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PARASITES OF JUVENILE BLUEGILL, *LEPOMIS MACROCHIRUS* AND YOUNG-OF-THE-YEAR LARGEMOUTH BASS, *MICROPTERUS SALMOIDES* IN THREE LAKES II AND GULL LAKE, MICHIGAN

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By

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ABSTRACT

PARASITES OF JUVENILE BLUEGILL, *LEPOMIS MACROCHIRUS* AND YOUNG-OF-THE-YEAR LARGEMOUTH BASS, *MICROPTERUS SALMOIDES* FROM THREE LAKES II AND GULL LAKE, MICHIGAN

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A total of 622 fish, 393 juvenile bluegill and 26 young-of-the-year (YOY) largemouth bass from Three Lakes II, Michigan (TL) and 117 juvenile bluegill and 86 YOY largemouth bass from Gull Lake, Michigan (GL) were examined for parasites. Monogene, trematode, cestode, acanthocephalan, nematode and protozoan parasites infected juvenile bluegill and YOY largemouth bass. Larval trematodes, particularly *Cryptogonimus* sp., were the most prevalent and abundant parasites in juvenile bluegill and YOY largemouth bass in both lakes. For bluegill in both lakes, the intestinal parasite component community diversity values (Shannon diversity) were not representative of total parasite component community diversity. Shannon diversity values for the total, enteric and parenteric component communities for TL largemouth bass were similar. Total parasite component community diversity of GL largemouth bass was higher than enteric or parenteric communities. Larval trematodes and parasites using small invertebrate intermediate hosts were the first parasites to colonize juvenile bluegill and YOY largemouth from both lakes. The percentage of the parasite species consisting of adult parasites generally increased with bluegill length in both lakes, but generally did not increase for YOY largemouth bass. Largemouth bass had higher parasite component community diversities than bluegill of the same age in both lakes.

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CHAPTER ONE

PARASITE INFRAPOPULATIONS AND COMMUNITIES OF JUVENILE BLUEGILL, *LEPOMIS MACROCHIRUS* AND LARGEMOUTH BASS, *MICROPTERUS SALMOIDES* IN THREE LAKES II, MICHIGAN

INTRODUCTION

Fish habitat (Esch, 1971; Wilson et al., 1996), diet and age (McDaniel and Bailey, 1974; Cone and Anderson, 1977; Hanek and Fernando, 1978a, 1978b; Bailey, 1984) are determining factors in the composition and structure of parasite communities in centrarchid fishes. The habitat in which a fish resides largely determines which parasites it may host. Habitat attributes such as substrate type, vegetation type and quantity play a major role in parasite intermediate hosts found in an area. Mollusks serving as intermediate hosts for trematode parasites, for instance, shed larval trematodes that may infect a fish by direct penetration. By sharing habitat with these mollusks, fish may become infected with these parasites. Habitat, in turn, influences diet by determining what prey items (which may be serving as intermediate hosts) are available to a fish. For example, copepods serve as intermediate hosts for several species of parasites that are acquired by fish through ingestion.

As a fish ages, it increases in size and surface area. With increased surface area, a fish increases its chances of becoming infected with parasites via direct penetration (Spall and Summerfelt, 1970). Also, some larval parasites, such as *Posthodiplostomum minimum*, are long-lived and accumulate in a fish over several years (Spall and Summerfelt, 1970; Hoffman, 1999). In bluegill, *Lepomis macrochirus* and largemouth bass, *Micropterus salmoides*, age may influence parasite communities because juveniles and adults have been shown to have different diets and habitats (Mittelbach, 1984; Werner and Hall, 1988; Olson, 1996; Post, 2003; Sammons and Maceina, 2005).

The life history traits of juvenile bluegill and young-of-the-year (YOY) largemouth bass should contribute to the development of a parasite fauna unique to their life stage. Adult bluegill spawn in vegetated littoral areas in May or June in Michigan when water temperature reaches approximately 20° C (Breder, 1936; Werner, 1967; Werner and Hall, 1988). After hatching approximately two weeks post-spawn (Breder, 1936), bluegill fry undergo a migration to the limnetic zone of a lake and remain there for approximately six to eight weeks (Werner, 1967; Werner and Hall, 1988). Juvenile fish then return to the vegetated littoral zone for the next two to three years (Werner and Hall, 1988) until they move to the limnetic zone of the lake for the duration of their life (Werner and Hall, 1988). The shift to the limnetic habitat gradually takes place in bluegill between 45 and 75 mm SL (Osenberg et al., 1992). At approximately 75 mm SL, bluegill switch to feeding almost exclusively in the limnetic zone of a lake (Werner and Hall, 1988), which is approximately commensurate with maturity (Osenberg et al., 1992).

Throughout life, bluegill prey on aquatic invertebrates that serve as intermediate hosts for many types of parasites (Zischke and Vaughn, 1962; Werner, 1969; McDaniel and Bailey, 1974; Sadzikowsi and Wallace, 1976; Cone and Anderson, 1977; Werner and Hall, 1988; Fisher and Kelso, 1990). However, the invertebrate prey available in the limnetic zone where bluegill spend their adult life differs from that available in the vegetated littoral zone where they live as juveniles (Mittelbach, 1984; Werner and Hall, 1988). This shift in diet and habitat may cause the parasite fauna to concurrently shift (Wilson et al., 1996). Additionally, the vegetated habitat of juvenile bluegill is habitat for many mollusks that serve as intermediate hosts for trematodes that shed larval parasites that directly penetrate bluegill (Wilson et al., 1996).

Largemouth bass spawn in April or May in Michigan in vegetated littoral areas (Breder, 1936) when the water temperature reaches approximately 15-18° C (Mittelbach and Persson, 1998). The YOY largemouth bass remain in the littoral zone for the first few weeks to months of life feeding on invertebrates (Gilliam, 1982; Olson, 1996; Post, 2003). When largemouth bass become large enough to eat fish, they switch to a piscivorous diet, primarily preying on juvenile bluegill (Gilliam, 1982; Olson, 1996; Post, 2003) and continue to prey on fishes throughout their life. Since largemouth bass eat aquatic invertebrates such as copepods, amphipods and mayflies for the first few weeks to months of life (Sule, 1981; Gilliam, 1982; Fischer and Kelso, 1990; Olson, 1996; Dibble and Harrel, 1997; Post, 2003), they may acquire parasites that use these invertebrates as intermediate hosts. As is the case with juvenile bluegill, while living in the vegetated littoral zone, largemouth bass are vulnerable to colonization by larval trematodes shed by mollusks. Since largemouth bass become piscivorous early in life, primarily eating juvenile bluegill, they may acquire parasites that use bluegill as intermediate or paratenic hosts.

Because juvenile and adult bluegill (Werner and Hall, 1988) and juvenile and adult largemouth bass (Werner and Hall, 1988; Sammons and Maceina, 2005) have different habitats and diets, parasite faunas should differ between juvenile (pre-reproductive) and adult (reproductively mature) fish. Most studies on the parasites of bluegill and largemouth bass are restricted to the examination of adult fish or fish of unknown age (see Hoffman, 1999 for a list of studies of bluegill parasites). Few studies report on changes in bluegill parasite communities with host age (McDaniel and Bailey,

1974; Cloutman, 1975) and only one study examines parasite community dynamics of largemouth bass with host age (Cloutman, 1975).

Studies on the parasite communities of juvenile bluegill and YOY largemouth bass are limited to Fischer and Kelso (1987, 1988, 1990), Landry and Kelso (1999) and Steinauer and Font (2003). All these studies were conducted in Louisiana which may not be indicative of the parasite communities of these fish in Michigan. Effects of fish age on parasite community composition and structure in juvenile bluegill and YOY largemouth bass were also not examined in the above studies. Fisher and Kelso (1987, 1988, 1990), Landry and Kelso (1999) and Steinauer and Font (2003) reported that parasite communities of juvenile bluegill and YOY largemouth bass were dominated by larval trematodes. However, not all larval trematodes in these studies were counted so the numeric role and the effect these parasites have on parasite community diversity of juvenile bluegill and YOY largemouth bass is not known.

The objectives of this study were to determine patterns of parasite infrapopulation abundance and prevalence for the most common parasites of three cohorts of juvenile bluegill (*Cryptogonimus* sp., *Posthodiplostomum minimum*, *Neascus* sp. and *Proteocephalus ambloplitis*) and YOY largemouth bass (*Cryptogonimus* sp. metacercariae, *Neascus* sp., *P. minimum*, *Diplostomum* sp., *Neoechinorhynchus cylindratus* and *Proteocephalus ambloplitis*) from Three Lakes II, Michigan; to determine patterns of parasite infracommunity diversity in three cohorts of juvenile bluegill; and finally, to describe parasite component community diversities in juvenile bluegill and YOY largemouth bass.

MATERIALS AND METHODS

Description of Study Site

Three Lakes II (Figure 1) (hereafter referred to as TL) is in Kalamazoo County, Michigan and is connected to two other lakes, Three Lakes I and Three Lakes III, by short (<1 km) channels (Mittelbach, 1984). Three Lakes II is a eutrophic lake with a surface area of 22 hectares and exhibits thermal stratification (Mittelbach, 1984). This lake has a broad littoral zone that extends up to 60 m from shore with a bottom that gradually slopes to a maximum depth of approximately 10 m (Mittelbach, 1984).

Fish Collection and Examination

Collection of fish took place in a shallow (<1.5 m) area on the southeast side of the lake where the yellow pond lily, *Nuphar lutea* was the dominant vegetation. A total of 393 juvenile bluegill (209 from 2003 and 184 from 2004) were collected by seine in June through November, 2003 and April through July, 2004. Twenty-six YOY largemouth bass were also collected by seine in July and September, 2003. Upon collection, fish were placed in aerated coolers and transported to the laboratory at Michigan State University.

Fish were killed within 48 hours of collection by an overdose of the anesthetic MS-222. The standard length (SL), distance from the tip of the snout to the end of the caudal peduncle, was measured in millimeters for each fish before being preserved in a vial of 70% ethyl alcohol. Five scales from each fish were removed from under the left pectoral fin below the lateral line for aging. Scales were mounted on glass slides and scale annuli were counted using dissecting and compound microscopes. Some fish were

examined immediately after euthanization so live parasites could be properly fixed for identification purposes.

The head of the fish was removed and the remainder of the fish was cut along the ventral surface to the vent. The stomach, pyloric ceca, intestine, gall bladder, liver, spleen, kidneys, heart, eyes, brain, gonads, nares, skin, fins, muscles, and gills were placed in Petri dishes containing tap water and examined for parasites. The location of all parasites and the number of all countable parasites (parasites except monogenes and protozoans) were recorded. Only prevalence of monogenes and protozoans was recorded because MS-222 may have caused some of these parasites to fall off the fish, so accurate counts of these parasites could not be made. Parasites were preserved in 70% ethyl alcohol.

Parasite Preparation and Identification

Protozoan parasites were identified on wet mount slides. Trematodes, monogenes, cestodes and acanthocephalans were rehydrated in a graded ethyl alcohol series and were left in each solution for approximately one hour. The rehydration series concentrations were as follows: 70% ethyl alcohol; 40% ethyl alcohol; 20% ethyl alcohol; and 100 % distilled water. Parasites were then placed in a Stentor dish of Grenacher's borax carmine stain overnight and then removed to another Stentor dish of distilled water for one hour. The parasites were then dehydrated in a graded ethyl alcohol series and were left in each solution for approximately one hour. The dehydration series concentrations were as follows: 20% ethyl alcohol; 40% ethyl alcohol; 70% ethyl alcohol; 80% ethyl alcohol; 95% ethyl alcohol; and two repetitions of 100% ethyl alcohol. Parasites were moved to a Stentor dish of xylene to clear for approximately one

hour and mounted on glass slides using Canada balsam diluted with xylene and covered with a glass coverslip. Nematodes were cleared by adding five drops of 100% glycerine daily until all ethyl alcohol evaporated and stored in vials of 100% glycerine.

Parasitological Terminology

A host is an animal which is infected with a parasite (Roberts and Janovy, 2004). A definitive host is one in which the parasite becomes sexually mature and produces some type of offspring (Roberts and Janovy, 2004). An intermediate host is one in which the parasite does not reach sexual maturity but undergoes growth and development necessary to infect the next host in its life cycle (Roberts and Janovy, 2004). A paratenic host is one in which the parasite does not reach sexual maturity and does not undergo growth and development necessary to infect the next host in the life cycle, yet still remains alive and infective (Roberts and Janovy, 2004). Parasite paratenic hosts bridge trophic gaps between intermediate and definitive hosts. For instance, adult largemouth bass infrequently eat copepods, the intermediate host for a cestode parasite of these fish. Bluegill can become infected with a larval stage of this cestode when eating an infected copepod (Hunter, 1928). The largemouth bass can become infected with this cestode parasite by eating an infected bluegill. A direct life cycle does not require an intermediate host for sexual reproduction (Roberts and Janovy, 2004). An indirect life cycle requires development in one or more intermediate hosts prior to sexual reproduction (Roberts and Janovy, 2004).

A parasite infracommunity is the community of all species of parasites in one host individual (Bush et al., 1997). A parasite component community is the community of all species of parasites infecting one host species in a geographic area (Bush et al., 1997).

Enteric parasites occur within the gastrointestinal tract and parenteric parasites live in sites outside of the gastrointestinal tract (Roberts and Janovy, 2004). Life cycles and life stage terminology of parasites found in the present study are in Appendix I.

The most common parasite species were defined as those with greater than 30% prevalence (arbitrarily determined) in examined fish for each host species. The term prevalence is the percentage of individuals in a sample infected with a parasite species (Bush et al., 1997). Abundance is the number of parasites of a species in a fish and mean abundance is the mean number of parasites of a species per examined fish in a sample (Bush et al., 1997). Species richness is the number of parasite species per host and mean species richness is the mean number of parasite species per fish in a sample. Adjusted species richness is the number of countable parasite species per host and mean adjusted species richness is the mean number of countable parasites per fish in a sample. Adjusted species richness was calculated in order for comparisons to be made between species richness and Brillouin's diversity and evenness values, which only include countable parasites.

Data Analysis

Names of fish cohorts correspond to the year those fish hatched. For example, fish that hatched in 2003 are referred to as the 2003 cohort of fish. The 2001 cohort of bluegill consisted of age 2 fish collected in June-October, 2003; the 2002 cohort of bluegill consisted of age 1 fish collected in June-October, 2003 and age 2 fish collected in April-July, 2004; and the 2003 cohort of bluegill consisted of age 0 fish collected in June-October, 2003 and age 1 fish collected in April-July, 2004. No fish with mature gonads

were examined in the present study. Mean fish lengths are expressed as mean ± standard deviation (SD) (range).

Prevalence and Mean Abundance of the Most Common Parasites

Mean parasite abundances are expressed as mean ± SD (maximum). Parasite abundance values were natural log transformed for normality. All statistical comparisons were considered significant at the α=0.05 level. Because multiple chi-square analyses were needed to detect significant differences in prevalence among cohorts of fish, Bonferroni corrections were used to compute a lower α-value to minimize experimentwise error. The new α-value for these tests was 0.02. Chi-square analyses were used to detect significant differences in prevalence of the most common parasite species by comparing numbers of infected and uninfected bluegill between sampling years irrespective of fish cohort and between fish cohorts irrespective of sampling year. An unpaired t-test was used to detect significant differences in mean abundances of the most common parasite species of juvenile bluegill between the 2003 and 2004 sampling years. In cases where variance was not equal between samples, a t-test assuming unequal variance was used. Analysis of variance (PROC MIXED, SAS 9.1) was used to test for significant differences in mean abundances of most common parasite species among cohorts of TL bluegill. Tukey's HSD was used for all pairwise comparisons between cohorts. Analysis of variance (PROC MIXED, SAS 9.1) was used to test for significant differences in mean abundances of most common parasite species among months of collection for TL bluegill. Tukey's HSD was used for all pairwise comparisons between months. Variance to mean abundance ratios were calculated for the most common parasites of the 2002 and 2003 cohorts of bluegill in order to infer that decreases in

prevalence and mean abundance were due to parasite-induced mortality of bluegill. Monthly patterns of infracommunities of the most common parasites of YOY largemouth bass were not examined due to low numbers of bass examined.

A Spearman's rank correlation was used to detect relationships between untransformed abundances of the most common parasite species and fish length for bluegill and largemouth bass irrespective of cohort and sampling year and for each cohort of bluegill. A Spearman's rank correlation was also used to detect relationships between untransformed abundances of the most common parasite species, Brillouin's diversity, evenness, species richness and adjusted species richness and fish length for juvenile bluegill in each cohort irrespective of sampling year.

Parasite Infracommunities

Mean Brillouin's diversity and evenness values, species richness and adjusted species richness values for parasite infracommunities are expressed as mean $\pm$ standard deviation (SD) (range). Parasite infracommunity diversity, evenness, species richness and adjusted species richness values were natural log transformed for normality. Values for Brillouin's index for use in diversity and evenness (Pielou, 1975; Magurran, 1988) were calculated for each fish examined using common logarithms for all countable parasites irrespective of their site of infection to measure diversity and evenness for the parasite infracommunity. Values for the Shannon diversity index were calculated for each host species in each lake using common logarithms for all countable parasites irrespective of their site of infection to measure diversity of the total parasite component community. Separate Shannon diversity values for each host species for total, enteric and

parenteric parasites were calculated to determine whether diversities of these parasite component communities were comparable.

All statistical comparisons were considered significant at the α=0.05 level. An unpaired t-test was used to detect significant differences in mean parasite infracommunity diversity, evenness, species richness and adjusted species richness of juvenile bluegill between the 2003 and 2004 sampling years. In cases where variance was not equal between samples, a t-test assuming unequal variance was used. Analysis of variance (PROC MIXED, SAS 9.1) was used to test for significant differences in mean parasite infracommunity diversity, evenness, species richness and adjusted species richness among cohorts of TL bluegill. Tukey's HSD was used for all pairwise comparisons between cohorts. Analysis of variance (PROC MIXED, SAS 9.1) was used to test for significant differences in parasite infracommunity diversity, evenness, species richness and adjusted species richness among months of collection for TL bluegill. Tukey's HSD was used for all pairwise comparisons between months.

Spearman's rank correlation was used to detect relationships between untransformed parasite infracommunity diversity, evenness, species richness, adjusted species richness and bluegill and largemouth bass length irrespective of cohort and sampling year and for each cohort of bluegill.

A t-test for two Shannon diversity values was used to compare enteric and parenteric component community diversity values to total component community diversity values in juvenile bluegill and YOY largemouth bass. This t-test was also used to compare total component community diversity between age-0 bluegill and YOY

largemouth bass. The variance of the parasite component community diversities for bluegill and largemouth bass was approximated by:

$$s^2 = \frac{\Sigma f_i \log^2 f_i - (\Sigma f_i \log f_i)^2 \, n^{-1}}{n}$$

where f_i= number of individuals of each species, and n= number of individuals of all species (Brower et al., 1993), for the test statistic:

$$t = \frac{H_1' - H_2'}{(s_1^2 + s_2^2)^{1/2}}$$

(Brower et al., 1993) which is compared to the Student's t-distribution with $\alpha = 0.05$ and degrees of freedom approximated by:

$$DF = \frac{(s^2_{H1'} + s^2_{H2'})^2}{\frac{(s^2_{H1'})^2}{n_1} + \frac{(s^2_{H2'})^2}{n_2}}$$

(Brower et al., 1993).

Mollusk Collection

Mollusks were collected three meters from shore starting at the midpoint of the fish collection area each month fish were sampled. Five one minute side-by-side transects were sampled by sweeping an aquatic D-frame dip net through the water column from the top layer of substrate, through the submergent vegetation up to the water's surface (Hairston et al., 1958; Brown, 1979). All contents of the nets were emptied into a container and preserved in 10% formalin or 70% ethyl alcohol in the field. Mollusks were identified to family with a key to aquatic snails of the United States (Burch, 1982, 1988; Burch and Tottenham, 1980) and counted.

RESULTS

Host Demographics

A total of 393 juvenile bluegill (209 from 2003 and 184 from 2004) and 26 YOY largemouth bass were examined from TL. Irrespective of cohort, bluegill collected in 2003 and 2004 had mean lengths of 31.8 ± 8.7 (16-54) mm and 28.1 ± 5.0 (20-42) mm, respectively. Bluegill collected in 2003 were significantly larger than those collected in 2004 ($t=4.61$, $p<0.01$, 345 d.f.). The 2001 cohort consisted of 66 age 2 bluegill collected in 2003; the 2002 cohort consisted of 63 age 1 bluegill collected in 2003 and 28 age 2 bluegill collected in 2004; and the 2003 cohort consisted of 80 age 0 bluegill collected in 2003 and 156 age 1 bluegill collected in 2004. Monthly mean lengths of fish by cohort are in Figure 2. Monthly water temperatures from TL are in Figure 3.

The YOY largemouth bass were collected in July and September, 2003 and consisted of 26 age 0 fish with a mean length of 38.4 ± 15.0 (19-69) mm. Largemouth bass from TL were significantly longer than age 0 bluegill ($t=-5.38$, $p<0.01$, 25 d.f.).

Parasites of Juvenile Bluegill and Young-of-the-Year Largemouth Bass

Prevalence and mean abundance ± SD (maximum) for all parasite species of juvenile bluegill by sampling year are in Table 1. Juvenile bluegill were infected with 71,400 parasites from fourteen countable parasite species: seven trematodes, *Azygia* sp., *Crepidostomum* sp., *Clinostomum* sp., *Cryptogonimus* sp., *Diplostomum* sp., *Neascus* sp. and *Posthodiplostomum minimum*; two cestodes, *Proteocephalus ambloplitis* and *Haplobothrium globuliforme*, two acanthocephalans, *Neoechinorhynchus cylindratus* and *Pomphorhynchus bulbocolli*; three nematodes, *Camallanus* sp., *Spinitectus* sp. and

Spiroxys sp. Bluegill were also infected with five non-countable parasite species: three monogenes, *Actinocleidus* sp., *Anchoradiscus* sp. and Monogene sp.; and two protozoans, *Myxobolus* sp. and *Trichodina* sp. Some individuals of *Crepidostomum* sp., *Spinitectus* sp., *Anchoradiscus* sp. and *Actinocleidus* sp. were gravid adults. Parenteric larval parasites, *Clinostomum* sp., *Cryptogonimus* sp., *Diplostomum* sp., *Neascus* sp., *P. minimum*, *P. ambloplitis*, *H. globuliforme*, *N. cylindratus* and *Spiroxys* sp. comprised 99.6% of all parasites counted. The larval trematode *Cryptogonimus* sp. accounted for 93.2% of all parasites.

Prevalence and mean abundance ± SD (maximum) for all parasites of YOY largemouth bass are in Table 2. Young-of-the-year largemouth bass were infected with 1,157 parasites from 10 countable parasite species: five trematodes, *Azygia* sp., *Cryptogonimus* sp., *Diplostomum* sp., *Neascus* sp. and *P. minimum*; one cestode, *P. ambloplitis*; two acanthocephalans, *N. cylindratus* and *P. bulbocolli*; two nematodes, *Camallanus* sp. and *Spiroxys* sp. Largemouth bass were also infected with three species of non-countable parasites: two monogenes, Monogene sp. and Monogene sp. A; and one protozoan, *Trichodina* sp. Some individuals of Monogene sp. A, *Cryptogonimus* sp. and *Camallanus* sp. were gravid adults. Parenteric larval parasites, *Cryptogonimus* sp. metacercariae, *Diplostomum* sp., *Neascus* sp., *P. minimum*, *P. ambloplitis* and *Spiroxys* sp. accounted for 95.8% of all parasites counted. Both adults and metacercariae of *Cryptogonimus* sp. were found. *Cryptogonimus* sp. metacercariae, which had the highest prevalence and mean abundance, accounted for 76.9% of all parasites. Many parasite species were common to both juvenile bluegill and YOY largemouth bass in TL, but a

larger percentage of the parasites of juvenile bluegill consisted of larval trematodes, particularly *Cryptogonimus* sp.

Prevalence and Mean Abundance of the Most Common Parasite Species

The most common parasite species of juvenile bluegill were *Cryptogonimus* sp., *Neascus* sp., *Posthodiplostomum minimum* and *Proteocephalus ambloplitis*. The most common parasite species of YOY largemouth bass were *Cryptogonimus* sp., *Neascus* sp., *Posthodiplostomum minimum*, *Diplostomum* sp., *Neoechinorhynchus cylindratus* and *Proteocephalus ambloplitis*. Abundance of the most common parasites was not consistently higher in one year than in another. Bluegill from 2003 had significantly higher prevalences of *Neascus* sp. (X^2=11.37, $p<0.01$) and *P. ambloplitis* (X^2=15.63, $p<0.01$) than bluegill from 2004. Bluegill from 2004 had significantly higher prevalences of *P. minimum* (X^2=23.07, $p<0.01$) than bluegill from 2003. There was no significant difference in prevalence of *Cryptogonimus* sp. between sampling years. Bluegill had significantly higher mean abundances of *Cryptogonimus* sp. ($t=6.89$, $p<0.01$, 393 d.f), *Posthodiplostomum minimum* ($t=8.71$, $p<0.01$, 393 d.f.) and *Neascus* sp. ($t=4.53$, $p<0.01$, 393 d.f.) in 2003 than 2004 and significantly higher mean abundances of *Proteocephalus ambloplitis* ($t=2.97$, $p<0.01$, 393 d.f.) in 2004 than in 2003.

Prevalence and mean abundance $\pm$ SD (maximum) for the most common parasite species of juvenile bluegill by cohort irrespective of collection year in Table 3. *Cryptogonimus* sp. and *P. minimum* were the most prevalent and abundant parasite species for all cohorts of juvenile bluegill. In general, the older cohorts of bluegill had higher prevalences of the most common parasites. The 2001 cohort of bluegill had significantly higher prevalences of *P. minimum* (X^2=14.41, $p<0.01$), *Neascus* sp.

(X^2=45.34, p<0.01) and *P. ambloplitis* (X^2=46.06, p<0.01) than the 2003 cohort of bluegill in TL. The 2002 cohort of bluegill had significantly higher prevalences of *P. minimum* (X^2=21.77, p<0.01), *Neascus* sp. (X^2=58.08, p<0.01) and *P. ambloplitis* (X^2=32.22, p<0.01) than the 2003 cohort of bluegill.

After the first year of life, abundance of the most common parasites did not significantly increase between the two oldest cohorts of bluegill. The 2002 and 2001 cohorts of bluegill had significantly higher mean abundances of *Cryptogonimus* sp. (ANOVA, $F_{2, 390}$=139.6, p<0.01), *Neascus* sp. (ANOVA, $F_{2, 390}$=44.59, p<0.01), *P. minimum* (ANOVA, $F_{2, 390}$=84.17, p<0.01) and *P. ambloplitis* (ANOVA, $F_{2, 390}$=35.58, p<0.01) than the 2003 cohort. There were no significant differences in mean abundances of any of the most common parasites between the 2001 and 2002 cohorts.

Prevalence and mean abundance $\pm$ SD for the most common parasites of juvenile bluegill by month and cohort are in Tables 4-6. With the exception of *P. ambloplitis*, the 2001 cohort had the highest mean abundances of the other most common parasites and the highest prevalence of *Neascus* sp. each month this cohort was collected. In the 2002 cohort of bluegill, mean abundances of *Cryptogonimus* sp., *Neascus* sp. and *P. minimum* decreased from May to June, 2004. In the 2003 cohort, mean abundances of *Cryptogonimus* sp. and *P. minimum* were significantly lower in May, 2004 than in October, 2003 and abundances of *Neascus* sp. and *P. ambloplitis* were lower (although not significant) in May, 2004 than in October, 2003. For the 2001 cohort of bluegill, there were significant differences among months for abundances of *Cryptogonimus* sp. (ANOVA, $F_{4, 61}$=4.61, p<0.01), *Neascus* sp. (ANOVA, $F_{4, 61}$= 12.77, p<0.01), *P.*

minimum (ANOVA, $F_{4, 61}$=11.68, p<0.01). There were significant differences among months for mean abundances of *Cryptogonimus* sp. (ANOVA, $F_{8, 82}$=3.57, p<0.01), *Neascus* sp. (ANOVA, $F_{8, 82}$=3.22, p<0.01) and *P. minimum* (ANOVA, $F_{8, 82}$=3.87, p<0.01) for the 2002 cohort of bluegill. The 2003 cohort of bluegill had significant differences among months for mean abundances of *Cryptogonimus* sp. (ANOVA, $F_{7, 228}$=42.06, p<0.01), *Neascus* sp. (ANOVA, $F_{7, 228}$=16.02, p<0.01) and *P. minimum* (ANOVA, $F_{7, 228}$=8.04, p<0.01).

Variance to mean abundance ratios of the most common parasite species by cohort and month for juvenile bluegill are in Tables 7 and 8. In the 2002 cohort of bluegill, variance to mean abundance ratios of *Cryptogonimus* sp. and *Neascus* sp. had the largest decreases between May and June, 2004. For the 2003 cohort of bluegill, the largest decreases in variance to mean abundance ratios occurred between October, 2003 and April, 2004 for *Cryptogonimus* sp. and *Neascus* sp. and rose for of *P. minimum* and *P. ambloplitis* between October, 2003 and April, 2004.

Significant Spearman's rank correlations irrespective of bluegill cohort were detected between abundances of *Cryptogonimus* sp. (r_S=0.71, p<0.01), *Neascus* sp. (r_S=0.52, p<0.01), *P. minimum* (r_S=0.56, p<0.01) and *P. ambloplitis* (r_S=0.31, p<0.01) and fish length. The 2001 cohort of bluegill had significant correlations between abundances of *Cryptogonimus* sp. (r_S=0.40, p<0.01), *P. minimum* (r_S=0.70, p<0.01), *Neascus* sp. (r_S=0.59, p<0.01), *P. ambloplitis* (r_S= -0.28, p=0.02) and bluegill length. The 2002 cohort

of bluegill had significant correlations between abundance of *Cryptogonimus* sp. (r_s=0.35, p<0.01), *P. minimum* (r_s=0.64, p<0.01), *Neascus* sp. (r_s=0.34, p<0.01) and fish length and a non-significant correlation between abundance of *P. ambloplitis* (r_s=-0.04, p=0.74) and fish length. The 2003 cohort of bluegill had significant correlations between abundance of *Cryptogonimus* sp. (r_s=0.30, p<0.01), *Neascus* sp. (r_s=0.25, p<0.01) and fish length and a non-significant correlation between abundance of *P. ambloplitis* (r_s=0.09; p=0.15) and length. In YOY largemouth bass, abundances of *Cryptogonimus* sp. metacercariae (r_s= -0.54, p<0.01), *Neascus* sp. (r_s=0.73, p<0.01), *N. cylindratus* (r_s=0.71, p<0.01) were significantly correlated with fish length.

Parasite Infracommunity Comparisons

Bluegill

Mean Brillouin's diversity, evenness, species richness and adjusted species richness for parasite infracommunities of juvenile bluegill by sampling year irrespective of cohort are in Table 9. For bluegill irrespective of cohort, the 2003 sampling year had significantly higher infracommunity diversity (t=3.44, p<0.01, 391 d.f.), species richness (t=5.66, p<0.01, 354 d.f.) and adjusted species richness (t=5.64, p<0.01, 359 d.f.).

Mean parasite infracommunity diversity, evenness, species richness and adjusted species richness for juvenile bluegill by cohort irrespective of sampling year are given in Table 10. The 2002 and 2001 cohorts of bluegill had significantly higher species richness (ANOVA, $F_{2, 290}$=85.23, p<0.01) and adjusted species richness (ANOVA, $F_{2, 290}$=76.13, p<0.01) than the 2003 cohort. Mean infracommunity diversity was

significantly higher in the 2002 cohort than in the 2003 cohort (ANOVA, $F_{2, 290}=5.47$, $p<0.01$), but mean infracommunity diversity in the 2001 cohort did not significantly differ from either the 2002 or 2003 cohorts.

Monthly mean parasite infracommunity diversity, evenness values, species richness and adjusted species richness for each cohort of bluegill are in Tables 11-13. In all cohorts of bluegill, infracommunity diversity and evenness generally increased from June through October, 2003. In the 2001 (Table 11) and 2002 (Table 12) cohorts of juvenile bluegill, species richness and adjusted species richness peaked in August. In the 2003 cohort (Table 13), species richness and adjusted species richness increased from August through April, 2004. In the 2002 cohort, there was a significant decrease in species richness and adjusted species richness and a decrease (although not significant) in diversity and evenness between May and June, 2004. In the 2003 cohort, there was a significant decrease in infracommunity diversity and evenness and no change in species richness and adjusted species richness between May and June, 2004. For the 2001 cohort of bluegill, there were significant differences among months for infracommunity diversity (ANOVA, $F_{4, 61}=5.44$, $p<0.01$), evenness (ANOVA, $F_{4, 61}= 7.37$, $p<0.01$), species richness (ANOVA, $F_{4, 61}=7.28$, $p<0.01$) and adjusted species richness (ANOVA, $F_{4, 61}=5.47$, $p<0.01$). There were significant differences among months for infracommunity diversity (ANOVA, $F_{8, 82}=2.72$, $p=0.01$), evenness (ANOVA, $F_{8, 82}=2.91$, $p<0.01$), species richness (ANOVA, $F_{8, 82}=3.87$, $p<0.01$) and adjusted species richness (ANOVA, $F_{8, 82}=3.10$, $p<0.01$) for the 2002 cohort of bluegill. The 2003 cohort

of bluegill had significant differences among months for infracommunity diversity (ANOVA, $F_{7, 228}=5.89$, $p<0.01$), evenness (ANOVA, $F_{7, 228}=7.59$, $p<0.01$), species richness (ANOVA, $F_{7, 228}=7.84$, $p<0.01$) and adjusted species richness (ANOVA, $F_{7, 228}=7.24$, $p<0.01$).

There were significant correlations between parasite infracommunity diversity ($r_S=0.13$, $p=0.01$), species richness ($r_S=0.61$, $p<0.01$) and adjusted species richness ($r_S=0.58$, $p<0.01$) of parasite infracommunities of bluegill and bluegill length, irrespective of cohort and collection year. Although there were significant positive correlations between all diversity metrics except evenness and bluegill length irrespective of cohort, this was not always the case within each cohort. For the 2001 cohort of bluegill, there were no significant correlations between parasite infracommunity diversity and evenness and species richness and adjusted species richness and fish length. For the 2002 cohort of bluegill, there was a significant correlation between adjusted species richness ($r_S=0.25$, $p=0.02$) and fish length. The 2003 cohort of bluegill had significant correlations between species richness ($r_S=0.30$, $p<0.01$) and adjusted species richness ($r_S=0.26$, $p<0.01$) and fish length.

Largemouth Bass

Mean parasite infracommunity diversity, evenness, species richness and adjusted species richness for YOY largemouth bass were 0.28 ± 1.4 (0.03-0.50), 0.54 ± 0.22 (0.10-0.83), 4.3 ± 1.4 (2-7) and 3.7 ± 1.3 (2-6) respectively. With the exception of species richness, all values of all diversity metrics significantly increased with age.

There were significant correlations between infracommunity diversity (r_s=0.55, $p<0.01$) and evenness (r_s=0.52, p=0.01) and adjusted species richness (r_s=0.40, p=0.04) and largemouth bass length.

Parasite Component Communities

Shannon diversity values (approximated variance) for the total, enteric and parenteric parasite component communities of bluegill irrespective of cohort were 0.14, 0.34 and 0.13, respectively. Age 0 bluegill had higher Shannon diversity values for the total and parenteric parasite component community. The Shannon diversity values for the total, enteric and parenteric parasite component communities of age 0 bluegill were 0.21, 0.09 and 0.21, respectively. Shannon diversity values for the total, enteric and parenteric component communities of largemouth bass were 0.40, 0.37 and 0.41 respectively, all of which were higher than Shannon diversity values found in either juvenile or age 0 bluegill. There were no significant differences in Shannon diversity values between the total and enteric or total and parenteric parasite component communities of juvenile bluegill irrespective of cohort or YOY largemouth bass. There were no significant differences between total parasite component communities of age 0 bluegill and YOY largemouth bass from TL. The Jaccard's coefficient for community similarity between parasite component communities of age 0 bluegill and YOY largemouth bass was 0.53.

Mollusk Abundances

Individuals of the snail families Lymnaeidae, Planorbidae, Physidae, the genus *Viviparus* sp. and the clam family Sphaeriadae were collected in TL. Abundances of mollusks by taxonomic group and month are in Figure 4. Mollusk abundances generally increased throughout July and August, declined through September and October and

declined between October and April. Mean number of trematodes per bluegill by month and number of mollusks collected per month are in Figure 5. In general, abundances of larval trematodes rose and fell in concert with mollusk abundances over the study period.

DISCUSSION

Parasites of Juvenile Bluegill and Young-of-the-year Largemouth Bass

Many of the parasite species found in the juvenile bluegill and YOY largemouth bass from TL have been found in previous studies of parasites of bluegill and largemouth bass in Michigan. Parasites of Michigan bluegill were summarized by Muzzall and Peebles (1998). The present study of TL bluegill is the first report of *Azygia* sp., *Cryptogonimus* sp., *H. globuliforme*, *Actinocleidus* sp. and *Anchoradiscus* sp. from Michigan bluegill. Reports on parasites of Michigan largemouth bass include Esch (1971), Hudson et al. (1994); Muzzall et al. (1995); Hudson and Bowen (2002); Gillilland and Muzzall (2004) and Muzzall and Gillilland (2004). The present study is the first report of *Azygia* sp., *Clinostomum* sp., *Cryptogonimus* sp. metacercaria and adults, *Diplostomum* sp., *Neascus* sp., *P. minimum*, *Camallanus* sp., monogene sp. A, *Trichodina* sp. and *Myxobolus* sp. from Michigan largemouth bass.

The present study notwithstanding, 22 parasite species have been reported from adult bluegill or bluegill of unknown age in Michigan (Muzzall and Peebles, 1998). Of those 22 species, seven (31%) are represented by larval or immature stages; five of which (23% of total parasite species) were larval trematodes. Prior studies of Michigan bluegill parasites have primarily surveyed adults which have a lower percentage of larval parasite species than juvenile bluegill in the present study. Parasites of juvenile bluegill in the present study hosted 19 parasite species—nine species (47%) were represented by larval or immature forms; five of which (26% of total parasite species) were larval trematodes.

Juvenile bluegill are an important intermediate host for many parasite species because they are a prey item for many vertebrate species (Muzzall and Peebles, 1998).

Although adult bluegill from Michigan have a larger percentage of adult parasite species (Muzzall and Peebles, 1998) than juvenile bluegill from the present study; 69% adult parasite species in adult bluegill compared with 53% adult parasite species in juvenile bluegill, similar percentages of the parasite species of adult and juvenile bluegill from TL are comprised of larval trematodes. Since larval trematodes are long-lived (Spall and Summerfelt, 1970), it may be that many of the larval trematodes of adult bluegill infect juveniles while they are living in the littoral zone. However, because mean abundances of larval trematodes are sometimes not reported in studies of parasites of Michigan adult bluegill (Esch, 1971), it is not known whether abundances of these parasites continue to increase as fish age.

The present study is the first in Michigan to report on the entire parasite community of largemouth bass, albeit largemouth bass were age 0. Esch (1971) did not include monogenes or copepods; Hudson et al. (1994), Muzzall et al. (1995), and Hudson and Bowen (2002) worked only with copepods; Gillilland and Muzzall (2004) reported on *P. ambloplitis*; and Muzzall and Gillilland (2004) worked only with acanthocephalan parasites of largemouth bass.

Esch (1971) reported that the parasite communities of adult largemouth bass in Michigan consisted of 83% adult parasite species and 17% larval or immature parasite species. In TL, of the 13 parasite species infecting YOY largemouth bass, 62% were adult parasite species and 46% of parasite species were represented by larval or immature forms. Percentages of adult and larval or immature parasite species do not add up to

100% because *Cryptogonimus* sp. was represented by both adult and larval forms. A greater percentage of the parasites of adult largemouth bass were adult species compared to YOY largemouth bass. Due to their size, adult largemouth bass are much less vulnerable to predation than YOY individuals; hence, parasite species using adult largemouth bass as an intermediate host may not be able to complete their life cycle. Additionally, since YOY largemouth bass spend more time in the littoral zone with snails shedding cercariae than adults (Gilliam, 1982; Sammons and Maceina, 2005), YOY largemouth bass should harbor more larval trematode parasite species than adults.

Neascus sp., *P. minimum*, *Camallanus* sp., *P. ambloplitis*, *Spinitectus* sp. and *N. cylindratus*, have been reported from juvenile bluegill and YOY largemouth bass in previous studies (Lemly and Esch, 1984; Fischer and Kelso, 1987, 1988, 1990; Camp, 1988; Landry and Kelso, 1999; Steinauer and Font, 2003). The mean abundances of *Cryptogonimus* sp. found in the present study are the highest metacercarial mean abundances reported in juvenile bluegill in the United States. In all previous studies of parasite communities of juvenile bluegill, as well as in the present study, larval trematodes had higher species richness and abundances than any other taxonomic group of parasites (Fischer and Kelso, 1987, 1988, 1990; Landry and Kelso, 1999; Steinauer and Font, 2003).

Prevalence and Mean Abundance of Most Common Parasites

Bluegill collected in 2003 had significantly higher mean abundances of *Cryptogonimus* sp., *P. minimum*, and *Neascus* sp. than bluegill in 2004. This is likely because bluegill collected in 2003 were significantly larger than bluegill in 2004. The oldest and longest cohort of bluegill, the 2001 cohort, was only collected in 2003.

Because bluegill from 2003, on average, were both older and larger than the bluegill from 2004, they had more time to acquire parasites and are more vulnerable to penetration by trematode cercariae by having more exposed surface area (Spall and Summerfelt, 1970), which led to higher mean abundances of *Cryptogonimus* sp. metacercaria, *P. minimum* and *Neascus* sp. Additionally, there were significant positive correlations between abundance of the four most common parasites and length of bluegill irrespective of cohort. Since parasite mean abundance and length of fish irrespective of cohort are highly correlated, it follows that mean abundances of parasites were significantly higher in 2003 than 2004.

In many cases, abundances of the most common parasites increased with increased fish length and also varied monthly. As previously discussed, length plays a role in mean abundance of larval trematode parasites because as a fish increases in length, surface area that can be penetrated by a parasite increases. Length also plays a role in larval trematode abundance because length and age in bluegill have a strong positive correlation and as fish age, they have had more time to accumulate larval trematodes. Month influences trematode abundances because water temperature, which varies by month, influences whether a snail sheds cercariae and also whether cercariae are sufficiently active to penetrate fish (Spall and Summerfelt, 1970). Cercariae of *P. minimum*, for instance, are not produced at temperatures below 15° C and are not active enough to penetrate fish at temperatures less than 18° C (Hoffman, 1958). During the study period, water temperatures in TL were not above 18° C until May (Figure 3). Since it takes approximately three weeks for the metacercariae of this species to be large enough to be detected in the fish (Spall and Summerfelt, 1970), prevalence and mean

abundance of this parasite would not be expected to increase until June, 2004. Since temperatures at TL were only recorded once a month during fish collection, it is not known if the water temperature was consistently above 18° C through May, 2004. Because the increase in prevalence and mean abundance was not observed until July (Tables 5 and 6), it seems likely that water temperatures were not consistently above 18° C until June.

Parasites altering the behavior of their fish intermediate hosts, which may lead to decreased fish survivorship, are well-documented (Barber et al., 2000, review; Marcogliese et al., 2001; Shirakashi and Goater, 2002; Barber et al., 2004; Seppala et al., 2004). In some cases, fish infected with parasites do not swim as well as uninfected fish or seek cover from predators as do uninfected fish (Barber et al., 2000). If fish with high parasite burdens have reduced swimming ability or do not seek cover when a predator is nearby, the fish with the highest abundances of parasites could be selectively preyed upon. Likewise, by interfering with the vision of a fish (Crowden and Broom, 1980; Brassard et al., 1982; Marcogliese et al., 2001; Shirakashi and Goater, 2002; Seppala et al., 2004), a parasite may inhibit the ability of a fish to escape predation because the predator cannot be as easily seen. If a bluegill intermediate host has a reduced ability to escape a predator definitive host, the probability of parasite transmission increases.

Bluegill with the highest abundances of *P. ambloplitis* may be experiencing some type of indirect parasite-induced mortality. The 2001 and 2002 cohorts of bluegill from TL had significantly higher prevalences of *P. ambloplitis* than the 2003 cohort of bluegill. When examining the relationship between abundance of this parasite and length by cohort, there was a significant positive correlation for the 2003 cohort, a non-

significant negative correlation in the 2002 cohort and a significant negative correlation between abundance and length of *P. ambloplitis* in the 2001 cohort of bluegill. This suggests that as fish age, the direction and the strength of the relationship between *P. ambloplitis* abundance and length becomes increasingly more negative. Because the relationship between abundance of this parasite and length becomes more negative, it may be that as fish age, the fish with the heaviest infections of *P. ambloplitis* are removed from the population in some way. There are many reports of parasite-induced host mortality in fishes (Barber et al., 2000, review; Coyner et al., 2001; Marcogliese et al., 2001; Shirakashi and Goater, 2002; Barber et al., 2004; Seppala et al., 2004). *Proteocephalus ambloplitis*, which causes significant damage to the liver and viscera of infected fish (Mitchell et al., 1983), was found in bluegill examined in the present study. Livers of juvenile bluegill infected with this parasite were filled with necrotic tissue and fibrous adhesions (B. Pracheil, personal observation) which likely led to poor health, and perhaps, increased vulnerability to predation.

Another possible explanation for the decline of *P. ambloplitis* with age is that juvenile bluegill may be eating fewer of the copepod intermediate hosts of this parasite. Osenberg et al. (1992) reported that bluegill between 45 and 75 mm SL spend some time foraging in limnetic areas of the lake. In the limnetic habitat, bluegill may not be ingesting the copepod intermediate hosts for *P. ambloplitis* as frequently as they did by strictly foraging in the littoral zone of the lake as they did when they were younger. However, this does not seem to be a likely explanation for decreases in prevalence and mean abundance of *P. ambloplitis* because Wilson et al. (1996) found limnetic adult

bluegill from another Michigan lake had higher prevalence and mean abundance of *P. ambloplitis* than fish of similar length in the littoral zone.

Cryptogonimus sp. and *Neascus* sp. had the largest decreases in prevalence and mean abundance accompanied by decreases in variance to mean abundance ratio between October, 2003 and May, 2004 (Tables 5-8). Parasite populations are typically overdispersed meaning many hosts have a few number of parasites and a few hosts have a large number of parasites. A decrease in variance to mean abundance ratio implies that after the decrease in mean abundance of these two parasite species from October through April and from May through June in the 2002 cohort and from October through May in the 2003 cohort, the overdispersion of these parasite species decreases. The decrease in degree of overdispersion of larval trematode populations suggests that these decreases may be due to mortality of the most heavily infected hosts (Kennedy, 1987). However, other factors which cannot be measured in a field study such as immigration of less heavily infected bluegill into the population or mortality of parasites in the most heavily infected bluegill could also produce a similar effect.

Heavy metacercarial burdens have been reported to decrease survivorship of juvenile bluegill. Lemly and Esch (1984), for instance, have experimentally shown that heavy infections of the larval trematode *Uvulifer ambloplitis* (a *Neascus*-type species) to be a causative agent for direct mortality of juvenile bluegill. Although the type of parasite-induced host mortality was not speculated, Fischer and Kelso (1988) attributed similar decreases in prevalence, mean abundance and variance to mean abundance ratio of *Allocanthochasmus* sp., to death of the most heavily infected juvenile bluegill. Indirect parasite-induced mortality of juvenile bluegill in TL caused by *Cryptogonimus*

sp. and *Neascus* sp. may be responsible for the concurrent decreases in prevalence, mean abundance and variance to mean abundance ratios of these parasites. *Cryptogonimus* sp., the most prevalent and abundant species reported in the present study and *Neascus* sp. were found largely in the muscle of the bluegill (Table 1) which could negatively impact swimming ability. *Cryptogonimus* sp. was also found in the brain which may affect cognition, on the gills which may influence gas exchange and waste removal and on the posterior exterior surface of the eyes, which may affect vision.

Indirect parasite-induced mortality of YOY largemouth bass caused by selective predation of the fish with the highest *Cryptogonimus* sp. metacercariae abundances may explain the significant negative correlation between abundance of *Cryptogonimus* sp. metacercariae and fish length. Most YOY largemouth bass do not survive to age 1 and mortality of many of them is due to predation by other juvenile and adult largemouth bass (Post et al., 1998). For instance, Post et al. (1998) estimated that by August, between 91 and 99% of YOY largemouth bass have been eaten by older largemouth bass when YOY populations ranged from 24,000 – 94,000 individuals. As in juvenile bluegill, *Cryptogonimus* sp. metacercariae encyst largely in the muscle, but also in the brain and on the gills, posterior exterior surface of the eye and on the gills. Metacercarial encystment in these areas of the fish may lead to decreased swimming ability, vision and/or gas exchange. In TL, if the YOY largemouth bass most heavily infected with *Cryptogonimus* sp. metacercariae are more vulnerable to predation, then the individuals with the lowest metacercarial abundances survive leading to the negative correlation between abundance of this parasite and length. *Cryptogonimus* sp. metacercariae stunting the growth of the YOY largemouth bass could also explain the significant

negative correlation between *Cryptogonimus* sp. abundance and fish length. In this case, the YOY largemouth bass with the highest abundances of *Cryptogonimus* sp. metacercariae would have a slower growth rate than fish with lower abundances. The larval trematode *Neascus* sp. has been shown to stunt the growth of juvenile bluegill (Lemly and Esch, 1984) and a similar phenomenon could be occurring with *Cryptogonimus* sp. in TL largemouth bass.

In YOY largemouth bass, metacercarial abundances of *Neascus* sp. increased significantly with increased length. These opposed relationships of metacercarial abundances to length for *Cryptogonimus* sp. and *Neascus* sp. may be due to habitat partitioning by the snail hosts of these parasites. *Physa* sp., one reported snail host of *Neascus* sp. (see Hoffman, 1999), is present in TL and is known to have variable habitat use in response to predation pressure (Turner, 1996; Bernot and Whittinghill, 2003) and parasite presence (Bernot, 2003). In response to these stimuli, snails may change their position in the water column (Turner, 1996; Bernot and Whittinghill, 2003). In TL, YOY largemouth bass were found in deeper areas of the littoral zone with less vegetation than juvenile bluegill (B. Pracheil, personal observation), an observation that was also noted by Fischer and Kelso (1990) in Louisiana. If snails infected with *Neascus* sp. are sharing this deeper, less vegetated habitat with YOY largemouth bass, these fish would be vulnerable to penetration by *Neascus* sp. and may have an increase in abundance of this parasite with length. However, since the snail host of *Cryptogonimus* sp. is not known, it is not possible to say whether the behavior of the snail host of this parasite can also be altered.

Parasite Infracommunities

In bluegill irrespective of cohort, parasite infracommunity diversity, species richness and adjusted species richness have significant positive correlations with fish length. This indicates that as a fish becomes older and longer, its parasite community becomes more diverse. This is similar to the findings of Cloutman (1975) and Fellis and Esch (2004) who reported increased parasite community diversity with increased adult bluegill length. This suggests that overall, parasite infracommunity diversity significantly increases with length, but length is not as important to diversity when looking at a smaller time scale, such as within a cohort. As fish become older and longer, they are able to eat a wider variety of parasite intermediate hosts, but they also increase their probability of being penetrated by cercariae due to increased surface area. The increase in larval trematode abundances, particularly *Cryptogonimus* sp., may be negating the positive effects on diversity caused by acquisition of more parasites through ingestion. It may also be that parasite infracommunities of the 2001 and 2002 cohorts of bluegill in TL have achieved maximum diversity and diversity measures will not increase until these fish primarily inhabit limnetic areas and are exposed to different parasite species from new intermediate hosts.

In the 2002 cohort, adjusted parasite species richness was significantly correlated with bluegill length but species richness was not. This suggests that length of fish may continue to be an important determinant of internal parasite communities, but not for external parasite communities. In the 2003 cohort of bluegill, species richness was the only diversity metric shown to be significantly influenced by length. It can be inferred that the factors structuring the internal parasite infracommunity and the entire parasite

infracommunity may vary in juvenile bluegill with age, such as diet and habitat, or that the factors structuring these communities may vary from year-to-year, such as temperature.

In addition to a decrease in mean abundance of *Cryptogonimus* sp., *Neascus* sp., *P. minimum* and *P. ambloplitis* in each cohort of juvenile bluegill in the spring, there are also simultaneous decreases in infracommunity diversity and evenness values in the 2002 and 2003 cohorts between April and June, 2004. Cloutman (1975) also found bluegill parasite community diversity values to decrease between April and May. In the present study, the magnitude of the decreases in diversity and evenness is not equal; diversity has a larger magnitude decrease than evenness. These decreases in infracommunity diversity and evenness values are concurrent with the decrease in abundances of the most common parasites. Based on data from the present study, the decrease in parasite mean abundance in April through June, 2004 may have led to a restructuring of the parasite community. This restructuring can be inferred from the decrease in the diversity to evenness ratio for *Cryptogonimus* sp. between May and June in the 2002 cohort and between April and May in the 2003 cohort. Because the drop in evenness is of a lower magnitude than the decrease in diversity, parasite individuals are more evenly distributed among species after the decrease in diversity and evenness. Increased evenness with respect to diversity between April and June, 2004 is likely a result of the decreased mean abundance of *Cryptogonimus* sp. and could also be brought about by increased mortality of heavily parasitized juvenile bluegill.

Parasite infracommunity diversity, evenness, species richness and adjusted species richness showed significant positive correlations with largemouth bass length.

This agrees with Cloutman (1975) who found that parasite community diversity of largemouth bass older than 12 months increased with age. As largemouth bass become older and longer, their gape size increases and allows them to eat a wider variety of prey, especially when they attain a size at which they can eat fish. As largemouth bass increase in size and become piscivorous, they eat juvenile bluegill serving as intermediate hosts for parasites such as *Cryptogonimus* sp. and *P. ambloplitis*. Parasite communities of largemouth bass in TL are not dominated by larval trematodes to the degree that parasite communities of juvenile bluegill are. Therefore, largemouth bass parasite infracommunity diversity values are higher than those of bluegill because individuals of the parasite species they harbor are more evenly distributed among species. Cloutman (1975) also found that parasite communities of largemouth bass older than 12 months were more diverse and had fewer larval trematodes than bluegill older than 12 months.

Parasite Component Communities

The Shannon diversity values for the total, enteric and parenteric parasite component communities of YOY largemouth bass are more similar to each other than those of juvenile bluegill. There is also a difference (although not significant) between Shannon diversity values for the total parasite component communities of age 0 bluegill and YOY largemouth bass. The variance values for the Shannon diversity t-test are approximated from the relative abundances of each species in a community. Since parasite individuals in this community are not evenly distributed among species in bluegill, a high variance value was generated. Variance values are a component of the approximation for degrees of freedom and also serve as the denominator in the t-test. High variance values lowers the degrees of freedom and the t-value which influence test

significance. The differences in the diversities of the total, enteric and parenteric parasite component communities of juvenile bluegill and total parasite component communities of age 0 bluegill and YOY largemouth bass were non-significant. However, it may be that this t-test may not be a robust method for detecting significant differences between parasite component communities in TL because enteric diversity of juvenile bluegill was more than two times higher than either total or parenteric diversity and total diversity of largemouth bass parasites was nearly twice that of age 0 bluegill. Because Shannon diversity values for the parasite component community only generate one diversity value per host species per site, as performed by Marcogliese and Cone (2001), other forms of statistical tests are not applicable.

Some surveys of fish parasite communities only census parts of the fish or do not include metacercarial abundances (Esch, 1971; Steinauer and Font, 2003). Results of the present study indicate that parasite community diversity values obtained from examination of certain parts of the fish may not be representative of the entire parasite community. Juvenile bluegill from TL had similar total and parenteric component community diversities, but the diversity of the enteric parasite component community is more than twice that of either the parenteric or total parasite component communities. The enteric parasite component communities of age 0 bluegill were much lower than the total or parenteric parasite component communities. In TL largemouth bass, the total, enteric and parenteric parasite component community diversities are similar. The present study shows that depending on the host species and age and study area, the diversity of the enteric component community may not be representative of total component community. Total and parenteric parasite component communities of juvenile bluegill

from the present study were dominated by larval *Cryptogonimus* sp. with very high mean abundances relative to other parasite species in the community. Conversely, one parasite species did not dominate the enteric parasite community; therefore, diversity values derived only from enteric parasites are not an adequate descriptor of the total parasite component community. In the case of juvenile bluegill from TL, the enteric parasite component community diversity is an overestimate of total component community diversity.

In the present study system, host life history can explain why age 0 bluegill have very different total, enteric and parenteric parasite component community diversities and YOY largemouth bass have similar total, enteric and parenteric parasite component community diversities. The parasite component communities of juvenile bluegill are dominated by larval trematodes. Juvenile bluegill live in vegetated areas containing mollusks that shed larval parasites that directly penetrate the fish (Wilson et al., 1996). These juvenile bluegill acquire these parasites passively by sharing habitat with mollusks that shed larval parasites.

Although the parasite communities of YOY largemouth bass are numerically dominated by larval trematodes, their larger gape size allows them to prey on a wider variety of intermediate hosts. Since largemouth bass are able to eat a wider variety of intermediate hosts, the diet of YOY largemouth bass is a more influential parasite community determinant than the diet of juvenile bluegill. Additionally, YOY largemouth bass in TL were found in deeper, less vegetated water than juvenile bluegill (B. Pracheil, personal observation). This deeper, less vegetated water may have less mollusks shedding larval trematodes; hence, YOY largemouth bass do not acquire as many larval

trematodes as do juvenile bluegill. Furthermore, the distribution of parasite individuals among species becomes more even due to the numerically lessened role of larval trematodes in the parasite component community, leading to similar total, enteric and parenteric parasite component community diversity in YOY largemouth bass.

Mollusk Abundances

Since larval trematodes, which are shed by mollusks and directly penetrate bluegill, numerically dominated the parasite community of juvenile bluegill in TL, mollusk abundance may have a large influence on parasite community structure. In general, an increase in numbers of mollusks found in the sampling area in concert with water temperature increasing above 18° (Hoffman, 1958) corresponded with an increase in the number of trematodes found per fish (Figure 4 and 5).

In the present study, decreases in the mean number of larval trematodes per fish cannot be directly attributed to decreases in mollusk numbers. Since metacercarial parasites are thought to be long-lived and accumulate in a fish over time (Spall and Summerfelt, 1970), a decrease in the mollusk abundances only has an effect on recruitment of new parasite individuals (depending on water temperature). Fewer mollusks may mean there are fewer larval parasites shed to penetrate fish. Decreases in numbers of trematodes per fish may be attributed to a larger proportion of younger, smaller fish examined in a month since younger fish have lower mean abundances of larval trematodes. Mortality of the most heavily infected bluegill also could explain the decline of the larval trematode community in concert with mollusk numbers in some months.

Summary

Several prior studies in other areas of the United States have shown larval trematodes to dominate the parasite fauna of juvenile bluegill (Fisher and Kelso, 1987, 1988, 1990; Landry and Kelso, 1999; Steinauer and Font, 2003). In some of these studies, including the present study in TL, larval parasites, particularly larval trematodes, have been implicated as potential causes of parasite-induced host mortality (Lemly and Esch, 1984; Fischer and Kelso, 1988). This suggests that larval trematodes may be a major selective pressure influencing the survivorship of juvenile bluegill.

In general, fish habitat and diet are the major determinants of parasite communities. Because parasite communities are structured as functions of these components, a better understanding of the diet and habitat of juvenile bluegill and YOY largemouth bass can be gained through surveying their parasite fauna. Juvenile bluegill in TL had an increase in parasite species richness with increased length and hence, with increased age. As juvenile bluegill in TL age, the decreasing importance of fish length on measures of parasite community diversity coupled with the recruitment of new parasite species suggests diet and habitat variability among juvenile age classes in TL. Finally, because fish parasite communities are functions of the diet and habitat of fish, the differences in parasite community composition and total community diversity between YOY bluegill and YOY largemouth bass in TL reinforces our knowledge of the diets and habitats of these fishes.

CHAPTER TWO

PARASITE INFRAPOPULATIONS AND COMMUNITIES OF JUVENILE BLUEGILL, *LEPOMIS MACROCHIRUS* AND LARGEMOUTH BASS, *MICROPTERUS SALMOIDES* IN GULL LAKE, MICHIGAN AND A COMPARISON OF PARASITE COMMUNITIES BETWEEN GULL LAKE AND THREE LAKES II, MICHIGAN

INTRODUCTION

Fish habitat (Esch, 1971; Wilson et al., 1996), diet and age (McDaniel and Bailey, 1974; Cone and Anderson, 1977; Hanek and Fernando, 1978a, 1978b; Bailey, 1984) are determining factors in the composition and structure of parasite communities in centrarchid fishes. The habitat in which a fish resides largely determines which parasites it may host. Habitat attributes such as substrate type, vegetation type and quantity play a major role in parasite intermediate hosts found in an area. Mollusks serving as intermediate hosts for trematode parasites, for instance, shed larval trematodes that may infect a fish by direct penetration. By sharing habitat with these mollusks, fish may become infected with these parasites. Habitat, in turn, influences diet by determining what prey items (which may be serving as intermediate hosts) are available to a fish. For example, copepods serve as intermediate hosts for several species of parasites that are acquired by fish through ingestion.

As a fish ages, it increases in size and surface area. With increased surface area, a fish increases its chances of becoming infected with parasites via direct penetration (Spall and Summerfelt, 1970). Also, some larval parasites, such as *Posthodiplostomum minimum*, are long-lived and accumulate in a fish over several years (Spall and Summerfelt, 1970; Hoffman, 1999). In bluegill, *Lepomis macrochirus* and largemouth bass, *Micropterus salmoides*, age may influence parasite communities because juveniles and adults have been shown to have different diets and habitats (Mittelbach, 1984; Werner and Hall, 1988; Olson, 1996; Post, 2003; Sammons and Maceina, 2005).

The life history traits of juvenile bluegill and young-of-the-year (YOY) largemouth bass should contribute to the development of a parasite fauna unique to their life stage. Adult bluegill spawn in vegetated littoral areas in May or June in Michigan when water temperature reaches approximately 20° C (Breder, 1936; Werner, 1967; Werner and Hall, 1988). After hatching approximately two weeks post-spawn (Breder, 1936), bluegill fry undergo a migration to the limnetic zone of a lake and remain there for approximately six to eight weeks (Werner, 1967; Werner and Hall, 1988). Juvenile fish then return to the vegetated littoral zone for the next two to three years (Werner and Hall, 1988) until they move to the limnetic zone of the lake for the duration of their life (Werner and Hall, 1988). The shift to the limnetic habitat gradually takes place in bluegill between 45 and 75 mm SL (Osenberg et al., 1992). At approximately 75 mm SL, bluegill switch to feeding almost exclusively in the limnetic zone of a lake (Werner and Hall, 1988), which is approximately commensurate with maturity (Osenberg et al., 1992).

Throughout life, bluegill prey on aquatic invertebrates that serve as intermediate hosts for many types of parasites (Zischke and Vaughn; 1962; Werner, 1969; McDaniel and Bailey, 1974; Sadzikowsi and Wallace, 1976; Cone and Anderson, 1977; Werner and Hall, 1988; Fisher and Kelso, 1990). However, the invertebrate prey available in the limnetic zone where bluegill spend their adult life differs from that available in the vegetated littoral zone where they live as juveniles (Mittelbach, 1984; Werner and Hall, 1988). This shift in diet and habitat may cause the parasite fauna to concurrently shift (Wilson et al., 1996). Additionally, the vegetated habitat of juvenile bluegill is habitat for many mollusks that serve as intermediate hosts for trematodes that shed larval parasites that directly penetrate bluegill (Wilson et al., 1996).

Largemouth bass spawn in April or May in Michigan in vegetated littoral areas (Breder, 1936) when the water temperature reaches approximately 15-18° C (Mittelbach and Persson, 1998). The YOY largemouth bass remain in the littoral zone for the first few weeks to months of life feeding on invertebrates (Gilliam, 1982; Olson, 1996; Post, 2003). When largemouth bass become large enough to eat fish, they switch to a piscivorous diet, primarily preying on juvenile bluegill (Gilliam, 1982; Olson, 1996; Post, 2003) and continue to prey on fishes throughout their life. Since largemouth bass eat aquatic invertebrates such as copepods, amphipods and mayflies for the first few weeks to months of life (Sule, 1981; Gilliam, 1982; Fischer and Kelso, 1990; Olson, 1996; Dibble and Harrel, 1997; Post, 2003), they may acquire parasites that use these invertebrates as intermediate hosts. As is the case with juvenile bluegill, while living in the vegetated littoral zone, largemouth bass are vulnerable to colonization by larval trematodes shed by mollusks. Since largemouth bass become piscivorous early in life, primarily eating juvenile bluegill, they may acquire parasites that use bluegill as intermediate or paratenic hosts.

Because juvenile and adult bluegill and juvenile and adult largemouth bass have different habitats and diets, parasite faunas should differ between juvenile (pre-reproductive) and adult (reproductively mature) fish. Most studies on the parasites of bluegill and largemouth bass are restricted to the examination of adult fish or fish of unknown age (see Hoffman, 1999 for a list of studies of bluegill parasites). Few studies report on changes in bluegill parasite communities with host age (McDaniel and Bailey, 1974; Cloutman, 1975) and only one study examines parasite community dynamics of largemouth bass with host age (Cloutman, 1975).

Studies on the parasite communities of juvenile bluegill and YOY largemouth bass are limited to Fischer and Kelso (1987, 1988, 1990), Landry and Kelso (1999) and Steinauer and Font (2003). All these studies were conducted in Louisiana which may not be indicative of the parasite communities of these fish in Michigan. Effects of fish age on parasite community composition and structure in juvenile bluegill and YOY largemouth bass were also not examined in the above studies. Fisher and Kelso (1987, 1988, 1990), Landry and Kelso (1999) and Steinauer and Font (2003) reported that parasite communities of juvenile bluegill and YOY largemouth bass were dominated by larval trematodes. However, not all larval trematodes in these studies were counted so the numeric role and the effect these parasites have on parasite community diversity of juvenile bluegill and YOY largemouth bass is not known.

The objectives of this study were to determine patterns of parasite infrapopulation abundance and prevalence for the most common parasites of three cohorts of the most common parasites of juvenile bluegill (*Cryptogonimus* sp., *Posthodiplostomum minimum*, *Neascus* sp. and *Diplostomum* sp.) and YOY largemouth bass (*Cryptogonimus* sp. adults, *Cryptogonimus* sp. metacercariae, *Pomphorhynchus bulbocolli* and *Camallanus* sp.); to determine patterns of parasite infracommunity diversity in juvenile bluegill; to describe parasite component community diversities in juvenile bluegill and YOY largemouth bass; and finally, to compare parasite communities of juvenile bluegill and YOY largemouth bass from Three Lakes II and Gull Lake, Michigan.

MATERIALS AND METHODS

Description of Study Site

Gull Lake (Figure 6) (referred to as GL from hereafter) is a mesotrophic lake of glacial origin located within Kalamazoo and Barry Counties in southwestern Michigan (Dexter, 1996). This surface area of the lake is 2,030 acres and it has a maximum depth of 110 feet (Dexter, 1996). Several springs along the lakeshore feed GL in addition to five inlets; Prairieville Creek at the north side, Long Lake, Miller Lake and Grass Lake at the west side and Wintergreen Lake on the east side. Gull Creek serves as the lake's only outlet (Dexter, 1996).

Fish Collection and Examination

Collection of fish took place in Miller's Marsh, a shallow area (<2 m) on the west side of the lake where the yellow pond lily, *Nuphar lutea* was the dominant vegetation. Bluegill were collected by seine in August through September, 2003 and May through June, 2004. Largemouth bass were collected in July through October, 2003. Upon collection, fish were placed in aerated coolers and transported to the laboratory at Michigan State University. Fish from GL were examined as described in Chapter One.

Parasite Preparation and Identification

Parasites were prepared and identified as described in Chapter One.

Parasitological Terminology

Ecological terms as used in the present study are defined in Chapter One. The most common parasite species were defined as countable parasite species with greater than 30% prevalence (arbitrarily determined) in each host species.

Data Analysis

Names of fish cohorts correspond to the year those fish hatched. For example, fish that hatched in 2003 are referred to as the 2003 cohort of fish. The 2002 cohort of bluegill consisted of age 1 fish collected in August and September, 2003; and the 2003 cohort of bluegill consisted of age 0 fish collected in August and September, 2003 and age 1 fish collected in May- July, 2004. No fish with mature gonads were examined in the present study. However, since no fish from the 2002 cohort were collected in the 2004 sampling year, by-cohort analyses were not conducted. Calculation and use of diversity values in the present study are presented in Chapter One.

Mean parasite abundance values are expressed as mean $\pm$ standard deviation (SD) (maximum). Mean fish length values and mean parasite infracommunity diversity, evenness, species richness and adjusted species richness values are expressed as mean $\pm$ SD (range). Parasite abundance, Brillouin's diversity and evenness values, species richness and adjusted species richness data were natural log transformed.

All statistical comparisons were considered significant at the α=0.05 level. Due to small sample sizes, all analyses for juvenile bluegill parasites are conducted irrespective of fish cohort. All analyses comparing bluegill and YOY largemouth bass use age 0 bluegill. Chi-square analyses were used to infer significant differences in prevalence by using numbers of fish infected and uninfected with the most common parasites of bluegill irrespective of fish cohort between sampling years. An unpaired t-test was used to detect significant differences in mean abundances of the most common parasites, mean Brillouin's diversity and evenness, parasite species richness and adjusted parasite species richness for juvenile bluegill irrespective of fish cohort between

sampling years. An unpaired t-test was also used to detect significant differences in Brillouin's diversity and evenness and species richness and adjusted species richness of parasite infracommunities of juvenile bluegill between GL and TL.

A Spearman's rank correlation was used to detect relationships between untransformed abundance of the most common parasite species, untransformed Brillouin's diversity and evenness and untransformed species richness and adjusted species richness and fish length for juvenile bluegill and YOY largemouth bass irrespective of cohort and sampling year.

A t-test for Shannon diversity values was used to compare enteric and parenteric component community diversity values to total component community diversity values and also to compare total component community diversity between juvenile bluegill and YOY largemouth bass. This t-test was also used to detect significant differences in parasite component communities of juvenile bluegill and YOY largemouth bass between GL and TL. Variance of parasite component community diversity for bluegill and largemouth bass was approximated by:

$$s^2 = \frac{\Sigma f_i \log^2 f_i - (\Sigma f_i \log f_i)^2 n^{-1}}{n^2}$$

where f_i= number of individuals of each species, and n= number of individuals of all species (Brower et al., 1993), for the test statistic:

$$t = \frac{H_1' - H_2'}{(s_1^2 + s_2^2)^{1/2}}$$

(Brower et al., 1993) which is compared to the Student's t-distribution with $\alpha = 0.05$ and degrees of freedom approximated by:

$$DF = \frac{(s^2_{H1'} + s^2_{H2'})^2}{\frac{(s^2_{H1'})^2}{n_1} + \frac{(s^2_{H2'})^2}{n_2}}$$

(Brower et al., 1993).

Fish of the same age and cohort were used when comparing Shannon diversity values and Jaccard's coefficients between lakes and fish species.

Mollusk Collection

Snails were collected, identified and counted as described in Chapter One.

RESULTS

Host Demographics

A total of 117 juvenile bluegill (52 from 2003 and 65 from 2004) and 86 young-of-the-year largemouth bass were examined. The mean length of juvenile bluegill irrespective of cohort for the 2003 and 2004 sampling years were 41.0 ± 13.0 mm (19-55 mm) and 35.2 ± 4.8 mm (26-48 mm), respectively. There was no significant difference in length of bluegill between years in this lake. The 2002 cohort of juvenile bluegill consisted of 33 age 1 fish from the 2003 sampling year with a mean length of 48.8 ± 3.4 mm (43-55 mm). The 2003 cohort of juvenile bluegill consisted of 19 age 0 fish from the 2003 sampling year with a mean length of 25.2 ± 4.7 mm (19-37 mm) and 65 age 1 fish from the 2004 sampling year with a mean length of 35.2 ± 4.8 mm (26-48 mm). Eighty-six age 0 YOY largemouth bass were collected in July- October, 2003 with a mean length of 37.0 ± 9.4 mm (21-61 mm). Water temperatures by month from GL are found in Figure 3.

Parasites of Juvenile Bluegill and Young-of-the-Year Largemouth Bass

Prevalence and mean abundance ± SD (maximum) for all parasite species of juvenile bluegill by sampling year are in Table 14. Juvenile bluegill were infected with 6634 countable parasites from 11 species: five trematodes, *Azygia* sp., *Cryptogonimus* sp., *Diplostomum* sp., *Neascus* sp. and *P. minimum*; two cestodes, *Proteocephalus ambloplitis* and *Haplobothrium globuliforme*, three acanthocephalans, *Leptorhynchoides thecatus*, *Neoechinorhynchus cylindratus* and *Pomphorhynchus bulbocolli*; and one nematode, *Spinitectus* sp. Five species of non-countable parasites also infected juvenile

bluegill: three monogenes, *Actinocleidus* sp., *Anchoradiscus* sp. and Monogenea sp.; and two protozoans: *Myxobolus* sp. and *Trichodina* sp. Some individuals of *Pomphorhynchus bulbocolli, Spinitectus* sp., *Actinocleidus* sp. and *Anchoradiscus* sp. were gravid adults. Parenteric larval parasites, *Cryptogonimus* sp., *Diplostomum* sp., *Neascus* sp., *P. minimum, P. ambloplitis, H. globuliforme* and *N. cylindratus* comprised 99.0% of all parasite individuals counted. *Cryptogonimus* sp. metacercariae accounted for 88.9% of all parasite individuals counted.

Prevalence and mean abundance ± SD (maximum) for parasites of YOY largemouth bass are in Table 15. Young-of-the-year largemouth bass were infected with 3297 countable parasites from 12 species: six trematodes, *Azygia* sp., *Clinostomum* sp., *Cryptogonimus* sp., *Diplostomum* sp., *Neascus* sp. and *P. minimum*; one cestode, *P. ambloplitis*; three acanthocephalans, *L. thecatus, N. cylindratus* and *P. bulbocolli*; and two nematodes, *Camallanus* sp. and *Spinitectus* sp. Four species of non-countable parasites: two monogenes, Monogenea sp. and Monogene sp. A; and two protozoans, *Myxobolus* sp. and *Trichodina* sp. also infected YOY largemouth bass. Both adults and metacercariae of *Cryptogonimus* sp. were found as well as enteric and parenteric *L. thecatus*. Some individuals of Monogene sp. A, *Cryptogonimus* sp. and *Camallanus* sp. were gravid adults. Parenteric larval parasites, *Clinostomum* sp., *Cryptogonimus* sp. metacercariae, *Diplostomum* sp., *Neascus* sp., *P. minimum, P. ambloplitis* and *L. thecatus* accounted for 44.4% of all parasites counted. *Cryptogonimus* sp. metacercaria, which had the highest prevalence and mean abundance, accounted for 41.6% of all parasites counted. Although juvenile bluegill and YOY largemouth bass had several parasite

species in common, larval trematodes comprised a much larger part of the parasite community in juvenile bluegill than in YOY largemouth bass.

Parasite species common to TL and GL bluegill were the monogenes, *Actinocleidus* sp. and *Anchoradiscus* sp.; the trematodes, *Azygia* sp., *Cryptogonimus* sp., *Diplostomum* sp., *Neascus* sp. and *P. minimum*; the cestodes, *P. ambloplitis* and *H. globuliforme*, the acanthocephalans, *N. cylindratus* and *P. bulbocolli*; the nematode, *Spinitectus* sp.; and the protozoans, *Myxobolus* sp. and *Trichodina* sp.

Prevalence and Mean Abundance of Most Common Parasites

The most common parasite species by host species were as follows: bluegill; *Cryptogonimus* sp., *Posthodiplostomum minimum*, *Diplostomum* sp., and *Pomphorhynchus bulbocolli*; largemouth bass: *Cryptogonimus* sp. adults, *Cryptogonimus* sp. metacercaria; *Pomphorhynchus bulbocolli* and *Camallanus* sp. Gull Lake bluegill had significantly higher prevalences of *Cryptogonimus* sp. (X^2=10.05, p<0.01), *P. minimum* (X^2=34.65, p<0.01), *Diplostomum* sp., (X^2= 18.20, p<0.01) and *P. bulbocolli* (X^2=24.67, p<0.01) in the 2004 sampling year than in 2003. In 2004, bluegill from GL had significantly higher mean abundances of *P. minimum* (t=-5.85, p<0.01, 83 d.f.) and *Diplostomum* sp. (t=-10.47, p<0.01, 68 d.f.) than in the 2003 sampling year. There was no significant difference in mean abundance between years for the other most common parasite species.

In GL bluegill, significant correlations were detected between abundance of *Cryptogonimus* sp. (r_s=0.63, p<0.01.), *P. bulbocolli* (r_s=0.38, p<0.01) and bluegill length (irrespective of cohort). In largemouth bass, there were significant correlations between

abundance of *Cryptogonimus* sp. metacercariae (r_s= -0.52, p<0.01), *P. bulbocolli* (r_s=0.61, p<0.01), *Camallanus* sp. (r_s= -0.37, p<0.01) and fish length.

Parasite Infracommunities

Brillouin's diversity, evenness, species richness and adjusted species richness of parasite infracommunities of juvenile bluegill by sampling year are in Table 16. Bluegill collected in 2004 from GL had significantly higher Brillouin's diversity (t= -5.55, p<0.01, 117 d.f.) and evenness (t= -4.28, p<0.01, 92 d.f.), species richness (t= -4.42, p<0.01, 85 d.f.) and adjusted species richness (t= -4.65, p<0.01, 82 d.f.) than bluegill collected in 2003.

There were significant correlations between parasite infracommunity diversity (r_s=0.13, p=0.01), species richness (r_s=0.61, p<0.01), adjusted species richness (r_s=0.58, p<0.01) and bluegill length. Mean diversity, evenness, species richness and adjusted species richness of parasite infracommunities of GL largemouth bass were 0.27 $\pm$ 0.14 (0-0.59), 0.57 $\pm$ 0.25 (0-1), 3.8 $\pm$ 1.8 (1-9) and 3.5 $\pm$ 1.6 (1-8), respectively. In largemouth bass, there were significant correlations between infracommunity diversity (r_s=0.55, p<0.01), evenness (r_s=0.52, p=0.01) and adjusted species richness (r_s=0.40, p=0.04) and fish length.

Parasite Component Communities

The Shannon diversity values of the total, enteric and parenteric parasite component communities of bluegill were 0.22, 0.38 and 0.21, respectively. The Shannon diversity values of the total, enteric and parenteric parasite component communities of age 0 bluegill were 0.24, 0.25 and 0.12, respectively. The Shannon diversity values for

the total, enteric and parenteric component communities of largemouth bass were 0.65, 0.53 and 0.13 respectively. There were no significant differences between total, enteric or parenteric parasite component communities of bluegill or YOY largemouth bass or in total parasite component communities between age 0 bluegill and YOY largemouth bass. The Jaccard's coefficient of community similarity for the parasite component communities of age 0 bluegill and YOY largemouth bass from GL was 0.47.

Mollusk Abundances

Abundances of mollusks by taxonomic group and month in GL are in Figure 8. Five taxonomic groups of mollusks were collected in GL; the snail families Planorbidae, Physidae and the snail genus *Viviparus* sp.; the clam family Sphaeriadae and the zebra mussel, *Dreissena sp.* Mollusk abundances generally declined between July and September and increased between June and July, 2004. Mean number of larval trematodes per bluegill by month and number of mollusks (excluding zebra mussels, which are not known to host any trematodes found in GL bluegill) collected per month are in Figure 8. Abundances of larval trematodes per bluegill decreased between August and September, 2003 and increased between June and July, 2004. Similarly, mollusk abundances decreased between August, 2003 and June, 2004 and increased between June and July, 2004.

Parasite Community Comparisons Between Three Lakes II and Gull Lake

Irrespective of cohort, bluegill from GL had significantly higher mean Brillouin's diversity ($t = -4.18$, $p<0.01$, 259 d.f.) and evenness ($t = -2.43$, $p=0.02$, 68 d.f.) than bluegill from TL. Irrespective of cohort, bluegill from TL had significantly higher mean species richness ($t = -4.86$, $p<0.01$, 65 d.f.) and adjusted species richness ($t = -4.63$,

$p<0.01$, 64 d.f.) than bluegill from GL. There were no significant differences in Brillouin's diversity, evenness, species richness or adjusted species richness of parasite infracommunities of YOY largemouth bass between GL and TL.

Total, enteric and parenteric parasite component community diversity values by lake and host species are in Figure 9. There were no significant differences in parasite component communities of bluegill between GL and TL or in largemouth bass between GL and TL although total component community diversity for each host species was highest in GL. Jaccard's coefficient for community similarity for parasite component communities of bluegill from TL and GL was 0.74 (Figure 10). Largemouth bass from GL and TL had a Jaccard's coefficient of parasite component community similarity of 0.93.

DISCUSSION

Parasites of Juvenile Bluegill and Young-of-the-Year Largemouth Bass

Many of the parasites found in the juvenile bluegill and YOY largemouth bass from GL in the present study have been found in previous studies of parasites of these fish in GL (Esch, 1971; Muzzall et al., 1995; Gillilland and Muzzall, 2004; and Muzzall and Gillilland, 2004). The present study is the first report of *Azygia* sp., *Cryptogonimus* sp., *Diplostomum* sp., *Neascus* sp., *P. minimum*, *Haplobothrium globuliforme*, *Neoechinorhynchus cylindratus*, *Actinocleidus* sp., *Anchoradiscus* sp., *Myxobolus* sp. and *Trichodina* sp. from GL bluegill; and *Clinostomum* sp., *Cryptogonimus* sp. metacercaria and adults, *Diplostomum* sp., *Neascus* sp., *P. minimum*, *Camallanus* sp., monogene sp. A, *Trichodina* sp. and *Myxobolus* sp. from GL largemouth bass.

The present study notwithstanding, 22 parasite species have been reported from adult bluegill or bluegill of unknown age in Michigan (Muzzall and Peebles, 1998 review). Of those 22 species, seven (31%) were represented by larval or immature stages; five of which (23% of total parasite species) were larval trematodes. Prior studies of Michigan bluegill parasites have largely surveyed adults which have a much lower percentage of larval parasite species than juvenile bluegill in the present study. Juvenile bluegill in GL hosted 15 parasite species; eight species (53%) were represented by larval or immature forms; four of which (27% of total parasite species) were larval trematodes. Juvenile bluegill are an important intermediate host for many parasite species because they are a prey item for many vertebrate species (Muzzall and Peebles, 1998).

Although adult bluegill from Michigan have a larger percentage of adult parasite species (Muzzall and Peebles, 1998) than juvenile bluegill from the present study, similar percentages of the parasite species of adult and juvenile bluegill from GL are comprised of larval trematodes. Since larval trematodes are long-lived (Spall and Summerfelt, 1970), it may be that many larval trematodes of adult bluegill infect bluegill while they are juveniles living in the littoral zone. However, because mean abundances of larval trematodes are sometimes not reported in studies of parasites of Michigan adult bluegill (Esch, 1971), it is not possible to know whether abundances of these parasites continue to increase as fish age.

The present study is the first in Michigan to report on the entire parasite community of largemouth bass, albeit largemouth bass in the present study are age 0. Esch (1971) did not include monogenes or copepods; Hudson et al. (1994), Muzzall et al. (1995), and Hudson and Bowen (2002) worked only with copepods; Gillilland and Muzzall (2004) reported on *P. ambloplitis*; and Muzzall and Gillilland (2004) worked only with acanthocephalan parasites of largemouth bass.

Esch (1971) reported parasite communities of adult largemouth bass in Michigan to consist of 83% adult parasite species and 17% larval or immature parasite species. In the present study in GL, of the 14 non-protozoan parasite species reported from YOY largemouth bass, 57% consisted of adult parasite species and 57% of parasite species were represented by larval or immature forms. Percentages of adult and larval or immature parasite species do not add up to 100% because *Cryptogonimus* sp. and *L. thecatus* were represented by both adult and larval or immature forms. A greater percentage of the parasites of adult largemouth bass consist of adult species than in YOY

largemouth bass. Due to their size, adult largemouth bass are much less vulnerable to predation than YOY largemouth bass; hence, parasite species using adult largemouth bass as an intermediate host may not be able to complete their life cycle.

Posthodiplostomum minimum, *Camallanus* sp., *P. ambloplitis* and *N. cylindratus*, have been reported from juvenile bluegill and largemouth bass in previous studies (Fischer and Kelso, 1987, 1988, 1990; Camp, 1988; Landry and Kelso, 1999; Steinauer and Font, 2003). The mean abundances of *Cryptogonimus* sp. reported in the present study are the highest metacercarial mean abundances reported in juvenile bluegill in the United States. In all previous studies of parasite communities of juvenile bluegill, as well as in the present study, larval trematodes had higher species richness and abundances than any other group of parasites (Fischer and Kelso, 1987, 1988, 1990; Landry and Kelso, 1999; Steinauer and Font, 2003).

Prevalence and Mean Abundance of Most Common Parasites

Posthodiplostomum minimum had significantly higher mean abundance in 2004 than in 2003. Fish accumulate *P. minimum* metacercariae as they age (Hoffman, 1958; Spall and Summerfelt, 1970). Bluegill collected in 2004 should have higher mean abundances of this parasite because they were, on average, older than fish in 2003.

Indirect parasite induced mortality caused by selective predation on the YOY largemouth bass with the highest *Cryptogonimus* sp. metacercariae abundances may explain the significant negative correlation between abundance of *Cryptogonimus* sp. metacercariae and fish length. Most YOY largemouth bass do not survive to age 1 and mortality of many of them is due to predation by other juvenile and adult largemouth bass (Post et al., 1998). For instance, Post et al. (1998) estimated that by August, between 91

and 99% of YOY largemouth bass have been eaten by older largemouth bass when YOY populations ranged from 24,000 – 94,000 individuals. As in juvenile bluegill, *Cryptogonimus* sp. metacercariae encyst largely in the muscle, but also in the brain and on the gills, posterior exterior surface of the eye and on the gills. Metacercarial encystment in these areas of the fish may lead to decreased swimming ability, vision and/or gas exchange. In GL, if the YOY largemouth bass most heavily infected with *Cryptogonimus* sp. metacercariae are more vulnerable to predation, then the individuals with the lowest metacercarial abundances survive leading to the negative correlation between abundance of this parasite and length.

This significant negative correlation between *Cryptogonimus* sp. metacercariae abundance and YOY largemouth bass length could also be explained by *Cryptogonimus* sp. stunting the growth of the YOY largemouth bass. In this case, the YOY largemouth bass with the highest abundances of *Cryptogonimus* sp. metacercariae would have a slower growth rate than fish with lower abundances. The larval trematode *Neascus* sp. has been shown to stunt the growth of juvenile bluegill (Lemly and Esch, 1984) and a similar phenomenon could be occurring with *Cryptogonimus* sp. in GL largemouth bass.

Abundance of *Camallanus* sp., which uses a copepod intermediate host, also had a significant negative correlation with fish length. As largemouth bass become older and attain a gape size large enough to eat fish, they transition from a diet of zooplankton and benthic invertebrates to piscivory (Olsen, 1996; Post, 2003). Since larger fish that have switched to piscivory may be eating copepods less frequently than they are eating smaller fish (Gilliam, 1982), abundance of *Camallanus* sp. might be expected to drop as largemouth bass become longer. Alternatively, *Camallanus* sp. has been reported in

centrarchid fishes as having seasonal fluctuations in prevalence and abundance, with both having their peak in the summer and declining throughout the fall months (Spall and Summerfelt, 1969; Stromberg and Crites, 1975; Steinauer and Font, 2003). As the largemouth bass in the present study became older and longer, it may be that the abundance of this parasite declined due to parasite senescence.

Two acanthocephalan species, *P. bulbocolli* and *L. thecatus* use amphipod intermediate hosts and had significant increases in abundances with bluegill length. *Leptorhynchoides thecatus* can use juvenile bluegill, a major prey-item for YOY largemouth bass, as a paratenic host (see Hoffman, 1999). Largemouth bass become infected with *L. thecatus* when they eat juvenile bluegill. Bluegill can also serve as definitive hosts for *P. bulbocolli* (see Hoffman, 1999). It has been shown that adults of *Pomphorhynchus laevis*, a congener of *P. bulbocolli*, can be transmitted post-cyclically, from the intestine of one fish to another (Kennedy, 1999). Instead of eating the amphipod intermediate host in this case, the largemouth bass may be acquiring this parasite by preying upon juvenile bluegill hosting this worm, which cannot occur until largemouth bass reach sufficient size. Since *P. bulbocolli* has a large bulb that becomes imbedded in the intestinal wall and grows larger as worms become older, it does not seem likely that large adult worms could be transmitted in this way. It may be that younger, smaller *P. bulbocolli* that have not fully imbedded themselves in the intestinal wall could be transmitted post-cyclically.

Parasite Infracommunities

Bluegill collected in 2004 had significantly higher mean Brillouin's diversity and evenness, species richness and adjusted species richness for the parasite infracommunity

than bluegill from 2003. This is caused by a decrease in the abundance of *Cryptogonimus* sp. and an increase in the abundances of several other parasite species in 2004 (Table 16).

There were significant positive correlations between parasite infracommunity diversity, species richness, adjusted species richness and length of juvenile bluegill. Fish length is an important determinant of parasite community richness. Parasite communities of adult bluegill have been shown to become more diverse with age (Cloutman, 1975). As bluegill increase in length and age in GL, they eat a larger variety of prey due to increased gape size and also eat more which increases the probability of acquiring a parasite via ingestion of an intermediate host. At 45-75 mm in SL, juvenile bluegill begin to forage in open water habitat (Osenberg et al., 1992). As fish begin to forage in this open water habitat, they eat intermediate hosts of new parasites and spend less time in the littoral zone where they are exposed to large numbers of *Cryptogonimus* sp. cercariae. Both the decreased exposure to cercariae and exposure to new parasites by ingestion of intermediate hosts leads to increased parasite community diversity in juvenile bluegill.

Infracommunity diversity and adjusted species richness have significant positive correlations with largemouth bass length. Because adjusted species richness has a significant positive correlation with length and species richness does not, this suggests that monogene and protozoan communities are not as heavily influenced by fish length as the internal parasite community. Species richness of monogenes and protozoans may be independent of length whereas species richness of countable parasite species are not. Monogenes and *Trichodina* sp. have direct life cycles and are acquired passively by the

fish which, in this system, may not be as dependent on fish length and acquisition of these parasites may be more heavily influenced by factors such as proximity to another fish host. If a fish is closer to a fish infected with a monogene or *Trichodina* sp., these parasites may have an easier time finding another fish host. *Myxobolus* sp., which was not a countable species, may be influenced by proximity to the tubificid worm intermediate host. Since life cycles of centrarchid species of *Myxobolus* sp. are not known, it is unclear whether length is a factor in presence of this parasite. In salmonid fishes, *Myxobolus cerebralis* recruitment by the fish may be somewhat length dependent in small fish because the infective stage to the fish host, the triactinomyxon spore, is released from the tubificid worm and penetrates the skin of the fish (Gilbert and Granath, 2003). If centrarchid fishes are infected with *Myxobolus* sp. in the same way, length may play a role in recruitment of this parasite because as a fish increases in length, they have more surface area to potentially be penetrated by the triactinomyxon spore. The countable parasites in this system are acquired both passively by fish, through cercarial penetration, and actively, through ingestion of an intermediate host. For countable parasites the actively acquired parasites are still a function of length because as fish increase in length, they have a larger gape size which allows them to eat a wider variety of prey that may be serving as intermediate hosts. Also, as fish become longer, they have greater surface area thus increasing the probability of being penetrated by cercariae.

Parasite Component Communities

The Shannon diversity values for the total, enteric and parenteric parasite component communities of YOY largemouth bass are less different than those of juvenile bluegill. There is also a difference (although not significant) between Shannon diversity

values for the total parasite component communities of age 0 bluegill and YOY largemouth bass. The variance values for the Shannon diversity t-test are approximated from the relative abundances of each species in a community. Since parasite individuals in this community are not evenly distributed among species in bluegill, a high variance value was generated. Variance values are a component of the approximation for degrees of freedom and the denominator in the t-test. High variance values lower the degrees of freedom and the t-value, both of which influence test significance. The differences in the diversities of the total, enteric and parenteric parasite component communities of juvenile bluegill and total parasite component communities of age 0 bluegill and YOY largemouth bass were non-significant. However, it may be that this t-test may not be a robust method for detecting significant differences between parasite component communities in TL because enteric diversity of juvenile bluegill was nearly two times higher than either total or parenteric diversity and total diversity of largemouth bass parasites was nearly three times higher than that of age 0 bluegill. Because Shannon diversity values for the parasite component community only generate one diversity value per host species per site, as performed by Marcogliese and Cone (2001), other forms of statistical tests are not applicable.

Some surveys of fish parasite communities only census parts of the fish or do not include metacercarial abundances (Esch, 1971; Steinauer and Font, 2003). Results of the present study indicate that parasite community diversity values obtained from examination of certain parts of the fish may not be representative of the entire parasite community. In the case of juvenile bluegill from GL, the total diversity of the component community was similar to the diversity of the parenteric component community, but the

diversity of the enteric parasite component community is more than twice that of either the parenteric or total parasite component communities. Total and parenteric parasite component communities of juvenile bluegill from the present study were dominated by larval *Cryptogonimus* sp. with very high mean abundances relative to other parasite species in the community. Conversely, one parasite species did not dominate the enteric parasite community; therefore, diversity values derived only from enteric parasites are not an adequate descriptor of the total parasite component community. Enteric parasite component community diversity is an overestimate of total component community diversity for GL juvenile bluegill. In GL largemouth bass, the total component community diversity is similar to enteric component community diversity, but much larger than parenteric component community diversity. In GL YOY largemouth bass, parenteric component community diversity is an underestimate of total diversity. The present study suggests that depending on the host species and study area, the diversity of the enteric component community may not be representative of total component community.

In the present study system, host life history can explain why age 0 bluegill have very different total, enteric and parenteric parasite component community diversities and YOY largemouth bass have similar total, enteric and parenteric parasite component community diversities. The parasite component communities of juvenile bluegill are dominated by larval trematodes. Juvenile bluegill live in vegetated areas containing mollusks that shed larval parasites that directly penetrate the fish (Wilson et al., 1996). These juvenile bluegill acquire these parasites passively by sharing habitat with mollusks that shed larval parasites.

When YOY largemouth bass begin eating bluegill, diet becomes a more important factor in the acquisition of parasites. Through their diet of juvenile bluegill, largemouth bass acquire parasites that use bluegill as intermediate and paratenic hosts such as *Cryptogonimus* sp., *P. ambloplitis* and *N. cylindratus*. There is a more even distribution of parasite individuals among parasite species due to the numerically lessened role in the parasite component community of directly penetrating larval trematodes due to the acquisition of new parasites, leading to similar total, enteric and parenteric parasite component community diversity in YOY largemouth bass.

Mollusk Abundances

In general, an increase in numbers of mollusks found in the sampling area in concert with water temperature increasing above 18° (Hoffman, 1958) was parallel with an increase in the number of trematodes found per fish (Figure 7 and 8). Because larval trematodes, which are shed by mollusks and directly penetrate bluegill, numerically dominated the parasite community of juvenile bluegill in GL, mollusk abundance had a large influence on parasite community structure.

In the present study, the decrease in the mean number of larval trematodes per fish in September cannot be directly attributed to concurrent decreases in mollusk abundances. Since metacercarial parasites are thought to be long-lived and accumulate in a fish over time (Spall and Summerfelt, 1970), a decrease in the mollusk abundances only has an effect on recruitment of new parasite individuals (depending on water temperature). Less mollusks may mean there are less larval parasites shed to penetrate fish. Decreases in numbers of trematodes per fish may be attributed to a larger

proportion of younger fish examined in a month since younger fish have lower mean abundances of larval trematodes.

Parasite Community Comparisons Between Gull Lake and Three Lakes II

There were no significant differences in Brillouin's diversity, evenness, species richness or adjusted species richness of parasite infracommunities of juvenile bluegill between GL and TL or of YOY largemouth bass between GL and TL. Additionally, there were no significant differences in total parasite component community diversity of juvenile bluegill or YOY largemouth bass between GL and TL. Esch (1971) suggested that the trophic status of a lake plays a role in the types of parasites harbored by centrarchids. Eutrophic lakes have better quality habitat for piscivorous birds, mammals and reptiles that can serve as definitive hosts for larval parasites hosted by fish (Esch, 1971). Due to the diversity of vertebrates associated with eutrophic lakes, Esch and Fernandez (1993) hypothesized that fish in these lakes should have more allogenic parasite species (parasite species using a terrestrial organism as a definitive host) and lakes with less available nutrients should have more autogenic parasite species (parasite species that use an aquatic organism as a definitive host). Esch (1971) found that adult bluegill and largemouth bass in GL contained 71% and 78% autogenic parasite species, respectively and 29% and 22% allogenic parasite species, respectively, compared to 67% autogenic and 33% allogenic parasite species in largemouth bass from eutrophic Wintergreen Lake. The parasite communities of juvenile bluegill from eutrophic TL contained 64% autogenic parasite species and 36% allogenic species whereas the parasite communities of juvenile bluegill in mesotrophic GL contained 72% autogenic species and 28% allogenic species. Young-of-the-year largemouth bass contained 60% autogenic

and 40% allogenic parasite species in TL and 64% autogenic and 36% allogenic parasite species in GL. Data from the present study agree with the percentages of autogenic and allogenic parasites in GL found by Esch (1971).

Data from the present study support the hypothesis proposed by Wisniewski (1958) and furthered by Esch (1971) that trophic level of the host is an important parasite community determinant. Juvenile bluegill in both lakes hosted similar parasite species and had similar percentages of their community comprised of adult parasites. Since juvenile bluegill are prey items of YOY largemouth bass, largemouth bass are on a higher trophic level than juvenile bluegill. If lake trophic status were more important than host trophic level, parasites of juvenile bluegill and YOY largemouth bass within a lake would be more similar to each other than parasites of the same host species between lakes. Young-of-the-year largemouth bass in both lakes had similar parasite species and had higher percentages of adult parasites in their community than juvenile bluegill from either lake. Additionally, juvenile bluegill are intermediate or paratenic hosts for *Cryptogonimus* sp., *P. ambloplitis*, and *L. thecatus*, all which use largemouth bass as definitive hosts.

The coefficient of community similarity for bluegill and largemouth bass from GL was approximately equal to the coefficient of community similarity for bluegill and largemouth bass from TL. The coefficients of community similarity show that parasite component communities of bluegill from TL, and GL and YOY largemouth bass from TL and GL were more similar to each other than parasite component communities of GL bluegill and largemouth bass and TL bluegill and largemouth bass. The present study suggests that trophic status of a fish host is a more important parasite community

determinant than lake trophic status because the coefficients of community similarity are more similar for the same host species in different lakes than for different host species in the same lake. If lake trophic status were more important than fish trophic status, the total parasite component communities of bluegill and largemouth bass within a lake would have higher coefficients of community similarity than parasite component communities of bluegill between lakes or largemouth bass between lakes.

Summary

Differences in parasite community composition between juvenile and adult bluegill and juvenile and adult largemouth bass in Michigan are a reflection of their diet and habitat. Adult bluegill occupy open water habitats (Werner and Hall, 1988) where they are less vulnerable to penetration by larval trematodes and, via exposure to different intermediate hosts, are also exposed to different parasites than littoral juvenile fish. A greater percentage of the parasites of juvenile bluegill in GL and TL are comprised of larval parasites than in adult bluegill previously studied in Michigan. These findings support the hypothesis that trophic level of the host is the most important determinant of the parasite community in fishes (Wisniewski, 1958; Esch, 1971). Because of their trophic level differences, juvenile bluegill and YOY largemouth bass occupy a different habitat and consume a different diet than adults of these species leading to a parasite fauna unique to their life stage.

CHAPTER THREE

ACQUISITION AND DYNAMICS OF THE PARASITE COMMUNITY IN JUVENILE BLUEGILL, *LEPOMIS MACROCHIRUS*, AND YOUNG-OF-THE-YEAR LARGEMOUTH BASS, *MICROPTERUS SALMOIDES* IN THREE LAKES II AND GULL LAKE, MICHIGAN

INTRODUCTION

The parasite communities of fish are a reflection of the diet and habitat of the fish host (Esch and Fernandez, 1993; Marcogliese, 2004). Habitat attributes such as vegetation type and quantity, and substrate type, play a major role in the parasite intermediate hosts found in an area. Mollusks serving as intermediate hosts for trematode parasites, for example, shed larval parasites that may infect a fish by direct penetration. Habitat also influences diet by determining what prey items (which may be serving as intermediate hosts) are available to a fish. Because parasite communities of fish are largely determined by fish diet and habitat, insights into the ecology and life history of a fish can be gained through examining its parasite fauna (Marcogliese, 2004).

The diet and habitat of bluegill change with age. After hatching approximately two weeks post-spawn (Breder, 1936), bluegill fry undergo a migration to the limnetic zone of a lake and remain there for approximately six to eight weeks (Werner, 1967; Werner and Hall, 1988). These fish then return to the vegetated littoral zone for the next two to three years (Werner and Hall, 1988) until they move to the limnetic zone of the lake for the duration of their life (Werner and Hall, 1988). The shift to the limnetic habitat gradually takes place in bluegill between 45 and 75 mm standard length (SL) (Osenberg et al., 1992). The switch to the limnetic zone of a lake as their primary habitat occurs at approximately 75 mm SL and is approximately commensurate with age of maturity (Osenberg et al., 1992). These changes in the diet and habitat may cause a concurrent shift in the parasite fauna (Wilson et al., 1996; Zelmer and Arai, 2004).

Young-of-the-year (YOY) largemouth bass also undergo diet shifts that may lead to changes in their parasite communities. Young-of-the-year largemouth bass remain in the littoral zone for the first few weeks to months of life feeding on invertebrates (Gilliam, 1982; Olson, 1996; Post, 2003). When they become large enough to eat fish, largemouth bass switch to a diet of piscivory, primarily preying on juvenile bluegill (Gilliam, 1982; Olson, 1996; Post, 2003) and continue to prey on fishes throughout their life. Since largemouth bass eat aquatic invertebrates such as copepods, amphipods and mayflies for the first few weeks to months of life (Sule, 1981; Gilliam, 1982; Fischer and Kelso, 1990; Olson, 1996; Dibble and Harrel, 1997; Post, 2003), they may acquire parasites that use these invertebrates as intermediate hosts. As is the case with juvenile bluegill, while living in the vegetated littoral zone, largemouth bass are vulnerable to colonization by larval trematodes shed by mollusks. Since largemouth bass become piscivorous early in life, primarily eating juvenile bluegill, they may also acquire parasites that use bluegill as intermediate or paratenic hosts. Since invertebrate and bluegill intermediate hosts may be harboring different larval parasites that can infect largemouth bass, the switch to piscivory may cause a shift in parasite communities of largemouth bass.

Many studies have reported on the parasite communities of bluegill (Esch, 1971; McDaniel and Bailey, 1974; Cloutman, 1975; Esch et al., 1976; Jilek and Crites, 1980; Fischer and Kelso, 1990; Fiorillo and Font, 1996; Wilson et al., 1996; Muzzall and Peebles, 1998; Steinauer and Font, 2003; Fellis and Esch, 2004; Bhuthimethee et al., 2005; Fellis and Esch, 2005), yet none of these studies have examined the chronology of parasite infection in bluegill. Only two of these studies have reported on parasite

communities of juvenile bluegill (Fisher and Kelso, 1990; Steinauer and Font, 2003), but neither of them focused on when parasite species initially colonized juvenile bluegill.

The objectives of the present study were to identify fish lengths at which parasite species first infected juvenile bluegill and YOY largemouth bass from Three Lakes II (TL) and Gull Lake (GL), Michigan and to determine if parasite community composition changed with length in juvenile bluegill from TL and GL and YOY largemouth bass from GL; and also to compare colonization of parasites in juvenile bluegill and YOY largemouth bass from TL and GL.

MATERIALS AND METHODS

Description of Study Sites

Study sites from TL and GL are described in Chapters One and Two.

Fish Collection and Examination

Descriptions of fish collections in TL and GL are in Chapters One and Two. Fish in both lakes were examined as described in Chapter One.

Parasite Preparation and Identification

Parasites from fish in both lakes were prepared and identified as described in Chapter One.

Data Analysis

The standard length (SL) of fish at which each parasite species was first acquired was identified for juvenile bluegill and YOY largemouth bass in TL and GL irrespective of fish cohort. Also, percentages of adult helminth parasite species in five mm length classes (arbitrarily determined) of juvenile bluegill and YOY largemouth bass were calculated to determine if parasite community structure changed as fish became older and larger. Adult parasite species in this analysis were *Actinocleidus* sp., *Anchoradiscus* sp., Monogene sp. A, Monogene sp., *Azygia* sp., *Crepidostomum* sp., *Cryptogonimus* sp. adults, *Leptorhynchoides thecatus*, *Neoechinorhynchus cylindratus*, *Pomphorhynchus bulbocolli*, *Camallanus* sp. and *Spinitectus* sp. Because there were no YOY largemouth bass from TL examined in several length classes, percentages of adult parasite species were not calculated for these fish.

RESULTS

The standard lengths (SL) at which TL and GL juvenile bluegill first acquired parasite species are in Figures 10 and 11. Numbers of juvenile bluegill in TL and GL examined in each length interval are in Appendices II and III. Larval trematodes such as *Cryptogonimus* sp. metacercariae and *Posthodiplostomum minimum*, the two most prevalent and abundant parasite species of juvenile bluegill (Tables 1 and 14), were the first parasites to colonize juvenile bluegill in both lakes. *Cryptogonimus* sp. was found in the smallest bluegill examined in each lake. *Proteocephalus ambloplitis* was the first parasite acquired through ingestion to colonize bluegill in TL. *Pomphorhynchus bulbocolli* was the first parasite acquired by ingestion by GL bluegill. Monogenes and protozoans did not appear to have any colonization patterns with length of juvenile bluegill in either lake.

The standard lengths at which TL and GL YOY largemouth bass first acquired parasite species are in Figures 12 and 13. Numbers of YOY largemouth bass in TL and GL examined in each length interval are in Appendix IV and V. *Cryptogonimus* sp. metacercariae, Monogene sp., *Cryptogonimus* sp. adults and *Proteocephalus ambloplitis* were the first species to colonize YOY largemouth bass from TL and were found in the smallest largemouth bass examined in TL. *Cryptogonimus* sp. metacercariae, *Trichodina* sp. and *Camallanus* sp. were the first species to colonize YOY largemouth bass from GL and were found in the smallest largemouth bass examined from GL. Monogenes and protozoans did not appear to have any colonization patterns with length of YOY largemouth bass from either lake.

The percentages of adult parasite species from TL and GL juvenile bluegill in five mm length classes are in Figures 14 and 15. No adult parasite species were found in the smallest length class (15-19 mm) of TL or GL juvenile bluegill. The percentage of adult parasite species in the parasite community generally increased with increased length of TL and GL juvenile bluegill.

Overall, 56% of parasite species from GL YOY largemouth bass were adults. The percentages of adult parasite species from GL YOY largemouth bass in five mm length classes are in Figure 16. The percentage of adult parasite species varied between 56-72% and did not show a general trend with increasing fish length.

DISCUSSION

Cryptogonimus sp. metacercariae were found in the smallest juvenile bluegill and YOY largemouth bass in TL and GL. Juvenile bluegill and YOY largemouth live in vegetated habitats with mollusks that shed trematode cercariae that can infect fish through penetration. Because larval trematodes, such as *Cryptogonimus* sp. metacercariae, are acquired passively by fish, it is not surprising that a larval trematode is among the first parasites acquired in both species of fish in both lakes. Since bluegill and largemouth bass in the present study had such high mean abundances of *Cryptogonimus* sp. metacercariae (Tables 2, 5, 14 and 15) there are likely a large number of cercariae in the environment. This large number of cercariae would increase the likelihood that even a very young and small fish would become infected with this parasite. Also, small fish have limited gape size and would not be able to eat the intermediate hosts for many of the adult parasite species found in the present study.

In general, for both fish species examined in TL and GL in the present study, parasites acquired via ingestion using the same intermediate host group are recruited within a narrow range of fish lengths. For example, in TL juvenile bluegill, all parasites using copepods as intermediate hosts (*Proteocephalus ambloplitis*, *Camallanus* sp., *Spiroxys* sp. and *Haplobothrium globuliforme*) were acquired between 17 and 23 mm. Parasites using larger intermediate hosts, such as *Spinitectus* sp. which likely uses a mayfly (Hoffman, 1999), are not recruited by bluegill until they reach larger lengths and have a larger gape size. In GL, the parasite species *P. ambloplitis* and *H. globuliforme*, are first acquired by juvenile bluegill between 28-30 mm SL.

The exception to recruitment of parasite species that use the same intermediate host group in a narrow range of lengths was *P. bulbocolli* in GL juvenile bluegill. *Pomphorhynchus bulbocolli* uses an amphipod intermediate host and was first acquired by bluegill in GL at 20 mm SL, but *Leptorhynchoides thecatus* which also uses an amphipod intermediate host was not first recruited until 32 mm SL. Esch et al. (1976) suggested that midges may be serving as intermediate hosts for this parasite in GL after examination of 6,000 amphipods in GL, none of which were infected with *P. bulbocolli*. However, there are no reports of midges hosting *P. bulbocolli* or other acanthocephalan species. The amphipod intermediate host of this parasite would be a large prey item for a 20mm bluegill, so it may be that *P. bulbocolli* is not using amphipods as intermediate hosts in GL. The notion of Esch et al. (1976) that amphipods may not serve as intermediate hosts for *P. bulbocolli* in GL is also supported by the recruitment data from TL bluegill. In TL bluegill, *P. bulbocolli*, the only parasite of TL bluegill using an amphipod intermediate host, is not first recruited by these fish until 32 mm SL. With the exception of *P. bulbocolli* in GL bluegill, parasites using amphipods as intermediate hosts are not acquired by bluegill until 32 mm SL.

In largemouth bass, the same general pattern exists that most of the parasites sharing the same intermediate host are recruited within a narrow range of lengths. In GL largemouth bass, both parasite species that use copepods as intermediate hosts, *Camallanus* sp. and *P. ambloplitis*, were recruited at 21 and 22 mm SL, respectively. In TL largemouth bass, two of the parasites using copepods as intermediate hosts, *Spiroxys* sp. and *Camallanus* sp were first recruited at 40 mm SL. However, *P. ambloplitis*, which also uses a copepod intermediate host, is first recruited by TL largemouth bass at 19 mm

SL. The sample size of fish in TL examined between 23 and 37 mm was small (n=11). *Spiroxys* sp. and *Camallanus* sp., which were infrequent parasites (Table 2), could have been recruited at smaller fish lengths, but they were not found due to small numbers of fish examined and low prevalence.

YOY largemouth bass have a higher percentage of adult parasite species than age 0 bluegill in either lake. By the end of the 2003 sampling year the mean length of age 0 bluegill is approximately 22 mm SL in TL and 26 mm SL in GL. Bluegill of this length have acquired eight parasite species in TL and four parasite species in GL, whereas YOY largemouth bass have acquired 16 parasite species in TL and 14 parasite species in GL. Since YOY largemouth bass have a larger gape size than bluegill, they are able to eat a wider variety of prey items that may be serving as parasite intermediate hosts.

In bluegill from TL and GL, percentages of the parasite community made up of adult parasite species generally increased with fish length. As juvenile bluegill begin to spend more time foraging in the limnetic zone of a lake, and their diet and habitat usage becomes more like that of adult bluegill, their parasite communities also become more similar to parasite communities of adult bluegill. Muzzall and Peebles (1998) reported adult parasite species comprised 69% of the adult bluegill parasite species from Michigan. As juvenile bluegill increased in length in the present study, the percentage of adult parasite species in the parasite community increased, but did not reach 69%. Osenberg et al. (1992) stated that juvenile bluegill approximately 45-75 mm in SL use both littoral and limnetic habitats. As juvenile bluegill spend an increasing amount of time foraging in the limnetic habitat, their percentage of adult parasite species may approach 69%, as in adult bluegill reported in Michigan (Muzzall and Peebles, 1998).

Gilliam (1982) reported that bluegill between 0-25 mm SL occupy a different position in the water column and are found different distances from shore than bluegill between 26-50 mm. Some of this habitat difference is attributed to larval bluegill living in the limnetic zone of the lake until they are approximately 12-14 mm SL (Werner, 1967; Werner and Hall, 1988). Data from the present study suggest that there may also be a slight habitat shift occurring in bluegill between 20 and 24 mm. In the 15-19 mm length class, bluegill have no adult parasites and between 20 and 24 mm, bluegill begin to acquire adult parasites. Since parasites are a reflection of the diet and habitat of a fish, it can be inferred that bluegill undergo a habitat and/or diet shift in this length range due to the dramatic shift in the percentage of adult parasite species in the parasite community of juvenile bluegill in TL and GL. However, *Azygia* sp. and *Camallanus* sp. are infrequent parasites (Tables 1 and 14). Since 11 bluegill were examined between 15-19 mm SL in TL and only one bluegill was examined within this length range in GL, it may be that bluegill between 15-19 mm SL had acquired these parasites, but they were not found due to small numbers of fish examined and low prevalences of these parasites. If adult parasites of these species had been acquired by juvenile bluegill between 15-19 mm SL, then the acquisition of adult parasites may be reflective of the return to the littoral areas of the lake from the open water (Werner, 1967; Werner and Hall, 1988).

Percentages of adult parasite species of GL YOY largemouth bass do not appear to have any visible trends with length. Until largemouth bass begin eating fish, their diet consists of invertebrates. Some of the invertebrates largemouth bass prey on serve as intermediate hosts for parasites that use largemouth bass as definitive hosts. Even though GL YOY largemouth bass are acquiring adult parasites through ingestion, they are still

vulnerable to penetration by trematode cercariae and their percentage of adult parasites fluctuates as these fish become longer. The majority of the diet of YOY largemouth bass consists of invertebrates until they are approximately 50 mm SL (Olson, 1996). Once a majority of the diet of YOY largemouth bass consists of fish (which may be serving as parasite intermediate hosts), there may be a shift to a larger percentage of the parasite species in the community being comprised of adults. Esch (1971) reported 83% of the parasite species of adult largemouth bass in GL as adults. In the present study, 10 fish were examined with lengths greater than 50 mm with 62% of their parasite species comprised of adults. Because YOY largemouth bass that have not switched to piscivory do not have the same diet and habitat as adults, the parasite communities of YOY largemouth bass may have less adult parasite species than adult largemouth bass.

Summary

The parasites hosted by a fish are a reflection of the diet and habitat of the fish host. Larval trematodes, particularly *Cryptogonimus* sp., are among the first parasites to colonize juvenile bluegill and YOY largemouth bass in TL and GL. The vegetated littoral habitat of these fish is home to many species of mollusks shedding cercariae that are passively acquired by fish. Because the diets and habitats of juvenile bluegill and YOY largemouth bass change over time, new parasites are acquired by these fish. In bluegill in TL and GL, the percentage of adult parasite species generally increases with increasing length. In YOY largemouth bass from GL, the percentage of the parasite community consisting of adult parasites generally does not increase with length and was lower than the percentage of adult parasites in piscivorous adult largemouth bass, which

may suggest that all YOY largemouth bass examined from GL had not switched to piscivory.

CONCLUSION

There are several similarities between parasite communities of TL and GL bluegill and between TL and GL bass that help to extend our general knowledge of parasite communities of juvenile centrarchid fishes. Fish species generally hosted the same parasite species between lakes and the most abundant parasites in each fish species in both lakes were larval trematodes. Prior studies in other areas of the United States have also shown larval trematodes to dominate the parasite fauna of juvenile centrarchid fishes (Fischer and Kelso, 1987, 1988, 1990; Landry and Kelso 1999; Steinauer and Font, 2003). In some of these studies, including the present study, larval parasites, particularly larval trematodes, have been implicated as potential causes of parasite-induced host mortality. This suggests that larval trematodes can be a major selective pressure influencing the survival of juvenile bluegill.

The trophic status of the lake in which a fish resides and the trophic status of the host are important determining factors of the parasite communities of juvenile bluegill and YOY largemouth bass. Data from the present study were in agreement with the percentage of autogenic and allogenic parasite species found in adult bluegill and largemouth bass in GL reported by Esch (1971). However, in the present study, juvenile bluegill parasite communities were more similar between lakes than juvenile bluegill and YOY largemouth bass within a lake. This suggests that trophic status of the host is a more important determining factor of the parasite community than the lake trophic status.

Fish habitat and diet are the major determinants of parasite communities. Because parasite communities are structured as functions of fish diet and habitat, our

knowledge of the diet and habitat of these fishes can be reinforced through surveying their parasite fauna. As juvenile bluegill in both lakes became longer and older, adult parasite species made up a greater percentage of the parasite community. Furthermore, juvenile bluegill and YOY largemouth bass acquired new penetrating larval trematode species and new parasite species with direct life cycles. This suggests that as juvenile bluegill and YOY largemouth bass age, their diet and/ or habitat change. This knowledge inferred from the parasite data in the present study corroborates with diet and habitat changes in juvenile bluegill and YOY largemouth bass documented by Gilliam (1982); Werner and Hall (1988); Osenberg et al. (1992), Olson (1993) and Post (2003).

Table 1. Prevalence, mean abundance ± SD (maximum) and site of infection of parasites of 393 juvenile *Lepomis macrochirus* in 2003 and 2004 from Three Lakes II, Michigan.

	2003	2004	Site of Infection
	n=209	n=184	
Monogenea			
Actinocleidus sp.	1%†	5%	Gills
	–	–	
	–	–	
Anchoradiscus sp.	2%	5%	Gills
	–	–	
	–	–	
Monogene sp.	9%	1%	Gills
	–	–	
	–	–	
Trematoda			
Azygia sp.	11%	4%	Stomach, Pyloric Ceca, Intestine
	0.2 ± 1.0‡	<0.1 ± 0.2	
	(7)	(1)	
Clinostomum sp.*	<1%	0%	Muscle
	<0.1 ± 0.1	–	
	(1)	–	
Crepidostomum sp.	0%	1%	Ceca
	–	0.1 ± 0.9	
	–	(12)	
Cryptogonimus sp.*	>99%	>99%	Muscle, Brain, Gills, Mesenteries
	244.2 ± 354.2	84.4 ± 150.3	
	(2387)	(1563)	
Diplostomum sp.*	12%	11%	Vitreous Humor
	0.3 ± 1.2	0.2 ± 0.8	
	(9)	(6)	
Neascus sp.*	50%	29%	Muscle, Mesenteries, Kidney
	3.3 ± 9.3	1.3 ± 3.3	
	(114)	(28)	
*Posthodiplostomum minimum**	62%	73%	Liver, Kidney Mesenteries, Gonad
	11.8 ± 15.8	3.8 ± 7.0	
	(93)	(57)	
Cestoda			
*Haplobothrium globuliforme**	7%	7%	Liver, Mesenteries, Gills
	0.1 ± 0.5	0.1 ± 0.3	
	(6)	(2)	

Table 1.

*Proteocephalus ambloplitis**	52% 0.9 ± 1.7 (13)	32% 0.6 ± 1.2 (9)	Liver, Mesenteries
Nematoda			
Camallanus sp.	<1% <0.1 ± 0.2 (1)	2% <0.1 ± 0.1 (1)	Intestine
Spinitectus sp.	17% 0.6 ± 1.8 (14)	11% 0.4 ± 1.3 (8)	Intestine
Spiroxys sp.*	4% <0.1 ± 0.3 (2)	1% <0.1± 0.1 (1)	Muscle
Acanthocephala			
Pomphorhynchus bulbocolli	<1% <0.1 ± 0.2 (2)	2% <0.1± 0.2 (2)	Liver
*Neoechinorhynchus cylindratus**	1% <0.1 ± 0.3 (5)	2% <0.1± 0.1 (1)	Intestine
Protozoa			
Myxobolus sp.	8% -- --	4% -- --	Gills
Trichodina sp.	6% -- --	10% -- --	Gills

Table 1 (con't).

* Indicates larval parasite.

† Parasite prevalence.

‡ Parasite mean abundance ± SD (maximum).

*Proteocephalus amboplitis**	52% 0.9 ± 1.7 (13)	32% 0.6 ± 1.2 (9)	Liver, Mesenteries
Nematoda			
Camallanus sp.	<1% <0.1 ± 0.2 (1)	2% <0.1 ± 0.1 (1)	Intestine
Spinitectus sp.	17% 0.6 ± 1.8 (14)	11% 0.4 ± 1.3 (8)	Intestine
Spiroxys sp.*	4% <0.1 ± 0.3 (2)	1% <0.1± 0.1 (1)	Muscle
Acanthocephala			
Pomphorhynchus bulbocolli	<1% <0.1 ± 0.2 (2)	2% <0.1± 0.2 (2)	Liver
*Neoechinorhynchus cylindratus**	1% <0.1 ± 0.3 (5)	2% <0.1± 0.1 (1)	Intestine
Protozoa			
Myxobolus sp.	8% – –	4% – –	Gills
Trichodina sp.	6% – –	10% – –	Gills

Table 1 (con't).

* Indicates larval parasite.

† Parasite prevalence.

‡ Parasite mean abundance ± SD (maximum).

Table 2. Prevalence (%), mean abundance ± SD (maximum) and site of infection of parasites of 26 young-of-the-year *Micropterus salmoides* from Three Lakes II, Michigan.

Parasite		Site of Infection
Monogenea		
Monogene sp. A	7%†	Gills
	--	
	--	
Monogenea sp.	42%	Gills
	--	
	--	
Trematoda		
Azygia sp.	15%	Stomach, Pyloric
	0.2 ± 0.5‡	Ceca, Intestine
	(2)	
Cryptogonimus sp.	4%	Stomach, Pyloric
	0.2 ± 0.6	Ceca, Intestine
	(3)	
Cryptogonimus sp.*	85%	Muscle, Cartilage,
	34.2 ± 55.1	Brain, Gills,
	(249)	Mesenteries
Diplostomum sp.*	35%	Vitreous Humor
	0.6 ± 1.0	
	(4)	
Neascus sp.*	50%	Muscle,
	2.4 ± 5.3	Mesenteries,
	(26)	Kidney
*Posthodiplostomum minimum**	38%	Liver, Kidney,
	1.0 ± 1.6	Cartilage, Gills,
	(6)	Mesenteries
Cestoda		
*Proteocephalus ambloplitis**	88%	Liver, Mesenteries,
	4.3 ± 2.9	Gonad
	(11)	
Nematoda		
Camallanus sp.	4%	Intestine, Pyloric
	0.1 ± 0.2	Ceca, Stomach
	(1)	

Table 2.

Spiroxys sp.*	4% 0.1 ± 0.3 (1)	Muscle
Acanthocephala		
Neoechinorhynchus cylindratus	35% 1.4 ± 4.1 (20)	Intestine
Pomphorhynchus bulbocolli	8% 0.1 ± 0.3 (1)	Intestine, Mesenteries, Muscle
Protozoa		
Trichodina sp.	8% -- --	Gills

Table 2 (con't).

* Indicates larval stage.

† Parasite prevalence.

‡ Parasite mean abundance ± SD (maximum).

Cohort	N	*Cryptogonimus* sp.	*Neascus* sp.	*Posthodiplostomum minimum*	*Proteocephalus ambloplitis*
2001		98%*	73%	95%	68%
	66	470.7 ± 489.9†	4.8 ± 6.9	18.2 ± 22.2	1.4 ± 1.9
		(2387)	(29)	(93)	(12)
2002		100%	62%	98%	55%
	91	265.5 ± 249.8	4.6 ± 12.6	14.6 ± 13.2	1.4 ± 2.1
		(1563)	(114)	(57)	(13)
2003		>99%	24%	72%	26%
	235	48.0 ± 71.3	0.8 ± 2.6	2.7 ± 3.0	0.3 ± 0.8
		(474)	(28)	(19)	(4)

* Parasite prevalence.

† Mean ± SD (maximum).

Table 3. Prevalence and mean abundance ± SD (maximum) of parasites of juvenile *Lepomis macrochirus* with greater than 30% overall prevalence by cohort from Three Lakes II, Michigan.

Month	N	*Cryptogonimus* sp.	*Neascus* sp.	*Posthodiplostomum minimum*	*Proteocephalus ambloplitis*
June, 2003	19	94%*	22%	89%	72%
		106.9 ± 116.7†	0.7 ± 1.8	8.1 ± 13.2	1.5 ± 1.4
		a‡	a	a	a
July	12	100%	70%	90%	60%
		602.8± 525.0	2.5 ± 2.9	7.0 ± 5.4	1.3 ± 1.6
		b	ab	a	a
August	20	100%	83%	100%	67%
		742.7± 597.2	4.4 ± 5.1	12.2 ± 14.8	1.7 ± 2.7
		b	b	a	a
September	9	100%	100%	100%	80%
		381.2± 182.7	9.1 ± 8.9	44.6 ± 23.6	1.0 ± 1.0
		b	b	b	a
October	6	100%	100%	100%	33%
		586.3± 430.5	17.8 ± 7.4	53.0 ± 21.8	0.7 ± 1.2
		b	c	b	a

* Parasite prevalence.

† Parasite mean abundance ± SD (maximum).

‡ Mean abundances followed by the same letter within the same column are not significantly different from each other.

Table 4. Monthly prevalence, mean abundance ± SD of parasites with greater than 30% overall prevalence from the 2001 cohort of *Lepomis macrochirus* from Three Lakes II, Michigan.

Table 5. **Monthly prevalence, mean abundance± SD of parasites with greater than 30% overall prevalence from the 2002 cohort of *Lepomis macrochirus* from Three Lakes II, Michigan.**

Month	N	*Cryptogonimus* sp.	*Neascus* sp.	*Posthodiplostomum minimum*	*Proteocephalus ambloplitis*
June, 2003	11	100%*	17%	100%	67%
		81.45 ± 64.6†	0.7± 1.8	4.8 ± 4.6	0.8 ± 0.9
		a‡	a	a	a
July	3	100%	40%	100%	80%
		441.0 ± 48.8	1.3± 1.2	6.3 ± 1.5	1.0 ± 1.0
		b	ab	abc	a
August	12	100%	58%	100%	67%
		257.2 ± 118.9	1.6± 1.7	6.8 ± 6.6	1.9 ± 1.4
		b	ab	a	a
September	21	100%	76%	100%	80%
		312.0 ± 206.0	8.5± 24.4	18.1 ± 11.7	1.3 ± 3.1
		b	ab	bc	a
October	16	100%	81%	100%	33%
		336.9 ± 345.6	7.4 ± 7.4	27.9 ± 10.4	1.3 ± 1.6
		b	b	c	a
April, 2004	3	100%	100%	100%	100%
		216.0 ± 165.0	8.7 ± 9.3	21.7 ± 9.1	2.0 ± 1.0
		ab	ab	abc	a
May	4	100%	100%	100%	25%
		452.8 ± 741.7	3.5 ± 2.4	31.0 ± 25.5	0.5 ± 1.0
		ab	ab	abc	a
June	4	100%	25%	75%	50%
		58.0 ± 119.0	0.3 ± 0.5	10.5 ± 10.7	3.5 ± 4.4
		ab	ab	ab	a
July	17	100%	65%	94%	47%
		224.6 ± 115.3	2.8 ± 3.4	6.7 ± 6.2	1.2 ± 1.6
		b	ab	a	a

Table 5.

* Parasite prevalence.

† Parasite mean abundance ± SD (maximum).

‡ Mean abundances followed by the same letter within the same column are not significantly different from each other.

Table 6. Monthly prevalence, mean abundance± SD of parasites with greater than 30% overall prevalence from the 2003 cohort of *Lepomis macrochirus* from Three Lakes II, Michigan.

Month	N	*Cryptogonimus* sp.	*Neascus* sp.	*Posthodiplostomum minimum*	*Proteocephalus ambloplitis*
June, 2003	2	100%* 26.0 ± 14.1† abcd‡	50% 0.5 ± 0.7 a	100% 5.5 ± 3.5 b	50% 0.5 ± 0.7 a
July	0	--√	--	--	--
August	5	100% 4.8 ± 3.4 a	29% 0 a	0% 0 a	20% 0.2 ± 0.4 a
September	35	100% 28.8 ± 15.0 cd	26% 0.4 ± 0.8 a	89% 2.7 ± 2.1 bc	23% 0.3 ± 0.5 a
October	38	100% 42.9 ± 41.7 cd	67% 0.8 ± 2.2 a	100% 4.6 ± 3.2 c	11% 0.1 ± 0.4 a
April, 2004	13	100% 20.8 ± 13.7 bc	38% 0.5 ± 0.8 a	85% 4.9 ± 5.4 bc	31% 0.8 ± 1.5 a
May	55	98% 11.9 ± 8.6 ab	13% 0.4 ± 1.3 a	62% 1.6 ± 2.1 ab	31% 0.4 ± 0.7 a
June	65	100% 44.18 ± 27.6 d	8% 0.2 ± 0.6 a	62% 1.7 ± 2.3 ab	31% 0.4 ± 0.6 a
July	23	100% 209.47 ± 129.5 e	78% 5.1 ± 6.1 b	78% 3.9 ± 3.2 c	47% 0.3 ± 0.9 a

Table 6.

* Parasite prevalence.

† Parasite mean abundance ± SD.

‡ Means followed by the same letter within the same column are not significantly different from each other.

√ Indicates no fish were examined.

Month	*Cryptogonimus* sp.	*Neascus* sp.	*Posthodiplostomum minimum*	*Proteocephalus ambloplitis*
June, 2003	51.26	22.8	12.53	2.05
July	5.39	0.25	0.59	3.33
August	164.98	1.90	6.37	1.09
September	382.74	69.95	7.55	7.29
October	354.41	7.99	3.89	2.01
April, 2004	126.10	9.96	3.80	0.50
May	1215.17	1.62	26.53	2.00
June	89.65	0.34	13.93	12.93
July	59.21	4.04	5.67	2.03

Table 7. Variance to mean abundance ratio for the most common parasites (parasites with >30% prevalence overall) for the 2002 cohort of *Lepomis macrochirus* from Three Lakes II, Michigan by month.

Month	*Cryptogonimus* sp.	*Neascus* sp.	*Posthodiplostomum minimum*	*Proteocephalus ambloplitis*
June, 2003	7.69	1.0	2.27	1.00
July	*	*	*	*
August	2.44	†	†	1.00
September	7.81	1.59	1.66	1.00
October	38.00	5.95	2.20	1.31
April, 2004	8.99	1.11	5.89	2.60
May	6.22	4.56	2.72	1.08
June	14.80	2.13	3.14	0.97
July	80.00	0.25	0.17	0.60

* Indicates no fish examined.

† Indicates no fish infected.

Table 8. Variance to mean abundance ratio for the most common parasites (parasites with >30% prevalence overall) for the 2003 cohort of *Lepomis macrochirus* from Three Lakes II, Michigan by month.

	2003	2004
Brillouin's diversity	0.16 ± 0.13 (0-0.97)	0.12 ± 0.10 (0-0.44)
Brillouin's evenness	0.30 ± 0.20 (0-1.00)	0.28 ± 0.24 (0-1.00)
Species Richness	3.7 ± 1.5 (1-9)	2.9 ± 1.5 (1-8)
Adjusted Species Richness	3.4 ± 1.3 (1-7)	2.7 ± 1.3 (1-6)

Table 9. Mean ± SD (range) of Brillouin's diversity and evenness and species richness and adjusted species richness for parasite infracommunities of *Lepomis macrochirus* from Three Lakes II, Michigan.

Cohort	Brillouin's Diversity	Brillouin's Evenness	Species Richness	Adjusted Species Richness
2001	0.15 ± 0.14 (0-0.97)	0.25 ± 0.19 (0-0.70)	4.5 ± 1.6 (1-9)	4.0 ± 1.3 (1-7)
2002	0.17 ± 0.14 (0-0.90)	0.28 ± 0.19 (0-1)	4.4 ± 1.3 (1-7)	4.0 ± 1.2 (1-7)
2003	0.13 ± 0.10 (0-0.44)	0.31 ± 0.23 (0-1)	2.6 ± 1.2 (1-8)	2.5 ± 1.1 (1-5)

Table 10. Mean ± SD (range) of Brillouin's diversity and evenness and species richness and adjusted species richness for parasite infracommunities of juvenile *Lepomis macrochirus* from Three Lakes II, Michigan by cohort.

	Brillouin's Diversity	Brillouin's Evenness	Species Richness	Adjusted Species Richness
June, 2003	0.21 ± 0.20* b†	0.34 ± 0.21 b	3.6 ± 1.2 a	3.0 ± 0.8 a
July	0.07 ± 0.07 a	0.08 ± 0.01 a	4.3 ± 1.6 a	3.8 ± 1.3 ab
August	0.11 ± 0.10 ab	0.16 ± 0.16 a	5.9 ± 1.3 b	5.1 ± 1.1 b
September	0.19 ± 0.06 b	0.35 ± 0.13 b	3.8 ± 0.7 a	3.8 ± 0.7 ab
October	0.22 ± 0.12 b	0.38 ± 0.20 b	4.2 ± 1.5 ab	4.0 ± 1.1 ab

* Mean ± SD.

† Means followed by the same letter within the same column are not significantly different from each other.

Table 11. Mean ± SD of Brillouin's diversity and evenness and species richness and adjusted species richness for parasite infracommunities of for the 2001 cohort of juvenile *Lepomis macrochirus* from Three Lakes II, Michigan by month.

	Brillouin's Diversity	Brillouin's Evenness	Species Richness	Adjusted Species Richness
June, 2003	0.21 ± 0.19* a†	0.38 ± 0.27 a	3.3 ± 1.2 ab	3.0 ± 0.8 a
July	0.04 ± 0.01 a	0.08 ± 0.01 a	3.7 ± 0.6 abc	3.3 ± 0.6 ab
August	0.11 ± 0.06 a	0.18 ± 0.10 a	4.8 ± 1.1 abc	4.3 ± 0.9 ab
September	0.20 ± 0.19 a	0.29 ± 0.18 a	4.4 ± 1.4 abc	4.1 ± 1.4 ab
October	0.21 ± 0.09 a	0.25 ± 0.14 a	4.4 ± 1.1 abc	4.1 ± 1.0 ab
April, 2004	0.27 ± 0.01 a	0.36 ± 0.13 a	5.6 ± 0.6 bc	5.6 ± 0.6 b
May	0.22 ± 0.14 a	0.39 ± 0.28 a	4.3 ± 1.9 abc	4.0 ± 1.4 ab
June	0.12 ± 0.08 a	0.27 ± 0.22 a	3.0 ± 1.4 a	3.0 ± 1.4 a
July	0.12 ± 0.07 a	0.21 ± 0.15 a	5.1 ± 1.0 c	4.2 ± 0.8 ab

* Mean ± SD.

† Means followed by the same letter within the same column are not significantly different from each other.

Table 12. Mean ± SD of Brillouin's diversity and evenness and species richness and adjusted species richness for parasite infracommunities of for the 2002 cohort of juvenile *Lepomis macrochirus* from Three Lakes II, Michigan by month.

	Brillouin's Diversity	Brillouin's Evenness	Species Richness	Adjusted Species Richness
June, 2003	0.22 ± 0.16* ab†	0.45 ± 0.17 ab	3.0 ± 1.4 ab	3.0 ± 1.4 abc
July	--‡	--	--	--
August	0.03 ± 0.07 a	0.04 ± 0.09 a	1.8 ± 0.4 a	1.2 ± 0.4 a
September	0.14 ± 0.06 b	0.37 ± 0.18 b	2.7 ± 0.8 a	2.5 ± 0.7 b
October	0.16 ± 0.09 b	0.39 ± 0.21 b	2.7 ± 1.1 a	2.7 ± 1.1 bc
April, 2004	0.20 ± 0.11 b	0.46 ± 0.24 b	2.8 ± 1.2 a	2.8 ± 1.2 bc
May	0.14 ± 0.11 b	0.40 ± 0.30 b	2.3 ± 1.0 a	2.2 ± 1.0 ab
June	0.08 ± 0.08 a	0.19 ± 0.15 a	2.3 ± 1.0 ab	2.2 ± 0.9 b
July	0.11 ± 0.07 ab	0.20 ± 0.12 ab	4.3 ± 1.4 b	3.6 ± 1.0 c

* Mean ± SD.

† Means followed by the same letter within the same column are not significantly different from each other.

‡ Indicates no fish were examined

Table 13. Mean ± SD of Brillouin's diversity and evenness and species richness and adjusted species richness for parasite infracommunities of for the 2003 cohort of juvenile *Lepomis macrochirus* from Three Lakes II, Michigan by month.

Table 14. Prevalence, mean abundance ± SD (maximum) and site of infection of parasites of 117 juvenile *Lepomis macrochirus* from Gull Lake, Michigan by year.

Parasite	Sampling Year 2003 n=54	2004 n=65	Site of Infection
Actinocleidus sp.	4% †	3%	Gills
	--	--	
	--	--	
Anchoradiscus sp.	2%	6%	Gills
	--	--	
	--	--	
Monogenea sp.	0%	2%	Gills
	--	--	
	--	--	
Trematoda			
Azygia sp.	0%	6%	Stomach, Ceca,
	--	0.1 ± 0.2	Intestine
	--	(1)	
Cryptogonimus sp.*	93%	100%	Muscle, Cartilage,
	50.2 ± 50.3‡	45.0 ± 42.2	Brain, Gills,
	(216)	(214)	Mesenteries
Diplostomum sp.*	4%	74%	Vitreous Humor
	<0.1 ± 0.1	3.7 ± 5.2	
	(1)	(29)	
Neascus sp.*	13%	22%	Muscle,
	0.3 ± 1.3	0.8 ± 2.1	Mesenteries, Kidney
	(9)	(12)	
*Posthodiplostomum minimum**	33%	80%	Liver, Kidney,
	0.8 ± 2.6	2.6 ± 2.5	Cartilage, Gills,
	(19)	(11)	Mesenteries, Gonad
Cestoda			
*Proteocephalus ambloplitis**	2%	6%	Liver, Mesenteries,
	<0.1 ± 0.1	0.1 ± 0.2	Gills
	(1)	(1)	

Table 14.

*Haplobothrium globuliforme**	0% -- --	2% <0.1 ± 0.1 (1)	Liver, Mesenteries
Nematoda			
Spinitectus sp.	22% 0.5 ± 1.3 (7)	20% 0.2 ± 0.5 (2)	Intestine
Acanthocephala			
Leptorhynchoides thecatus	4% <0.1 ± 0.2 (1)	14% <0.1 ± 0.2 (1)	Intestine
*Leptorhynchoides thecatus**	6% 0.1 ± 0.4 (2)	28% 0.1 ± 0.3 (1)	Liver, Mesenteries
*Neoechinorhynchus cylindratus**	2% <0.1 ± 0.1 (1)	1% <0.1 ± 0.1 (1)	Liver
Pomphorhynchus bulbocolli	67% 1.6 ± 1.6 (5)	20% 0.2 ± 0.6 (3)	Intestine
Protozoa			
Myxobolus sp.	4% -- --	2% -- --	Gills
Trichodina sp.	2% -- --	2% -- --	Gills

Table 14 (con't).

* Larval or immature stage

† Prevalence

‡ Mean abundance ± SD (maximum)

Table 15. Prevalence, mean abundance ± SD (maximum) and site of infection of parasites of 86 juvenile *Micropterus salmoides* from Gull Lake, Michigan.

Parasite		Site of Infection
Monogenea		
Monogene sp. A	1%†	Gills
	--	
	--	
Monogenea sp.	9%	Gills
	--	
	--	
Trematoda		
Azygia sp.	17%	Stomach, Ceca,
	0.4±1.4‡	Intestine
	(10)	
Clinostomum sp.*	1%	
	>0.1± 0.1	
	(1)	
Cryptogonimus sp.	33%	Stomach, Ceca,
	11.4± 39.1	Intestine
	(281)	
Cryptogonimus sp.*	83%	Muscle, Cartilage,
	16.0± 28.0	Brain, Gills,
	(136)	Mesenteries
Diplostomum sp.*	3%	Vitreous Humor
	>0.1± 0.2	
	(1)	
Neascus sp.*	7%	Muscle,
	0.3± 1.8	Mesenteries,
	(16)	Kidney
Posthodiplostomum	7%	Liver, Kidney,
*minimum**	0.1± 0.3	Cartilage, Gills,
	(1)	Mesenteries
Cestoda		
Proteocephalus	6%	Liver, Mesenteries,
*ambloplitis**	0.1± 0.4	Gonad
	(2)	

Table 15.

Nematoda		
Camallanus sp.*	47% 2.7± 5.1 (26)	Intestine, Ceca, Stomach
Spinitectus sp.	10% 0.4± 2.1 (18)	Intestine, Ceca, Stomach
Acanthocephala		
Leptorhynchoides thecatus	19% 0.4± 1.3 (10)	Intestine
*Leptorhynchoides thecatus**	27% 0.5± 1.3 (10)	Mesenteries, Liver
Neoechinorhynchus cylindratus	13% 0.2± 0.6 (3)	Intestine
Pomphorhynchus bulbocolli	72% 5.8± 6.9 (28)	Intestine, Mesenteries, Muscle
Protozoa		
Myxobolus sp.	6.9% -- --	Gills
Trichodina sp.	17.4% -- --	Gills

Table 15 (con't).

* Indicates larval stage

† Prevalence

‡ Mean abundance ± SD (maximum)

	Sampling Year	
	2003	2004
Brillouin's diversity	0.10 ± 0.09 (0-0.296)	0.20 ± 0.12 (0-0.46)
Brillouin's evenness	0.25 ± 0.23 (0-0.90)	0.39 ± 0.21 (0-0.84)
Species Richness	2.5 ± 1.1 (0-5)	3.6 ± 1.2 (1-7)
Adjusted Species Richness	2.4 ± 1.0 (0-5)	3.5 ± 1.2 (1-7)

Table 16. Mean ± SD (range) of Brillouin's diversity and evenness and species richness and adjusted species richness for parasite infracommunities of juvenile *Lepomis macrochirus* from Gull Lake, Michigan from the 2003 and 2004 sampling years.

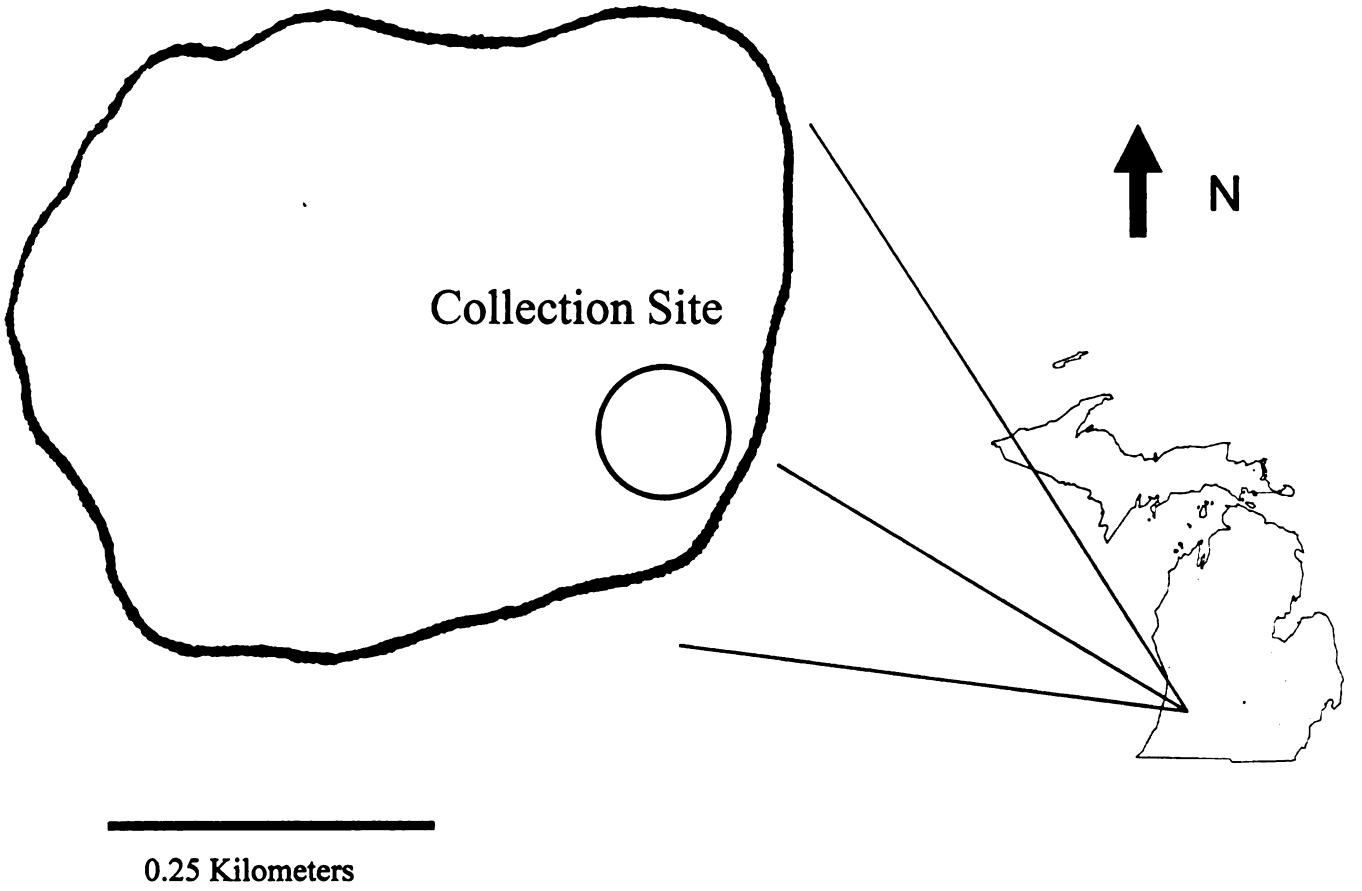


Figure 1. Map of Three Lakes II, Michigan with collection site.

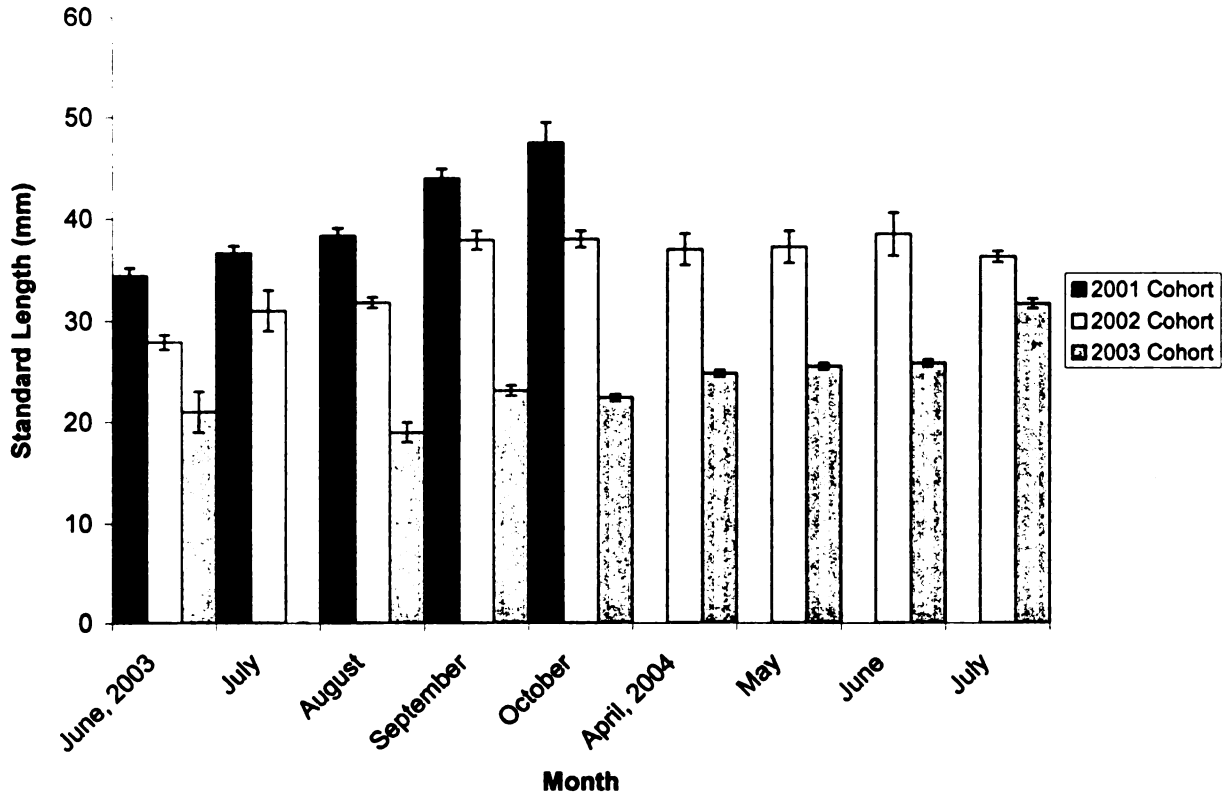


Figure 2. Mean lengths of *Lepomis macrochirus* by cohort from Three Lakes II, Michigan by month. Standard error bars are included on mean length bars.

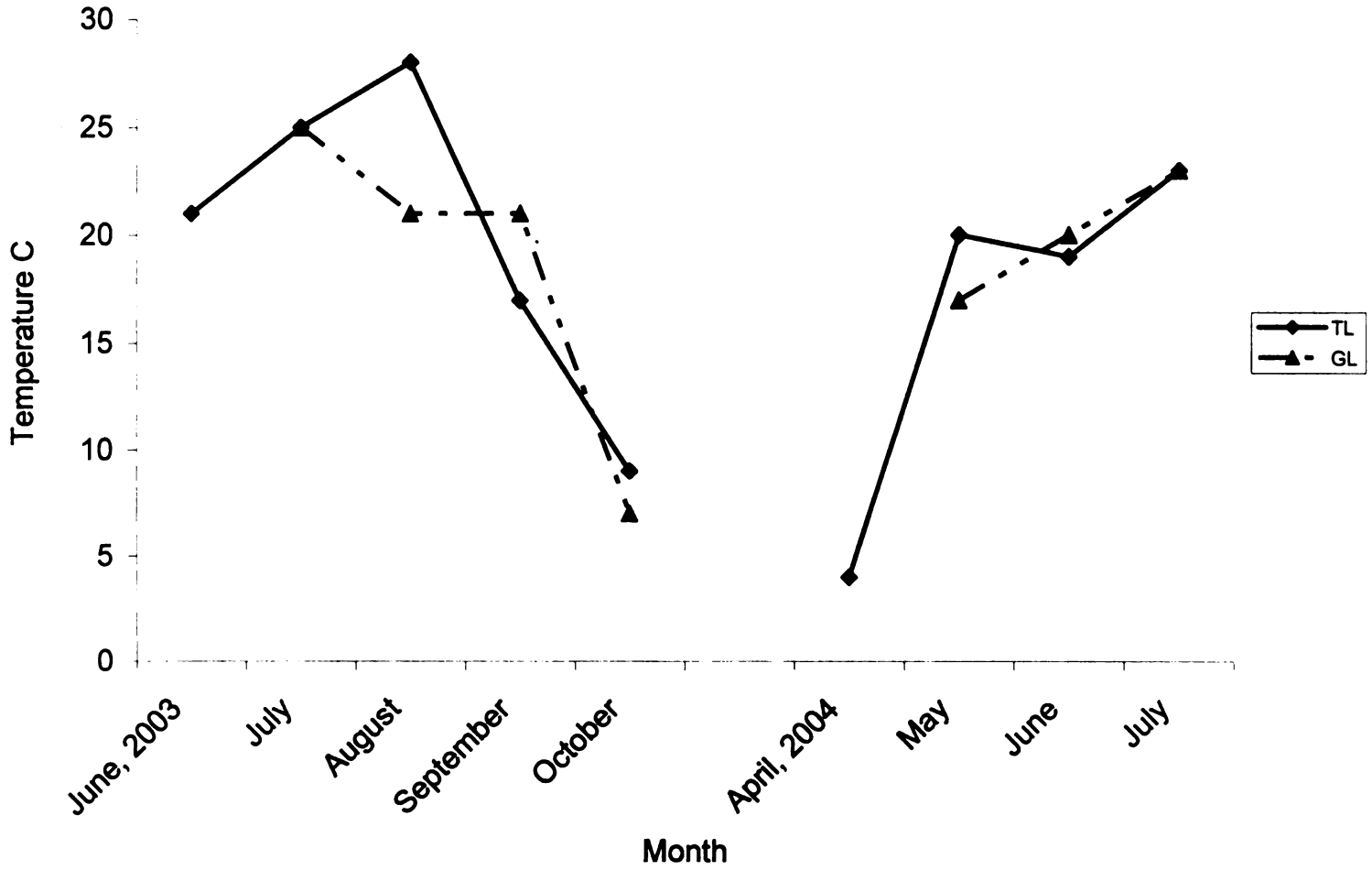


Figure 3. Water temperature at 0.5 m depth in the littoral zones of Three Lakes II (TL) and Gull Lake (GL), Michigan by month.

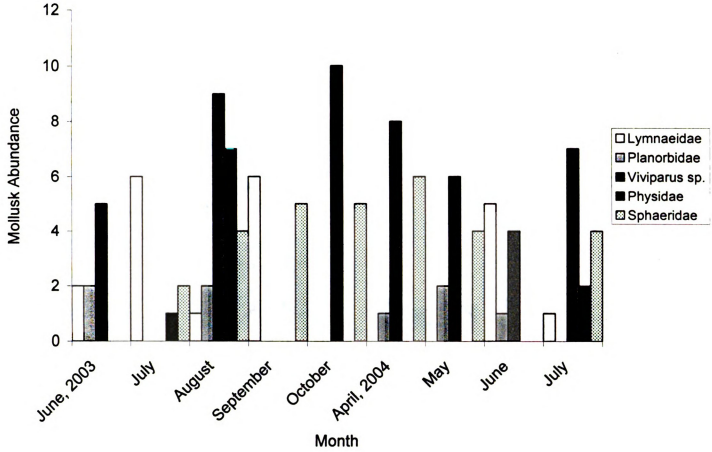


Figure 4. Monthly abundance of mollusks by taxonomic group from Three Lakes II, Michigan.

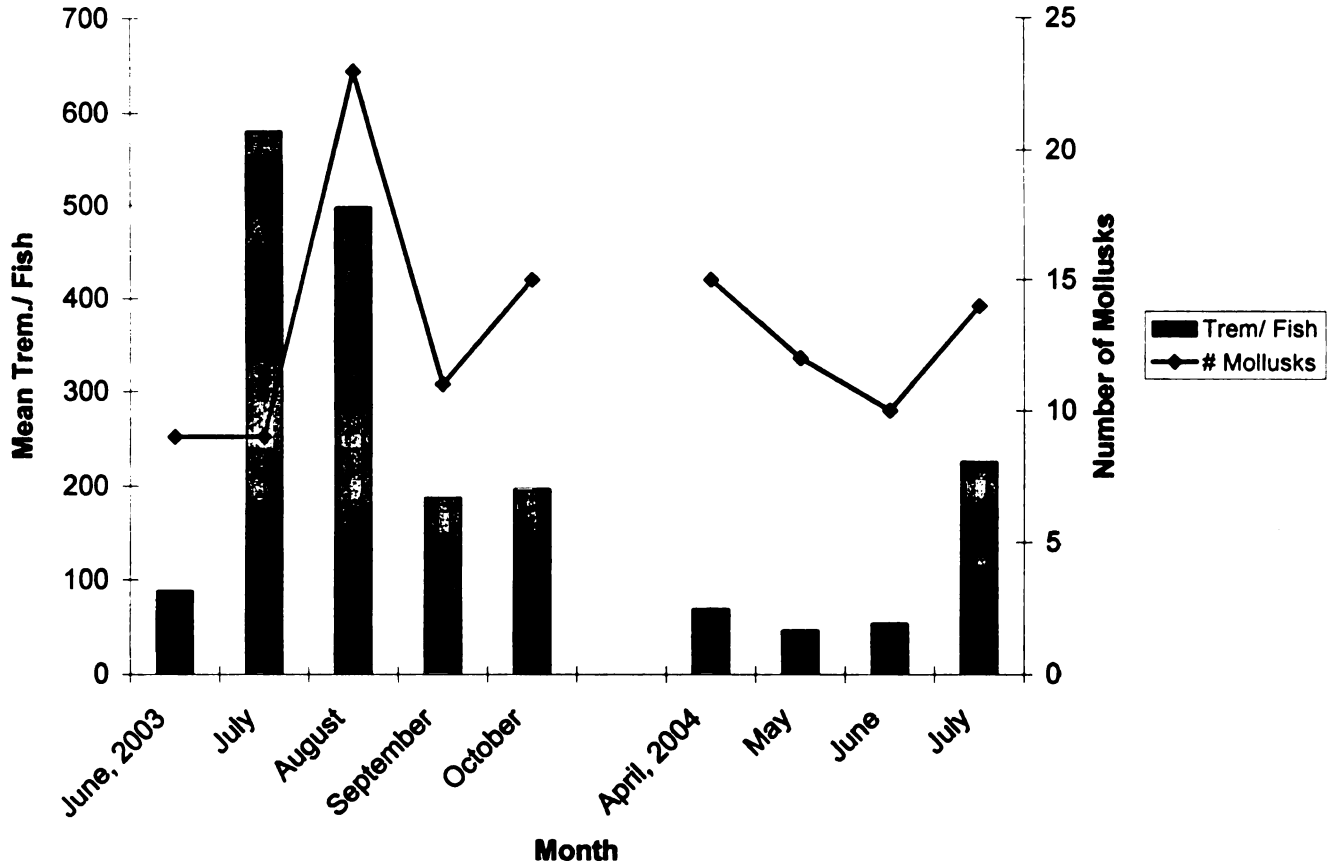


Figure 5. Monthly mean larval trematodes per *Lepomis macrochirus* irrespective of cohort and total mollusks collected per month from Three Lakes II, Michigan.

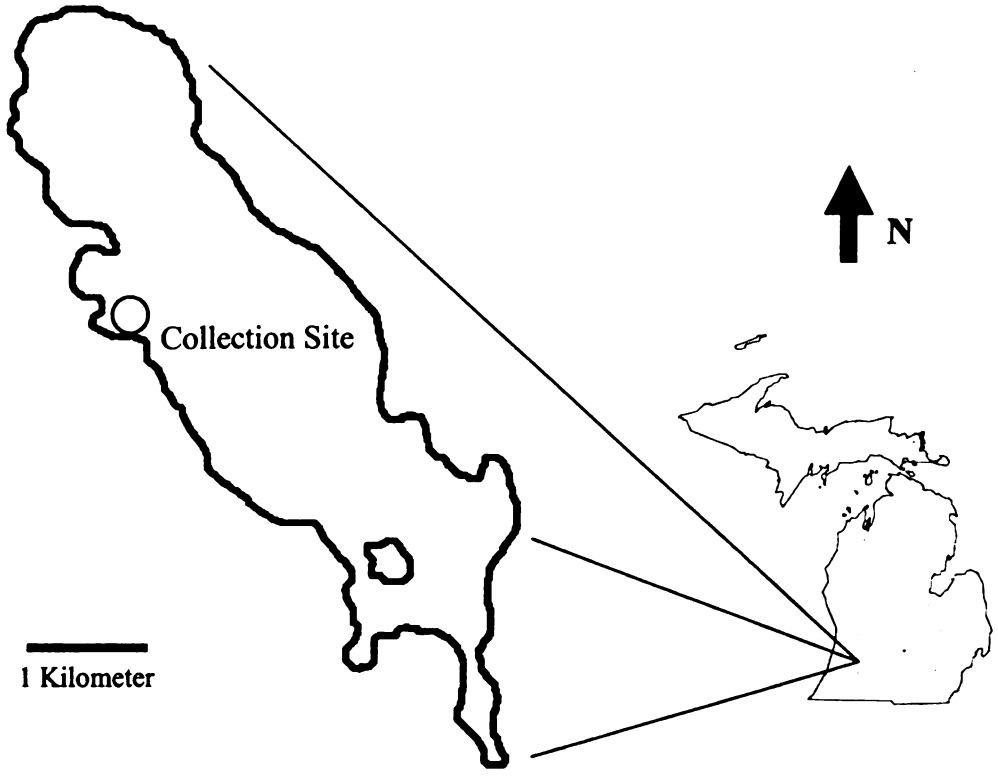


Figure 6. Map of Gull Lake, Michigan with collection site.

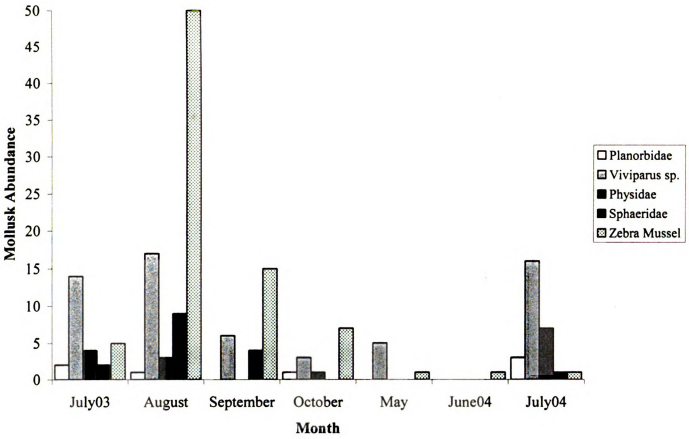


Figure 7. Monthly abundance of mollusks by taxonomic group from Gull Lake, Michigan.

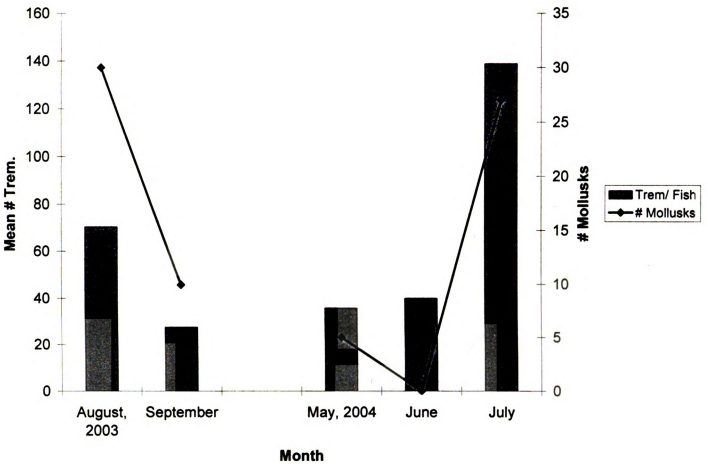


Figure 8. Monthly mean trematodes per *Lepomis macrochirus* and total mollusks collected per month from Gull Lake, Michigan.

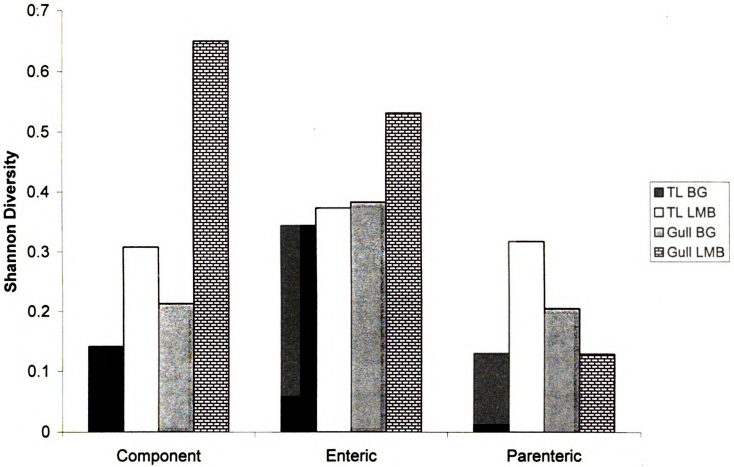


Figure 9. Shannon diversity values for total, enteric and parenteric parasite component communities for *Lepomis macrochirus* (BG) and *Micropterus salmoides* (LMB) from Three Lakes II and Gull Lake, Michigan.

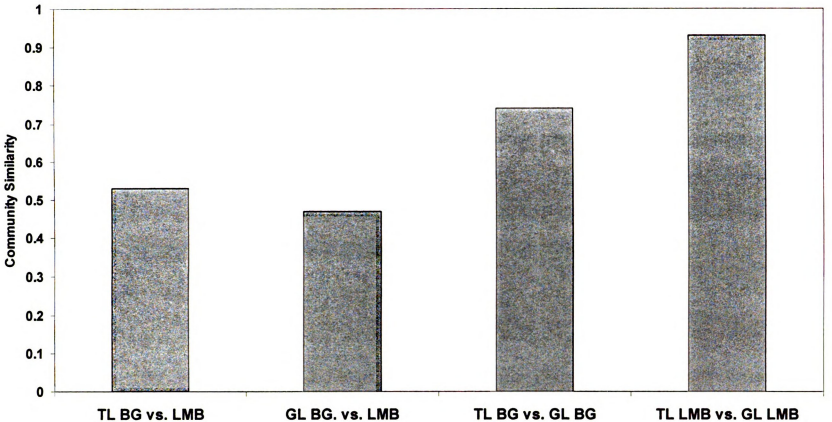


Figure 10. Jaccard's coefficient of community similarity for parasite communities of juvenile bluegill and young-of-the-year largemouth bass from Three Lakes II and Gull Lake, Michigan.

Figure 11. Length of fish at first occurrence of parasite species from 392 juvenile *Lepomis macrochirus* from Three Lakes II, Michigan. Numbers above vertical lines represent the first occurrence of a parasite species and represent parasite species as follows: 1—*Cryptogonimus* sp. metacercaria; 2—*Proteocephalus ambloplitis*, 3—*Trichodina* sp., 4—*Posthodiplostomum minimum*, 5—*Neascus* sp., 6—*Azygia* sp., 7—*Camallanus* sp., 8—*Spiroxys*, 9—*Neoechinorhynchus cylindratus*, 10—*Haplobothrium globuliforme*, 11—*Anchoradiscus* sp., 12—Monogene sp., 13—*Diplostomum* sp., 14—*Spinitectus* sp., 15—*Myxobolus* sp., 16—*Actinocleidus* sp., 17—*Pomphorhynchus bulbocolli,* 18—*Clinostomum* sp., 19—*Crepidostomum* sp. Height of lines arbitrarily determined.

* Parasite species that is acquired by direct penetration or a parasite species with a direct life cycle.

† Adult parasite species.

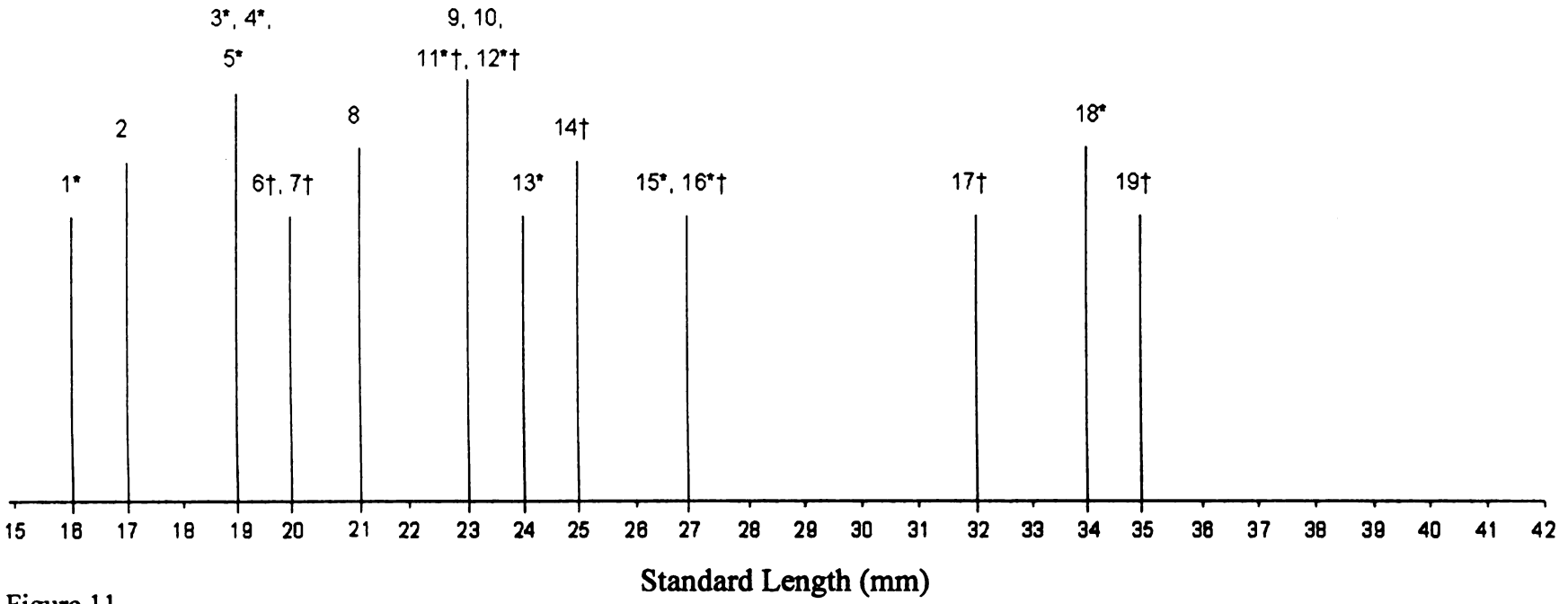

3*, 4*,
5*
9, 10,
11*†, 12*†
8
14†
18*
2
1*
6†, 7†
13*
15*, 16*†
17†
19†
15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42
Standard Length (mm)

Figure 11.

Figure 12. Length of fish at first occurrence of parasite species from 117 juvenile *Lepomis macrochirus* from Gull Lake, Michigan. Numbers above vertical lines represent the first occurrence of a parasite species and represent parasite species as follows: 1—*Cryptogonimus* sp. metacercaria; 2— *Posthodiplostomum minimum*, 3—*Diplostomum* sp., 4—*Pomphorhynchus bulbocolli*, 5—Monogene sp., 6—*Proteocephalus ambloplitis*, 7—*Neascus* sp., 8—*Anchoradiscus* sp., 9—*Neoechinorhynchus cylindratus*, 10—*Haplobothrium globuliforme*, 11—*Leptorhynchoides thecatus*, 12—*Spinitectus* sp., 13—*Azygia* sp., 14— *Actinocleidus* sp., 15—*Trichodina* sp., 16— *Myxobolus* sp. Height of lines arbitrarily determined.

* Parasite species that is acquired by direct penetration or a parasite species with a direct life cycle.

† Adult parasite species.

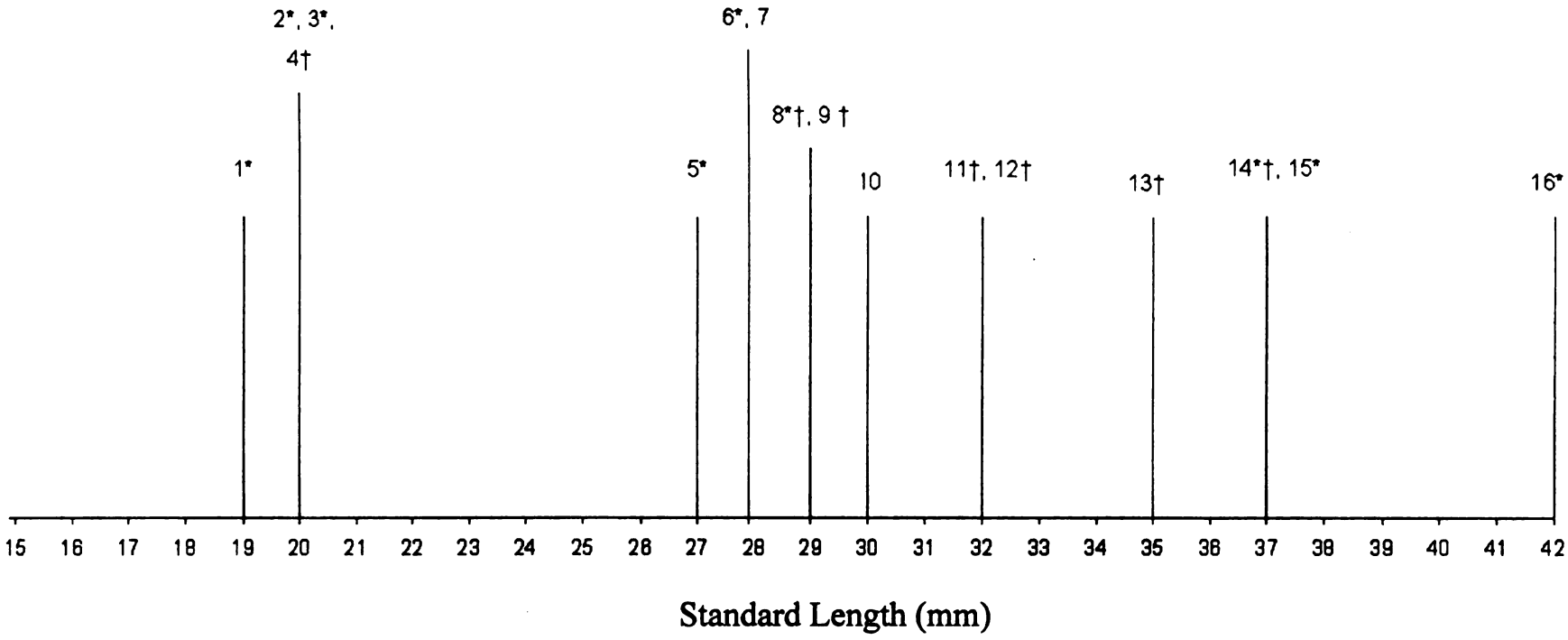

2*, 3*,
4†
6*, 7
8*†, 9 †
1*
5*
10
11†, 12†
13†
14*†, 15*
16*
15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42
Standard Length (mm)

Figure 12.

Figure 13. Length of fish at first occurrence of parasite species from 26 young-of-the-year *Micropterus salmoides* from Three Lakes II, Michigan. Numbers above vertical lines represent the first occurrence of a parasite species and represent parasite species as follows: 1—*Cryptogonimus* sp. metacercaria; 2— Monogene sp., 3—*Cryptogonimus* sp. adult, 4—*Proteocephalus ambloplitis*, 5—*Trichodina* sp., 6—Monogene sp. A, 7—*Azygia* sp., 8—*Posthodiplostomum minimum*, 9—*Neascus* sp., 10—*Diplostomum* sp., 11—*Neoechinorhynchus cylindratus*, 12—*Pomphorhynchus bulbocolli*, 13—*Spiroxys* sp., 14— *Camallanus* sp. Height of lines arbitrarily determined.

* Parasite species that is acquired by direct penetration or a parasite species with a direct life cycle.

† Adult parasite species.

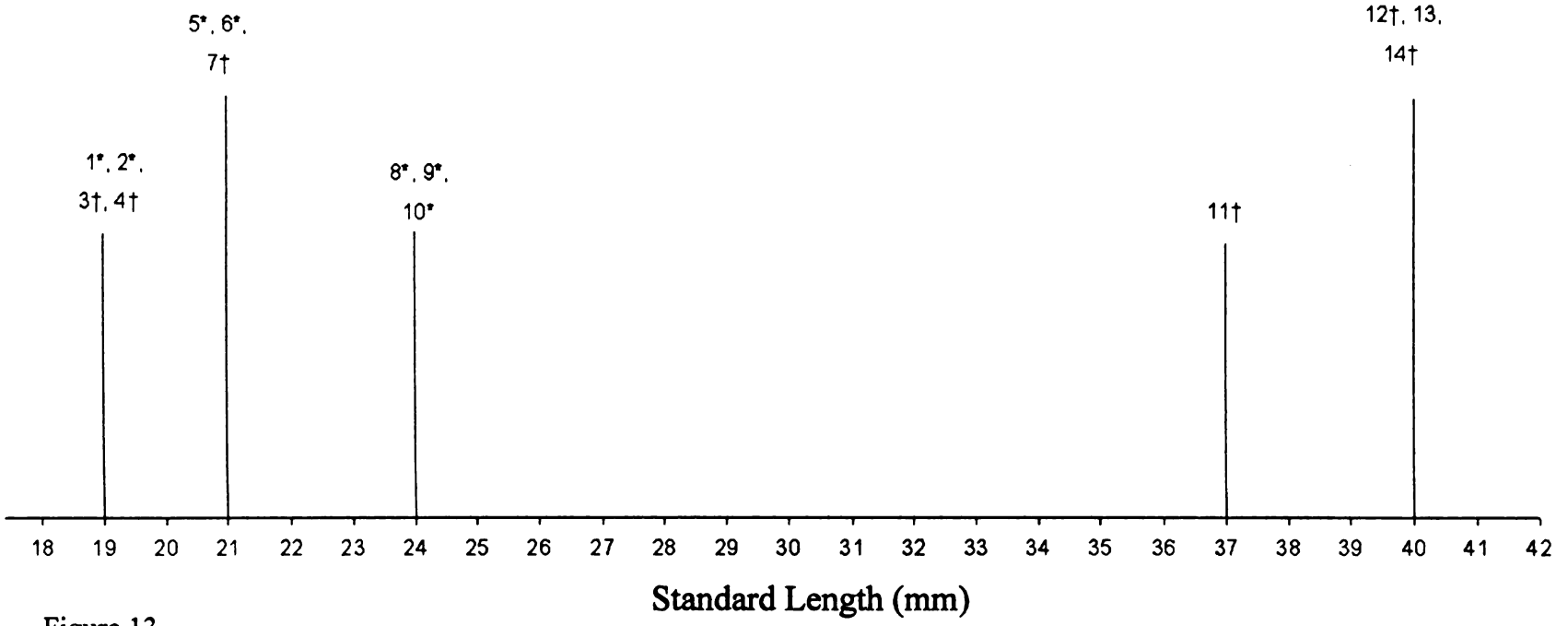

1*, 2*,
3†, 4†
5*, 6*,
7†
8*, 9*,
10*
11†
12†, 13,
14†
18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42
Standard Length (mm)

Figure 13.

Figure 14. Length of fish at first occurrence of parasite species from 86 young-of-the-year *Micropterus salmoides* from Gull Lake, Michigan. Numbers above vertical lines represent the first occurrence of a parasite species and represent parasite species as follows: 1—*Cryptogonimus* sp. metacercaria; 2— *Trichodina* sp., 3—*Camallanus* sp., 4—*Posthodiplostomum minimum*, 5—*Diplostomum* sp., 6—*Proteocephalus ambloplitis*, 7—*Leptorhynchoides thecatus*, 8—*Pomphorhynchus bulbocolli.*, 9—Monogene sp., 10—*Cryptogonimus* sp. 11—*Azygia* sp., 12—*Spinitectus* sp., 13—Monogene sp. A, 14—*Myxobolus* sp., 15—*Neoechinorhynchus cylindratus*, 16—*Clinostomum* sp. Height of lines arbitrarily determined.

* Parasite species that is acquired by direct penetration or a parasite species with a direct life cycle.

† Adult parasite species.

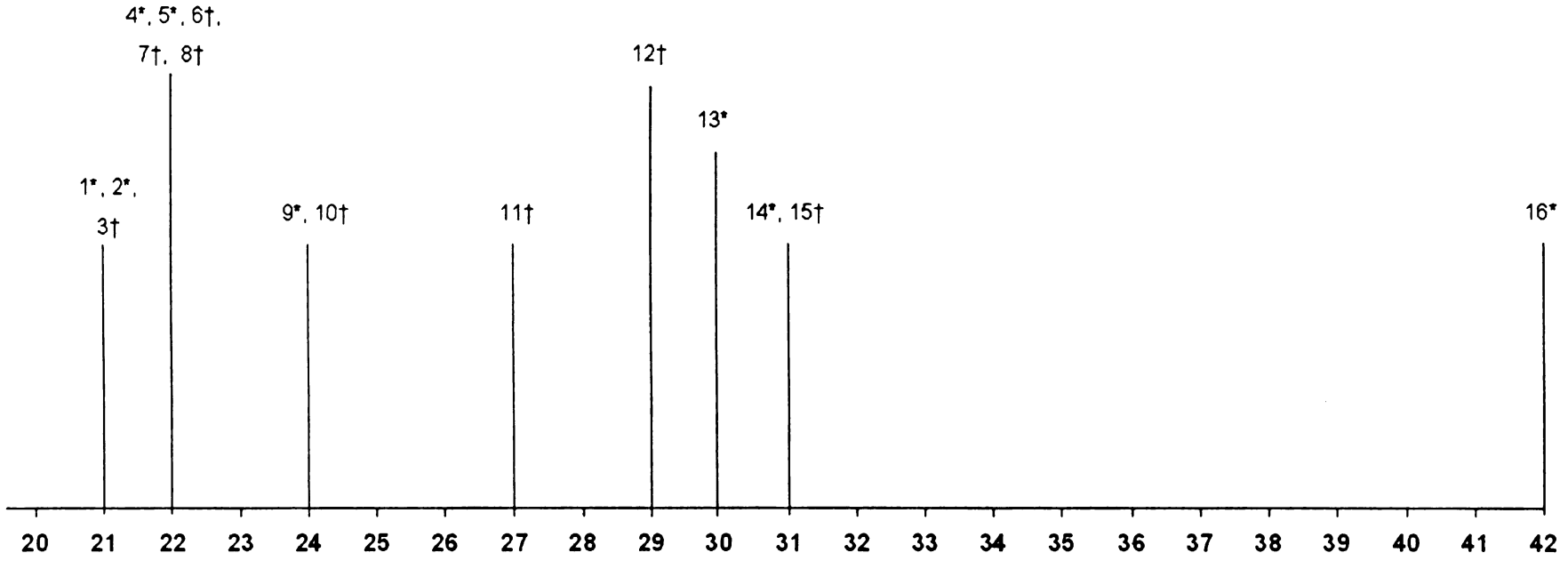

4*, 5*, 6†,
7†, 8†
12†
13*
1*, 2*,
3†
9*, 10†
11†
14*, 15†
16*
20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42
Standard Length (mm)

Figure 14.

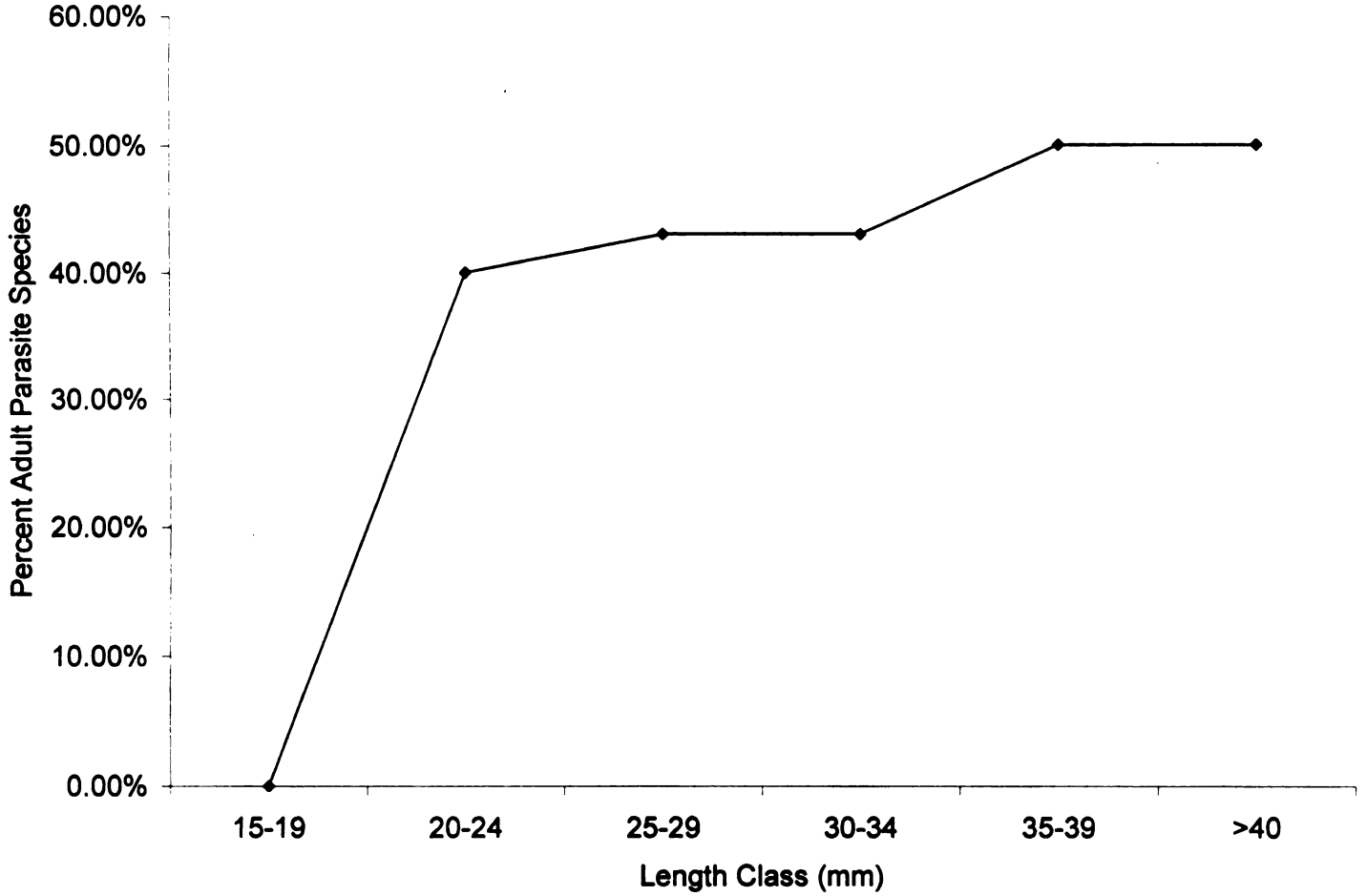


Figure 15. Percentage of adult parasite species of 392 juvenile *Lepomis macrochirus* from Three Lakes II, Michigan in five mm length classes.

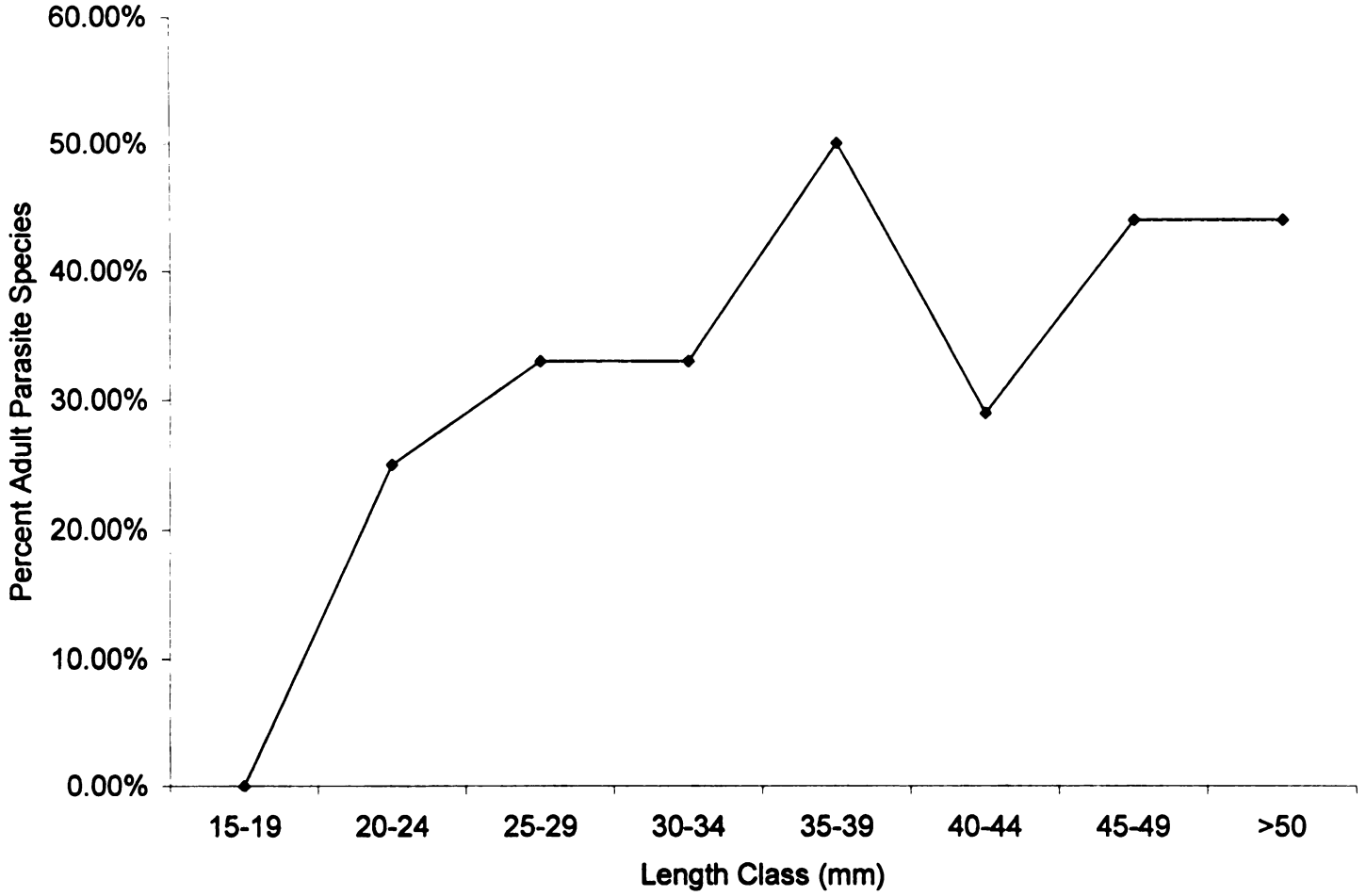


Figure 16. Percentage of adult parasite species of 117 juvenile *Lepomis macrochirus* from Gull Lake, Michigan by five mm length classes.

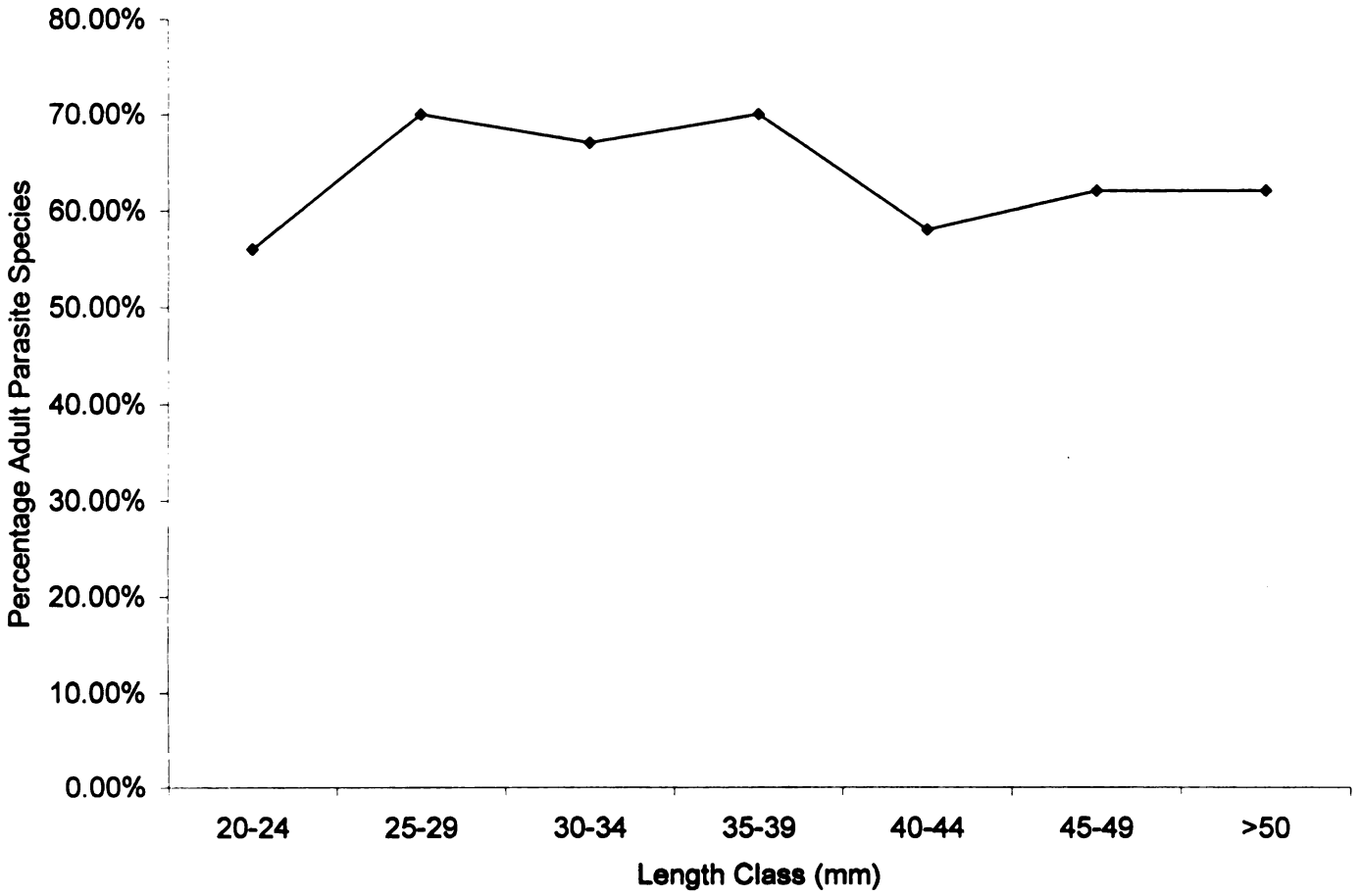


Figure 17. Percentage of adult parasite species of 86 young-of-the-year *Micropterus salmoides* from Gull Lake, Michigan by five mm length classes.

APPENDIX I

Protozoa

Life cycles of parasites in this group are highly variable. Some parasites in this group have a direct life cycle, while others require an intermediate host. The parasite *Trichodina* sp., which was encountered in the present study, has a direct life cycle (Hoffman, 1999). The parasite *Myxobolus* sp., which was also found in the present study, requires a tubificid worm intermediate host (Markiw and Wolf, 1983). Fish become infected with this parasite when triactinomyxon spores are released from the tubificid worm and attach to the fish (El-Matbouli and Hoffman, 1989) or penetrate the fish and travel throughout the body of the fish via the circulatory system (Gilbert and Granath, 2003).

Trematoda

Life cycles of parasites in this group are also variable, but most species require use of a mollusk intermediate host. In aquatic systems, eggs, which contain a developing embryo, are shed by adults in the feces of the definitive host and hatch into miricidia when contacting water (Roberts and Janovy, 2004). These miricidia then penetrate the soft tissue of a mollusk or the trematode eggs are eaten by a mollusk intermediate host where they develop into either a sporocyst or redia (depending on the parasite species) (Roberts and Janovy, 2004). Sporocysts may go through several generations of producing daughter sporocysts before producing either cercariae, which is the infective stage to the fish, or redia which produce cercariae that are shed by the mollusk and directly penetrate or are ingested by the fish host (Roberts and Janovy, 2004).

Cercariae in many of the trematode species in the present study encyst in soft tissue after penetrating the fish. Once encysted, these larval parasites are called metacercariae. Two exceptions found in the present study are the trematode *Azygia* sp. that has cercaria that are eaten by the fish definitive host (Sillman, 1962) and the trematode *Diplostomum* sp., has cercaria that will not encyst, but will instead localize unencysted in the vitreous humor of the eye of the fish intermediate host (Hoffman, 1999).

Monogenea

Monogenea do not use an intermediate host for development; typically after copulation (with the exception of one family), eggs are formed and released (Roberts and Janovy, 2004). Once in the water, the egg releases into an oncomiracidium, a larval stage, that swims to find a suitable host (Roberts and Janovy, 2004). All monogene species encountered in the present study produce eggs that hatch in the water into an oncomiracidium.

Eucestoda

Two variations of cestode lifecycles are used by parasite species found in the present study. Adult worms of *Proteocephalus ambloplitis* live in the pyloric ceca and small intestines of largemouth bass. Fertilized eggs are produced after copulation and are passed out in the feces of the fish which are ingested by the appropriate copepod or amphipod intermediate host and eventually develop into the plerocercoid I (Hunter, 1928; Fisher and Freeman, 1969, 1973). If an appropriate definitive or paratenic host eats a crustacean intermediate host containing a mature pleroceroid I, the plerocercoid I burrows through the fish gut into the body cavity where it develops into the plerocercoid

II stage (Fisher and Freeman, 1969, 1973; Freeman, 1973). If a paratenic host harboring the initial plerocercoid II stage is eaten by the proper definitive host, the worm again burrows through the gut wall into the body cavity in order to undergo further growth and development (Fischer and Freeman, 1973). In the definitive host, the initial plerocercoid II will develop parenterically into the middle plerocercoid II. Upon receiving the right stimulus, which may be a rise in temperature, an increase in fish gonadotropic and gonadal hormones, an increase in photoperiod or a combination of these factors, the middle plerocercoid II moves back into the lumen of the intestine where it will develop into an adult worm capable of sexual reproduction (Fischer and Freeman, 1969, 1973; Freeman, 1973; Esch et al., 1975).

Haplobothrium globuliforme uses a bowfin, *Amia calva*, definitive host (Hoffman, 1999). The worm will pass eggs in the feces of the fish which are ingested by the copepod intermediate host (Hoffman, 1999). Within the copepod, the egg develops into a procercoid (Hoffman, 1999). When a copepod infected with a mature procercoid is eaten by a fish second intermediate host, the procercoid burrows through the gut wall and encysts in the liver developing into a plerocercoid (Hoffman, 1999). The worm completes its life cycle when a fish intermediate host with a mature plerocercoid is eaten by the bowfin definitive host (Hoffman, 1999).

Nematoda

Nematodes have highly variable life cycles. The species of nematodes involved in the present study are *Spinitectus* sp., *Camallanus* sp., and *Spiroxys* sp. Adults of *Camallanus* sp. live in the intestine of fish where eggs are fertilized and larvae are produced within the female (Stromberg and Crites, 1974). Female worms hang out the

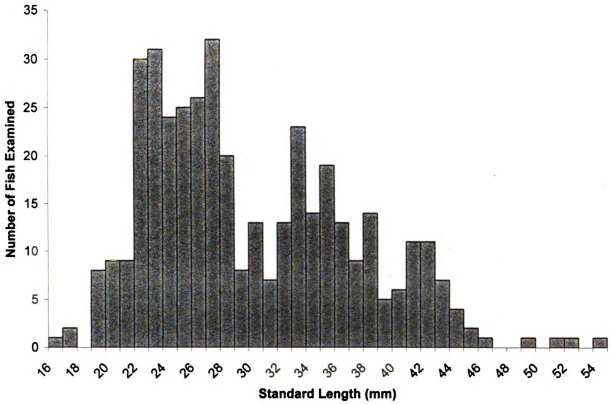
vent of fish and the female worm bursts when coming into contact with water, thus releasing larvae (Stromberg and Crites, 1974). Larvae are eaten by copepods and molt twice before they are infective to the fish definitive host (Stromberg and Crites, 1974). Adults of *Spinitectus* sp. live in the intestine of fish, where they mate and produce eggs (Jilek and Crites, 1982). Eggs are passed from the female worm into the intestinal lumen of the fish and into the environment via the feces of the definitive host. The eggs are ingested by an arthropod intermediate host which may be a mayfly nymph, dragonfly nymph, stonefly larvae or collembolan larvae, where the eggs hatch and larval worms develop (Jilek and Crites, 1982). When an arthropod with mature larvae is ingested by a bluegill or other definitive host, the larval worms establish in the intestine of the fish (Jilek and Crites, 1982). Adults of *Spiroxys* sp. live in the gastrointestinal tract of turtles (Hedrick, 1935). Eggs of *Spiroxys* sp. are passed from the female worm and shed in the feces of the definitive host (Hedrick, 1935). Larvae hatch from eggs upon coming into contact with water and are eaten by a copepod first intermediate host (Hedrick, 1935). The copepod with mature larvae is then eaten by a second intermediate host, which may be either a dragonfly nymph or a fish, such as a bluegill and largemouth bass, where the larvae will undergo development necessary to infect the definitive host (Hedrick, 1935).

Acanthocephala

For acanthocephalans using fish as definitive hosts, eggs are passed from female worms into the lumen of the intestine and passed into the aquatic environment via feces (Schmidt, 1985). The egg is then ingested by an aquatic crustacean and hatches into an acanthella which develops into a cystacanth, the infective stage to the definitive host (Schmidt, 1985).

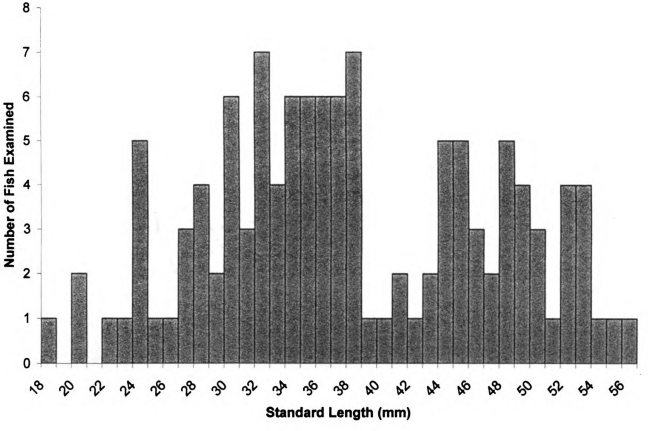
APPENDIX II

Numbers of *Lepomis macrochirus* from Three Lakes II, Michigan by standard length (mm).



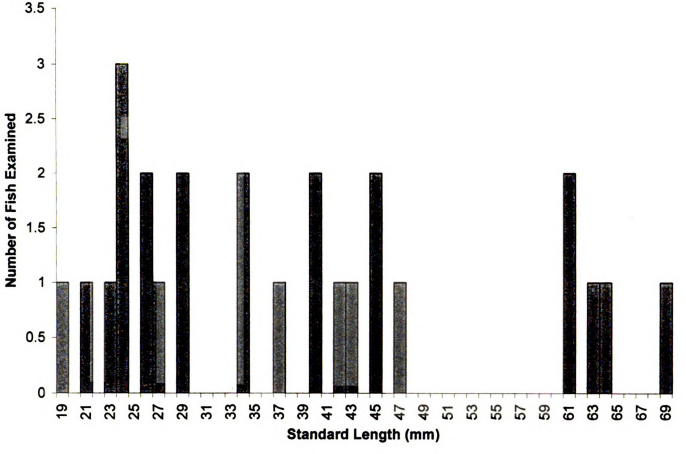
APPENDIX III

Numbers of *Lepomis macrochirus* from Gull Lake, Michigan by standard length (mm).



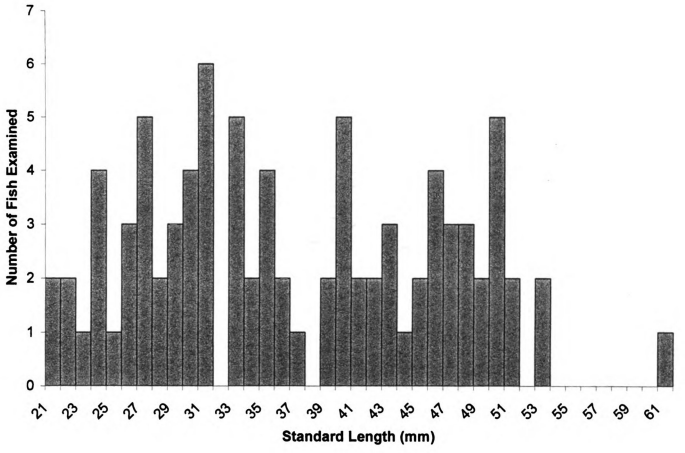
APPENDIX IV

Numbers of *Micropterus salmoides* from Three Lakes II, Michigan by standard length (mm).



APPENDIX V

Numbers of *Micropterus salmoides* from Gull Lake, Michigan by standard length (mm).



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