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The parasite–host relationship of glochidia (Mollusca: Margaritiferidae) on the gills of young-of-the-year Atlantic salmon (*Salmo salar*)

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The relationship between condition of overwintering young-of-the-year salmon (*Salmo salar*) and levels of infection by glochidia of the freshwater mussel *Margaritifera margaritifera* was investigated at two sites in South River, Nova Scotia, which contained significantly different concentrations of adult *M. margaritifera*. Although the salmon at site A (which had 5.1 times fewer freshwater mussels than site B) were significantly larger than the salmon at site B, there was no correlation between size of salmon and abundance of glochidia. Mean condition factor (K) was lower at site B. There was a significant increase in K in spring, which was most likely due to spring growth as there was no significant decrease in glochidia abundance. Significant, negative regressions were found only in January and February, when 24 and 66% of the variation in K, respectively, could be explained by the abundance of glochidia on the gills. Abundance and prevalence of infection did not change significantly between October and March. There was, however, a 45% decrease in infections of over 300 glochidia after December, which may have been due to host mortality. The mean size of glochidia increased between October and November, levelled off between December and March, and increased again in April. In May there was no further increase in growth, which is believed to be due to the loss of larger glochidia from the gills at that time. The data suggest an increasingly detrimental impact to juvenile salmon over winter as a function of the time and degree of infection (i.e., intensity, abundance) with mussel glochidia.

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La relation entre la condition physique de jeunes saumons (*Salmo salar*) de 1 an en hiver et la gravité des infections de glochidies chez les moules d'eau douce *Margaritifera margaritifera* a fait l'objet d'une étude en deux endroits à concentrations significativement différentes de moules adultes, dans la rivière South, Nouvelle-écosse. Bien que la taille des saumons du site A (habité par 5,1 fois moins de moules que le site B) se soit avérée significativement plus grande que celle des saumons du site B, il n'y avait pas de corrélation entre la taile des poissons et l'abondance des glochidies. Le coefficient d'embonpoint moyen (K) était plus faible au site B. Il s'est produit une augmentation significative de la valeur de K au printemps, augmentation probablement due à la croissance printanière, puisqu'il ne s'est pas produit de diminution significative de l'abondance des glochidies. Des régressions négatives significatives n'ont été constatées qu'en janvier et février; 24% de la variation de K en janvier et 66% en février d'expliquaient par l'abondance des glochidies sur les branchies. L'abondance et la fréquence des infections n'ont pas changé significativement d'octobre à mars. Cependant, il s'est produit une diminution de 45% des infections graves (plus de 300 glochidies) après décembre, peut-être à cause de la mortalité des hôtes. La taille moyenne des glochidies a augmenté entre octobre et novembre, s'est stabilisée entre décembre et mars et a augmenté de nouveau en avril. En mai, la croissance a cessé, probablement parce que les glochidies les plus grosses avaient quitté les branchies à ce moment. Les résultats indiquent que la gravité des infections (i.e., intensité, abondance) de glochidies chez les moules et le moment où les saumons sont atteints ont un effet de plus en plus délétère sur les jeunes saumons à mesure que progresse l'hiver.

[Traduit par la rédaction]

Introduction

The parasitism of the gills of salmonid fishes by glochidia of pearly river mussels (Mollusca: Margaritiferidae) is common in Holarctic streams and rivers (Murphy 1942; Taylor and Uyeno 1965; Clarke 1981; Young and Williams 1984). Despite the prevalence of the phenomenon, relatively little is understood about the parasite–host relationship in the wild or of the potentially deleterious impacts to the infected fish. Murphy (1942) and Meyers and Millemann (1977) each reported mortalities in experimentally infected brown trout (*Salmo trutta*), Atlantic salmon (*S. salar*), cutthroat trout (*S. clarki*), rainbow trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*), and chinook salmon (*O. tshawytscha*). In contrast, Young et al. (1987) found no mortality or change in growth rate in experimentally infected brown trout. The only known field study to investigate the development and abundance of glochidia over winter, that by Young and Williams (1984) in Scotland, did not explore the possibility of mortalities in infected brown trout.

In eastern Canada, where Atlantic salmon is a commercially important resource, glochidia infections have been found on the gills of this species in several river systems (Hare and Frantsi 1974; Hare and Burt 1975). As in Scottish streams (see Young and Williams 1984), glochidia remain attached to the gills of the host over winter until they metamorphose and drop off in the spring. Previous research has identified the winter season as a critical period for survival of Atlantic salmon (Gardiner and Geddes 1980; Myers et al. 1986), especially young-of-the-year fish experiencing their first winter (Lindroth 1965). Factors, such as parasite abundance, could affect growth or the amount of energy reserves required for overwintering and, hence, survival. To determine the effect of glochidial parasitism, young-of-the-year Atlantic salmon were examined between autumn and spring in a Nova Scotian river where glochidia infestation had previously been reported (Hare and Frantsi 1974). Two hypotheses were formulated and investigated: first, that the condition factor of individual salmon would show an inverse relationship to the "abundance" of the parasites (Margolis et al. 1982) and second, that "intensity" and "prevalence" of glochidia (Margolis et al. 1982) in the host population was a function of localized stream densities of adult mussels. Finally, to better understand the aspects of the life-history and biology of glochidia, individuals were measured during each monthly

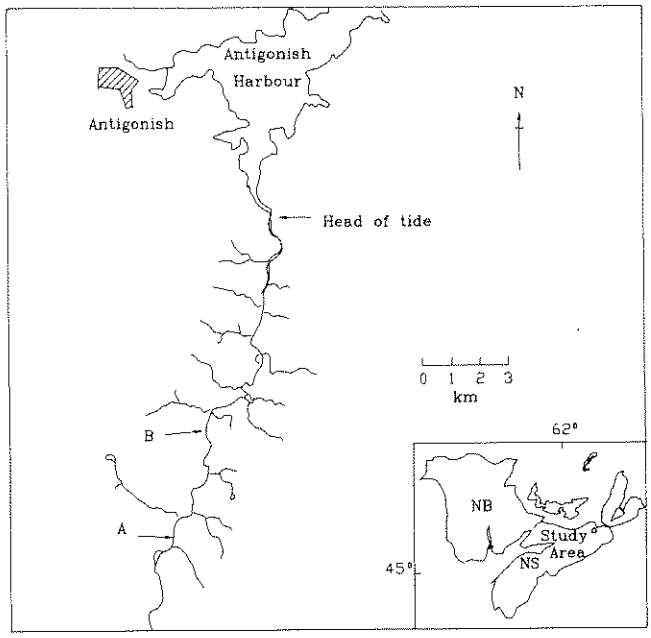

FIG. 1. Map showing the South River system and the location of the two sampling sites.

collection to determine the duration of the parasitic phase and whether size variations over the winter represented glochidial growth or recruitment.

Materials and methods

The two sampling sites (A and B) used for this study are approximately 4 km apart in the midreaches of South River (Fig. 1) in Antigonish County, Nova Scotia (45°36′N, 61°54.8′W). A description of the river and the two study sites was provided by Cunjak (1988*a*).

Between 15 October 1987 and 21 May 1988, monthly collections of young-of-the-year (YOY) wild Atlantic salmon were made from each site by electrofishing. The exception to this schedule was March 1988 when no fish samples were collected at either site owing to ice and high water conditions. Collections from each site comprised the first 9–12 YOY salmon encountered (i.e., no selection). Fish were subsequently weighed (g), measured for fork length (FL, cm), dissected for sex determination, individually labelled, and frozen until examination for parasites in the laboratory. The October collections were of YOY salmon prior to their movement beneath rocks, whereas spring (May) collections occurred after salmon had vacated winter shelters; November to April collections (inclusive) were of salmon that were hiding beneath rocks as part of their normal diurnal winter behaviour pattern (Cunjak 1988*a*).

Adult freshwater pearl mussels, *Margaritifera margaritifera* (identification verified by J. Topping, Mollusc Unit, Canadian Museum of Nature, Ottawa), were enumerated at each of the study sites in mid-May to determine relative population densities. Counts were made by a diver who moved along 1 m wide transects criss-crossing the stream (same transects used by Cunjak (1988*a*) for underwater counts of juvenile salmon). No other freshwater mussel species were found in these sections of South River and, hence, it was assumed that all glochidia found in this study were *M. margaritifera*.

In the laboratory, YOY salmon were dissected and individual gill arches examined microscopically (120–250× magnification). Glochidia were enumerated for each individual gill arch (numbered anterior to posterior, 1–4) and for left and right sides of the fish. Straight-line measurements of glochidia size were taken from the fringe to the ventralmost margin of the valve, using a calibrated micrometer at 100× magnification. All glochidia were removed from the host-epithelial sheath and measured individually up to a maximum of approximately 50/fish; for the more heavily infected fish, subsamples of approximately 50 glochidia were measured. All glochidia were the hookless type.

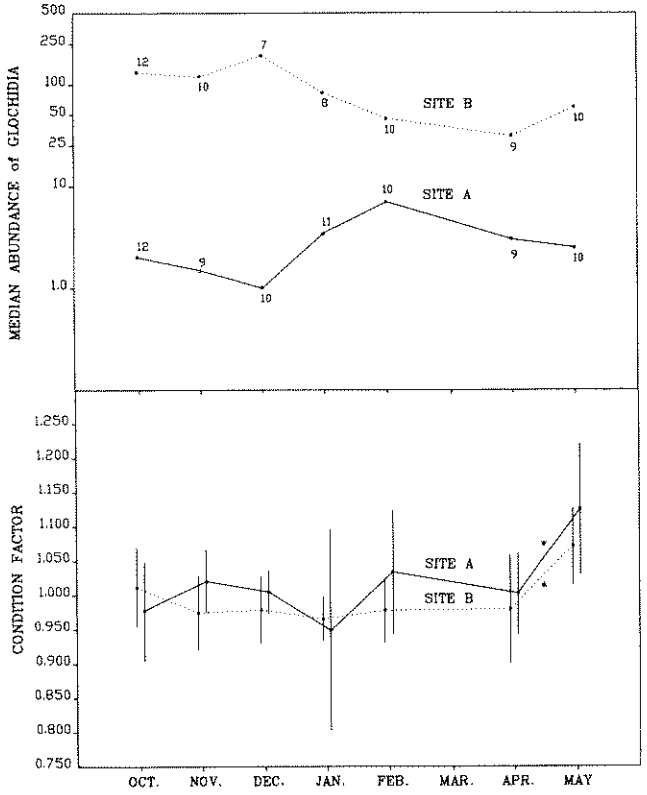

FIG. 2. Monthly changes in the condition factor of the salmon (lower panel) and median abundance of glochidia (upper panel) attached to the gills of young-of-the-year Atlantic salmon at two study sites at South River, Nova Scotia. Numbers in the upper panel refer to sample sizes; vertical lines in the lower panel represent standard deviations (1 SD). *, significant ($p < 0.05$) differences between consecutive months.

All statistical analyses were performed using the SAS computer software system (SAS Institute Inc. 1982) and significance was defined as $p < 0.05$ unless otherwise stated. Student's *t*-tests were used in testing for intersite differences and for differences between host sexes for the variables of condition factor, FL, abundance, and glochidia size. ANOVA was used to test for differences between sampling dates; a posteriori Student–Newman–Keuls' test was used to distinguish interdate differences. Where assumptions of homoscedasticity were violated, nonparametric Kruskal–Wallis test and *t*-test approximations (SAS Institute Inc. 1982) were employed. Simple linear correlation and regression were used to test the relationship between abundance and FL and between abundance and condition factor, respectively. Prevalence and intensity of infection are defined *sensu* Margolis et al. (1982). Median abundance is defined as the midvalue in the abundance data set (which includes uninfected hosts); we prefer its use here because it is less affected by extreme values than the mean.

Results

The population density of *M. margaritifera* was 5.1 times greater at site B than site A; there were 24 mussels found per 97 m^2 (i.e., 0.25 mussels $\cdot m^{-2}$) at site A compared with 115 mussels per 91 m^2 (i.e., 1.26 mussels $\cdot m^{-2}$) at site B.

The abundance of mussel glochidia on the gills of YOY salmon (dates pooled) was significantly ($p < 0.001$) higher ($\bar{X} = 191.7$, $n = 70$) at site B (where adult mussel density was greater) compared with site A ($\bar{X} = 31.5$, $n = 66$). There were marked intersite differences in median abundance on every sampling date (Fig. 2). No significant differences ($p > 0.450$)

TABLE 1. Prevalence (*%P*), intensity (*I*), and abundance (*A*) (±1 SD) of glochidia on the gill arches of young-of-the-year *Salmo salar* from the two study sites at South River, Nova Scotia, between October 1987 and May 1988

	Site A			Site B		
Month	*%P*	*I*	*A*	*%P*	*I*	*A*
Oct.	58.3	1–122	12.3 (34.7)	91.7	1–544	153.3 (191.5)
Nov.	60.0	1–64	17.7 (26.5)	100.0	4–555	162.3 (181.5)
Dec.	44.4	2–18	3.7 (6.6)	90.0	1–1105	335.5 (407.3)
Jan.	60.0	1–1052*	107.6 (331.8)	100.0	9–424	162.2 (167.5)
Feb.	80.0	1–193	36.6 (61.2)	80.0	2–935	180.6 (295.7)
Mar.	—	—	—	—	—	—
Apr.	88.9	1–45	9.8 (14.4)	100.0	3–745	188.0 (232.7)
May	50.0	5–111	18.2 (36.5)	90.0	5–570	149.0 (185.1)

*One fish with 1052 glochidia. Intensity of infection for the rest of the sample scored as 1–9.

were found between sampling dates, at either site, indicating that mean abundance of the parasite was similar throughout the period under study.

Monthly prevalence, intensity, and abundances of infection (Table 1) showed a significant difference between levels of infection at the two sites for each month except January, where a single fish caught at site A harboured an exceptionally large number of glochidia ($n = 1052$), raising the abundance 30-fold and the standard deviation 3-fold. No other examples of such extreme overdistribution were observed in any of the other samples collected. There were no significant monthly changes in prevalence or abundance at each individual site. The high levels of infection found at site B in December (abundance = 335 ± 407.3), however, were not observed in subsequent samples from the same site. The consistently high prevalence at site B between October and December and the marked increase in abundance of infection over the same period indicated that new infections may have continued to be acquired up until December. This observation is reinforced by the lack of significant difference in size of glochidia between October and November. There was similar evidence of new infections at site A until November. However, with the exception of the individual fish with 1052 glochidia, no salmon were found there in December or January with infections of over 18 glochidia. Prevalences and intensities of glochidia at sites A and B in February, April, and May were indistinguishable from those found in October.

Although all the salmon sampled in this study were from the same age-class (i.e., YOY), mean FL of salmon from site A (6.2 cm, range = 5.0–8.6 cm) was significantly greater ($p < 0.05$) than those from site B (5.9 cm, range = 4.5–7.9 cm). The difference between sites was consistent on every sampling date with the difference of 0.10 cm FL in October increasing to 0.47 cm in May. There was no significant correlation between size (FL) and glochidia abundance at site A ($r = 0.065$, $p > 0.600$) or at site B ($r = -0.117$, $p > 0.300$) when dates were pooled. Similarly, host sex had no significant effect ($p > 0.200$) on glochidia abundance at either site.

K of YOY salmon (Fig. 2) did not differ significantly between sites ($p > 0.200$) unlike the situation for fish size or parasite abundance. Mean condition of YOY salmon from site B was 0.995 compared with 1.013 at site A (where mean FL was greatest and parasite abundance least). Although the calculated values varied markedly among individuals and dates (Fig. 2), mean condition factor was generally higher for salmon from site A, after October. The only exception was the January sample (Fig. 2) where a single individual from site A had 1052 glochidia. The same individual had the lowest condition factor found in the present study ($K = 0.572$). This individual depressed the mean *K* for the whole sample, since no other salmon from site A in January had more than nine glochidia on its gills (Table 1). Significant ($p < 0.01$) changes in mean condition factor between months were only noted between April and May (Fig. 2). This was probably a result of growth rate increases in spring when mean FL similarly increased significantly ($p < 0.01$).

To determine if glochidia abundance affected the condition of YOY salmon, linear regression (with sites pooled) was used. The analysis yielded a significant ($p < 0.005$) slope but explained only 6% of the variation in the data. Assuming that an increased abundance (e.g., >50 glochidia) on the gills of YOY salmon had an increasingly negative impact on individual fish, we excluded those data where salmon had less than a certain level of parasite abundance. The best fit was realized for YOY salmon with >200 glochidia ($n = 24$ salmon) on their gills; a significant ($p > 0.005$), negative slope was found but still only explained 31% of the variation in condition factor. When the data were subdivided by sampling date, significant, negative regressions ($p < 0.05$) were found in January and February where 24 and 66% of the variation in *K*, respectively, was explained by the abundance of glochidia on the gills.

The mean size (diameter) of glochidia (Table 2) was not significantly different ($p > 0.300$) between site B ($n = 919$) and site A ($n = 312$); diameters ranged between 0.11 and 0.38 mm. However, mean size varied significantly ($p < 0.001$) among the sampling dates (sites pooled). Linear regression of glochidia size by sampling date showed a significantly positive slope between October and May ($p < 0.001$) such that mean size in the spring (April, May) was significantly greater ($p < 0.05$) than in autumn (October). Based on mean diameter measurements (Table 2), glochidia showed significant ($p < 0.05$) growth between October and December sampling dates when water temperatures declined steadily from 6 to 1.5°C. No growth was demonstrated during winter, when water temperature averaged 1.5°C (range = 1.0–2.0°C from December to February). Growth of glochidia began again in April when water temperatures increased to 5.0°C.

There was no significant difference ($p > 0.700$) in the abundance of glochidia (Table 3) between the left or right gills of YOY salmon, at either of the study sites. There were,

TABLE 2. Size of glochidia subsampled from the gills of young-of-the-year Atlantic salmon at two sites along South River from October 1987 to May 1988

Study site	Month of sample						
	Oct.	Nov.	Dec.	Jan.	Feb.	Apr.	May
A	0.20±0.047	0.23±0.043	0.27±0.040	0.27±0.044	0.27±0.038	0.30±0.040	0.29±0.027
B	0.20±0.036	0.26±0.040	0.28±0.034	0.27±0.040	0.28±0.040	0.31±0.035	0.31±0.031

NOTE: Values are means ± SD (mm). Horizontal lines beneath adjacent mean values represent nonsignificant ($p > 0.05$) differences based on Student–Newman–Keuls' multiple range test.

TABLE 3. Abundance of glochidia on gill arches of young-of-the-year Atlantic salmon from the two study sites of South River, Nova Scotia

Gill arch	n	Mean	SD	Minimum	Maximum
Site A					
L1	67	4.5	24.3	0	198
L2	67	3.1	15.5	0	126
L3	67	3.9	16.5	0	131
L4	66	2.2	6.5	0	45
R1	67	6.1	32.6	0	264
R2	67	4.3	19.5	0	155
R3	67	3.9	13.7	0	98
R4	67	3.1	10.1	0	69
Site B					
L1	73	27.1	40.7	0	238
L2	73	27.8	39.0	0	199
L3	73	22.0	31.5	0	157
L4	71	17.7	24.5	0	113
R1	73	29.5	44.9	0	226
R2	73	22.8	28.6	0	122
R3	73	23.8	31.1	0	124
R4	72	18.9	28.7	0	126

NOTE: Arches are numbered anterior to posterior. L, left-side; R, right-side; n, total number of gill arches examined; SD, standard deviation.

however, notable differences in abundance among the gill arches (Table 3). Glochidia were most frequently attached to the first (anterior) gill arch; a maximum of 200 glochidia were found attached to this arch in the most heavily infested YOY salmon. The high variation in abundance of glochidia (Table 3) accounted for the nonsignificant differences ($p > 0.200$) in mean abundance among the gill arches at both study sites.

Discussion

Glochidia abundance on the gills of young-of-the-year Atlantic salmon varied markedly among individuals as well as between the two study sites. Ten percent of the salmon (14/141) had over 400 glochidia on their gills and all but one of these salmon were from site B, which had the higher density of adult *Margaritifera margaritifera*. Salmon from site B consistently had a significantly higher abundance of glochidia compared with site A. These results support our hypothesis that parasite abundance (and prevalence) is a function of localized adult mussel densities.

Foci of infection based on localized distribution of other life-history stages is common in host–parasite systems and the basis for use of parasites as biological tags (Margolis 1963). The overdistribution of glochidia collected for this study and, hence, the large standard deviations within individual samples is a common host–parasite distribution pattern, where the host is exposed to several waves of infection and where the infective stages of the parasite are not randomly distributed (Crofton 1971), as is the case with glochidial infections (Murphy 1942; Tedla and Fernando 1969).

That mean abundance was similar among the sampling dates indicates that glochidia were not lost over the course of the parasitic phase. This is similar to the findings of Young et al. (1987) for experimental infections of brown trout, but it contrasts with a field study in Scotland where only 5% of the glochidia on the gills of wild brown trout survived from September to May (Young and Williams 1984). Since our study commenced in October, it is possible that initial infections in August or September were higher than those found thereafter. Young and Williams (1984) offered such an explanation to account for the lack of significant differences in abundance between December and May.

The temporally similar (and spatially specific) levels of abundance of glochidia suggest that, at least for South River populations, YOY salmon are relatively sedentary during the winter months. Cunjak (1988*a*), in studying the winter behaviour of YOY salmon at these same study sites, noted that salmon spent the day beneath stones, although there was evidence of feeding activity (based on stomach analyses), presumably during crepuscular and (or) nocturnal hours.

The impact of glochidia parasitism on the condition of YOY salmon (our second hypothesis) was less clearly defined. However, there was evidence that mean size (FL) was significantly less among salmon from site B (where glochidia were most prevalent). In addition, declining fish condition was best correlated to increased parasite loads (i.e., >200 glochidia/salmon), especially by late winter (February), since environmental parameters were similar at both sites.

Moles (1983) documented mortalities in recently emerged coho salmon (*Oncorhynchus kisutch*) with infestations of >50 glochidia (Anodontidae), as well as reduced growth rates and fat content at lower levels of parasite abundance. Murphy (1942) reported significant mortalities (16–52%) in YOY rainbow trout and brown trout that were experimentally infected with glochidia of *M. margaritifera* at levels similar to those found in the present study. Young et al. (1987), however, found no mortality or reduced growth in YOY brown trout that were experimentally infected (median abundance: 22–1489 glochidia/fish).

Fish size and the amount of energy reserve are important factors for winter survival in fishes (Hunt 1969; Oliver et al. 1979; Gardiner and Geddes 1980; Post and Evans 1989). The results of our research suggest that heavy parasite loads are contributing to the poorer condition and smaller size of YOY salmon at site B, which may then result in death, either directly

(e.g., interference with gill circulation; Murphy 1942) or indirectly via secondary infection. Murphy (1942) attributed the deaths of infected trout to saprolegnian infections via lesions in the gills after the "release" of encysted glochidia. If mortalities are occurring in heavily infected YOY salmon at South River, we believe that they are occurring in the spring (April–May) as water temperatures and the concomitant metabolic costs of overwintering (see Cunjak 1988*b*) are increasing in parallel with the nutritional requirements, which are derived solely from the host (Murphy 1942), for glochidial growth and metamorphosis.

Hare and Frantsi (1974) studied the effects of several different parasites on salmonids from fish hatcheries, including glochidia of the hookless type, and found no pathological effects despite intensities of infection at one hatchery ranging from 1 to 5204. They did not indicate, however, whether or not they followed infection through to glochidial loss in spring, which is when acute pathological effects have been cited by other workers (Murphy 1942; Taylor and Uyeno 1965). Hare and Frantsi (1974) found glochidia exclusively on juvenile Atlantic salmon and, since previous authors (Murphy 1942; Taylor and Uyeno 1965) had found *M. margaritifera* on other salmonids including *Oncorhynchus*, it is possible that the glochidia investigated by Hare and Frantsi were not this species.

Glochidia of adult *M. margaritifera* in South River are discharged in September as inferred from previously published growth rates of glochidia (Murphy 1942; Young et al. 1987), from studies on the biology of this species in Massachusetts (Smith 1976), as well as from their initial measurements in the October samples. Based on the more frequent occurrence of glochidia on anterior gill arches, entry and subsequent attachment is most likely via inhalant water currents through the buccal cavity rather than via the opercular opening.

Growth of glochidia continued through November, ceased during winter, and resumed in April as water temperatures began increasing. The maximum sizes (diameters) of 0.38 mm found in May are similar to the sizes at metamorphosis documented for this species by Murphy (1942: 0.39–0.42 mm) and Young et al. (1987: 0.35 mm). Therefore, we believe that the largest glochidia had metamorphosed and were "releasing" from fish hosts at the time of our May sample. This scenario would explain the nonsignificant difference in mean sizes of glochidia measured between April and May (Table 2).

In conclusion, our study has shown that (*i*) glochidia abundance on the gills of YOY salmon was highly variable but was strongly influenced by localized densities of adult *M. margaritifera*, (*ii*) glochidia abundance did not change significantly over the course of the study (October–May), and (*iii*) growth of glochidia followed the pattern of water temperature, with no growth during the coldest months (December–February). Our data are not sufficiently conclusive to define the relationship between glochidia infestation and winter survival of YOY salmon. The data do, however, suggest an increasingly detrimental impact as a function of time and the degree of infestation. In this regard, we propose the following scenario for the situation at South River based on our preliminary observations. Moderately to heavily infested YOY salmon display a continuous decline in condition from October to February and March. As water temperatures increase in April, glochidial growth increases with all nutrition derived from the host. In May, with further increases in water temperatures and continued growth, glochidia metamorphose and detach from the host. The resultant lesions and weakened condition of the most parasitized fish may contribute to secondary infections and ultimately death. Secondary bacterial and fungal infestations of ectoparasitic lesions and their pathogenic consequences are well documented (Reichenbach-Klinke 1965). We strongly encourage further research to investigate the relationship between glochidia parasitism and fish survival in the wild and to further test this hypothesis. The results presented demonstrate a definite potential for *M. magaritifera* population densities of over 1.26 mussels/m^2 to impact negatively on the overwintering capability of YOY salmon.

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