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THE PARASITES OF LAKE FISHES

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Introduction

Since the times of Van Beneden and Leuckilart animal parasites have been intensively studied, but little effort has been made to determine the amount or frequency of parasitic infection under natural conditions; except for those species directly related to man and his domestic animals. Many species of parasites that infest fishes have been, and are being, described, but few accurate observations that relate to their abundance and the factors which make them numerous or few have been made.

Van Cleave (1919) found that half the species of fishes that he examined from Douglas Lake, Michigan, were infected with acanthocephalans, and he determined the percentage of infection for sixteen species. La Rue (1914), Marshall and Gilbert (1905), Smallwood (1914), and Ward (1910) made incidental observations concerning the number of parasites present in certain fishes. Surber (1913) remarks on the small percentage of natural infections with glochidia. The white crappie, which carries more species of glochidia than any other fish, he found to show an infection of only 0.7 per cent, and the sheepshead, known to carry two species of glochidia, had 3.7 per cent.

Zschokke (1902) found that salmon lost a large number of their parasites while migrating up the Rhine. But Ward (1909) points out that such migrations are not always conducive to parasitic losses, for the Alaskan salmon during its journey inland acquires a copepod which is never found in salt water.

Little is known of the effects of seasonal succession on the life cycles of the parasites of fishes. Van Cleve (1916) states that acanthocephalans vary greatly in this respect and cites two species in one genus which, though occurring in the same host, mature at different seasons. Hausmann (1897) found that perch had very few trematodes in the spring. In studying frogs, Ward (1909) found the lowest percentage of infection in late spring or early summer, and a maximum was reached during hibernation. There is a great need of more information concerning the seasonal prevalence of the parasites of all aquatic animals.

Of the factors that control the occurrence of fish parasites there is also a dearth of knowledge. Hausmann (1897) states that when fishes eat little on account of cold or heat, parasites are few; and he assigns an important role to temperature as a factor in parasitic infection. He also points out that most parasites enter fishes with food. Ward (1909) stresses the fact that parasites respond to changes in the habits of their hosts to such a degree that their presence or absence furnishes evidence of particular habits. Pratt (1919) affirms that epidemics of fish parasites are apt to occur when the water is warm and that small inclosed bodies of water harbor more parasites than those of larger size because fishes cannot escape by migration.

The present paper describes the results of statistical studies on the occurrence of fish parasites in different types of lakes. The writer was led to make such studies in attempting to discover why fishes fail to grow much in certain bodies of water while they may attain large size in other bodies near by. It seemed desirable to learn whether particular lakes showed specificities in regard to the numbers and kinds of parasites present and whether there is correlation between the presence and size of particular fishes and the presence or absence of parasites. The work began in 1917 and was at first confined to the yellow perch. Observations were made on specimens from sixteen lakes on three different river systems. Later, more extensive observations were made on five different types of lakes where the parasites of all available species of fishes were studied.

In studying fishes for parasites they were always examined while fresh, as it was found that results from old or preserved fishes were of little value. The skin, fins, mouth and gills were first scrutinized; then the specimen was opened from vent to throat, and the visceral organs were examined. The contents of the alimentary canal were stripped out on a glass plate and the canal itself was opened from end to end with scissors. The food and faecal matter were carefully teased across under a binocular microscope. The number and location of all parasites was entered on a form sheet, one sheet being used for each fish examined. Parasites were placed in corrosive sublimate solution and alcohol. Later they were stained and mounted. In this paper all measurements of fishes are given in millimeters and do not include the tail fin. In the tables "+" indicates less than 0.05.

The work could never have been completed without the cheerful and excellent assistance rendered by Drs. George R. LaRue and H. J. Van Cleave, who identified Proteocephalidae and Acanthocephala, respectively. Others who deserve thanks for identifications are Dr. A. R. Cooper, tapeworms; Prof. H. S. Davis, Sporozoa; Dr. A. D. Howard, glochidia; Prof. J. P. Moore, leeches; and Prof. C. B. Wilson, copepods. Mr. Leslie Tasche assisted the writer in the field; Misses Henrietta Achtenberg and Marion E. Lamont, and Mr. J. C. Stucki mounted slides.

Before all the factors which influence parasitism in fishes are known, if they ever are, parasitologists and ecologists will have to labor for several generations. This paper is, of course, only a beginning in the ecology of fish parasites and is concerned particularly with certain Wisconsin lakes.

PARASITES OF THE YELLOW PERCH

From June, 1917, to May, 1918, the yellow perch from the deep waters of Lake Mendota were examined each month, except during December. During the summer and at intervals throughout the year perch from four other lakes on the Yahara River and from the shallow waters of Lake Mendota were also examined. The results of these studies are given in table 1. The parasites found in the perch in these lakes were as follows:

TREMATODA

Diplostomum cuticola Van Nordmann

This trematode was common, occurring in small cysts in the skin and fins, and sometimes on the gills. The cysts are easily seen on account of the black pigment that surrounds them and gives infected fishes a speckled appearance. Their distribution on the bodies of 335 perch from all the lakes studied averaged as follows: pectoral fins 1; pelvic fins 0.9; anal fin 0.5; caudal fin 1.3; dorsal fins 1; anterior dorsal 0.4; posterior dorsal 0.5; gills +; opercles 1.3; ventrum 1.4; tail +; dorsum 2.4; sides 3.3.

Bunodera luciopercae O. F. Müller

A parasite that was found only in the intestine and the intestinal caeca.

Clinostomum sp.?

Large white cysts enclosing this parasite occurred in the flesh just beneath the skin; sometimes on the gills and in the eye sockets.

Acanthocephala

Echinorhynchus thecatus Linton

This hook-headed worm occurred as an intestinal parasite and in cysts in the peritoneum.

Neoechinorhynchus cylindratus (Van Cleave)

An intestinal parasite.

Acanthocephalan cysts

These cysts were mostly those of *Echinorhynchus thecatus* Linton, but as it is not certain that they all belonged to that species, they are not definitely assigned to it.

Nematoidea

Dacnitoides cotylophora Ward and Magath

This nematode was an intestinal parasite in the perch.

Icthyonema cylindraceum Ward and Magath

A filarial worm that occurred in cysts in the peritoneum and liver.

Cestoidea

Proteocephalus sp.?

Most of the intestinal proteocephalids were *P. pearsei* La Rue. Perhaps all belonged to this species.

Proteocephalid cysts

Encysted proteocephalids were commonly encountered; usually in the liver, but often in the peritoneum. Those identified were the cysts of *Proteocephalus ambloplitis* (Leidy).

Bothriocephalus cuspidatus Cooper

This tapeworm was found in the intestine of the perch.

GLOCHIDIA

Probably all the glochidia observed were *Lampsilis luteola* Lamarck, which is the most abundant species in the lakes along the Yahara River.

Piscicolaria sp. ?

This leech was usually attached about the bases of the fins.

Unknown cysts

Very often cysts were encountered among the viscera that could not be identified.

The four lakes along the Yahara River decrease in size and depth downstream and come thus in the following order: Mendota, Monana, Waubesa, Kegonsa (Table 3). Lake Wingra is small, shallow, and is connected with Lake Monona through a narrow, swampy stream. In general the perch increase in size downstream, but average smaller in Lake Wingra than in Lake Mendota (Pearse and Achtenberg, 1920).

The results from the five Yahara lakes may properly be compared for the months of July, August, and September, when collections were made in all of them. During that time the total average parasitism* for each lake was: Mendota, deep 66.7 (60.7); Mendota, shallow 120.9 (67.7); Monona 84.8 (18.8); Wingra 38.8 (38.6); Waubesa 24.9 (16.4); Kegonsa 40.9 (13.4). The figures in parenthesis represent the total average infection without the averages for *Diplostomum cuticola,* which, when it occurs in very large numbers on even one fish, may change the total very much. The figures in parenthesis are probably better as a basis for comparison. In any case it is apparent that a decrease in infection is generally correlated with larger size in these lakes. Before the writer had studied lakes along other rivers he thought that a greater infection might occur in deeper lakes, or in those nearer the headwaters of a stream.

The different kinds of parasites varied greatly in abundance in the lakes. Table 1 shows that the perch in the shallow water

*Average total number of parasites per fish.

of Lake Mendota have more parasites than those at greater depths and that Lake Mendota has a higher percentage of infection than any of the other lakes. If the highest percentage of infection with a particular parasite makes a lake "first," the lakes rank about as follows:

Mendota, shallow: 6 firsts; 6 seconds; 2 thirds; all species present.

Mendota, deep: 5 firsts; 1 second; 2 thirds; 4 species absent.

Wingra: 3 firsts; 1 third; 1 fourth; 1 fifth; 2 sixths; 6 species absent.

Waubesa: 1 first; 2 seconds; 3 thirds; 2 fourths; 2 fifths; 4 species absent.

Kegonsa: 1 first; 2 seconds; 2 thirds; 1 fourth; 3 fifths; 3 species absent.

Monona: 1 first; 2 seconds; 1 third; 1 fourth; 2 sixths; 6 species absent.

That Monona ranks last is probably explained by the fact that it is heavily contaminated with organic matter from the city of Madison. It is on the whole the most barren of the lakes and contains fewest fishes.

Glochidia, leeches, intestinal proteocephalids, and acanthocephalans are apparently more abundant in shallow water. All encysted parasites are somewhat more abundant in deep water. Lake Kegonsa has a much higher infection with bothriocephalids than any other lake, and also has many *Dacnitoides*.

The data in table 1 are rearranged in table 3 to show the average infection of the perch in the Yahara lakes by months. It will be noted that the maximum infections were in spring. This was due largely to the increase of acanthocephalans at that season. Winter came next, autumn was third, and summer showed the lowest infection. The different parasites reached their seasons of greatest numbers as follows:

Spring: acanthocephalans; Bunodera.

Summer: glochidia—which were found at no other season.

Autumn: bothriocephalids, Diplostomum, Clinostomum, Icthyonema, and proteocephalid cysts.

Winter: Dacnitoides; intestinal proteocephalids; unknown visceral cysts.

In order to compare other lakes with deep, fertile lakes along the Yahara, eleven lakes on the Oconomowoc and Fox Rivers were visited during August, 1917. The general characteristics of these lakes are given in table 3. Those on the Oconomowoc were deep, with sandy and pebbly shores. Those on the Fox (except Green Lake, which was much like those on the Oconomowoc River) were shallow with swampy shores.

Table 3 shows that the average infection was about equal on the Oconomowoc (15.2) and Fox (14.4) Rivers; the latter perhaps having a slight excess because eight parasites showed the highest infection average on it—to five on the former. The Yahara lakes showed about two-thirds the infection (9.3) of those on the other two rivers, and the infection average of only two parasites exceeded those of the same parasites in the lakes on the other rivers. In table 4 the lakes of each river system are arranged in order, with that nearest the headwaters on the left. It will be seen that only on the Yahara was infection greater toward the headwaters.

During August infection with all trematodes, intestinal proteocephalids, glochidia, and leeches was greater in the Fox River lakes; in the Oconomowoc lakes acanthocephalans, Icthyonema cysts, proteocephalid cysts, and unknown cysts were most abundant. The Yahara lakes showed the highest infections with acanthocephalan cysts and Bothriocephalus.

Except for Diplostomum, the trematodes were most abundant in the shallow lakes. Acanthocephala occurred in largest numbers in the deep, sandy, and rather barren Oconomowoc lakes; but acanthocephalan cysts reached their greatest numbers in the deep, fertile Yahara lakes. Dacnitoides was somewhat more abundant in the shallow lakes than in the sandy, barren, deep lakes and was absent from the deep, fertile lakes. Icthyonema cysts reached their maximum in Lake Poygan (shallow, swampy) but on the whole were slightly more abundant in the deep, sandy, Oconomowoc lakes. Intestinal proteocephalids *(P. pearsei* La Rue) also were prevalent in the shallow, swampy lakes, but encysted proteocephalids, mostly *P. ambloplitis* (Leidy), reached their maximum in the sandy, deep lakes. Bothriocephalids were most abundant in the deep fertile lakes. Glochidia and leeches reached their maxima in the shallow, swampy lakes. Unknown visceral cysts were most common in the sandy, deep lakes.

According to their degree of average infection the sixteen lakes rank in the following order: Green 59.1; Monona 42.1; Beaver 32.7; Poygan 32.2; Mendota shallow 31.1; North 30; la Belle 30, Oconomowoc 25.5; Butte des Morts 19.2; Pine 17; Mendota deep 15.3; Okauchee 14.5; Puckaway 14.1; Wingra 9.5; Waubesa 6.5, Winnebago 3; Kegonsa 0.5. If Diplostomum cysts are disregarded the order is as follows: Beaver 32.1; Poygan 30.7; North 26; Mendota, shallow 23.3; Butte des Morts 19.1; Mendota, deep 14.7; Oconomowoc 14.2; Puckaway 14; Pine 10.8; Wingra 9.4; Monona 7.1; Green 7.1; la Belle 6.5; Okauchee 2.9; Waubesa 2.5; Winnebago 1; Kegonsa 0.2. There is no apparent relation between river systems, depth, fertility, character of shore and the general abundance of parasites. This appears to indicate that all parasites are not influenced by the same factors. There is also no apparent relation between the size of the perch in various lakes and the degree of parasitic infection, but when there are more fishes per unit of area there is a heavier infection.

Phyllodistomum superbum Stafford was found in the urinary bladders of many perch in the lakes along the Fox River, but was never observed in any of the two thousand perch that the writer has examined in the lakes on the Mississippi drainage. This parasite is apparently confined to the St. Lawrence drainage system.

The food of the perch examined was carefully recorded during August, 1917. For the three river systems it may be summarized as follows; the figures after the foods indicating the average percentage eaten:

	Yahara	Oconomowoc	Fox
Number examined	58	30	32
Average length	157	160	180
Insect eggs			0.1
Fish remains	10.3	32.7	6.9
Chironomid larvae	42.6	1.0	1.1
Caddis-fly larvae	1.8	2.3	7.6
Unidentified insect larvae			0.4
Chironomid pupae		0.2	1.2
Corixa	0.1		6.6
Grasshoppers			2.5
Sialis larvae			11.6
Mites	+		0.5
Crayfishes	0.7	22.0	43.6
Amphipods, unidentified	7.1	0.2	

	Yahara	Oconomowoc	Fox
Hyalella	2.0		1.9
Ostracods	0.2		
Cyclops	+		
Leptodora	2.9		2.4
Daphnia	21.4		0.4
Cladocera, unidentified	1.1		
Sphaeridae	+		
Snails	3.0	20.9	2.0
Leeches	0.1	16.6	0.6
Bryozoa	1.5		
Plants	4.1	1.9	
Silt and sediment			3.3
Unidentified	0.1	2.1	4.0

From these figures it appears that a diet of fishes, insects, crayfishes, snails, and leeches is associated with parasitic infection more than chironomid larvae and cladocerans, but the observations cover too limited a period to be of much significance.

COMPARISON OF THE FISH PARASITES OF FIVE WISCONSIN LAKES

As the study of the yellow perch in sixteen lakes had not given results of particular value, it was decided to study the parasites of all the fishes available in several different types of lakes. According to this plan five Wisconsin lakes were studied intensively during the summers of 1919 and 1920. Accounts of the food and distribution of the fishes in these lakes have already been published (Pearse, 1921, 1921a). All the lakes were of considerable size and depth. Their general characteristics are given in table 5. Lake Geneva is deep, clear, and its deepest parts are without oxygen in summer. Mendota is deep, turbid and the water below 8 to 12 meters is without oxygen for three months during summer and early autumn. Pepin is the shallowest of the lakes, but it has the greatest area of any lake except Michigan. Its temperature is nearly uniform from top to bottom and it forms a part of the Mississippi River. Green Lake is deep and has a small surface area; it is sharply stratified thermally but has plenty of oxygen at the bottom at all seasons. Lake Michigan is clear, cool, and of course, has a very large volume of water compared to the other lakes. In regard to "fertility," as judged by the probable amount of food for fishes per unit of area, the lakes rank in about the following order: Mendota, Green, Geneva, Michigan, Pepin (Pearse, 1921, pp. 19, 58). Detailed accounts of the general characteristics of these lakes and of routine catches in them have been published (Pearse, 1921, 1921a).

Green Lake and Lake Mendota were studied during August, 1919. The lakes investigated in 1920 were studied as follows: Pepin: June 20 to July 25; Lake Michigan: July 27 to August 7; Geneva: August 8 to 25.

Attention will now be directed to a detailed consideration of the parasites that were found to infest Wisconsin lake fishes and the parts of fishes' bodies that they frequented. Although unidentified parasites of various groups occurred in a number of fishes, they are not given in the following lists.

PROTOZOA

Myxobolus cysts were found once in Lake Mendota on the gills of a yellow perch. Doubtless other protozoan parasites occurred, but were not observed.

TREMATODA

Acetodextra amiuri Pearse

Found in the swim bladders of the yellow, black, and speckled bullheads in Lake Pepin; in the black and speckled bullheads in Lake Michigan.

Acrolechanus petalosa (Lander)

Common in the sand sturgeon in Lake Pepin.

Allocanthocasmus varius Van Cleave

Occurred in the white bass in Lake Pepin; free in the intestine and encysted in the liver.

Allocreadium armatum (MacCallum)

Found in intestine of the sheepshead in Lake Pepin and Lake Michigan.

Allocreadium boleosomi Pearse

In intestines of the Johnny darter and log-perch in Lake Pepin.

Piscicola punctata (Verrill)

Leeches, identified by the writer, occurred as follows: Lake Mendota: carp, bluegill, largemouth black bass; Green Lake: pumpkinseed.

Piscicola milneri (Verrill)

Found in Lake Michigan on a cisco—*Leucichthys hoyi* (Gill), and the lota.

Piscicolaria sp.?

Professor J. P. Moore identified specimens from the following sources: Lake Geneva: rock bass, yellow perch; Lake Pepin: black and yellow bullheads, channel cat; Lake Michigan: rock bass, smallmouth black bass.

Placobdella montifera Moore

Occurrence: Lake Geneva: smallmouth black bass; Lake Pepin: carp and hackleback sturgeon.

Placobdella parasitica (Say)

Occurrence: Lake Mendota: bluegill; Green Lake: pickerel, top minnow.

Placobdella picta (Verrill)

Occurred in Lake Michigan on the sucker and perch.

Lamellibranchiata

During all the studies described in this paper glochidia were never found on any part of fishes except the gills. In Lake Mendota the yellow perch was infected with *Lampsilis luteola* (Lamark). In Lake Pepin the yellow perch was infected with *Lampsilis luteola* (Lamark) and *Quadrula plicata* (Say); the sauger, with *Quadrula metaneura* (Say) ("probably"), *Lampsilis recta* (Lamark), *L. ligamentina* (Lamark); the mud cat, with unidentified glochidia.

Copepoda

Achtheres ambloplitis Kellicott

In Lake Michigan on the gills of a cisco—Leucichthys harengus (Richardson), the lota, and smallmouth black bass.

Achtheres coregoni (Smith)

On the gills of the lake trout in Lake Michigan.

Achtheres corpulentus Kellicott

On the gills of a cisco—*Leucichthys johannae* (Wagner), in Lake Michigan.

Achtheres micropteri Wright

On the gills of the smallmouth black bass in Lake Geneva.

Achtheres pimelodi Kroyer

On the gills of the channel cat in Lake Pepin.

Argulus sp.?

An unidentified Argulus was found on a carp in Lake Mendota.

Argulus appendiculosus Wilson

Found in Lake Pepin on the mud cat.

Argulus catostomi Dana and Herrick

Under the opercula and on the gills of suckers in Lake Geneva and Lake Mendota.

Argulus maculosus Wilson

On the yellow bullhead in Lake Pepin.

Ergasilus caeruleus Wilson

On the gills of fishes: Lake Mendota: yellow perch; Lake Michigan: rock bass, sucker, a cisco—*Leucichthys harengus* (Richardson), and yellow perch.

Ergasilus centharchidium Wright

In Lake Michigan on the gills of the rock bass.

Pisces

Icthyomyzon concolor (Kirtland)

This lamprey was taken in Lake Pepin on a spoonbill.

Discussion and Conclusions

A summary of the parasites found in the five lakes studied is given in table 4. The writer had expected to publish six additional tables giving the number of fishes infected and total average infection for each parasite but the space available will not permit this. Those interested in such detailed information may obtain it by letter. Lake Mendota in all respects contained the smallest number of parasites—the average number in each fish being 2.0; the average number of species of fishes each parasite infected, 4.7; and the average number of individual fishes infected by each parasite, 1.4. Lake Pepin had the largest average number of parasites per fish (5.0); Green Lake the largest average number of species of fishes infected by each species of parasite (8.1); and Lake Geneva the largest average number of individuals infected by each parasite (2.2).

The lakes with the widest range of territory and opportunity for fishes to invade the greatest variety of habitats have the highest average infection per fish (Pepin, 5.0; Michigan, 3.9). However, the fishes in Pepin, with its shifting, sandy bottom and lack of thermal stratification, have 22 per cent more parasites than Michigan, with its soft mud bottom and cold deeper water. The two lakes with the largest average number of species of fishes infected per species of parasite include the one with a large number of species of fishes and habitats (Pepin, 8.1) and the one with the smallest number of species of fishes and the least variety of habitats (Geneva, 6.6). The lakes having the largest number of individuals infected by each parasite include one with the least range and variety of habitats (Geneva, 2.2), one with wide range and variety of habitats (Michigan, 2.1), and one in which there was little variety in the shore habitats and a sharp distinction between deep and shallow water habitats (Green, 2.1).

The lake in which there was the least infection by parasites (Mendota) had the largest number of fishes per unit of area (Pearse, 1921, p. 24), the most abundant food supply, the greatest degree of stagnation in the deeper water during summer. Table 4 shows, however, that this lake had the second largest number of species of parasites which showed the largest number of highest infection averages; and that it was excelled in this only by Lake Pepin, which had nearly twice as many species of fishes, the scantiest food supply, and the greatest parasitic infection. Taking the number of species of parasites that showed the highest average infections as a criterion, the lakes rank in the following order: Pepin, Mendota, Michigan, Green, Geneva. This order indicates that there is a direct relation between variety of habitat and amount of infection.

Taking the total number of species of fish parasites present as a criterion the lakes rank in the following order: Pepin 70, Michigan 60, Mendota and Green 44, Geneva 35. This indicates that variety of habitat is correlated with a large number of species of parasites (and fishes) as well as a large amount of infection. In other words the lake with the largest variety of habitats has the greatest variety of fishes and parasites.

Arranged in order of average infection the fishes in each of the five lakes in which extensive observations were made rank as follows:

Lake Geneva: Rock bass 9.4, pumpkinseed 5.0, smallmouth black bass 4.0, sucker 2.2, cisco 1.0, largemouth black bass 0.8, wall-eyed pike 0.6, pickerel 0.5, bluegill 0.5, perch 0.5, brook trout 0, shiner *(Notropis hudsonius)* 0.

Lake Mendota: White bass 13.2, wall-eyed pike 12.7, dogfish 8.3, smallmouth black bass 6.6, sucker 4.0, long-billed gar 3.[illegible], tadpole cat 2.8, pumpkinseed 2.6, speckled bullhead 2.4, largemouth black bass 2.4, Johnny darter 2.0, bluegill 1.6, perch 1.4, yellow bullhead 1.3, rock bass 1.1, pickerel 1.1, cisco 0.8, black crappie 0.7, top minnow 0.3, shiner *(Notropis heterodon)* 0.2, silversides 0.1, carp 0.1, blunt-nosed minnow +, bream 0, buffalo 0, miller's thumb 0.

Lake Pepin: Mud cat 462, lake carp 116.6, eel 40, dogfish 37, spoonbill 19, smallmouth buffalo 17, yellow bass 16, quillback 13.2, river carp 5, sucker 4.7, black bullhead 3.7, skipjack 3.[illegible] pickerel 3.1, speckled bullhead 2.9, white bass 2.9, channel cat 2.7, tadpole cat 2.5, mongrel buffalo 2, hackleback sturgeon 1.8, sauger 1.7, wall-eyed pike 1.6, pumpkinseed 1.3, white crappie 1, yellow perch 0.9, shiner *(Notropis heterodon)* 0.8, short-headed redhorse 0.7, long-billed gar 0.6, largemouth black bass 0.5, bluegill 0.5, mooneye 0.4, white-nosed sucker 0.4, black crappie 0.4, Johnny darter 0.2, shiner *(Notropis atherinoides)* 0.2, log perch 0.2, carp 0.1, shiners *(Notropis jejunus* and *N. hudsonius)* 0.1, pirate perch +, gizzard shad 0, lamprey 0.

Green Lake: Pumpkinseed 29.7, blunt-nosed minnow 22.5, sucker 21.4, rock bass 8.9, bluegill 4.2, yellow bullhead 2.5, smallmouth black bass 2.5, cisco 2.4, carp 2, speckled bullhead 1.9, top minnow 1.1, largemouth black bass 0.8, yellow perch 0.4, pickerel 0.4, Johnny darter 0.1, shiner *(Notropis atherinoides)* 0.

Lake Michigan: Whitefish 31.1, smallmouth black bass 28.9, blackfin 27.8, pumpkinseed 18.9, carp 15, rock bass 12.6, lake trout 9.2, speckled bullhead 6.5, chub 5.8, mud puppy 5, black bullhead 4.1, bloater *(Leucichthys harengus)* 3.9, lota 3.9, bloater *(Leucichthys hoyi)* 2, log perch 1.5, pickerel 1.4, cottid 1.3, sucker 1.2, top minnow 1, Iowa darter 0.9, long-nosed sucker 0.8, Johnny darter 0.8, yellow perch 0.5, bream +, shiners *(Notropis atherinoides* and *N. hudsonius)* +, blunt-nosed minnow 0, yellow bullhead 0.

It would not be proper to add the average infections in different lakes in order to compare infection in different species of fishes, for the total infection in different lakes varies greatly. Each species should be given a rating which will compare it with all others in each lake. The writer has therefore used the following formula in order to give to each fish a relative percentage (P).

$$P=100-\frac{100}{N}\times R$$

N is the number of fishes examined in the lake; *R*, the rank of the particular species of fish in the lake according to its average infection. For example twelve species were examined in Lake Geneva $(\frac{100}{12})$. The largemouth black bass ranks sixth $(\frac{100}{12}\times 6)$. For this species $P=100-\frac{100}{12}\times 6=50$. Using this method for each lake and averaging the relative percentages for all species of fishes that occurred in two or more lakes, the fishes rank in the following order: dogfish 90, smallmouth black bass 78, white bass 78, rock bass 73, pumpkinseed 71, sucker 68, black bullhead 66, tad-pole cat 64, wall-eyed pike 61, speckled bullhead 60, long-billed gar 56, bluegill 55, yellow bullhead 55, all species of ciscoes 54, largemouth black bass 45, pickerel 42, carp 40, buffalo *(Ictiobus cyprinella)* 36, log perch 35, blunt-nosed minnow 32, top minnow 32, yellow perch 31, shiner *(Notropis heterodon)* 30, Johnny darter 30, black crappie 27, shiner *(Notropis atherinoides)* 14, bream 11, shiner *(Notropis hudsonius)* 11.

In general the fishes that frequent vegetation show the highest infection with parasites, those that frequent the bottom and open water are intermediate, and the small fishes that live in shallow water have fewest parasites. Doubtless many factors influence the prevalence of fish parasites, and much is yet to be learned before general laws that will enable one to predict the degree of infection that will be probable in a particular locality are formulated.

There are many ways in which parasites may infect fishes. The most important means of infection are: (1) food, (2) the active migration of the parasite to its host, (3) and accidental contamination from bottom mud, vegetation, or other material. Van Cleave (1920) and Mrázek (1891) have found parasites encysted in amphipods. The observations described in this paper show that the fishes in Lake Michigan that feed largely on amphipods are heavily infected with the parasites these crustaceans are known to carry. Several types of parasites are found encysted in fishes and fish-eaters often have a heavy infection. Hausmann (1897) believed that fishes acquired parasites chiefly through their food, and he was doubtless right, as intestinal parasites are most abundant. In general the fishes that eat the greatest variety of food have the most parasites, but there are some notable exceptions to this. The dogfish, wall-eyed pike, and gar, for example, subsist largely on fishes (Pearse 1918) and are heavily infected.

Little is known of the active migration of fish parasites to their hosts. The distribution of the cuticular cysts of Diplostomum indicates that infection may occur in such a way. Faust (1918) notes that Bunodera has been known to wander out of dead fishes. Perhaps parasites may infect a second host after leaving the first.

The acquiring of parasites from the accidental ingestion of eggs or other stages may be characteristic of certain parasites that are erratic in their occurrence—like intestinal nematodes.

The susceptibility of the host is an important factor in determining the degree and frequency of parasitic infection. *Proteocephalus pinguis* was never found by the writer except in the pickerel; *P. ambloplitis* was found in a number of hosts. Fasten (1913) has studied a parasitic copepod which kills brook trout in great numbers, but will not live on the German brown trout. Howard (1914) cites similar instances among glochidia. Fish parasites may show considerable specificity for certain hosts and hosts may possess a varying degree of immunity. The black crappie, for example, appears to be immune to many parasites that attack other Centrarchidae. The largemouth and smallmouth black bass are closely related, but during the present investigations the latter always carried more parasites. The pumpkinseed was always more heavily infected than the bluegill. Perhaps some of these differences are due to differences in habitats, but some are undoubtedly due to susceptibility. Furthermore, there is general similarity between the parasites of the Siluridae and certain Percidae which leads one to believe that infection may be limited at least in part by certain chemical substances which are present in or absent from the bodies of fishes.

Surber (1913) has remarked on the remarkably small percentage of fishes that carry glochidian parasites in nature. Van Cleave (1919) showed that only half the species of fishes in a Michigan lake were infected with ancanthocephalans. Infection depends on so many factors and opportunities that it is to be expected that parasites will frequently fail to reach their hosts.

Most fish parasites do little harm to their hosts. Pratt (1919) states that nematodes are most injurious and that trematodes do the least harm. While his generalizations may apply to the parasites of certain marine fishes, like the cod, the writer does not believe they are generally applicable to the fresh-water fishes in the United States. The most injurious parasites (leaving out the Protozoa, which the writer has not studied) appear to be the larval tapeworms, which destroy liver tissue; acanthocephalans, which cause ulcers in the wall of the intestine; and copepods, which suck blood from the gills. Glochidia, nematodes, and leeches are usually too few in numbers to do serious damage. Tapeworms and trematodes often occur in enormous numbers but do not appear to do much injury. The writer has never examined a dogfish that did not contain numerous tapeworms; yet all appeared to be in good condition.

The migrations of fresh-water fishes doubtless afford them opportunity to acquire and shed parasites (Ward 1909): The fishes that travel most and invade the greatest variety of habitats in general have the most parasites.

Seasonal changes doubtless have a marked effect on certain fish parasites. It was found that perch have most parasites in spring, although some species of parasites were more abundant at other seasons. Ward (1909), Marshall and Gilbert (1905) and Van Cleave (1916) have also made observations on the abundance of parasites at various seasons, but such information is as yet too limited for generalization.

Hausmann (1897) thought that perch had few parasites when little food was eaten on account of low temperature. In the writer's experience perch have not been found to refrain from eating during winter and they have more parasites in winter than in autumn or summer. Pratt (1909) says that epidemics of trematodes are likely to occur when the water is warm. The writer has found no evidence that this is the case, at least in fresh-water fishes.

Some parasites are apparently limited to particular drainage systems. *Phyllodistomum superbum* Stafford was quite common in the urinary bladder of perch in several lakes on the St. Lawrence drainage but was never observed in a single one of the several thousand perch examined from the lakes on the Mississippi drainage. Perhaps this trematode entered the St. Lawrence drainage after the Mississippi separated from it. Other cases of this kind probably occur but too few specimens have yet been examined to demonstrate them.

Contrary to Pratt's (1919) assertion, the size of a lake does not appear to be correlated with the degree of parasitic infection of its fishes. The density of the population may sometimes be of importance. However, the fishes of Lake Mendota, which has the densest population of any of the five lakes studied extensively by the writer, has the fewest parasites and the fishes in the depth of Lake Michigan, where the population is scanty, have many: There is, in general, no direct relation between number of fishes and number of parasites.

The habitats of fishes are of course important in their relation to parasitic infection. While a variety of habitats is desirable for the growth of fishes, it gives opportunity for acquiring more parasites. A wide range also gives more opportunities for acquiring parasites than a restricted one. Ward (1910) has pointed out that "the parasitic fauna of any animal is primarily a function of its habitat". The observations reported in this paper indicate that the fishes in comparatively barren lakes have an unusual number of visceral cysts and acanthocephalans—perhaps because they wander about more in search of food. Visceral cysts appear to be more abundant in deep water fishes than in those from shallow water. Linton (1910) found that marine fishes in shallow water had fewer parasites than those at greater depths. He believed this was because the former had less opportunity to wander about and become infected. In fresh-water the writer has found infection to be greater on the whole in shallow water—probably because there is a greater variety of habitats and secondary hosts there.

The ecological factors that appear to be important in relation to parasitic infection have now been discussed. Perhaps only one thing has been made clear—that, "now we see through a glass darkly". The writer makes no apology for this final conclusion. There is great need for more information in regard to the ecology of parasitism, not only among fishes but among all animals. It is hoped that this paper may help to interest fishermen, parasitologists, geographers, and ecologists in the opportunities that are open for research on the parasites of fishes. The fisherman must in the future learn to increase his catch by the control of parasites. There are many undescribed species and life histories that await discovery by the parasitologist. The zoogeographer has unusual opportunities for study—parasites depend on one or more hosts for their distribution and are hence conservative in their migrations. The ecologist may disclose the most intricate and interesting relations to be found in nature.

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TABLE 1. *Total average infection of the yellow perch in the lakes along the Yahara River during July, August, September, 1917.*

Parasite	Mendota, Deep	Mendota, Shallow	Monona	Wingra	Waubesa	Kegonsa
Number examined	30	44	30	26	36	26
Diplostomum cuticola	6.0	53.2	66.0	0.2	8.5	27.5
Bunodera lucioperсae	0.3	7.2	....	....	....	....
Clinostomum	0.1	0.1	....	....	....	....
Echinorhynchus thecatus	....	0.8	0.3	....	0.3	0.1
Neoechinorhynchus cylindratus	....	0.1	....	....	0.1	....
Acanthocephalan cysts	3.9	5.0	....	8.5	1.2	2.4
Dacnitoides cotylophora	3.8	2.1	0.1	0.6	1.0	3.6
Ichthyonema cysts	16.1	8.6	0.3	1.5	2.8	0.7
Proteocephalus, intestinal	0.6	2.5	1.3	2.6	0.4	....
Proteocephalus, cysts	32.4	26.1	14.1	24.5	1.4	1.0
Bothriocephalus cuspidatus	....	0.1	0.9	....	0.1	4.4
Glochidia	0.3	11.8	....	....	0.6	....
Piscicolaria	....	0.1	....	0.2	....	0.1
Unknown cysts	3.2	3.2	1.8	0.7	2.5	1.1
Total	66.7	120.9	84.8	38.8	24.9	40.9
Total without Diplostomum	60.7	67.7	18.8	38.6	16.4	13.4

TABLE 2. *Showing average infection by months in the Yahara River lakes, 1917–1918. After October, perch were not examined from any lake except Mendota, with the exception of seven specimens from Kegonsa in November.*

Month	Number examined	*Dipostomum cuticola*	*Bunodera luciopercae*	*Clinostomum* cysts, sk. n. gills	*Echinorhynchus thecatus*	*Neoechinorhynchus cylindratus*	*Acanthocephalan* cysts, visceral	*Dacnitoides cotylophora*	*Ichthyonema* cysts, visceral	*Proteocephalids*, intestinal	*Proteocephalid* cysts, visceral	*Bothriocephalus cuspidatus*	*Glochidia*, gills	*Piscicolaria*	Unknown visceral cysts	Total
June........	45	5.1	.....	+	.....	.....	.....	1.0	0.2	.....	6.2	0.2	2.1	.....	0.4	15.2
July.........	79	11.5	+	.....	0.2	+	1.0	1.3	0.7	0.1	7.9	+	2.1	+	0.	25.3
August......	62	8.9	1.2	.....	0.1	.....	0.3	0.1	1.5	0.4	5.5	0.1	.....	.....	0.4	18.5
September...	56	6.4	0.1	+	+	+	2.2	0.7	2.8	0.8	3.2	0.8	.....	0.1	1.2	18.2
October......	31	6.3	2.0	.....	.....	0.3	0.3	0.3	4.3	0.3	3.3	0.2	.....	+	0.7	18.0
November...	13	19.1	1.0	0.2	0.2	.....	.....	.....	4.7	.....	13.8	.....	.....	.....	.....	39.0
January.....	20	4.5	1.8	.....	.....	23.7	0.3	21.5	2.1	0.9	3.5	0.1	.....	.....	1.3	59.7
February....	10	0.5	0.9	.....	.....	5.3	2.8	.....	2.0	0.3	11.0	.....	.....	.....	0.4	23.2
March.......	20	0.4	3.1	.....	.....	18.4	17.6	.....	1.5	0.5	3.6	.....	.....	.....	.....	45.1
April........	7	0.1	3.7	.....	7.5	9.1	114.6	.....	1.3	.....	0.7	.....	.....	.....	.....	137.0
May.........	8	1.5	2.7	.....	0.1	29.4	76.3	.....	5.4	0.3	1.6	.....	.....	0.1	.....	117.4
Total......	..	64.3	16.5	0.2	8.1	86.2	215.4	24.9	26.5	3.6	60.3	1.4	4.2	0.2	4.9	516.6
Average...	..	5.8	1.5	+	0.7	7.8	19.6	2.3	2.4	0.3	5.5	0.1	0.4	+	0.4	46.8

he Yahara River lakes, from any lake except …egonsa in November.

Bothriocephalus cuspidatus	Glochidia, gills	Piscicolaria	Unknown visceral cysts	Total
0.2	2 1	.....	0.4	15.2
+	2.1	+	0.	525.3
0.1	.....	.....	0.4	18 5
0.8	.....	0.1	1.2	18.2
0.2	.....	+	0.7	18.0
.....	.....	.....	.....	30.0
0.1	.....	.....	1.3	50.7
.....	.....	.....	0.4	23.2
.....	.....	.....	.....	45.1
.....	.....	.....	.....	137 0
.....	.....	0.1	.....	117.4
1.4	4.2	0.2	4.0	516.6
0.1	0.4	+	0.4	46.8

TABLE 3. *Showing average number of parasites infecting perch from 16 lakes during August, 1917. The results from lakes on three drainage systems are summarized.*

	Yahara River							Oconomowoc River							Fox River					
	Mendota, deep	Mendota, shallow	Monona	Wingra	Waubesa	Kegonsa	Average	Beaver	Pine	North	Okauchee	Oconomowoc	Lac la Belle	Average	Puckaway	Green	Poygan	Butte des Morts	Winnebago	Average
Depths, meters	25.6	25.6	22.5	4.3	11.1	9.6	14.6	15.0	27.4	23.7	28.6	19.1	14.2	21.3	1.6	72.2	3.3	3.4	6 4	17.4
Surface area, square kilometers	39.4	39.4	14.1	2.2	8.2	12.7	15.3	12.4	30.6	18.0	42.8	25.6	46.1	29.3	1.3	29 7	4 5	18 2	55.8	21.9
Number examined	10	10	10	10	11	7	10	10	4	1	3	10	2	5	7	6	8	10	1	6
Number infected	10	10	10	10	8	3	8	10	4	1	3	10	2	5	7	6	8	10	1	6
Diplostomum cuticola	0.6	7.8	35.0	0.1	4.0	0.3	8.0	0.6	6.2	4.0	11.6	11.3	23.5	9.5	0.1	52 0	1.5	0 1	.....	10 7
Bunodera lucioperCae	.....	6.6	.....	.....	.....	.....	1.1	1.1	.....	.....	.....	.....	.....	0.1	11.0	.....	2 5	10.9	2 0	5 2
Clinostomum marginatum	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	2.5	.....	0 3	.....	.....	0 5
Phyllodistomum superbum	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0 3	0.3	.....	0.1
Allocreadium armatum	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	3.2	0.6	.....	0.7
Echinorhynchus thecatus	.....	0.1	.....	.....	0.2	.....	+	.....	.....	.....	.....	0.6	.....	0.1	.....	.....	0.1	0.2	.....	+
Neoechinorhynchus cylindratus	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0.2	.....	+	.....	.....	.....	.....	.....	.....
Acanthocephalan cysts, visceral	1.5	0.6	.....	0.5	.....	.....	0.4	.....	0.2	.....	.....	.....	.....	+	.....	1 5	0.2	.....	.....	0.3
Dacnitoides cotylophora	.....	0.1	.....	.....	0.2	.....	+	0.2	1.2	.....	.....	1.6	.....	0.5	.....	1 0	1.1	.05	.....	0.5
Ichthyonema cysts, visceral	3.2	3.0	.....	1.7	1.3	.....	1.5	.....	0.5	7.0	2.6	4.4	.....	2.4	0.1	0.2	10.0	0.1	.....	2.1
Proteocephalids, intestinal	.....	1.9	0.3	.....	.....	.....	0.3	0.4	.....	4.0	.....	.....	.....	0.7	.....	2 3	.....	.....	.....	1 4
Proteocephalid cysts, visceral	8.7	10.8	6 5	7.0	.....	.....	5.5	23.8	8.2	15.0	.....	6.7	6.5	10.0	0.4	0.8	12.0	4 8	1 0	3 8
Bothriocephalus cuspidatus	.....	0.1	0.3	.....	.....	.....	0.1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Glochidia	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1 4	.....	0.3
Piscicolaria	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	0.1	.....	.....	+
Unknown *cysts*, visceral	1.3	0.1	.....	0.2	0.8	0.2	0.4	6.6	0.7	.....	0.3	0.7	.....	1.4	.....	1 3	0 9	0 3	.....	0.5
Total	15.3	31.1	42.1	9.5	6.5	0.5	17.3	32.7	17.0	30.0	14.5	25.5	30.0	24.7	14.1	59 1	32.2	19.2	3.0	25 1
Total without *diplostomum*	14.7	23.3	7.1	9.4	2.5	0.2	9.3	32.1	10.8	26.0	2.9	14.2	6.5	15.2	14.0	7.1	30 7	19 1	1.0	14 4

TABLE 4. *Summary of the average infection with fish parasites in five Wisconsin lakes during summer. + indicates less than 0.01 per cent.*

	Geneva	Mendota	Pepin	Green	Michigan
Trematodes	0.31	0.09	0.51	0.09	0.28
Trematodes, encysted	1.25	0.46	0.10	1.70	0.12
Tapeworms	0.39	0.23	0.67	0.45	0.50
Tapeworms, encysted	0.12	0.28	1.19	0.09	0.06
Nematodes	0.04	0.05	0.07	0.01	0.27
Nematodes, encysted	0.02	0.13	+	+	0.11
Acanthocephalans	0.24	0.12	0.18	0.41	1.79
Acanthocephalans, encysted	0.04	0.12	0.10	0.12	0.08
Unknown cysts	0.06	0.49	1.36	0.12	0.14
Leeches	0.01	0.02	0.02	0.02	0.03
Glochidia	—	+	0.80	—	0.01
Copepods	+	+	+	—	0.32
Protozoan cysts	—	+	—	—	—
Parasitic fishes	—	—	+	—	—
Total average infection[6]; parasites per fish	2.3	2.0	5.0	3.0	3.9
Average number of species of fish infected by each parasite	6.6	4.7	5.0	8.1	5.3
Average number of infections by all species of parasites	2.2	1.4	1.5	2.1	2.1

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