Population Biology of the Trematode Uvulifer ambloplitis (Hughes, 1927) in Juvenile Bluegill Sunfish, Lepomis macrochirus, and Largemouth Bass, Micropterus salmoides

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POPULATION BIOLOGY OF THE TREMATODE UVULIFER AMBLOPLITIS (HUGHES, 1927) IN JUVENILE BLUEGILL SUNFISH, LEPOMIS MACROCHIRUS, AND LARGEMOUTH BASS, MICROPTERUS SALMIOIDES

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ABSTRACT: Prevalence and intensity of *UVulifer ambloplitis* were monitored in a population of juvenile bluegill sunfish, *Lepomis macrochirus*, and largemouth bass, *Micropterus salmoides*, from March 1979 through November 1982. Prevalence of *U. ambloplitis* in bluegill did not drop below 30% for any month and often reached 100%, with intensities ranging from 1 to 269 cysts per fish. Significant differences occurred in the intensity between size classes of bluegill, but not between sexes. Prevalence of cysts in largemouth bass did not exceed 26% and the intensity did not exceed 12 cysts per fish. The frequency distribution of *U. ambloplitis* in bluegill closely fit the negative binomial model. Recruitment of *U. ambloplitis* by caged bluegill began in May and ended in September, with maximum recruitment occurring in July. Both the prevalence and intensity of *U. ambloplitis* were exceptionally high in bluegill in the present study as compared with other locations. This may be due to the breeding behavior of the definitive host and population biology of the small intermediate host combining to maximize parasite transmission and recruitment. Seasonal changes in the degree of overdispersion of *U. ambloplitis* suggest that parasite-related mortality of bluegill occurs during the winter.

Aside from the study by McDaniel and Bailey (1974), little ecological information is available for the seasonal periodicity of *UVulifer ambloplitis*, a causative agent for black-spot disease of fishes. The few ecological data which do exist were gathered from laboratory studies conducted shortly after the life cycle of *U. ambloplitis* was determined. Hunter and Hamilton (1941) examined the mechanism of cercaria penetration and cyst formation. Fischthal (1949), and Lemly and Esch (1983) studied the ability of the metacercariae to overwinter. Krull (1934) and Hunter and Hunter (1938) reported that heavy infections caused reduced weight gain and death in some hosts. However, their conclusions were based on recruitment of very large numbers of cercariae (hundreds) in a very short time (hours), a situation which is highly artificial and which resulted in the establishment of a much larger number of cysts (tenfold greater) than had ever been observed in nature. Thus, the hypothesis that host mortality would occur in natural populations of fishes was quite speculative and, in reality, an unconfirmed extrapolation from the laboratory experiments. More recently, Meyer (1958), Kakonge (1972), and Harrison and Hadley (1982) have suggested that infections of *Neascus* spp. could regulate host population growth due to the elimination of the most heavily infected fishes. However, this notion was not supported with quantitative data on mortality. To date, the only attempt to ascertain the effect of black grubs, or black-spot parasite, on fishes under natural conditions involved an unidentified species of *Neascus* (Rahideau and Self, 1953). Thus, the ecology of *U. ambloplitis* in natural populations of fishes remains largely unknown.

As previously noted (Lemly and Esch, 1984a), preliminary observations in a small pond located in the Piedmont area of North Carolina suggested that some heavily infected bluegill, *Lepomis macrochirus*, do not survive winter. The present report extends these observations and presents information relative to certain aspects of the population biology of the parasite in juvenile bluegill and largemouth bass, *Micropterus salmoides*.

**MATERIALS AND METHODS**

**Study area**

Reed’s Pond is a small (2.0 ha), eutrophic farm pond located in Davidson County, in the Piedmont area of North Carolina. It is steeply banked and thus possesses a minimal littoral zone. It has a maximum depth of 10 m and a mean depth of 2.5 m. Water quality characteristics were measured monthly and are presented elsewhere (Lemly, 1983).
Population biology of *Lepomis macrochirus* and *Micropterus salmoides*

The density of juvenile bluegill (≤70 mm total length) in the littoral zone of Reed’s Pond was estimated on the 15th (±2 days) of each month. Sweep samples were taken at 2 sites with an 8.0 x 1.5 m seine having a mesh size of 0.5 cm². The bluegill obtained were counted and, based on the area covered by the sweep, converted to a density estimate expressed as the number of individuals/m². The density of juvenile largemouth bass (≤70 mm total length) was also estimated from the same sweep samples. Except for a subsample which was removed for further study, all of the fishes were returned to the pond. Visible mortality due to handling was rare, involving only a few of the several hundred fishes that were processed. A sweep sample could not be taken during January 1981 due to a thick covering of ice on the pond and, consequently, the fishes for that month were collected with minnow traps.

The age structure of the juvenile bluegill population was determined by counting scale annuli for all individuals from the monthly subsamples. Details of the procedure and validation of this method of aging are given by Bagenal (1973) and Regier (1962).

Population biology of *Uvulifer ambloplitis*

Prevalence and intensity of *U. ambloplitis* were monitored for the juvenile bluegill population in Reed’s Pond from March 1979 through November 1982 (definitions of prevalence and intensity are those of Margolis et al., 1982). A subsample of the monthly sweep samples was retained (50-60 fish) and returned to the laboratory. The fish were divided into 3 size classes (≤30 mm, 31-70 mm, 71-70 mm total length) and 10 individuals of each size class were selected by assigning random numbers (Sokal and Rohlf, 1969; Rohlf and Sokal, 1969). The number of pigmented cysts present in each of these 30 fish was counted. Periodically, a larger sample size (100) was obtained to ensure that counting cysts in 30 fish was consistent in yielding an accurate assessment of the prevalence and intensity of parasitism in the bluegill population. Chi-square analysis indicated that the smaller sample (30) was adequate to obtain a valid measure of both parameters. When possible, the sex of individuals 40–70 mm t.l. was determined. Prevalence and intensity of *U. ambloplitis* were also determined for the juvenile largemouth bass in Reed’s Pond during August and September of each year. For comparative purposes, the prevalence and intensity of *U. ambloplitis* were determined for juvenile centrarchids collected from several other lakes, ponds, and streams in the region.

To study the dynamics of recruitment of *U. ambloplitis*, uninfected bluegill were maintained in 6 liveboxes in the littoral zone of Reed’s Pond from January through December 1981. The liveboxes, measuring 75 x 75 x 75 cm, were covered by 0.5 cm³ hardware cloth. On the first day of each month (except January), all of the fish in each livebox were removed and 10 new uninfected bluegill (30–70 mm t.l.) added. Since up to 3 wk may be required to produce a pigmented cyst, bluegill removed from liveboxes were held in aquaria in the laboratory for at least 21 days prior to counting the cysts. Uninfected bluegill were obtained from a recently constructed pond stocked with hatchery-reared fish in which *U. ambloplitis* had not yet become established.

Enumeration of cysts of *Uvulifer ambloplitis*

Cysts of *U. ambloplitis* were counted in 1 of 2 ways. Freshly killed fishes with relatively few cysts (<50/ fish) were placed on a surface having a strong backlight (i.e., a light table) and thoroughly examined on both sides with the aid of a magnifying lens. The translucent nature of the tissue in small centrarchids, combined with the large size (0.5-1.5 mm) and black color of pigmented cysts, allowed direct enumeration without dissection. Most of the fishes with more than 50 cysts, and all of the fishes that had been preserved prior to examination, were dissected with the aid of a binocular dissection microscope in order to count cysts. The dissection involved careful sectioning and inspection of all muscle tissue and a thorough examination of the lining of the peritoneal cavity and fibrous tissue of the throat, eyes, and brain.

Data analysis

Data that were found to be heteroscedastic (non-normally distributed) when compared to a normal probability plot, were transformed (log, square root, or arcsine transformation) prior to analysis in order to meet the assumptions of normality required by parametric statistical tests.

Single classification and two-way analysis of variance (ANOVA) were used to compare prevalence and intensity of parasitism, cyst location, persistence of pigmented cysts, and survival of *U. ambloplitis*. Frequency distributions of *U. ambloplitis* were compared to the Poisson and negative binomial models and tested for closeness of fit using Chi-square analysis. Variance to mean intensity ratios were compared using multiple polynomial regression for linear models (SAS time series analysis procedure = REG, Statistical Analysis Systems Institute, Cary, NC). Any statistical probability less than 5 percent (*P* < 0.05) was considered significant.

**RESULTS**

Population biology of *Lepomis macrochirus* and *Micropterus salmoides*

Data from sweep samples indicated that the seasonal population dynamics of bluegill and largemouth bass in the littoral zone of Reed’s Pond remained quite consistent throughout the study (Fig. 1). Maximum abundance of bluegill (24–26 individuals/m²) occurred from June through September, and maximum abundance of largemouth bass (8–9 individuals/m²) during May and June. The age distribution of bluegill indicated that virtually all were young-of-the-year (0+) from May through February. Annulus formation occurred in March and, consequently, a number of fish age 1+ were present during March and April until they grew beyond the limits of the largest size class used (≤70 mm t.l.) in the present study.
Table I. Statistical summary for ANOVA of prevalence and intensity of parasitism by Uvulifer ambloplitis between size classes of bluegill from Reed’s Pond, March 1979 through November 1982.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prevalence</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Size class</td>
<td>2</td>
<td>119.44</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Month</td>
<td>11</td>
<td>26.30</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Intensity</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Size class</td>
<td>2</td>
<td>155.21</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Month</td>
<td>11</td>
<td>124.40</td>
<td>&lt;0.05</td>
</tr>
</tbody>
</table>

* Size classes compared were: <30 mm LTL, 31–50 mm LTL, 51–70 mm LTL.

Population biology of Uvulifer ambloplitis

Except for a brief period in spring (April–May), prevalence of *U. ambloplitis* in bluegill was generally high throughout the year, often reaching 100 percent (Fig. 2). Even during the spring, prevalence did not drop below 50 percent. Analysis of variance indicated that differences in the prevalence of parasitism were significant between size classes of bluegill and between months (Table I). The intensity of parasitism (Figs. 3–5) varied greatly from season to season, with maxima occurring in September and minima occurring in March or April. Individual fish were found to harbor up to 269 cysts during September.

Significant differences occurred in the intensity of parasitism between the size classes of bluegill (Table I), but not between sexes. Maximum intensity was greatest in the 31–50 mm LTL size class. Both the mean and range of intensity decreased sharply for each size class after September, but the prevalence remained high (80–100 percent, Fig. 2).

The pattern of prevalence and intensity of *U. ambloplitis* in juvenile largemouth bass from Reed’s Pond was different from that which occurred in bluegill. The prevalence never exceeded 26% and the intensity of infection never exceeded 12 cysts per host (Table III).

During September, especially, the frequency distribution of cysts of *U. ambloplitis* was highly contagious in bluegill. Variance to mean ratios (s^2/\bar{X}) for intensity of parasitism fluctuated greatly during the course of a year, but were consistently largest in September or October, decreasing sharply (10–15-fold) by December (Fig. 6). Low s^2/\bar{X} values persisted until the following spring. These seasonal fluctuations in variance-mean ratios were significant (Table III). The observed frequency distribution of cysts among bluegill could not be adequately described by the Poisson distribution (Fig. 7); it was not, however, significantly different from the negative binomial model (Fig. 7).

Recruitment of *U. ambloplitis* by caged bluegill in the littoral zone began in May and ended in September (Fig. 8). Maximum recruitment occurred in July and was quite similar among the 3 size classes. No differences in recruitment were observed among bluegill held at different locations around the pond. Recruitment never exceeded 25 cysts/fish during the 1-month exposure period. Consequently, compounding the monthly maximum over the entire 5 month recruitment period (25 × 5) would not yield an intensity of cysts/fish comparable to that commonly observed in the bluegill population of Reed’s Pond (150–230 cysts/fish).

Table II. Prevalence and intensity of Uvulifer ambloplitis in juvenile largemouth bass (≤ 70 mm total length) from Reed’s Pond.

<table>
<thead>
<tr>
<th>Year and month</th>
<th>n</th>
<th>Prevalence (%)</th>
<th>Range of intensity (cysts per fish)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979 August</td>
<td>50</td>
<td>26</td>
<td>0–12</td>
</tr>
<tr>
<td>September</td>
<td>50</td>
<td>8</td>
<td>0–0.5</td>
</tr>
<tr>
<td>1980 August</td>
<td>50</td>
<td>24</td>
<td>0–24</td>
</tr>
<tr>
<td>September</td>
<td>50</td>
<td>24</td>
<td>0–24</td>
</tr>
<tr>
<td>1981 August</td>
<td>50</td>
<td>24</td>
<td>0.7–24</td>
</tr>
<tr>
<td>September</td>
<td>30</td>
<td>20</td>
<td>0–0.5</td>
</tr>
<tr>
<td>1982 August</td>
<td>50</td>
<td>12</td>
<td>0–6</td>
</tr>
<tr>
<td>September</td>
<td>50</td>
<td>12</td>
<td>0–10</td>
</tr>
</tbody>
</table>

Table III. Statistical summary for multiple polynomial regression analysis of variance to mean ratios of intensity of Uvulifer ambloplitis in bluegill from Reed’s Pond, March 1979 through March 1982.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>5</td>
<td>21.4500</td>
<td>24.812</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Error</td>
<td>30</td>
<td>3.8645</td>
<td>3.8645</td>
<td>0.093</td>
</tr>
</tbody>
</table>

* R-square = 0.8053, W: Normality = 0.310

* Cubic model.
† Shapiro-Wilk statistic (W).
Figure 1. Estimated density (number/m²) of bluegill and largemouth bass (<70 mm total length) in the littoral zone of Reed's Pond, March 1979 through November 1982.

Figure 2. Prevalence of parasitism by *U. ambloplitis* in bluegill from Reed's Pond, March 1979 through November 1982. *n* = 10 fish per data point.
**DISCUSSION**

As compared with other sites in the USA and Canada (Dechtiar, 1972; Cone and Anderson, 1977), both the prevalence and intensity of *Unilifer ambloplitis* were exceptionally high in bluegill from Reed's Pond. This condition in Reed's Pond was also atypical of Piedmont North Carolina (Lemly, 1983) and may be attributable to 2 factors. First, kingfishers may congregate at this pond in spring (Lemly and Esch, 1984a). This...
would produce a period of maximum parasite egg input into the pond which coincided with the occurrence of maximum snail density, ultimately resulting in relatively high cercariae production in July. Second, the greatest numbers of juvenile bluegill were present in the littoral zone in July. As a result, it is suggested all 3 hosts in the parasite’s life cycle were simultaneously brought to

Figure 5. Mean (o) and range (T) of intensity of parasitism by *Uvulifer ambloplitis* in bluegill from Reed’s Pond, March 1979 through November 1982. n = 10 fish per data point; all fish were 51-70 mm total length.

Figure 6. Variance to mean ratios of the intensity of *Uvulifer ambloplitis* in bluegill from Reed’s Pond, March 1979 through November 1982. n = 10 fish per data point.
Figure 7. Observed, Poisson (○), and negative binomial expected (●) frequency distributions of *Uralifer ambloplitis* in bluegill from Reed's Pond, March 1979 through November 1982; n = 493 (1979), 566 (1980), 543 (1981), 612 (1982); all fish were ≥70 mm total length. Probabilities for goodness of fit tests (Chi-square) between expected and observed frequency distributions were: $P > 0.05$ negative binomial, $P < 0.001$ Poisson (1979); $P > 0.05$ negative binomial, $P < 0.001$ Poisson (1980); $P > 0.05$ negative binomial, $P < 0.001$ Poisson (1981); $P > 0.05$ negative binomial, $P < 0.001$ Poisson (1982).

Together in high numbers and in very close spatial association, the opportunity for parasite transmission would thus be maximized. However, the period of optimal transmission was brief. During August the density of snail hosts (*Helisoma trivolvis*) was reduced, cercarial production declined, and the kingfishers probably dispersed after the young were fledged.

Pigmented cysts, produced during spring and summer, were shown to persist throughout the winter (Lemly and Fisch, 1983). This observation is important since it indicates that cysts produced during the spring and summer are maintained over the winter and not lost. Thus, the decline in the intensity of cysts observed for the bluegill in Reed's Pond between September and December cannot be ascribed to the destruction of cysts via a host response. Earlier observations made on the overwintering of cysts of *U. ambloplitis* by Fischthal (1949) are thus confirmed.

It is of interest that largemouth bass in Reed's Pond were not nearly as heavily parasitized by *U. ambloplitis* as juvenile bluegill, even though both species were collected from the same areas in the littoral zone and should, therefore, have had the same probability of acquiring cercariae. This pattern was also observed among bass and bluegill from other lakes and ponds in the area (Lemly, 1983). While it is possible that, even within the small area covered by the sweep samples, differences in habitat preference by these 2 species of fish resulted in differential exposure to cercariae, it seems more likely that bluegill are more suitable hosts for this parasite. Although no experimental data are available, it may be that cercariae of *U. ambloplitis* are recruited equally well by bluegill and largemouth bass, but have a differential capacity to become established and encyst. Differences in the microenvironment of host tissues are well known to influence the invasion and establishment of parasites (Mettrick and Podesta, 1974; Holmes, 1976; Nicol, 1979; Cook et al., 1980).

The frequency distribution of *U. ambloplitis*...
in bluegill was adequately described by the negative binomial model. In this respect, cysts of *U. ambloplitis* occurred in a clumped, or contagious, pattern similar to that which had been reported for a number of other trematode parasites of fishes (Pennyucick, 1971; MacKenzie and Livesidge, 1975; Lester, 1977; Rau and Gordon, 1978; Gordon and Rau, 1982).

The degree of overdispersion, as measured by the ratio of variance to mean intensity, rose through the spring and summer as parasites were recruited and then reached a maximum in September when intensities were greatest. By this time, parasite recruitment had stopped. Assuming no death of hosts or parasites, and no movement of uninfected fish into or out of Reed's Pond, the ratio should have remained constant for the rest of the year. However, a precipitous drop occurred, and by December the ratio was from 10–100 fold lower. Such a decrease in the variance/mean ratio has been suggested to indicate mortality through elimination of heavily parasitized hosts (Crofton, 1971; Pennyucick, 1971; Lester, 1977; Gordon and Rau, 1982). However, it should be noted that all of these studies were based on indirect estimates of mortality, subject to many variables which would be impossible to assess *a posteriori*, e.g., parasite natality, parasite mortality, expulsion of parasites, emigration or immigration of hosts, and birth of new hosts. Conclusions drawn from these studies are tenuous at best. Conclusive evidence presented elsewhere (Lemly and Esch, 1984b) indicates that the decrease in the variance/mean ratio between September and December in the present study was due to parasite-induced host mortality.

**ACKNOWLEDGMENTS**

Our sincere thanks to Mr. Lester Reed for providing us complete and unrestricted access to his pond to conduct these studies; also to Dr. Michael Riggs for his assistance in the statistical analyses and Mrs. Cathy Lemly for typing the manuscript. Publication costs were supported by a grant from the Wake Forest University Research and Publication fund.

**LITERATURE CITED**


Cone, D. K., and R. C. Anderson. 1977. Parasites


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