Occurrence of Glochidia in Stream Drift and on Fishes of the Upper North Fork Holston River, Virginia

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ABSTRACT: Occurrence of glochidia in stream drift, and prevalence and intensity of glochidial infestations on host fishes were recorded in the upper North Fork Holston River near McCrady, Virginia, between June 1981 and June 1982. Glochidia of Lampsilinae were collected in drift samples year-round, peaking in abundance during June and July. Glochidia of the Ambleminae were in the drift from June to mid-August. Of 4800 fish (41 species) examined for infestations, 14% carried encysted glochidia. Eleven fish species in the Centrarchidae, Cottidae and Percidae were infested with lampsiline glochidia, with prevalence highest in March. Amblemine glochidia occurred only in 12 species of the Cyprinidae, with prevalence highest in July. Prevalence and intensity of infestations were highest in fish hosts of the Ambleminae. Previous accounts of host specificity, based on laboratory experiments with naiades, were corroborated by field observations.

INTRODUCTION

Nearly all freshwater mussel species (Unionidae) pass through a larval parasitic or glochidial stage (Howard and Anson, 1922; Allen, 1924; Howard, 1951). Gravid female mussels release these glochidia either individually through minute pores in their marsupial gills or as clusters (conglutinates) through the excurrent aperture. Estimates of the number of glochidia released by each female range from ca. 100,000 to 3.5 million, depending on the species and size of female (Surber, 1912; Yeager and Neves, 1986). This tremendous reproductive potential is greatly diminished, however, if the numbers of available hosts are inadequate at the time the glochidia are in the water column. Contact between glochidia and host is a low-probability but annual event, facilitated by the respiratory or feeding activities of fishes (Dartnall and Walkey, 1979; Zale and Neves, 1982a; Neves *et al.*, 1985), and perhaps behavioral characteristics of some mussel species (Davenport and Warmuth, 1965; Wood, 1974). Reproductive success therefore depends on the broadcasting of prodigious numbers of glochidia to increase the likelihood of encounters with suitable hosts.

The unionid fauna in North American rivers is dominated by three subfamilies of mussels (naiades), each of which has slightly different reproductive characteristics. Mussels in the subfamilies Anodontinae and Lampsilinae are winter or long-term brooders (bradytictic) that spawn in summer, retain glochidia in their gills throughout the winter, and release them during the following spring. The Ambleminae are summer or short-term brooders (tachytictic) that spawn in spring and release glochidia in summer. Glochidia of species in each of these subfamilies can be distinguished by size and valve morphology (Coker *et al.*, 1921; Zale and Neves, 1982b).

The prevalence of glochidial infestations has been reported for various species of mussels and on certain species of fish (Coker *et al.*, 1921; Tedla and Fernando, 1969; Giusti *et al.*, 1975), but no investigator has attempted to describe this parasitic relationship for an ecological assemblage of mussels and fishes. Objectives of this study were to

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document the annual cycle of glochidia in stream drift, quantify the prevalence and intensity of glochidial infestations in fishes and identify the fish taxa important to the reproductive success of naiades in the upper North Fork Holston River, Virginia. Parasitological terminology is according to Margolis *et al.* (1982).

MATERIALS AND METHODS

Study area.—Fieldwork was conducted along a 350-m reach (36°55′N, 81°40′W) of the North Fork Holston River at North Holston Ford (NHF), near McCrady, Smyth County, Virginia, from June 1981 to June 1982. The North Fork is a fourth-order stream in the Ridge and Valley Province of southwestern Virginia, and flows southwesterly for 218 km before joining the South Fork near Kingsport, Tennessee. North Holston Ford, at river mile 86.9 (river km 139), has an average width of ca. 30 m; the substrate consists primarily of cobbles and mixed sand and gravel. Mean water depths ranged from less than 30 cm in summer to more than 1 m in spring. This site was chosen because the assemblage of both mussels and fishes is diverse (Kitchel, 1985; Widlak and Neves, 1985): 15 species of naiades, including the endangered shiny pigtoe (*Fusconaia edgariana*), occur in the study area (Table 1). Based on 60 random 0.5-m^2 quadrat samples taken at NHF, the mean density of naiades was ca. 100/10 m^2 (Table 1).

Water temperatures were monitored from January 1981 to June 1982 with a 30-day recording thermograph. Mean river discharge during the study period, obtained at a gauging station of the U.S. Geological Survey at river mile 85.0 (river km 136), ranged from 1.44 m^3/sec in August 1981 to 25.93 m^3/sec in February 1982. Water quality data collected at North Holston Ford were summarized by Widlak and Neves (1985).

Glochidia.—Seasonality of glochidia in the stream drift was determined by setting three drift nets (30 x 30 cm, 130-μm mesh) ca. 5 m apart along a transect of the river at each of four stations. Stations 1 and 4 were immediately (within 5 m) upstream and downstream, respectively, from the largest mussel assemblage; stations 2 and 3 were 50

TABLE 1.—Species composition and mean density of naiades at North Holston Ford

Subfamily and species[a]	Mean density (no./10m^2)
Ambleminae	
Fusconaia edgariana (Lea, 1840)	5.0
Fusconaia barnesiana (Lea, 1838)	<0.1
Pleurobema oviforme (Conrad, 1834)	10.0
Lexingtonia dolabelloides (Lea, 1840)	5.3
Anodontinae	
Alasmidonta viridis (Rafinesque, 1820)	<0.1[b]
Lasmigona costata (Rafinesque, 1820)	<0.1[b]
Lampsilinae	
Lampsilis ventricosa (Barnes, 1823)	<0.1[b]
Lampsilis fasciola (Rafinesque, 1820)	1.3
Villosa nebulosa (Conrad, 1834)	19.7
Villosa vanuxemi (Lea, 1834)	12.0
Ptychobranchus fasciolaris (Rafinesque, 1820)	3.3
Ptychobranchus subtentum (Say, 1825)	7.0
Actinonaias pectorosa (Conrad, 1834)	1.3
Medionidus conradicus (Lea, 1834)	35.3
Toxolasma lividus (Rafinesque, 1831)	<0.1[b]
Total	100.3

[a]Nomenclature according to Stansbery and Clench (1974)
[b]Found in qualitative samples only

m apart within this area of greatest mussel density. Based on results of previous work with glochidial release periods (Zale and Neves, 1982b), Stations 1 and 4 were sampled twice monthly from June to August 1981, and monthly from September to April 1982; stations 2 and 3, because of higher mussel densities, were sampled weekly from June to August 1981 and monthly thereafter through April 1982. Ice and flood conditions in winter and a storm in May 1982 prevented the collection of six samples. On each sampling date, nets were set for 2 hr between 1000 and 1500 hr, a time period when glochidia are most likely to occur in the drift (Kitchel, 1985). Water depth and current velocity were measured with a pygmy meter at each net to compute water volume filtered, and later the density of glochidia. Drift samples were preserved in 10% buffered formalin.

In the laboratory, samples were stained with rose bengal and then rinsed on 0.5-mm and 130-μm mesh screens to remove organic debris and silt. Each sample was examined in a gridded petri dish with a dissecting microscope (20X). Glochidia were removed, counted and identified to subfamily on the basis of their size and shape (Zale and Neves, 1982b; Kitchel, 1985). Densities for each station and date were calculated as the weighted mean of all three nets, based on water volume filtered. Two-way analysis of variance (ANOVA) was used to compare densities among stations and sampling dates (Zar, 1974).

Fish.—The study area (350 m) was divided into seven 50-m sections and sampled by a crew of three persons with a direct current backpack electroshocking unit and dip nets to obtain a representative sample of the fish species and estimate their relative abundance within each section. Section 1 was a shallow run furthest upstream, with primarily cobble substrate; sections 2, 3 and 4 were swift riffles with coarse substrates and a pool along one bank; sections 5, 6 and 7 were primarily pool habitats with silt and bedrock substrates. Six of the sections were sampled twice monthly from June to August 1981 and monthly from September 1981 to June 1982. Section 3, with the greatest density of mussels, was sampled weekly from June to August 1981 and monthly thereafter through June 1982. High water conditions occasionally prevented sampling in winter and spring.

All larger fish (>80 mm total length) captured were anaesthetized, identified, counted and examined for glochidial infestations on fins or gills. Fish infested with glochidia were preserved in 10% buffered formalin; uninfested fish were released. All fish less than 80 mm were preserved for later examination. In the laboratory, opercular flaps were removed from each fish, and gills and fins were examined under a dissecting microscope. Glochidia were identified to subfamily and counted. Monthly prevalence and intensity of infestations by glochidia were tabulated for each fish species. Chi-square contingency tables were used to test for differences in prevalence of infestation among fish species and between two mussel subfamilies. Anodontinae were too poorly represented for analysis; only two were collected. We used Spearman rank correlations to test the possible association between infestations and densities of glochidia in the drift.

RESULTS

Examination of 160 drift samples collected from June 1981 to April 1982 revealed temporal patterns of glochidia in stream drift (Fig. 1). The greatest number of glochidia and highest water velocities usually were obtained along the left bank on each sampling date. Densities of lampsiline glochidia were significantly higher at stations 2 and 3 than at stations 1 and 4 throughout the year ($P<0.05$). Densities of amblemine glochidia were highest at station 3, but did not differ significantly among the other three stations during the summer release period ($P<0.05$). Differences in lampsiline densities were highly significant ($P<0.01$) among sample dates, but there was no significant difference in amblemine densities during the summer release period. Lampsiline glochidia were collected throughout the year, peaking in abundance from mid-June to mid-July and remaining at low densities in autumn and winter. Highest densities at stations 2 and 3 — 6 and 8.2 glochidia/10 m^3 of water sampled, respectively — were in April. In contrast, amblemine glochidia were present in the drift only from June to mid-August. In July, densities were as high as 34 glochidia/10 m^3 at station 2 and 117/10 m^3 at station 3. Water temperatures associated with these peak abundances were 7-17C for Lampsilinae and 20-28C for Ambleminae. These temporal trends in abundance of glochidia occurred at all four drift sampling stations.

Of 4800 fish examined for glochidial infestations between June 1981 and June 1982, 691 (14%) carried encysted glochidia (41 species of fish in seven families collected; 23 species in four families infested). The fish assemblage at the site was dominated numerically by cyprinids (39%), percids (28%), centrarchids (19%) and cottids (9%). Host specificity was evident, in that many of the more abundant fish species were frequently infested on various sampling dates, but several of the 18 species that were not infested, such as the northern hogsucker (*Hypentelium nigricans*) and banded darter (*Etheostoma zonale*), were relatively common (Table 2).

Amblemine glochidia were encysted only in the gill lamellae of 12 cyprinid species. Prevalence of infestation, based on all cyprinids examined, was nearly 18% (Table 3). However, if only fish examined during the summer release period for amblemine species are considered, infestations occurred in 23% of the cyprinids at NHF. Abundance of each of these 12 species hosting glochidia was not significantly correlated with prevalence of infestation ($P = 0.5$). For example, stonerollers (*Campostoma anomalum*), river chubs (*Nocomis micropogon*) and telescope shiners (*Notropis telescopus*) were relatively abundant, but the percent infested was low. Percentage of infestations was highest in moderately abundant species such as saffron shiners (*Notropis rubricroceus*) (53%), Tennessee shiners (*Notropis leuciodus*) (51%) and whitetail shiners (*Notropis galacturus*) (48%).

Eleven species of centrarchids, cottids and percids were infested with lampsiline glochidia (Table 4). Of 2655 fish of these three families examined, 356 (13%) carried glochidia. Species abundance again was not significantly correlated with prevalence of infestation ($P = 0.5$). Frequencies of infestation were low in some commonly collected

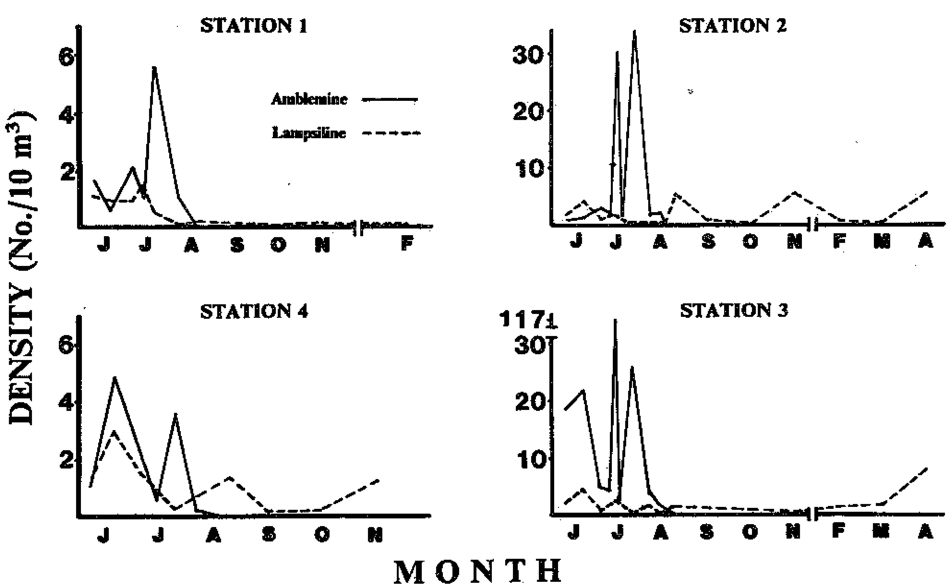

Fig. 1.—Densities of glochidia in stream drift at four stations, June 1981-April 1982

species, such as greenside darters (*Etheostoma blennioides*) (2%), Tennessee snubnose darters (*E. simoterum*) (3%), and smallmouth bass (*Micropterus dolomieui*) (8%), but were relatively high in less abundant species such as bluebreast darters (*E. camurum*) (18%) and logperch (*Percina caprodes*) (18%).

Mean prevalence of amblemine glochidia on cyprinids increased from 23% in June to 29% in July, and dropped to 8% in August (Table 3). No infestations were seen after late August. This temporal trend in infestations was similar to the pattern of occurrence of amblemine glochidia in stream drift (Fig. 1); however, this association was not statistically significant ($P<0.1$).

Mean prevalence of lampsiline glochidia on fish was highest in spring (March) and gradually declined through August (Table 4). Frequency of infestation then increased through autumn and winter. Fewer fish were collected in winter and spring than in summer and autumn, but the high frequencies of infestation in rock bass, banded sculpins and redline darters contributed to the apparently low degree of seasonality in the Lampsilinae.

Most fish with glochidia had light infestations, averaging 1–10 glochidia, on their

TABLE 2.—Prevalence of glochidial infestations on fish species at North Holston Ford, June 1981-June 1982

Species[a]	No. examined	Percent infested: Ambleminae	Percent infested: Lampsilinae
Cyprinidae			
Telescope shiner (*Notropis telescopus*)	499	12	<1
Stoneroller (*Campostoma anomalum*)	442	2	0
Tennessee shiner (*N. leuciodus*)	273	51	<1
Common shiner (*N. cornutus*)	157	15	0
River chub (*Nocomis micropogon*)	144	8	0
Warpaint shiner (*Notropis coccogenis*)	102	16	0
Whitetail shiner (*N. galacturus*)	73	48	0
Popeye shiner (*N. ariommus*)	51	24	0
Saffron shiner (*N. rubricroceus*)	47	53	0
Silver shiner (*N. photogenus*)	28	11	0
Rosyface shiner (*N. rubellus*)	15	7	7
Mirror shiner (*N. spectrunculus*)	1	100	0
Cottidae			
Banded sculpin (*Cottus carolinae*)	413	0	12
Centrarchidae			
Rock bass (*Ambloplites rupestris*)	688	0	20
Smallmouth bass (*Micropterus dolomieui*)	106	0	8
Bluegill (*Lepomis macrochirus*)	48	0	6
Redbreast sunfish (*L. auritus*)	45	0	11
Largemouth bass (*M. salmoides*)	5	0	20
Percidae			
Redline darter (*Etheostoma rufilineatum*)	842	0	15
Greenside darter (*E. blennioides*)	162	0	3
Tennessee snubnose darter (*E. simoterum*)	129	0	3
Bluebreast darter (*E. camurum*)	72	0	18
Logperch (*Percina caprodes*)	28	0	18
Total	4370		

[a]Species (No.) examined but not infested: *Ichthyomyzon bdellium* (3); *Hypentelium nigricans* (154); *Moxostoma erythrurum* (55); *Catostomus commersoni* (1); *Noturus insignis* (51); *Ictalurus nebulosus* (2); *Ictalurus natalis* (1); *Hybopsis dissimilis* (29) *Phenacobius uranops* (10); *Rhinichthys atratulus* (6); *Semotilus atromaculatus* (1); *Cottus baileyi* (3); *Lepomis megalotis* (29); *Pomoxis nigromaculatus* (6); *Etheostoma zonale* (66); *Etheostoma maculatum* (27); *Percina macrocephala* (5); *Percina aurantiaca* (1)

gills (Table 5). Overall, 79% of lampsiline-infested hosts had 10 or fewer glochidia attached compared with 47% for amblemine-infested hosts. The highest infestation consisted of 140 amblemine glochidia on a whitetail shiner (*Notropis galacturus*) in July, and 230 lampsiline glochidia on a rock bass (*Ambloplites rupestris*) in May. Amblemine glochidia were found only on gill lamellae, whereas lampsiline glochidia were occasionally seen on the inner membrane of the opercular flap and on the lateral or caudal fins of heavily infested fish. Although the seven river sections sampled for fish differed in habitat type and availability, the prevalence of glochidial infestations on fishes was similar among sections; 24 ($\pm$4.9 SD) % for Ambleminae and 12 ($\pm$6.3 SD) % for Lampsilinae.

Discussion

The period of glochidial release by amblemine species at North Holston Ford, June to mid-August, concurs with that reported for other short-term brooders (Surber, 1912; Matteson, 1948; Yokley, 1972; Wiles, 1975; Yeager and Neves, 1986). These earlier studies of mussel reproduction relied on observations of gravid females or host infestations to define the times of release and were essentially correct for short-term brooders. However, the nearly continuous occurrence of lampsiline glochidia in our stream drift samples, particularly their consistent presence in autumn and winter, differs from the generally accepted notion of seasonality in reproduction of Lampsilinae, and consequently the occurrence of hosts infested with glochidia. Early observations of gravid mussels noted variation in breeding (release) periods among individuals and species, particularly for these long-term brooders (Connor, 1907, 1909; Ortmann, 1909, 1919). Discharge of glochidia by individual females was therefore considered to be brief, not spanning the entire release period for a population or a species. Recent studies on long-term brooders have relied on the same criteria (gravidity, host infestations), with little consideration for individual variation. Lack of sexual dimorphism in most species, unknown sex ratios and small sample sizes contribute to the difficulty of describing components of the reproductive cycle of the Lampsilinae based primarily on the presence or absence of gravid individuals in field collections. Discrete periods of glochidial release by lampsiline species, as described in previous studies, should therefore be considered principal and not inclusive release periods. Our results and those of Zale and Neves (1982b) indicated that the release of glochidia by some individuals in populations of

TABLE 3.—Prevalence of infestation (number examined, percent infested) by amblemine glochidia on fish. Mean percent is the ratio of number infested to total number examined

	1981						1982	
	June		July		Aug.		June	
Species	No.	%	No.	%	No.	%	No.	%
Stoneroller	41	10	128	4	135	0	11	9
River chub	17	6	41	20	48	2	5	20
Common shiner	26	35	57	12	40	10	16	19
Mirror shiner	0	0	1	100	0	0	0	0
Popeye shiner	12	8	17	41	12	17	4	50
Rosyface shiner	1	0	6	17	3	0	2	0
Saffron shiner	11	64	16	88	6	33	4	50
Silver shiner	20	10	5	20	2	0	1	0
Telescope shiner	114	11	140	19	88	6	54	26
Tennessee shiner	55	53	71	89	62	27	34	88
Warpaint shiner	12	42	37	14	22	9	8	50
Whitetail shiner	16	31	26	73	6	50	9	89
Mean %		23		29		9		44

lampsiline species is nonsynchronous and may be nearly year-round, except during the period of embryogenesis.

Fish host specificity was apparent for mussel species at NHF; not only species with identified fish hosts but also those with unknown hosts (Fuller, 1974; Zale and Neves, 1982a). The lack of correlation between prevalence of infestation on fish species and their relative abundance, and the absence of glochidia on members of the lamprey, sucker and catfish families support that conclusion. Although the seven fish species in these three families were not infested at NHF, they do serve as hosts for other mussel species (Howard and Anson, 1922; Fuller, 1974). The importance of sunfishes and darters as hosts for the Lampsilinae in Virginia confirms field observations for other species of naiades in the Mississippi River drainage (Fuller, 1974).

Overall prevalence of glochidial infestation on fishes, 23% for amblemine mussels and 13% for lampsiline species, was similar to results of previous studies on individual naiad species, which ranged from 6% to 35% (Trdan, 1981; Neves and Zale, 1982a; Threlfall, 1986). The greater prevalence and intensity of infestations by amblemine vs. lampsiline mussels on fish hosts is noteworthy and is possibly related to the mode of infestation. Release of conglutinates (packets of glochidia) by amblemine species may result in a higher intensity of infestation, particularly if they elicit a feeding response by

TABLE 4.—Prevalence of infestation (number examined, percent infested) by lampsiline glochidia on fish, June 1981-June 1982. Mean percent is the ratio of number infested to total number examined

	June		July		Aug.		Sept.	
Species	No.	%	No.	%	No.	%	No.	%
Rock bass	132	33	163	29	168	3	31	0
Redbreast sunfish	0	0	23	17	10	0	0	0
Bluegill	5	40	7	14	13	0	4	0
Smallmouth bass	10	20	16	13	39	0	10	10
Largemouth bass	0	0	3	0	0	0	0	0
Banded sculpin	68	21	97	7	132	0	10	0
Redline darter	64	36	231	12	295	0	103	14
Greenside darter	39	5	47	0	54	0	1	1
Tennessee snubnose darter	36	11	24	0	30	0	0	0
Bluebreast darter	8	38	10	10	25	4	0	
Logperch	8	38	10	10	7	0	0	0
Mean %		26		15		1		9

TABLE 4.—(Cont.)

	Oct.		Nov.-Jan.		Feb.-Mar.		Apr-May		June	
Species	No.	%	No.	%	No.	%	No.	%	No.	%
Rock bass	19	0	25	4	4	25	24	33	102	28
Redbreast sunfish	1	0	2	0	0	0	0	0	9	11
Bluegill	6	0	10	0	0	0	0	0	3	0
Smallmouth bass	13	23	5	0	0	0	8	0	5	0
Largemouth bass	0	0	0	0	0	0	0	0	2	50
Banded sculpin	34	18	36	33	4	25	10	80	22	9
Redline darter	56	36	18	39	24	58	24	58	27	22
Greenside darter	12	0	2	0	1	0	1	100	5	20
Tennessee snubnose darter	19	0	16	0	0	0	0	0	4	0
Bluebreast darter	10	40	2	100	0	0	6	17	11	9
Logperch	1	0	0	0	0	0	1	100	1	0
Mean %		19		19		48		45		21

host fishes. This reproductive attribute is particularly effective for infesting mobile, diel sight-feeders such as cyprinids (Fraser and Cerri, 1982).

Since glochidia survive for only a few days if they are unable to parasitize a suitable host (Surber, 1912), peak infestations of fish hosts would be expected to coincide with the period of peak glochidial release. Due to the prolonged release period and the potentially long period of encystment (which is temperature-dependent), peak infestations occurred shortly after maximum densities of glochidia in stream drift. Infestations were fewer in benthic fish having subterminal mouths (greenside and snubnose darters, stonerollers) than on closely related species with terminal mouths. As judged by the hypotheses proposed to explain modes of infestation—ingestion of drifting glochidia and respiratory action of host fish—the difference in mode of feeding among darter species at NHF supports the former hypothesis for these and other small species categorized as drift-feeders.

The low prevalence of infestation and low densities of glochidia on most parasitized fish illustrate the relative inefficiency of reproduction for naiades. An average of less than 10 glochidia per infested fish appears to be typical for most mussel populations (Coker *et al.* 1921; Trdan, 1981; Threlfall, 1986), except in areas with extremely high mussel densities (Stern and Felder, 1978). Naiades, best described as long-lived and r-selected species, have generally low but prolonged rates of recruitment to sustain their populations. The glochidial stage is considered to be an adaptation for dispersal, and co-evolution of mussels and fish hosts may explain the specificity observed in such old and diverse assemblages as those in the upper Tennessee River drainage. For example, the seasonal movements of drift feeders such as cyprinids, generally upstream in spring and summer and downstream in autumn (Mendelsen, 1975; Fraser and Sise, 1980; Storck and Momot, 1981), would be of dispersal value to sedentary mussels. If home range mechanisms are unimportant in the overall population dynamics of cyprinids in rivers (Linfield, 1985), then these highly mobile species would provide an effective mode for colonization by mussels. Conversely, however, the more sedentary species such as darters and sculpins, which are benthic and share the same riffle habitats with mussels (Reed, 1968; Brown and Downhower, 1982), are typically abundant and readily available as hosts. Their limited use by the mussel assemblage at North Holston Ford indicates that other factors are important for host suitability. Hypotheses on host fish use and specificity in diverse ecosystems vs. nonspecificity in less diverse systems can be postulated on evolutionary and ecological principles. However, until fish hosts are iden-

TABLE 5.—Intensity of infestations by amblemine and lampsiline glochidia on fish, June 1981-June 1982

No. glochidia	No. Fish June	July	Aug.	Sept.-May	June
		Ambleminae			
1-10	59	122	31	0	51
11-20	10	13	3	0	9
21-40	4	13	0	0	1
>40	3	10	2	0	4
Total	76	158	36	0	65
		Lampsilinae			
1-10	43	47	5	52	21
11-20	17	16	0	29	7
21-40	17	19	0	16	7
>40	19	12	1	22	6
Total	96	94	6	119	41

tified for more mussel species in various types and sizes of aquatic communities, explanations for host specificity remain largely conjecture.

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