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Demonstrating the practical impact of studies on biotic interactions and adaptation of a threatened unionoid mussel (*Margaritifera margaritifera*) to its host fish (*Salmo trutta*)

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Abstract

1. To understand the ecological factors behind the decline of functionally important threatened species with complex life cycles, many different life-cycle stages need to be investigated. The highly threatened unionoid freshwater mussels, with their complex life cycle, including a parasitic stage on host fish, often have a large influence on biodiversity and ecosystem functioning.
2. The overall aim of the present article is to summarize and discuss the impact of two articles published in *Aquatic Conservation: Marine and Freshwater Ecosystems* (AQC) on biotic interactions and adaptation of a threatened unionoid mussel (*Margaritifera margaritifera*) to its host fish (*Salmo trutta*).
3. The two *AQC* publications described research on the influence of population size and density of mussels and host fish, and host–parasite interactions between mussels and their host fish, on the recruitment of juvenile mussels.
4. The results from these publications filled gaps in knowledge and resulted in recommendations and incentives for conservation. The results and method development have been used in practical conservation work with threatened mussel species and have been implemented and cited in management handbooks. The outcome of the publications has been implemented in large conservation and restoration projects, and in several recent scientific publications.
5. Specifically, the results from one publication showed that ecological parameters such as mussel and host fish density and population size influenced recruitment of the threatened freshwater pearl mussel. The results from the second publication showed that understanding host–parasite interactions is important for comparing the suitability of host fish strains, and that host fish strains differ in their suitability for mussel infestations. In combination, the articles show that integrating ecological parameters of threatened mussels and their host fish with host–parasite interaction experiments can be an important influence on conservation recommendations, adaptive management and national management programmes for threatened species.

KEYWORDS
conservation evaluation, fish, invertebrates, stream

1 | INTRODUCTION

Preserving biodiversity, and ecosystem functions and services, is of major global concern (Cardinale et al., 2012). Biodiversity and ecosystem functioning are influenced by habitat type and reflect different ecological levels, from species to communities. The effects of species on biodiversity and ecosystem functioning is not evenly distributed, and in many communities only a few species, such as ecosystem engineers and keystone species, have strong ecological effects (Brodie, Redford, & Doak, 2018). Given the conservation value and the importance of protecting and designing effective conservation programmes for functionally important aquatic species, greater knowledge is needed of species-specific threats and ecology (Schneider, Nilsson, Höjesjö, & Österling, 2019). This article discusses the impact of two previous publications in *Aquatic Conservation: Marine and Freshwater Ecosystems* (*AQC*) on the conservation and management of the freshwater pearl mussel (*Margaritifera margaritifera*).

Where functionally important threatened species have complex life cycles, understanding the ecological factors causing their decline requires the study of many life-cycle stages (Österling, 2015). The ecology of the host also needs to be considered for species with life cycles that include parasitic stages (Österling, Greenberg, & Arvidsson, 2008). Hosts differ in their ecological characteristics, such as density, distribution, and migration patterns, and thus affect the parasitic life stages of threatened species. Hosts also affect their parasites through internal immunological processes within the host, which can have impacts on the recruitment of post-parasitic life stages (Zuk & Stoehr, 2002). Such processes also affect co-evolutionary dynamics, resulting in species-specific and local adaptations between the parasite and the host (Blanquart, Kaltz, Nuismer, & Gandon, 2013; Kaltz & Skyhoff, 1998).

The highly threatened unionoid freshwater mussels (45% of the species are classified as Near Threatened, Threatened, and Extinct; the International Union for Conservation of Nature (IUCN), 2020) affect biodiversity and ecosystem functioning (Aldridge, Fayle, & Jackson, 2007; Limm & Power, 2011; Vaughn, Nichols, & Spooner, 2008). Preserving the ecosystem functions and services provided by unionoid freshwater mussels (Vaughn, 2018; Lopes-Lima et al., 2017) has resulted in the formalization of international and national legal frameworks (Schneider et al., 2019). The unionoid mussels have an obligate parasitic stage on one or more host fish species (Bauer, 2001). Juvenile mussels are the most sensitive life stage, with sedimentation, acidification and water quality among the most recognized threats (Österling, Arvidsson, & Greenberg, 2010; Strayer, Downing, Haag, King, & Layzer, 2004; Vaughn & Taylor, 2000). There is a lack of understanding, however, on the potential effects of host fish ecology and host–parasite interactions on the status, ecology, and host–parasite interactions of unionoid mussels (Schneider, Nilsson, Höjesjö, & Österling, 2017).

The threatened freshwater pearl mussel spawns during summer, with the female mussels releasing their glochidia larvae from late summer to early autumn (Hastie & Young, 2003; MÖ, BML, & BA, unpubl. data), which then attach to the gills of a host fish: the brown trout (*Salmo trutta*) and/or the Atlantic salmon (*Salmo salar*). Encysted on the fish gills, the parasitic glochidia grow and metamorphose into mussels, and after 10–12 months (Hastie & Young, 2001) the juvenile mussels release themselves from the fish gills and start their sedentary life in the river bed (Bauer, 2001). Although human threats to the juvenile mussels are well known and understood (Geist, 2011; Österling et al., 2010), the influence of population size and density of mussels and host fish, and the interactions between mussels and their host fish, on the recruitment of juvenile mussels has not been studied to the same extent. Two publications in AQC: 'Recruitment of the threatened mussel *Margaritifera margaritifera* in relation to mussel population size, mussel density and host density' (Arvidsson, Karlsson, & Österling, 2012) (article 1, hereafter referred to as A1) and 'Impact of origin and condition of host fish (*Salmo trutta*) on parasitic larvae of *Margaritifera margaritifera*' (Österling & Larsen, 2013) (article 2, hereafter referred to as A2), reported the effects of such ecological factors and host–parasite interactions on mussel recruitment.

When A1 and A2 were planned and designed, the knowledge of the importance of host fish ecology and host–parasite interactions on recruitment of juvenile mussels was scarce; thus, the aim of the present article is to summarize and discuss the impact of A1 and A2 on recommendations for conservation, adaptive management, management handbooks, and funding from national and international conservation funding organizations.

2 | SUMMARY OF THE ARTICLES

2.1 | A1 – 'Recruitment of the threatened mussel *Margaritifera margaritifera* in relation to mussel population size, mussel density and host density' (Arvidsson, Karlsson, & Österling, 2012)

Although the abiotic factors responsible for the decline and extinction of freshwater pearl mussel populations are well known, biotic factors may also be important for successful recruitment. In this article, we presented the results from a large-scale investigation on the relationship between the recruitment of freshwater pearl mussel in relation to mussel population size, mussel density, and host density. We assumed that population size and density affected reproduction, such that reproduction and glochidia production in small and sparse mussel populations are low, and lead to low infestation rates on host fish. Host fish density has been shown to be important for glochidial infestation, with a potential positive influence on recruitment (Österling et al., 2008). Recruitment success may differ, however, depending on the age of the host fish, as host fish become more resistant to infestation as they get older (Bauer, 1987a; Bauer & Vogel, 1987). We found that mussel population size and density were positively related to recruitment and to juvenile mussel density, with juvenile mussel density giving a more accurate measure of recruitment. The density of young-of-the-year host fish and older brown trout were both positively related to recruitment, and the density of both age classes of fish was positively related to juvenile mussel density. This effect decreased at trout densities higher than 10 per 100 m^2. Moreover, mussel population size and density were relatively more important to recruitment than trout density. We suggested that conservation managers should apply measures that favour mussel density, and trout density of up to around 10 per 100 m^2, to increase juvenile mussel recruitment. We also suggested that mussel beds could be managed, where one possible measure within small and sparse mussel populations is to concentrate the mussels in localities where trout density is high. Similarly, young-of-the-year trout may be introduced to areas with high mussel density as they tend to be relatively stationary during their first summer through to early autumn, which is the period when the mussels spawn. By contrast, and as older trout were also found to influence recruitment, older trout could be infested with glochidia larvae and act as dispersal vectors for the mussels. These measures may increase mussel larval infestation rates, mussel recruitment, and mussel population distribution.

2.2 | A2 – 'Impact of origin and condition of host fish (*Salmo trutta*) on parasitic larvae of *Margaritifera margaritifera*' (Österling & Larsen, 2013)

Where threatened species have a parasitic stage in their life cycle, the host can influence the growth and survival of the parasite (Dodd, Barnhart, Rogers-Lowery, Fobian, & Dimock, 2005; Haag & Warren, 1998; McNichols, Mackie, & Ackerman, 2011; Strayer et al., 2004). Even so, local adaptation may result in increased parasitic growth and survival, resulting in increased parasitic survival and recruitment rates. Likewise, local evolutionary pressure may cause reduced growth and survival of parasites locally through adaptive defence traits (Dodds & Whiles, 2004).

After attachment to the host fish, the parasitic mussels grow from 0.05–0.07 mm to 0.40–0.50 mm before they release themselves from the host fish (Bauer, 1987a; Bauer, 1987b; Hastie & Young, 2001; Young & Williams, 1984). For a few weeks after encapsulation on the host, the level of encystment decreases, with abundance continuing to decrease relatively slowly until the juvenile mussels fall off the fish (Hastie & Young, 2001; Young & Williams, 1983). It has been found that encystment abundance is higher on sympatric brown trout strains compared with allopatric brown trout strains (Taeubert, Denic, Gum, Lange, & Geist, 2010), indicating that co-evolutionary interactions between mussels and their host fish favour the adaptation of the mussel to the fish.

In an aquarium experiment described in A2, the objective was to compare the encystment and growth of mussel larvae on its sympatric brown trout strain with three allopatric strains without any previous contact with mussels. At the end of the experiment, one of the allopatric strains had higher encystment abundance and growth compared with the other three strains. Thus, the potential production of juvenile mussels may be restricted during the parasitic life stage on sympatric brown trout populations. There was a significant positive relationship between the mean condition factor of the host fish and the shell length of the mussels, which may be a result of innate differences in resources and immune defence among the brown trout populations.

This experiment showed that conservation managers should be aware of co-evolutionary relationships between unionoid mussels and their host fish. Conservation managers could also perform experiments similar to the one presented here: for example, when evaluating host fish strains used for host fish introductions or when using host fish for mussel breeding programmes.

3 | IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

The results presented in A1 and A2 have resulted in recommendations and incentives for conservation. The results from the large-scale A1 study on the importance of host fish density on mussel recruitment fills a gap in our knowledge, with implications for the conservation of freshwater pearl mussel. Surprisingly, and in contrast to other findings, trout older than young-of-the-year appear to be important hosts. In fact, trout older than young-of-the-year influenced juvenile recruitment positively to a higher degree than young-of-the-year trout. These findings, combined with the methods developed in A2, resulted in an investigation showing that trout older than young-of-the-year are also functionally important hosts (Österling, 2015). Based on the results in A1, we could recommend minimum densities for different age classes of host fish that are needed for successful recruitment of juvenile mussels. The results also showed the positive influence of mussel density and mussel population size on recruitment, adding to the complexity of ecological factors important for mussel recruitment. The effect of mussel density and population size on mussel recruitment was relatively more influential than trout density. Restoration that aims to increase trout densities seems to be important not only for the recruitment and survival of juvenile mussels, but also in producing higher population sizes and densities of adult mussels, with a positive influence on spawning (Österling, 2015), glochidia density on host fish, and ultimately juvenile recruitment (Österling et al., 2008; Schneider et al., 2019).

The results from A2 demonstrated the value of performing experiments on the suitability of host fish strains. A trout strain living in sympatry with a mussel population, which was shown not to be the most suitable strain, may be restricting recruitment. The infestation method that was used in A2 can thus be applied by conservation managers when planning captive breeding programmes or host fish introductions. The results from A2 also suggest that host fish populations that are geographically close could be used as donor populations if trout strains living in sympatry with mussels are extinct. This is in accordance with the IUCN guidance for reintroduction, where it is stated that the geographically closest population should be used when reintroducing threatened species (International Union for Conservation of Nature Species Survival Commission (IUCN SSC), 2013).

4 | DEMONSTRATED IMPACTS OF OUR AQC ARTICLES

4.1 | Adaptive management

Adaptive management is probably an ideal approach when managing threatened unionoid mussels, given their complex life cycle and the many potential damaging impacts of human disturbances affecting all life stages, including the host. Studies that increase the knowledge of host fish ecology and host–parasite interactions, such as those reported in A1 and A2, should therefore be applied in conservation programmes. The results from A1 and A2 will be implemented in the Swedish programme for threatened species (Henrikson & Söderberg, pers. comm.). This national programme, which is authorized by the Swedish Agency for Marine and Water Management, and shall be applied by county administrative boards and other authorities, aims to increase the status of threatened species, suggesting conservation management based on an adaptive management approach. For example, the results from A1, combined with the method developed in A2, resulted in the advice to manage trout older than young-of-the-year because older age classes are functionally important hosts (Österling, 2015). In addition, the results and methods from A1 and A2 have been applied to the European LIFE project 'UC4LIFE' (LIFE10 NAT/SE/000046, 2012–2016) and to the recently started LIFE project 'LIFE CONNECTS' (LIFE 18 NAT/SE/000742, 2019–2025), in which the results form an important background to large restoration projects. The results and methods developed in A1 and A2 were also important factors in obtaining funding from sources such as World Wide Fund for Nature (WWF) Sweden, the Fortum Nordic Environmental Fund, the Swedish Knowledge Foundation, the non-governmental organization the Swedish Society for Nature Conservation (SSNC), and county administrative boards. Applications recently submitted that include host fish ecology and infestation experiments have also been highly influenced by these publications.

4.2 | Management handbooks

The results from the research in A1 and A2 have been implemented and cited in published and unpublished management handbooks: the Swedish programme for threatened species and the Norwegian action plan for the freshwater pearl mussel (Larsen, 2018) are two examples. The results and methods developed from A1 and A2 have also contributed to management handbooks for another unionoid mussel species, the thick-shelled river mussel *Unio crassus* (Lundberg & Österling, 2016). In addition, we have been invited by county administrative boards and private companies to present the results from A1 and A2, and how the findings from these articles can be applied to practical conservation work.

4.3 | Influence on conservation-related research

The scientific publication of results, and the development of new science based on previous research and publications, is important when working with adaptive management. Many scientific publications on conservation have been based on the results and method development in A1 and A2, such as how land use influences recruitment by its effect on brown trout densities (Österling & Högberg, 2014), or on the reproductive potential of another threatened unionoid mussel, *U. crassus*, with the aim of prioritizing conservation locations in management action (Schneider et al., 2019). The latter study found that host fish density was also affecting the recruitment potential of *U. crassus*, extending the results in A1 more widely (Schneider et al., 2019). The results and methods developed in A2 have influenced new conservation publications. For example, the methods developed in A2 were used when discriminating between the two potential host fish species, brown trout and Atlantic salmon, in two rivers in Sweden (Österling & Wengström, 2015; Wacker, Larsen, Karlsson, & Hindar, 2019), and how brown trout from different rivers and of different ages influence the suitability and functioning of the parasitic glochidia in an aquarium experiment (Österling, 2015). The results from both A1 and A2 were also used to compare the suitability and glochidia density of sea-migrating trout and tributary-resident trout, and showed the importance of creating free migration routes for the host fish, acting as dispersal vectors for the mussel (Österling & Söderberg, 2015).

The results and methods developed in A1 and A2 have contributed to the following conclusions in various scientific articles on behavioural ecology: (i) the infestation of glochidia on host fish can impair drift feeding and competition between individual host fish (Österling, Ferm, & Piccolo, 2014); (ii) not only foraging, but also activity and dominance are reduced in juvenile brown trout when trout are infested with glochidia (Filipsson et al., 2018); (iii) glochidia infestation can increase the metabolic rate and haematocrit in juvenile brown trout (Filipsson et al., 2017); and (iv) the individual activity of brown trout can alter their exposure to parasitic glochidia infestation (Wengström et al., 2016). These findings have implications for conservation: for example, when fish are artificially infested with glochidia in the laboratory and released back into a river with the aim of strengthening juvenile recruitment. Experiments based on the methods in A2 can then be designed to find the optimal infestation loads, relating the costs of glochidia infestation on host fish to the benefits of juvenile mussel production.

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