CLEAR TECHNICAL REPORT 190

Impact of *Camallanus oxcephalus* on Lake Erie Fishes: Study II

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I. SUMMARY

The study of the impact of *Camallanus oxycephalus* involved four areas of intensive investigation; 1) identity of the parasite, 2) life history, 3) pathology and 4) ecology and interactions of the population in the western Lake Erie system. The identity of the parasite was determined by study and redescription of numerous adult specimens. The life history of the parasite was studied experimentally and in the natural environment. The intermediate host is *Cyclops bicuspidatus* and *Cyclops vernalis*. Although many species of aquatic arthropods eat the larvae, only copepods may transmit the infection. The efficiency of infection of copepods is very high. Fish may become infected by eating copepods with the infective larvae. Large predatory species may also acquire the infection by eating smaller infected fish.

The first stage larvae may live for 24-39 days at normal extreme summer water temperatures. The ability to infect

the copepod decreases rapidly. No penetration occurs after 18 days at 25°C. The larvae are also relatively intolerant to NaCl solutions. Survival was significantly altered at 1% NaCl and only lasted 3 days at 3% NaCl. Free-living larvae are very active and experiments indicated that this activity "attracts" copepods. Penetration of the copepod gut was primarily a mechanical phenomenon.

No pathogenesis was observed which could be directly attributed to the worms. The intestinal mucosa is penetrated and the nematodes feed on blood and tissue. Mechanical injury, especially in heavy infections, could lead to secondary invasion of pathogens and fish death. Extremely heavy infections might also kill fish.

Analysis of past records strongly indicates that this parasite has become more abundant in western Lake Erie. This may be due, in part, to changes in the plankton and benthic communities. The great increase in prevalence coincides with the rise in abundance of gizzard shad and alewife. Both fish are infected with _C. oxycephalus_, particularly shad, and transmit the disease to fish that eat them.

The population biology and ecology of _C. oxycephalus_ in western Lake Erie was intensively investigated in white bass. The parasite is distributed as a negative binomial through all segments of the fish population in all seasons. No difference exists between infections of male and female fish. Larger fish generally are more heavily infected. Approximately 80-90% of all adult bass are infected. The worms live for only one year and die in July when larvae are dispersed. The heaviest infections are found in July and August when most worms are larvae. The mean worm burden decreases from August to the following July. This reduction in the worm population is believed to be caused by worm density of the parasite. Growth of females is arrested over winter, then proceeds at a very rapid rate during April, May and June. Male and female nematodes copulate in autumn but eggs are not fertilized until April. Larvae are released simultaneously. Dispersal in the population occurs during the maximum density period of the copepod intermediate host. Relative success of each parasite generation may be affected by the abundance of copepods, gizzard shad and alewife, water temperature and other factors affecting the timing of parasite transmission.

II. CONTENTS

III. BACKGROUND

Camallanus oxycephalus is a common and widespread nematode in fishes in eastern North America. It occurs in 52 species of fishes, most of which are cypriniform and perciform. This parasite has been reported from as many as 26 species in Lake Erie. Since its first report in Lake Erie in 1927, it has apparently attracted much attention from sportsmen and commercial fishermen. During late spring and summer, these worms, which are bright red in color, protrude from the rectum of fish and are readily observable. Fish infected with this parasite are unsightly and discourage fishermen.

In a preliminary study of C. oxycephalus in western Lake Erie, we were impressed with the great abundance of this worm. Some populations of fishes, such as white bass and crappies were 100% during some seasons and often very heavily infected. Comparison of our findings with previous studies suggested that the prevalence of C. oxycephalus has increased sharply in recent years. In addition, our data also suggested that the intensity of infection increased as well.

The great abundance of this parasite and the accurate information available to us concerning the history of this species in Lake Erie presented a unique opportunity to study this parasite population and its interaction with Lake Erie fish. Because white bass were common, heavily infected and easily collected, much of our work centers around this fish. Other fish, however, were studied, to accurately assess the host-parasite interactions in the Lake Erie system. The gathering of information on pathology, transmission, life history, morphology, abundance and population ecology would allow us to construct certain hypotheses about how this population of parasites maintains abundance in western Lake Erie. Such insights might develop into generatizations and useful information concerning parasite communities in aquatic systems. This information could be applied to management practices to control the spread of harmful parasitic species in general and of _C. oxycephalus_ in particular.

IV. OBJECTIVES

This very broad and inclusive study of a host-parasite interaction was divided into three jobs, each with specific objectives. These jobs were entitled 1) descriptive investigations, 2) experimental investigations, and 3) population investigations. Under job one, our first objective was to describe accurately the species _Camallanus oxycephalus_ Ward and Magath, 1916. Although this worm has been commonly collected for about 60 years, its specific description has been poor, making identification nearly impossible. Also under job one, we planned to describe any evidence of disease associated with the attachment of this worm to host gut tissue. The experimental aspects of this study revolved about the transmission pathways of the parasite, its life history and development and an analysis of the biology of the dispersal agent and its interaction with the lake environment. The third job is broadly defined. It includes the gathering of information on the incidence, intensity of infection, and seasonality of the parasite and correlating this data with information gathered from Jobs I and II in order to construct hypotheses about population regulation, transmission and factors contributing to parasite success in western Lake Erie.

V. PROCEDURES

This project was in residence at the Franz Theodore Stone Laboratory at Put-in-Bay, Ohio, from June through mid-September. During the last part of September, the laboratory was moved to the parasitological laboratory in the zoology department of Ohio State University at Columbus. The project worked out of Columbus for the remainder of the year. Fish for the study were obtained from 14 locations in western Lake Erie and Sandusky Bay. They were collected by otter trawl, commercial trap nets, commercial shore seines, gill nets, fyke nets, minnow seines and angling. Young of the year fish for experimental procedures were taken with dip nets, minnow seines and shallow water otter trawl, maintained in laboratory holding tanks and treated with Nox-Ich and Maracyn to prevent disease. These fish were fed frozen minnows and chopped earthworms. Invertebrate animals for experimental work were obtained with plankton nets and dip nets. Copepods were maintained in 3 gallon canisters and fed *Paramecium* and brine shrimp.

First-stage larvae of *C. oxycephalus* were maintained in filtered lake water and stored in constant temperature cabinets at 15°, 20°, and 25°C. Fresh larvae were offered to various invertebrates in finger bowls. Quantified infection experiments with copepods were conducted by exposing 10 larvae to a single copepod in 2 ml of lake water for 24 hours. Development of the larval stages of *C. oxycephalus* was studied every 24 hours by sacrificing infected copepods and studying living worms.

Fish were infected with *Camallanus* in several ways. Some young of the year white bass and yellow perch were anesthetized with Quinaldine (.025 ml/3 gal) and infected with a stomach tube. Infected copepods were also exposed to minnow fry and these fry exposed to young fish, passing the infection along. Development of *Camallanus* within white bass and yellow perch was studied by sacrificing fish every 48 hours and studying living and preserved worms. Drawings were made with the aid of a drawing tube mounted upon a wild microscope.

Population data was gathered by sampling white bass, yellow perch and freshwater drum bi-weekly. Data on fish size, sex, season, incidence, intensity of infection, site selection, and structure of worm population was kept. Approximately 6,600 worms were measured and body volume calculated. In addition, 13 other species of fishes were surveyed for Camallanus. Data from all fishes were keypunched on computer cards and analyzed using standard statistical programs on the IBM 370/165 at Ohio State University. Plankton samples were taken 3 times per week between May and September with a 2 liter Kemmerer water bottle.

White bass intestines containing Camallanus adults and larvae were fixed for histological examination by placing them in alcoholic Bouin's for at least 24 hours. Bouin's was washed from the tissue with 70% ethanol. Tissue was dehydrated and embedded in paraplast and sectioned at 6-10 microns. Sections were stained with Mallory's triple stain and Hematoxylin and Eosin.

VI. FINDINGS

Intermediate Host Determination and Larval Development

Gravid female nematodes were placed in lake water, allowed to rupture and active, first-stage larvae were collected and exposed to various aquatic invertebrates (Table 1). Although many of these arthropods ate the larvae, penetration through the gut wall and

TABLE 1
EXPERIMENTAL DETERMINATION OF THE INTERMEDIATE HOST

Potential Host	Larvae Eaten	Larvae Penetrated
Gammarus	+	−
Hyalella	+	−
Asellus	+	−
Cyclops	+	+
Diaptomus	+	+
Daphnia	−	−
Bosmina	−	−
Chironomus	+	−
Cricotopus	+	−
Stenonema	−	−
Ostracoda	+	−

migration to the hemocoel occurred only in copepods. Active larvae were frequently observed moving about in amphipod and midge larvae guts, but no penetration occurred. Larvae were allowed to remain with these arthropods for several days and specimens dissected periodically but no nematodes were found in any animals except copepods.

When penetration occurred, it was usually within 2 hours. Larvae thrashed vigorously in the copepod gut, punched a hole in the gut wall and slipped into the hemocoel quickly. First-stage larvae remain active within the hemocoel for several days, but become quiescent. Shortly after penetration, the anterior portion of the thin-walled esophagus thickens, becoming more distinct. The posterior portion becomes lined with cells indistinguishable from the intestinal cells. The intestinal wall becomes thicker with more cells and the lumen becomes wider and straightens out. The genital primordium remains unchanged.

The first molt occurs on the 3rd day post infection at 25°C and on the 5th day p.i. at 20°C. The molt is readily observed at the posterior end of the larvae. The stoma of the second-stage larva is round and the minute dorsal spine is absent.

A great change in the anterior end of the worm occurs during development of the second-stage larva. The buccal cavity inflates, laterally, forming the buccal valves, and the esophagus moves posteriorly. The stoma changes from a circular opening to a dorso-ventral oval. The anterior part of the esophagus becomes muscular and the posterior portion differentiates from the intestine.

The second molt occurs on the 6th day after infection at 25°C and on the 10th day after infection at 20°C. This molt can be easily detected because the 3d stage larva has 3 mucrones on the tail. The stoma is dorso-ventrally elongated but no circumoral papillae are present. The buccal capsule is composed of two weakly sclerotized lateral valves, pale yellow in color, and divided into two chambers. The esophagus is distinctly divided into an anterior muscular portion and a posterior glandular portion. The entire worm has a distinct orange color.

The third-stage larvae lie coiled and inactive in the copepod hemocoel. If the copepod contains only one or two worms, they are usually found dorsal to the gut. The larvae are immediately infective after the third molt. Infected copepods were placed in 1 ml of 1) Ringer's Solution, 2) Pepsin-HCl + Ringer's and 3) Fish Bile + Ringer's in separate depression slides to determine what released escape activity of the larvae. Copepods died quickly in each solution. Larvae remained coiled and motionless in Ringer's Solution for several hours. Immersion in the pepsin-HCl solution caused some larval activity after 35 minutes and continued for 3 hours but larvae remained coiled. The bile solution caused larval activity within 5-10 minutes. Larvae uncoiled and moved about so violently that it caused flexing of the entire dead copepod body. These larvae moved throughout the body punching their heads into appendages and lashing vigorously about the hemocoel. No larvae escaped, although activity continued for 3 hours. Some infected copepods were placed in pepsin-HCl for 1 hour, then in the bile solution. A high percentage of larvae escaped from these copepods through the tail.

Spot-tail shiner fry (Notropis hudsonius) were collected with a dip net and exposed to infected copepods in large finger bowls for three days. Dissection of these fish revealed developing third-stage Camallanus larvae. Shiner fry exposed to infected copepods were placed into a 15 gallon aquarium with 5 yearling yellow perch (Perca flavescens). The perch were observed feeding upon the shiner fry. All the perch were sacrificed after 5 days and 4 of these fish contained developing 3d stage larvae. All control fish were free of infection.

Third-stage larvae from fish are morphologically similar to larvae from copepods except they are larger (Max. length = 1.241 mm as opposed to 0.671 mm). The third molt occurs 9-10 days after infection. The most striking change following this molt is in the buccal capsule. It's color is a deep bronze, the ridges are longitudinal and the two chambers are fused into a single one. Five pairs of circumoral papillae occur around the stoma. The tail has three small mucorones.

The final molt occurs at different times for the male and female. The male 4th stage larvae reach a maximum length of 1.90 mm and molt on the 17th or 18th day after infection at $26^{\circ}C$. The female larvae attain a maximum length of 2.60 mm and molt 24 days after infection. Adult worms have dorsal and ventral tridents associated with the buccal capsule. The tail is rounded and smooth, without mucorones.

The experimental determination of the life history elucidates several important points on the transmission of Camallanus oxycephalus. One, infective first-stage larvae must be eaten by the intermediate host. Transmission of this parasite depends, in part, upon the trophic dynamics of this host. Two, the intermediate host may only be a copepod. Although many aquatic arthropods eat these larvae, development to the stage infective to fish occurs only in copepods. This is a relatively important finding because transmission of the parasite can be narrowed to the interaction between the plankton community and fish. The parasite contacts the fish populations through a single route. Three, the infection may be passed from one fish to another. This, too, is a significant finding of this study. The ability to be transferred in such a manner provides a zone of overlap between plankton feeding fish and fish eating fish, thus widening the potential range of hosts. Many fish, far removed from plankton feeding, are open to infection if they feed upon forage fish. It is likely that the large sport fish, such as white bass, black bass, yellow perch, walleye, northern pike, drum, crappies and rockbass become infected by eating infected forage species.

<u>Summary of the Experimental Life History</u> (Fig. 1)

1. Ovoviviparous females exposed to lake water when fully gravid rupture and release 7,000-10,000 infective first-stage larvae.
2. Active 1st stage larvae are eaten by a variety of aquatic arthropods, but penetration through the gut wall into the hemocoel occurs only in copepods.
3. There is little observable development until the 1st molt, which occurs 3-5 days after infection.
4. Many morphological changes begin to take place in the second-stage larva. Most notably, the buccal capsule begins to form.
5. The second molt occurs 6-10 days after infection.
6. Third-stage larvae are distinct; the buccal capsule is divided into two chambers, the tail terminates in three mucrones and living worms are bright orange in color.
7. Escape activity of the third-stage larvae is stimulated by bile. Actual escape may depend in part on the softening of the copepod exoskeleton by pepsin and HCl.
8. Infection may be acquired by large fish either by directly ingesting infected copepods or eating smaller fishes carrying the worms. The parasite may be passed from plankton to plantivorous fish to piscivorous fish in this manner.

9. The third molt occurs on the 18th day after infection. Fourth-stage larvae have a one chambered buccal capsule, circumoral papillae and three mucrones on the tail.

10. The final molt occurs on the 18th day after infection for males and 24 days after infection for females. Adult nematodes have dorsal and ventral tridents associated with the buccal capsule and a smooth, blunt tail.

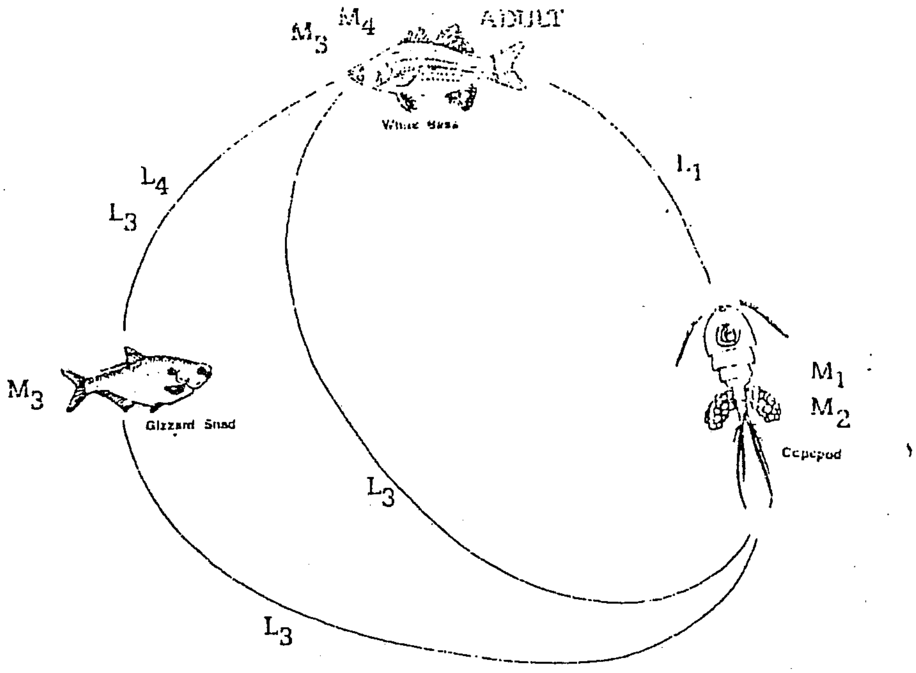

Fig. 1. Life History of Camallanus oxycephalus.

Biology of the Dispersal Agent

Because the ability of the first-stage larva to infect the intermediate host may be affected by its interaction with the environment, a series of experiments were conducted with the larvae to determine the nature of the interaction and its effect on infectivity. Among the most important are the effect of temperature on survival, the relationship between infectivity and age, salinity tolerance and the relationship between larval activity and consumption rate by the intermediate host.

To determine a basal efficiency of infection, copepods (*Cyclops bicuspidatus*, *C. vernalis*, *Diaptomus* sp.) were exposed to freshly released infective larvae of *Camallanus oxycephalus*. Table 2 summarizes these experiments.

TABLE 2
INFECTION OF COPEPODS BY 1st STAGE LARVAE

Copepod	No. L_1 exposed	No. L_1 eaten	No. L_1 penetrated	
Cyclops	800	508 (.635)	360	P_e = .709
Diaptomus	108	1 (.009)	0	

It is clear that cyclopoid copepods ingest _Camallanus_ larvae much more readily than do calanoid copepods. This is probably related to the feeding habits of the copepods, since cyclopoids are predacious and scavengers, while calanoids are filter feeders. Although we were able to produce infections in calanoid copepods, these experiments allow us to confine epidemiological considerations of the intermediate host to the dynamics of cyclopoid copepod populations. The experiments also revealed a very high efficiency of infection (P_e) by the dispersal agent. This high efficiency is an important factor in the local abundance of _C. oxycephalus_ in western Lake Erie.

Survival of the infective dispersal agent was definitely affected by temperature. Figure 2 shows the survivorship curve determined at 20°C and 25°C. These temperatures were selected because they approximate the extreme water temperatures in western Lake Erie during June and July when larvae are in the water. Larvae survived 39 days at 20°C but only lived 24 days at 25°C. More than half of the larvae lived 28 days at the lower temperature, while 50% survival was reached between 17 and 18 days at the higher temperature. Not only did the larvae survive for a longer period of time at 20°C but the decline in survival was more gradual than at 25°C. Figure 3 shows the effect of NaCl concentration on larval survivorship. A 1% solution of NaCl was clearly detrimental to larvae, significantly

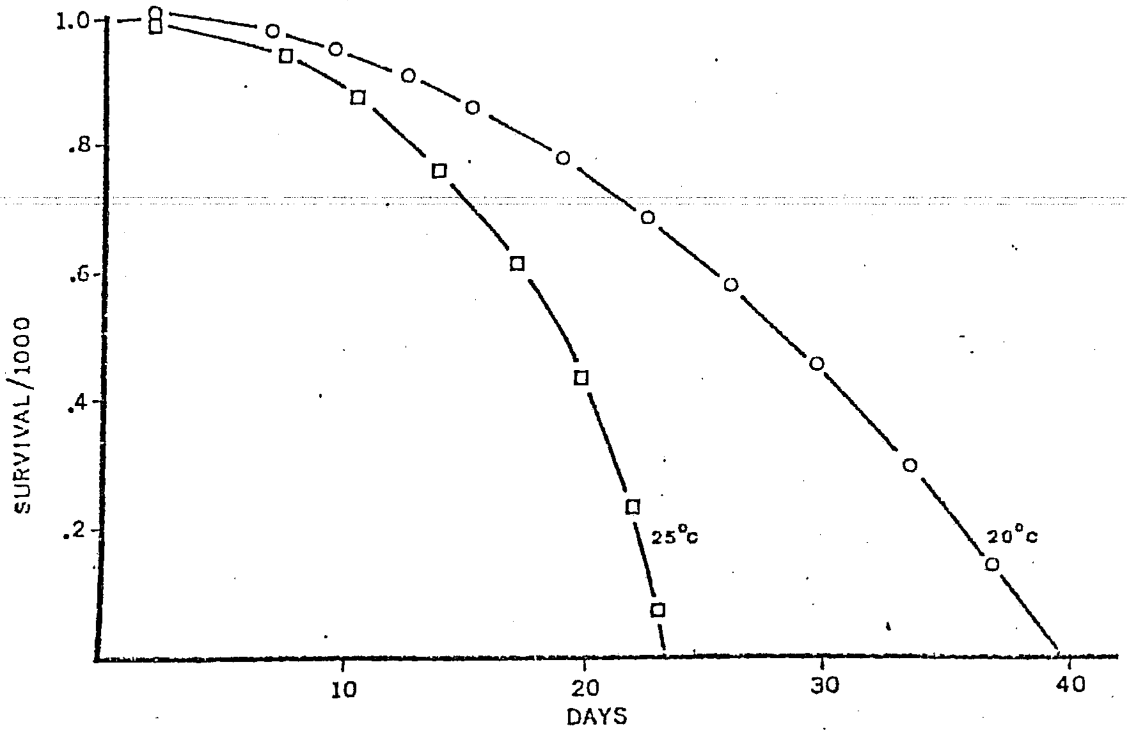

Fig. 2. Survival of first-stage larvae of C. oxycephalus at 20°C and 25°C.

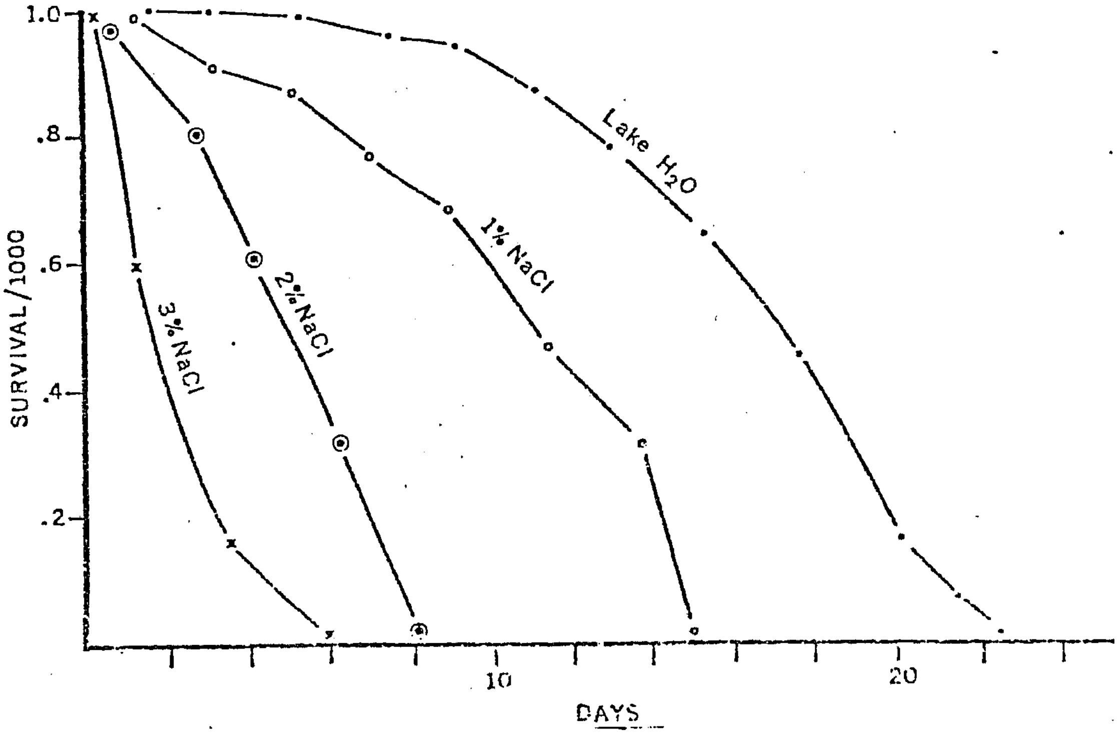

Fig. 3. Survival of first-stage larvae of C. oxycephalus in saline solutions at 25°C.

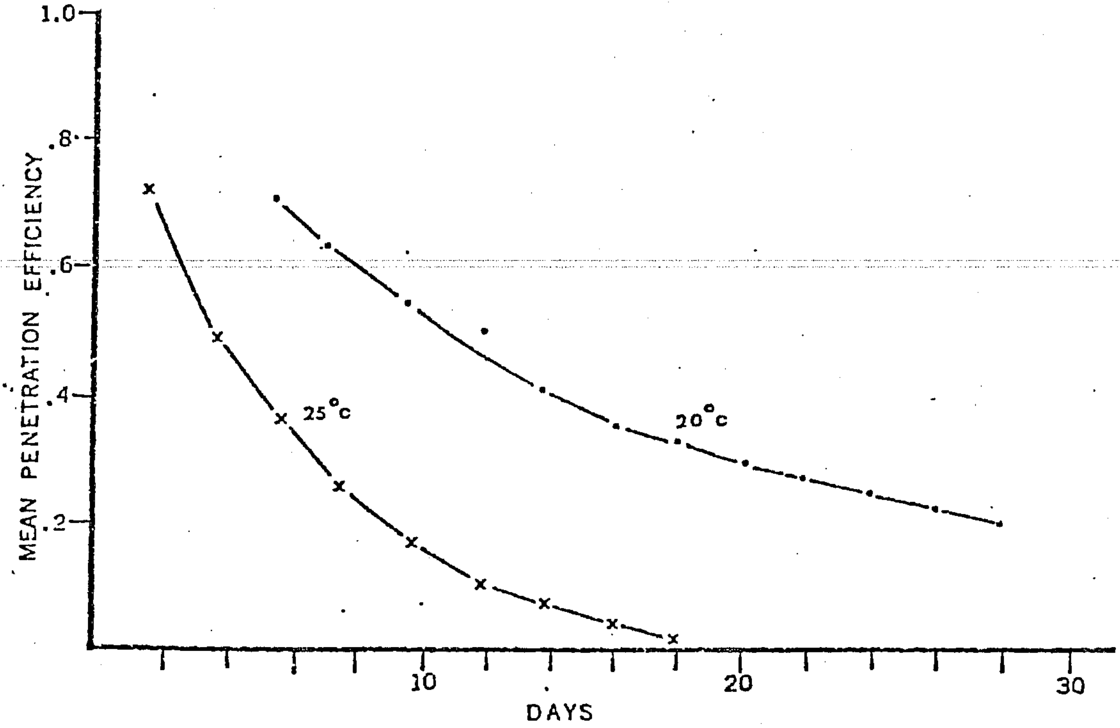

Fig. 4. Relationship between penetration efficiency and age of C. oxycephalus larvae at 20°C and 25°C.

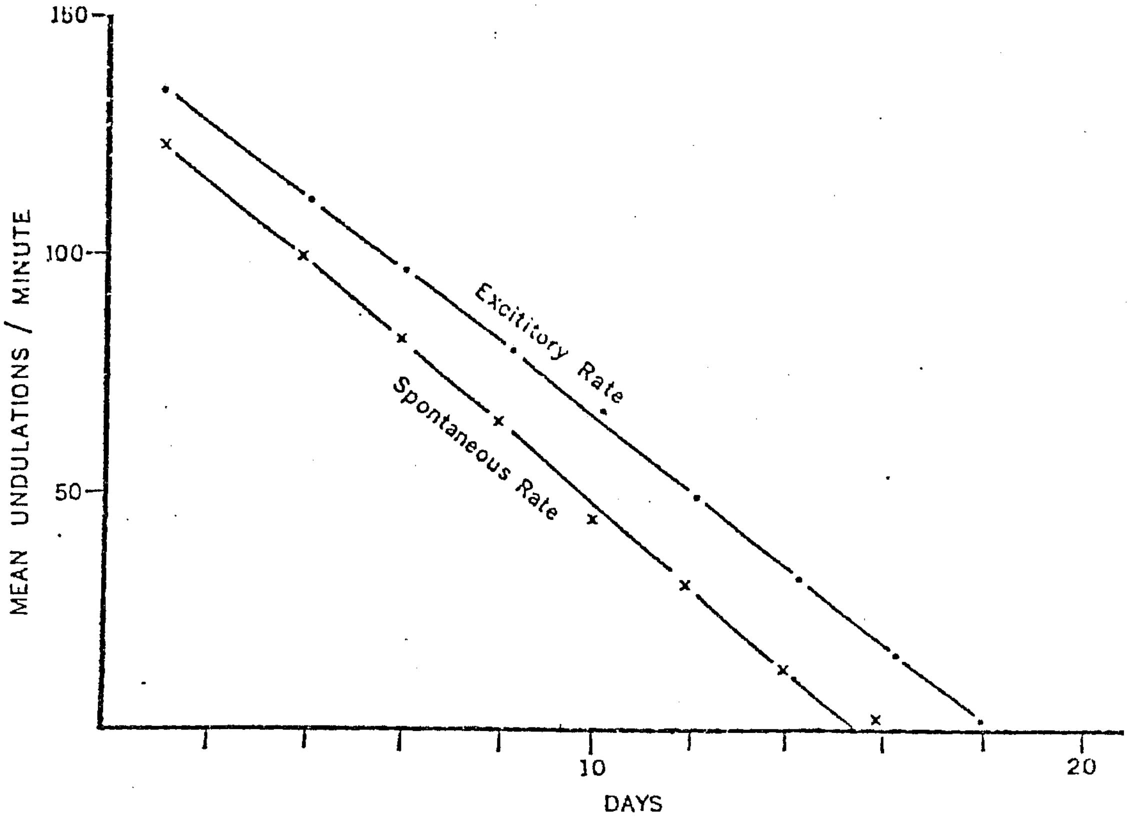

Fig. 5. Relationship between rate of activity and age of first-stage larvae of C. oxycephalus at 25°C.

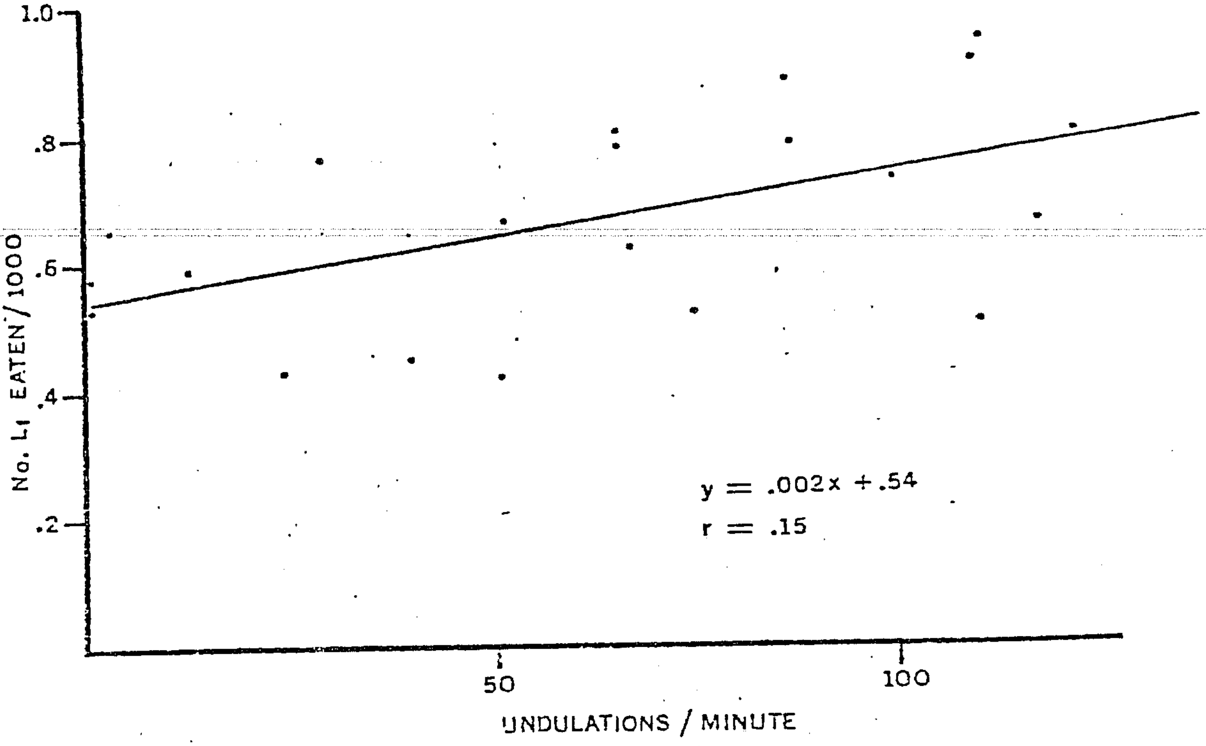

Fig. 6. Relationship between activity rate and L_1 ingestion of Cyclops.

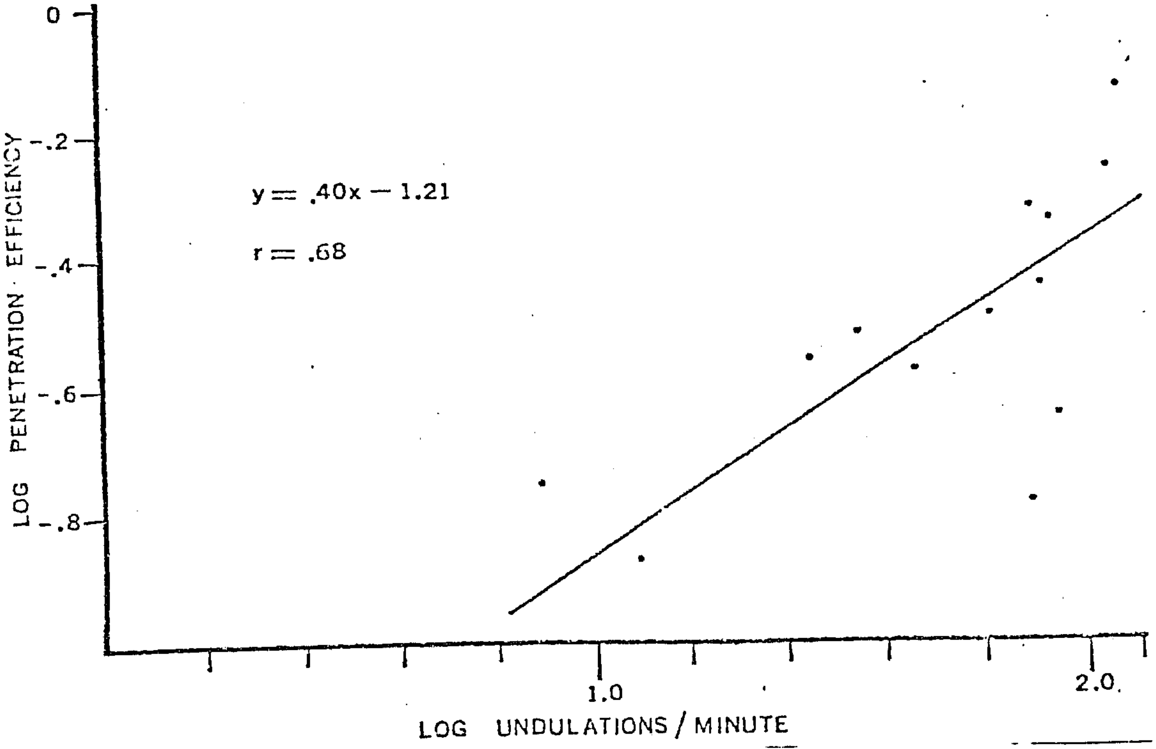

Fig. 7. Relationship between the log penetration efficiency and the log activity rate.

decreasing their survival. Higher concentrations of NaCl reduced survival more rapidly. Most larvae exposed to 3% NaCl were crenated and exhibited abnormal twitching after 24 hours.

Although the larvae survived 39 days and 24 days in filtered lake water at 20° and 25° respectively, the ability to penetrate the copepod gut wall was lost before the larvae died (Figs. 2 and 4). The penetration efficiency decreased logarithmically with the age of the larvae. The decrease was rapid at both temperatures. No larvae penetrated the gut wall after 18 days at 25°C. Penetration efficiency had not reached 0 when the 20° experiment was terminated at 28 days.

The initial rate of larval activity was high. Fresh, undisturbed larvae exhibited a mean rate of 130 undulations per minute. The decline in spontaneous activity was linear and the slope was -8.55 (Fig. 5). Spontaneous activity ceased after 16 days at 25°C. The mean excitatory rate was consistantly higher than the mean spontaneous rate, but was maintained for less than 1 minute after the larvae were disturbed. The maximum excitatory rate was 142 undulations per minute, slightly less than a 10% increase over the spontaneous rate. The slope of the excitatory line (-7.61) was nearly equal to that of the spontaneous line. No excitatory activity could be elicited after 18 days.

The relationship between the mean spontaneous activity rate and the number of larvae eaten by Cyclops (Fig. 6) was a positive linear function. Statistical analysis of the regression coefficient indicated that this was a highly significant relationship ($F = 8.06$, $P < .01$). This suggests that active larvae are more likely to be eaten by copepods than sluggish or inactive larvae. The expenditure of energy in maintaining a constant movement by the larvae, then appears "ecologically justified" since this movement apparently attracts copepods and significantly increases the probability of intermediate host infection. The conservation of energy resources by Camallanus larvae, for prolonged survival at a low activity rate does not seem an effective tactic because larvae liberated into the plankton fall rapidly through the water column and are probably lost in the sediments. In addition, cyclopoid copepods are abundant for only several weeks during the year. Thus, copepods and infective dispersal agents overlap temporarily for only a short time, and there would be little selective advantage in prolonged survival of larvae.

Because the rate of activity declines linearly while the penetration efficiency declines logarithmically (Figs. 4 and 5), it was initially thought that larval activity alone did not account for penetration of the copepod gut wall. Analysis of the log transformation values for penetration efficiency and activity and their relationship (Fig. 7), however, yielded a highly significant correlation coefficient ($t = 4.22$; $P < .01$). This indicates that larval activity is the most important factor in penetration of the copepod gut wall.

Pathogenecity in Fish

Repeated analyses of the histopathology associated with adult *Camallanus oxycephalus* has not revealed any definite, significant disease in white bass. The nematodes clearly penetrate the rectal mucosa, grasp the submucosa and feed upon blood and tissue fluid. The reaction to this invasion is minimal and there is limited damage associated with it. Although no heavy infections were studied histologically, it is unlikely that there is any significant structural damage caused by *Camallanus*. The minimal structural damage to the rectal mucosa, however, might be sufficient to allow secondary invasion of normal bacterial flora and subsequent disease. There are other cases on record of parasite-disease complexes caused in this manner. This was not investigated, but might be the subject in future investigations of any white bass mortality.

Changes in the Prevalence of *C. oxycephalus* in Lake Erie

Seventeen species of fishes were examined for *C. oxycephalus* in western Lake Erie. Sixteen of these fishes were found to be parasitized. These data were compared to the previous findings of

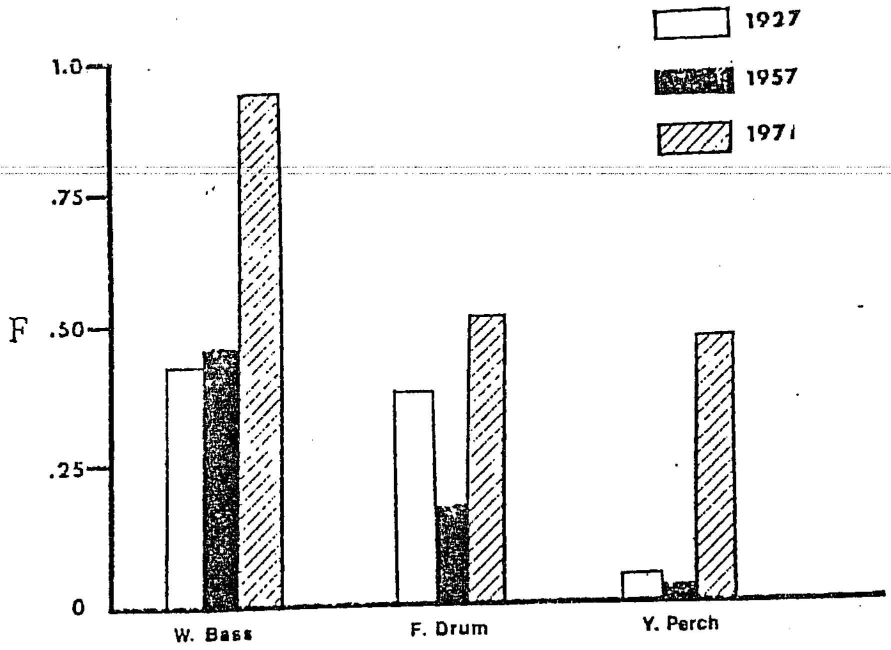

Fig. 8. Frequency of *C. oxycephalus* in Lake Erie fish.

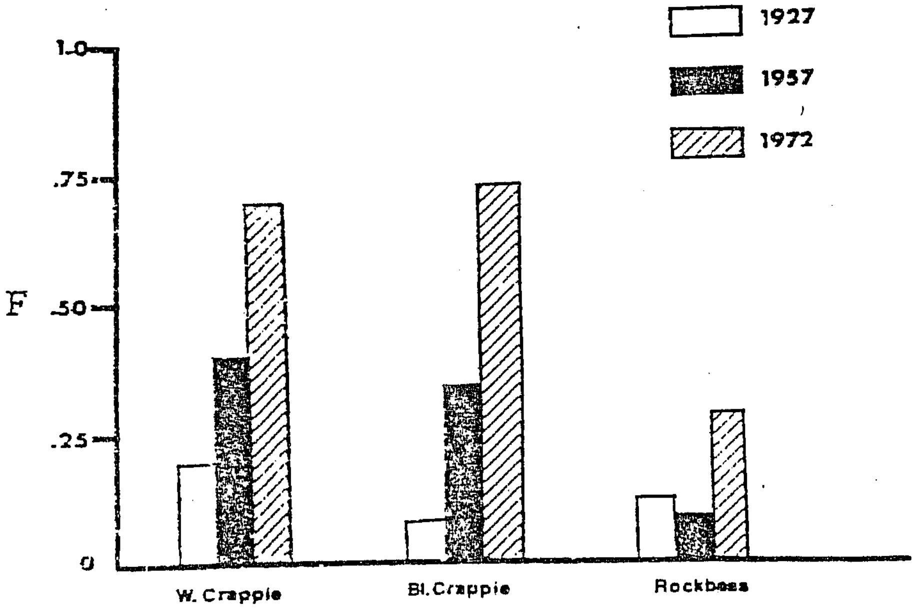

Fig. 9. Frequency of *C. oxycephalus* in Lake Erie fish.

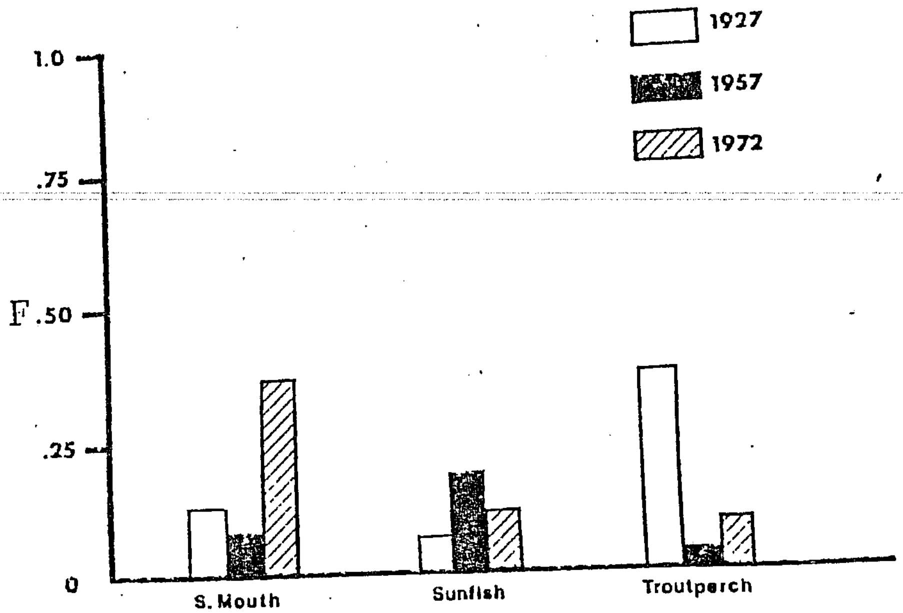

Fig. 10. Frequency of C. oxycephalus in Lake Erie fish.

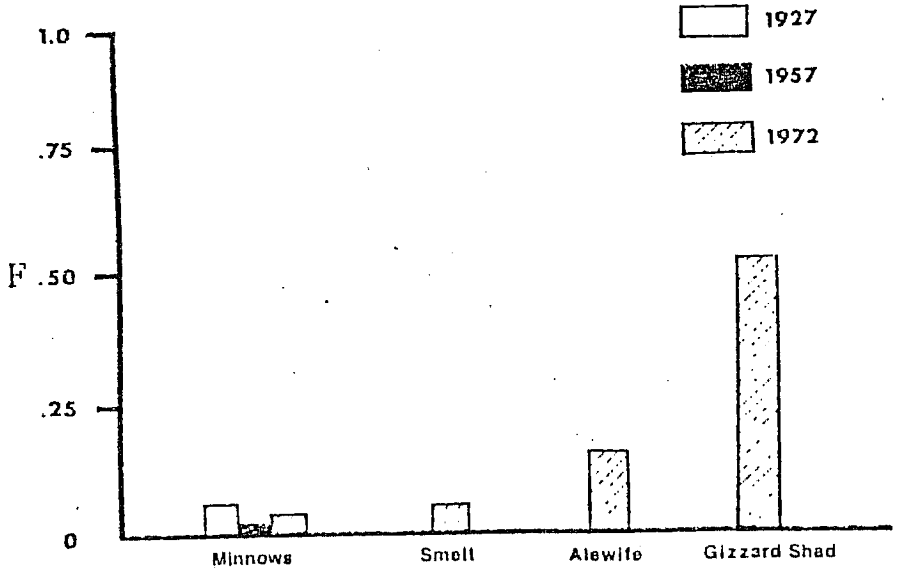

Fig. 11. Frequency of C. oxycephalus in Lake Erie fish.

TABLE 3
CHANGES IN THE FREQUENCY OF *Camallanus oxycephalus* IN LAKE ERIE FISHES 1957-1972

Fish	1957 N	1957 F	1972 N	1972 F	z
Morone chrysops (Adult)	53	.472	83	.952	+6.233**
M. chrysops (YOY)	--	----	170	.641	
Aplodinotus grunniens (Adult)	88	.143	67	.507	+4.727**
A. grunniens (YOY)	--	----	300	.500	
Perca flavescens (Adult)	93	.054	114	.475	+8.816**
P. flavescens (YOY)	--	----	64	.016	
Pomoxis annularis	53	.396	48	.708	+3.270**
P. nigromaculatus	29	.310	37	.730	+3.428**
Ambloplites rupestris	75	.107	22	.273	+1.983**
Lepomis gibbosus	58	.069	28	.107	+ .606
Micropterus dolomieui	55	.078	40	.375	+3.574**
Stizostedion vitreum	33	.212	13	.691	+3.092**
Percopsis omiscomaycus	63	.032	13	.077	+ .761
Ictalurus punctatus	39	.026	57	.157	+2.047**
Notropis hudsonius	77	.013	60	0	- .619
N. atherinoides	39	0	240	.011	+ .523
N. spilopterus	68	.015	24	.167	-2.923**
Osmerus mordax (YOY)	61	0	50	.040	+1.633
Dorosoma cepedianum (YOY)	27	0	360	.533	+5.333**
Alosa pseudoharengus (YOY)	14	0	190	.121	+1.388

N = sample size; F = frequency of infection; ** denotes dignificant z-value

TABLE 4
CHANGES IN THE FREQUENCY OF *Camallanus oxycephalus* IN LAKE ERIE FISHES 1927-1957

Fish	1927		1957		
	N	F	N	F	z
Morone chrysops (Adult)	32	.469	53	.472	- .006
M. chrysops (YOY)	9	.220	--	----	
Aplodinotus grunniens (Adult)	45	.400	88	.143	-2.888**
Perca flavescens (Adult)	45	.022	93	.054	+1.000
P. flavescens (YOY)	15	0	--	----	
Pomoxis annularis	17	.231	53	.396	+1.231
P. nigromaculatus	9	.111	29	.310	+1.192
Ambloplites rupestris	12	.116	75	.107	- .090
Lepomis macrochirus	10	.100	74	.311	+1.384
L. gibbosus	23	.143	58	.069	+ .441
Micropterus dolomieui	80	.125	55	.078	- .855
M. salmoides	24	.041	40	.175	+1.576
Stizostedion vitreum	48	.104	33	.212	+1.403
Etheostoma/Percina	93	.161	127	.102	- .418
Percopsis omiscomaycus	46	.369	63	.032	-4.746**
Ictalurus punctatus	29	.034	39	.026	- .178
Notropis hudsonius	83	.036	77	.013	- .958
N. atherinoides	81	.012	39	0	- .706
N. spilopterus	49	.101	68	.015	-2.300**

N = sample size; F = frequency of infection; ** denotes significant z-value

Bangham and Hunter (1939) and Bangham (1957) to ascertain if any trend could be seen in the abundance of this parasite. Figures 8-11 illustrate the nature and magnitude of the frequency of infection in important Lake Erie fishes. Tables 3 and 4 show the precise frequency values of Camallanus in Lake Erie fish among the three studies and the statistical analysis of the changes in prevalence.

It is clear immediately that the frequency of occurrence of C. oxycephalus was quite high in many of the 1972 fish. Highest frequencies occurred in predatory species such as Morone chrysops, Pomoxis spp., Stizostedion vitreum. Low frequencies occurred in plankton feeders with the exception of Dorosoma cepedianum and young of the year drum (Aplodinotus grunniens).

A comparison of the prevalence of C. oxycephalus between 1927 and 1957 (Table 4) reveals a significant decrease in three species; drum, troutperch (P. omiscomaycus) and spot-fin shiner (N. spilopterus). The prevalence of the worm remained essentially unchaged in 14 species of fish between 1927 and 1957. A study of the 1957 and 1972 data, however, shows a significant increase of Camallanus in 11 species of Lake Erie fish (Table 3). The prevalence of Camallanus remained unchanged in 6 species and declined in none. It is apparent that C. oxycephalus has become more common in Lake Erie since 1957. Troutperch were the only fish to exhibit a decline in prevalence of the parasite since 1927. Although no data for young of the year white bass are available for 1957, direct comparison of the 1972 data with the 1927 values revealed a significant increase in Camallanus (z = +2.586). A similar comparison of yellow perch showed that although adult fish are more frequently parasitized, the frequency in young of the year has not changed significantly (z = +.498).

In addition to the increase in frequency of infection of white bass the data suggest that the intensity of infection has also risen. Only 18% of the 1927 white bass carried more than 10 worms each, while 45% of the 1972 adult white bass had at least 10 worms. Thus, the mean worm burden in the white bass population appears to have increased.

The magnitude of the changes in prevalence of C. oxycephalus in the fish community as a whole is illustrated in Fig. 12. This figure compares the sequence of infection frequencies ordered from highest to lowest for each year studied. The numbers do not correspond to specific fish, so that the changes in specific fish is not illustrated. Rather, the graph represents the shift in abundance of the parasite population. It is clear from this figure that no significant change in prevalence of C. oxycephalus occurred in the fish community between 1927 and 1957. The curves for these two years are characterized by relatively low frequencies of infection, sloping gradually from a high of about .47 to .01. The 1972 curve

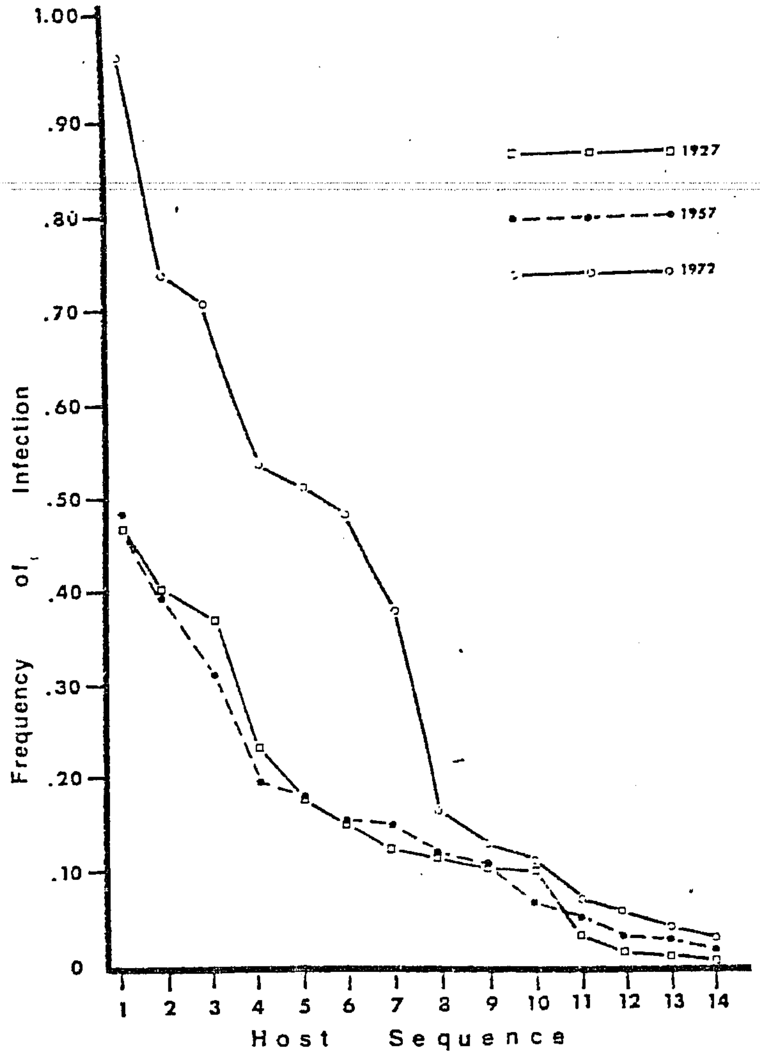

Fig. 12. Comparison of the prevalence of C. oxycephalus in Lake Erie in 1927, 1957 and 1972.

represents a significant increase of great magnitude in the prevalence of the parasite. Several groups of fish can be defined based upon infection frequency. One species (white bass) occurs at the .90 level, three species (white crappie, black crappie, walleye) occur around .70 and three species (freshwater drum, gizzard shad and yellow perch) occur around .50. The 1972 curve declines sharply after these seven high frequency values through two intermediate frequencies (.40-.20). The remaining seven values are low, occurring around or below .15. The fish exhibiting the low frequencies of infection are all plankton feeders except the catfish and pumpkinseed. In contrast, the 1927-57 curves have only a single species in the high frequency group (ca. .50), three or four species in the intermediate group and the majority (12) in the low frequency group.

Based upon this analysis of the prevalence of Camallanus in 16 species of Lake Erie fish, the parasite appears to be far more abundant than in past years. In addition, this analysis suggests that the shift upward has occurred since around 1957. Only troutperch of all the fish examined, had a lower frequency of infection with Camallanus in 1972 than in 1927. Nine of the 11 species with higher frequencies of infection are predatory species which include a significant portion of fish in their diet. All 6 species with unchanged infection frequencies are either plankton feeders or consume benthic arthropods.

Because the increase in the prevalence of C. oxycephalus in western Lake Erie has been largely in piscivorous fish, it seems likely that the increase has been caused by a rise in infected forage fish. The ability of C. oxycephalus to be carried from forage fish to predatory fish was demonstrated experimentally. The discovery of a high frequency of *Camallanus* in gizzard shad was a particularly significant finding in this regard. Although this fish was known from Lake Erie as early as 1848, Miller (1957) pointed out that it has only become abundant in Lake Erie since the 1950's. Bodola (1964) noted the rapid rise of gizzard shad especially in the western basin, since around 1950 and he stated that it had an important effect upon lake ecology. We frequently found shad in white bass and crappie stomachs indicating that the increase in shad has been exploited by some predatory fish. The rapid rise in a forage fish which becomes frequently infected and is preyed upon by many susceptible fish has increased the transmission of *C. oxycephalus* to its final host. This mechanism would also produce heavier infections in predatory fish and might be responsible for some fish mortality. The data available place the rise in gizzard shad stocks in the same time period as the increase in the prevalence of *Camallanus*, lending additional credibility to the hypothesis that shad are responsible, in part, for the abundance of the parasite.

Changes in the Lake Erie benthic fauna may have indirectly influenced the abundance of *Camallanus*. Britt, *et al.* (1973) documented the decline in abundance of the mayfly nymph *Hexagenia* since 1953. They noted a large decrease in *Hexagenia* after 1959.

This reduction in food resource may have forced such generalized feeders as perch, drum, and catfish into eating greater amounts of forage. The concomitant rise of gizzard shad during this period increased the exposure of these fish to infection with *Camallanus*.

Ecology of *Camallanus oxycephalus* in western Lake Erie

To more fully understand the interaction of *C. oxycephalus* with its various life history components in the western Lake Erie system, an examination of certain host and parasite population phenomena was initiated. Such a study might help to determine how the abundance of this parasite is maintained, what factors might cause flucuations in the parasite population and finally, if any of these factors could be manipulated to reduce the abundance of the parasite.

The parasite occurred in 16 species of fish, but was most intensively investigated in white bass. All size classes of white bass were infected. The difference in incidence and intensity of infection between male and female fish was tested with the Mann-Whitney-U test and found to be not significant. Only a general relationship was evident between fish length and infection intensity (Figs. 13 and 14) because of the large degree of overdispersion in the sample. Infections from adult and young of the year fish were fit to the Poisson series, but agreement was very poor. Because the ratio of variance to mean was high, the negative

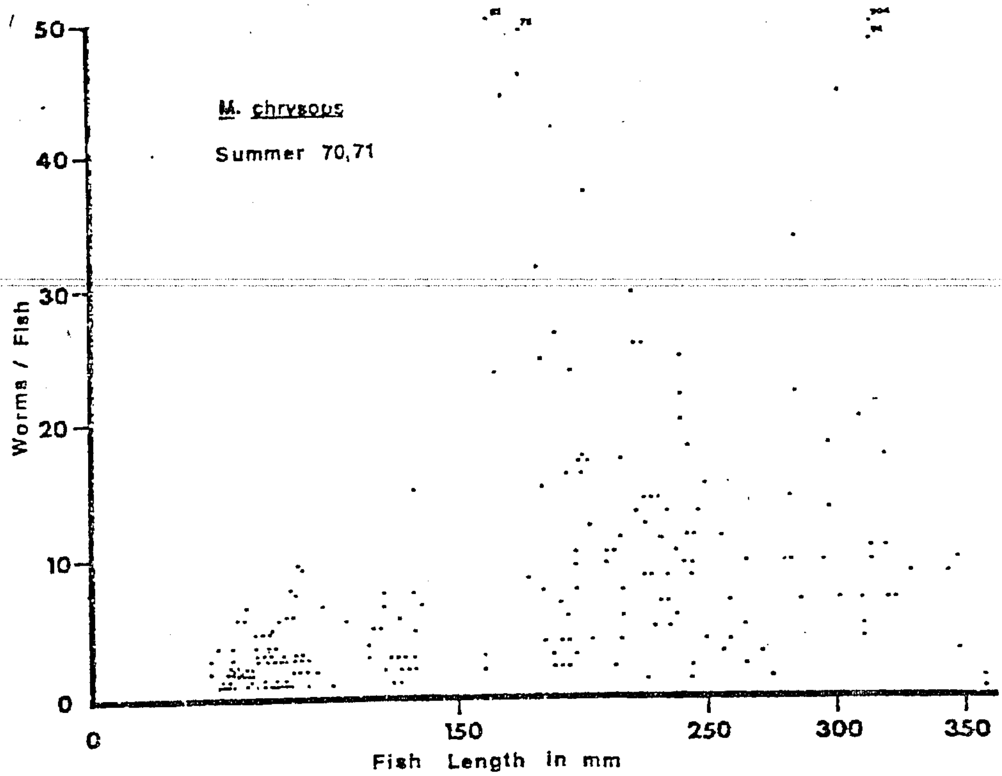

Fig. 13. Relationship between infection intensity and fish length for white bass - Summer 1970, 1971.

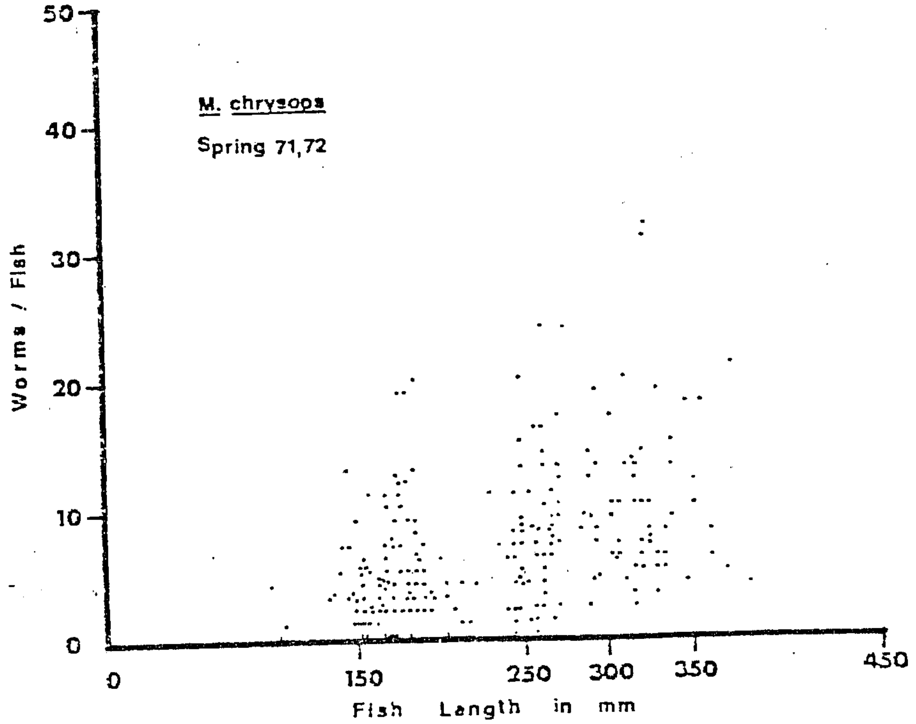

Fig. 14. Relationship between infection intensity and fish length for white bass - Spring 1971, 1972.

binomial distribution was fit to the data and agreement was good. The negative binomial, which is one of several overdispersed distributions, then is taken to be a satisfactory model of _Camallanus_ in western Lake Erie fish. Data for freshwater drum, yellow perch, and gizzard shad also approximate the negative binomial.

TABLE 5

RELATIONSHIP OF WHITE BASS LENGTH TO THE INCIDENCE AND INTENSITY OF INFECTION WITH _C. oxycephalus_

Length Group of Fish (mm)	No. Fish Examined	No. Fish Infected	% infected	Mean Worm Burden
< 100	254	182	71.7	1.97
101-150	93	80	86.0	4.14
151-200	158	134	84.8	8.04
201-250	132	107	81.1	8.78
251-300	110	100	90.9	7.54
300 <	102	93	91.2	11.11

Table 5 illustrates the percentage infection and the mean intensity of infection in six size groups of fish. Adult fish one year or older (over 150 mm) generally had a higher incidence and higher mean worm burden than young of the year fish. The heaviest worm burdens were always in large adult fish. The percentage of infection did not change with fish size in adult fish. These data indicate that white bass in western Lake Erie are frequently and heavily infected with Camallanus.

The structure of the parasite population varied considerably with the seasons. The population was composed entirely of adult worms during all months except July, August and September (Table 6). During July and August, the population consisted mostly of third and fourth stage larvae. This indicates that 1) the worms live for approximately one year, 2) worms die during early summer and 3) fish are re-infected in July and August. Old and new generations of the parasite can easily be differentiated by size and degree of maturation. Year old males and females averaged 4.57 mm and 18.18 mm in length respectively. The ratio of new males to new females is approximately 2:1 during August, but changes to 1:1 in September. This initial sex ratio is caused by the different molting times in the fourth-stage larvae. The sex ratio remains 1:1 until the following July, when females begin to die before males, producing a 2:1 ratio again.

Seasonal variation in the infection of adult white bass is evident in Table 7. While there is little change in the percentage of infection during the year, there is a marked decrease in the

TABLE 6

SEASONAL CHANGES IN THE POPULATION STRUCTURE OF *C. oxycephalus*

Month	% Males	% Females	% L_4	% L_3
June	48.2	51.8	0	0
July	11.6[a]	6.4[a]	58.4	14.3
	5.2[b]	3.9[b]		
August	1.0[a]	0.1[a]	43.1	9.2
	29.1[b]	17.5[b]		
September	51.6	45.6	3.2	0
October	51.2	48.8	0	0
November	50.5	49.5	0	0
April	49.2	50.8	0	0
May	47.9	52.1	0	0

a = year old adults; b = new adults

TABLE 7

SEASONAL CHANGES IN THE INFECTION OF ADULT WHITE BASS

Year and Month		Number of Fish Examined	Infected	Percent Infected	Mean Worm Burden
1970	November	15	14	93.3	10.9
1971	April	20	20	100.0	8.1
	May	36	33	91.7	5.4
	June	49	47	95.9	7.9
	July	52	47	90.4	2.2 adults 13.5 juveniles
	August	29	28	96.6	0.5 adults 14.6 juveniles
	September	20	20	100.0	12.3
	November	9	9	100.0	11.5
1972	April	23	22	95.7	8.4
	May	43	43	100.0	7.5
	June	40	36	90.0	5.7
	July	69	43	62.3	2.7 adults 0.0 juveniles
	August	89	70	78.6	0.3 adults 6.1 juveniles
	October	31	29	93.4	4.6
	November	16	15	93.8	2.8

mean worm burden between July and the following June. The infection increases rapidly in July, but a net loss of worms occurs as early as September. The decrease in the parasite population continued throughout the year so that the mean number of reproducing females in June is 30-60% less than the original number of immature females found the previous August. The 1970-71 and 1971-72 generations of C. oxycephalus were very similar in seasonal timing and size. The absence of larvae and lower incidence of the parasite in July 1972 indicates that the 1972-73 generation was delayed and not as effective in reaching the white bass population as in previous years. The November mean worm burden was markedly lower than the 1970 and 1971 values. The loss of worms from white bass appears partially related to fish size but may be directly related to the population density of worms within fish. Data from 1970-71 and 1971-72 were grouped and the mean worm burdens in four size groups of fish were plotted for six seasonal time periods (Fig. 15). It appears that the C. oxycephalus population remains relatively stable in the fish with summer mean worm burdens of 10 worms or less. The two fish groups with high summer infections lost 50-60% of their nematodes. The initial worm burdens do not correlate with size completely since more worms occurred in the 1+ fish than in the 2+ fish. These data suggest the possibility of a density-dependent

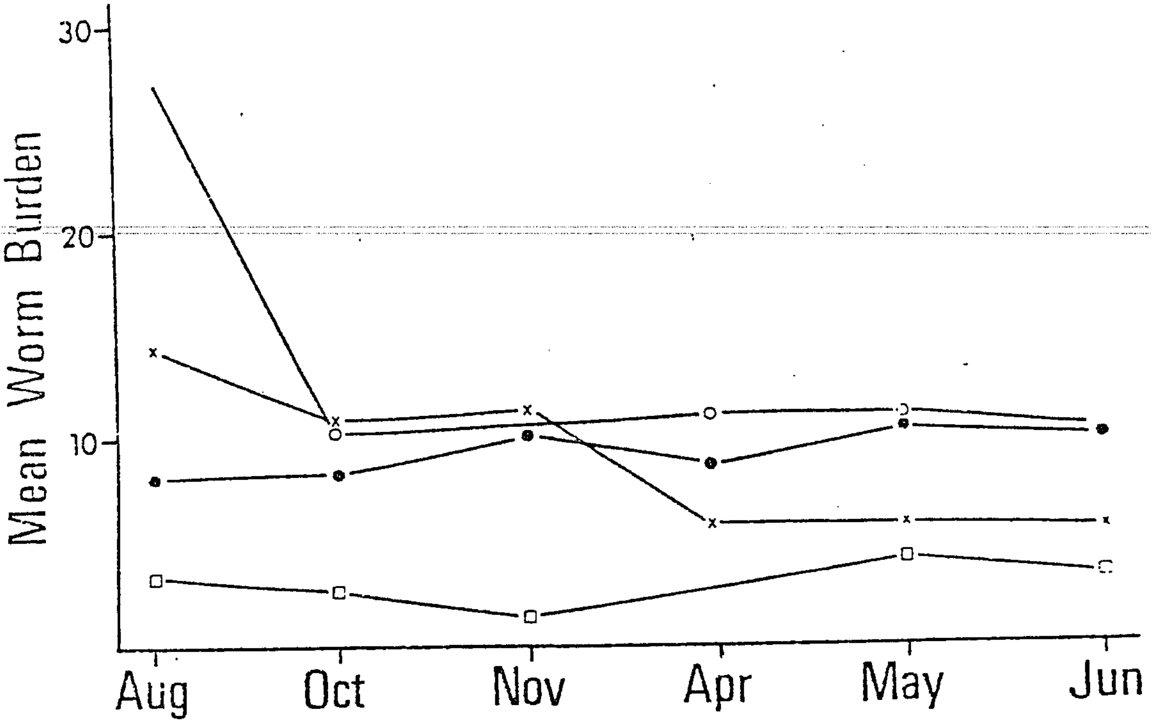

Fig. 15. Seasonal variation in the mean worm burden of <u>C. oxycephalus</u> in different age groups of white bass, □ - 0+ years (0–150mm), x – 1+ years (151–250mm), ● - 2+ years (251–300mm), o - 3+ years (over 300mm).

regulatory mechanism might be related to fish size because larger fish have more gut volume and therefore could support a higher density of parasites. This is suggested in Fig. 15, where 1+ fish had a greater initial worm density with greater worm mortality than the 2+ fish which had a lower worm density with no apparent worm mortality.

When a new generation of worms enters the white bass in July, they are distributed throughout the entire intestine. During July, when most worms are larvae, they occurred primarily in the intestine (Table 8). A maturational site selection occurs and by August, two-thirds of the worms are found in the rectum. No worms occur anterior to the rectum between October and the following June. The worms remain in the rectum until death. Infected fish become obvious in April and May when growing female nematodes begin to protrude from the fish rectum and are readily observable with the unaided eye.

TABLE 8

SEASONAL CHANGES IN SITE SELECTION OF _C. oxycephalus_ IN ADULT WHITE BASS

Month	worms in small intestine No.	worms in small intestine %	worms in large intestine No.	worms in large intestine %
June	0	0.0	386	100.0
July	458	66.5	231	33.5
August	210	36.1	370	63.9
September	42	18.3	188	81.7
October	0	0.0	34	100.0

The seasonal growth pattern of C. oxycephalus was established by plotting mean body length against time. Figure 16 reveals that the growth pattern for two generations was very similar and exhibits the following four characteristics: 1) the initial, autumn growth rate of female worms was more rapid than that of males; 2) female growth was arrested between November and April; 3) the difference in mean male body length between November and April was significant, ($t = 2.888$, $P < .005$) indicating that males continued to grow through the winter; 4) females resumed

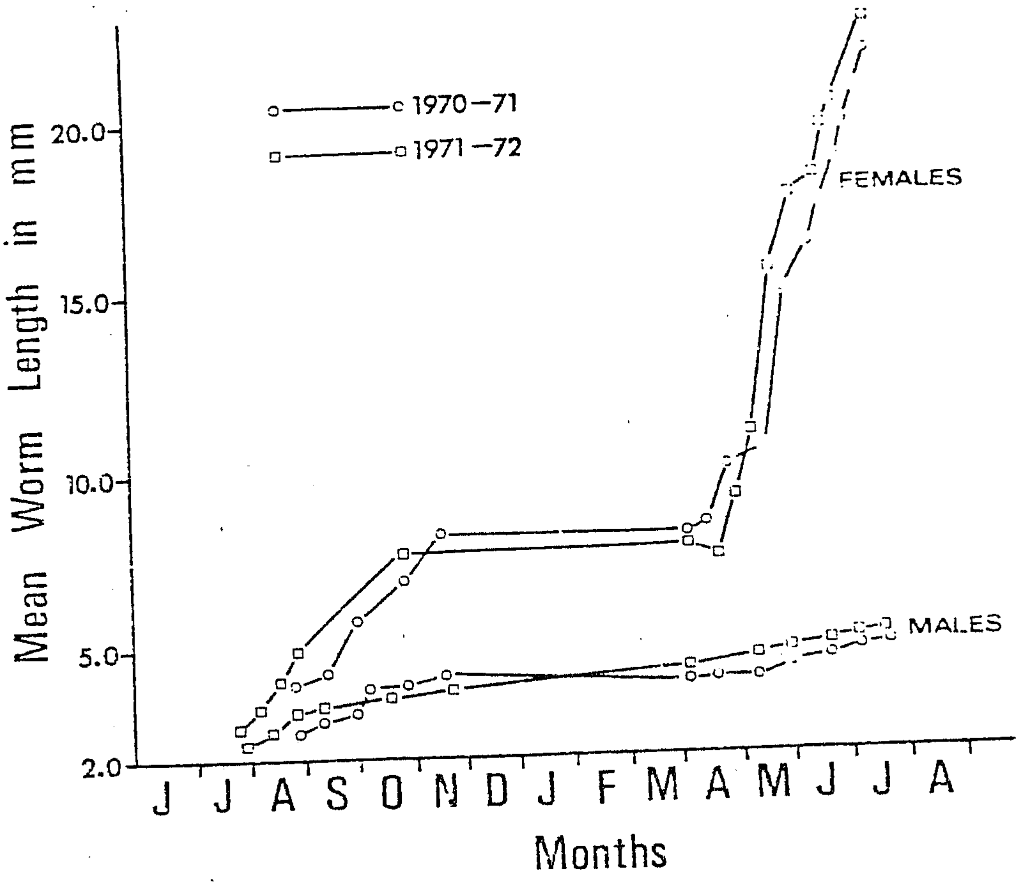

Fig. 16. Seasonal growth pattern of C. oxycephalus in western Lake Erie.

growth at an extremely rapid rate in April and continued growing until death, reaching a length 4-5 times longer than males. Sperm cells were found in the uteri of female worms in October and November and were carried through the winter, indicating copulation occurs in the autumn. Fertilization occurs in April when ova are shed into the uterus. Development of the embryos is relatively synchronous. Development is complete by mid-June and the female uterus is filled with active, first-stage larvae. Gravid females contain about 7,000 to 10,000 larvae. Most larvae are dispersed simultaneously when the female ruptures and prolapses the uterus through the body wall.

The cyclopoid copepod populations in western Lake Erie, composed predominantly of Cyclops bicuspidatus and Cyclops vernalis, reach an annual maximum density in June and July but are otherwise low throughout the rest of the year. Calanoid copepods are most dense in September (Britt, et al., 1973). Our sampling determined that this pulse of cyclopoids in 1971, 1972 and 1973 was composed of two separate peaks. Figure 17 shows that the dispersal period of C. oxycephalus coincides with the annual maximum cyclopoid density. A close examination of Figure 17 reveals some subtle differences in this synchrony among the three years. The summer of 1972 was unusually cold in northwestern Ohio. The abundance of cyclopoids was less than in 1971 and 1973. In addition, the two

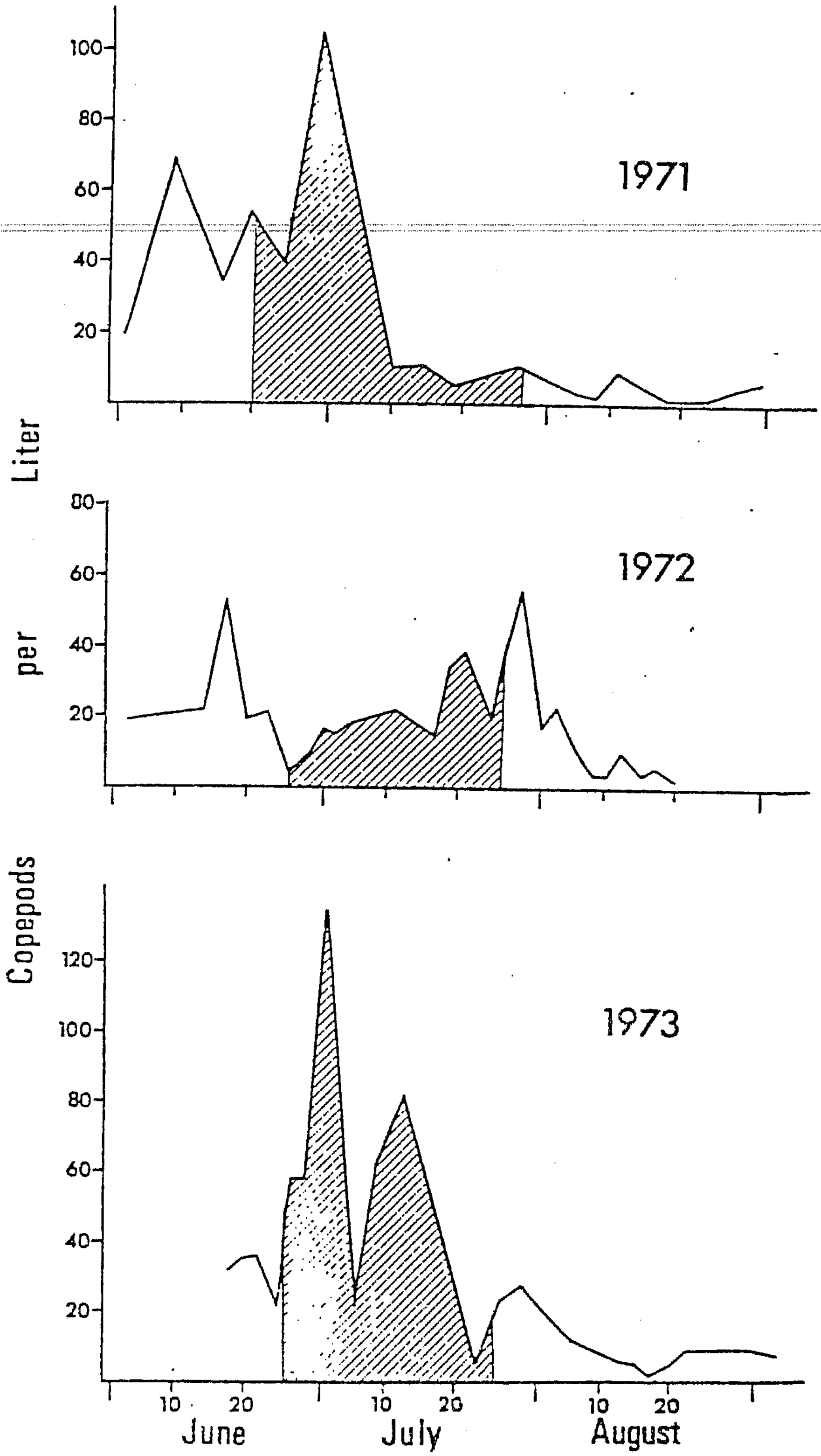

Fig. 17. Density of cyclopoid copepods and the dispersal period of Camallanus oxycephalus in western Lake Erie. Shaded area is copepod density during dispersal of larvae.

peak densities within the copepod pulse were 42 days apart, compared to the 10-20 day peak separation in 1971 and 1973. We arbitrarily designated the copepod populations to be "abundant" when they were at least as dense as 20/liter, since this density rarely occurs during non-pulse periods. The effectiveness of worm dispersal can be compared among the 3 years by dividing the number of dispersal days with abundant copepods by the total number of dispersal days (Table 9).

TABLE 9

EFFECTIVENESS OF C. oxycephalus DISPERSAL

	Total Dispersal Days	"Abundant" Copepod Days	% Effectiveness
1971	38	19	50
1972	30	11	36
1973	29	26	89

It is clear from Table 9 that the effectiveness of larval dispersal was much less than in 1971 or 1973.

Examination of forage fish revealed C. oxycephalus larvae in the following species: Alewife (Alosa pseudoharengus), gizzard shad, spotfin shiners (Notropis spilopterus), emerald shiners (N. atherinoides), and smelt (Osmerus mordax). Camallanus occurred most frequently in gizzard shad (71%) and with much less frequency in spotfins (16%), alewife (15%), smelt (4%) and emeralds (1%). Spot-tail shiners (N. hudsonius) which are a very common forage species, were not infected. The distribution of Camallanus within these fish populations does not remain stable. Table 10 illustrates how the distribution in young gizzard shad changed over a 2-1/2 week period. The incidence of the parasite decreased by 50%. This was caused by parasite mortality. Most of the August 5 worms were 3d stage larvae. Most of the August 23 worms were 4th stage larvae, indicating that the worms undergo the 3d molt in shad. No adult worms were found, which suggests that the final molt does not occur in gizzard shad, and that 4th stage larvae eventually die and pass out of the fish. Thus, C. oxycephalus larvae remain within the gizzard shad population for only several weeks and thus the period during which the parasite can be transferred to the white bass population is short.

Analysis of the total lengths of 256 young of the year gizzard shad found in 67 white bass stomachs taken between August and November revealed a prey size selection by different size white

TABLE 10

DISTRIBUTION OF *C. oxycepahlus* IN YOUNG GIZZARD SHAD

No. Worms X	Number of fish with X worms August 5	August 13	August 23
0	23	34	46
1	27	23	21
2	18	15	10
3	8	5	1
4	2	0	1
5	1	1	0
6	0	2	0
No. Fish	80	80	79
Size range (mm)	30-45	34-67	41-60
% infected	71.2	57.9	42.5
% L_3	72.2	57.6	29.2
% L_4	27.8	42.4	70.8
% Adults	0	0	0
Total worms	108	85	48
Mean infection	1.9	1.8	1.4

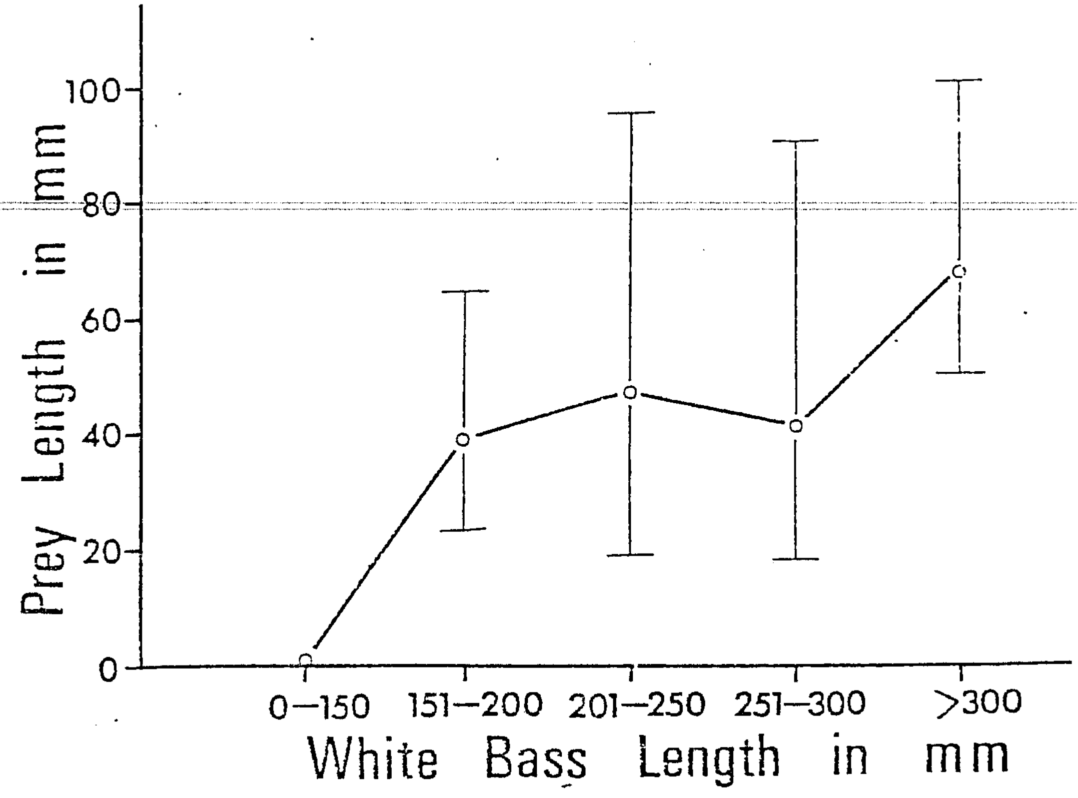

Fig. 18. Food size selection on young of the year gizzard shad by 5 size groups of white bass. O indicates mean prey length and vertical bars indicate selection range.

bass (Fig. 18). No shad under 19 mm long was taken by any bass. Although maximum prey size was 100 mm, shad over 80 mm were rarely found in bass stomachs. White bass 201-300 mm in length selected shad throughout the entire 19-100 mm length interval, although the mean length was 40 mm. Large bass, however, showed a preference for large shad (mean length = 66.8 mm) and ate no fish less than 50 mm long. Small bass (151-200 mm) showed a preference for small shad (mean length = 39.4 mm) and ate no fish longer than 64 mm. Gizzard shad were not recovered from white bass less than 170 mm in length.

Young of the year gizzard shad grow rapidly, reaching maximum prey size (100 mm) for white bass as early as September. If white bass feed only upon 19–100 mm shad, transmission of _C. oxycephalus_ would be affected by a combination of 1) parasite distribution in the shad population, 2) growth rate of shad and 3) relative abundance of shad. Extreme water temperatures may alter the transmission by raising or lowering the availability of the parasite to predatory fish. Gizzard shad abundance may fluctuate from year to year. During years of relatively few shad, predators may select more shiners or alewife, which are not as frequently infected, resulting in few _Camallanus_ reaching the final host and reproducing.

VII. RECOMMENDATIONS

At present, there appears to be little that fisheries biologists can do to reduce the abundace of _Camallanus_ _oxycephalus_ in Lake Erie. This system is simply too large for effective management. The spreading of this parasite, however, could be minimized if fish taken from the lake for fish-out ponds are captured during periods of low infection. This period extends from late June to late July. However, relatively low infections are found in April and May, so that fish can be taken and transported from Lake Erie from April to mid July. No fish should be taken between mid July and April.

The control of this parasite anywhere depends upon elimination of forage fish which become infected and transmit the parasite to predatory species. It is recommended that gizzard shad and alewife not be used in ponds where Camallanus is an undesirable parasite.

Although no direct pathological effect is known to occur in connection with C. oxcephalus, some secondary bacterial, fungal or viral infection is possible, particularly in heavily infected fishes. It is apparent that gizzard shad abundance has been related to the increase of C. oxycephalus in Lake Erie fish. If this parasite continues to increase in abundance as a result of changes in the Lake environment, some mortality is likely. To this end, future investigations of white bass mortality, if any, should encompass an assessment of the role of C. oxycephalus as well as other parasites, in the health of the fish population.

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