

The depressed river mussel *Pseudanodonta complanata* as an occasional host for the European bitterling *Rhodeus amarus*

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Abstract – This study explores the utilisation of European freshwater mussels as hosts by the European bitterling (*Rhodeus amarus*) at their current sympatric occurrence range. Our study confirms *Pseudanodonta complanata* as a suitable, occasional host for bitterling. The spawning relationship of *R. amarus* with freshwater mussels has physiological costs for the hosts, leading to resource competition and potential negative effects on host fertility. Further research is needed to assess the dynamics of host-parasite interactions, mussel adaptations to prevent parasitism, and the consequences of the bitterling recent and possible future expansion in Europe for mussel populations.

Keywords: Species coexistence / reproductive strategies / host-parasite relationship / invasive species / threat

The European bitterling *Rhodeus amarus* (Bloch, 1782) is a freshwater fish that exhibits a spawning relationship with freshwater mussels. Females bitterling develop long ovipositors to place their eggs inside the gills of a mussel through its exhalant aperture. The male releases its sperm in front of the inhalant aperture, and the fertilised eggs subsequently complete their development inside the mussel gill, bitterling juveniles emerging after approximately a month (Smith *et al.*, 2004). Freshwater mussels require suitable fish hosts for the successful development of their own larvae, called glochidia. Depending on the mussel species, glochidia must spend time attached to a fish host to undergo metamorphosis into juvenile mussels and complete their life cycle, relying on food resources obtained from the host. Freshwater mussels employ a myriad of strategies to infest their hosts (Barnhart *et al.*, 2008; Modesto *et al.*, 2018) and some of them, such as *Unio crassus* Philipsson, 1788, have evolved species-specific behaviours to attract fish (Aldridge *et al.*, 2023). However, the roles of host and parasite in the relationship between freshwater mussels and bitterling have been shown to be variable, and can potentially be reversed (Reichard *et al.*, 2012). *R. amarus* is rarely a host for the glochidia of European freshwater mussels, and the presence of bitterling embryos in mussels is associated with physiological costs to the mussel

host (Smith *et al.*, 2001; Mills *et al.*, 2005; Prié, 2017; Methling *et al.*, 2019). Bitterling embryos compete with the mussel hosts for oxygen, damage the gills and disrupt filtration (Stadnichenko and Stadnichenko, 1980; Smith *et al.*, 2001), potentially also competing for nutrients (Spence and Smith, 2013). The presence of developing bitterling embryos in the gills may also adversely affect host growth (Reichard *et al.*, 2006). Therefore, the European bitterling should be regarded as a mussel parasite (Sousa *et al.*, 2020; Brian *et al.*, 2022). As such, the degree of historical coexistence between bitterling and mussel populations in Europe is crucial to the understanding of their relationship from an evolutionary viewpoint (Van Damme *et al.*, 2007).

Here, we report that a rare European unionid, *Pseudanodonta complanata* (Rossmässler, 1835), serves as a host for bitterling, and further discuss research directions to address the consequences for *P. complanata* and other mussel populations of the expansion of *R. amarus* in Europe. Until now, a single documented instance of *R. amarus* utilising *P. complanata* as a host is based on a specimen from the River Cam in the United Kingdom in 1995 (Smith *et al.*, 2004).

During a survey of the River Warta in Poland in July 2023, we examined 25 individuals of *P. complanata* and found one specimen that hosted a single bitterling embryo (visually identified) at the eyed stage (Fig. 1). We additionally checked for the presence of bitterling embryos in the other freshwater mussel species found at this site: for *Anodonta anatina*

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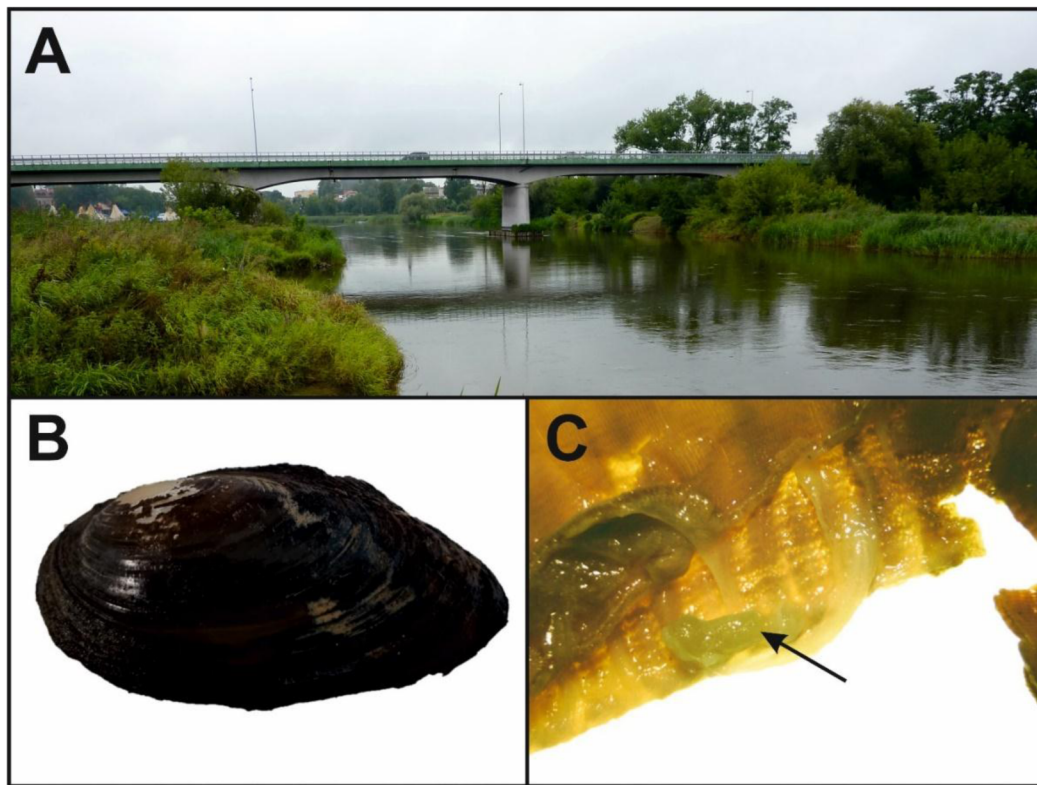


Fig. 1. A – Sampling site on the River Warta, Poland (coordinates: N 51.968589, E 18.793521; photo by G. Zięba); B – Shell of *Pseudanodonta complanata* infested by bitterling embryo (photo by D. Halabowski); C – The bitterling embryo in the gills of *P. complanata* (photo by D. Halabowski).

Table 1. Mussels utilised by bitterlings at the studied site.

| Species | Number of investigated mussels | Number of mussels used by bitterlings | Prevalence |
|---------------------------------|--------------------------------|---------------------------------------|------------|
| <i>Anodonta anatina</i> | 25 | 1 | 4% |
| <i>Pseudanodonta complanata</i> | 25 | 1 | 4% |
| <i>Unio pictorum</i> | 22 | 4 | 18% |
| <i>Unio tumidus</i> | 29 | 12 | 41% |

(Linnaeus, 1758), one individual contained a bitterling embryo, for *Unio pictorum* (Linnaeus, 1758) four individuals contained bitterling embryos and eggs, and for *U. tumidus* (Philipsson, 1788) 12 individuals contained bitterling embryos and eggs (Tab. 1). These results match previous studies, as it is known that *A. anatina*, *U. pictorum*, and *U. tumidus* are hosts for the European bitterling (Balon, 1962; Wiepkema, 1961; Reynolds *et al.*, 1997). Furthermore, it is also known to date that among co-occurring mussel species *U. crassus* (Tatoj *et al.*, 2017), *A. cygnea* (Linnaeus, 1758) (Reynolds *et al.*, 1997), *Pseudunio auricularius* (Spengler, 1793) (Soler *et al.*, 1999), *Microcondylaea bonellii* (Férussac, 1827) (Sousa *et al.*, 2020), *U. mancus* Lamarck, 1819, and *Potomida litoralis* (Cuvier, 1798) are suitable native European hosts for the European bitterling (Prié, 2017).

This study reinforces the hypothesis of Soler *et al.* (2019), stating that *Rhodeus amarus* can utilise all European unionid species within its current range, including rare European species as occasional hosts, including *Unio crassus*

(Tatoj *et al.*, 2017; Lewisch *et al.*, 2023) and *Pseudanodonta complanata* (Smith *et al.*, 2004; this study). However, despite their capacity for using a wide range of hosts, field and laboratory studies show that European bitterling are choosy about which species of freshwater mussel they use for oviposition (Balon, 1962; Aldridge, 1997; Kondo *et al.*, 1984; Smith *et al.*, 2000; Reichard *et al.*, 2010, 2015; Soler *et al.*, 2019; Sousa *et al.*, 2020). It has been demonstrated that both the number of previously laid eggs and mussel species affect oviposition decisions, although not the number of eggs laid by the female bitterling when oviposition occurs (Smith *et al.*, 2000). Smith *et al.* (2000) showed that among four mussel species (*Anodonta anatina*, *A. cygnea*, *U. tumidus*, *U. pictorum*), female bitterling can distinguish between host species and also the ‘quality’ of the host based on the number of previously laid eggs. *A. anatina* was the most frequently chosen species, while bitterling avoided spawning in *A. cygnea*, and relatively few *A. cygnea* released young bitterlings. Moreover, embryo mortality occurred at different

rates in different mussel species. Yet, in water bodies where only *A. cygnea* was present, bitterling readily utilised this species as a host. As a result, bitterling appear to select hosts depending on mussel availability, but modulate host preference based on temporal variation in mussel quality (Smith *et al.*, 2000). Therefore, in the presence of other species of freshwater mussels, *A. cygnea* and other rare mussel species are only occasional hosts for the European bitterling. This is consistent with our results as, while the relative abundance of *P. complanata* (22%) in our studied site was higher than for *U. pictorum* (18%), the latter was utilised more often by bitterlings.

The presence of *R. amarus* in Central and West Europe may be relatively recent (Reichard *et al.*, 2007; Van Damme *et al.*, 2007). A comprehensive study of historical records suggests a rapid expansion of *R. amarus* from the Pontic region (Van Damme *et al.*, 2007). Climate change has been identified as a significant factor influencing the spread of invasive fish species, as it can create favourable conditions for the establishment and expansion of invasive fish populations, including bitterling (Van Damme *et al.*, 2007; Rahel and Olden, 2008; Hellmann *et al.*, 2008). Additionally, intentional or accidental introductions of *R. amarus* to new regions cannot be excluded (*e.g.*, waterways connecting previously separated systems, releases by hobbyists and anglers). Considering the potential further expansion of *R. amarus* in Europe and its negative impact on the physiological condition of mussels, along with the threatened status of freshwater mussels in Europe (Lopes-Lima *et al.*, 2017; Sousa *et al.*, 2023), efforts to introduce or conserve *R. amarus* in some locations, especially in areas where mussels are endangered, should be discouraged. Indeed, a reconsideration of the protective status of *R. amarus* in Europe appears necessary (Van Damme *et al.*, 2007). For example, in Poland, where *R. amarus* is under partial protection (Regulation, 2016), *R. amarus* is the fourth most abundant fish species in inland waters (The Chief Inspectorate of Environmental Protection; Ichthyofaunal monitoring results from 2011–2022), its range expands and local populations steadily increase, making it the most abundant species among the protected freshwater fishes. In the Czech Republic, *R. amarus* is listed as a near-threatened species on the Red List (Lusk *et al.*, 2017) and, at the same time, is considered a non-native species (Barankiewicz *et al.*, 2021). Despite its expanding range in Europe, there is currently no evidence that *R. amarus* has contributed to the decline of freshwater mussel populations, though this may reflect a lack of appropriate research to address this question.

Although freshwater mussels have evolved to mitigate the impacts of parasitism by bitterling (Smith *et al.*, 2000; Reichard *et al.*, 2010), freshwater mussel species that have no exposure to bitterling may not have appropriate adaptive responses to cope with parasitism. Therefore, there is an urgent need to determine the potential threat to native mussels from *R. amarus* (Rouchet *et al.*, 2017; Sousa *et al.*, 2020), which may contribute to the conservation of European mussel species.

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