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Seasonal prevalence, intensity of infestation, and distribution of glochidia of *Anodonta grandis simpsoniana* Lea on yellow perch, *Perca flavescens*[1]

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Five fish species were sampled at regular intervals in Narrow Lake, central Alberta, and examined for the prevalence and intensity of infestation by glochidia larvae of *Anodonta grandis simpsoniana*. Yellow perch (*Perca flavescens*) collected between January and May were infested with glochidia, whereas perch captured between June and October were free of larvae. The prevalence of infestation increased gradually from 86 to 95% between January and May, and the intensity of infestation increased from 5.7 to 49.4 glochidia per fish over the same period. Glochidia were found on most external body surfaces, including the gills. Glochidia attached preferentially to some anatomical areas, especially pectoral and pelvic fins. Furthermore, the relative importance of certain attachment sites differed significantly among sampling dates. Neither sex, size (length or weight), or age of perch significantly affected the intensity of infestation per fish. However, small (4.4–6.0 cm), 1- and 2-year-old fish carried more than 12 times the number of glochidia per gram of body weight than large (12.1–15.7 cm), 4- to 7-year-old fish. Both perch behavior and distribution and clam reproduction and distribution provide possible explanations for the observed patterns in the prevalence and intensity of infestation and in the distribution of the glochidia on the host.

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Cinq espèces de poissons ont été échantillonnées à intervalles réguliers dans le lac Narrow, au centre de l'Alberta, dans le but d'y étudier la prévalence et la gravité des infestations par des glochidies d'*Anodonta grandis simpsoniana*. Seules les perchaudes, *Perca flavescens*, récoltées entre janvier et mai étaient infestées par les glochidies; les perchaudes capturées entre juin et octobre ne portaient pas de glochidies. La prévalence des infestations a augmenté graduellement de 86 à 95% entre janvier et mai et la densité des larves est passée de 5,7 à 49,4 par poisson durant cette période. Les glochidies occupaient presque toutes les surfaces externes du corps, y compris les branchies; elles s'attachaient préférentiellement à certaines zones anatomiques, notamment les nageoires pectorales et pelviennes. De plus, l'importance relative des sites d'attachement différait significativement d'un moment à un autre. Ni le sexe, ni la taille (longueur ou masse), ni l'âge des perchaudes n'etaient reliés de façon significative à la densité de glochidies par individu. Cependant, les petits poissons (4,4–6,0 cm) de 1 ou 2 ans supportaient plus de 12 fois le nombre de glochidies par gramme de masse corporelle que les gros poissons (12,1–15,7 cm) de 4 à 7 ans. La prévalence et la gravité des infestations de même que la répartition des glochidies sur les hôtes peuvent s'expliquer à la fois par le comportement et la répartition des perchaudes et par la reproduction et la répartition des anodontes.

[Traduit par la rédaction]

Introduction

The glochidial larvae of nearly all freshwater clams are obligate parasites on fish (for exceptions see summary in Heard 1975). Female clams retain glochidia for various lengths of time in a modified portion of their gills, the marsupium (Lefevre and Curtis 1910), and release the larvae if, for example, a passing fish stimulates light-sensitive mantle spots (Clarke 1981). Survival of released glochidia is limited to a few days (Tedla and Fernando 1969). Therefore, recent host infestation indicates the presence of clams carrying mature larvae (Giusti *et al.* 1975). After successful attachment to the host, most glochidia metamorphose to small clams within a few weeks and then excyst to start their life as free-living juveniles in the substrate (Clarke 1981). It is generally assumed that, for a given clam species, one or only a few fish species are suitable hosts for glochidial attachment and metamorphosis. However, for many species of clams, the host(s) are unknown and little information exists about the timing, duration, and intensity of glochidial infestation. Furthermore, although there is some information on the attachment sites occupied by glochidia on their fish hosts (Dartnall and Walkey 1979; Dudgeon and Morton 1984), a rigorous quantitative analysis of such distribution patterns is lacking. Knowledge of the attachment sites and changes in their relative importance over the infestation period provides valuable information about the ecological relationships of host and parasite.

Of all North American members of the family Unionidae, *Anodonta grandis simpsoniana* has the northernmost distribution (Clarke 1981). Some aspects of its biology in central Alberta have recently been studied (Hanson *et al.* 1988*a*, 1988*b*, 1989), but no data exist on most aspects of the reproduction, the fish hosts, and the parasitic glochidial phase of this subspecies. This paper describes the host specificity and the seasonal prevalence and intensity of glochidial infestation on yellow perch, *Perca flavescens*. Also considered were the topographical distribution of the glochidia on the host and the effects of fish size (age) and sex. A companion paper examines the timing of clam reproduction in the lake, the number of glochidia produced, and the fraction of glochidia attaching to fish and surviving to age 2 or older (Jansen and Hanson 1991).

Material and methods

Fish and glochidia sampling

Between 13 March 1988 and 24 March 1989, fish were collected from Narrow Lake (54°35′ N; 113°37′ W) and examined for attached glochidia of *A. g. simpsoniana*, the single unionid species occurring in the lake (Hanson *et al.* 1988*a*). Narrow Lake, located in the southern ecotone of the mixed-wood boreal forest of central Alberta, is small (1.14 km^2), deep (mean depth, 14.4 m), and moderately productive (mean summer epilimnetic chlorophyll *a*, 12.9 μg/L) (Prepas and

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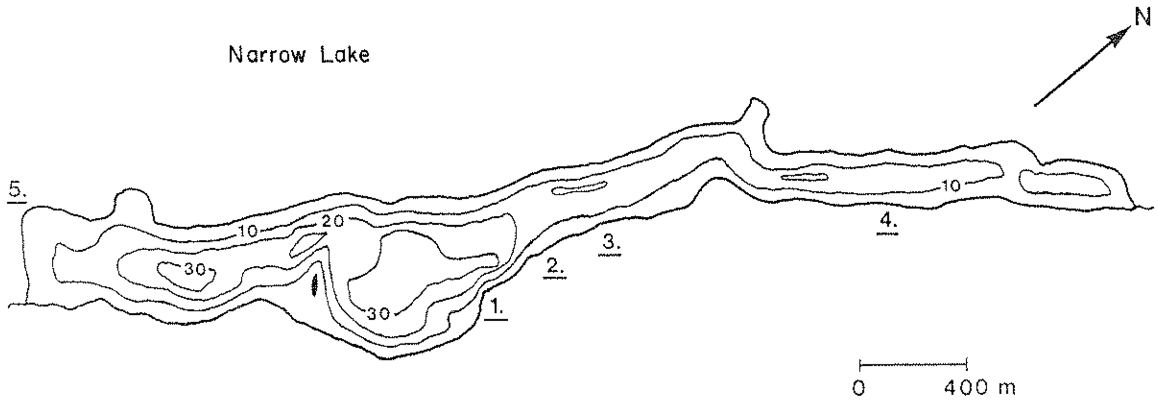


FIG. 1. Bathymetric map of Narrow Lake (contours in metres) showing sites where yellow perch were collected.

Trimbee 1988). Fish sampling was conducted at 2- to 4-week intervals between April and October, and in January and March. A total of five sampling sites were chosen where clams are known to occur in the lake (Fig. 1). During the open-water season (late April to mid-November), fish were collected from all sites, using a 15.5 × 1.8 m floating bag seine with 6 mm (stretched) knotless mesh, a 56 × 3 m sinking bag seine with 9.0 mm knotless mesh, and Windermere perch traps. Traps were used exclusively during a 2-week period immediately following ice-off when they were deployed at depths of 3–6 m near sites 1 and 2. While the lake was covered with ice, in January and March, fish were caught in 5–10 m of water by hook and line at site 1. For each sample, fish were sorted by species, and the prevalence (percentage of fish parasitized) and intensity (total number of glochidia per infested fish) of glochidia infestation were determined separately. The topographic pattern of glochidia distribution was studied only on yellow perch since it was the only species observed to carry glochidia (Table 1).

Upon capture, the sex, age, wet weight (±0.01 g), and total length (TL; ±0.1 cm) of each fish were determined. Perch were sexed by the macroscopic appearance of their gonads. To determine age, both opercular bones were removed (after recording the number of glochidia), cleaned, and the growth rings (annuli) were counted following a technique similar to that of Le Cren (1947). Perch carcasses were then frozen (−18°C) and stored individually in air-tight bags for later analysis of glochidia distribution. As indicated by the firm attachment of the glochidia after thawing, this procedure did not appear to result in loss of larvae. Glochidia were identified and counted under a dissecting microscope. For each of the following locations, the number of glochidia was determined separately: head, gills, pectoral fins, pelvic fins, flanks, abdomen, anal region, anal fin, caudal fin, first dorsal fin, and second dorsal fin. The location of each glochidium was recorded in more detail for the head (e.g., eye, preoperculum), gills (e.g., first gill arch, filaments), and fins (e.g., base, dorsal margin). The anal region represented the anus and the immediately surrounding area; the abdomen was the unpigmented ventral area between the anal region and head; and the flanks were the pigmented areas extending between head, abdomen, anal region, and caudal peduncle. To test the hypothesis that the pattern of glochidia settlement on the fins reflects their size or margin length, the maximal fin ray length of the pelvic, pectoral, anal, and caudal fins was measured (±0.2 mm) using an ocular micrometer. To monitor temperature, one key component of the abiotic environment that potentially affects the timing of reproductive events in unionids (Giusti *et al.* 1975), the water temperature of Narrow Lake, was measured continuously between 27 April and 14 October by a Ryan recorder (Ryan Institute Incorporated) placed at 1 m depth.

Data analysis

A single perch was caught in March of 1989 (Table 1) and it was pooled with the March 1988 sample. Perch captured between 26 April 1988 and 4 May 1988, and from 18 to 21 May 1988, are referred to as April and May samples, respectively, in all figures and tables. To determine the effect of fish size on the intensity and topographical distribution of glochidia infestation, perch caught in April and May were categorized into four size classes: I, ≤6.0 cm; II, 6.1–9.0 cm; III, 9.1–12.0 cm; and IV, >12.0 cm. The perch population of Narrow Lake is severely stunted (Jansen and Mackay 1991); fish used in this analysis were 4.4–15.7 cm TL and were 1–7 years old. Differences in the intensity of infestation and in the distribution of glochidia among these size classes were also tested after adjusting for body weight (BW; number of glochidia per gram of body wet weight). This analysis was restricted to those perch caught in April and May, because only at these times did the fish samples adequately represent the entire size spectrum of the population and show an approximately even sex ratio.

Differences among sampling dates in the intensity and topographical distribution, and the sex or size classes of the perch were tested by one-way or two-way analysis of variance (ANOVA), using the Statistical Analysis System (SAS Institute Inc. 1985). When appropriate, Duncan's multiple-range test was used to identity means that differed between groups, when comparisons were made among more than two groups. A probability of $p \leq 0.05$ was considered significant. Since in most cases variances were heterogeneous, data were transformed logarithmically ($\log(x + 1)$), which resulted in uniform variances. For clarity of presentation, arithmetic means of the untransformed data with standard errors have been used in all figures and tables.

Results

Prevalence and intensity

Of the five fish species present in Narrow Lake, only yellow perch were infested with glochidia (Table 1). However, sample sizes of the other four species were small. No glochidia were recovered from yellow perch between mid-June and October, whereas nearly every fish was infested between January and the middle of May. During this latter period, the prevalence of infestation continuously progressed from 86 to 100%, and the intensity increased almost 9-fold, from 5.7 to 49.1 glochidia per fish (Table 2; Fig. 2). This significant ($p \leq 0.0001$) increase was partially due to the appearance of individual fish with massive infestations, but mainly reflected a general increase in the parasite load of all fish (Fig. 3). Whereas in January all perch were relatively lightly infested (maximally 16 glochidia), by mid-May most (i.e., the mode) fish carried 20–40 glochidia (Fig. 3) and, on a few individuals, up to 196 larvae had successfully attached.

Topographical distribution

The increase in the intensity of infestation was not uniform among the body parts examined. The mean number of glochidia on the head ($p \leq 0.0001$), gills ($p \leq 0.0001$), pectoral fins

TABLE 1. Prevalence of glochidia of *Anodonta grandis simpsoniana* on five fish species caught at Narrow Lake between March 1988 and March 1989

Date	Species				
	CI	EE	EL	LL	PF
12–13 March 1988	0 (0)	0 (0)	0 (0)	0 (1)	15 (17)
26 April 1988 – 4 May 1988	0 (2)	0 (5)	0 (12)	0 (5)	52 (55)
18–21 May 1988	0 (1)	0 (7)	0 (5)	0 (3)	22 (22)
13 June 1988 – 9 October 1988	0 (3)	0 (11)	0 (12)	0 (2)	0 (246)
21–22 January 1989	0 (0)	0 (0)	0 (1)	0 (0)	6 (7)
24 March 1989	0 (0)	0 (0)	0 (0)	0 (1)	1 (1)

NOTE: The number in parentheses indicates the number of fish caught. CL, *Culea incostans*; EE, *Etheostoma exile*; EL, *Esox lucius*; LL, *Lota lota*; PF, *Perca flavescens*.

TABLE 2. Seasonal changes in the number of glochidia of *Anodonta grandis simpsoniana* attached to yellow perch from Narrow Lake

Location	Month			
	January (n = 7)	March (n = 18)	April (n = 55)	May (n = 22)
Head	0.14±0.14*b*	0.50±0.10*b*	0.47±0.11*b*	3.00±0.76*a*
Gills	1.14±0.34*b*	1.61±0.38*b*	1.02±0.25*b*	6.55±1.11*a*
Pectoral fins	1.14±0.46*b*	3.17±0.51*b*	5.45±1.16*b*	11.68±3.27*a*
Pelvic fins	1.43±0.75*c*	2.67±0.58*b,c*	7.07±1.30*b*	10.86±2.62*a*
Flanks	0.14±0.14*a*	0.22±0.13*a*	0.62±0.24*a*	1.09±0.37*a*
Abdomen	0.57±0.30*a*	0.44±0.17*a*	1.07±0.21*a*	1.00±0.35*a*
Anal fin	0.29±0.18*b*	0.83±0.19*b*	2.09±0.44*a,b*	4.50±1.26*a*
Caudal fin	0.71±0.47*a*	0.50±0.17*a*	0.38±0.11*a*	1.05±0.51*a*
Dorsal fins	0.14±0.14*c*	0.50±0.26*b,c*	2.80±0.79*b*	8.68±2.21*a*
Total	5.71±1.81*c*	10.72±1.92*c*	21.20±3.38*b*	49.09±9.92*a*

NOTE: Values are given as means ± SE. The number of perch examined is indicated in parentheses. Means followed by the same letter are not significantly different among dates.

($p \leq 0.005$), pelvic fins ($p \leq 0.05$), anal fin ($p \leq 0.01$), and dorsal fins ($p \leq 0.0001$) differed significantly among sampling dates and increased from January to May, whereas the number of glochidia on the abdomen, flanks, and caudal fins remained similar for this period (Table 2). Consequently, the relative contributions of the abdomen and the caudal fin to the overall glochidia load each decreased from approximately 10% in January to about 2% in May (Table 3).

Between 65% (January) and 84% (April) of all glochidia attached to the fins (Table 3). Pectoral and pelvic fins consistently showed the highest individual counts on all sampling dates, each pair of fins contributing between 20 and 33% to the total number of glochidia. This predominance of pectoral and pelvic fins as sites of attachment was not simply a matter of fin size. For each millimetre of margin length, measured as the extension of the longest fin ray, pectoral (0.6 glochidia/mm) and pelvic (0.7 glochidia/mm) fins had significantly more glochidia ($p \leq 0.001$) than either the anal fin (0.25 glochidia/mm) or the caudal fin (0.05 glochidia/mm). Among other body parts, glochidia were found preferentially on the gills, which, except for the April sample, contributed between 13 and 20% to the total glochidia count (Table 3). The mean number of glochidia attached to both dorsal fins increased more than 60-fold between January and May (Table 2) and their relative contribution to the total glochidia count increased from 3 to 19% for this period (Table 3).

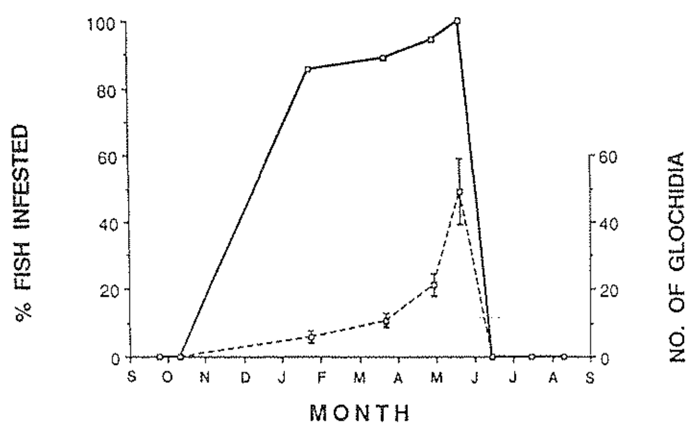


FIG. 2. Seasonal variation in the prevalence (% fish infested; solid line) and mean (±SE) intensity (number of glochidia per fish; broken line) of infestation of glochidia of *A. g. simpsoniana* on yellow perch from Narrow Lake.

The distribution of glochidia on the fins, head, and gills was not random, but followed a consistent pattern that was independent of season. On the head, glochidia were found in four locations: nostrils, eyes, opercular series (opercular, subopercular, and preopercular), and the branchiostegal rays. The latter, especially the soft tissues between individual bones, was the attachment site of almost 80% of all glochidia found on the

TABLE 3. Numerical and percentage distribution of glochidia of *Anodonta grandis simpsoniana* infesting yellow perch from Narrow Lake

Location	January *N*	January %	March *N*	March %	April *N*	April %	May *N*	May %
Head	1	2.5	9	4.7	26	2.2	66	6.1
Gills	8	20.0	29	15.0	56	4.8	144	13.3
Pectoral fins	8	20.0	57	29.5	300	25.7	257	23.8
Pelvic fins	10	25.0	48	24.9	389	33.4	239	22.1
Flanks	1	2.5	4	2.1	34	2.9	24	2.2
Abdomen	4	10.0	8	4.2	59	5.1	22	2.0
Anal region	0	0	5	2.6	12	1.0	15	1.4
Anal fin	2	5.0	15	7.8	115	9.9	99	9.2
Caudal fin	5	12.5	9	4.7	21	1.8	23	2.1
Dorsal fins	1	2.5	9	4.7	154	13.2	191	17.7
All fins	26	65.0	138	71.5	979	84.0	809	74.9
Other locations	14	35.0	55	28.5	187	16.0	271	25.1
Total	40		193		1166		1080	

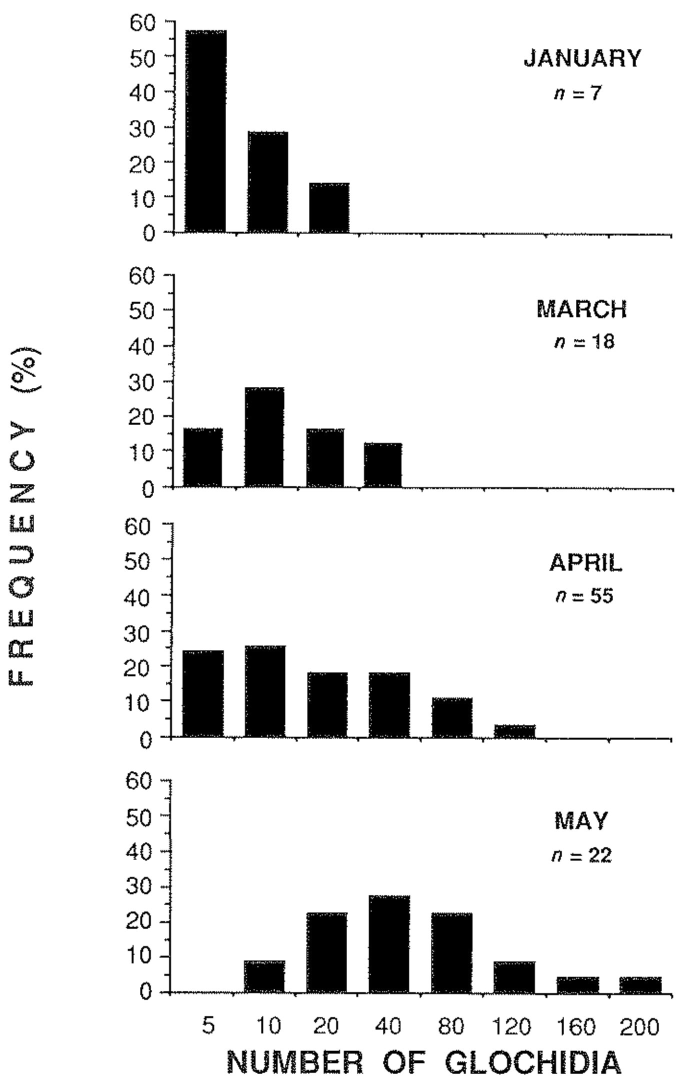


FIG. 3. Frequency distribution of the number of glochidia per fish of *A. g. simpsoniana* infesting yellow perch from Narrow Lake. The fish sample size is indicated for each date. Numbers below the abscissa represent the upper limit of the class boundary.

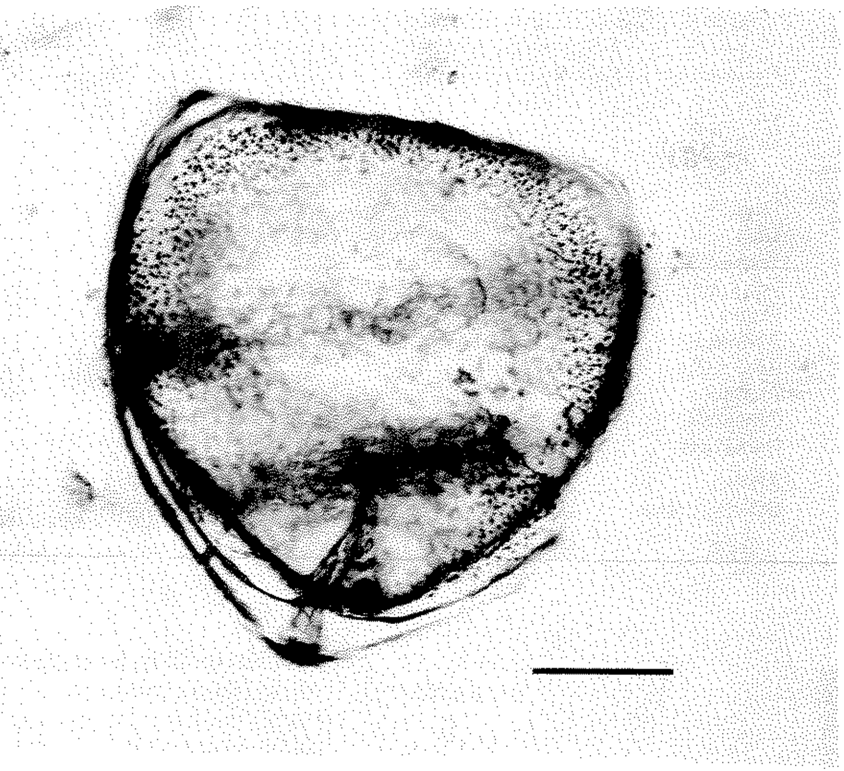
head. On the gills, most glochidia were located on the filaments with no distinct preference for any one branchial arch, and some larvae attached to the arch itself. On the pectoral fins, glochidia preferentially settled on the ventral and posterior margins, attaching to the 11th, 12th, and 13th fin rays (Figs. 4 and 6). On the pelvic fins, glochidia were found mainly on the lateral and posterior margins (Fig. 6). Almost all glochidia on the anal fin and second dorsal fin attached to the distal margin. Most of the few glochidia found on the caudal fin were attached to the posterior margin of the ventral lobe. On the first dorsal fin, glochidia encysted in the connecting epithelium with highest densities typically between the 3rd and 6th dorsal spine (Fig. 5).

Effect of sex and size of fish

All perch caught in January and March were females. During April and May, the mean number of glochidia (±SE) attached to female (20.1 ± 4.3; n = 22) and male (34.8 ± 5.8; n = 49) perch was not significantly different. The mean TL was 9.05 cm for females and 8.95 cm for males. Despite this similarity in the total number of glochidia, female and male perch differed significantly in the glochidia count of two anatomical areas: males had significantly more glochidia (3.6 larvae; $p \leq 0.01$) on their anal fin than females (0.9 larvae). Conversely, twice as many glochidia were attached to the gills of females (4.2) compared with the gills of males (2.1; $p \leq 0.05$).

There was no significant correlation ($F_{1,73} = 0.47$; $p = 0.49$) between TL of individual perch and total number of attached glochidia per fish. Also, fish length did not significantly affect (p = 0.19) the intensity of infestation between each of the four size classes: I, 17.0 ± 3.0 glochidia; II, 32.7 ± 5.1; III, 30.7 ± 10.7; and IV, 26.8 ± 9.2. Furthermore, none of the different anatomical areas, except the gills (p = 0.01), showed a significant difference in the number of glochidia among the above size classes. For the gills, fish of size class II carried significantly more glochidia than those of size class IV.

The mean number of glochidia per gram of BW decreased continuously and significantly ($p \leq 0.0001$) with increasing body size classes; the smallest perch carried more than 12 times as many glochidia as the largest perch (Table 4). The absence of a significant difference in the absolute glochidia count per fish among size classes noted earlier for the caudal fin, dorsal fin, 4



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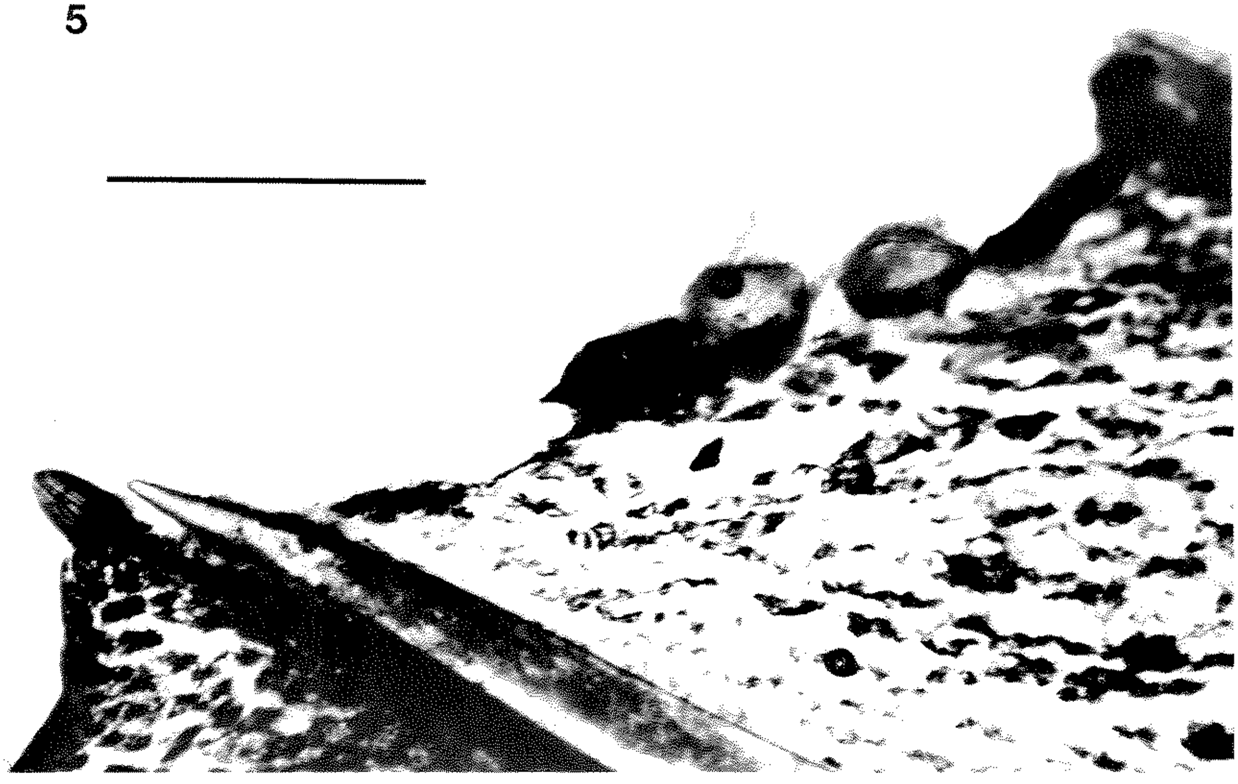

FIG. 4–5. Glochidia of *A. g. simpsoniana* infesting yellow perch from Narrow Lake. Fig. 4. Glochidium showing spined hook on 11th fin ray of pectoral fin. Scale bar: 100 μm. Fig. 5. Distal margin of first dorsal fin between 3rd and 4th spine. Scale bar: 1 mm.

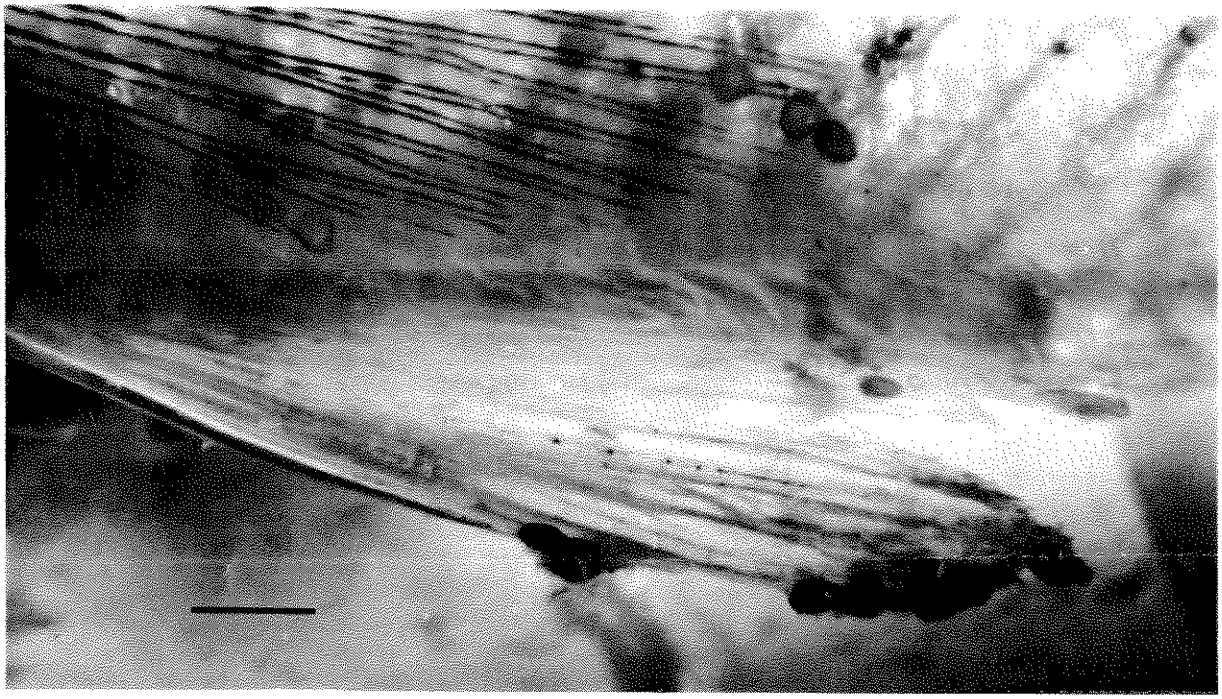

FIG. 6. Glochidia of *A. g. simpsoniana* infesting yellow perch from Narrow Lake. Left pectoral and pelvic fins showing typical locations of glochidia. Scale bar: 1 mm.

TABLE 4. Number of glochidia of *Anodonta grandis simpsoniana* on four size classes of yellow perch caught between 26 April 1988 and 21 May 1988 at Narrow Lake

	Size class (cm)			
Location	≤6.0 (*n* = 11)	6.1–9.0 (*n* = 35)	9.1–12.0 (*n* = 22)	>12.1 (*n* = 9)
Head	0.72±0.19*a*	0.43±0.10*a,b*	0.12±0.06*b,c*	0.01±0.01*c*
Gills	0.97±0.39*a*	1.03±0.20*a*	0.23±0.12*b*	0.03±0.02*b*
Pectoral fins	2.01±0.60*a,b*	2.71±0.63*a*	0.98±0.40*b,c*	0.12±0.05*c*
Pelvic fins	4.75±1.13*a*	2.69±0.63*b*	0.85±0.27*b,c*	0.35±0.17*c*
Flanks	0.15±0.10*a*	0.26±0.08*a*	0.07±0.04*a*	0.07±0.07*a*
Abdomen	1.41±0.43*a*	0.29±0.09*b*	0.13±0.04*b*	0.02±0.01*b*
Anal fin	1.82±0.56*a*	0.92±0.23*b*	0.31±0.15*b,c*	0.08±0.01*c*
Caudal fin	0.42±0.28*a*	0.13±0.04*a*	0.11±0.06*a*	0.01±0.01*a*
Dorsal fins	0.72±0.30*a*	1.10±0.27*a*	0.60±0.31*a*	0.36±0.15*a*
Total	13.40±2.29*a*	9.68±1.75*a*	3.34±1.31*b*	1.06±0.36*b*

NOTE: The number of perch examined is indicated in parentheses. Values are given as means (±SE) of the number of glochidia per gram of perch body weight. Means followed by the same letter are not significantly different among size classes.

and flanks persisted even when the data were expressed on a weight specific basis.

Because the size limits for size classes I to IV approximately coincided with the length range of fish age 1, 2, 3, and 4–7 years, respectively, and because perch older than 5 years were not well represented in the present samples, the effect of fish age on the intensity and topographical distribution of glochidia infestation was considered identical to that of the effect of size.

Discussion

Host specificity

It appears that yellow perch is the single host for *A. g. simpsoniana* in Narrow Lake. Since the geographical distribution of *A. G. simpsoniana* (Clarke 1981) extends past the northern limit of the distribution of yellow perch (Scott and Crossman 1973), clearly, *A. g. simpsoniana* must have some other host fish. However, according to Clarke (1981), no information on the fish host(s) of this subspecies has been published. According to Fuller (1974), *A. g. grandis* naturally infests three of the five fish species occurring in Narrow Lake: yellow perch, Iowa darter, and brook stickleback. Because of their small sample sizes, the latter two species cannot be dismissed as potential hosts of *A. g. simpsoniana*. Nevertheless, it is possible that this subspecies has a smaller host spectrum than *A. g. grandis*. Yellow perch (Wootten 1973; Fuller 1974; Giusti *et al.* 1975) and Eurasian perch, *P. fluviatilis*, (Tedla and Fernando 1969) are commonly infested by many other species of the genus *Anodonta*, although Wiles (1975) was unable to find glochidia of *Anodonta* sp. on yellow perch at times they infested other hosts. Among the remaining fish species present in Narrow Lake, northern pike is a known host for *A. cygnea* (Giusti *et al.* 1975).

Although Tedla and Fernando (1969) claim that there is no host selection by glochidia of *Lampsilis radiata siliquoidea*, at least partial host specificity (i.e., only a few species of a fish assemblage are hosts, or the prevalence and intensity of infestation differs dramatically between species) is commonly observed among the larvae of unionids (Lefevre and Curtis 1910; Zale and Neves 1972; Giusti *et al.* 1975; Dudgeon and Morton 1984). Furthermore, Wood (1974) found that successful encystment of glochidia of *A. cygnea* after initial attachment relies on a continuous chemical stimulus by the host tissue, which only certain fish can provide.

Prevalence and intensity of infestation and distribution of glochidia

From the natural incidence and intensity of infestation of yellow perch in Narrow Lake, the extrusion of glochidia from adult *A. g. simpsoniana* appears to occur in late fall or early winter. No fish were obtained between 10 October and 20 January, so the precise timing of the onset of glochidia release cannot be ascertained. However, considering the relatively high prevalence of infestation by January (present study), and the gradual increase in prevalence between initial and maximal infestation for *A. cygnea* (Giusti *et al.* 1975), it is likely that glochidia were first released by adult clams in Narrow Lake well before January. Such an early date also corresponds to the general breeding cycle of *A. grandis* (Clarke 1973). No data are available on the first appearance of glochidia of *A. grandis* on fish hosts and on how long fully developed larvae are retained in the marsupium before their release, however, the pattern in relative frequency of clams carrying glochidia (Jansen and Hanson 1991) suggests that clams retain them from September to May at least in some years. Because of this latter feature of unionid life history, glochidia infestation on a host does not reliably determine the start of the reproductive cycle.

There are two plausible interpretations for the observed numbers of glochidia on fish: glochidia may accumulate until they are released (excyst) synchronously, or glochidia are acquired and released simultaneously over an extended period of time and the number of glochidia on the fish represents the balance of these two processes. Although the present data provide no direct evidence for either, the seasonal pattern of glochidia infestation and the temperature regime of Narrow Lake indirectly support the first interpretation. For example, the more than doubling of the number of glochidia infesting perch between April and May indicates that glochidia accumulated on the host before a common release or that the rate of acquisition by far exceeded the release rate of glochidia. In either case, the above increase in the glochidia count suggests that larvae were still being released by the clams until at least 21 May, which corresponds well to the end of the gravid period of *A. g. simpsoniana* in Narrow Lake (Jansen and Hanson 1991).

The complete absence of glochidia on perch, only 23 days after levels of infestation had reached a previous maximum, indicates that excystment of juvenile clams proceeds rapidly at least at summer temperatures. Such findings are similar to that for glochidia of *A. cygnea* on *P. fluviatilis* (Giusti *et al.* 1975). These authors implicated water temperature as the key factor stimulating both the release of larvae from the parent and the excystment of glochidia from the host; infestation started once temperatures fell below 10°C and excystment proceeded when temperatures reached approximately 15°C in spring. Similarly, glochidia of *A. cygnea* occurred on *Gasterosteus aculeatus* only when water temperatures were below 12°C (Dartnall and Walkey 1979). If these values also apply to *A. g. simpsoniana*, larvae in Narrow Lake may have been released by the parent any time after 19 October and glochidia started to excyst by 26 May, when minimum daily water temperatures permanently remained below 10°C and exceeded 15°C, respectively. If so, the parasitic period of *A. g. simpsoniana* on *P. flavescens* may last up to 6 months.

The number of glochidia attached to perch increased throughout the period of infestation and more than doubled between 30 April and 21 May. Both perch behavior and clam distribution provide possible explanations for this pattern. In January and March, 85% of all perch were caught at water depths of more than 6 m and no fish were obtained at a depth of less than 5 m. These results are in agreement with the view that perch move offshore in the fall and remain there until the following spring (Hasler 1945; Keast 1977). According to Hanson *et al.* (1988*b*), the density of *A. g. simpsoniana* (and thus the chance of encountering glochidia) is approximately 15 times higher in the littoral zone of Narrow Lake than at water depths >6 m. Unless clams show similar seasonal migrations as perch, these fish must have been exposed to low densities of gravid *A. g. simpsoniana* during fall and winter. Furthermore, prevailing light intensities at 6 m water depth under ice and snow cover must have been minimal. Although no information is available on the photosensitivity of the mantle spots of unionids (Clarke 1981), it is likely that the method of directed massive glochidia release on to a host is less effective at this time of the year. If they do not immediately attach to a host after release by the parent, glochidia sink to the sediment and, being incapable of further movement (Lefevre and Curtis 1910), are entirely dependent on the host to make physical contact. Only perch that were actively feeding on benthic invertebrates (W. A. Jansen, unpublished data) were caught in January and March. Perch foraging on benthic invertebrates often adopt an almost vertical position in the water column, just above the sediment, forcefully penetrating the substrate to "flush out" prey, which is then captured mainly by suction feeding (W. A. Jansen, personal observation). These fish not only potentially expose the head to a direct stream of glochidia expelled by the parent or to those resting on the sediment, but also resuspend larvae into the water column and channel them across the gill surfaces. It is not known whether all perch feed to a similar extent during winter, and particularly if there are sexual differences in food consumption. If such differences exist, as suggested in this study by the complete absence of males in the samples from January and March, then the intensity of glochidia infestation recorded at those times may have been positively biased and higher than the actual population average. Differences in the disposition of clams to release larvae in response to temperature, photoperiodic, or light intensity stimuli provide an alternative or complementary explanation for the seasonal pattern in the intensity of infestation.

The presence of glochidia of *A. g. simpsoniana* on the gills of *P. flavescens* is in itself remarkable. Lefevre and Curtis (1910) claimed that the hooked glochidia of *Anodonta* sp. never permanently attach to the gills of fish (they may initially hold on, but drop off after a few hours). This view was supported more recently by Dudgeon and Morton (1984), who did not report glochidia on the gills of four artificially infested host fish of *A. woodiana*. However, Giusti *et al.* (1975) and Dartnall and Walkey (1979) found that fewer than 5% (*Esox lucius*) to almost 60% (*Tinca tinca*) of all glochidia of *A. cygnea* had settled on the gills of various host species. Also, Wootten (1973) found up to 39 glochidia of *Anodonta* sp. per fish on the gills of five different fish species, including *P. fluviatilis*, and Threlfall (1986) found 71% of all glochidia of *A. cataracta* on the gills of *G. aculeatus*. Finally, Wiles (1975) states that glochidia of *Anodonta* sp. occurred only on the gills of various fish hosts. Clearly, hooked glochidia are less restricted in their capability to attach to different host tissues than it has been previously assumed.

The significant seasonal differences in the relative importance of attachment sites other than head and gills are more difficult to explain. Presumably, the anterior and ventral position of the pectoral and pelvic fins, and, in the case of the pectorals, their importance in low speed locomotion (including frequent movement independent of the body) results in increased exposure to glochidia. The only other available study of glochidia (*A. cygnea*) distribution on *P. fluviatilis* (Giusti *et al.* 1975) confirms the general pattern found in the present study. In Narrow Lake, the continuous increase in the contribution of the dorsal fin to the total glochidia load between January and May was mainly due to a few heavily infested individuals. In these cases, the most accessible attachment sites may have been unavailable to newly arriving larvae because of crowding of those already established, and glochidia infested alternative locations.

Effect of sex and size of fish

The intensity of infestation was independent of the sex or the size of fish regardless of sampling date (April or May). If perch behavior affects the probability of glochidia settlement, these results indicate that possible behavioral differences between males and females during and after the end of the spawning season are not sufficient to cause preferential attachment of glochidia to fish of one particular sex. For *G. aculeatus* infested by *A. cygnea* (Dartnall and Walkey 1979) and *A. cataracta* (Threlfall 1986), the effect of sex was also nonsignificant.

With regard to fish size, the published results are equivocal. Threlfall (1986) found no relationship between fish length or weight and the intensity of glochidia infestation, whereas Dartnall and Walkey (1979) observed a general increase in glochidia infestation with increasing fish size. Conversely, a negative correlation to glochidia load and fish size was reported by Tedla and Fernando (1969) for larvae of *L. r. siliquoidea* on *P. flavescens*. To reconcile these results and those of the present study, it is useful to look at the data in more detail. The sticklebacks ranged in size from about 20 to 40 mm (Dartnall and Walkey 1979). Possibly, unionid clams require a stimulus of a certain strength to activate their photosensitive glochidia release mechanism. If the smallest sticklebacks did not provide such a signal, they would not have been exposed to direct, en masse, release of larvae by the parent, thus explaining the substantially lower numbers of glochidia in some of the two or three smallest size categories used by Dartnall and Walkey (1979). Table 1 in Tedla and Fernando (1969) indicates that perch 116–125 mm long carried approximately twice the number of glochidia infesting perch either <116 mm or 126–215 mm in length. All of these heavily infested perch, if used in the present study, would have been classified in the two largest size groups, thereby leading to a partial reversal of the results. Obviously, conflicting findings with regard to the effect of fish size on glochidia attachment have to be interpreted with caution. Nevertheless, the results by Tedla and Fernando (1969) agree with those of this study, that is, smaller perch carry more glochidia per unit body surface area than larger perch.

Tedla and Fernando (1969) suggested that differences in immunological reaction and behavior between young and old fish are responsible for the differences in the intensity of glochidia infestation. Indeed, perch show ontogenetic diet shifts, the younger (smaller) individuals feeding primarily on zooplankton and the older (larger) on benthic invertebrates (e.g., Hartmann and Nümann 1977; Keast 1977). These dietary differences are apparently reflected in the schooling behavior of perch. When perch of mixed age classes school in the littoral zone of Narrow Lake, older fish often maintain a position closer to the sediment, whereas the younger fish swim closer to the water surface, thus forming a gradient of increasing size with depth (W. A. Jansen, personal observation). Considering this structure of perch aggregations and the pattern of glochidia distribution, it is surprising that the smaller fish carry the relatively heavier glochidia load. Unless differences in the timing of certain daily activities or in the choice of a nighttime resting area between smaller and larger perch (Helfman 1979) favor the exposure of smaller fish to glochidia, interpretations other than behavioral differences as the primary effect of fish size on the relative intensity of glochidia infestation have to be sought.

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