The Freshwater Pearl Mussel: A Costly Stowaway or an Important Habitat Engineer?

J. Höjesjö, N. Wengström, and M. Österling

Abstract The freshwater pearl mussel (FPM) (*Margaritifera margaritifera*) has a fascinating lifecycle that includes a parasitic life stage on host fish; the brown trout (*Salmo trutta*) and/or the Atlantic salmon (*Salmo salar*) (Geist et al., Aq Conser: Mar Freshw Ecosystems. 16:251–266, 2006) in order to successfully reproduce. Freshwater mussels, including the FPM, have large effects on ecosystem functions in streams and rivers. The FPM is thus an important habitat engineer and keystone species where healthy populations indicate a well-functioning ecosystem (Geist, Hydrobiol 644: 69–88, 2010). In this chapter, our aim is to provide a general overview of the present knowledge regarding the FPM and (1) the interaction with its host fish (2) its habitat requirements, (3) the threats to the mussel, and (4) successful restoration measures.

Keywords Freshwater pearl mussel · Brown trout · Host fish · Parasite-host interaction · Restoration

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1 Distribution and Life History of the Freshwater Pearl Mussel

The freshwater pearl mussel (FPM) (*Margaritifera margaritifera*) has a Holarctic distribution covering parts of North America on the Atlantic coast from Newfoundland, Canada, down to Delaware and Pennsylvania, USA (Walker 1910). In Europe, the species occur in Austria, Belgium, Czechia, Denmark, Estonia, Finland, France, Germany, Ireland, Latvia, Lithuania, Luxembourg, Norway, Poland, Portugal, Slovakia, Spain, Sweden, and the United Kingdom (Geist 2010; Moorkens et al. 2017). The species is decreasing throughout its distribution range (Quinlan et al. 2015), and it is believed to have gone extinct in Belarus, Denmark, Lithuania, and Poland (Lopes-Lima et al. 2017). It is on the IUCN red list of threatened species in the category endangered (EN) (Moorkens et al. 2017).

The FPM is a relatively large mussel that can grow to 160 mm with a thick and heavy shell that enables it to inhabit streams with high discharge (Dunca et al. 2011). They have separate sexes but can also switch to hermaphroditism (Bauer 1987; Grande et al. 2001). The age of maturity is reached at an age of 10–15 years, and they reproduce until they die (Bauer 1987). The size of the glochidia (larval stage of the FPM) is between 45 and 70 μm and a female can produce 2–4 million larvae every reproductive season. The FPM are known for their long longevity (>80 years) and the oldest documented individual was dated 280 years (Dunca et al. 2011; Lopes-Lima et al. 2017).

Life history traits like body size, glochidia size, lifespan, brooding period, gill brooding area, host infection strategy, and host use, are only known for some of the >800 species of freshwater mussels (Graf and Cummings 2007). The life cycle and life history of the freshwater pearl mussel are relatively well-known and described in Fig. 1.

The reproductive period of the FPM takes place annually between June and October. Females carry the glochidia in special pouches on the gills (both gill pairs) called marsupia. The FPM are short-term breeders meaning that the females only carry the glochidia for 5–7 weeks before releasing them into the water. The release of glochidia into the water column is a synchronized temperature-driven event; Hastie and Young (2003) reported that within Scottish rivers generally at least 300-degree days were needed before glochidia release. The glochidia then must attach to a host fish, exclusively brown trout (*Salmo trutta*) and/or Atlantic salmon (*Salmo salar*) in Europe and possibly brook charr (*Salvelinus fontinalis*) (Ziuganov et al. 1994) in North America for approximately 10–12 months from late summer until early summer the next year (Taeubert et al. 2013; Taeubert and Geist 2017). During the parasitic stage where they develop and metamorphose from a glochidia into a juvenile mussel, the larvae grow 6–10 times in size before they excyst off the fish (Hastie and Young 2003; Young and Williams 1984). Temperature is also important here and Marwaha et al. (2017) predicted that the number of excysted individuals increased from 5.63 at 11 °C to 35.65 at 18 °C. After excystment, the juvenile mussels bury themselves in the substrate for approximately 5 years (Young and

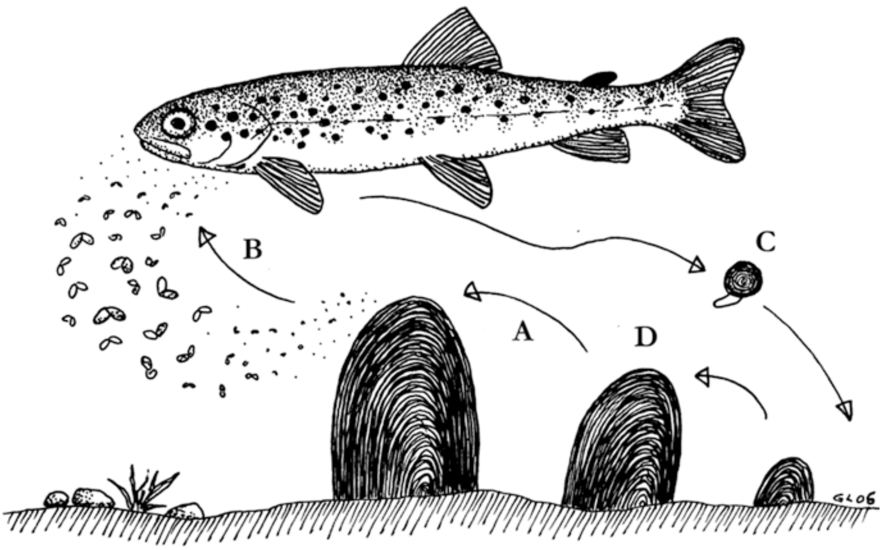

Fig. 1 The life cycle of the freshwater pearl mussel. (**a**) Males release sperm that females inhale, and the eggs get fertilized. (**b**) Females release mature glochidia that get encysted on the gills of the host fish. (**c**) Juvenile mussels excyst from the host. (**d**) Juvenile mussels grow into adult sexually mature mussels. Drawing by Gunnar Lagerkvist

Williams 1984; Bauer 1992, 1998) before they emerge to the gravel bed and mature at a size of 65 mm (Hastie et al. (2000).

2 Preferences

2.1 Habitat Preference

The FPM lives in running water, in northern Europe generally at sites located downstream of lakes, which secure the mussels from droughts (Degerman and Tamario 2017). The FPM are distributed both in small shallow streams at a depth of a few cm but also in large rivers with a depth over 10 meters. Streams with healthy FPM populations, which include mussels of all age classes, are clear with low turbidity and well-oxygenated hyporheic zones, and poor in phosphorous and nitrogen (Boon et al. 2019, Geist and Auerswald 2007; Österling et al. 2008 and 2010). Mussels can be found in a variety of substrate types, from fine substrates such as silt and sand to mixtures of sand and larger substrates such as pebbles, cobbles, and boulders. The general within-stream distribution of the FPM is patchy. Interactions with the host fish (Haag and Warren 1998; Hastie and Young 2001; Hastie and Young 2003) and with physical factors such as substrate structure and water flow (Hastie et al. 2000; Brown and Banks 2001; Box et al. 2002), sedimentation (Box and Mossa 1999), and water chemistry (Bauer 1988; Buddensiek et al. 1993) are believed to contribute to the distribution of the FPM. Some studies suggest a positive relationship between host and mussel densities (Arvidsson et al. 2012) but only until a certain threshold is reached (Geist et al. 2006). This suggests that beyond this threshold, further eutrophication may only be beneficial for the host, but not for the juvenile pearl mussels when buried within the stream bed facing an increasing risk of embeddedness and depletion of oxygen (Geist and Auerswald 2007). Hastie et al. (2000) computed habitat suitability curves and reported that water depths of 0.3–0.4 m and current velocities of 0.25–0.75 m/s at intermediate water levels were optimal but also that riverbed characteristics were the most important physical parameter for predicting FPM distribution. Hence, stability of sediments during flooding and low shear stress are important factors that are probably associated with FPM assemblages (Lehner et al. 2006; Strayer 1999; Hastie et al. 2001). In streams where high turbidity and sedimentation load results in the large cover of fine material, unfavorable conditions such as low oxygen levels and a high degree of embeddedness can be detrimental for juvenile mussels, hence why only adult mussels exist here (Geist and Auerswald 2007; Österling et al. 2008).

2.2 Host Preference

The glochidia infection is associated with a cost for the host fish, and the glochidia larvae can thus act as a selective force resulting in a potential mussel–salmonid host coevolution (Douda et al. 2017; Chowdhury et al. 2021). Whether the FPM can live as a parasite on one or both fish species when they co-occur is complex and not fully understood. According to Salonen et al. (2017), the occurrence of glochidia infestation is highest on Atlantic salmon in large main channels where salmon is the dominant host. In small tributaries without presence of Atlantic salmon, brown trout is a functional host. Thus, FPM glochidia can be adapted to either Atlantic salmon *or* brown trout in some rivers, even though both species live in sympatry (Larsen et al. 2000a, 2000b; Larsen 2012; Dunca and Larsen 2012). Salonen et al. (2017) reported that the FPM generally prefers *S. salar* rather than *S. trutta* as a host, even if both can be suitable hosts. Moreover, Geist et al. (2018) detected two main conservation units of pearl mussel in Ireland: one mostly salmon-dependent Western cluster and one trout-dependent central–eastern cluster. Other studies have shown that FPM can also parasitize only *S. trutta* during sympatric conditions with *S. salar* (Hastie and Young 2001, 2003; Österling and Wengström 2015).

The host suitability also differs among host fish strains, and although no clear pattern of local adaptation to the host fish has been shown in some studies (Karlsson et al. 2014; Wacker et al. 2019; Österling and Larsen 2013), Taskinen and Salonen (2022) recently validated the hypothesis that glochidia can show local adaptation by being more successful when attached to local fish strains which are of crucial importance for management. Wacker et al. (2019) could also show that when both salmon and trout were exposed to larvae originating from "salmon- and trout-mussel," respectively, salmon-mussel larvae almost never infected brown trout and vice versa suggesting that host specificity can explain variation in natural infection among FPM populations. In addition, Taubert et al found evidence of local co-adaptation between pearl mussel and brown trout with different rates of metamorphosis success on different strains of FPM where the brown trout strain originating from the natural pearl mussel distribution range was identified as the most suitable host. Lastly, in a comparison between tributary-resident and sea-migrating *S. trutta* as hosts for the FPM, the sea migrating strain was the most suitable host (Österling and Söderberg 2015), which adds to the complex interactions between the FPM and its host fish species. Thus, to be able to manage mussel populations, careful selection and management of appropriate host fish strains is mandatory for sustainable conservation and more research on adaptation and suitability between different mussel and host fish strains and species are needed.

3 Threats

Freshwater mussels are among the most threatened aquatic species on the planet (Lydeard et al. 2004; Goodrich et al. 2022). Factors affecting the species and leading to impoverishment of populations are habitat destruction and degradation, loss of host fish, commercial exploitation, and biological invasions (Bogan 2008). Since the 1960s enigmatic mass mortality events have occurred in North America and recently these mass mortality events have also happened in parts of Europe (Haag et al. 2019; Wengström et al. 2019). Erosion and high loads of fine sediments have been correlated with low or no juvenile recruitment success (Österling et al. 2010; Geist and Auerswald 2007; Denic and Geist 2015; Hoess and Geist 2020). Climate change with drought, floods, and increased sediment depositions have also been shown to affect mussel populations with catastrophic results (Hastie et al. 2001; Sousa et al. 2018; Baldan et al. 2020, 2021). A lack of host fish is another major threat to the freshwater pearl mussel and there is a low probability of finding juvenile mussels in streams with densities of host fish below 5 fish/100 m^2 (Degerman et al. 2013). In contrast, a high density of host fish and a large fish species richness can be indicative of non-functional streams for the FPM (Geist et al. 2006). Mass mortality events in FPM populations have often been described as enigmatic without any obvious causes but with a new focus on mussel health assessments knowledge about pathogens associated with mass mortality events has been gained (Waller and Cope 2019; Haag 2019; Richard et al. 2020, 2021).

Free-living FPM glochidia have a high natural mortality since they lack swimming ability, drift with the current, and have to find a host fish. If they attach to a non-functional host fish, they will be fended off from the fish and die (Jansen et al. 2001). During the drift, there are also several predators such as fish, copepods, and flatworms that consume glochidia (Jansen et al. 2001). Glochidia and juveniles are vulnerable to acidification and their survival decreases with decreasing pH, below pH 4.5 they will not survive for more than 24 hours (Taskinen et al. 2011).

Wengström and Höjesjö (2020) found no juvenile recruitment in streams with pH < 6.0.

Habitat alterations like channelizing and man-made barriers are common threats to the FPM in headwaters and tributaries. For example, small hydropower plants have been shown to have a negative impact on freshwater pearl mussels (Sousa et al. 2020). Hydropower plants have a negative effect through modified downstream flows, channel morphology, water temperature, sediment transport and deposition, and as fish barriers (Couto and Olden 2018).

Historically, adult freshwater pearl mussels have been caught and killed to collect pearls, and this eradicated populations from many streams (Bauer 1988; Makhrov et al. 2014). In Sweden in the late seventeenth century more than two million freshwater pearl mussels were killed every year to support the king's demand for pearls (Awebro 1995).

In Europe, invasive species like the signal crayfish (*Pacifastacus leniusculus*) and brook trout (*Salvelinus fontinalis*) have been shown to be a threat to the FPM (Sousa et al. 2019; Salonen et al. 2016). Laboratory experiments suggest that especially younger mussels were more vulnerable to predation by signal crayfish (Sousa et al. 2019). In Europe, brook trout can be infected by FPM glochidia but in most cases the larvae will fall off before metamorphosis is complete (Salonen et al. 2016). Both signal crayfish and brook trout have negative effects on the population size of brown trout which can ultimately reduce the number of suitable hosts for the freshwater pearl mussel (Peay et al. 2009; Lovén Wallerius et al. 2017; Lovén Wallerius et al. 2022).

4 Interaction with Salmonids

The definition of a parasite is usually simplified into "an organism that lives on or in an organism of another species, known as the host, from the body of which it obtains nutrients" or "an organism that lives and feeds on or in an organism of a different species and causes harm to its host" (Crofton 1971). Generally, parasites affect their hosts negatively, which in many cases may lead to reduced fitness of the host (Lehmann 1993; Moore 2002). It has been argued that the relationship between the FPM and their host fishes can be considered as either parasitic, mutualistic, or commensal (Ziuganov et al. 1994; Skinner et al. 2003; Geist 2010; Barnhart et al. 2008). The presence of adult mussels might for example reduce the content of particulate matter and nutrients in the water column by their filtering activity and by the creation of microhabitats for juvenile fishes (Ziuganov et al. 1994; Skinner et al. 2003). However, the FPM clearly fulfills the criteria for a parasitic relationship where the glochidia larvae thrive as encysted parasites on the gills of juvenile salmonids for almost a year from which they obtain energy that allows them to grow and metamorphose into a juvenile free-living mussel. The infection load on the gills of salmonids in nature can be very high, reaching up to the 1000s of glochidia at least during the initial phase of infection (Österling et al. 2008; Hastie and Young

2003). However, the glochidia load generally decreases within a couple of months and there are also reports on differences in infection rate both between year classes where young of the year salmonids generally have a higher degree of infection and between strains of fish suggesting an active and evolving immune response in the fish (Hastie and Young 2001). A lower infection load has also been found after a second infection in the laboratory. Clearly, brown trout can eliminate FPM glochidia by both tissue and humoral reaction so that repeated exposures strengthen the immunologic responses indicating an acquired immunity against FPM (e.g., Bauer 1987; Zotin and Zyuganon 1994; Hastie and Young 2001; Bauer and Vogel 1987; Chowdhury et al. 2018; Marwaha et al. 2019). Hence, for efficient conservation of the FPM it is important to emphasize the availability of young of the year fish that are immunologically more naive than older cohorts.

Clearly, the number of glochidia established on the fish and the growth of glochidia might be expected to adversely impact host fish directly or indirectly, but the understanding of how glochidia of FPM affect brown trout both in terms of direct costs (e.g., growth and survival) and indirectly (altered behavior and competitive interactions) is very limited. Below we aim to summarize the current knowledge on the effects that the glochidia infection might have on juvenile salmonid fish host.

4.1 Direct Effects

Mortality of infected salmonids in nature and/ or at low infestation rates are not well examined but Taeubert and Geist (2013) detected host fish mortality at an infection rate of ~350 glochidia/g fish weight and a mortality of 60% at the highest infection rates (~900 glochidia/g fish weight). For the surviving host fishes, a high infection load decreased swimming performance, with infection intensity of ~900 glochidia/g fish reducing the critical swimming speed of the host by ~20% compared to infection with 6 glochidia/g fish weight. In contrast, Chowdhury et al. (2021) used a much lower degree of infestation (~140 glochidia/g fish) and could not see any difference in mortality in brown trout due to infection of FPM. Recent studies have also shown that glochidia encystment increases respiration where trout encysted with glochidia took almost 6 h. longer to reach basal levels compared with trout without glochidia (Thomas et al. 2013) and standard metabolic rate (SMR) in infected host fish were on average 26% higher than non-infected fish (Filipsson et al. 2017). There are to our knowledge only two studies that have examined the effects on growth rate in host fish being infected with glochidia from FPM; Treasurer et al. (2006) could not detect any effect of FPM infection on the growth of Atlantic salmon at an early stage but a negative effect after 15 weeks which again disappeared by the end of the first year. In contrast, Chowdhury et al. (2021) reported how non-infected trout gained 11% more weight than infected trout no matter season and/ or density of food. In agreement Terui et al. 2017, using a similar host–parasite system (larval parasites of the freshwater mussel *Margaritifera laevis* and its salmonid fish host *Oncorhynchus masou masou*) showed reduced growth in smaller host fish. These studies suggest that at least for highly infected fish the FPM will act as a parasite with a resulting increased mortality, impaired swimming capability, reduced metabolic rate, and most likely a reduced growth rate.

4.2 Indirect Effects

Foraging behavior and competitive interactions in salmonids have been thoroughly investigated (Lima and Dill 1990, Keenleyside and Yamamoto 1962,) and there is a number of papers describing how drift-feeding salmonids forage at a focal point where their net energy intake (NEI) will be maximized (Bachman 1984; Fausch 1984; Hughes et al. 2003; Piccolo et al. 2014) and how the relative dominance rank will influence foraging and habitat utilization where the dominant fish usually is winning the position with the greatest NEI potential (Hughes 1992), thus achieving the greatest potential fitness (Nilsson et al. 2004; Höjesjö et al. 2002, 2004). This theoretical framework has been used to predict behavior (Hughes 1992), distribution (Hughes and Dill 1990), growth (Hayes et al. 2000), and production (Hayes et al. 2007) of stream salmonids (Piccolo et al. 2014). However, parasitic infections of the FPM will most likely affect both inter- and intraspecific interactions among the juvenile salmonids such as dominance behavior and competition for food and territories (Barber et al. 2000; Österling et al. 2014). Österling et al. (2014), for example found that uninfected juvenile brown trout had higher drift foraging rates than infected fish and were able to capture more prey items further away from a focal point. Furthermore, Filipsson et al. 2016 studied the pairwise interaction between an infected and a non-infected brown trout and showed how high encystment rates decreased prey items caught, activity, and the number of initiated interactions relative the non-infected individual. Low glochidia loads, however, did not seem to affect feeding or competitive interactions suggesting a threshold in glochidia load before any negative effect on host fish performance can be detected. There is to our knowledge, only one study on the performance of infected host fish in the field; Wengström (2022) showed that infected fish covered a larger range in the field compared with non-infected and utilized habitats with different bottom substrates and velocities in the autumn. Similarly, using chub (*Squalius cephalus*) as a model species, Horký et al. (2014), have shown that chub infected by the larval stage of the freshwater bivalve; the duck mussel (*Anodonta anatina*) dispersed less far upstream and maintained position further from the riverbank.

5 The FPM as Habitat Engineers

Freshwater mussels are described as umbrella species and keystone species because of their effect on the ecosystem in streams and rivers (Collier et al. 2016; Geist 2010; Dudgeon et al. 2006; Strayer et al. 2004) and the FPM is the first species for which a standardized monitoring approach has been developed (Boon et al. 2019). Their filter feeding transfers the energy of phytoplankton, bacteria, and organic particles from the free-flowing water to the benthos. The mussels release nutrients such as phosphorous and nitrogen, some of which can be assimilated by algae and macrophytes, thereby positively affecting their growth (Howard and Cuffey 2006; Strayer et al. 1994; Vaughn 2010, 2018; Vaughn and Hakenkamp 2001). Hence, the mussels can strongly affect the number of suspended particles in the open water (Lummer et al. 2016), some of the filtered materials are converted and biodeposited as feces and pseudofeces providing food for the secondary production of benthic fauna (Aldridge et al. 2007; Limm and Power 2011; Vaughn et al. 2008). When insect larvae, which are a dominant part of this increased faunal production, hatch and become flying adults, many of them ultimately end up in the terrestrial ecosystem, providing food for terrestrial predators (Vaughn 2018). However, the effects of mussels on macroinvertebrates may be less strong in agriculturally impacted catchments (Richter et al. 2016). It has also been proposed that the increased abundance of benthic fauna can provide food for fish, thereby increasing fish densities (Ziuganov et al. 1994; DuBose et al. 2020). Mussel beds can constitute a dominant part of the benthic biomass, and the physical structure provides a habitat for other benthic fauna and fish (Spooner et al. 2013). Finally, mussels can stabilize the sediment, and when they move vertically and horizontally in the sediment, they cause bioturbation leading to increased oxygen concentrations in the sediment (Vaughn and Hakenkamp 2001; Gutiérrez et al. 2003; Strayer 2008, Boeker et al. 2016).

6 Reintroducing the FPM, Successful Examples on Habitat Restoration and Artificial Infection

Several actions have been taken to secure the future of the FPM in Austria, Czech Republic, England, Finland, France, Germany, Ireland, Luxembourg, Norway, Scotland, Spain, Sweden, and Wales (Moorkens 2011; Gum et al. 2011; Wengström 2012). There are different methods to apply when trying to revive FPM populations (McMurray and Roe 2017).

Controlled propagation—Includes the collection of gravid females or wild glochidia, inoculation of host fish, recovery and care of juveniles, captive grow-out, and captive breeding, usually within a controlled environment.

Controlled propagation/captive breeding is a method that is widely used in several European countries (Gum et al. 2011). It is often applied in EU-funded LIFE projects and the method is quite costly (Moorkens 2018), but since it is performed in a controlled environment, data can be quantified and the chance of enhancing the results is greater than with other methods. Using this methodology, Hruška (2001) produced several thousands of FPM over a period of 3 years. Here, maintained infected fish were hosted under controlled conditions from which excysted juveniles were collected daily and transferred to boxes in the stream.

Augmentation—The addition of individuals of a species within the geographic boundaries of an existing local population.

Augmentation involves the methods of moving adult/juvenile mussels between sites in the same basin, and the release of infected fish hosts using glochidia and fish hosts from the same basin. These methods are used to support already existing populations with recruitment problems. These actions should only be performed when all reasons for the species decline are understood, and the cause of the problems are managed (McMurray and Roe 2017). In the river Lutter, Germany, the release of artificially infected fish hosts has been a success with a self-sustaining FPM population after 10 years (Altmüller and Dettmer 2006). The river had previous severe problems with high sedimentation loads from ditches but the sedimentation have been reduced over a period of 10 years using sediment traps. Today the population of FPM contains more than 80% juvenile FPM. Another good example of the method comes from the Southwest of Sweden where the Swedish Anglers Association (SAA) has released infected brown trout into a small creek since 2011. This creek had in 2011 no known individuals of FPM. In the same year, the SAA also performed a site-specific restoration at five sites in this creek, adding boulders and gravel to enhance the environment for the brown trout. After 10 years, the first juvenile FPM were found at two of the restored sites.

Reintroduction—The release of a species at a location where it is not currently present and that is outside the geographic boundaries of existing local populations or metapopulations, but where there is evidence for the former presence of the species in historical times.

There are few studies describing different strategies to enhance the chance of a successful reintroduction of FPM (Bolland et al. 2010; Geist 2010; Moorkens 2018), but all of them emphasize the importance of habitat quality regarding the requirements of the FPM, and they do not recommend any actions before the requirements are fulfilled. Unfortunately, there are to our knowledge no scientific papers describing the results from any of the recommended actions where the habitat has been restored prior to the release of juvenile or adult FPM. This is something that needs to be investigated in the future. Such measures are, however, associated with the risk of spreading diseases and parasites, which must be taken into consideration when reintroduction programs are being planned (Brian et al. 2021).

7 The Future

There are numerous studies on the ecology of salmonids and on the ecology of freshwater pearl mussels, but surprisingly few on the interaction between these species and the effects of the infection. In this chapter, we have tried to summarize what we know and highlight the current knowledge gaps. One part that clearly is missing and where more knowledge is needed is the effects on the long-term fitness and life history tactics on fish that have been infected with larvae. Here, more field-based studies are needed to validate the movement and habitat choice of host fish on a finer scale, perhaps by using detailed habitat mapping, pit-tagged fish and a combination of stationary and portable antennae. In such a setup, it would also be possible to investigate to what extent the FPM are spread to different regions using the salmonid host as a vector.

To understand what determines a successful reintroduction it is also important to increase our knowledge on parasite-host coevolution. More infection experiments, using different strains of fish and stages may inform managers if the parasitic stage and combination of host is functioning properly and to what extent it can be improved especially in the long term. Such experiments may have applications in breeding programs for mussels.

It is also of uttermost importance to predict how this system will be affected by climate change, i.e., an increasing temperature. At present, it is clearly the juvenile fish (under yearlings, 0 + fish) with their poorer immune responses that are the better target for the larvae. However, salmonid fry might emerge earlier with a prolonged growth rate as an effect of an increasing temperature. If this imposes a shift in habitat from shallow riffle habitats to deeper habitats earlier in the season (Kaspersson and Höjesjö 2009; Höjesjö et al. 2016) there is a risk of a potential mismatch between the availability of suitable host and glochidia larvae at the given time frame.

Invasive species is also of major concern and we need to learn more. Brook trout has not been reported to act as a functional host of FPM in Europe. Instead, the larvae generally are repelled from the brook trout after a few weeks. This could be problematic in regions of a relatively high density of brook trout where the number of successful infections will be reduced due to the decreased likelihood of finding a suitable host.

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