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ORIGINAL ARTICLE

The endangered freshwater pearl mussel *Margaritifera margaritifera* shows adaptation to a local salmonid host in Finland

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Abstract

1. The freshwater pearl mussel *Margaritifera margaritifera* (FPM) is an endangered unionid which has a glochidium larva that attaches to the gills of Atlantic salmon *Salmo salar* or brown trout *S. trutta*, although some FPM populations have been shown to exclusively attach to only one of these species. The origin of host fish populations may be crucial for conservation actions for this mussel species, but the relative suitability of local (sympatric) and non-local (allopatric) salmonid populations as the hosts for FPM has been studied only rarely. We hypothesised that FPM glochidia would show adaptation to local salmonid strains and, therefore, that they would be more successful (abundant, larger) attached to sympatric than to allopatric fish.
2. Here, we investigated the infection success (abundance and growth of encysted larvae in fish) of FPM in local versus non-local fish by caging different strains of brown trout and Atlantic salmon in rivers where FPM populations are present.
3. Higher abundances of glochidia in local fish were observed in three brown trout streams, and larger glochidia were found in sympatric hosts in one brown trout stream and in one salmon river. Furthermore, non-local allopatric fish were not better hosts than local fish in any of the FPM populations tested, neither in brown trout or salmon rivers and neither in abundance nor size of larvae. Therefore, the results supported the hypothesis that glochidia show local adaptation by being more successful when attached to local fish strains.
4. Thus, the local, sympatric fish strain should be preferred in FPM conservation programmes that involve captive breeding of juvenile mussels and introduction of host fish, but the regional assessment of local host dependency of FPM also would be important outside the current study area.
5. The results also indicate the importance of restoration of original salmonid populations in FPM rivers to enable the natural, effective reproduction cycle of FPM in their original, sympatric hosts, and thus to promote the recovery of endangered FPM populations.

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KEYWORDS
conservation, glochidia, host–parasite co-evolution, local adaptation, Unionoida

1 | INTRODUCTION

Freshwater mussels (Unionida) have declined globally (Haag & Williams, 2014; Lydeard et al., 2004). For example, populations of the freshwater pearl mussel, *Margaritifera margaritifera* (FPM), have collapsed dramatically during recent decades (Bauer, 1988; Cosgrove et al., 2000; Geist, 2010; Jung et al., 2013; Lopes-Lima et al., 2017) and the species is now classified as critically endangered in Europe (Cuttelod et al., 2011). Furthermore, young mussels often are absent or rare in many remnant FPM populations (Cosgrove et al., 2000; Geist, 2010), indicating unsuccessful reproduction and probable extinction debt.

The reproduction cycle of Unionida (Hyriidae, Unionidae and Margaritiferidae) is complex, and includes an obligatory parasitic stage, the glochidium larva, which infects fish or amphibian hosts (Barnhart et al., 2008; Bauer, 2001; Lopes-Lima et al., 2017). For European FPM, the salmonids brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*) are the suitable host fishes (Bauer, 1987; Hastie & Young, 2001; Salonen et al., 2016; Young & Williams, 1984), although Danube salmon (*Hucho hucho*) may be an additional but poor host (Taeubert & Geist, 2017). The parasitic phase of FPM in the gills of host is of exceptionally long duration at almost one year, and is characterised by a remarkable growth (Bauer, 1987; Denic et al., 2015; Salonen et al., 2016). Thus, the infectivity of glochidia and performance of FPM during the parasitic life cycle stage are important factors concerning the reproduction and furthermore the full dispersal and recruitment of this threatened mussel species.

FPM inhabit only rivers and streams. One reason for their low recruitment and decline is low density or the complete absence of suitable fish hosts as a consequence of migration obstacles and/or overfishing (Cosgrove et al., 2000; Geist, 2010; Oulasvirta, 2011). Therefore, stocking of host salmonids, with or without encysted FPM glochidia, often has been used to promote restoration of FPM populations (Bauer, 1988; Geist et al., 2006; Simon et al., 2015). Captive FPM breeding programmes, in which FPM juveniles are cultivated in fish in captivity to be released into rivers, also have been started recently (Eybe et al., 2013, 2015; Gum et al., 2011; Hoftyzer et al., 2008; Thomas et al., 2010). However, the source of the salmonid hosts in relation to FPM origin may have important consequences for the success of both of the above conservation actions, because it has been observed recently that FPM populations inhabiting large river channels often prefer Atlantic salmon as their host, whereas FPM in smaller streams may use only brown trout as their host (Karlsson et al., 2014; Österling & Wengström, 2015; Salonen et al., 2017; Wacker et al., 2019). In addition to this host specificity, populations or strains within a host species also may vary in their suitability (Jung et al., 2013; Österling & Larsen, 2013; Taeubert et al., 2010). Therefore, the potential degree of local/non-local adaptation (i.e., the preference for either sympatric or allopatric fish hosts within the suitable species) needs further investigation. In fact, identification of primary mussel and host fish relationships and compatibilities recently were ranked as one of the urgent research priorities in conservation of endangered freshwater mussels by Ferreira-Rodríguez et al. (2019). So far, only Österling and Larsen (2013) have addressed host strain specificity experimentally by using FPM and a host fish strain originating from the same river. Interestingly, they found that an allopatric, non-local brown trout strain appeared to be the best host for FPM, having greater glochidia abundance and larger size (Österling & Larsen, 2013). Furthermore, Jung et al. (2013) found glochidia survival, growth and prevalence to be higher in brown trout originating from a different country to the FPM. In addition, no signs of local adaptation were observed in the relationship between *Margaritifera laevis* and its salmonid host *Oncorhynchus masou masou* in Japan (Kitaichi et al., 2021). By contrast, Taeubert et al. (2010) showed that brown trout that originated outside the distribution range of FPM were poorer hosts than trout from within the FPM range, and that the more local (although not sympatric) host fish were the most suitable hosts.

Local adaptation, higher infection success and fitness of parasites in their local (sympatric) than in non-local (allopatric) host populations, has been found frequently in host–parasite associations (e.g., Ebert, 1994; Greischar & Koskella, 2007; Kaltz & Shykoff, 1998; Saarinen & Taskinen, 2005). However, local maladaptation, when local host individuals are less suitable hosts than those from a non-local population, also has been observed (Kaltz et al., 1999). Generally, theories predict that in a given host–parasite relationship the most rapidly evolving partner (i.e., the one having a shorter generation time, higher mutation rate or higher migration rate [gene flow]), usually is locally adapted whereas the other partner is not (Blanquart et al., 2012; Gandon, 2002; Gandon & Michalakis, 2002; Lively, 1999). Migration rate of FPM can be expected to be lower than that of the salmonid host since the migration of FPM depends on movements of fish hosts carrying their larvae; therefore, this should decrease the probability of local adaptation in FPM with respect to fish. In addition, and unlike the majority of parasites, the generation time of FPM (with a life span of 40–200 years and age at first reproduction of 10–15 years (Bauer & Wächtler, 2000; Jung et al., 2013; Young & Williams, 1984)), is much longer than that of salmonids (typical life span <10 years and at first reproduction <5 years; see, e.g., Klemetsen et al., 2003). Thus, theoretically, local maladaptation should be observed in FPM (see, e.g., Blanquart et al., 2012), providing better infectivity in allopatric salmonid hosts. Furthermore, the likelihood of local adaptation of the parasite should, theoretically, increase with virulence (i.e., highly pathogenic parasites are more frequently locally adapted than less harmful parasites [Gandon, 2002; Lively, 1999]). Although FPM infection is associated with harm and even mortality to the fish (Chowdhury, Marjomäki, et al., 2021; Marwaha et al., 2021; Österling et al., 2014; Taeubert & Geist, 2013),

and induces acquired immunity in salmon and trout (Chowdhury et al., 2018), FPM generally are considered a benign rather than a virulent parasite (e.g., Ziuganov, 2005) which also should decrease the tendency for local adaptation by FPM. Finally, the partner having the larger population size often is the one that is locally adapted, and usually this is the parasite rather than the host (Ebert, 1994; Price, 1980). In the present host–parasite case, current populations of FPM probably are smaller than that of the salmonid species, but the historical population sizes of FPM have probably been enormous. However, high host specificity often leads to local adaptation of parasites (Gandon, 2002), and as the survival of parasites depends critically on compatibility with the local host, the parasite is, in general, expected to have a stronger selection pressure on compatible host genotypes than vice versa (Douda et al., 2017). Furthermore, local adaptation by parasites generally is found when host migration is low, and parasites disperse at the same rate (or slightly more) than their hosts (Lively, 1999). In the current case, movement by adult mussels is minor, so they disperse only as larvae relying on the host, which suggests local adaptation, although the migration and gene flow of salmonid hosts between rivers also can be very low (Palstra & Ruzzante, 2010; Verspoor, 1997).

In light of these different scenarios, we studied the potential local adaptation of FPM to salmonid host strain. According to the studies and theories mentioned above, we expected adaptation by FPM to local host populations within the most suitable host species, because the high specialisation observed in FPM between host species (Salonen et al., 2017) should favour local adaptation (Gandon, 2002). Thus, our hypotheses were that (a) glochidia will be more infective to local host stains than to non-local host strains, and (b) glochidia will grow faster in local than non-local host strains.

2 | METHODS

Performance of FPM, measured as prevalence and abundance of encysted FPM glochidia in fish gills and as length of glochidia, in local and non-local hosts was investigated by conducting a series of transplant (cage) experiments, with as fully reciprocal design (see Kawecki & Ebert, 2004) as logistic challenges permitted. The experiments were carried out in 2011–2013 by placing fish in cages close to FPM beds in tributaries of the River Iijoki (catchment of 14,200 km^2, Baltic Sea drainage), in the main channel of the River Simojoki (catchment of 3160 km^2, Baltic Sea drainage) and in tributaries of the River Luttojoki (the River Tuloma catchment of 21,500 km^2, Barents Sea drainage) in Finland (Figure 1). The experiments involved both of the two suitable host species for European FPM (Atlantic salmon and brown trout) (Salonen et al., 2016), and in each experiment fish from a local population and from two non-local populations within the same species were used (Table 1).

Brown trout strains were caged in six FPM streams, four of them belonging to the River Iijoki and two to the River Tuloma catchment (Table 1; Figure 1). In these streams, brown trout was the only salmonid and/or the most suitable host for FPM (Salonen et al., 2017). Atlantic salmon strains were caged in two FPM rivers (Table 1; Figure 1), representing former (River Livojoki) and present (River Simojoki) spawning grounds of Atlantic salmon. Therefore, both these rivers are referred to as salmon rivers, and the FPM populations in these rivers are specialised to use salmon as their host (Salonen et al., 2017). For protection of FPM, the exact locations of these caging experiments are not given but can be provided upon request. The characteristics of each study river are given in Table S1.

The sea-migrating (anadromous) brown trout and Atlantic salmon strains originating from the River Iijoki were obtained from fish farms where they have been maintained by the Natural Resource Institute Finland (Luke) since damming of the Iijoki main channel for hydropower production in the 1960s (see, e.g., Erkinaro et al., 2011). Before building of the dams, the anadromous Iijoki brown trout also may have migrated to spawn in the smaller streams included in this study, but as it generally, according to local knowledge, preferred the main channel for spawning, this strain also was considered a non-local fish in these stream experiments. Farmed Rautalampi brown trout (a strain originating

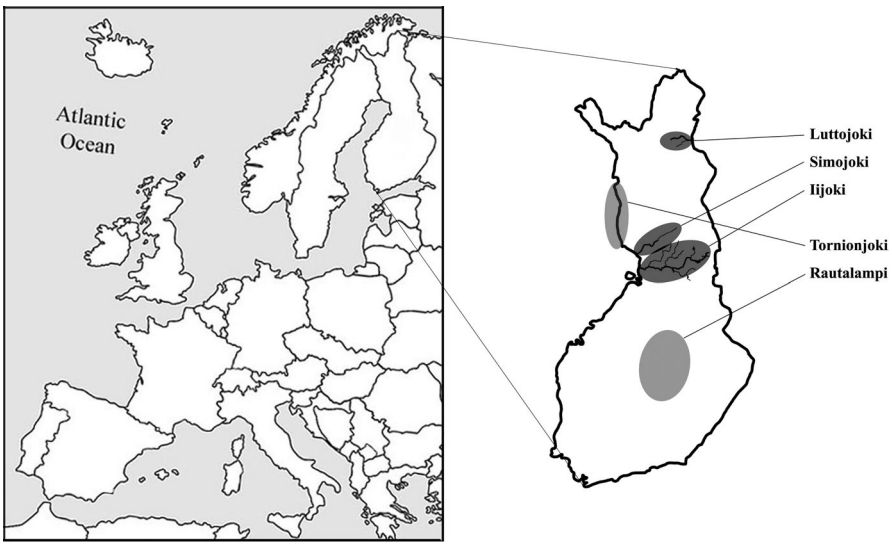

FIGURE 1 Map showing Finland in Europe and the three northern Finnish catchments where the cage experiments were performed (dark grey), and the location of all catchments from where the fish strains used in the experiments originated. The River Iijoki catchment included Ala-Haapuanoja, Lohijoki, Porraslammenoja and Portinjoki streams, and River Livojoki, and the River Luttojoki area included Hanhioja stream and the River Kolmosjoki (Table 1)

TABLE 1 The caging rivers, the brown trout and Atlantic salmon strains compared (^{L} indicates the local partner) and the results of statistical analyses for the differences in abundance of FPM infection and in length of FPM glochidia between the partner strains

				Abundance of glochidia			Length of glochidia		
Species	**River**	**Strains compared**		**Analysis**	***p***	***H***	**Analysis**	***p***	***H***
Brown trout	Ala-Haapuanoja	Ala-Haapuanoja^{L}	Rautalampi	M-W	0.795	0	ANOVA	0.784	0
		Ala-Haapuanoja^{L}	Iijoki	M-W	0.036**	local		0.646	0
		Iijoki	Rautalampi	M-W	0.021**	n.a.		0.299	0
	Lohijoki	Lohijoki^{L}	Portinjoki	M-W	>0.999	0	-		
		Lohijoki^{L}	Iijoki	M-W	0.528	0	-		
		Portinjoki	Iijoki	M-W	0.174	0	-		
	Porraslammenoja	Porraslammenoja^{L}	Rautalampi	M-W	0.105	0	ANOVA	0.946	0
		Porraslammenoja^{L}	Iijoki	M-W	>0.999	0		0.939	0
		Iijoki	Rautalampi	M-W	<0.001***	n.a.		0.252	0
	Portinjoki	Portinjoki^{L}	Lohijoki	M-W	>0.999	0	-		
		Portinjoki^{L}	Iijoki	M-W	>0.999	0	-		
		Lohijoki	Iijoki	M-W	0.570	0	-		
	Hanhioja	Hanhioja^{L}	Kolmosjoki	ANOVA	<0.001***	local	ANOVA	<0.001***	local
		Hanhioja^{L}	Luttojoki		<0.001***	local		0.944	0
		Kolmosjoki	Luttojoki		0.608	0		<0.001***	n.a.
	Kolmosjoki	Kolmosjoki^{L}	Hanhioja	ANOVA	0.441	0	ANOVA	0.799	0
		Kolmosjoki^{L}	Luttojoki		0.011**	local		0.732	0
		Hanhioja	Luttojoki		0.236	0		0.293	0
Atlantic salmon	Livojoki	Iijoki^{L}	Simojoki	M-W	0.312	0	M-W	0.108	0
		Iijoki^{L}	Torniojoki	M-W	0.132	0	M-W	0.474	0
		Simojoki	Torniojoki	M-W	>0.999	0	M-W	0.009	n.a.
	Simojoki	Simojoki^{L}	Iijoki	M-W	>0.999	0	M-W	0.052*	local
		Simojoki^{L}	Torniojoki	M-W	>0.999	0	M-W	0.906	0
		Iijoki	Torniojoki	M-W	>0.999	0	M-W	0.019	n.a.

Note: ANOVA with Tukey's post hoc test (ANOVA) or Mann–Whitney *U* test (M-W) were used. Statistical significances (after Bonferroni correction when necessary): ***highly significant, $p < 0.001$; **significant, $0.010 \le p < 0.050$; and *marginally significant, $0.050 \le p < 0.100$. 'H' refers to study hypotheses: local = support for local adaptation, n.a. = statistically significant difference but neither of the strains could be assigned as local, and 0 = H_0 hypothesis (no difference) not rejected.

from southern Finland; Figure 1) and Tornionjoki salmon (Figure 1) also were available, while resident brown trout from the streams/rivers Alahaapuanoja, Lohijoki, Porraslammenoja, Portinjoki, Hanhioja, Kolmosjoki and Luttojoki (a resident strain originating from headwaters above the FPM habitats and above the spawning ground of Atlantic salmon of the River Luttojoki main channel), as well as anadromous Atlantic salmon from Simojoki strain were collected by electrofishing.

For the caging experiments, cylindrical steel cages (height 250 mm, diameter 490 mm, mesh 5.7 mm) with two to three replicates per fish strain were used, except for the Porraslammenoja stream, in which only one tank of local trout existed owing to the low availability of 0+ wild trout. The number of fish individuals cage^{-1} population^{-1} was generally between 20 and 30, with some exceptions resulting from low catch of natural fish (Figures 2–4). Cages were placed in the rivers in early autumn shortly before the start of FPM glochidia release and removed after the release so that the caging period varied from 7 to 9 weeks (Table 2). The fish were not provided with food during caging. Loss of fish during caging was minor, ≤ 2 fish per cage.

The farmed fish used in the experiments had not been in contact with FPM earlier. Size differences of the wild fish caged generally were small (Table S2), indicating that every fish belonging to the age group 0+ (hatched in the previous spring and thus having no FPM infection before). In 2011, fish of different ages were caged, but only the 0+ individuals were included in statistical analyses to exclude the potential effects of previous FPM contact (Hastie & Young, 2001). As an exception, in the experiments at the River Tuloma catchment the size differences (Table S2; Hanhioja and Kolmosjoki) between fish groups were considerable, probably indicating that the largest Luttojoki fish also included older individuals. However, these fish were collected from an FPM-free area and they then had no previous contact with FPM. Thus, these fish were included to analyses, and in these experiments the glochidia numbers were standardised by dividing the number by fish mass (Taeubert et al., 2010) to exclude the potential effect of larger host size (i.e., gill area) on the results.

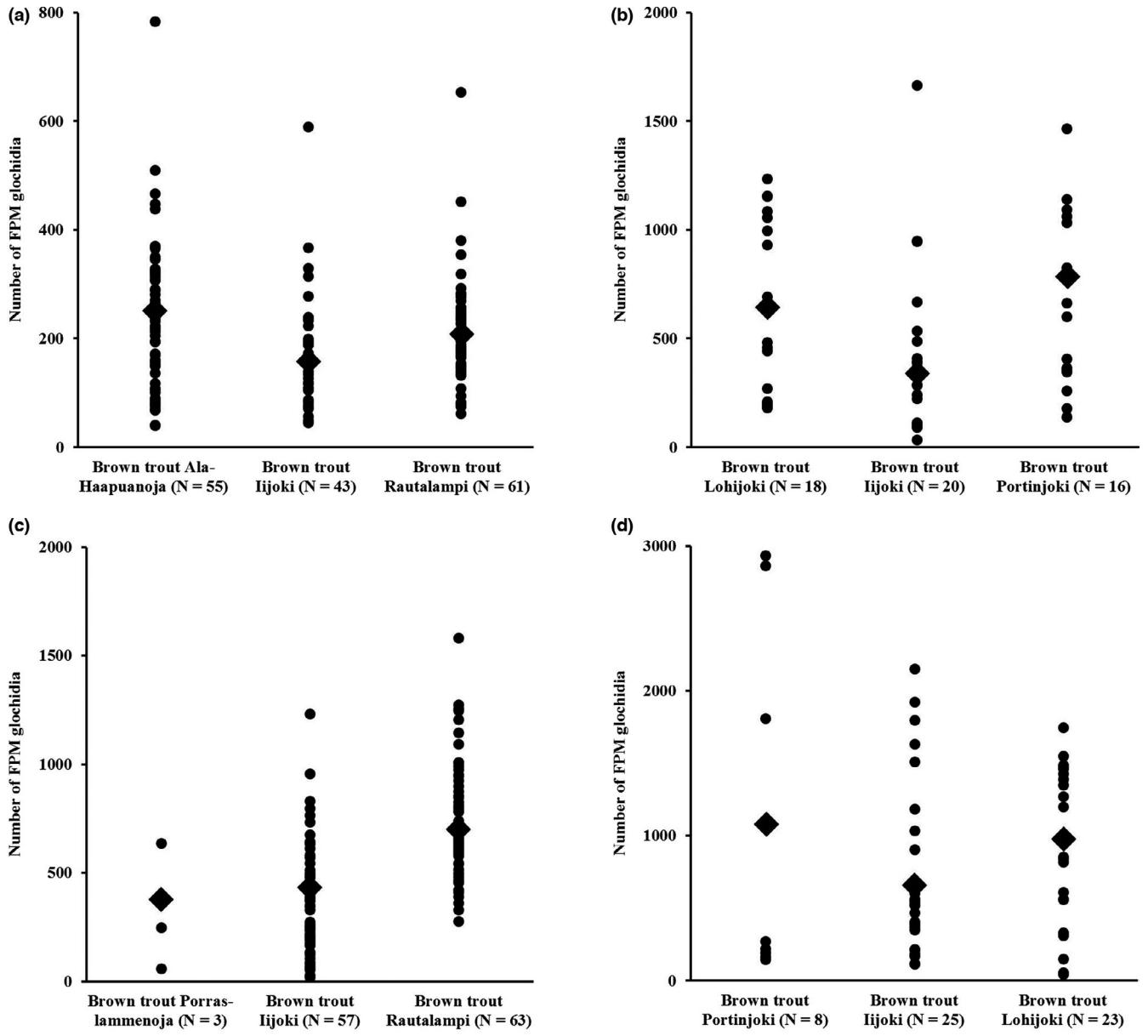

FIGURE 2 Abundance (number) of FPM glochidia in different brown trout strains caged in the streams Ala-Haapuanoja (a), Lohijoki (b), Porraslammenoja (c) and Portinjoki (d), all belonging to the River Iijoki catchment. The individual dots represent the number of larvae in individual fish, and the diamond is the mean abundance of the strain

After caging, fish were killed with a sharp blow on the head and transported to the laboratory on ice. However, in 2011 only around a third of the fish from each group were killed immediately after the caging, while the rest were transported to Konnevesi Research Station (University of Jyväskylä) where they were maintained — to monitor the growth of glochidia — in individual, flow-through aquaria, and examined at varying intervals during the next 8 months, when total length and fresh mass were measured. Then gills were dissected and pressed between two large glass plates and the number of FPM glochidia in each gill was counted microscopically using transmitted light. Length (the longest diameter) of glochidia was measured microscopically from a randomly selected subsample of larvae ($n = 10$) using an ocular scale in 2012–2013 experiments (Table 1).

2.1 | Data analysis

Differences in the prevalence of FPM infection (percentage of fish carrying encysted FPM glochidia) between different salmonid strains were analysed using χ^2 test. For analyses of glochidia abundance (average number of FPM glochidia fish^{-1}) and glochidia length between different strains, parametric tests (ANOVA and Tukey's post hoc test) for comparisons of means were applied (with variable transformation if necessary), but if the assumptions of parametric testing were not met, nonparametric rank order tests (Mann–Whitney *U* test) were applied (details in Table 1). In the case of glochidia length, fish-individual-specific mean glochidium length was used as the response variable (i.e., individual fish as the statistical unit).

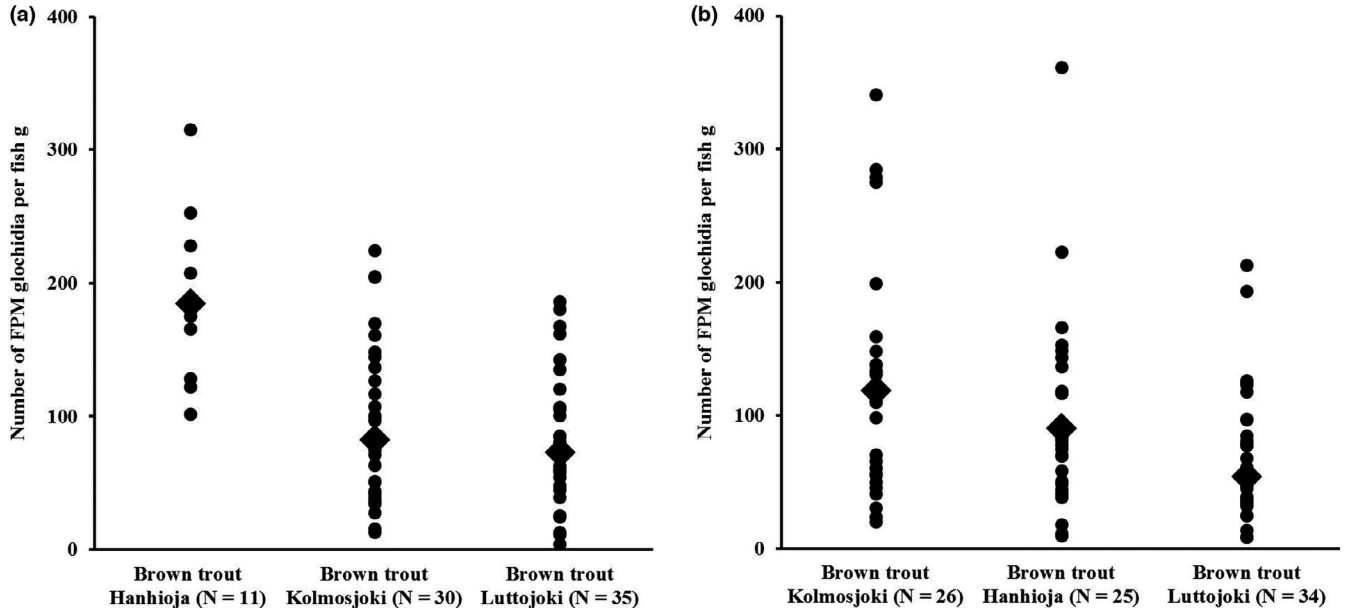

FIGURE 3 Abundance (number) of FPM glochidia in different brown trout strains caged in Hanhioja stream (a) and Kolmosjoki river (b) in the River Tuloma catchment. The values were exceptionally given and analysed per g fish body mass as a result of potential differences in the size of the fish compared (see Table S2). The individual dots represent the fish-mass corrected number of larvae in individual fish, and the diamond is the mean abundance of the strain

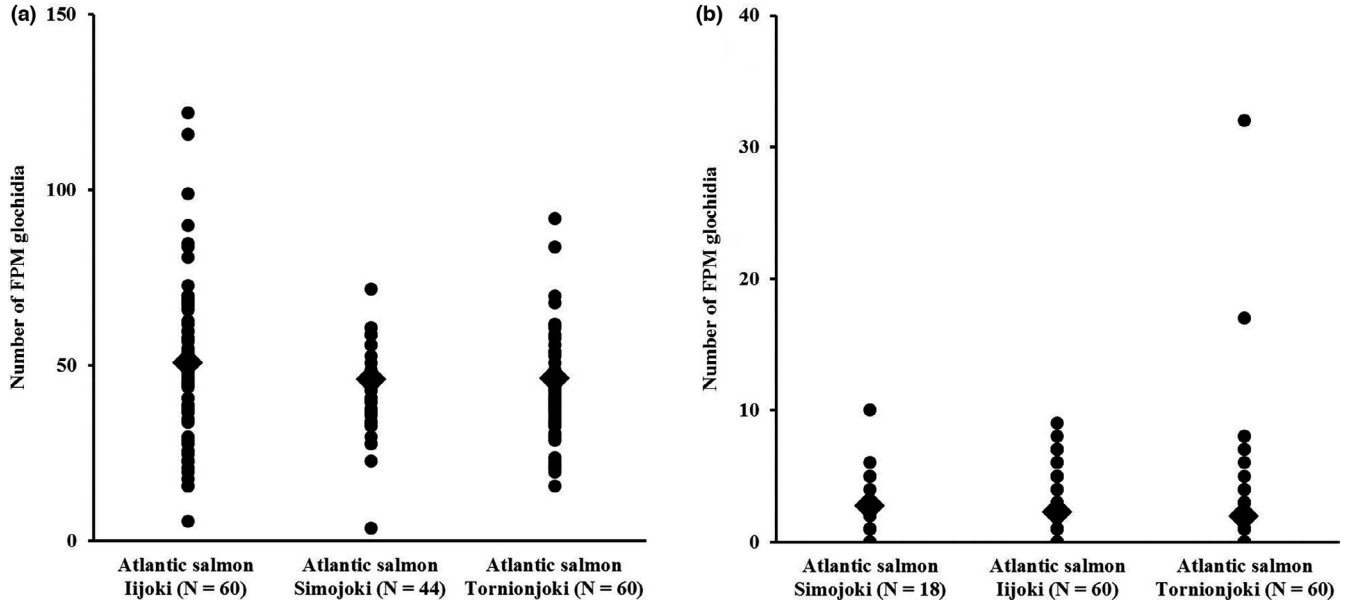

FIGURE 4 Abundance (number) of FPM glochidia in different Atlantic salmon strains caged in the River Livojoki (a) and River Simojoki (b). The individual dots represent the number of larvae in individual fish, and the diamond is the mean abundance of the strain

Before the comparisons between different salmonid strains, the significance of differences in prevalence and abundance between the replicate cages (and between the examination dates in the 2011 experiments), were analysed. Differences between the replicates or between the 2011 examination dates within any fish strain in any experiment were non-significant ($p > 0.05$ in all cases). Thus, data from the replicate cages were pooled for the subsequent analyses. Statistical analyses were performed with SPSS v22.0.01 (IBM Corporation, Armonk, NY, USA) and Bonferroni correction was applied in multiple comparisons.

3 | RESULTS

3.1 | Brown trout experiments in the River Iijoki catchment

FPM glochidia were found in every fish individual from both local and non-local strains after 7.5 weeks caging in each of the four brown trout streams (Ala-Haapuanoja, Lohijoki, Porraslammenoja and Portinjoki) in the River Iijoki catchment. Thus, there were no differences in the prevalence of FPM infection between any strains.

TABLE 2 Length (mean ± *SE*) of FPM glochidia in different brown trout and Atlantic salmon strains after the caging period shown in the first row

	27.08–18.10.2012		23.08–04.10.2012		20.08–16.10.2013	
Species and strain	**Ala-Haapuanoja**	**Porraslammenoja**	**Hanhioja**	**Kolmosjoki**	**Livojoki**	**Simojoki**
Brown trout Ala-Haapuanoja	80 ± 0.9					
Brown trout Porraslammenoja		119 ± 4.5				
Brown trout Hanhioja			102 ± 1.7	82 ± 1.6		
Brown trout Kolmosjoki			91 ± 1.5	83 ± 1.7		
Brown trout Luttojoki			102 ± 1.5	85 ± 0.9		
Brown trout Iijoki	82 ± 1.3	119 ± 4.5				
Brown trout Rautalampi	79 ± 2.0	121 ± 2.6				
Atlantic salmon Iijoki					113 ± 1.1	91 ± 1.8
Atlantic salmon Simojoki					117 ± 1.6	100 ± 3.0
Atlantic salmon Tornionjoki					110 ± 1.2	98 ± 2.0

Among the brown trout caged in the Ala-Haapuanoja stream, the abundance of FPM infection in local trout was significantly higher than that in anadromous Iijoki trout, but was not statistically different from that in non-local Rautalampi trout (Table 1; Figure 2). The abundance of FPM infection in local fish did not differ statistically from either of the non-local fish strains in the Lohijoki, Porraslammenoja and Portinjoki streams (Table 1; Figure 2). Significant differences in abundance were found between the non-local strains in the Ala-Haapuanoja and Porraslammenoja streams, but not in the Lohijoki and Portinjoki streams (Table 1; Figure 2).

There were no statistically significant differences in the length of encysted FPM glochidia between any of the different brown trout strains in the Ala-Haapuanoja and Porraslammenoja streams (Tables 1 and 2).

3.2 | Brown trout experiments in the River Tuloma catchment

FPM glochidia were found from all fish individuals after 6 weeks caging in the River Tuloma catchment. Thus, there were no differences in prevalence of FPM infection between any of the three trout strains tested in the Hanhioja and Kolmosjoki streams.

The abundance of FPM infection in the Hanhioja stream was significantly higher in local Hanhioja trout than in non-local Luttojoki and Kolmosjoki trout (Table 1; Figure 3). The abundance of FPM infection in the River Kolmosjoki also was significantly higher in local trout than in non-local Luttojoki trout, but did not differ significantly from the abundance in the other non-local strain. In both rivers the non-local strains did not differ significantly from each other in terms of glochidia abundance (Table 1; Figure 3).

Among the fish caged in the Hanhioja stream, the glochidia in the local trout were significantly larger than those in the non-local Kolmosjoki trout (Tables 1 and 2). The difference in length of glochidia between the non-local strains also was statistically significant in the Hanhioja experiment (Tables 1 and 2). There were no significant differences in glochidia length between any of the different fish strains in the River Kolmosjoki (Tables 1 and 2).

3.3 | Atlantic salmon experiments

FPM glochidia were found in all (100%) salmon individuals after 8 weeks caging in the River Livojoki (Iijoki catchment), meaning there were no differences in the prevalence between different salmon strains in that river. In the main channel of the River Simojoki, 72% of local Simojoki salmon, 72% of non-local Iijoki salmon and 63% of non-local Tornionjoki salmon were parasitised by FPM glochidia. These differences in prevalence were not significant (χ^2 test, Bonferroni-corrected $p > 0.999$ in all three comparisons).

There were no differences in the abundance of FPM infection between any of the salmon strains in the River Livojoki (Table 1; Figure 4). Likewise, no differences in the abundance were observed between salmon strains in River Simojoki (Table 1; Figure 4).

There were no statistically significant differences in glochidia length between the local and non-local salmon caged in the River Livojoki, while a significant difference between non-local strains was found (Tables 1 and 2). The FPM glochidia in the River Simojoki were marginally significantly larger in the local salmon than in the non-local Iijoki salmon (Tables 1 and 2), while the difference from the other non-local strain was not significant (Table 1). There also was a significant difference in glochidia length between non-local strains in the River Simojoki (Tables 1 and 2).

4 | DISCUSSION

Our results support the local adaptation hypothesis, that is better infection success of a parasite in a local, sympatric host. This is in line with the general idea that parasites usually are adapted to the host

genotype most frequently encountered in a habitat (Ebert, 1994; Greischar & Koskella, 2007; Kaltz & Shykoff, 1998). Local adaptation of FPM was not as clearly obtained from several brown trout rivers, but in none of these rivers were the fish from non-local, allopatric strains better hosts than the local fish. No clear indication of local adaptation was observed in the Atlantic salmon experiments but, as in the brown trout rivers, in none of the salmon rivers was the non-local fish the better host. Thus, there was no support for the local maladaptation hypothesis in this parasite–host relationship from any of the experiments in this study. Interestingly, both Karlsson et al. (2014) and Geist et al. (2018) found the genetic differentiation among mussel populations that use only trout as their host to be very large, and significantly larger than among salmon-specialised mussel populations. This genetic differentiation may be one explanation for the higher local adaptation observed in mussels that use brown trout as their host. However, in Swedish catchments where different host species (salmon, resident brown trout, anadromous trout) occur, no genetic evidence for such co-adaptation was found (Geist et al., 2010), stressing the importance of a regional assessment of host dependency.

Many freshwater mussel species are endangered throughout the world (Lydeard et al., 2004). However, surprisingly, the potential local adaptation of mussels to their fish hosts has been studied only rarely, even though laboratory breeding and translocation programmes to restore and re-establish populations of endangered mussels are used widely (Eybe et al., 2013, 2015; Gum et al., 2011; Hoftyzer et al., 2008; Thomas et al., 2010). Previously, Rogers et al. (2001) addressed the question of adaptation of freshwater mussels to their local fish host and found evidence for local adaptation in tan riffleshell (*Epioblasma florentina walkeri*) and fantail darter (*Etheostoma flabellare*). Furthermore, Douda et al. (2017) observed an ability to exploit foreign host fishes when studying infectivity of the invasive freshwater mussel *Sinanodonta woodina* at a global scale, and no evidence for population-specific adaptation in the original range of *S. woodiana*, indicating the importance of geographical scale and possibility of host counter-adaptation in studies of local adaptation of freshwater mussels to their fish hosts. Therefore, local adaptation (or maladaptation) and population-level differences in host compatibility of freshwater mussels with respect to fish host population could be an important factor affecting the success of conservation operations with mussels, which should be studied further so that potential association-specific differences can be taken into account to increase the success of conservation of freshwater mussels (Douda et al., 2014; Ferreira-Rodríguez et al., 2019). Huber and Geist (2019) have shown that non-sympatric fishes can be suitable hosts for duck mussel (*Anodonta anatina*), but also, interestingly, found differences in duration of the metamorphosis/ development of glochidia between different host fish species – something that to our knowledge has not yet been studied for the freshwater pearl mussel. Determining metamorphosis success rate and juvenile quality of FPM (see Douda et al., 2020) may yield other new research directions in the area of population-level host suitability and local adaptation. Finally, as FPM glochidia infestation may provide protection for host fish against bacterial disease (Chowdhury, Roy, et al., 2021), yet unknown features of the co-evolutionary relationship between endangered FPM and their salmonid hosts – in addition or related to local adaptation – may be recovered through successful conservation programmes.

According to the theoretical models of host–parasite coevolution, our findings of adaptation of FPM to local brown trout should be related either to a higher migration rate or a higher population size of FPM relative to brown trout (see review by Blanquart et al., 2012). The River Tuloma catchment, where both the studied FPM populations exhibited clear adaptation in parasitising brown trout from the local populations, is the area where the largest Finnish FPM populations are found (see Oulasvirta, 2011). Thus, local adaptation of FPM in the tributaries of the River Tuloma catchment could be linked to the large number of FPM populations and individuals, which fuels the capacity of FPM for evolutionary adaptations (e.g., Blanquart et al., 2012). This area also is a hotspot of genetic diversity of FPM in Europe (Geist & Kuehn, 2008), which also may have increased the ability of FPM to evolutionarily differentiate in order to more successfully parasitise the local than the allopatric salmonids (see Blanquart et al., 2012). Furthermore, historically (before any anthropogenic effects and, thus, decline in water quality) the number of mussels in these populations may have been enormous, possibly resembling the contemporary population in the geographically adjacent River Varzuga where c. 2 million FPM individuals have been estimated (Ziuganov et al., 1994).

Intuitively, using sympatric fish and FPM, and stocking captive-bred FPM juveniles to the river from where their parental FPM originated (see, also, results by Denic, Taeubert, Lange, et al., 2015), should be the recommended practice. However, previous tests of the potential differences in the suitability of different salmonid strains as host for FPM have found that an allopatric, non-local brown trout strain from another drainage (Österling & Larsen, 2013), or from another country (Jung et al., 2013) was a better host for FPM than a (more) local strain, opposite to our findings. By contrast, Taeubert et al. (2010) showed that brown trout that originated outside the distribution range of FPM were poorer hosts than trout from within the FPM range, and the more local (although not sympatric) host was the most suitable, consistent with our results. Thus, the geographical scale at which fish strains are tested may affect the findings of local adaptation/maladaptation studies. Furthermore, in many catchments ancient links between FPM and their original, historically sympatric salmonid populations have been altered or erased by relatively recent fish transfers or barriers to migration created by humans. The data in this study came from catchments that generally can be considered to be closer to their natural state than, for example, rivers in central Europe (Jung et al., 2013); especially the small headwater streams, where the links to local adaptation were stronger. Thus, fisheries management may explain why local adaptation has not been detected everywhere, as in the studies of Österling and Larsen (2013) and Jung et al. (2013).

Owing to the enormous collapse of FPM populations during the last century, the conservation of FPM requires artificial propagation, including captive breeding techniques and restoring suitable host fish populations via restocking (Geist, 2010; Gum et al., 2011), an approach that would be useful for other mussel species, too (Douda et al., 2014). Although host specificity by FPM is well known, the present study provides confirmation that it exists and demonstrates a novel approach to determining host–parasite relationships at the population level. In conclusion, for the conservation of FPM, it is important to know the potential patterns of local adaptation of FPM with respect to fish host populations. Our results suggest that parasitism of FPM glochidia in terms of abundance and growth is most successful in a sympatric fish host – that is, in fish originating from the same area, or river, as the mussel. Although stocking or using allopatric salmonid hosts can be and has been applied in the conservation of this parasite species, the best success of these actions is likely to come with use of original, sympatric fish with respect to a given FPM population.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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