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**Microhabitat analysis of bass tapeworm, *Proteocephalus ambloplitis*, infrapopulations in four species of centrarchids from Gull Lake, Michigan.**

presented by

**Merritt Gale Gilliland III**

has been accepted towards fulfillment
of the requirements for

**M.S.** degree in **Zoology**

Patrick M. Muzzall
Major professor

Date July 31, 2002

# MICROHABITAT ANALYSIS OF BASS TAPEWORM, PROTEOCEPHALUS AMBLOPLITIS, INFRAPOPULATIONS IN FOUR SPECIES OF CENTRARCHIDS FROM GULL LAKE, MICHIGAN

By

Merritt Gale Gillilland III

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Zoology
Ecology, Evolutionary Biology, and Behavior Program

2002

ABSTRACT

MICROHABITAT ANALYSIS OF BASS TAPEWORM, PROTEOCEPHALUS AMBLOPLITIS, INFRAPOPUALTIONS IN FOUR SPECIES OF CENTRARCHIDS FROM GULL LAKE, MICHIGAN

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A total of 242 centrarchids (54 *Micropterus dolomieu*, 88 *M. salmoides*, 50 *Ambloplites rupestris* and 50 *Lepomis macrochirus*) were collected from April – September 2000 and April – July 2001 from five locations in Gull Lake, Michigan and examined for *Proteocephalus ambloplitis*. The overall prevalence of *P. ambloplitis* in smallmouth and largemouth bass was 100%. The number of *P. ambloplitis*, from each microhabitat in the fish host, was compared between females and males of the same species and females and males of different species. *Proteocephalus ambloplitis* had a significantly higher overall mean intensity ± SD (72.5 ± 44.8) and a higher mean intensity in the ovaries (34 ± 18.9) of smallmouth bass when compared to largemouth bass. In smallmouth bass the gonads were most heavily infected and in largemouth bass the liver and mesentery were the most infected organs. Rock bass and bluegill were examined to investigate their role in the transmission of *P. ambloplitis* to the definitive host. Based upon the dietary composition of the smallmouth and largemouth bass, other second intermediate hosts may also be involved in the transmission of *P. ambloplitis*. *Proteocephalus ambloplitis* may be contributing to a reduction in the reproductive potential of smallmouth bass from Gull Lake, Michigan.

## DEDICATION

I would like to dedicate this thesis to my parents, Gale and Mary Gillilland, for a lifetime of encouragement and for helping me through all the rough spots.

## ACKNOWLEDGMENTS

To begin with, I would like to thank my advisor, Dr. Patrick M. Muzzall, for his help and guidance over the years. Thank you also to my guidance committee, Dr. Donald Hall and Dr. Thomas Coon, for their constructive criticism throughout this project. Acknowledgments are due to Mr. Jim Dexter, Michigan Department of Natural Resources (MDNR), for helping to get this project started and for giving me many helpful tips along the way; Mr. Bob Day and Mr. Jim Grant, Michigan Department of Environmental Quality (MDEQ), for allowing me use of an MDEQ fyke net; and to Dr. Michael Klug and Dr. Steve Hamilton, Kellogg Biological Station (KBS), for allowing me use of the boathouse, boats, and many other facilities at KBS. Much thanks to the residents of Gull Lake who readily caught fish for me throughout the summers of 2000 and 2001: Mr. Doyle Boss, Mr. Dennis McGraill, Mr. Bob Smith, Mr. Dale Boersma, and Mr. Lloyd Anspaugh. I would especially like to give thanks to Mr. Doyle Boss "Master Fisherman" for his enormous help in the field and for sharing his vast knowledge on the art of bass fishing. Thank you to Mr. Karl Strauss, Dr. Matt Zwiernik and Dr. Denise Kay, Aquatic Toxicology Laboratory (ATL), for granting me access to an electrofishing boat and for helping to catch fish; Mr. Dan Anson, MDNR, for catching largemouth bass in April 2001; and Dr. John Giesy (ATL), for helping with the 3-Way and 2-Way ANOVA. I am especially grateful to my father, Mr. M. Gale Gillilland Jr., and my nephew, Mr. Ryan Gillilland, for helping me fish, even though we did not catch much. Lastly, thanks to my wife, Carolyn, for all of her support, encouragement, and assistance in the field on several occasions.

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# INTRODUCTION

Bass tapeworm, *Proteocephalus ambloplitis* Leidy, 1887 (Eucestoda: Proteocephalidae) is a common parasite of fishes from North American lakes (Hoffman, 1999). It is a ployzoic cestode, which is nearctic in distribution, has a heteroxenous life cycle, and is simultaneously hermaphroditic with cross-fertilization. The definitive hosts are usually in the genera *Micropterus* and *Ambloplites* (Centrarchidae). Fischer and Freeman (1969) suggested that *P. ambloplitis* is one of the most common parasites of the smallmouth bass, *Micropterus dolomieu.* Fish in many families are known to be second intermediate hosts of *P. ambloplitis*, such as: Catostomidae, Centrarchidae, Ictaluridae, Lepisosteidae, Percidae, and Salmonidae (Becker and Brunson, 1968; and Amin, 1990). This parasite is found less frequently in fishes from lotic environments probably due to the habitat requirements of the crustacean first intermediate host (Vernard, 1940).

*Proteocephalus ambloplitis* can affect reproduction in the fish definitive host (Fischer and Freeman, 1969; Esch and Huffines, 1973; Esch et al., 1975, McCormick and Stokes, 1982). The scar tissue formed by the movements of larval bass tapeworm through the gonads can cause a decline in the number of eggs released or number of sperm produced (Esch and Huffines, 1973; McCormick and Stokes, 1982). Eventually, as the scar tissue becomes more numerous, castration of the fish host may occur. It has been suggested that the bass tapeworm may be contributing to a decline in the reproductive potential of smallmouth bass, *Micropterus dolomieu*, in Gull Lake, Michigan (Esch and Huffines, 1973; Dexter, 1996). According to Dexter (1996), Gull Lake offers more suitable habitat for smallmouth bass than largemouth bass, *M.*

*salmoides*. The lake is mesotrophic, having cool and clear water, with little vegetation. According to net surveys, however, largemouth bass are the more abundant species (Dexter, 1996). It is usually thought that weedy lakes with mud bottoms, ponds, and sluggish streams are habitats for largemouth bass, and that smallmouth bass are found more often in large, cool, clear lakes and streams (Hubbs and Bailey, 1938). Anecdotal surveys over the last 50 years from Gull Lake have reported a high level of parasitism, especially in the gonads of smallmouth bass, by *P. ambloplitis* (see Dexter, 1996). Esch and Huffines (1973), also reported that infections of *P. ambloplitis* in smallmouth bass were extensive and that larval *P. ambloplitis* may "be an important factor in regulating the population of smallmouth bass" in Gull Lake.

One would assume the mean intensity of *P. ambloplitis* to be higher in smallmouth bass than in largemouth bass, if indeed *P. ambloplitis* is affecting the reproductive potential of smallmouth bass to such an extent that largemouth bass are out breeding them, thus becoming more abundant. Furthermore, one would also expect the mean intensity of *P. ambloplitis* to be higher in the gonads of smallmouth bass. Three hypotheses were formed for this study, they were: 1) the mean intensity of *P. ambloplitis* is significantly higher in smallmouth bass when compared to the largemouth bass; 2) the mean intensity of *P. ambloplitis* is significantly higher in the gonads of smallmouth bass when compared to largemouth bass; 3) bluegill are contributing more to the transmission of *P. ambloplitis* than rock bass based upon smallmouth and largemouth bass diets.

Esch et al. (1975) reported the prevalence of *P. ambloplitis* in smallmouth bass from Gull Lake. By comparing these data generated by Esch et al. (1975) to those observed in the present study it will be determined if the prevalence of *P. ambloplitis* has

increased in smallmouth bass over time. Esch (1971) also reported the prevalences of adult and gravid *P. ambloplitis* in smallmouth bass and largemouth bass. Rock bass, and bluegill were not infected with adult or gravid worms from Gull Lake. Esch (1971) did not report the prevalence of plerocercoids in any of these fish species and only noted if they were present or absent. One objective of this study will be to compare the prevalence of adult and gravid *P. ambloplitis* in the present study to other studies that were performed in Gull Lake.

This is the first study to quantify the mean intensity of *P. ambloplitis* in smallmouth bass and largemouth bass by specific organ of infiltration in North America. By examining the infrapopulation biology of *P. ambloplitis* in these two centrarchid species it will be possible to compare microhabitat utilization of this worm. This microhabitat analysis will allow for statistical comparisons within a fish species and between smallmouth and largemouth bass.

## REVIEW OF THE LITERATURE

### Life Cycle

Cooper (1915), Moore (1926), Bangham (1927), Hunter (1927), and Hunter (1928) attempted to understand the complete life cycle of *P. ambloplitis*. However, it was not until the work of Fischer and Freeman (1969, 1973) and Freeman (1973) that the entire life cycle was revealed (Figure 1). Adult and gravid worms live in the lumen of the gut or pyloric ceca of the definitive host. The gravid proglottids and eggs are passed with the fish feces and enter the aquatic environment. Upon contact with the water the eggs

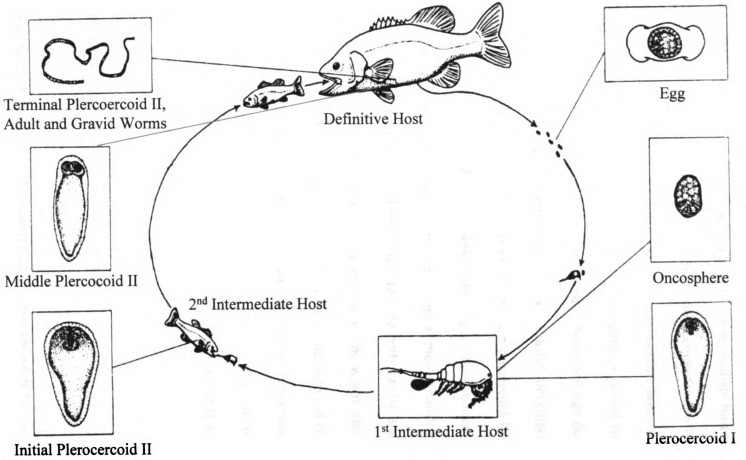


**Figure 1. Life cycle of *Proteocephalus ambloplitis* (Modified from Hugghins, 1959).**

are released from the proglottids and settle onto the substrate and surrounding submergent vegetation. Five species of cyclopoid copepod crustacean (*Cyclops albidus, C. leuckarti, C. prasinus, C. vulgaris*, and *C. serulatus*), and one amphipod crustacean (*Hyalella azteca*) may ingest the eggs becoming a first intermediate host (Hunter, 1928). The egg hatches, releasing the oncosphere, which then penetrates the hemocoel of the crustacean and the plerocercoid I develops. The first intermediate host may then be eaten by the fish second intermediate host, usually a centrarchid or percid fish (Fischer and Freeman, 1969). After consumption, the plerocercoid I bores through the gut and enters the body cavity of the fish second intermediate host. Further development may occur parenterally, which results in the formation of the initial plerocercoid II. The definitive hosts, which are usually the smallmouth bass or the largemouth bass, eat the fish second intermediate host becoming infected. The ingested initial plerocercoid II does not attach to the gut wall of the definitive host but bores into the body cavity and encysts within various organs and tissue (Eure, 1976). Development of the worm continues within the viscera of the definitive host, which produces the middle plerocercoid II. The parenteric middle plerocercoid II waits for some cue, which may be temperature-dependent or hormonal, and then migrates from the viscera back into the lumen of the gut or pyloric ceca (Esch et al., 1975). There it becomes a terminal plerocercoid II and completes the life cycle by developing into the adult and gravid worm.

**Host Terminology for *Proteocephalus ambloplitis***

Fischer and Freeman (1973) stated that it is not known if fish other than bass are

second intermediate hosts or paratenic hosts. A paratenic or transport host is described as being "an organism which serves to transfer a larval stage or stages from one host to another but in which little or no development takes place" (Anderson, 1992). *Proteocephalus ambloplitis* plerocercoids do increase in size within the fish second intermediate host but do not develop into the middle plerocercoid II (Fischer and Freeman, 1973). Further development is required parenterally in the bass definitive host in order for the middle plerocercoid II to move into the gut lumen, and become gravid. Even though some growth does take place in the fish second intermediate host the development is not essential in order to infect the definitive host. Bass, primarily fingerlings, have been shown to acquire *P. ambloplitis* by ingesting infected crustaceans without the need of the fish second intermediate host (Moore, 1926). In this case, the ingested plerocercoid I would leave the gut, enter the viscera, and develop into the middle plerocercoid II.

Bass can become infected by cannibalism or by eating other infected definitive host species. If a bass infected with the middle plerocercoid II is eaten by another bass that fish could become infected. The ingested middle plerocercoid II may either be passed with the feces or it may move through the gut wall, and enter the viscera. It is also possible for a bass to ingest an infected crustacean and become infected.

**Life Stage Terminology for *Proteocephalus ambloplitis***

Freeman (1973) redescribed the different life stages of *P. ambloplitis*, based upon his work regarding the ontogeny of cestodes. The definition of a procercoid is "a metacestode which does not develop a scolex" (Freeman, 1973). *Proteocephalus*

*ambloplitis* in the crustacean first intermediate host has a scolex and does not fit the definition of a procercoid. Freeman (1973) concluded that procercoids with a scolex needed a different name that would better describe the morphological characteristics seen in the crustacean first intermediate host. Freeman (1973) suggested the terms below be used when referring to different life stages of *P. ambloplitis*. In the crustacean first intermediate host the term "procercoid" is changed to "acaudate invaginated glandacetabulo-plerocercoid". This term is very descriptive of the cestodes morphology; "acaudate" refers to the absence of the cercomer, the prefix "gland -" describes the secretory apical end, and the suffix "- acetabulo" refers to the acetabulum or suckers. The new term for visceral worms in the fish second intermediate and definitive host is "invaginated glandacetabulo-plerocercoid II" which replaces "plerocercoid". Lastly, the term "acetabulo-plerocercoid before proglottisation" describes the plerocercoids within the gut lumen of the definitive host. The loss of the prefix "gland -" describes the loss or reduction of the apical organ during penetration into the gut of the bass. Modified forms of these terms will be used herein and are in accordance with Fisher and Freeman (1973).

**Pathology associated with *Proteocephalus ambloplitis***

The effects of *P. ambloplitis* on fish second intermediate and definitive hosts have been investigated by Amin (1990), Bailey (1984), Becker and Brunson (1968), Esch and Huffines (1973), Esch et al. (1975), Fischer and Freeman (1969), Hugghins (1959), Joy and Madan (1989), McCormick and Stokes (1982), and Moore (1926). The movement of the plerocercoid II through the viscera can have severe effects on fish health and

reproduction. It has been demonstrated that fibrosis of the gonadal tissue can occur if penetrated by parenteric plerocercoids, which could ultimately lead to "parasitic castration" and a decrease in reproductive potential of the fish host. Moore (1926), stated (pg. 91) "... infestation by the worms inhibits the development of both egg and spawn and promotes general sterility", and Hugghins (1959) suggested (pg. 40) that *P. ambloplitis* is "the most damaging tapeworm of fresh-water fishes."

Esch and Huffines (1973) examined the histopathology associated with *P. ambloplitis* from the smallmouth bass of Gull Lake, Michigan. They reported a definite reduction in the reproductive potential of bass based on histologic study. They also found the damage usually more severe in young males. Similarly, Esch et al. (1975) found the most extreme pathology in the testes of young male smallmouth bass. Esch and Huffines (1973) observed extensive scarring throughout the oviducts of females and that cysts containing necrotic tissue were present, suggesting this could prevent the shedding of eggs.

McCormick and Stokes (1982) reported on the severity of *P. ambloplitis* infections in female *M. dolomieu* from northeastern Minnesota, and found parenteric plerocercoids invading advanced vitellogenic oocytes. The damage to the oocytes was extensive and the nutrient rich yolk material was lost and absorbed by the worm. Joy and Madan (1989) found 85% of *M. salmoides* and 91% of spotted bass, *M. punctulatus*, infected with *P. ambloplitis* from Beech Fork Lake, West Virginia. Liver damage was characterized by the paucity of bile ducts, congested blood vessels, replacement of liver parenchyma by plerocercoids, fibrous adhesions, and collagen formation. Joy and Madan (1989) concluded the severe damage to the liver of these fish may play an important role

in regulating bass populations in this lake. These authors suggested, that based on intensity, *M. salmoides* is the favored host species. Fischer and Freeman (1969) found all 877 *M. dolomieu* examined from Lake Opeongo, Ontario, infected with parenteric plerocercoids. These authors suggested that the wandering plerocercoids could damage the gonads to such an extent that spawning is inhibited.

Amin (1990) studied *P. ambloplitis* in 13 species of fish from 2 southeastern Wisconsin lakes. He determined that 55% of the plerocercoids in smallmouth bass, found during the summer, were associated with the gonads. Further, the plerocercoid penetration of the ovarian expansive stroma was commonly observed and the unilateral hypertrophy of the ovaries resulted in the destruction of many eggs. Damage was also done to the hepatic tissue of bluegill by parenteric plerocercoid movement through the viscera. Bailey (1984) reported that plerocercoids of *P. ambloplitis* were causing the formation of fibrotic liver cysts in the bluegill intermediate host. This author described the cysts as being composed of strands of melanotic connective tissue that were restricted to areas of plerocercoid infection.

**Seasonal Patterns of *Proteocephalus ambloplitis***

The parenteric middle plerocercoid II in the bass definitive host migrates from the viscera to the gut lumen or pyloric ceca to finish development by becoming gravid. The timing of this movement has been theorized by many researchers as being seasonal. In the early spring fish have no *P. ambloplitis* in the digestive tract, but as the water warms the plerocercoids migrate to the gastrointestinal tract. Throughout the summer the

prevalence of adult and gravid *P. ambloplitis* in the gastrointestinal tract increases. Furthermore, as the fall season approaches water temperature begins to drop and the adult and gravid worms in the gastrointestinal tract are voided and no enteric worms are reported from fish in the winter season (Esch et al., 1975), even though they did not examine any fish from the winter.

Some aspect of the seasonal patterns of *P. ambloplitis* in bass and other fish from the United States and Canada has been investigated by Fischer and Freeman (1969, 1973), McDaniel and Bailey (1974), Cloutman (1975), Esch et al. (1975), Eure (1976), Ingham and Dronen (1982), Amin (1990), Amin and Cowen (1990), Fischer and Kelso (1990), and Szalai and Dick (1990). Although all of these studies correlate temperature and season to the plerocercoid migration, they suggest that hormones may be a factor due to the correlation with spawning times.

Fischer and Freeman (1969) investigated the seasonal patterns of *P. ambloplitis* in smallmouth bass from Lake Opeongo, Ontario. They found that a rise in temperature from 4°C to 7°C triggered the migration of parenteric plerocercoids into the gut lumen. They followed up this finding with lab experiments and were able to duplicate this temperature-dependent migration of *P. ambloplitis* in smallmouth bass. These authors also reported that as the summer progressed the incidence of *P. ambloplitis* in the gut declined, became less frequent in the early fall, and did not persist in the gut during the winter. It was also noted that no worms were found in the gut during the month of April, however; parenteric plerocercoids were found penetrating the gut wall in May and early June.

Esch et al. (1975) studied the population biology of *P. ambloplitis* in smallmouth

bass from Gull Lake, Michigan. These researchers found that as the lake warmed from 4°C in April the prevalence of adult *P. ambloplitis* in the gut increased. The overall percent occurrence of adult worms reached 50% in late May and remained that way until the prevalence decreased in late August. Similar to Fischer and Freeman (1969), Esch et al. (1975) also suggested that smallmouth bass in Gull Lake are free of *P. ambloplitis* in winter. Esch et al. (1975) did not report the intensity of *P. ambloplitis* in smallmouth bass from Gull Lake. It was also reported by Esch et al. (1975) that the recruitment of adult tapeworms occurs only once a year in bass. Esch at al. (1975) and Fischer and Freeman (1969) are in agreement that it is the rise in temperature from 4°C to 7°C that is essential for the migration into the gut, and that event would only occur once in the spring. Finally, Esch et al. (1975) suggested that other events might influence plerocercoid migration, such as increasing photoperiod or increases in gonadotrophic and gonadal hormones.

# MATERIALS AND METHODS

## Description of Study Area

Gull Lake is located within Barry and Kalamazoo Counties in southwestern Michigan (Figure 2). Gull Lake is mesotrophic and has a drainage area of approximately 17,000 acres and the total surface area of lake is 2,030 acres (6.4 kilometer long and 1.6 kilometer wide); the deepest area of the lake is 33.5 meter while 30% of the lake is less then 3 meter deep and the lake bottom is composed primarily of sand, gravel, and rubble; water quality is excellent (Esch, 1971; Dexter, 1996).

## Sampling and Examination of Fish

Four species of centrarchids were examined for *P. ambloplitis* in this study. Two species (smallmouth bass, *Micropterus dolomieu* and largemouth bass, *M. salmoides*) are considered definitive hosts; the remaining two species (rock bass, *Ambloplites rupestris* and bluegill, *Lepomis macrochirus*) are considered second intermediate hosts. Fish were collected in April – September 2000 and April – July 2001 from five different sampling sites KBS-1, KBS-2, Miller's Marsh, South Lake, and North Lake (Figure 2). KBS-1, KBS-2, South Lake and North Lake have sand and cobble substrate with no vegetation; fish were caught at the depth of 2 – 8 meters. Miller's Marsh is approximately 1 – 3 meters in depth and has a soft bottom with submergent and emergent vegetation, and woody debris. Smallmouth bass were not collected from this site. Fish caught from

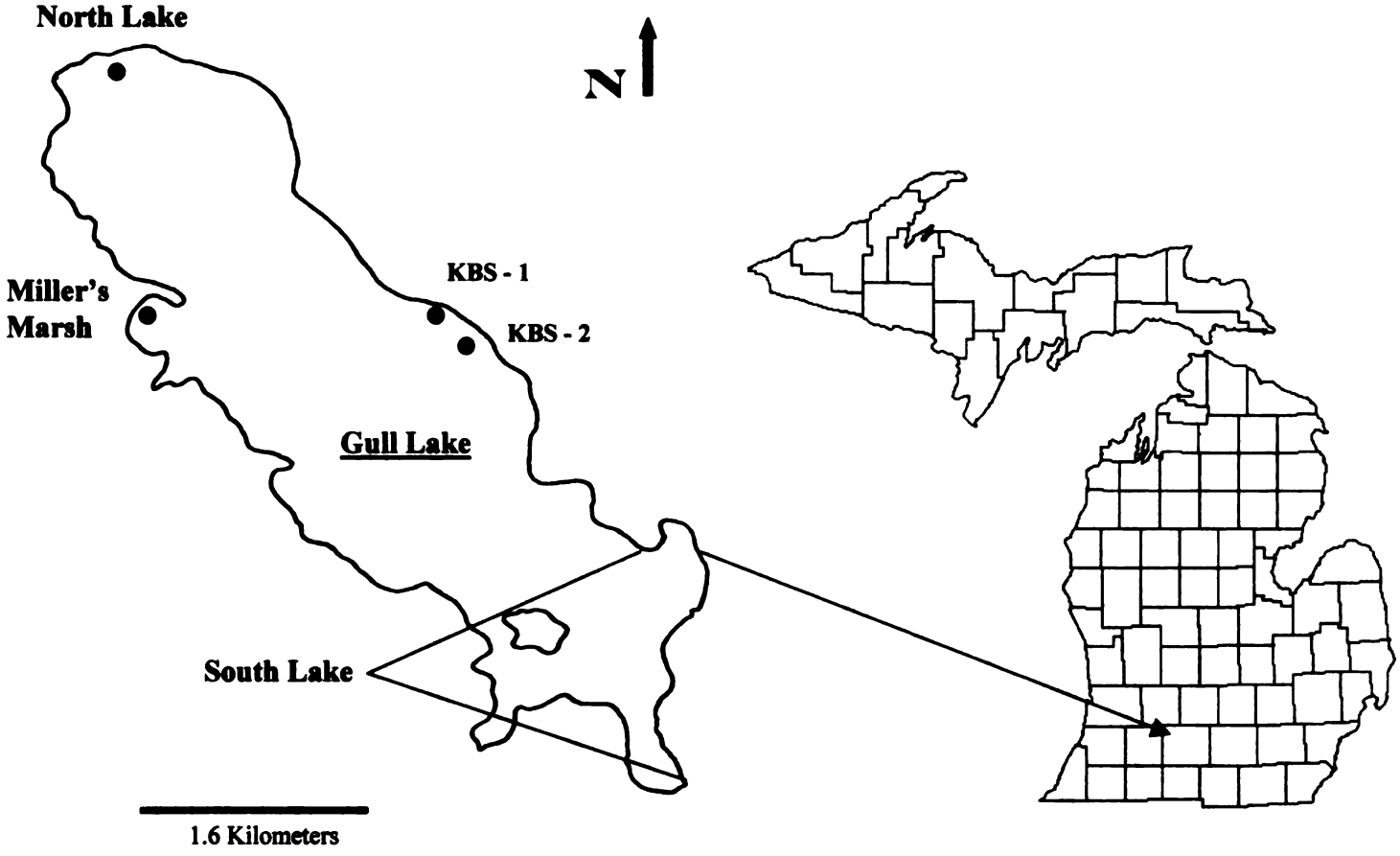


**Figure 2. Location of Gull Lake, Michigan, and five sampling sites where centrarchids were collected in 2000 and 2001.**

different sites were combined for the analyses. Fish were collected during three seasons that are defined as: spring (April and May), summer (June – August), and fall (September). Water temperature was also taken at the depth of 1 meter at the time of sampling (Appendix A).

Several different methods were used to capture fish. The most successful one was angling, using either worm and bobber rigs or artificial lures. Fish were also sampled using a 30.5 x 1.2 meter shallow water fyke net with 3 centimeter mesh size, and by electrofishing. Fish collected for this project by residents of Gull Lake were frozen and picked up at a later date. Fish that I collected were placed within coolers of water and transported to Michigan State University, killed by an overdose of the anesthetic MS-222 (Tricaine methane sulfonate), put into zip-lock bags, individually labeled, frozen, and examined later. Two fish were examined within 2 hours of collection to obtain live worms.

At time of necropsy the fish was sexed and standard length measurement (mm) was taken. Organs and tissues (testes, ovaries, liver, spleen, mesentery, stomach, intestine, and pyloric ceca) were removed and placed into separate petri dishes. Each organ and tissue was then carefully dissected and all life stages of *P. ambloplitis* were counted, removed, and preserved in 70% ethyl alcohol. In many cases the amount of fibrous adhesions surrounding the organs was great, and many organs could not be differentiated. However, with great care, the fibrous adhesions were peeled away from the organs. This peeling procedure also removed the mesentery; therefore both tissue types (mesentery and fibrous adhesions) were placed into a petri dish and examined.

**Worm Identification**

Amin and Boarini (1992) described the various plerocercoids of *P. ambloplitis* from several fish species using morphometric characteristics that were given as a mean (mm) ± SD. The initial plerocercoid II from the bluegill has a body length of 11.10 ± 9.20, scolex width 0.95 ± 0.23, lateral sucker diameter 0.29 ± 0.10, and accessory apical sucker diameter 0.28 ± 0.11. The middle plerocercoid II and initial plerocercoid II from the body cavity of *Micropterus* spp. have a body length of 4.69 ± 6.53, scolex width 0.60 ± 0.20, lateral sucker diameter 0.20 ± 0.06, and accessory apical sucker diameter 0.20 ± 0.06. The terminal pleroceroid II from the gut lumen of *Micropterus* spp. has a body length of 41.34 ± 44.49, scolex width 0.71 ± 0.16, lateral sucker diameter 0.29 ± 0.05, and accessory apical sucker diameter of 0.05 ± 0.07.

Adult and gravid worms were identified according to Hoffman (1999). The vestigial apical sucker is present; testes are dorsal to the uterus; cirrus pouch is lateral, extending over 1/3 of the proglottids; vitellaria are marginal; vaginal opening is lateral and anterior to genital atrium; eggs are dumbbell shaped, and embryonated. All gravid worms were identified by having the characteristic dumbbell shaped eggs. Drawings of various life stages are in Figure 3.

**Worm Preparation**

Live worms were removed and placed in a petri dish containing hot water (~ 80° C). After 30 minutes the worms had relaxed, died and were then preserved in 10%

formalin. Worms removed from frozen fish were preserved in 70% ethyl alcohol. Preserved worms were then stained using borax carmine and dehydrated in a graded ethanol series. Stained worms were cleared in xylene and permanently mounted onto slides using Canada Balsam.

**Definition of Terms**

Prevalence is defined as the percentage of fish infected with *Proteocephalus ambloplitis*, mean intensity is the mean number of *P. ambloplitis* in infected fish, mean abundance is the mean number of *P. ambloplitis* in all fish examined. The definitive hosts are the smallmouth bass and largemouth bass; second intermediate hosts are the rock bass and bluegill. Even though rock bass have been shown to serve as definitive hosts in other studies, I feel since no enteric worms were found in this species it is more appropriate to classify this fish as a second intermediate host in Gull Lake. Life cycle terminology that I use is in accordance with Fischer and Freeman (1973). In the fish second intermediate host the term initial plerocercoid II will be used to describe the worms. Four different developmental stages of *P. ambloplitis* were found in the fish definitive host, they are, middle plerocercoid II (found in the visceral organs), terminal plerocercoid II, adult worm, and gravid worm (found in the lumen of the digestive tract). Adult worms are strobilized but are not producing eggs; gravid worms are strobilized and are producing eggs. Infrapopulation will be defined as all of the parasites of a single species in one host (Esch and Fernandez, 1993). In this study I will define 2 major types of infrapopulations within each fish host, they are the parenteric infrapopulation (located

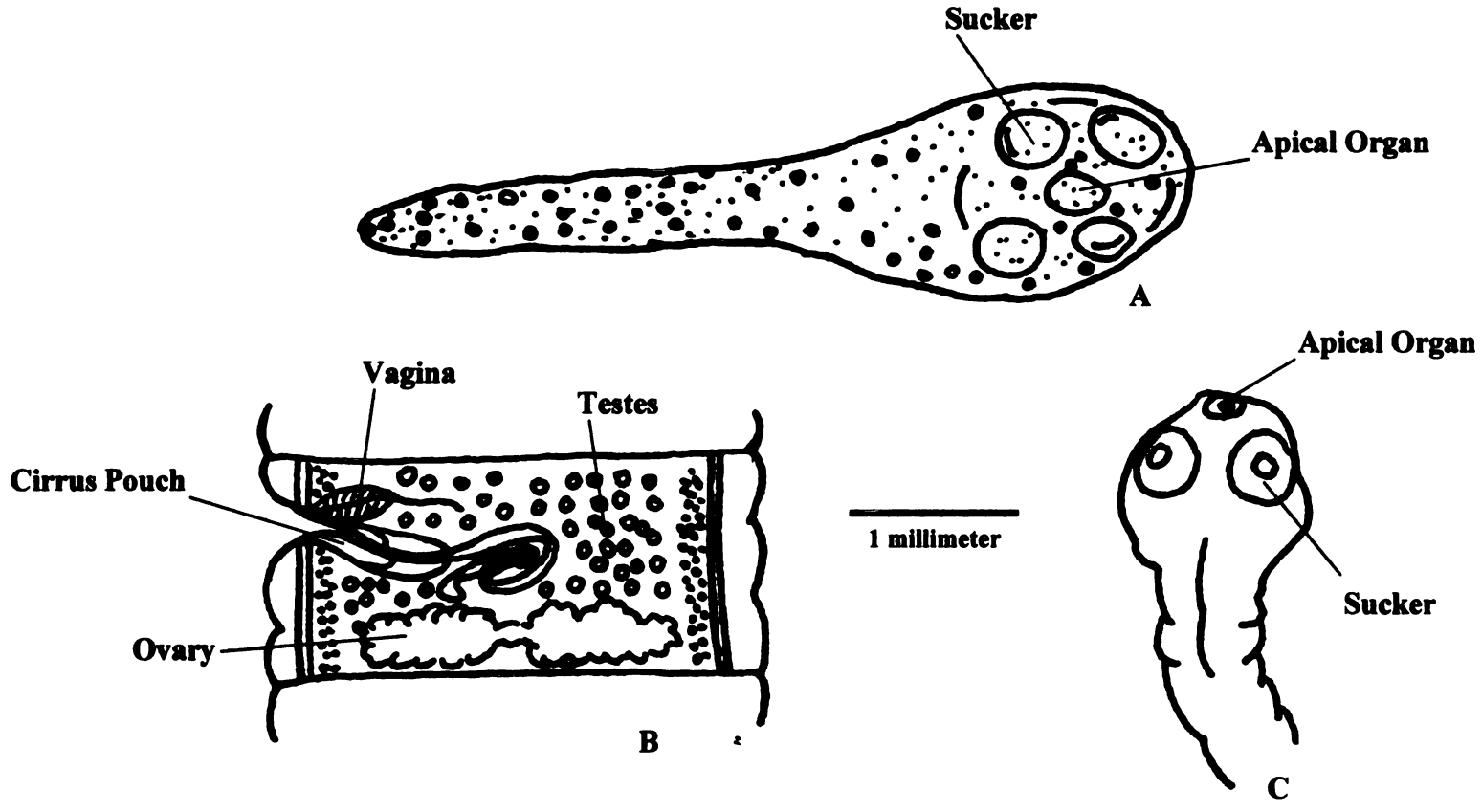


**Figure 3. Bass tapeworm; A) plerocercoid – initial and middle, B) adult proglottid, and C) scolex.**

outside the digestive tract) and enteric infrapopulation (located inside the digestive tract). Both infrapopulations are comprised of several microhabitats. The parenteric infrapopulation is comprised of six microhabitats and they are the gonad (combined female and male fish), testes, ovaries, liver, spleen, and mesentery. Worms recovered from these microhabitats were all plerocercoids (initial or middle). The enteric infrapopulation is comprised of two microhabitats and they are the pyloric ceca and small intestine. Worms recovered from these microhabitats were of three different developmental stages (terminal plerocercoid, adult, and gravid).

**Data Analysis**

A three-way nonparametric ANOVA was used to evaluate differences in the mean intensity and test for interaction between fish species (smallmouth bass and largemouth bass), sex, and microhabitat. A two-way nonparametric ANOVA and Tukey's posthoc test was used to evaluate differences in the mean intensity and test for interaction between sex and microhabitat within fish species. Further analyses within fish species were done by rank transforming the data and using a one-way ANOVA and Tukey's posthoc test for multiple comparisons. A Mann–Whitney *U*-test was used to compare overall mean intensity of *P. ambloplitis* between male and female fish of the same species and overall mean intensity among fish species. A Kruskal–Wallis nonparametric one-way ANOVA test was used to compare mean intensity and fish lengths among months sampled. Paired and unpaired t-tests were used to compare male and female fish lengths. Chi-square analysis was performed to compare the prevalence of intestinal

worms in smallmouth bass for each month to look for a seasonal pattern in the summer and fall, and to compare the prevalence of worms found in rock bass and bluegill. A Spearman's rank correlation coefficient was generated to investigate if a correlation existed between the number of worms and fish length. All mean intensity and mean abundance values are expressed as a mean ± standard deviation (SD). All descriptive and statistical calculations were done using E-Z Stat for windows® version 1.0.1; Systat 10® for windows; and PC – SAS version 8.1® for windows.

# RESULTS

## THE DEFINITIVE HOSTS

### Smallmouth Bass - Descriptive Statistics

A total of 54 (32 female and 22 male) smallmouth bass was collected in June – September 2000 and in May - June 2001 and examined for *P. ambloplitis* from Gull Lake. The number of fish examined, mean lengths and length ranges per month can be found in Appendix B. The mean length (mm) for all fish was 223.1 ± 42.1. The mean length for female and male fish was 224.9 ± 41.7 and 218.9 ± 42.8, respectively. There was no statistical difference between the lengths of female and male fish (Unpaired t-test, t = 0.514, d.f. = 52, $P$ = 0.608). The mean length of smallmouth bass, per month, significantly varied over the June – September 2000 sampling period (Kruskal-Wallis test, $H$ =26.6, d.f. = 3, $P < 0.001$); fish from 2001 were not included in this analysis because only three fish were examined in two months. This difference occurred because the fish sampled in September 2000 were smaller than fish sampled from other months. The mean lengths of smallmouth bass in 2000 and 2001 were 221.4 ± 42.5 and 250.0 ± 18.1, respectively. There was no statistically significant difference in the mean length between 2000 and 2001 (Unpaired t-test, t = -1.15, d.f. = 52, $P$ = 0.255).

### *Proteocephalus ambloplitis* in Smallmouth Bass

The overall prevalence and mean intensity of *P. ambloplitis* in smallmouth bass was 100% and 72.5 ± 44.8, respectively, in 2000 - 2001. The mean intensity of *P.*

*ambloplitis* in female and male fish was 80.4 ± 48.6 and 60.9 ± 36.7, respectively. There was a statistically significant difference in the mean intensity of *P. ambloplitis* among the months sampled in 2000 (Kruskal-Wallis test, $H = 13.8$, d.f. = 3, $P = 0.003$); fish from 2001 were not included in this comparison because the sample sizes were too small (Figure 4). This difference occurred because the fish in September 2000 were statistically smaller than fish sampled from other months, and they had fewer worms. The mean intensity of *P. ambloplitis* was not significantly different during June, July, and August 2000 (Kruskal-Wallis test, $H = 0.972$, d.f. = 2, $P = 0.615$). The mean intensity of *P. ambloplitis* in 2000 and 2001 were 73.7 ± 45.4 and 52.3 ± 31.5, respectively. There was no statistically significant difference in the mean intensity between the years 2000 and 2001 (Mann-Whitney *U*-test, $U = 97$, d.f. = 52, $P = 0.459$) however; these results may be biased since only two fish were examined in 2001. A total of 3,926 *P. ambloplitis* was found in smallmouth bass, including all life stages. The number of *P. ambloplitis* from each microhabitat is in Figure 5. A significant correlation did exist between fish length and the number of *P. ambloplitis* (Spearman's correlation, $r_s = 0.497$, $P < 0.001$), Figure 6.

**Parenteric Microhabitats in Smallmouth Bass**

The prevalence, mean intensity, and mean abundance of *P. ambloplitis* in each microhabitat of combined female and male fish (Table 1), only female fish (Table 2), and only male fish (Table 3) were calculated. A total of 3,581 worms were recovered from parenteric microhabitats. This accounts for 91.2% of all the worms recovered from this

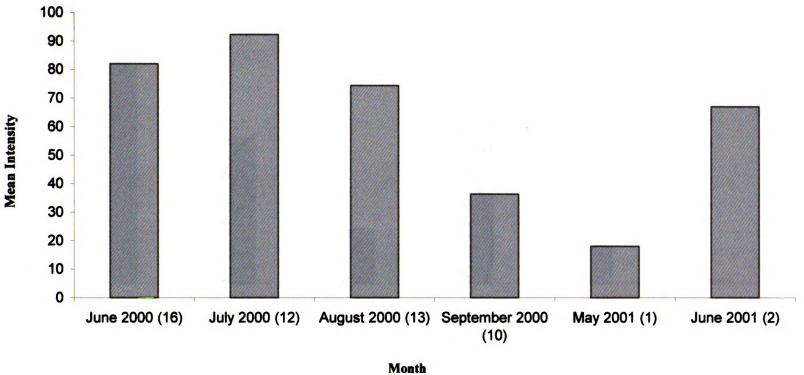


**Figure 4. Mean intensity (number of smallmouth bass examined) per month for *Proteocephalus amblopl itis* collected in 2000 and 2001.**

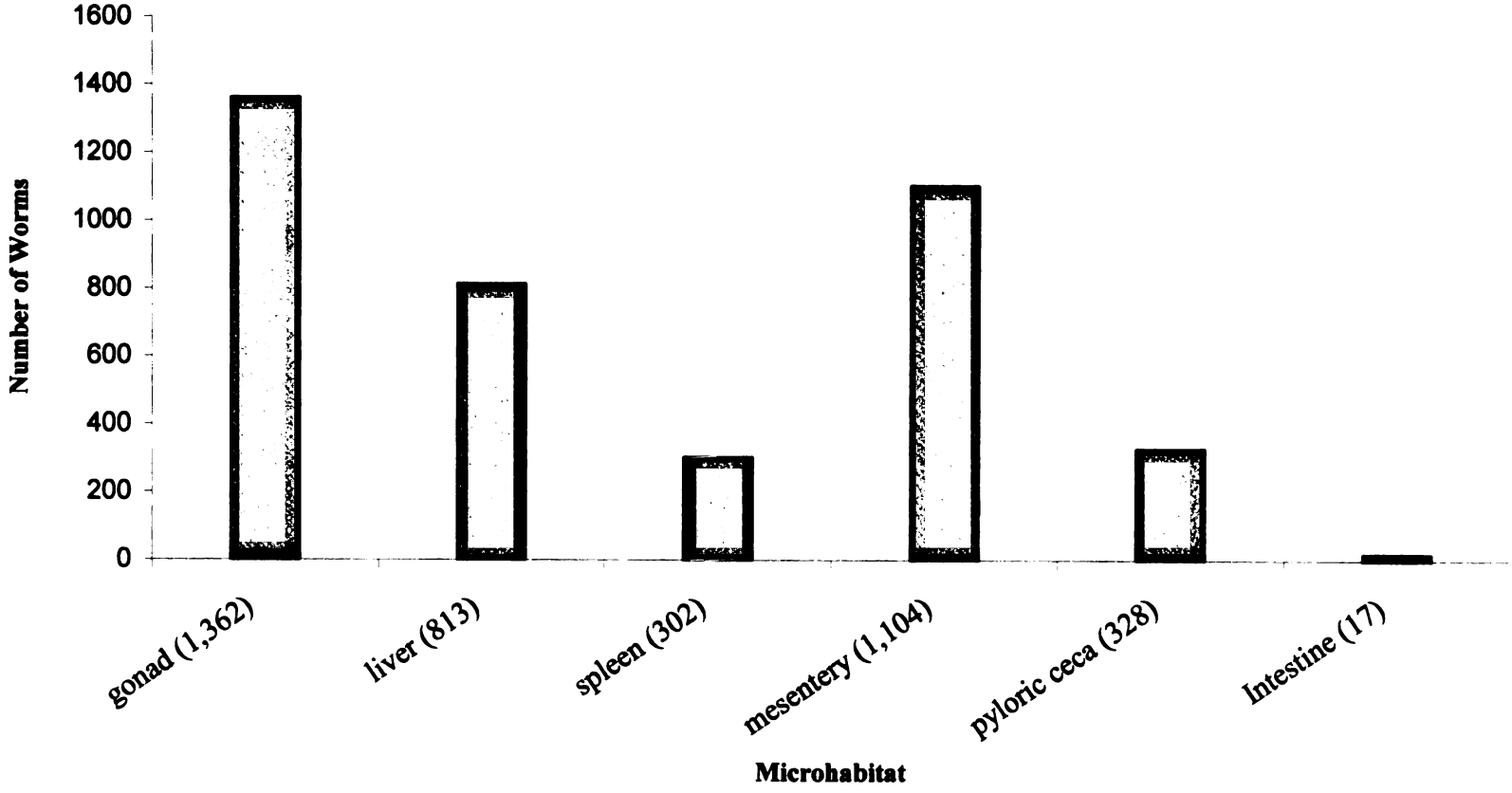


**Figure 5. Six microhabitats where *Proteocephalus ambloplitis* was found (number of worms removed) in smallmouth bass collected in 2000 and 2001.**

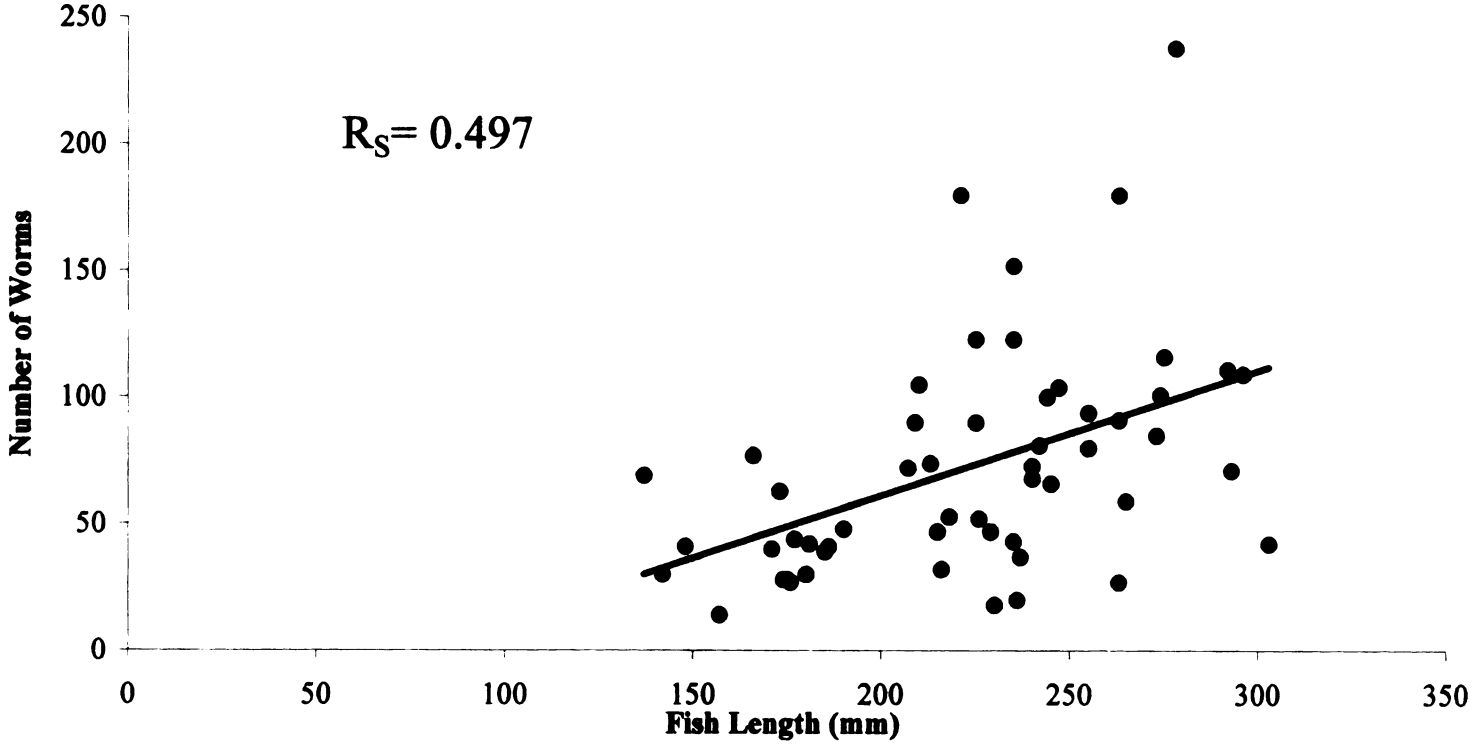


**Figure 6. Spearman's rank correlation coefficient showing a relationship between length and number of worms in smallmouth bass collected in 2000 and 2001.**

parenteric microhabitats. This accounts for 91.2% of all the worms recovered from this fish species. All worms found in parenteric microhabitats were middle plerocercoid II stages. A nonparametric two-way ANOVA was used to evaluate differences in mean intensity and test for interaction between two main effects (sex and microhabitat) in smallmouth bass. A statistically significant difference was found between the sexes (2-Way ANOVA, $F = 4.63$, d.f. = 1, $P = 0.032$) and between microhabitats (2-Way ANOVA, $F = 19.99$, d.f. = 3, $P < 0.0001$). Since there was significant interaction between main effects (2-Way ANOVA, $F = 4.85$, d.f. = 3, $P = 0.028$) no further analyses could be done to test for differences between the sexes.

**Table 1. The prevalence, mean intensity, mean abundance, and range of *Proteocephalus ambloplitis* from 6 microhabitats in smallmouth bass collected in 2000 - 2001.**

| Microhabitat | Prevalence | Mean Intensity ± SD | Mean Abundance ± SD | Range |
|---|---|---|---|---|
| **Parenteric** | | | | |
| Gonads | 96 | 26.2 ± 18.6 | 25.2 ± 18.9 | 0 - 76 |
| Liver | 100 | 15.1 ± 13.4 | 15.1 ± 13.4 | 0 - 77 |
| Spleen | 85 | 4.5 ± 6.7 | 5.6 ± 6.6 | 0 - 38 |
| Mesentery | 100 | 20.4 ± 15.5 | 20.4 ± 15.5 | 3 - 86 |
| **Enteric** | | | | |
| Pyloric ceca | 50 | 12.1 ± 14.1 | 6.1 ± 11.6 | 0 - 31 |
| Intestine | 18.5 | 1.7 ± 0.82 | 0.31 ± 0.74 | 0 - 39 |

When analyzing the mean intensity of *P. ambloplitis* from parenteric microhabitats found in only female fish (Table 2) highly significant differences occurred (1-Way ANOVA, $F = 31.59$, d.f. = 3, $P < 0.0001$). A statistically significant difference in the mean intensity existed between the ovaries and liver, ovaries and spleen, and ovaries and mesentery ($P < 0.05$ for all pair-wise comparisons, Tukey's test).

When analyzing the mean intensity of *P. ambloplitis* from parenteric microhabitats found in only male fish (Table 3) a significant difference occurred (1-Way ANOVA, $F = 4.72$, d.f. = 3, $P < 0.001$). A statistically significant difference in the mean intensity existed between the testes and spleen ($P < 0.05$, Tukey's test). Significant differences did not occur when the testes were compared to the liver and mesentery ($P > 0.10$ for all pair-wise comparisons, Tukey's test).

**Table 2. The prevalence, mean intensity, mean abundance, and range of *Proteocephalus ambloplitis* from 6 microhabitats in female smallmouth bass collected in 2000 - 2001.**

| Microhabitat | Prevalence | Mean Intensity ± SD | Mean Abundance ± SD | Range |
|---|---|---|---|---|
| **Parenteric** | | | | |
| Ovaries | 94 | 34.0 ± 18.9 | 31.9 ± 20.1 | 0 - 76 |
| Liver | 100 | 14.9 ± 14.4 | 14.9 ± 14.4 | 3 - 77 |
| Spleen | 84 | 5.5 ± 4.3 | 4.7 ± 4.4 | 0 - 19 |
| Mesentery | 100 | 21.5 ± 18.2 | 21.5 ± 18.2 | 4 - 86 |
| **Enteric** | | | | |
| Pyloric ceca | 44 | 12.6 ± 10.1 | 5.5 ± 9.1 | 0 - 31 |
| Intestine | 25 | 1.75 ± 0.88 | 0.43 ± 0.87 | 0 - 3 |

**Table 3. The prevalence, mean intensity, mean abundance, and range of *Proteocephalus ambloplitis* from 6 microhabitats in male smallmouth bass collected in 2000 - 2001.**

| Microhabitat | Prevalence | Mean Intensity ± SD | Mean Abundance ± SD | Range |
|---|---|---|---|---|
| **Parenteric** | | | | |
| Testes | 100 | 15.5 ± 11.8 | 15.5 ± 11.8 | 1 - 43 |
| Liver | 100 | 15.2 ± 11.9 | 15.2 ± 11.9 | 1 - 52 |
| Spleen | 86 | 8.1 ± 9.0 | 6.9 ± 8.8 | 0 - 38 |
| Mesentery | 100 | 18.9 ± 10.5 | 18.9 ± 10.5 | 3 - 47 |
| **Enteric** | | | | |
| Pyloric ceca | 38 | 7.7 ± 7.3 | 2.9 ± 5.8 | 0 - 21 |
| Intestine | 3 | 2.0 | 0.06 ± 0.35 | 0 - 2 |

**Enteric Microhabitats in Smallmouth Bass**

A total of 345 worms were recovered from enteric microhabitats. This accounts for 8.7% of all the worms recovered from this fish species. Developmentally, 122 (35.3%) terminal plerocercoid II, 64 (18.5%) adult, and 159 gravid (46.0%) worms were found in smallmouth bass. The mean intensity of all life stages of *P. ambloplitis* from enteric microhabitats, in combined female and male fish, was calculated (Table 1). A statistically significant difference in the mean intensity existed between the pyloric ceca and small intestine (Mann-Whitney *U*-test, $U = 226$, d.f. = 35, $P < 0.001$). The overall prevalence of adult and gravid worms in smallmouth bass was 43%. When the prevalence of combined adult and gravid *P. ambloplitis* was compared among months sampled from 2000 - 2001 significant differences were found ($\chi^2 = 18.19$, d.f. = 4, P = 0.0025). The prevalence was highest in June 2001, however this prevalence may be misleading since only two fish were examined (Figure 7). When the prevalence of adult and gravid *P. ambloplitis* was compared among months in 2000 significant differences were found ($\chi^2 = 14.86$, d.f. = 3, P = 0.0025), Figure 7.

**Largemouth Bass - Descriptive Statistics**

A total of 88 (44 female and 44 male) largemouth bass was collected in April – September 2000 and in April – July 2001 and examined for *P. ambloplitis* from Gull Lake. The number of fish examined, mean lengths and length ranges per month can be found in Appendix C. The mean length (mm) for all fish was 214.7 ± 39.7. The mean

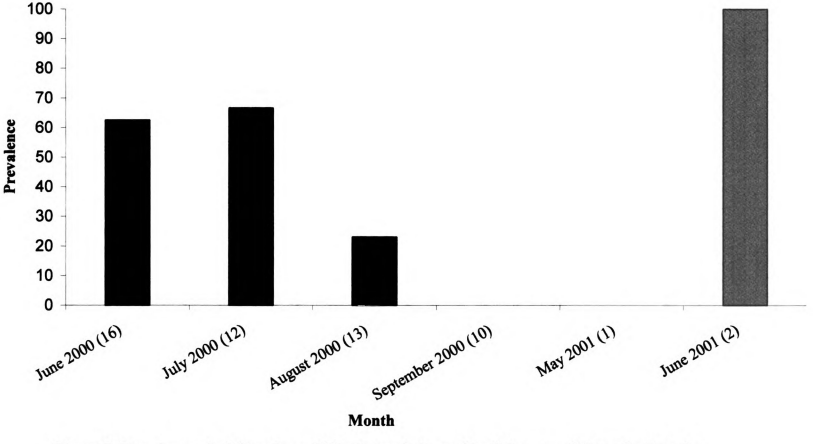


**Figure 7. Prevalence of adult and gravid *Proteocephalus amblopl itis* removed from the digestive tract of smallmouth bass (number of fish examined) for each month sampled in 2000 and 2001.**

length for female and male fish was 226.3 ± 45.3 and 203.2 ± 29.4, respectively. A significant difference existed between the lengths of female and male fish (Paired t-test, t = 3.5, d.f. = 43, $P = 0.001$). This is probably due to the April 2001 sample, which was primarily made up of large females (Appendix C). The mean length of largemouth bass, per month, was significantly different over the two-year sampling period (Kruskal-Wallis test, $H = 40.3$, d.f. = 6, $P < 0.001$). The mean lengths of largemouth bass in 2000 and 2001 were 199.9 ± 27.4 and 231.0 ± 44.8, respectively. The mean length was significantly larger in the fish sampled from 2001 compared to 2000 (Mann-Whitney *U*-test, $U = 1{,}422$, d.f. = 86, $P < 0.001$). Again, this occurred because the fish sampled from April 2001 were much larger than fish examined in any other months.

### *Proteocephalus ambloplitis* in Largemouth Bass

The overall prevalence and mean intensity of *P. ambloplitis* in largemouth bass was 100% and 18.1 ± 12.9, respectively, in 2000 - 2001. The mean intensity of *P. ambloplitis* in female and male fish was 17.9 ± 12.8 and 18.4 ± 13.2, respectively. There was no statistical difference between the mean intensity of *P. ambloplitis* in female and male fish (Paired t-test, t = -0.177, d.f. = 43, $P = 0.859$). The mean intensity was not significantly different among the months sampled 2000 – 2001 (Kruskal-Wallis test, $H = 9.1$, d.f. = 6, $P = 0.163$), Figure 8; the sample from September 2000 was removed because the sample size was too small. The mean intensity of *P. ambloplitis* in 2000 and 2001 was 18.1 ± 14.4 and 18.3 ± 11.3, respectively. There was no statistically significant difference in the mean intensity between the years 2000 and 2001 (Mann-Whitney *U*-test,

$U$ = 1,042, d.f. = 86, $P$ = 0.526) however these results may be biased since too few fish were collected in April, July and September 2000. A significant correlation did not exist between fish length and number of *P. ambloplitis* (Spearman's correlation, $r_s$ = -0.168, $P$ = 0.116). A total of 1,607 *P. ambloplitis* was found in largemouth bass, including all life stages. The number of *P. ambloplitis* removed from each microhabitat can be found in Figure 9.

**Parenteric Microhabitats in Largemouth Bass**

The prevalence, mean intensity, and mean abundance of *P. ambloplitis* within each microhabitat of combined female and male fish (Table 4), only female fish (Table 5), and only male fish (Table 6) was calculated. A total of 1,554 worms were recovered from parenteric habitats. This accounts for 96.7% of all the worms recovered from this fish species. All worms found in parenteric microhabitats were middle plerocercoid II stages. A nonparametric two-way ANOVA was used to evaluate differences in mean intensity and test for interaction between two main effects (sex and microhabitat) in largemouth bass. A statistically significant difference was found between the microhabitats (2-Way ANOVA, $F$ = 27.52, d.f. = 3, $P$ < 0.0001). No statistically significant differences were found between the sexes (2-Way ANOVA, $F$ = 0.02, d.f. = 1, $P$ = 0.889). Since there was no significant interaction between main effects (2-Way ANOVA, $F$ = 0.93, d.f. = 3, $P$ = 0.475) further analyses could be done to test for differences between microhabitats (Table 4). A statistically significant difference in the mean intensity existed between the liver and gonads, and the mesentery and gonads ($P$ <

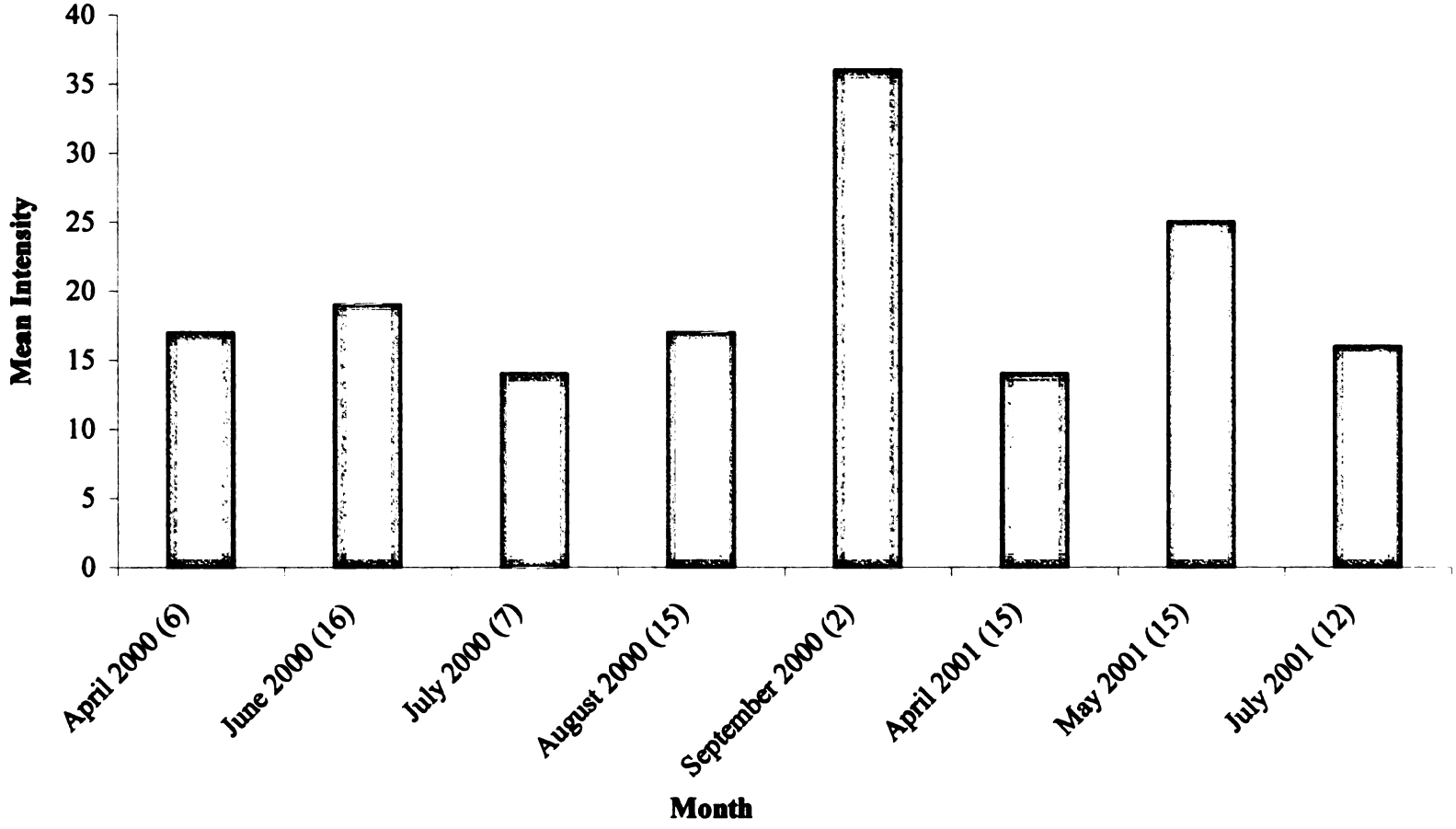


**Figure 8. Mean intensity (number of largemouth bass examined) per month for *Proteocephalus amblopitis* collected in 2000 and 2001.**

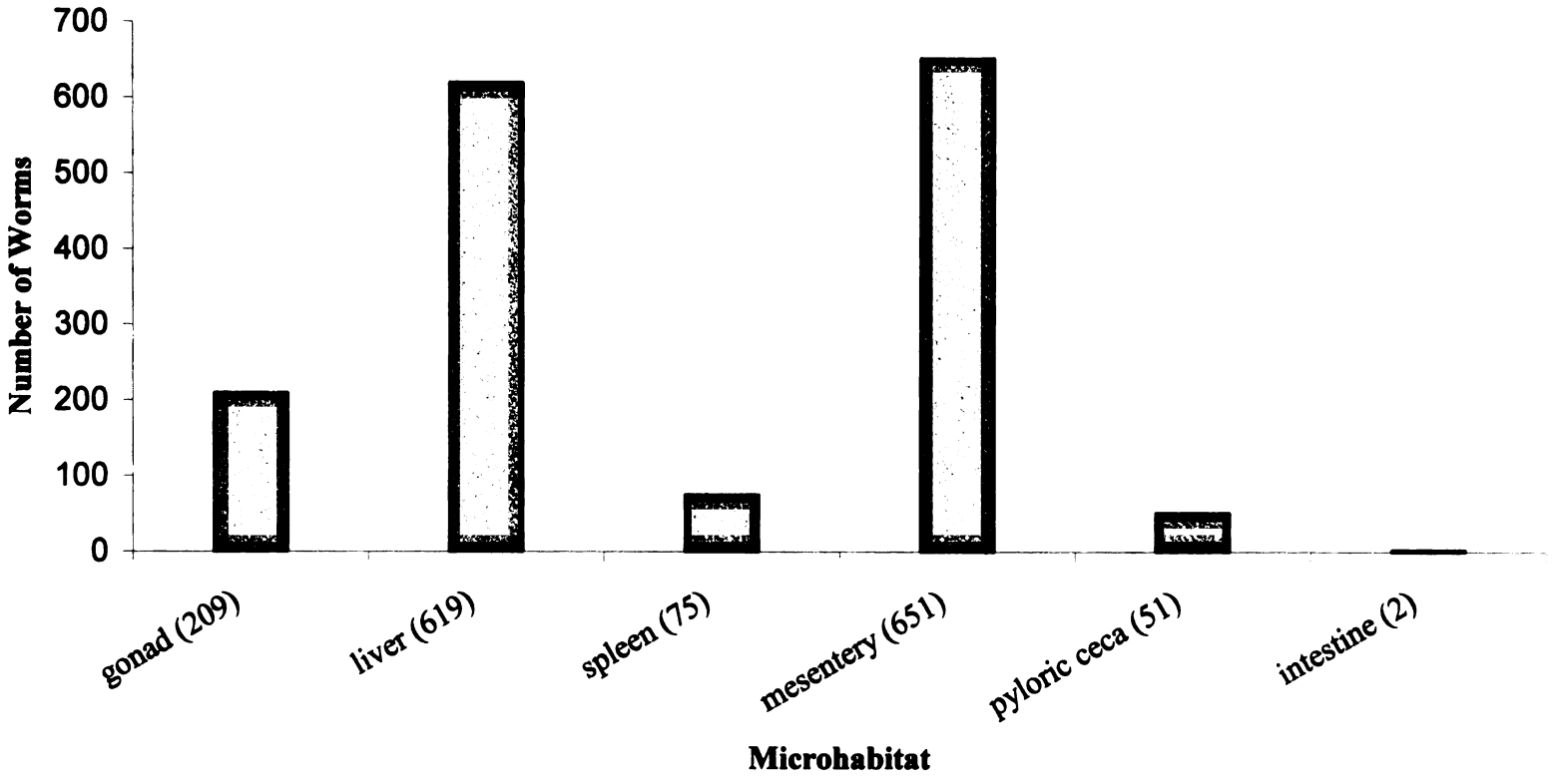


**Figure 9. Six microhabitats where *Proteocephalus ambloplitis* was found (number of worms removed) in largemouth bass collected in 2000 and 2001.**

0.05, for all pair-wise comparisons, Tukey's test). Significant differences did not occur when the gonads were compared to the spleen ($P > 0.05$, Tukey's test).

**Table 4. The prevalence, mean intensity, mean abundance, and range of *Proteocephalus ambloplitis* from 6 microhabitats in largemouth bass collected in 2000 - 2001.**

| Microhabitat | Prevalence | Mean Intensity ± SD | Mean Abundance ± SD | Range |
|---|---|---|---|---|
| **Parenteric** | | | | |
| Gonads | 64 | 3.7 ± 3.0 | 2.3 ± 3.1 | 0 - 19 |
| Liver | 86 | 8.1 ± 8.4 | 7.0 ± 8.3 | 0 - 44 |
| Spleen | 41 | 2.1 ± 1.5 | 0.85 ± 1.4 | 0 - 7 |
| Mesentery | 93 | 7.9 ± 7.8 | 7.3 ± 7.8 | 0 - 44 |
| **Enteric** | | | | |
| Pyloric ceca | 13 | 4.4 ± 3.5 | 0.55 ± 1.9 | 0 - 12 |
| Intestine | 2 | 1.0 | 0.02 ± 0.14 | 0 - 1 |

**Table 5. The prevalence, mean intensity, mean abundance, and range of *Proteocephalus ambloplitis* from 6 microhabitats in female largemouth bass collected in 2000 - 2001.**

| Microhabitat | Prevalence | Mean Intensity ± SD | Mean Abundance ± SD | Range |
|---|---|---|---|---|
| **Parenteric** | | | | |
| Ovaries | 70 | 3.2 ± 1.9 | 2.3 ± 2.2 | 0 - 9 |
| Liver | 86 | 8.2 ± 9.0 | 3.2 ± 2.0 | 0 - 44 |
| Spleen | 41 | 1.8 ± 1.5 | 0.7 ± 1.3 | 0 - 7 |
| Mesentery | 87 | 7.1 ± 6.0 | 4.5 ± 6.1 | 0 - 34 |
| **Enteric** | | | | |
| Pyloric ceca | 18 | 5.5 ± 3.5 | 1.0 ± 2.5 | 0 - 12 |
| Intestine | 2 | 1.0 | 0.02 ± 0.15 | 0 - 1 |

**Enteric Microhabitats in Largemouth Bass**

A total of 53 worms were recovered from enteric microhabitats. This accounts for 3.3% of all the worms recovered from this fish species. All stages found in the digestive tract were terminal plerocercoid II; no adult or gravid worms were found. Worms were

**Table 6. The prevalence, mean intensity, mean abundance, and range of *Proteocephalus ambloplitis* from 6 microhabitats in male largemouth bass collected in 2000 - 2001.**

| Microhabitat | Prevalence | Mean Intensity ± SD | Mean Abundance ± SD | Range |
|---|---|---|---|---|
| **Parenteric** | | | | |
| Testes | 57 | 4.3 ± 3.9 | 2.4 ± 3.7 | 0 - 19 |
| Liver | 86 | 8.1 ± 7.9 | 6.9 ± 7.8 | 0 - 31 |
| Spleen | 50 | 3.9 ± 3.3 | 1.9 ± 3.0 | 0 - 5 |
| Mesentery | 98 | 8.6 ± 9.2 | 8.4 ± 9.1 | 0 - 44 |
| **Enteric** | | | | |
| Pyloric ceca | 9 | 2.2 ± 1.5 | 0.20 ± 0.76 | 0 - 4 |
| Intestine | 0 | 0 | 0 | 0 |

found more often in the pyloric ceca than in the intestine in which only two worms were found (Table 4).

**Descriptive Comparisons Between Smallmouth Bass and Largemouth Bass**

The mean length (mm) for smallmouth and largemouth bass were 223.1 ± 42.1 and 214.7 ± 39.7, respectively. No statistical difference existed between the lengths of these two fish species (Unpaired t-test, t = 1.18, d.f. = 140, $P$ = 0.239). Female smallmouth and largemouth bass had mean lengths of 224.9 ± 41.7 and 226.3 ± 45.3, respectively, and they were not significantly different (Unpaired t-test, t = - 0.132, d.f. = 74, $P$ = 0.894). Male smallmouth bass and largemouth bass had mean lengths of 218.9 ± 42.8 and 203.2 ± 29.4, respectively, and they were not significantly different (Mann-Whitney $U$-test, $U$ = 590, d.f. = 64, $P$ = 0.149). Similar lengths indicate similar ages of fish and thus eliminating any age biases.

**Comparisons of *Proteocephalus ambloplitis* between smallmouth bass and largemouth bass**

The overall mean intensity of *P. ambloplitis* in smallmouth bass and largemouth bass was 72.5 ± 44.8 and 18.1 ± 12.9, respectively. The overall mean intensities of *P. ambloplitis* were significantly higher in the smallmouth bass than in largemouth bass (Mann-Whitney *U*-test, $U = 4{,}452$, d.f. = 140, $P < 0.001$). The prevalence and mean intensity of *P. ambloplitis* for combined female and male smallmouth and largemouth bass by microhabitat are in Table 7. The prevalence and mean intensity of *P. ambloplitis* removed from parenteric microhabitats in female smallmouth and largemouth bass was compiled (Table 8). The overall mean intensity of *P. ambloplitis* in female smallmouth and largemouth bass was 80.4 ± 48.6 and 17.9 ± 12.8, respectively. The mean intensity of *P. ambloplitis* was significantly higher in female smallmouth bass (Mann-Whitney *U*-test, $U = 1{,}352$, d.f. = 74, $P < 0.001$) than female largemouth bass. The prevalence and mean intensity of *P. ambloplitis* removed from parenteric microhabitats in male smallmouth and largemouth bass was compiled (Table 9). The overall mean intensity of *P. ambloplitis* in male smallmouth and largemouth bass was 60.9 ± 36.7 and 18.4 ± 13.2, respectively. The mean intensity of *P. ambloplitis* was significantly higher in male smallmouth bass (Mann-Whitney *U*-test, $U = 878$, d.f. = 63, $P < 0.001$) than male largemouth bass.

A nonparametric three-way ANOVA was used to evaluate differences in mean intensity and test for interaction among three main effects (sex, microhabitat, and species) between smallmouth and largemouth bass. A statistically significant difference was

found among the microhabitats (3-Way ANOVA, $F = 29.09$, d.f. = 3, $P < 0.0001$) and between species (3-Way ANOVA, $F = 203.86$, d.f. = 1, $P < 0.0001$). No statistically significant differences were found between the sexes (3-Way ANOVA, $F = 3.2$, d.f. = 1, $P = 0.0744$). Since there was significant interaction between all three main effects (3-Way ANOVA, $F = 6.41$, d.f. = 3, $P = 0.0003$) no further analyses could be done to test for differences in the mean intensity of *P. ambloplitis* between the two fish species.

**Table 7. The prevalence (P) and mean intensity (MI) of *Proteocephalus ambloplitis* in smallmouth bass and largemouth bass examined from Gull Lake Michigan collected in 2000 – 2001.**

| | Smallmouth Bass | | Largemouth Bass | |
|---|---|---|---|---|
| **Microhabitat** | **P (%)** | **MI ± SD** | **P (%)** | **MI ± SD** |
| **Parenteric** | | | | |
| Gonad | 96 | 26.2 ± 18.6 | 64 | 3.7 ± 3.0 |
| Liver | 100 | 15.1 ± 13.4 | 86 | 8.1 ± 8.4 |
| Spleen | 85 | 4.5 ± 6.7 | 93 | 7.9 ± 7.8 |
| Mesentery | 100 | 20.4 ± 15.5 | 41 | 2.1 ± 1.5 |
| **Enteric** | | | | |
| Pyloric ceca | 50 | 12.1 ± 14.1 | 13 | 4.4 ± 3.5 |
| Intestine | 18.5 | 1.7 ± 0.82 | 2 | 1.0 |

**Table 8. The prevalence (P) and mean intensity (MI) of *Proteocephalus ambloplitis* from parenteric microhabitats in female smallmouth and largemouth bass examined from Gull Lake, Michigan, collected in 2000 – 2001.**

| | Smallmouth Bass | | Largemouth Bass | |
|---|---|---|---|---|
| **Microhabitat** | **P (%)** | **MI ± SD** | **P (%)** | **MI ± SD** |
| Ovaries | 94 | 34.0 ± 18.9 | 70 | 3.2 ± 1.9 |
| Liver | 100 | 14.9 ± 14.4 | 86 | 8.2 ± 9.0 |
| Spleen | 84 | 5.5 ± 4.3 | 41 | 1.8 ± 1.5 |
| Mesentery | 100 | 21.5 ± 18.2 | 87 | 7.1 ± 6.0 |

**Table 9. The prevalence (P) and mean intensity (MI) of *Proteocephalus ambloplitis* from parenteric microhabitats in male smallmouth and largemouth bass examined from Gull Lake, Michigan, collected in 2000 – 2001.**

| | Smallmouth Bass | | Largemouth Bass | |
|---|---|---|---|---|
| **Microhabitat** | **P (%)** | **MI ± SD** | **P (%)** | **MI ± SD** |
| Testes | 100 | 15.5 ± 11.8 | 57 | 2.4 ± 3.7 |
| Liver | 100 | 15.2 ± 11.9 | 86 | 6.9 ± 7.8 |
| Spleen | 86 | 8.1 ± 9.0 | 50 | 1.9 ± 3.0 |
| Mesentery | 100 | 18.9 ± 10.5 | 98 | 8.4 ± 9.1 |

## THE SECOND INTERMEDIATE HOSTS

### Rock Bass - Descriptive Statistics

A total of 50 (25 female and 25 male) rock bass was collected in April – September 2000 and examined for *P. ambloplitis* from Gull Lake. The number of fish examined, mean lengths and length ranges per month can be found in Appendix D. The mean length (mm) for all fish was 151.7 ± 23.4. The mean length for female and male fish was 153.4 ± 26.2 and 150.2 ± 20.7, respectively. There was no significant difference between the lengths of female and male fish (Paired t-test, t = 0.504, d.f. = 24, P = 0.618). The mean lengths of rock bass, per month, were significantly different over the 6-month sampling period (Kruskal-Wallis test, $H$ = 20.4, d.f. = 5, $P$ <0.001), with July and April having fish with the largest mean lengths.

### *Proteocephalus ambloplitis* in Rock Bass

The overall prevalence and mean intensity of *P. ambloplitis* in rock bass was 32% and 3.5 ± 3.6, respectively, in 2000. Only the initial plerocercoid II was found in rock bass. The mean intensity of *P. ambloplitis* in female and male fish was 5.2 ± 3.7 and 2.8 ± 3.4, respectively. There was no statistical difference between the mean intensity of *P. ambloplitis* in female and male fish (Mann-Whitney $U$-test, $U$ = 40, d.f. = 14, $P$ = 0.176). A total of 57 *P. ambloplitis* was found in rock bass. A significant correlation did not exist between fish length and number of *P. ambloplitis* (Spearman's correlation, $r_s$ = 0.434, $P$ = 0.092). The prevalence, mean intensity, and mean abundance of *P.*

*ambloplitis* from each microhabitat of combined female and male fish (Table 10) was calculated.

**Table 10. The prevalence, mean intensity, mean abundance, and range of *Proteocephalus ambloplitis* from 4 microhabitats in rock bass collected in 2000.**

| Microhabitat | Prevalence | Mean Intensity ± SD | Mean Abundance ± SD | Range |
|---|---|---|---|---|
| **Parenteric** | | | | |
| Gonad | 4 | 2.0 ± 1.4 | 0.08 ± 0.44 | 0 - 3 |
| Liver | 22 | 2.0 ± 1.2 | 0.44 ± 1.0 | 0 - 4 |
| Mesentery | 10 | 5.4 ± 2.5 | 0.54 ± 1.7 | 0 - 8 |
| Spleen | 4 | 1.0 | 0.04 ± 0.19 | 0 - 1 |

**Bluegill - Descriptive Statistics**

A total of 50 (24 female and 26 male) bluegill was collected in May – September 2000 and examined for *P. ambloplitis* from Gull Lake. The number of fish examined, mean lengths and length ranges per month can be found in Appendix E. The mean length (mm) for all fish was 122.4 ± 24.0. The mean length for female and male fish was 115.2 ± 25.8 and 129.1 ± 20.5, respectively. There was a significant difference between the lengths of female and male fish (Unpaired t-test, t = 2.11, d.f. = 48, P = 0.039). The mean lengths of bluegill, per month, were significantly different over the 5-month sampling period (Kruskal-Wallis test, $H$ = 17.2, d.f. = 3, $P < 0.001$), with May and August having fish with the largest mean lengths.

***Proteocephalus ambloplitis* in Bluegill**

The overall prevalence and mean intensity of *P. ambloplitis* in bluegill was 44%

and 1.8 ± 1.9, respectively, in 2000. Only the initial plerocercoid II was found in bluegill. The mean intensity of *P. ambloplitis* in female and male fish was 2.2 ± 2.4 and 1.3 ± 0.5, respectively. There was no statistical difference between the mean intensity of *P. ambloplitis* in female and male fish (Mann-Whitney *U*-test, $U = 70.5$, d.f. = 20, $P = 0.446$). A total of 40 *P. ambloplitis* was found in bluegill. A significant correlation did not exist between fish length and number of *P. ambloplitis* (Spearman's correlation, $r_s = 0.584$, $P = 0.565$). The prevalence, mean intensity, and mean abundance of *P. ambloplitis* from the two microhabitats of combined female and male fish (Table 11) was calculated. Only the liver and mesentery were found infected and no statistical difference in the mean intensity of *P. ambloplitis* was found between these microhabitats (Mann-Whitney *U*-test, $U = 38$, d.f. = 20, $P = 0.900$). There was no statistically significant difference in the mean intensity of *P. ambloplitis* when compared between rock bass and bluegill (Mann-Whitney *U*-test, $U = 206$, d.f. = 36, $P = 0.385$). There was no statistically significant difference in the number of worms when compared between rock bass and bluegill ($\chi^2 = 2.58$, d.f. = 1, $P > 0.05$).

**Table 11. The prevalence, mean intensity, mean abundance, and range of *Proteocephalus ambloplitis* from 2 microhabitats in bluegill collected in 2000.**

| Microhabitat | Prevalence (%) | Mean Intensity ± SD | Mean Abundance ± SD | Range |
|---|---|---|---|---|
| **Parenteric** | | | | |
| Liver | 36 | 1.7 ± 1.6 | 0.64 ± 1.3 | 0 - 8 |
| Mesentery | 8 | 1.5 ± 0.57 | 0.12 ± 0.43 | 0 - 2 |

## DISCUSSION

Esch et al. (1975) suggested that as water temperature rose from 4° C to 7° C in Gull Lake, parenteric plerocercoids moved from the viscera to the digestive tract of smallmouth bass, thus showing a seasonal pattern in movement. In the present study a seasonal pattern would indicate that in spring (April and May) the worms begin to move from the viscera into the digestive tract, as summer progresses (June – August) the prevalence of worms in the digestive tract increases, and as fall (September) approaches the number of worms in the digestive tract decreases. In the year 2000 the prevalence (P) of adult and gravid worms in June was (P = 63%), then peaked in July (P = 67%), and declined in August (P = 23%) with no enteric worms found in September. While these data generated in the present study do indicate a seasonal pattern, a relationship to water temperature cannot be made. In 2000 and 2001, the water temperature reached 10° C in late March before sampling was done.

Esch (1971) reported that the prevalence of adult *P. ambloplitis* in smallmouth bass and largemouth bass was 43% and 12%, respectively, from Gull Lake. In the present study adult and gravid *P. ambloplitis* were never reported from the digestive tract of largemouth bass. However, the terminal plerocercoid II was found in the digestive tract of largemouth bass in the present study. It is believed that these worms would have developed into adult worms if the fish had not been caught. Similar to what I found, Esch (1971) did not find adult or gravid *P. ambloplitis* in the digestive tract of rock bass. Esch (1971) found plerocercoids in all 4 fish species examined in this study, but did not give prevalences.

Esch (1971) reported that the prevalence of adult *P. ambloplitis* was 43% during

the summer months. Esch et al. (1975) demonstrated that the prevalence of adult *P. ambloplitis* reached a maximum of 50% during the summer. In the present study I report the prevalence of adult and gravid *P. ambloplitis* reached a maximum of 51% in the summer of 2000 (this is the average prevalence for June, July, and August 2000). Interestingly, the prevalence of adult and gravid *P. ambloplitis* has decreased in the largemouth bass to zero. Esch et al. (1975) reported that adult and gravid worms were never found in smallmouth bass less than 200 millimeters (mm). Adult and gravid worms occurred in fish less than 200 mm in the present study. One male fish (181 mm) from June 2000 had 6 adult worms and 5 gravid worms. Another male fish (175 mm) from August 2000 harbored 6 gravid worms.

It is not known why largemouth bass have lower mean intensities of *P. ambloplitis* compared to smallmouth bass; a possible reason may have to do with where each fish species spawns. This author speculates that worm recruitment may be highest during the fishes mating season (April – May), because the two bass species do not mate in similar habitats. However, this is merely speculation since so few fish were collected during the actual spawning times for both fish species. Smallmouth bass will nest in areas of sand, gravel or rubble while largemouth bass usually prefer soft bottoms with vegetation and other woody debris (Hubbs and Bailey, 1938). Perhaps, it is during mating time when smallmouth bass are eating more second intermediate hosts.

Neither rock bass nor bluegill was ever found in the stomachs of smallmouth and largemouth bass. The diet of smallmouth and largemouth bass was comprised primarily of crayfish, *Orconectes propinquus*, which was common in the lake (personal observation). Fingerling basses and minnows were also found in the stomach of the two

definitive host species, but much less frequently as crayfish. Since rock bass are often found in weedy, benthic habitats one might expect not to find them too often in the guts of smallmouth and largemouth bass. One would expect that open water bluegill would make up a portion of smallmouth and largemouth bass diets.

It is not known what proportion of the bass diet is comprised of other centrarchids in Gull Lake (James Dexter, personal communication). In the present study crayfish were the primary food item found in the stomach and digestive tract of basses, comprising approximately 95% of their diet. Since crayfish were abundant in the bass diet it was speculated that they may be a second intermediate host for *P. ambloplitis*. However, cestodes have never been reported as utilizing crayfish or other decapods as a second intermediate host. Twenty-two crayfish, *O. propinquus*, were collected in July 2001 from KBS-1 and examined for *P. ambloplitis* plerocercoids. None of the crayfish examined were infected with *P. ambloplitis*. Minnows were also found in the stomachs of the basses. Likewise, cyprinids have never been reported as a second intermediate host for *P. ambloplitis* (Hoffman, 1999 and Amin, 1990). It may be possible that minnows are involved in the transmission of *P. ambloplitis* to the bass definitive host. Fingerling smallmouth and largemouth bass were also found in the stomachs, but they were found even less frequently then minnows. Fingerling basses have been shown to be a potential second intermediate host through cannibalism (Szalai and Dick, 1990). Further study should be performed to examine what part fingerling bass, minnows, and crayfish play in the transmission of *P. ambloplitis*.

The mean intensity and prevalence of *P. ambloplitis* in smallmouth and largemouth bass have been reported from several locations in North America. It would

seem that infections of *P. ambloplitis* vary from each system studied, in regards to which fish host has higher mean intensities and prevalences. Amin (1990) reported, that of the 22 smallmouth and 116 largemouth bass examined in Wisconsin, prevalences were 18% and 43%, respectively. Amin and Cowen (1990) also reported that plerocercoids of *P. ambloplitis* in smallmouth and largemouth bass from Silver Lake, Wisconsin, had prevalences of 50% and 56%, respectively, and from Tichigan Lake, Wisconsin, prevalences of zero and 14%, respectively. Similar to the present study, Ingham and Dronen (1982) and Szalai and Dick (1990), from Texas and Saskatchewan, respectively, reported only finding plerocercoids of *P. ambloplitis* in largemouth bass and never any adult worms. Ingham and Dronen (1982) demonstrated that the prevalence of *P. ambloplitis* plerocercoids was as high as 50%. Szalai and Dick (1990) reported the prevalence of *P. ambloplitis* plerocercoids was highest (91%) in 2 - 4 year old largemouth bass. Eure (1976) reported finding adult worms in largemouth bass from South Carolina with the mean number of worms ranging from 0.5 – 3.0. Not similar to the present study, Joy and Madan (1989) concluded, based upon the mean intensity of *P. ambloplitis* plerocercoids, largemouth bass are the favored host species in Beech Fork Lake, Wisconsin. The prevalence of *P. ambloplitis* plerocercoids in the present study for smallmouth and largemouth bass was 100% and are the highest reported to date in North America.

Rock bass and bluegill have been shown in many studies to serve as second intermediate hosts for *P. ambloplitis*. Amin (1990) reported that *P. ambloplitis* was found to be common in rock bass from Wisconsin, and had prevalences ranging from 12 – 100% in spring, summer and fall. Harley and Keefe (1970) indicated that 11 encysted

*P. ambloplitis* were recovered in 60 bluegill from Kentucky. Cloutman (1975) reported that the mean abundance of *P. ambloplitis* ranged from 0.1 – 6.0 in bluegill from Arkansas. Jilek and Crites (1980) found *P. ambloplitis* in bluegill from five different inland lakes from Ohio, and had prevalences ranging from 7.4 – 84.8%. Fischer and Kelso (1990) showed that *P. ambloplitis* in bluegill captured from the littoral zone in a Louisiana Pond had a prevalence and mean intensity (± SD) of 20.7% and 4.0 ± 6.2, respectively. Amin (1990) reported the prevalence of *P. ambloplitis* in bluegill from Wisconsin ranged from 36 – 66% in the spring, summer and fall. Wilson et al. (1996) demonstrated that the prevalence and mean intensity (± SD) of *P. ambloplitis* in bluegill from Holcomb Lake, Michigan, was 83% and 15.3 ± 24.5, respectively. The results of the present study are similar to what other studies have reported in regards to the mean intensity and prevalence of *P. ambloplitis* plerocercoids from rock bass and bluegill in North America.

The fact that smallmouth bass had higher mean intensities of *P. ambloplitis* in the ovaries compared to other microhabitats may indicate that this cestode is contributing to a decline in this fish population from Gull Lake. Female smallmouth bass harbor more worms in the ovaries than any other organ when compared to male smallmouth bass and to male and female largemouth bass. The damage done to the ovaries was often so severe it was difficult to differentiate an ovary from the mass of fibrotic and necrotic tissues that surrounded and infiltrated it. This gross pathology is consistent with the histopathology reported by Esch and Huffines (1973), and observations made by McCormick and Stokes (1982). Amin (1990) reported that the unilateral hypertrophy of the ovaries could result in the destruction of many eggs. In the present study, infected female smallmouth bass

very often (> 60%) exhibited severe unilateral hypertrophy of the ovaries. This usually was identified by one ovary being 2 – 3 times as large as the other.

The infected ovaries of smallmouth bass were characterized by being white in color, poorly vascularized, and having the appearance of a deflated balloon; the uninfected ovaries were much larger, robust, and yellow in color. In contrast, infected and uninfected ovaries of largemouth bass were similar in appearance, pink and red in color, highly vascularized, and robust in appearance. The ovaries of smallmouth bass had the appearance of strands or threads that were made up of the plerocercoids, fibrotic tissue, and necrotic tissues, thus giving the ovary an appearance likened to a ball of yarn. This stranded appearance was also described by Bailey (1984) from the liver of bluegill. It is hard for this author to believe that the ovaries could function properly, if at all. Furthermore, I observed the damage to the gonads worsened as the fish became larger and older. A significant positive correlation was found between fish length and the number of *P. ambloplitis* only in the smallmouth bass. This indicates that as the fish becomes larger they acquire more worms and this too would cause increased damage to the gonads. However, not significant, the number of *P. ambloplitis* decreased as length increased in largemouth bass. It is not known why there is a trend of decreasing worms with increasing length in largemouth bass.

The ovaries of smallmouth bass had significantly higher mean intensities of *P. ambloplitis* compared to any other visceral organ within the female fish. McCormick and Stokes (1982) indicated that the nutrient rich yolk of the eggs is often absorbed by the plerocercoids. Perhaps these plerocercoids are attracted to the ovary because of this nutrient rich yolk. It is also possible that the ovaries have higher mean intensities of *P.*

*ambloplitis* because of the large surface area compared to the smaller surface area of the testes. The ovary becomes very large, especially during the mating season of the fish; it may be that the large surface area makes the ovaries more susceptible to colonization by the invading plerocercoids. In female largemouth bass it is not the ovaries that have higher mean intensities of *P. ambloplitis* but the liver and mesentery.

The mean intensity of *P. ambloplitis* in the testes of smallmouth bass was not significantly different from those of the liver and mesentery. In fact, the mesentery had higher mean intensities of *P. ambloplitis*, although not significant. Within smallmouth bass the ovaries harbored more worms than the testes. This demonstrates that if the reproductive potential of smallmouth bass is decreasing it may be happening because of the high mean intensity of *P. ambloplitis* in female fish. Esch and Huffines (1973) reported the damage caused by *P. ambloplitis* is usually more severe in young males and that they may suffer from a decline in sperm producing tissue. Similarly, Esch et al. (1975) found the most extreme pathology in the testes of young male smallmouth bass. Neither of these two studies reported the mean intensity of *P. ambloplitis*, but is based on histopathology. It may be possible that even though the mean intensity of *P. ambloplitis* is lower in male smallmouth bass than female smallmouth bass that the pathology caused by this worm is also severe in males. Male smallmouth bass have higher worm burdens than do male largemouth bass. Clearly, this indicates that overall the gonads of the smallmouth bass have much higher mean intensities of *P. ambloplitis* than those of largemouth bass.

The gonads of largemouth bass had fewer worms than that of the liver and mesentery. This may indicate that *P. ambloplitis* is not affecting the reproductive

potential of largemouth bass as drastically as it may be in the smallmouth bass. In both the female and male largemouth bass it was the other visceral organs that had higher mean intensities of *P. ambloplitis*.

*Proteocephalus ambloplitis* has a significantly higher overall mean intensity in smallmouth bass when compared to largemouth bass. This clearly indicates that *P. ambloplitis* infections are worse in smallmouth bass. It is also evident that the gonads, especially the ovaries, of smallmouth bass may be damaged so severely as to impair proper function. Impaired function of the gonads could cause a decline in the reproductive potential of smallmouth bass and ultimately contribute to their declining numbers.

## CONCLUSION

It would seem that smallmouth bass are experiencing an increase in the mean intensity of *Proteocephalus ambloplitis* through the life span of the fish. As the fish ages, the infections become more severe, with increasing scar tissue formation (fibrous adhesions and necrotic tissue) and the recurring penetration of worms over time. Several residents and avid fishermen of Gull Lake were interviewed over the course of this study. These interviews indicated that a common fishing practice is to only keep fish between 355 – 432 millimeters, and to release the larger fish (> 441 millimeters). If this is a common fishing practice then this might be contributing to a decrease in smallmouth bass numbers. As fish become larger the pathology caused by *P. ambloplitis* becomes worse. If the smaller, younger, reproductively viable fish were taken from the breeding stock, then the larger fish should be present in higher numbers. If these larger fish are rendered sterile, but still go through spawning behaviors they could be contributing to an overall decline in the abundance of smallmouth bass from Gull Lake. It is the suggestion of this author that the larger fish are caught and removed from the breeding population. This may allow for the smaller fish, which have less severe infections, to spawn and reproduce.

More research is warranted to investigate if smallmouth bass are producing fewer offspring than largemouth bass. To test this in a lake system, experiments could be designed to count the number of smallmouth bass nesting and quantify the number of eggs produced and compare these findings to that of largemouth bass. This would give more support to the hypothesis that smallmouth bass are experiencing a decline in their numbers due to bass tapeworm interaction.

Fingerling bass are known to acquire *P. ambloplitis* by eating infected zooplankton. It is not known how long the bass tapeworm can persist or survive in the fish host. Further study should investigate bass tapeworm infections in fingerling bass and attempt to understand how long worms can survive in fish when the infections are acquired as fingerlings. Further study should be done to investigate what role, if any, crayfish play in the transmission of *P. ambloplitis*. *Orconectes propinquus* is known to raid the nests of smallmouth bass and consume the fish eggs. Even though decapods have never been reported as second intermediate hosts for cestodes a study is still warranted, based upon the large amount of crayfish that are eaten by smallmouth bass and largemouth bass.

# APPENDIX A

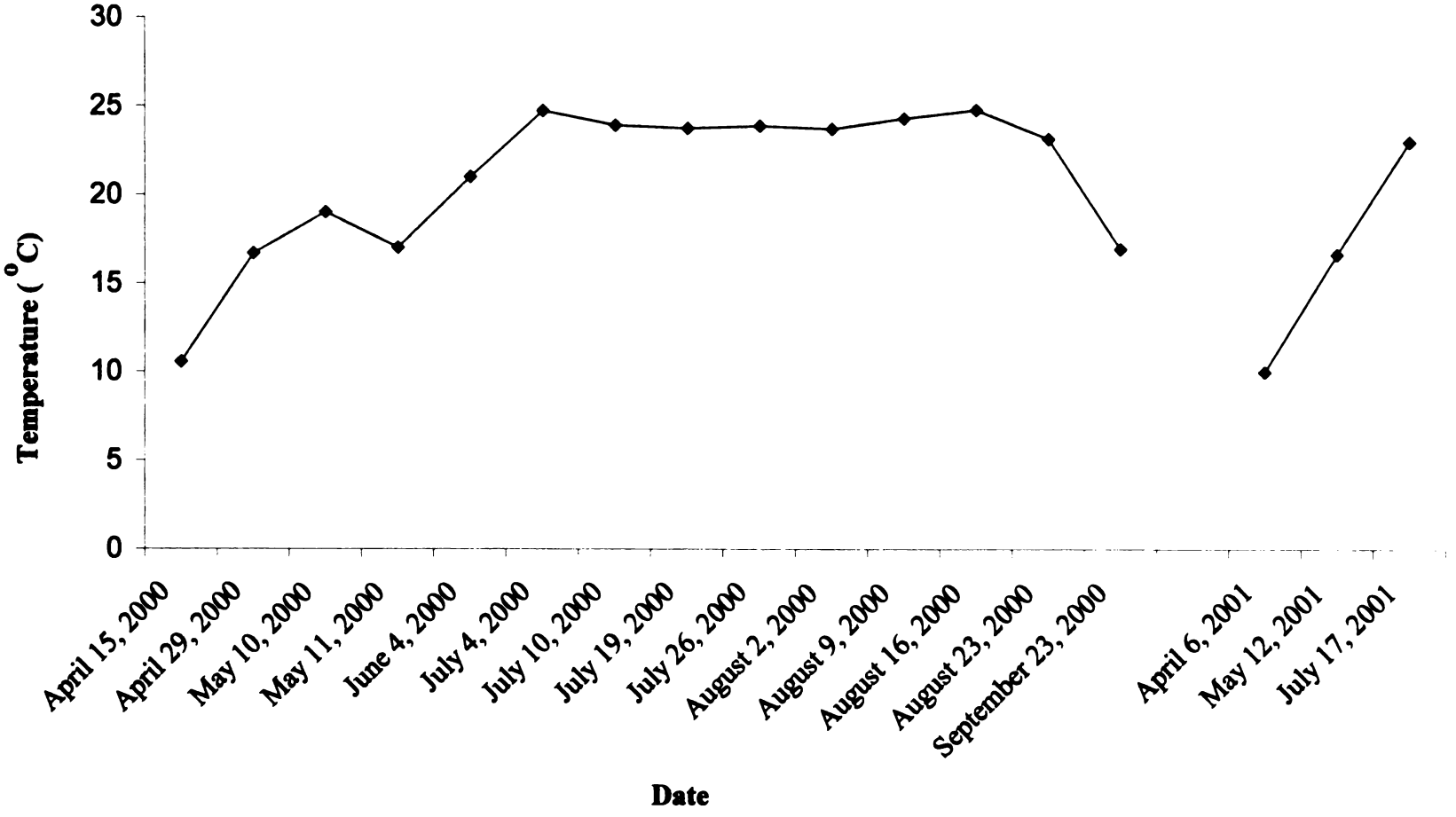


**Figure A.1. Water temperature recorded at 1 meter depth from Gull Lake, Michigan in 2000 and 2001.**

# APPENDIX B

**Table B.1. Number of smallmouth bass examined, mean length, and length range per month sampled from Gull Lake, Michigan in 2000 and 2001.**

| Month | Number Examined | Mean Length (mm) ± SD | Range (mm) |
|---|---|---|---|
| June 2000 | 16 | 224.5 ± 42.7 | 181 – 274 |
| July 2000 | 12 | 265 ± 56.4 | 225 – 303 |
| August 2000 | 13 | 219.7 ± 40.1 | 166 – 263 |
| September 2000 | 10 | 166.2 ± 14.5 | 137 – 186 |
| May 2001 | 1 | 230 | 230 |
| June 2001 | 2 | 257.5 ± 10.6 | 255 - 265 |

# APPENDIX C

**Table C. 1. Number of largemouth bass examined, mean length, and length range per month sampled from Gull Lake, Michigan in 2000 and 2001.**

| Month | Number Examined | Mean Length (mm) ± SD | Range (mm) |
|---|---|---|---|
| April 2000 | 6 | 239. 3 ± 34.6 | 192 – 280 |
| June 2000 | 16 | 191.3 ± 20.5 | 148 – 221 |
| July 2000 | 7 | 193.4 ± 21.6 | 160 – 219 |
| August 2000 | 15 | 198.1 ± 23.0 | 155 – 240 |
| September 2000 | 2 | 187.5 ± 10.6 | 180 – 195 |
| April 2001 | 15 | 275.1 ± 30.8 | 217 – 315 |
| May 2001 | 15 | 209.8 ± 29.1 | 131 – 248 |
| July 2001 | 12 | 202.5 ± 31.7 | 150 – 248 |

# APPENDIX D

**Table D. 1. Number of rock bass examined, mean length, and length range per month sampled from Gull Lake, Michigan in 2000.**

| Month | Number Examined | Mean Length (mm) ± SD | Range (mm) |
|---|---|---|---|
| April 2000 | 3 | 164.6 ± 8.38 | 155 – 170 |
| May 2000 | 4 | 157.0 ± 30.1 | 123 – 196 |
| June 2000 | 15 | 145.6 ± 17.8 | 126 – 197 |
| July 2000 | 7 | 165.5 ± 20.7 | 135 – 204 |
| August 2000 | 15 | 153.5 ± 11.6 | 138 – 170 |
| September 2000 | 6 | 120.8 ± 24.8 | 72 – 141 |

# APPENDIX E

**Table E. 1. Number of bluegill examined, mean length, and length range per month sampled from Gull Lake, Michigan in 2000.**

| Month | Number Examined | Mean Length (mm) ± SD | Range (mm) |
|---|---|---|---|
| May 2000 | 2 | 132.0 ± 12.7 | 123 - 141 |
| June 2000 | 12 | 116.3 ± 21.7 | 89 – 145 |
| July 2000 | 12 | 112.6 ± 14.1 | 86 – 132 |
| August 2000 | 15 | 143.8 ± 19.1 | 108 – 175 |
| September 2000 | 9 | 106.1 ± 24.2 | 68 - 136 |

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