloplites rupestris*			X	↓	➢ Reduced trophic position of native competitor	Vander Zanden et al. (1999)
	Oncorhynchus mykiss			X	↓	➢ altered the foraging behaviour of native fish (*Salvelinus malma*) ➢ Reduced aquatic-terrestrial coupling	Baxter etl. (2004, 2007)
	Neogobius melanostomus	X	X		↓	➢ Reduction of invertebrate and fish abundance and biomass	e.g. Kornis et al. (2012), Clark et al. (2022), Mikl et al. (2017)
		X			↑	➢ Predation by fish (e.g. *Perca fluviatilis, Sander lucioperca*)	Hempel et al. (2016), Almqvist et al. (2010)
Crayfish	*Procambarus clarkii*		X	X	↓	➢ Reduction of the abundance and biomass of macrophytes	e.g. Feminella and Resh, 1989; Matsuzaki et al., 2009; Angeler et al., 2001; Anastácio et al., 2005
			X	X	↓	➢ Reduction of invertebrate abundance and biomass	e.g. Momot, 1995; Cicala et al., 2023; Haubrock et al., 2019
				X	↑	➢ Shortening of the energy pathway by making the detrital energy pool available through consumption of basal resources	e.g. Geiger et al., 2004; Carvalho et al., 2016
		X			↑	➢ Predation by fish ➢ Predation by birds ➢ Predation by mammals	e.g. García-Berthou, 2002; Correia, 2001
Amphipod	*Dikerogammarus villosus*	Mechanism under field situation not clear yet; contrasting results regarding feeding strategy and the importance of predacious behaviour			↓	➢ Reduction of the abundance of macroinvertebrate species	e.g. Dick and Platvoet, 2000; Rewicz et al. 2014; Gergs and Rothhaupt, 2015

			X		↓↑	➢ Contrasting results on leaf litter decomposition in comparison to native amphipod species	Boeker and Geist, 2015; MacNeil et al., 2011; MacNeil and Briffa, 2019; Bundschuh et al., 2013; Truhlar et al., 2014
Mussel	*Dreissena polymorpha / bugensis*		X		↓	➢ Reduction of phytoplankton biomass and seasonality by filtration	e.g. Fahnenstiel et al., 2010; Holland, 1993; Nicholls and Hopkins, 1993; Bastviken et al., 1998; Naddafi et al., 2007
				X	↓	➢ Reduction of zooplankton populations ➢ Change in resource utilization of planktivorous fish	e.g. Fahnenstiel et al., 2010; Baer et al., 2022; Trumpickas et al., 2022
		X			↑	➢ Increase of most benthic invertebrates due to biodeposition of pelagic organic material	e.g. Griffiths, 1993; Mörtl and Rothhaupt, 2003; Mitchell et al., 1996; Stewart and Haynes, 1994
		X			↑	➢ Predation by water birds and increase in their wintering abundances ➢ Predation by native as well as invasive fish	e.g. Hamilton et al., 1994; Mitchell et al., 2000; Cleven and Frenzel, 1993; Werner et al., 2005

4. Conclusion

Although biological invasions, particularly in freshwater systems, are considered an increasing threat to native biodiversity (Chandra and Gerhardt, 2008; Sala et al., 2000) and have received increasing attention over the last decades, mechanistic knowledge regarding the impact on community and food web structure of the invaders in general in the field is still largely unknown and often limited to case studies of single well-studied species. From our point of view, to further the mechanistic knowledge of the trophic impact, different perspectives need to be considered simultaneously. The autecological perspective should consider the trophic properties of an invasive species as important species characteristics and are the basal information. Moreover, the synecological importance of these autecological species characteristics is also dependent on ecosystem characteristics like available substrate, habitat connectivity, various environmental conditions such as light availability or temperature, and potential anthropogenic stressors. Hence, to gain knowledge on the trophic impact investigation of the relevance of an invader’s autecological capabilities under given complex biotic and abiotic conditions in the field is mandatory, which cannot be simulated in the laboratory. However, the existing knowledge is scattered across multiple local studies, focusses especially on a few species and is biased towards temperate ecosystems of the northern hemisphere. Therefore, we need to address at least three research questions concerning the success of invasions, management of invasive species, and predictions of future invasions. First, more empirical research is needed to determine whether non-native species are the cause of ecosystem degradation or merely a concurrent phenomenon. Our analysis indicates that most invasive species tend to colonize river reaches that are engineered and dominated by boulders. This raises the question of whether the prevalence of invasive species in degraded areas is due to the availability of niches, as native species may avoid these engineered reaches. Alternatively, invasive species might apply strong top-down pressures on native communities, thereby creating the necessary niche availability. Both of these potential mechanisms are suggested by the "passenger-driver hypothesis" (MacDougall and Turkington, 2005), but currently, there is no evidence available to determine which of these mechanisms is responsible for the establishment of invasive species. Nonetheless, conserving shallow, hydromorphologically diverse shores appears to be a promising strategy for maintaining high levels of diversity and functionality in native communities, while also potentially limiting niche opportunities for non-native species in human-altered riverine ecosystems. Secondly, what measures exist to control or even reduce non-native populations, and would invader eradication lead back to unaltered or even pristine food webs? Removal or trapping as a means to actively control non-native populations may primarily work for larger, conspicuous species (Hein et al., 2007) but may be ineffective for most invasive macroinvertebrates with smaller body sizes. Such species could be controlled by facilitating populations of native predators (Green and Grosholz, 2021). Despite some examples showing the success of food web control on non-native species (Adams and Marks, 2016; Hein et al., 2007), the efficiency and the lack of unwanted side effects still need to be demonstrated. A promising yet unexplored opportunity to control non-native populations is to restore engineered shorelines in navigable rivers. As outlined above, most non-native species prefer modified or engineered river reaches, and it remains to be tested if restoration of such reaches returns communities and food webs to the uninvaded state. Finally, can the existing knowledge be used to create a predictive framework for the impacts of invasive species on food webs, for instance, by grouping invaders by trophic position? Our synthesis in Table 1 shows that effects are rather species-specific and potentially caused by the taxonomic and, therefore also, autecological diversity of invasive species, even with the restriction on animal species. Moreover, it can be assumed that the effects in the field can also vary as a result of differences in environmental conditions. However, the synthesis also shows similarities between invasive species, such as positive bottom-up effects on native species while serving as prey organisms for native predators.

Addressing these questions and topics necessitates more targeted empirical research, including manipulative experiments and field surveys across the invasion range, to fully understand the functional impacts of invasive species. This would potentially allow a better generalisation of effects and lead to more precise recommendations for the management of invasive species not only in freshwater ecosystems.

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