STUDIES ON THE POPULATION BIOLOGY OF *PROTEOCEPHALUS AMBLOPLITIS* (CESTODA) IN THE SMALLMOUTH BASS

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Adult *P. ambloplitis* (Leidy) in Gull Lake, Kalamazoo County, Michigan, was highly seasonal, being recruited in late May and turned-over in September and October. The prime infection rate of adult cestodes was approximately 50% and was usually restricted to sexually mature smallmouth bass. Based on temperature profiles and seasonal periodicity of adult worms in Gull Lake (a northern U. S. lake) and upon similar observations in Par Pond, South Carolina (a southern U. S. lake), it was suggested that hormones may be of significance in stimulating parenteric plerocercoids to migrate into the gut. A comparison between infrapopulation densities of adult *P. ambloplitis* and acanthocephalans suggested that there was an absence of negative, interspecific interaction. A comparison between the densities of acanthocephalans and adult tapeworms with the number of pyloric ceca present in each host suggested that the potential space available was not being fully exploited by any of the enteric helminths.

INTRODUCTION

The plerocercoid of the bass tapeworm, *Proteocephalus ambloplitis*, has long been recognized as a potential threat to bass breeding stock (1). Esch and Huffines (2) described the gonadal and other lesions produced by larval *P. ambloplitis* in smallmouth bass from Gull Lake, Kalamazoo County, Michigan, U.S.A. They reported the most severe pathology was seen in testes of younger males. Their conclusion was, however, that the intensity of parenteric plerocercoids in Gull Lake bass was insufficient to produce sterility. While direct empirical evidence was lacking they did infer that the larval cestode might be involved in maintaining the bass population within the carrying capacity of Gull Lake.

The earliest description of the complete life history of *P. ambloplitis* was given by Hunter (1). He contended that eggs, shed by the adult tapeworm, are ingested by cyclopoid crustaceans. After hatching, and migration of the oncosphere to the hemocoel, the embryo was said to transform into a procercoid. Then, on ingestion by a fingerling bass, the procercoid migrated to the parenteric organs and developed into a plerocercoid. The adult tapeworm then developed in large bass after ingestion of plerocercoid-infected fingerlings, completing the life cycle.

Recent studies by Fischer and Freeman (3) have presented new field and experimental evidence which suggests that a portion of the life cycle outlined by Hunter (1) was in error. Their investigations indicate that parenteric plerocercoids may migrate directly into the lumen of the intestine or pyloric ceca where they then develop into the adult tapeworm; in essence, the proposed pathway would result in a form of "internal autoinfection" by the parasite. Experimentally, they have shown that migration from the parenteric viscera into the gut was triggered when the water temperature was elevated from 4 to 7 C. In addition, they indicated that plerocercoids generally did not migrate into the intestine when bass were smaller than 15 cm and that none penetrated the gut of bass less than 10.7 cm. They also suggested, "that other factors such as the hormonal state of the host, for example, may enhance the effect of temperature."

The present study was undertaken in an effort to analyze various aspects of the dynamics of *Proteocephalus ambloplitis* populations in Gull Lake, Kalamazoo County, Michigan. In view of the suggested role of temperature in triggering plerocercoid migration, special effort was given to following seasonal changes in populations of adult *P. ambloplitis* and in comparing the timing of these changes with existing temperatures.

Proc. Okla. Acad. Sci. 55: 122-127 (1975)

MATERIALS AND METHODS

Approximately 400 smallmouth bass, *Micropterus dolomieui* (Lacepede), were caught by hook and line and by gill netting in Gull Lake, Kalamazoo County, Michigan. Fish were collected each month from April through October in the years 1967, 1968, 1972 and 1973.

The alimentary canal was removed and separated into stomach, pyloric ceca and intestine. The number of ceca was determined. Acanthocephalans and tapeworms were counted in each area of the gut.

Hereafter, cestodes shedding eggs will be referred to as adults, segmented tapeworms will be called segmented adults while non-segmented forms in the alimentary canal will be referred to as enteric plerocercoids.

Two tapeworm species were removed from bass. *Proteocephalus ambloplitis* can be distinguished from the other cestode commonly seen (*P. fluviatilis* Bangham) since the former produces eggs with dumbbell shaped, external egg membranes; *P. ambloplitis* proglottids also possess a well developed, vaginal sphincter muscle.

Weekly temperature readings were made at a depth of one meter over a three year period (1970-72). For each consecutive three week period beginning in April and extending into October, the average median temperature was used to establish a temperature profile (Fig. 1).

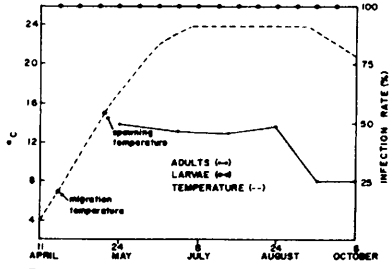

FIGURE 1. A temperature profile for Gull Lake showing the infection rates of *Proteocephalus ambloplitis* adults and plecocercoids in smallmouth bass, *Micropterus dolomieui*.

RESULTS

According to Fischer and Freeman (3), plercercoid migration from parenteric sites into the gut of smallmouth bass from Lake Opeongo (Algonquin Park, Ontario, Canada) occurred when water temperature was elevated from 4 to 7 C (these bass had been maintained at 4 C for several months prior to manipulation of the water temperature). In Gull Lake the elevation of water temperature from 4 to 7 C occurred in mid-April. Yet, enteric plerocercoids and segmented adults were not seen in most fish until May 20, a full five weeks after the stimulating temperature of 7 C had been reached. In the present study, only one bass in 32 examined had segmented adults or enteric plerocercoids prior to May 20. Between May 20 and May 28, when the first adult (egg-shedding) *P. ambloplitis* was observed, 37 bass were autopsied. Of these, nine were found to possess segmenting adults or enteric plerocercoids. After May 28, approximately 50% of the sexually mature smallmouth bass were found to have adult *P. ambloplitis*, although in late August this number began to decline. The appearance of substantial numbers of enteric *P. ambloplitis* in Gull Lake was thus correlated with a water temperature of 14 C or higher, not the lower temperature (7-12 C) associated with Lake Opeongo bass (3).

The water temperature in Gull Lake rose, reaching a peak during the first week of July. Except for minor fluctuations, high temperatures persisted until early September. Throughout most of the period of elevated water temperature, the infection rate remained constant with approximately 50% of the sexually mature bass (>200 mm length) having adult *P. ambloplitis* (Fig. 1). During the last two, three-week sampling intervals the infection rate dropped to approximately 25%. It is reasonable to conclude that smallmouth bass in Gull Lake are free of *P. ambloplitis* in the winter; a similar conclusion was reached by Fischer and Freeman (3) for Lake Opeongo bass. Apparently, disappearance of this parasite from bass during winter, is strictly a phenomenon of northern latitudes, since *P. ambloplitis* adults have been found in largemouth bass caught in January in Par Pond, Savannah River Plant, Aiken, South Carolina (4). The lowest minimum surface temperature in Par Pond in January of 1972 was 8.0 C; the average minimum temperature in the same month was 11.5 C. This is close to the critical temperature (7-12 C) reported by Fischer and Freeman (3) as

being necessary for stimulating parenteric plerocercoid migration.

For bass longer than 220 mm, there was only minor fluctuation in incidence and density of adult tapeworms (Table 1). If pre-spawn bass, sexually immature bass (<200 mm) and bass from late summer are excluded from the total sampled, then the incidence of infection is approximately 50%.

The most abundant enteric helminths in the bass were the acanthocephalans, *Neoechinorhynchus cylindratus* and *Leptorhynchoides thecatus*. The former was restricted to the intestine while the latter species was primarily a parasite of the pyloric ceca with lesser incidence in the anterior quarter of the intestine. Since there is overlap in the area of attachment for *Proteocephalus ambloplitis* and *Leptorhynchoides thecatus*, the possibility of competitive interaction was considered. An estimate of the interaction was made by comparing the density of tapeworms and accenthocephalans in relation to the number of pyloric ceca in 147 bass. Use was made of the rank correlation statistics (5) on the assumption that if densities of the two species were inversely proportional, then evidence of negative interaction could be inferred. Based on an analysis of bass having dual infections of acanthocephalans and adult tapeworms, the rank correlation coefficient (r_s = 0.181, d.f = 38, $p > 0.40$) indicates that density of tapeworms was independent of the density of acanthocephalans.

A prime factor in limiting the density of a given population is the amount of space available for exploitation. If the number of pyloric ceca per fish is variable, then the amount of space available for attachment will also be variable. To estimate the space available for exploitation, the number of enteric parasites and the number of pyloric ceca in 147 bass were correlated. Ninety-one percent of the bass had between 11 and 15 ceca (range = 8-16) with an approximately normal distribution (Fig. 2); sex and size of the bass were independent variables.

The mean number of adult tapeworms in bass with 11 ceca was 3.7; for those with 12 ceca, the mean was 10.9; with 13 ceca, it was 7.1 and with 14 ceca, the mean number was 9.5. There were not enough infected bass with eight, nine, ten or 15

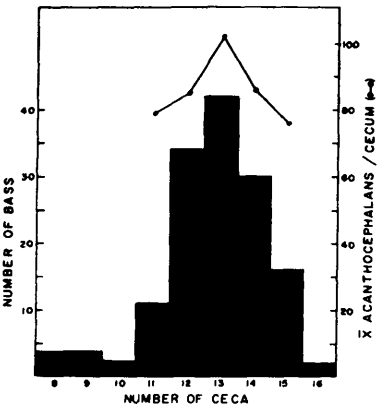

FIGURE 2. The frequency distribution for pyloric ceca per bass and acanthocephalans per bass cecum in the Gull Lake smallmouth bass population.

ceca to provide a reliable estimate of mean worm burdens. Variability in the mean number of tapeworms, number of pyloric ceca, and ranges in tapeworm density per infected fish (11 ceca, 1-11 tapeworms; 12 ceca, 1-35; 13 ceca, 1-20; 14 ceca, 3-20), strongly suggest that the number of tapeworms is independent of the number of pyloric ceca present in each bass. While the number of tapeworms present and the number of pyloric ceca available for exploitation are apparently independent variables, the same cannot be said for the density of acanthocephalans in relation to the number of ceca present in each bass (Fig. 2). Thus, when the mean number of acanthocephalans per cecum is compared with bass having 11 through 15 ceca, the resulting curve appears normal and closely approximates the frequency distribution of ceca per bass in the total bass population.

The frequency distribution for *P. ambloplitis* infected and non-infected bass is shown in Fig. 3. Since the variance exceeds the mean ($\bar{X}$ = 4.06; variance = 39.94) for adult tapeworms, the distribution does not fit a Poisson and is thus clumped, or contagious. Whether the parenteric plerocercoid population is also non-randomly distributed is not known.

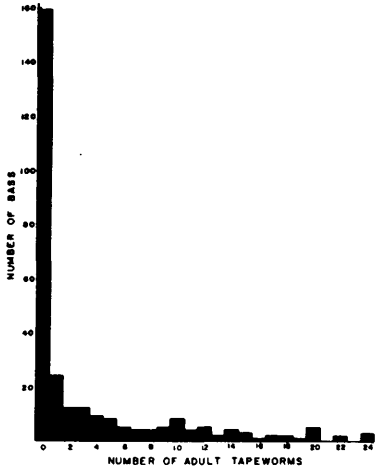

FIGURE 3. Frequency distribution of *Proteocephalus ambloplitis* adults in the Gull Lake smallmouth bass population. The totals exclude all bass taken prior to May 28 plus all bass less than 20 mm in length.

DISCUSSION

The significant finding by Fischer and Freeman (3) was the role of temperature in stimulating the migration of parenteric plerocercoids of *P. ambloplitis*. They state that "when bass, kept over winter at 4 C, were raised to 7 C or higher, some parenteral plerocercoids left the viscera and penetrated into the gut lumen". Because of differential effects, based on bass size, they also state "that other factors, such as the hormone state of the host, may enhance the effect of temperature". We believe that their passing reference to the potential role of hormones deserves greater consideration in identification of the migration stimulus for parenteric plerocercoids in bass. Thus, based on the results of studies presented herein and upon those of Eure (4), we feel either that *P. ambloplitis* — bass systems in Gull Lake and Lake Opeongo are variable because of differential latitudinal distribution, or that breeding condition (more likely hormone state) of the host is important in stimulating parenteric plerocercoids to migrate, or that a combination of these hypotheses along with temperature, is involved.

TABLE 1. *Infection rates by adult* Proteocephalus ambloplitis *in the gut of bass according to size class (standard length) of host bass.*

	ALL BASS			SUMMER BASS[a]		
Size (mm)	Infected	Non-Infected	% Infected	Infected	Non-Infected	% Infected
<200	1(1.0)[b]	53	2	—	—	—
200-219	4(4.5)	15	21	4(8.7)	5	44
220-239	21(8.5)	20	51	16(10.0)	11	59
240-259	14(7.9)	24	37	12(8.3)	11	52
260-279	14(5.7)	38	27	12(4.8)	20	38
280-299	22(7.4)	32	41	22(7.4)	22	50
300-319	17(8.2)	33	34	16(7.6)	16	50
320-339	6(8.3)	10	38	5(9.6)	5	50
340-359	4(9.0)	7	36	3(5.3)	1	75
360-379	5(9.2)	7	42	5(9.2)	3	63
380-399	6(11.2)	6	50	5(10.6)	4	56
>400	2(10.5)	18	10	2(10.5)	3	40
Total	116	263	31	102	101	50

[a] Prime infection group (excluded from consideration are bass taken before May 27, bass less then 200 mm and bass taken after August 24).

[b] Density per infected host.

There are several observations which would suggest that hormonal state, in addition to temperature, may be related to stimulation of parenteric plerocercoid migration. First, it was clearly shown that most bass less than 200 mm, and, therefore, sexually immature individuals, were without adult *P. ambloplitis* even though all those sampled had parenteric plerocercoids. Second, our data and those of Fischer and Freeman (3), indicates that recruitment of adult tapeworms is an event which occurs but once each year in bass. Yet in both lakes, the water temperature remains high throughout the summer and 100% of the sexually mature bass possess parenteric plerocercoids. An explanation offered by Freeman (personal communication) for this seeming paradox is that the stimulation for plerocercoid migration is not high water temperature *per se*, but the *rise* in water temperature from 4 to 7 C or higher and the maintenance of fish at this temperature for at least two days. The rise in water temperature once in the spring would thus coincide with the single period of recruitment which also occurs in the spring. We feel that other springtime events such as increasing photoperiod and an unique combination of gonadotrophic and gonadal hormones, could also be potential stimuli for migration of parenteric plerocercoids.

Perhaps the main objection to the temperature hypothesis (3) is the finding by Eure (4) of adult *P. ambloplitis* in largemouth bass in Par Pond, near Aiken, South Carolina, during the month of January. He also points out that the seasonal peak in density of *P. ambloplitis* in largemouth bass in Par Pond is in midwinter, i.e. December through February. The peak does not coincide with a rise in water temperature from 4 to 7 C since in Par Pond it does not drop below 8.0 C. The presence of adult worms in midwinter, the probable recruitment of adult worms in January and February, and the fact that water temperature does not drop as low as 4 C at any time of the year, do not necessarily negate Fischer and Freeman's (3) temperature hypothesis. These observations do strongly suggest other interrelated factors may be necessary to provide the necessary stimulus for parenteric plerocercoid migration.

It is clear that a number of host and environmental factors are involved in regulating the infrapopulations of *P. ambloplitis* in bass and other centrarchid fish. (An infrapopulation is defined as including all members of a single species of parasite within an individual host) (6). Since the parasite fauna in a host population in nature is seldom composed of a single species, it is conceivable that competitive interaction, either intra- or interspecific, may limit densities of one or more of the species comprising the parasitofauna of *Micropterus dolomieui*. Based on rank correlation coefficients, it does not appear that negative interaction by acanthocephalans is involved in regulating the density of the bass tapeworm. In this regard, however, it is unusual that the number of acanthocephalans per cecum would parallel the bell-shaped frequency distribution of bass having between 11 and 15 ceca. It would seem more logical that the mean number of acanthocephalans per cecum would continue to increase until the carrying capacity had been reached; the resulting frequency distribution would then reach and maintain some asymptote. Because of a general lack of information regarding the nature of host and parasite physiology, it is difficult to do more than report the apparent anomaly and reserve speculation until such time as more information can be obtained.

The result of the collage of interacting and independent host and environmental variables is the establishment of isolated parasite infrapopulations which collectively represent an important segment of the suprapopulation (the suprapopulation includes all members of all life cycle stages of a given parasite species within all the hosts in an ecosystem). The frequency distribution in Figure 3 is a way of depicting the infrapopulation subsets within hosts which were sampled in the course of this study. An attempt was not made to fit the data for parasites in the smallmouth bass to any theoretical distribution. However, the variance was larger than the mean number of *P. ambloplitis* within Gull Lake bass and, according to Li and Hsu (7), when the variance exceeds the mean, the distribution is overdispersed and hence, non-random. The non-random character of the *P. ambloplitis* infrapopulations reported herein is difficult to assess since it is not known if the skewed character of the infrapopulations is due to a host factor which differentially affects individual plerocercoid

migration, or to variation in successful recruitment of plerocercoids when the bass ingests either a plerocercoid-infected centrarchid or procercoid-infected cyclopoid crustacean. Because of the differences in infection rates between the sexes, the latter explanation may be correct, i.e., the sexes might have a difference in feeding behavior or a variation of successful establishment in a host due to an enhancing or inhibiting factor(s) associated with sex.

If an understanding of the population dynamics of *P. ambloplitis* in smallmouth bass is to be achieved, then it is imperative that the nature of the stimulating cue for plerocercoid migration first be determined. Because of the potential interactions between temperature and hormones under *in vivo* conditions, it appears that the most efficient way of elucidating the triggering mechanism(s) would be to employ *in vitro* culture methods. Such a procedure would allow separation of these two variables and other host or environmental factors which might be involved in triggering growth and development of larval *P. ambloplitis* to the adult stage.

ACKNOWLEDGMENTS

We want to thank Dr. George Lauff, Director, W. K. Kellogg Biological Station for use of space and facilities in the conduct of these studies and for permitting us the use of temperature data from Gull Lake. We thank Dr. R. S. Freeman for his many comments and constructive criticisms of the manuscript. We also thank Mrs. Carolyn Buckland for her work on the illustrations.

This work was supported in part by a grant from Wake Forest University Research and Publication Fund. The preparation of the manuscript was supported by the U. S. Energy Research and Development Administration under Contract AT (38-1)-819 between the University of Georgia and the U. S. Energy Research and Development Administration.

REFERENCES

1. G. W. HUNTER, J. Parasit. 14: 229-242 (1928).
2. G. W. ESCH and W. J. HUFFINES, J. Parasit. 59: 306-313 (1973).
3. H. FISCHER and R. S. FREEMAN, J. Parasit. 55: 766-774 (1969).
4. H. E. EURE, Ph. D. Dissertation, Wake Forest University, Winston-Salem, North Carolina, 1974.
5. W. J. DIXON and F. J. MASSEY, *Introduction to Statistical Analysis*, McGraw-Hill Book Company, Inc., New York, Toronto, London, 1957.
6. G. W. ESCH, J. W. GIBBONS and J. E. BOURQUE, An Analysis of the Relationship Between Stress and Parasitism. Amer. Midland Naturalist, in press.
7. S. LI and H. HSU, J. Parasit. 37: 32-41 (1951).