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A Long-term Study on the Population Biology of *Crepidostomum cooperi* (Trematoda: Allocreadidae) in the Burrowing Mayfly, *Hexagenia limbata* (Ephemeroptera)

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ABSTRACT: A 16-year study (1969-1984) considered aspects of the population biology of *Crepidostomum cooperi* (Trematoda: Allocreadidae) in the burrowing mayfly *Hexagenia limbata* (Ephemeroptera). The study site was Gull Lake, a mesoeutrophic system in southwestern lower Michigan. Prevalence of *C. cooperi* metacercariae was, except for one period of 2 consecutive years, significantly higher in female subimagoes. Prevalence in male mayflies varied between 75% and 90% in all but 4 years; among females it was >90% in all but 3 years. Densities of metacercariae were consistently higher in female mayflies in all 16 years. There was a significant increase in density of the parasite from 1969 through 1976, followed by a significant decrease over the next 6 years; densities have risen substantially in the last 2 years. The prevalence and abundance of *C. cooperi* in mayfly nymphs was higher in shallow parts of the littoral zone (3 m) than at 5 or 7 m. The pattern of distribution of the parasite in mayfly nymphs and subimagoes is believed to be related to the eutrophication which has occurred in the lake during the past 15-20 years.

INTRODUCTION

Long-term studies on the population biology of parasites are few. Those which have lasted for more than a few years have been mostly of helminth parasites in aquatic ecosystems (Peterson, 1971; Smith, 1973; Kennedy and Rumpus, 1977; Kennedy, 1981; Aho *et al.*, 1982; Camp *et al.*, 1982). Because of a lack of effort in this area, there is a serious gap in our knowledge regarding long-term changes in patterns of host-parasite interactions.

For the past 16 years, we have examined various aspects of the population biology of the allocreadid trematode, *Crepidostomum cooperi*, in the burrowing mayfly *Hexagenia limbata*. Aside from the significance of the long-term data base, we have had the opportunity of conducting the study in a system which has been subjected to substantial perturbation over the same time.

Because of nutrient loading, primarily from faulty septic systems in the drainage basin, Gull Lake (located in Kalamazoo Co., Michigan) has undergone eutrophication over the past 20-25 years (Moss, 1972). Along with a decline in water quality, there has been a concomitant disruption in the community structure and dynamics of both the flora and the fauna.

Prior to the onset of eutrophication, the lake had large areas of marl-mud substrate which were capable of supporting populations of the burrowing mayfly. With eutrophication, however, parts of the hypolimnion with a marl-mud substratum can no longer support *Hexagenia limbata* because of anoxia. Because of hypolimnetic anoxia, we hypothesized that mayflies are now restricted to shallower, less suitable areas in the littoral zone of the lake. With this redistribution, we proposed that recruitment of the parasite would be enhanced since nymphs of the mayfly would be in greater proximity with sphaeriid clams, the first intermediate host of the parasite.

In our 16-year study, we have undertaken to answer questions relating eutrophication, the distribution and abundance of the mayfly in the lake, and long-term changes in density and prevalence of the parasite in the mayfly intermediate host. Of particular

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interest to us is the recently completed construction of a sewer system to service the Gull Lake drainage basin. Reversal of the eutrophication process should occur and, indeed, be complete within 5-10 years. We now have the opportunity of following changes in the parasite-mayfly system and of testing predictions based on the first 16-year data set.

MATERIALS AND METHODS

Subimagoes of the burrowing mayfly (*Hexagenia limbata*) were collected each August at the W. K. Kellogg Biological Station from 1969 through 1984. The mayflies had recently emerged from Gull Lake. Mayflies were placed in 70% ethanol, and later sexed and examined for the number of *Crepidostomum cooperi* metacercariae.

During the summer of 1984, mayfly nymphs were collected from two stations in Gull Lake; one site (RTP) was located just off Ross Township Park near the W. K. Kellogg Biological Station and the other approximately 2 miles N at the northwestern end of the lake (NP). Thirty grabs were made at each site with a 6-inch Ekman dredge from depths of 3, 5 and 7 m. The grab samples were separately washed through a series of hardware-cloth screens with the smallest mesh size of 1.5 x 2.0 mm. Mayfly nymphs were placed in 70% ethanol and returned to the laboratory. The number of metacercariae in each nymph was counted; the nymphs were sexed and measured to the nearest millimeter in total length.

Water quality characteristics of Gull Lake prior to 1971 have been described by Moss (1972). Information regarding data on water quality subsequent to 1971 was obtained from Drs. Patricia Lane, George Lauff and Robert Wetzel. In 1984, dissolved oxygen and temperature were measured at the two collecting sites described above, as well as at six stations, 18-30 m deep.

Host and parasite life histories. — The life history characteristics of the burrowing mayfly *Hexagenia limbata* have been described by Hunt (1953). In Gull Lake, the emergence of subimagoes begins approximately 1 August each year, and continues 4-6 weeks. After the final molt and copulation, females oviposit on the lake surface and then die; following copulation, males remain on land, dying in vegetation along the lake shore. After development, eggs hatch and small nymphs appear. For approximately 1 year, nymphs grow in size, molting 28-29 times in the process. Subimagoes begin emerging around 1 August of the next year. Throughout the aquatic phase of the life cycle, nymphs reside in U-shaped burrows constructed in the marl-mud sediments of the lake. Generally, eggs are deposited in shallow water; eggs then hatch and nymphs grow in size, moving into deeper and deeper water (Hunt, 1953).

Crepidostomum cooperi (Allocreadidae: Trematoda) is a common parasite of centrarchid fishes throughout the U.S.A. and Canada (Hoffman, 1967). The life cycle of *C. cooperi* was described by Hopkins (1934). Adult parasites are typically found in the pyloric ceca of definitive hosts which, in Gull Lake, include bluegill (*Lepomis macrochirus*), rock bass (*Ambloplites rupestris*), and smallmouth bass (*Micropterus dolomieu*) (Esch, 1971). Eggs which are shed into water hatch quickly, releasing miracidia which then penetrate sphaeriid clams. Following sporocyst development in the clam, cercariae are released into the water. Infection of *Hexagenia limbata* occurs when cercariae make contact with nymphs. Upon penetration, a cyst wall is secreted around each of the metacercariae. Generally, cysts occur in the gill filaments and muscles supporting the gills. When nymphs molt to become subimagoes, metacercariae become directly associated with the abdominal wall and can easily be seen using an ordinary dissecting microscope. The life cycle of the parasite is completed when the mayfly is consumed by a centrarchid fish. Mayflies possessing metacercariae may be eaten by fish at any time, but most frequently they are consumed during the period of emergence and when adult females oviposit on the lake surface.

Definitions and terminology. — Mean density, as used herein, is the number of parasites divided by the number of hosts sampled. Prevalence is the percentage of infected hosts

in the sample. An infrapopulation refers to all of the metacercariae of *Crepidostomum cooperi* within a single subimago (for a discussion of the concept, see Esch *et al.*, 1975).

Data analysis.—Data were analyzed using the Statistical Analysis System (SAS Inc., Raleigh, N.C.). Chi-square tests were used to compare prevalence of the parasite in male and female mayflies. Student's t-test was used to compare mean densities of metacercariae in the two sexes of host during each year. A quadratic regression analysis (RSREG procedure of SAS) was used to test for the significance of long-term changes in density of metacercariae among male and female mayflies. Analysis of variance was performed using the procedure described by Zar (1984).

RESULTS

With the exception of 4 nonconsecutive years, the prevalence of *Crepidostomum cooperi* metacercariae in male subimagos remained between 75.0 and 90.6% (Table 1). In 1969, 1972 and 1980, prevalence was less than 75%, while in 1978, it approached 95%. Among female subimagos, the prevalence was generally more than 90%, dropping below this level in 1969, 1972 and 1980, the same 3 years when prevalence was also lower among male subimagos. In each year of the study, except 1978 and 1979, the prevalence of metacercariae in female subimagos was significantly higher than that in males. The patterns of change in prevalence from one year to the next over the 16-year period were virtually identical for the two sexes; the only exception was in 1978 when prevalence increased among males to the point where it approximated that in females.

The mean density, variance and variance/mean ratios were computed for metacercariae among female subimagos (Table 2). During the 1st 8 years, mean density increased and was paralleled by changes in both variance and variance/mean ratios. Beginning in 1977, however, mean density declined over the next 6 years. Both variance and variance/mean ratio followed a similar pattern of decline in these years. In 1983 and 1984, density and variance increased dramatically while the variance/mean ratio remained low. Among males, mean densities of metacercariae increased during the 1st 8 years, although the magnitude of change was not as large as among the females (Table 2). Over the next 6 years, mean density in males declined, but changes were erratic, with the 14-year peak occurring in 1978. In 1983 and 1984, density and variance increased perceptibly while variance/mean ratios stayed low. Mean densities of metacercariae

TABLE 1.—Comparison of prevalence of *C. cooperi* among male and female mayflies, 1969-1984

Year	Prevalence		Chi square	$\bar{z}P$
	Male	Female		
1969	60.6(33)*	86.2(101)	10.08	0.0015
1970	78.7(216)	93.0(212)	17.71	0.0001
1971	80.4(224)	93.2(222)	16.13	0.0001
1972	60.7(410)	83.2(236)	34.81	0.0001
1973	81.2(202)	94.8(154)	14.40	0.0001
1974	88.2(268)	95.7(277)	10.62	0.0011
1975	85.3(92)	94.8(122)	33.83	0.0001
1976	82.3(196)	91.9(142)	6.09	0.0136
1977	86.1(106)	98.2(100)	10.03	0.0015
1978	94.6(93)	96.6(149)	0.59	0.4424
1979	85.1(141)	91.8(97)	2.37	0.1235
1980	70.4(71)	84.6(123)	5.49	0.0191
1981	81.1(90)	94.8(116)	9.61	0.0019
1982	75.0(108)	92.0(89)	10.03	0.0015
1983	85.3(68)	97.8(89)	6.80	0.001
1984	90.6(128)	99.0(96)	5.33	0.01

*Numbers sampled in parentheses

riae were significantly higher among females in all years of study. The *t*-values for comparing mean densities of metacercariae among males and females in a specific year are not given, but the lowest one was $t = 2.80$ ($df = 188$, $p < 0.005$) in 1982.

The shape of the spreads of the means and the variance/mean ratios over the 1st 14 years was roughly parabolic, suggesting a quadratic relationship between the response variables (\bar{X} and S^2/\bar{X}) and time. Therefore, a least squares fit of the following two models was made for the mean density and variance/mean density data (Table 3).

Fits to the quadratic model were significant for mean density vs. time (1969-1982) in both male ($p = 0.045$) and female ($p = 0.007$) hosts, marginally significant ($p = 0.064$) for the variance/mean density ratio vs. time among female mayflies, but not significant ($p = 0.341$) for the variance/mean density ratio vs. time among males. The quadratic models of the mean density provided marked improvement in the overall R^2 , while quadratic models of the variance/mean density ratio did not. In all cases, the models predicted local maxima of the mean density and variance/mean density functions during 1976.

Metacercariae among both males and females were contagiously distributed in each of the 16 years; the smallest chi-square value for goodness of fit was 99.2 ($p < 0.0001$). Among males, the percentage of hosts carrying approximately 50% of the parasites ranged from a low of 7.0% in 1969 to a high of 23.4% in 1984 (Table 4). There was no clear or consistent pattern of change among males during the course of the study. The median density for the 50% cut-off ranged from a low of three to a high of eight (the median density represents the accumulative number of parasites necessary to represent approximately 50% of the total sampled, *e.g.*, male mayflies with three or fewer metacercariae/individual carried 50% of the total parasites counted in 1969). The maximum number of parasites in a single male subimago ranged from a low of 12 in 1969 and 1980 to a high of 29 in 1972.

Among female subimagos (Table 4), the percentage of hosts carrying approximately 50% of the parasites ranged from a low of 13.5 in 1982 to a high of 29.2 in 1984. The median density ranged from 5 to 22. The high median densities in 1976, 1977, 1978 and 1984 coincided with the years when mean densities were highest. The maximum number of metacercariae in a single female in any year was 79 in 1977.

At RTP, the mean densities of mayfly nymphs varied with depth, with the largest

TABLE 2.—Mean density, variance and variance/mean ratio for metacercariae in male and female mayflies, 1969-1984

Year	\bar{X}		S^2		S^2/\bar{X}	
	Male	Female	Male	Female	Male	Female
1969	1.6(33)*	4.2(101)	5.1	17.1	3.1	4.1
1970	2.5(216)	5.3(212)	6.2	22.5	2.5	4.3
1971	3.9(224)	9.5(222)	16.5	57.6	4.3	6.1
1972	2.3(410)	6.6(236)	8.9	54.6	3.8	8.3
1973	3.1(202)	8.3(154)	9.7	35.6	3.1	4.3
1974	4.5(268)	8.6(277)	17.2	36.5	3.8	4.3
1975	4.2(92)	9.2(122)	23.8	81.9	5.7	8.9
1976	4.9(196)	16.8(142)	23.7	233.3	4.8	13.9
1977	3.5(106)	15.5(100)	18.9	181.3	5.4	11.7
1978	5.7(93)	14.8(149)	20.5	133.5	3.6	9.1
1979	3.1(141)	9.8(97)	10.4	93.2	3.3	9.6
1980	2.3(71)	8.2(123)	6.3	46.4	2.7	5.7
1981	3.2(90)	8.7(116)	10.0	65.6	3.1	7.5
1982	3.6(108)	6.0(89)	18.0	53.9	5.1	9.0
1983	4.7(68)	11.5(89)	13.5	74.2	2.9	6.5
1984	5.6(128)	16.5(96)	16.9	128.2	3.0	7.8

*Numbers sampled in parentheses

TABLE 3.—Results of the quadratic regression analysis

Host sex	Response variable	R ² for quadratic model	Improvement in R ² over linear model	Significance (P value) of quadratic model SS	B ₀	B ₁	B ₂
Male	\bar{X}	.431	+ .351	0.0450	+1.124	+0.742	-0.044
Female	\bar{X}	.590	+ .486	0.0074	+0.083	+2.953	-0.177
Male	S ² \bar{X}	.177	+ .139	0.3414	+2.495	+0.431	-0.025
Female	S ² \bar{X}	.393	+ .171	0.064	+1.736	+1.588	-0.083

numbers at 7 m (Table 5). This trend was not apparent at NP. Prevalence of metacercariae in both male (Table 6) and female (Table 7) nymphs varied with depth at both collecting sites. The exception to this pattern occurred at RTP where prevalence of metacercariae was highest at 5 m rather than 7 m. Mean density of *Crepidostomum cooperi* was highest in shallow water and least at 7 m for both collecting sites. A statistical summary for ANOVA (Table 8) of metacercariae in male and female nymphs at depths of 3, 5 and 7 m shows significant differences among both sexes at both sites, with most of the variation occurring within groups.

DISCUSSION

Long-term changes in prevalence and mean density.—There have been relatively few long-term studies on the consistency in prevalence or mean density of parasites from hosts within aquatic ecosystems. As a consequence, it is difficult to generalize about patterns of change. However, investigations which have lasted over 4 years indicate that the magnitude of change over time is relatively small. Petersson (1971) reported that the prevalence of the tapeworm *Triaenophorus crassus* in whitefish, *Coregonus* spp., from a series of Scandinavian lakes ranged from 45.2-53.1% over 8 years. In a 20-year study, prevalence of the tapeworm *Eubothrium salvelini* in smolts of *Onchorhynchus nerka* from Babine Lake in Canada, was fairly constant except for two brief periods, one lasting two consecutive summers and a second for three consecutive summers (Smith, 1973). During those years in which infection declined, Smith noted that the seasonal appearance of potential intermediate hosts (copepods) and the presence of infected definitive hosts were asynchronous. For 9 years recently, Kennedy and Rumpus (1977) examined prevalence and density of the acanthocephalan *Pomphorhynchus laevis* in the amphipod, *Gammarus pulex*, and in dace, *Leuciscus leuciscus*, from the River Avon in southwestern England. They showed that neither prevalence of infection nor mean parasite densities varied significantly.

TABLE 4.—Percentage of male and female hosts carrying approximately 50% of the parasites in a given year, the median for the sample, and the maximum number of parasites in a single host

Year	(1)		(2)		(3)		Maximum number of parasites in a single host	
	% Hosts		% Parasites		Median		Male	Female
	Male	Female	Male	Female	Male	Female		
1969	7.0	20.0	50.0	50.0	3	5	12	21
1970	12.7	22.2	43.0	50.9	4	12	15	25
1971	10.7	21.1	44.6	50.6	8	16	21	56
1972	21.7	15.3	51.4	51.1	6	14	29	37
1973	17.3	23.4	46.7	48.4	5	12	16	30
1974	21.3	26.7	52.0	52.1	6	11	21	26
1975	17.4	21.3	48.7	48.8	7	10	21	37
1976	18.0	21.1	50.0	50.1	8	21	22	57
1977	17.9	22.7	47.6	47.5	8	21	21	79
1978	22.6	22.1	49.8	47.4	8	22	21	66
1979	16.3	19.6	48.0	47.0	7	15	16	60
1980	19.7	22.8	55.0	50.5	4	13	12	26
1981	14.4	18.1	50.0	47.9	6	14	13	41
1982	13.0	13.5	45.6	49.5	8	11	19	30
1983	19.1	24.7	52.3	50.1	7	18	14	47
1984	23.4	29.2	50.7	52.4	8	20	24	63

(1) Represents the percentage of hosts examined which carry the percentage of parasites given in column (2). (3) The median indicates an accumulative number of parasites necessary to present approximately 50% of the total sampled, e.g., individuals with five or less (1969) carried 50% of the total parasites in the sample

If we assume that one consequence of ecosystem stability will be long-term consistency in prevalence and density of certain parasite species, then it also might be assumed that the same parasite species can be influenced by natural or artificial perturbations. Support for such assertions is inferred from results of short-term investigations of parasite population dynamics in thermally-altered ecosystems (Eure and Esch, 1974; Eure, 1976; Sankurathri and Holmes, 1976) and by the long-term studies of Aho *et al.* (1982) and Camp *et al.* (1982). The latter two groups of investigators followed changes in prevalence and density of metacercariae of two strigeid trematodes in mosquitofish for 53 months in a thermally altered cooling reservoir in South Carolina. They suggested that the observed patterns of change were due to normal seasonal changes, a combination of erratic water temperatures caused by the "on again-off again" operations of the nuclear production facility, and by possible changes in foraging behavior of the definitive host. The results of the present study support the notion that parasite population dynamics may be significantly affected by ecosystem perturbation.

Moss (1972) conclusively showed that the hypolimnion in Gull Lake underwent progressive deoxygenation from 1966 to 1971. Hypolimnetic anoxia increased to the point that just prior to the time of the autumn turnover in 1978, oxygen depletion was complete from the lake bottom to the thermocline. Dissolved oxygen profiles at six sites in early July 1984 showed that oxygen was present in the hypolimnion. However, the impact of eutrophication was nonetheless clear, with an average of 14.2 mg/liter oxygen in the middle of the thermocline and an average of 6.0 mg/liter in the bottom meter of the hypolimnion at the same six sites. Moreover, the substratum samples taken at each of these sites were foul-smelling and there was a total absence of mayfly nymphs, clearly suggesting a lack of oxygen at the lake bottom. Eutrophication in Gull Lake has been attributed to excessive use of lawn fertilizers and to faulty septic systems (Moss, 1972; Tague, 1977).

Eutrophication has substantial and far-reaching effects on the abundance and functional characteristics of flora and fauna (Edmonson, 1972; Moss, 1972). Prior to 1984, there was no direct evidence that the population biology or distribution of *Hexagenia limbata* had been affected by eutrophication. Although there are no data prior to 1984 regarding the distribution of mayfly nymphs in Gull Lake, it can be surmised that they were present in deeper parts of the lake prior to the onset of eutrophication, and even

TABLE 5.—Mean density of *H. limbata* per 0.6 m² of substrate at three depths for NP and RTP in Gull Lake, July 1984

	RTP \bar{X} density $\pm S^2$	NP \bar{X} density $\pm S^2$
3M (30)*	2.1 \pm 3.0	1.8 \pm 3.1
5M (30)	3.5 \pm 7.0	3.0 \pm 10.6
7M (30)	5.8 \pm 6.5	2.5 \pm 4.5

*30 grabs with the Ekman dredge

TABLE 6.—Prevalence, mean parasite density and mean length of male *H. limbata* nymphs from various depths at two collecting sites in Gull Lake, July 1984

Site	Depth	N	Prevalence	$\bar{X} \pm S^2$ parasite density	$\bar{X} \pm S^2$ length of nymphs
NP	3 M	21	85.7%	1.8 \pm 2.5	17.8 \pm 5.0
RTP	3 M	19	84.2%	2.3 \pm 3.1	17.7 \pm 4.5
NP	5 M	54	61.1%	1.0 \pm 1.9	16.9 \pm 6.6
RTP	5 M	35	77.7%	1.7 \pm 3.1	17.5 \pm 7.1
NP	7 M	29	27.6%	0.3 \pm 0.4	17.7 \pm 10.4
RTP	7 M	68	32.4%	0.4 \pm 0.5	14.9 \pm 6.5

for some time following the onset of eutrophication. This is because substantial parts of the deeper parts of the lake have marl-mud substrates which provide conditions which are suitable for colonization by mayfly nymphs (Hunt, 1953). Hunt also indicated that when oxygen concentrations fall below 1.5 mg/L, nymphs exhibited signs of stress and abandoned their burrows. It is further known that water depth does not limit colonization by mayflies (Lyman, 1943), that nymphs avoid light, and that their abundance is reduced in dense stands of aquatic vegetation, especially *Chara* sp. (Hunt, 1953). Evidence gathered in 1984 indicates that mayflies are absent in the parts of the lake covered by hypolimnetic water, indicating that eutrophication has affected distribution of the mayflies, and probably their numbers as well. As a consequence, mayflies have been forced to survive in shallower, less desirable parts of the lake. Moreover, we hypothesized that the mayflies have been forced into parts of the lake where the probability of acquiring metacercariae was enhanced because these same areas also support substantial populations of sphaeriid clams, the first intermediate host for *Crepidostomum cooperi*. Evidence to support the hypothesis comes from studies on the differential distribution of parasites in nymphs during the summer of 1984. The metacercariae are thus more prevalent and in higher densities in shallower parts of the lake. With increasing depth, metacercariae prevalence and densities decline.

The long-term changes in the density of metacercariae are more difficult to explain. However, we believe that the eutrophication process has, in part at least, contributed to the increase in densities in the 16 years of the study. If nymphs are deprived of oxygen and forced to survive in shallow littoral areas of the lake, then they will acquire more metacercariae. The trend of metacercariae densities has been upward since 1969 when densities were 4.15 in females and 1.64 in males. The increases were almost steady until 1976, when peaks of 16.80 and 4.91 were observed in females and males, respectively. There was then a more or less steady decline until 1983 and 1984 when densities jumped sharply. We originally speculated that the decline observed between 1976 and 1982 was related to subtle changes in water quality which may have been occurring because of the restrictions on the use of phosphate-containing lawn fertilizers. With the sudden increases in densities in 1983 and 1984, this hypothesis must now be rejected. A serious problem in dealing with a long-term data set such as this is that there is little

TABLE 7.—Prevalence, mean parasite density and mean length of male *H. limbata* nymphs from various depths at two collecting sites in Gull Lake, July 1984

Site	Depth	N	Prevalence	$\bar{X} \pm S^2$ parasite density	$\bar{X} \pm S^2$ length of nymphs
NP	3 M	35	85.7%	3.7 \pm 12.5	22.5 \pm 17.1
RTP	3 M	40	80.0%	3.8 \pm 25.9	19.3 \pm 25.9
NP	5 M	49	69.4%	2.0 \pm 3.9	22.3 \pm 18.7
RTP	5 M	60	90.0%	3.1 \pm 8.0	19.8 \pm 17.7
NP	7 M	60	61.0%	1.7 \pm 14.2	21.3 \pm 15.3
RTP	7 M	84	45.2%	1.4 \pm 16.7	15.5 \pm 6.4

TABLE 8.—Statistical summary for ANOVA of metacercariae in male and female nymphs at depths of 3, 5 and 7 M at NP and RTP in July 1984

	df	F	P	Variation among groups	Variation within groups
NP	2141	7.75	<0.001	12.57%	87.43%
RTP	2183	5.91	<0.001	7.76%	92.24%
NP	2101	31.82	<0.001	12.18%	87.82%
RTP	2109	34.10	<0.001	30.24%	69.76%

with which it can be compared. However, with the promise of complete reversal of eutrophication in the lake following the construction of a sewage system and the disuse of septic systems, further insight into the problem of long-term change in this host-parasite system is possible.

Relationship of parasitism and host sex.—Differences in abundance and prevalence of parasites in male and female hosts have frequently been reported (Addis, 1946; Beck, 1952; Esch, 1967; Novak, 1975; Esch *et al.*, 1975). In these cases, host sex has been shown to affect establishment, growth, egg production or asexual reproduction for a variety of parasitic organisms. While we observed a clear and consistent difference in prevalence (except 1978 and 1979) and density of *Crepidostomum cooperi* in male and female *Hexagenia limbata* during this study, the mechanism for generating these differences remains unknown. Esch and Hazen (1982) clearly demonstrated a linear relationship between host size and parasite density within each sex and this is a likely explanation for our results.

While parasite density may simply be a function of host size, the relationship is not inconsequential with regard to transmission dynamics of the parasite. Following the last molt, from subimago to adult, males congregate at dusk in a mating swarm above vegetation along the lake shore. Females fly into the swarm and, while in flight, are caught by males and inseminated. After swarming, males light on vegetation along the shore and die. Any metacercariae in male subimago or adult male mayflies cannot, therefore, be transmitted to a definitive host. After insemination, females return to the lake, deposit their eggs after landing on the water surface and then also die. The activity associated with ovipositing by the female will, in many cases, attract predaceous fish, many species of which can serve as definitive hosts for *Crepidostomum cooperi*. Except for the time during which they emerge from the lake, females are most vulnerable to predation while ovipositing. Thus, metacercariae in female mayflies have a much higher probability of reaching a definitive host and maturing to the adult stage. There is, therefore, a distinct selective advantage for metacercariae present in female *Hexagenia limbata*.

Dispersion of metacercariae in mayflies.—The variance/mean density ratio is an indicator of the degree of clumping and, in all years in the study, the parasites were contagiously distributed among the hosts. Between 1969 and 1982, the variance/mean density ratio and the mean density closely paralleled one another. However, in 1983 and 1984, when densities increased sharply, the variance/mean ratio stayed down. This 2-year trend is in marked contrast to the 3 years from 1976-1978 when both the variance/mean ratio and the density were high. Relationships between variance/mean ratio and mean density have been considered by several investigators in recent years (Anderson and Gordon, 1982; Gordon and Rau, 1982). They have asserted that changes in parasite frequency distribution under certain conditions can be used as a basis for inferring evidence of parasite-induced host mortality. The pattern of change which took place in the metacercariae frequency distribution and mean density in 1983 and 1984 would fall within the conditions they identify as being necessary for inferring parasite-induced host mortality. On the other hand, Kennedy (1984) has recently urged caution in making inferences about changing relationships between mean densities and variance/mean ratios. While we concur, we cannot exclude the possibility of parasite-induced host mortality, especially considering the highly perturbed nature of Gull Lake.

Curve fitting and theoretical models aside, Crofton (1971) emphasized that the essential feature of a parasite distribution is that it be clumped. The significance of contagiously distributed populations rests, in part, with limiting any interaction between a host and parasite to a small segment of the host population containing a large segment of the parasite population. The percentage of the host population carrying approximately 50% of the parasites was remarkably consistent over the 16 years of this study, especially among females. This consistency is even more remarkable when one considers the large changes in mean density which occurred during the same time. In

1969, the mean density was 4.15 and the percentage of the females with 50% of the parasites was 20.0, while in 1976 the mean density was 16.80, and 21.1% of the hosts carried 50.1% of the parasites. The long-term consistency emphasizes the extent of synchronization in host and parasite life history patterns, even during the extensive environmental perturbation such that has occurred in Gull Lake.

Long-term trends in the prevalence and density of parasite populations should follow one of two patterns. Consistency in these population parameters over a long-term interval could be due to long-term stability in physicochemical factors. It could also be a consequence of density-dependent regulatory mechanisms which affect the populations, such as proposed by Anderson and May (1978) and May and Anderson (1978). An inconsistent pattern of change over the long term could be the result of environmental perturbation, or variability in nesting or foraging behavior of potential intermediate or definitive hosts (Aho *et al.*, 1982; Camp *et al.*, 1982). Based on the results of the present study, it is clear that the pattern of change over the years in Gull Lake has been inconsistent in one sense and consistent in another. Thus, densities have risen and fallen in an undefined manner, yet the long-term trend in density has clearly been to increase.

A continuation of this study, in view of the reversal of eutrophication which should occur in the next 5-10 years, should provide valuable insight into the population biology of both *Crepidostomum cooperi* and *Hexagenia limbata*. Moreover, it will provide useful insight into the long term changes in the population biology of this host-parasite system.

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