Knowl. Manag. Aquat. Ecosyst. 2025, 426, 4
© M. Pfeiffer *et al.*, Published by EDP Sciences 2025
https://doi.org/10.1051/kmae/2024026

www.kmae-journal.org

Knowledge & Management of Aquatic Ecosystems

Journal fully supported by Office français de la biodiversité

SHORT COMMUNICATION OPEN ACCESS

The Asian clam *Corbicula fluminea*, an accidental host for the European bitterling *Rhodeus amarus*

Michael Pfeiffer*, Manuel Mildner, Christian Patrick Günter and Magnus Leschner

Gobio, Weißerlenstraße 2, 79108 Freiburg-Hochdorf, Germany

Received: 16 November 2024 / Accepted: 20 December 2024

Abstract – European bitterling (*Rhodeus amarus*) embryonic development depends entirely on freshwater mussels of the family Unionidae as host. As almost all the six widespread European unionid mussel species are declining in Southwestern Germany, this could result in the loss of spawning habitats for *R. amarus* in the future. However, there is evidence even for a further expansion of this fish species in the Upper Rhine valley. As this expansion takes place in conjunction with a considerable spread of the non-indigenous freshwater mussel *Corbicula fluminea*, it is hypothesized that *C. fluminea* might also serve as a suitable host for *R. amarus*. Our study for the first time reports successful oviposition of *R. amarus* into *C. fluminea*. However, there is a lack of any evidence of bitterling embryo development in *C. fluminea*. In the presence of both *U. crassus* and *C. fluminea*, *R. amarus* exhibits a preference for unionid mussels for oviposition, prior to *C. fluminea*. Consequently, *C. fluminea* seems to be an accidental host for *R. amarus* and there seem to be other causes for its range expansion.

Keywords: Freshwater mussel / species coexistence / reproductive ecology / host preference / invasive species

The European bitterling (*Rhodeus amarus* (Bloch, 1782); hereafter simply referred to as bitterling unless otherwise specified) is the only bitterling species native to Central and West Europe (Kottelat and Freyhof, 2007). It has a unique strategy for reproduction: Bitterlings rely heavily on the presence of live freshwater mussels from the Unionoidea superfamily (mainly species from the Unionidae family, and to a lesser extent on bivalves from the Margaritiferidae family; reviewed in Smith *et al.*, 2004) for reproduction. Females use long ovipositors to deposit their eggs in the gills of a clam through the clam's exhalation siphon (Aldridge, 1999; Smith *et al.*, 2004). Bitterling embryonic development takes place inside the mussel, where the embryos remain for approximately one month.

Many of the 16 freshwater bivalves of the Unionoidea superfamily that occur naturally in Europe are in severe decline and are therefore considered highly endangered (Lopes-Lima *et al.*, 2017). Due to the unique spawning symbiosis between bitterlings and Unionid mussels, the distribution of European bitterlings should also be restricted in the absence of their hosts. However, it can be observed that the bitterlings distribution area in the Upper Rhine valley has continuously increased over the last decade, despite the steady decline of unionid mussel species in the same area (Dußling *et al.*, 2018; Büro Gobio, 2022). This contradictory trend is difficult to explain, given that the European bitterling is dependent on Unionid host mussels for its development.

Like the European bitterling, the East Asian freshwater mussel *Corbicula fluminea* (O. F. Müller, 1774) has also been steadily spreading into the Upper Rhine Valley since the late 19th century. Some bitterling species in Asia and Europe use freshwater mussels outside the Unionoidea superfamily. For example, the Asian bitterling *Sinorhodeus microlepis* is specialised in using only *C. fluminea* for sexual reproduction (Li *et al.*, 2017). As the cyprinid subfamily Acheilognathinae is mainly distributed in Asia (Fricke *et al.*, 2023), it is conceivable that there is a causal relationship between the mutual dispersal of *R. amarus* and *C. fluminea* in Europe. Although oviposition of *R. amarus* in the invasive zebra mussel *Dreissena polymorpha* was observed by Bartáková and Reichard (2017), breeding success has not been documented. It is currently unknown whether the genus *Corbicula* also serves as a host for the European bitterling.

We tested the theory that bitterlings select *Corbicula* as potential hosts for their progeny. Furthermore, it is not clear whether the evolved defences of Asian *Corbicula* against bitterling parasitism will also result in the successful expulsion of bitterling eggs and embryos. Theoretically, the bitterling offspring could successfully develop in *Corbicula* mussels.

To test our hypothesis, we kept European bitterlings and Asian *C. fluminea* together in a tank for several weeks and recorded their behaviour. Our experimental animals originate

*Corresponding author: pfeiffer@gobio-online.de

from an area where both species co-exist, the Dreisam-Glotter drainage in south-west Germany. Ten individuals of young European bitterling fishes were caught in the river Glotter in summer 2019. Specimens of *C. fluminea* were collected from Lake Moosweiher in January 2020. Both species were kept in a 50-litre tank. Bitterlings were fed daily with standard fish food. The bitterling's behaviour was recorded when clear signals for prespawning behaviour were observed, such as mussel inspection, head-down posture, skimming, sperm release, quivering, female leading of the male, and spawning. If oviposition was successful, the *C. fluminea* individuals were removed, opened, and inspected for bitterling eggs in the inner tissue of the clam using a stereomicroscope (Nikon SMZ 1500).

To determine the preferred host of *R. amarus* when coexisting, we combined two individuals of *U. crassus* and three individuals of *C. fluminea* with ten bitterlings from the Glotter river in a 50-litre tank. The *U. crassus* and *C. fluminea* individuals were collected in April 2020 from the Krebsenbächle stream in the north of Freiburg. This location was chosen because *R. amarus* is absent, ensuring that no mussels were already infected with bitterling eggs. Once again, the behaviour of the bitterlings was recorded when clear signals of pre-spawning behaviour were observed.

Another experiment investigated the host preferences of *R. amarus* in their natural environment. The Schutter and the Herrenmühlebach are two rivers in the Upper Rhine Valley where live specimens of *C. fluminea*, *R. amarus*, and the thick-shelled river mussel (*Unio crassus*) coexist. Thus, bitterlings can use either *U. crassus* or *C. fluminea* as a host at both locations. In April and May, the bitterling fish were in their mating season, as indicated by their bright nuptial coloration. It is likely that the bitterlings have already deposited their eggs in their host mussel.

In April 2020, we collected 47 living *C. fluminea* from the Schutter. In May 2020, a further 18 *C. fluminea* individuals were taken from the Herrenmühlebach. In the laboratory, the collected *C. fluminea* individuals were opened and examined for bitterling eggs or embryos in the inner tissue of the mussel. In April 2020, we collected one individual of *U. crassus* from the Schutter. The two valves were carefully opened on-site without causing any damage. The inner tissue was examined for bitterling eggs or embryos, and subsequently, *U. crassus* was returned to the Schutter.

Shortly after the fish were placed in the aquarium, the male bitterlings developed their nuptial colouration. This change in colour persisted for several weeks even in the absence of a host clam. Subsequently, males showed mating behaviour (males frequently chasing females), albeit with a reduced spectrum. Female bitterlings also developed an ovipositor, but it was regularly retracted and not ready to spawn.

Shortly after placing *C. fluminea* individuals in the aquarium, both male and female bitterlings approached the clams and examined them by facing the siphons (head down posture); see supplementary video). Soon after, the female ovipositor extended to its maximum length. Both sexes showed clear signals of pre-spawning behaviour as described in Duyvené de Witt (1955) and Wiepkema (1961):

1. quivering of the male in front of the female,
2. frequent pursuance of females by males,
3. male leading the female to the mussel,
4. skimming (male and female dip forward frequently over the mussel).

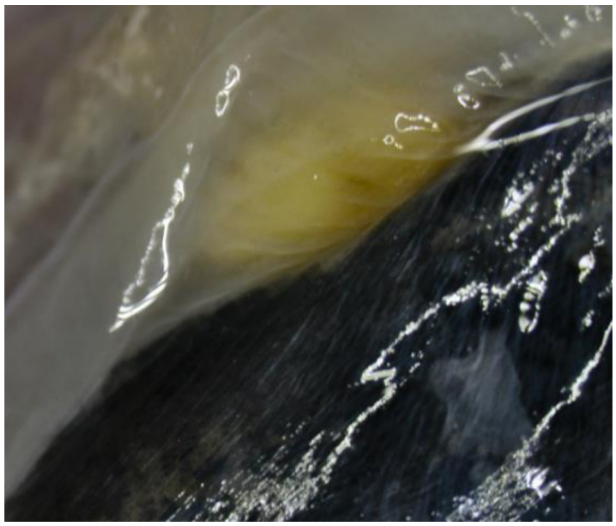

Fig. 1. Bitterling embryo that has not developed further in the gills of *Corbicula fluminea* (photo by M. Pfeiffer).

The skimming behaviour can be considered as failed spawning (female misses the exhalant siphon with its ovipositor) and sperm release attempts (Smith *et al.*, 2001). At one instance, sperm release of the male and immediate successful spawning of the female could be recorded (see supplementary video). These spawning periods (when the males showed a bright mating dress, the females extended their ovipositor and both sexes showed distinct behaviour) alternated with periods of inactivity. During the inactive periods, the nuptial coloration and ovipositor length were reduced.

The presence of bitterling eggs was confirmed by dissection of the *C. fluminea* specimens used. However, living embryos have never been found on the gills, only embryos that have not developed any further (Fig. 1). Additionally, we did not observe any juvenile bitterlings that had successfully developed and been released into the open water.

When both *U. crassus* and *C. fluminea* are present, bitterlings clearly prefer *U. crassus* for oviposition. Additionally, *R. amarus* larvae were only found in the two *U. crassus* individuals (Fig. 2), indicating a preference for this species over *C. fluminea*.

None of the 47 *C. fluminea* individuals collected from the Schutter, nor the 18 from the Herrenmühlebach, hosted bitterling eggs or embryos. In the gills of *C. fluminea*, gelatinous oval structures measuring 1–2 mm were occasionally observed (Fig. 3). Whether these objects were bitterling eggs or simply fat globules could not be determined. On the other hand, live bitterling embryos were found in the few *U. crassus* collected at the same location in the river Schutter (Fig. 3). This observation supports the results of the laboratory tests.

Our results indicate that *C. fluminea* is not a preferred host for the European bitterling. This is evidenced by the fact that

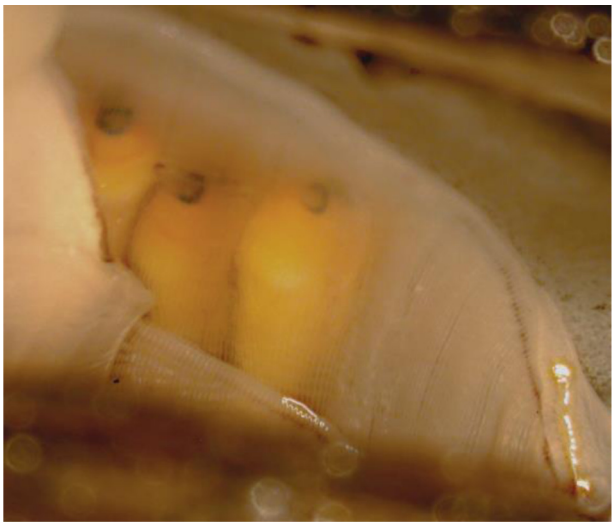

Fig. 2. Bitterling embryo that has not developed further in the gills of *Corbicula fluminea* (photo by M. Pfeiffer).

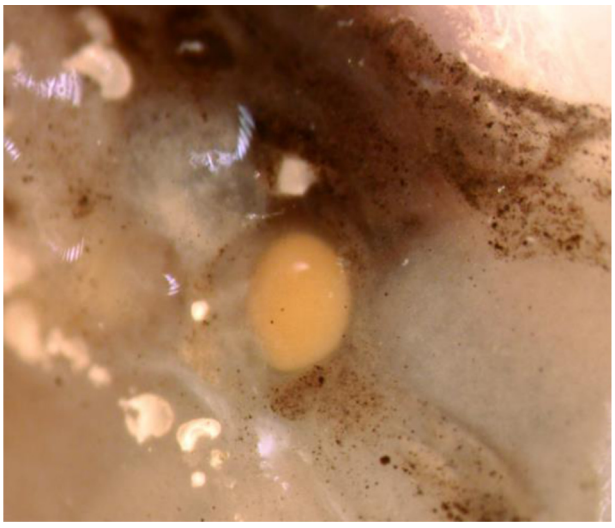

Fig. 3. Gelatinous oval structures (bitterling eggs or fat globules) in the gills of *Corbicula fluminea* (photo by M. Pfeiffer).

C. fluminea is only used in the absence of unionid mussels. While European bitterlings occasionally use *C. fluminea* individuals for reproduction, this does not result in successful larval development within the mussel body. In accordance with the host preference and host suitability hypothesis evidenced by Reichard *et al.*, (2007a), the general anatomy of *C. fluminea* seems to be unsuitable for successful bitterling embryo development. In the study by Reichard *et al.*, (2007a), the authors found no bitterling eggs or embryos in *C. fluminea*.

Thus, the current range extension of the European bitterling appears not to be associated with the substantial spread of *C. fluminea* in Europe. It is more likely that *R. amarus* benefits from a general temperature rise caused by climate change (van Damme *et al.*, 2007; Hellmann *et al.*, 2008; Rahel and Olden, 2008), potentially resulting in an extension of the spawning season, faster larval/juvenile development, and improved habitat suitability. With a prolonged breeding season, a single unionid individual (like *Unio crassus* in the Schutter) might be used several times for oviposition.

Almost all bitterling species in the subfamily Acheilognathinae – including the genus Rhodeus – are restricted to Asia (Arai, 1988; Okazaki *et al.*, 2001) and share a long co-evolution with native Asian mussel species. This led to the development of defence mechanisms against bitterling infection in Asian freshwater mussels (*e.g.* egg/embryo ejection and others; Reichard *et al.*, 2006), reported for *Sinanodonta woodiana* (Reichard *et al.*, 2007b). However, Unionid mussels native to Europe have not yet developed measures to avoid bitterling oviposition. Given that *R. amarus* is considered to be a parasite on European unionid bivalves with likely detrimental effects on its hosts (Reichard *et al.*, 2006, 2007a; Sousa *et al.*, 2020), further expansion and population growth of *R. amarus* must be viewed critically, especially given that all unionid bivalves in Europe are highly threatened (Lopes-Lima *et al.*, 2017; Sousa *et al.*, 2023).

The introduction and subsequent dispersion of the Asian clam *Corbicula fluminea* outside its native range (Southeast Asia) is one of the most dramatic events of non-indigenous invasive species (NIS) success in aquatic ecosystems (Crespo *et al.*, 2015; Nentwig *et al.*, 2018). These NIS, whether introduced accidentally or deliberately, are considered the most devastating environmental problem today, causing high ecological, economic, and conservation costs. The first records of *C. fluminea* in Europe date back to the early 1980s (Mouthon, 1981). It was introduced by cargo shipping upstream of the Rhine River as a stowaway in ballast water. Since then, it dispersed inexorably in Germany, now colonizing *e.g.* the entire Rhine and many connected water bodies up to the Lake Constance, Neckar, Oder, Weser, Elbe, and Danube (Alf, 1991; Kinzelbach, 1991; Boschert *et al.*, 1996; Rey and Ortlepp, 1997; Titttizer and Taxacher, 1997; Schniebs and Winkelmann, 2001; Jueg and Zettler, 2004; Werner and Mörtl, 2004; Wilke, 2007).

The high reproductive fitness of *C. fluminea* (short generation times, rapid growth, rapid sexual maturity, and great fecundity) enabled this species to frequently predominate the benthic substrate of populated streams (Sousa *et al.*, 2008; Geist *et al.*, 2023). *C. fluminea* seems to prevail over the native unionid mussels regarding interspecific competition for the same resources (Ferreira-Rodríguez *et al.*, 2018). Therefore, *C. fluminea* represents a significant threat to the continued existence of all European unionid bivalves and the implementation of urgent conservation measures is imperative.

It is unknown whether conservation efforts for unionid mussels will be successful in the future (Lopes-Lima *et al.*, 2017), but on a local scale, many populations in Southwestern Germany are facing extinction. However, if a local population of Unionids becomes extinct, the socially connected bitterling population in the same location will also die. It is therefore highly likely that the European expansion of *R. amarus* will slow down or even come to a halt.

Supplementary material

Movie S1. The video presents a series of oviposition attempts by Rhodeus amarus in Corbicula fluminea.

The Supplementary Material is available at https://www.kmae-journal.org/10.1051/kmae/2024026/olm.

References

Aldridge DC. 1999. Development of European bitterling in the gills of freshwater mussels. *J Fish Biol* 54: 138–151.

Alf A. 1991. Neu- und wiedergefundene Arten des Makrozoobenthon im Neckar. *Lauterbornia* 8: 71–76.

Arai R. 1988. Fish systematics and cladistics. In Uyeno T and M, eds. Ichthyology Currents, Asakura Shoten, Tokyo, 4–33.

Araujo R, Moreno D, Ramos M. 1993. The Asiatic clam *Corbicula fluminea* (Müller, 1774) (Bivalvia: Corbiculidae) in Europe. *Am Malacol Bull* 10 1: 39–49.

Bartáková V, Reichard M. 2017. No effect of recent sympatry with invasive zebra mussel on the oviposition decisions and reproductive success of the bitterling fish, a brood parasite of unionid mussels. *Hydrobiologia* 794: 153–166.

Boschert M, Heitz A, Heitz S, Laufer H, Münch C, Josef Ruf J, Rademacher M, Saumer F, Schneider F, Uhl A, Westermann K, Westermann S, Hanspeter Zimmermann H. 1996. Die Körbchenmuscheln *Corbicula fluminea* und *Corbicula fluviatilis* am südlichen Oberrhein – Dokumentation der Neufunde. *Naturschutz südlicher Oberrhein* 1: 211–225.

Büro Gobio 2022. *Die Kleine Flussmuschel, Unio crassus (PHILIPSSON, 1788), in Baden-Württemberg*, available at https://www.gobio-online.de/forschung.php – 2024/06/19.

Crespo D, Dolbeth M, Leston S, Sousa R, Pardal MÂ. 2015. Distribution of *Corbicula fluminea* (Müller, 1774) in the invaded range: a geographic approach with notes on species traits variability. *Biol Invasions* 17: 2087–2101.

den Hartog C, van den Brink FWB, van der Velde G. 1992. Why was the invasion of the river Rhine by *Corophium curvispinum* and *Corbicula* species so successful? *J Nat Hist* 26: 1121–1129.

Dußling U, Baer J, Gaye-Siessegger J, Schuman M, Blank S, Brinker A. 2018. Das große Buch der Fische Baden-Württembergs. *Ministerium für Ländlichen Raum und Verbraucherschutz Baden-Württemberg, Stuttgart*, 372 p.

Duyvené de Wit JJ. 1955. Some observations on the European bitterling (*Rhodeus amarus*). *Suid-Afrikaanse Joernaal van Wetenskap* 51: 249–251.

Ferreira-Rodríguez N, Sousa R, Pardo I . 2018. Negative effects of *Corbicula fluminea* over native freshwater mussels. *Hydrobiologia* 810: 85–95.

Fricke R, Eschmeyer WN, Van der Laan R. 2023. *Eschmeyer's catalog of fishes: Genera, species, references*. Available from: http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp#Acheilognathidae

Geist J, Benedict A, Dobler AH, Hoess R, Hosse P. 2023. Functional interactions of non-native aquatic fauna with European freshwater bivalves: implications for management. *Hydrobiologia* 1: 1–24.

Halabowski D, Reichard M, Pyrzanowski K, Zięba G, Grabowska J, Smith C, Przybylski M. 2024. The depressed river mussel *Pseudanodonta complanata* as an occasional host for the European bitterling *Rhodeus amarus*. *Knowl Manag Aquat Ecosyst* 425: 3.

Hellmann JJ, Byers JE, Bierwagen G, Dukes JS. 2008. Five potential consequences of climate change for invasive species. *Conserv Biol* 22: 534–543.

Jueg U, Zettler ML. 2004. Die Molluskenfauna der Elbe in Mecklenburg-Vorpommern mit Erstnachweis der Grobgerippten Körbchenmuschel *Corbicula fluminea* (O. F. Müller 1756). *Mitteilungen der Naturforschenden Gesellschaft Mecklenburg* 41: 85–89.

Kinzelbach R. 1991. Die Körbchenmuscheln *Corbicula fluminalis*, *Corbicula fluminea* und *Corbicula fluviatilis* in Europa (Bivalvia: Corbiculidae). *Mainzer Naturwissenschaftliches Archiv* 29: 215–228.

Kottelat M, Freyhof J. 2007. Handbook of European freshwater fishes. *Kottelat, Cornol & Freyhof, Switzerland and Berlin*, 646 p.

Li F, Liao T-Y., Arai R, Zhao L. 2017. *Sinorhodeus microlepis*, a new genus and species of bitterling from China (Teleostei: Cyprinidae: Acheilognathinae). *Zootaxa* 4353: 69.

Lopes-Lima M, Sousa R, Geist J, Aldridge DC, Araujo R, Bergengren J, Bespalaya Y, Bódis E, Burlakova L, Van Damme D, Douda K, Froufe E, Georgiev D, Gumpinger C, Karatayev A, Kebapçi Ü, Killeen I, Lajtner J, Larsen BM, Lauceri R, Legakis A, Lois S, Lundberg S, Moorkens E, Motte G, Nagel KO, Ondina P, Outeiro A, Paunovic M, Prié V, von Proschwitz T, Riccardi N, Rudzīte M, Rudzītis M, Scheder C, Seddon M, Şereflişan H, Simić V, Sokolova S, Stoeckl K, Taskinen J, Teixeira A, Thielen F, Trichkova T, Varandas S, Vicentini H, Zajac K, Zajac T, Zogaris S. 2017. Conservation status of freshwater mussels in Europe: state of the art and future challenges. *Biol Rev* 921: 527–607.

Mouthon J. 1981. Sur la presence en France et au Portugal de *Corbicula* (Bivalvia, Corbiculidae) originaire d'Asie. *Basteria* 45: 109–116.

Nentwig W, Bacher S, Kumschick S, Pyšek P, Vilà M. 2018. More than "100 worst" alien species in Europe. *Biol Invasions* 20: 1611–1621.

Nesemann H. 2018. *Corbicula largillierti* im Oberrhein (Hessen), neu erkannt in Deutschland. *Mitteilungen der Deutschen Malakozoologischen Gesellschaft* 98: 65–68.

Okazaki M, Naruse K, Shima A, Arai R. 2001. Phylogenetic relationships of bitterlings based on mitochondrial 12S ribosomal DNA sequences. *J Fish Biol* 58: 89–106.

Rahel F, Olden J. 2008. Assessing the effects of climate change on aquatic invasive species. *Conserv Biol* 22, 3: 521–533.

Reichard M, Ondračková M, Przybylski M, Liu H, Smith C. 2006. The costs and benefits in an unusual symbiosis: experimental evidence that bitterling fish (Rhodeus sericeus) are parasites of unionid mussels in Europe. *J Evol Biol* 19: 788–796.

Reichard M, Liu H, Smith C. 2007a. The co-evolutionary relationship between bitterling fishes and freshwater mussels: insights from interspecific comparisons. *Evol Ecol Res* 92: 239–259.

Reichard M, Przybylski M, Kaniewsk P, Liu, H, Smith C. 2007b. A possible evolutionary lag in the relationship between freshwater mussels and European bitterling. *J Fish Biol* 70: 709–725.

Rey P, Ortlepp J. 1997. Koordinierte biologische Untersuchungen im Hochrhein 1995; Makroinvertebraten. *Schriftenreihe Umwelt* 283: 115 p.

Schniebs K, Winkelmann C. 2001. Erste Nachweise der Körbchenmuschel *Corbicula fluminea* in Sachsen. *Lauterbornia* 41: 53–54.

Smith C, Rippon K, Douglas A, Jurajda P. 2001. A proximate cue for oviposition site choice in the bitterling (*Rhodeus sericeus*). *Freshw Biol* 46: 903–911.

Smith C, Reichard M, Jurajda P, Przybylski M. 2004. The reproductive ecology of the European bitterling (*Rhodeus sericeus*). *J Zool* 262, 2: 107–124.

Sousa R, Bogan AE, Gonçalves DV, Lajtner J, Prié, V, Riccardi, N, Lopes-Lima M. 2020. *Microcondylaea bonellii* as a new host for

the European bitterling *Rhodeus amarus*. *Knowl Manag Aquat Ecosyst* 421: 4.

Sousa R, Zając T, Halabowski D *et al.*, 2023. A roadmap for the conservation of freshwater mussels in Europe. *Conserv Biol* 37, 2: 13994.

Sousa R, Antunes C, Guilhermino L. 2008. Ecology of the invasive Asian clam *Corbicula fluminea* (Müller, 1774) in aquatic ecosystems: an overview. *Ann Limnol* 44, 2: 85–94.

Titttizer T, Taxacher M. 1997. Erstnachweis von *Corbicula fluminea/ fluminalis* (Müller 1774) (Corbiculidae, Mollusca) in der Donau. *Lauterbornia* 31: 103–107.

Turner H, Kuiper JGJ, Thew N, Bernasconi R, Rüetschi, J, Wüthrich M, Gosteli M. 1998. Fauna Helvetica 2: Atlas der Mollusken der Schweiz und Liechtensteins. *Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft*: 527 p.

Van Damme D, Bogutskaya N, Hoffmann R, Smith C. 2007. The introduction of the European bitterling (*Rhodeus amarus*) to west and central Europe. *Fish Fish (Ox)* 8: 79–106.

Werner S, Mörtl M. 2004. Erstnachweis der Fluss-Körbchenmuschel *Corbicula fluminea* im Bodensee. *Lauterbornia* 49: 93–97.

Wiepkema PR. 1961. An ethological analysis of the reproductive behaviour of the bitterling (*Rhodeus amarus* Bloch). *Arch Neerl Zool* 14: 103–199.

Wilke H-J. 2007. Erstnachweis von *Corbicula fluminea* in der Hohensaaten-Friedrichsthaler-Wasserstraße/Oder (Brandenburg). *Lauterbornia* 59: 63–65.

Cite this article as: Pfeiffer M, Mildner M, Günter CP, Leschner M. 2025. The Asian clam *Corbicula fluminea*, an accidental host for the European bitterling *Rhodeus amarus*. *Knowl. Manag. Aquat. Ecosyst.*, 426, 4. https://doi.org/10.1051/kmae/2024026.