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The role of chosen fish species as hosts for larvae of the protected thick-shelled river mussel *Unio crassus* Philipsson, 1788

All species of large freshwater mussels of the family Unionidae are included on the European Red List of threatened animals. For this reason, improving our understanding of their ecology is becoming increasingly important, particularly from the perspective of effective conservation and management. The thick-shelled river mussel, *Unio crassus* Philipsson, 1788, which has recently been treated as a species complex under the collective name *Unio crassus*, was historically one of the most widespread and abundant freshwater mussel species in Europe. Today, however, it is declining at an alarming rate. In Poland, the species is legally protected under national legislation and the EU Habitats Directive, and it is classified as Endangered (EN) on the IUCN Red List.

Unionid mussels have a highly specialized reproductive strategy. They produce larvae, known as glochidia, which develop in specialized gill chambers called marsupia. Once mature, the glochidia are released into the water column. To complete their development, they must spend a short parasitic phase attached to suitable fish hosts. After several weeks, they detach from the host as free-living juvenile mussels. This means that the ecology of unionid mussels cannot be fully understood without considering fish communities, because interactions with fish are essential for completing their life cycle under natural conditions. The series of articles presented here addresses issues that have so far been poorly explored, and in some cases almost entirely overlooked, in studies on the ecology and conservation of the thick-shelled river mussel.

The first article focuses on the so-called “dilution effect”, examining a situation in which the presence of an abundant but ineffective host may reduce the reproductive success of *U. crassus*. The study centres on the relationship between the mussel and two numerically dominant fish species: the Eurasian minnow, *Phoxinus phoxinus* (Linnaeus, 1758), which was the main effective host in the studied population, and the gudgeon, *Gobio gobio* (Linnaeus, 1758), which intercepts glochidia but does not allow them to complete metamorphosis. Combining field data from the Warkocz River with a controlled experiment, the study shows that *G. gobio* may act as a “dead-end” host, removing part of the larval pool that would otherwise be available to suitable hosts. The experiment confirmed that glochidia attached to *G. gobio*, but did not transform into juvenile mussels, whereas larvae attached to *P. Phoxinus* successfully completed metamorphosis. At the same time, field analyses of co-occurrence revealed a negative relationship between the number of glochidia recorded on *G. gobio* and *P. phoxinus*, particularly at low mussel densities. This indicates that the dilution effect is context-dependent: it becomes especially important in small, declining populations, where part of the glochidial pool may be intercepted by species that do not support larval transformation, further reducing reproductive efficiency.

The second article approaches host quality from a different angle: taxonomy and biogeography. It examines the smallhead sculpin, *Cottus microstomus* Heckel, 1837, as a previously unrecognized host for larvae of two species belonging to the *U. crassus* complex: *U. crassus* sensu stricto and *U. nanus*

Lamarck, 1819. Until now, the European bullhead, *Cottus gobio* Linnaeus, 1758, has been widely regarded as one of the most important hosts for this mussel complex. However, taxonomic revisions have shown that in parts of Central and Eastern Europe, including the Vistula River basin, the species co-occurring with the *U. crassus* complex is not *C. gobio*, but *C. microstomus*. This created an important knowledge gap: it was unclear whether *C. microstomus* could function as an effective host. A controlled experiment demonstrated that *C. microstomus* allows glochidia to successfully transform into juvenile mussels, and that its effectiveness is comparable to that of *P. phoxinus*, a widely recognized suitable host. This finding is important not only from the perspective of evolutionary biology, but also for conservation, as it shows that the composition of fish host species used by the *U. crassus* complex may vary regionally and requires precise taxonomic identification of fish hosts. The case of this cryptic sculpin species also suggests that phylogenetic relatedness may serve as a useful indicator of potential host suitability when the host status of a species is unknown.

The final article focuses on the actual availability of suitable fish hosts in the right place and at the right time, namely during the period when female thick-shelled river mussels release their glochidia. The study involved repeated fish sampling in several rivers that differed in abiotic conditions and fish community structure: the Warkocz, Cedron, Nida and Czarna Włoszczowska rivers. In addition, PIT-tag monitoring was used in the Smuga Umianowicka to assess the exposure and potential dispersal capacity of fish occurring near a mussel bed. In parallel, the reproductive phenology of *U. crassus* was monitored at each site to determine the timing of glochidial release. The results show that the timing of glochidial release varies among rivers and years, while the proportion of host fish present during the mussel breeding period ranged from 12.5% to 57%. One of the most important conclusions of this study is that, in most cases, fish communities were dominated by species that do not serve as hosts for *U. crassus* larvae. Effective reproduction in *U. crassus* therefore depends on the stable availability of suitable hosts during the larval release period. The most stable and widespread host species were *P. phoxinus* in foothill rivers and *L. cephalus* in lowland streams. Tagging data further confirmed that chub were consistently present near mussel beds and, at the same time, showed the potential to move over considerable distances, which may facilitate long-distance dispersal of glochidia. Importantly, the proportion of host fish was usually lower outside the glochidial release period. This means that habitat assessments and fish monitoring carried out outside the mussel's reproductive window may fail to reflect the true availability of suitable hosts.