

Studies on the Seasonal Dynamics of *Crepidostomum cooperi* in the Burrowing Mayfly, *Hexagenia limbata*¹

GERALD W. ESCH AND TERRY C. HAZEN

Department of Biology, Wake Forest University, Winston-Salem, North Carolina 27109 and
Department of Biological Sciences, University of Puerto Rico, Rio Piedras, Puerto Rico 00926

ABSTRACT: Recruitment of metacercariae of *Crepidostomum cooperi* by nymphs of *Hexagenia limbata* in Gull Lake, Michigan, begins in June and continues through August. The seasonal dynamics of adults of *C. cooperi* is characterized by their disappearance from centrarchid definitive hosts during the fall months. More than 99% of the metacercariae in subimagoes of *H. limbata* occur in the abdomen and >70% in IV, V, and VI abdominal segments; the distribution of metacercariae among the abdominal segments is virtually identical in the two sexes. During April and May and among the smallest nymphs during periods of recruitment, metacercariae distributions were best fit by the Poisson. With one exception, following the initiation of recruitment and continuing throughout each sampling period, the negative binomial model provided the best fit to observed frequency distributions of metacercariae in larger nymphs and subimagoes. Based on these observations, it is suggested that the frequency distributions are generated by the compounding of Poisson variates which arise as a consequence of random waves of invasion by cercariae.

Crepidostomum cooperi Hopkins, 1931, is one of the most common and geographically widespread of the allocreadid trematodes. It has been reported from at least 20 genera of fishes throughout the United States and Canada (Hoffman, 1967). There are, however, only three studies which provide any data regarding seasonal dynamics or other ecological information for the parasite. Two of these (Cannon, 1972; McDaniel and Bailey, 1974) documented seasonal changes in the definitive host and the third (Hazen and Esch, 1977) examined seasonal dynamics in an intermediate host, *Hyaella azteca*.

For the past 12 years, the population biology of *C. cooperi* in the burrowing mayfly, *Hexagenia limbata*, has been studied in Gull Lake, Michigan, U.S.A. (Esch and Hazen, manuscript in preparation). As a part of this investigation, and because so little is known about the seasonal dynamics of the parasite, the present study was undertaken.

Study Area

Gull Lake is spring-fed, mesotrophic tending toward eutrophic, and is located in southwestern, lower Michigan. The lake is 9.7 × 1.6 km, has a surface area of 822 ha, and reaches a maximum depth of 31 m. The lake is predominantly marl. Dominant aquatic macrophytes include *Chara* spp., *Najas flexilis*, *Myriophyllum heterophyllum*, *Potamogeton* spp., *Utricularia* sp., *Elodea canadensis*, and *Vallisneria americana* (Moss, 1972). The parasite fauna for Gull Lake centrarchids was described by Esch (1971).

Methods

Mayfly nymphs were collected from several locations at approximately 4-m depths using an Ekman-type grab sampler. Mayflies were separated from the

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Table 1. Distribution of *Crepidostomum cooperi* in the abdominal segments of male and female subimagoes.

Segment	Percent metacercariae/segment	
	Males (N = 151)	Females (N = 314)
Thorax	<1.0	<1.0
I	3.3	5.1
II	11.3	8.9
III	13.2	11.1
IV	19.2	20.7
V	29.1	26.1
VI	20.5	26.4
VII	4.0	3.2
VIII	0.0	<1.0

sediments and other debris by washing through a screen having a mesh size of 0.20 mm. Nymphs collected in this manner were immediately preserved in 70% ethanol and returned to the laboratory for microscopic examination. Metacercariae of *C. cooperi* were recorded and pertinent data regarding host sex and size were noted.

Beginning in late July, subimagoes of *H. limbata* were collected on the evening of their emergence from the lake. The positive phototaxis exhibited by the subimagoes facilitated their capture from window screens and light posts. Mayflies were immediately placed in 70% ethanol and returned to the laboratory for study. Metacercariae were counted with the aid of an ordinary 40× dissecting microscope. Host sex, total length and/or abdominal length were recorded.

The life cycle characteristics of *H. limbata* have been well documented by Hunt (1952); in Gull Lake, *H. limbata* has a 1-year cycle, with emergence beginning in late July and continuing into September. The life cycle pattern of *C. cooperi* was initially described by Hopkins (1934). In Gull Lake, the definitive hosts for *C. cooperi* include bluegill, *Lepomis macrochirus*, rock bass, *Ambloplites rupestris*, and smallmouth bass, *Micropterus dolomieu*. The primary second intermediate host in Gull Lake is *H. limbata*, although the amphipod, *Hyaella azteca*, also serves as an important second intermediate host.

Data were analyzed using an HP3000 computer. The negative binomial, log-normal, and Poisson models were all fitted to the observed distributions using the procedure of Bliss and Fisher (1953). An estimate of goodness of fit was obtained by the value of χ^2 derived from comparing observed and expected frequencies. The procedures used were similar to those of Lester (1977).

Results

Metacercariae of *Crepidostomum cooperi* are restricted almost entirely to the abdominal segments of *H. limbata* subimagoes (Table 1), with less than 1% of the parasites encysted in the head and thoracic regions. The fourth, fifth, and sixth abdominal segments carry nearly 70% of all metacercariae present in the host. There is no apparent difference in the distribution of metacercariae in subimagoes of the two sexes.

Nymphs collected in April and May had few metacercariae; those which were present were randomly distributed (Table 2). Parasites which were present were

Table 2. Seasonal changes in various population parameters of *C. cooperi* metacercariae in nymphs and subimagoes of *H. limbata*.

Date	Stage of host (sex)	Prevalence	\bar{x} (N)	Variance	Dispersion pattern	k	P
4/2	Nymph (not sexed)	6%	0.06 (33)	0.06	Random	—	—
4/17	Nymph (not sexed)	9%	0.15 (73)	0.29	Random	—	—
5/2	Nymph (not sexed)	8%	0.10 (70)	0.11	Random	—	—
5/23	Nymph (not sexed)	4%	0.05 (69)	0.08	Random	—	—
7/7	Nymph (male)	45%	0.97 (86)	3.83	Contagious	0.54	0.067
7/29	Nymph (male)	71%	1.90 (77)	3.61	Contagious	1.15	0.366
7/30	Subimago (male)	75%	1.96 (105)	4.04	Contagious	1.95	0.875
7/30	Subimago (female)	89%	6.01 (104)	37.82	Contagious	1.38	0.030*
8/28	Subimago (male)	86%	3.26 (76)	14.89	Contagious	1.37	0.425
8/28	Subimago (female)	96%	7.00 (91)	39.74	Contagious	1.65	0.971

* While overdispersed, the negative binomial model did not provide a satisfactory fit to the observed frequency distribution.

most probably recruited during the previous fall. Recruitment of metacercariae by nymphs of *H. limbata* begins in June and continues at least through August. After the onset of parasite recruitment in June, and continuing through the August collections, metacercariae were contagiously distributed among both nymphs and newly emerged subimagoes. The negative binomial model provided an adequate fit for all samples after May 23 except among female subimagoes collected on July 30. A separate collection made approximately two weeks later revealed a mean density of 9.19 metacercariae/host and the negative binomial provided a satisfactory fit to the observed distribution ($k = 1.32$; $P = 0.738$). The value of k , which is an index of overdispersion, ranged from 0.54 (indicating a high degree of contagion) to 1.95 (indicating less overdispersion).

The prevalence and mean infrapopulation densities of *C. cooperi* metacercariae were measured in three, arbitrarily established, size classes of nymphs collected on July 7 and July 23 (Table 3). For each date, there was a positive relationship between total body length and the prevalence and density of the parasites. The parasites were randomly distributed in the smallest nymphs (<19 mm) collected on both dates in July. Metacercariae were overdispersed in all other size classes during each sampling period. In the two larger size classes collected in July, the

Table 3. Various population parameters of *C. cooperi* metacercariae within male nymphs of different size classes during early and late July.

Size range (mm)	July 7					
	Prevalence	\bar{x} (N)	Variance	Dispersion pattern	k	P
≤19	33%	0.37 (45)	0.28	Random	—	0.067
20–23	40%	1.04 (25)	4.12	Contagious	0.388	0.237
≥24	69%	1.38 (16)	2.25	Contagious	2.51	0.567
July 29						
≤19	47%	0.77 (17)	1.07	Random	—	0.564
20–23	73%	1.67 (43)	3.99	Contagious	1.59	0.245
≥24	88%	4.18 (16)	13.65	Contagious	1.89	0.993

Table 4. Changes in various population parameters of *C. cooperi* metacercariae within subimagoes of varying abdominal lengths.

Abdomen length (sex)	Prevalence	\bar{x} (N)	Variance	k	P
13 mm (male)	60%	1.67 (15)	5.38	0.77	0.450
14 mm (male)	84%	3.02 (51)	8.70	1.89	0.793
15 mm (male)	85%	2.63 (80)	4.77	3.24	0.482
16 mm (male)	88%	3.28 (50)	11.68	1.79	0.360
17 mm (female)	91%	3.91 (23)	10.81	2.50	0.837
18 mm (female)	86%	3.69 (58)	10.01	2.04	0.385
19 mm (female)	89%	5.89 (92)	30.30	1.29	0.219
20 mm (female)	89%	5.39 (74)	20.33	1.47	0.573
21 mm (female)	100%	7.63 (18)	49.36	1.72	0.855

negative binomial model provided a satisfactory fit to the observed frequency distributions.

The mean density of *C. cooperi* metacercariae in subimagoes was positively correlated ($r = 0.922$) with length of the abdomen, increasing from 1.67 in males with abdomens 13–14 mm in length to 7.63 in females with abdominal lengths of 21–22 mm (Table 4). In all size classes, metacercariae were overdispersed; the negative binomial model provided a satisfactory fit to the observed frequency distribution of parasites in subimagoes within each size class. The pattern of overdispersion is clear in all size classes, with the majority (>50%) of the metacercariae occurring in approximately 20% of the hosts.

The positive relationship between prevalence of *C. cooperi* metacercariae and size of *H. limbata* is also consistent for the other dominant intermediate host in Gull Lake. Thus, the prevalence of metacercariae in amphipods, *Hyalella azteca*, increased from <1% among individuals with <17 antennal segments to >25% among individuals with >25 antennal segments (Fig. 1).

Discussion

The recruitment of *C. cooperi* by mayfly nymphs in Gull Lake is clearly a seasonal phenomenon, beginning in June and continuing at least through August. This pattern, not surprisingly, is similar to that which occurs among *Hyalella azteca* in the same system (Hazen and Esch, 1977). Unpublished observations by one of us (GWE) also indicate that the prevalence of *C. cooperi* adults in centrarchid definitive hosts is also highly seasonal, with parasites present in each month from May through September, but absent during the winter. Collectively, the seasonal dynamics of *C. cooperi* in the second intermediate and definitive hosts suggest that the parasite overwinters as an egg, or in the first intermediate host (fingernail clams of the genus *Sphaerium*). While we have no direct observation to support the contention, indirect evidence from Gale (1973) suggests that *C. cooperi* occurs in *Sphaerium transversum* from Pool 19 in the Mississippi River during the winter months.

The seasonal pattern of *C. cooperi* metacercariae and adults in Gull Lake is similar to that reported by Cannon (1972) among yellow perch, *Perca flavescens*, in Lake Opeongo, Ontario, Canada, but not for *Lepomis* spp. in Little River, Oklahoma, U.S.A. (McDaniel and Bailey, 1974). Thus, the latter investigators

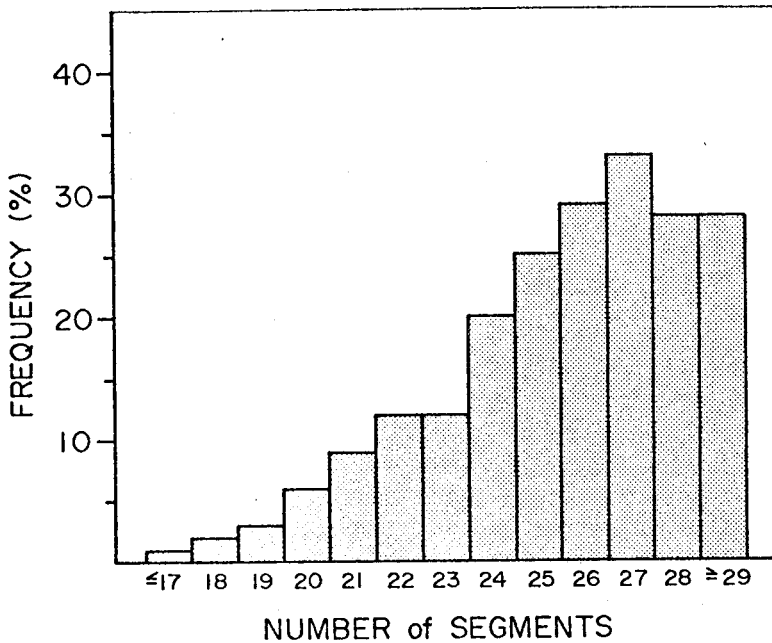


Figure 1. Relationship between prevalence of *C. cooperi* and numbers of antennal segments of *Hyalella azteca*; numbers of antennal segments are also a function of size and age for *H. azteca*.

reported peak prevalence during the winter months and then an almost linear decline until September when infection percentages reach zero. The similarity in seasonal dynamics of *C. cooperi* in Gull Lake and Lake Opeongo and its decline to zero during the summer months in Little River would be expected if, as proposed by Chubb (1979), water temperature is a major factor in regulating the population biology of *C. cooperi*. It is clear, however, that the seasonal periodicity of *C. cooperi* must also be synchronized with the seasonal dynamics of intermediate and definitive host populations. Thus, in Gull Lake, the burrowing mayfly, *Hexagenia limbata*, follows a 1-year cycle (rather than two years as in other lake systems), with peak emergence in August–September and maximum growth rates from May through July of each year. It would consequently be advantageous for the parasite to be recruited by the intermediate host during that time when probability of transmission to the definitive host is maximized. Since size selective predation is known to be a strategy of the bluegill (Werner and Hall, 1974) and probably of other centrarchid hosts in Gull Lake as well, then it would be best to have greater transmission during the months of June through August when nymphs of *H. limbata* grow to their greatest size.

Anderson (1978) proposed that three processes are most important in producing what he termed, "stable dynamical equilibrium," or regulation. These are: (1) density-dependent constraints on parasite population growth; (2) nonlinear, parasite-induced host mortality; and (3) overdispersion of parasite infrapopulations within their hosts. It was Crofton (1971), however, who first emphasized that "it is overdispersion and the relationship of parasite density to lethal factors which produce a disparity in parasite and host deaths." It is clear that *C. cooperi*

metacercariae are highly overdispersed and that the negative binomial model provided the best fit for the observed frequency distributions. The data presented herein do not suggest whether *C. cooperi* and *H. limbata* may be acting in a mutually regulatory fashion. The only feature which may be suggestive of regulation is that k values are low. According to Anderson and May (1978), a "high degree of overdispersion tends to confer stability"; this is, however, but one of several conditions which must be met in order to have effective regulation.

The mechanisms which may operate to generate overdispersion and, more precisely, a frequency distribution to which the negative binomial model can be fitted, are several. According to Crofton, these include: (1) compounding of Poisson variates through a series of random waves of infection; (2) clumped, or contagious distribution of infective agents; (3) increasing the probability of infection by a previous infection; (4) decreasing the chance of further parasite recruitment because of previous infection; (5) altering the probability of infection by changes in size or age of the host; (6) changing the probability of infection with time. The mechanism by which the overdispersion of *C. cooperi* metacercariae was generated has not been determined experimentally, but based on several life history features of the parasite and host, a reasonable hypothesis may be formulated. First, the parasite is randomly distributed among mayfly nymphs during the months of April and May, suggesting that recruitment by nymphs occurred during the previous fall and that it was probably a consequence of random exposure to cercariae shed from *Sphaerium* spp. during the tail-end of the seasonal cycle. Second, small nymphs collected on July 7 and July 29 had metacercariae which were dispersed in a random fashion. These nymphs, being smaller, were probably also younger and, as a consequence, were less likely to have been exposed to infection for as long a period of time as the larger individuals. The existence of randomly dispersed metacercariae in smaller nymphs, collected from the same location as larger nymphs having contagiously distributed metacercariae infrapopulations, tends to suggest that overdispersion was generated by the compounding of Poisson variates. Such a contention is further supported by the knowledge that nymphs do not move about in the substrate once construction of a burrow has been completed (Hunt, 1952); they are, therefore, sedentary and would unlikely be exposed to contagiously distributed masses of infective agents. The other five possibilities identified by Crofton (1971) as mechanisms for generating overdispersion which can be described by the negative binomial model seem less likely to have occurred than the first. The absence of any evidence indicating that probabilities of infection may be increased or decreased by changes in size, age, or as a function of differences in sample sizes, seem to support our assertion that *C. cooperi* overdispersion is generated by random waves of infection by cercariae shed from infected *Sphaerium*.

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Literature Cited

- Anderson, R. M. 1978. The regulation of host population growth by parasitic species. *Parasitology* 76:119-157.
- Anderson, R. M., and R. M. May. 1978. Regulation and stability of host-parasite population interactions. I. Regulatory processes. *J. Anim. Ecol.* 47:219-247.
- Bliss, C. I., and R. A. Fisher. 1953. Fitting the negative binomial distribution to biological data. *Biometrics* 9:176-200.
- Cannon, L. R. G. 1972. Studies on the ecology of the papillose allocreadid trematodes of the yellow perch in Algonquin Park, Ontario. *Can. J. Zool.* 9:1231-1239.
- Chubb, J. C. 1979. Seasonal occurrence of helminths in freshwater fish. Part II. Trematoda. In W. H. R. Lumsden, R. Muller, and J. R. Baker, eds. *Advances in Parasitology*. Vol. 17. Academic Press, New York.
- Crofton, H. D. 1971. A quantitative approach to parasitism. *Parasitology* 62:179-193.
- Esch, G. W. 1971. Impact of ecological succession on the parasite fauna in centrarchids from oligotrophic and eutrophic ecosystems. *Am. Midl. Nat.* 86:160-168.
- Gale, W. F. 1973. Predation and parasitism as factors affecting *Sphaerium transversum* (Say) populations in Pool 19, Mississippi River. *Res. Popul. Ecol.* 14:169-187.
- Hazen, T. C., and G. W. Esch. 1977. Studies on the population biology of two larval trematodes in the amphipod, *Hyalella azteca*. *Am. Midl. Nat.* 98:213-219.
- Hoffman, G. L. 1967. *Parasites of North American Freshwater Fishes*. University of California Press, Berkeley and Los Angeles. 486 pp.
- Hopkins, S. A. 1934. The papillose Allocreadidae. III. *Biol. Monogr.* 13:45-124.
- Hunt, B. P. 1952. The life history and economic importance of the burrowing mayfly, *Hexagenia limbata*, in southern Michigan lakes. *Bull. Inst. Fish. Res.* 4:1-151.
- Lester, R. J. G. 1977. An estimate of the mortality in a population of *Perca flavescens* owing to the trematode *Diplostomum adamsi*. *Can. J. Zool.* 55:288-292.
- McDaniel, J. S., and H. H. Bailey. 1974. Seasonal population dynamics of some helminth parasites of centrarchid fishes. *Southwest. Nat.* 18:403-416.
- Moss, B. 1972. Studies on Gull Lake, Michigan. II. Eutrophication evidence and prognosis. *Freshwater Biol.* 2:309-320.
- Werner, E. E., and D. H. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042-1052.