Host-Parasite Relations of Certain Endoparasitic Helminths of the Channel Catfish and White Crappie in an Oklahoma Reservoir[1]

RICHARD D. SPALL and ROBERT C. SUMMERFELT

Oklahoma Cooperative Fishery Unit[2]
Oklahoma State University
Stillwater, Oklahoma 74074

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Abstract

Fifteen identified species and 13 genera, of endoparasitic helminths (Digenea, Eucestoda, Nematoda, Acanthocephala) were collected from 207 white crappie and 189 channel catfish June, 1967, through September 1968, from a 3,300-acre, turbid reservoir in northcentral Oklahoma. Differences in the prevalence and intensity of helminths from six reservoir collection sites were not statistically significant. Statistically significant differences in intensity and prevalence of certain helminth were found among different age classes of the hosts. Ontogenetic changes in the food habits of channel catfish, from a diet of invertebrates to fish, were apparently the reason for changes in the occurrence of many enteric helminths. The occurrence of some helminths, however, was independent of age. Changes relating to age in the crappie were limited to the occurrence of *Posthodiplostomum minimum* where multiple generations of metacercariae accumulate in older fish. These metacercariae occurred in significantly higher numbers in males. Otherwise the occurrence of parasitism did not differ significantly between the sexes. Seasonal differences in parasitism, heretofore rarely studied, were pronounced, reflecting changes in feeding, metabolism, and the reproductive cycle of the host, and the annual life cycle characteristics of the parasite. Some parasites, such as *Dacnitoides robusta,* were absent in the channel catfish in the winter but abundant in the summer. Conversely, proteocephalid tapeworms from the channel catfish were abundant in the winter and infrequent in the summer. Observations on the pattern of seasonal variation in prevalence and degree of infection of *Posthodiplostumum minimum* in the white crappie suggests that it may contribute to summer mortality of its host.

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Introduction

Much has yet to be learned of the life history of endoparasitic helminths, and of factors contributing to natural mortality of fishes. Seasonal changes in the parasitocenoses of fishes are related to the reproductive cycle, feeding ecology and migratory patterns of the host, which are atuned to annual environmental changes. Environmental changes influence the development and infectivity of the helminths and determine the abundance of their intermediate hosts. Except for reports by Bogitsh[2], Chubb[4], Connor[5], and Holl[15], knowledge of seasonal and annual variation in parasitic incidence in fishes is limited.

This study reports observations on seasonal changes in the endohelminth parasites of the channel catfish *(Ictalurus punctatus)* and white crappie *(Pomoxis annularis)* in Lake Carl Blackwell, a 3,300-acre, watershed reservoir located in the Permian Redbeds Plains physiographic region of northcentral Oklahoma. The influence of age, sex, and habitat of the host are also described.

Methods

Fish were collected from June, 1967, through September, 1968, primarily by use of sinking 150-ft. experimental gill nets, and to a lesser extent by use of rotenone cove samples, frame nets, barrel traps and by electrofishing.

Six major reservoir areas were sampled, each assumed to represent a different habitat type (Fig. 1). The reservoir, 30-years-old at the time of this study, was relatively shallow allowing strong southwesterly winds to keep it circulating almost continually throughout the year, which resulted in relatively uniform physical and chemical conditions. Another consequence of this mixing was the suspension of a high concentration of colloidal clay particles. The turbidity, inversely related to water depth, increased appreciably from west to east along the main axis of the reservoir. Transparency, measured by a Secchi disc, was usually less than one meter in the deeper, east areas *(A* and *E)* and graded downward to 20 cm or less in the western end of the lake (Area *D*). As a result of high turbidity, the lake was largely devoid of rooted vegetation and therefore lacked suitable habitat for many possible intermediate hosts. For example, snails of the genus *Heliosoma* were not found and *Physa* were limited to a few areas of apparent heavy sediment deposition with high organic content.

The names used in the text generally follow those prescribed by Hoffman[14]. Fixing, storing, staining and mounting of helminths, as well as histological sectioning techniques, followed the procedures outlined by Humason[18] or as recommended by E. D. Besch (1967, Dean, College Vet. Med., Louisiana State University, personal communication).

Results

Fourteen species of endohelminths were found in channel catfish and ten in white crappie (Table 1). Channel catfish contained a greater variety and a heavier parasitic load of digenetic trematodes and eucestodes than crappie. Crappie lacked acanthocephala. Greater similarity between crappie and catfish were observed in the number and abundance of nematodes than in the other major taxa.

TABLE 1. *Prevalence and intensity of endoparasitic helminths in channel catfish and white crappie from Lake Carl Blackwell, Oklahoma* [1]

Taxon	Prevalence (%) M	Prevalence (%) F	Prevalence (%) Total	Mean Intensity M	Mean Intensity F	Mean Intensity Total
CHANNEL CATFISH (67 males; 82 females)						
Digenea:						
Phyllodistomum lacustri	26.9	28.0	27.5	1.1	1.3	1.2
Crepidostomum ictaluri	9.0	2.4	5.4	3.0	3.0	3.0
Alloglossidium corti	0	1.2	0.7	0	11.0	11.0
Eucestoda:						
Proteocephalidea (see text)	76.1	80.5	78.5	10.5	14.4	12.7
Corallobothrium fimbriatum and *C. giganteum*	71.6	77.0	75.6	10.2	13.4	11.9
Proteocephalus spp.	19.4	32.9	26.8	3.5	4.0	3.8
Nematoda:						
Contracaecum spiculigerum[2]	28.4	20.7	24.2	1.8	3.4	2.5
Camallanus oxycephalus	17.9	17.1	17.4	1.8	2.8	2.3
Rhabdochona decaturensis	47.8	56.2	52.4	4.8	4.6	4.7
Spinitectus carolini	17.9	18.3	16.8	1.9	1.9	1.9
Dacnitoides robusta	3.0	6.1	4.7	1.5	3.2	2.7
Spiroxys sp.[2]	1.5	0	0.7	2.0	0	2.0
Spiruroidea[2]	1.5	0	0.7	3.0	0	3.0
Acanthocephala:						
Leptorhynchoides thecatus	1.5	0	0.7	1.0	0	1.0
WHITE CRAPPIE (76 males; 100 females)						
Digenea:						
Posthodiplostomum minimum[2]	85.5	72.0	77.8	14.6	17.0	15.8
Eucestoda:						
Proteocephalidea including *Proteocephalus ambloplitis*[2]	10.5	3.0	6.3	1.0	1.0	1.0
Nematoda:						
Camallanus oxycephalus	64.5	66.0	65.4	3.6	3.4	3.5
Spinitectus gracilis	3.9	6.0	5.1	1.0	1.3	1.2
Rhabdochona cascadilla and *R. decaturensis*	11.8	13.0	12.5	1.7	2.5	2.2
Spiroxys sp.[2]	2.6	0	1.3	2.5	0	2.5
Contracaecum sp.[2]	9.2	13.0	11.4	1.4	1.4	1.4
Ascaroidea[2]	2.6	1.0	1.7	2.5	1.0	2.0
Spiruroidea[2]	1.3	0	0.6	1.0	0	1.0

[1]Data for collections from June, 1967 through May, 1968.
[2]Immature or larval form.

Digenea

Posthodiplostomum minimum (MacCallum, 1921) metacercariae (larval genus *Neascus)* were found in crappie but not catfish. Other Digenea found in this study were found in the catfish but not the crappie. *P. minimum* were most abundant in the liver of crappie but were commonly found in the kidney, spleen, heart and pericardium and less commonly under the serosa of the gut or the mesovarium. There have been numerous reports of *P. minimum* from fishes in this region[25].

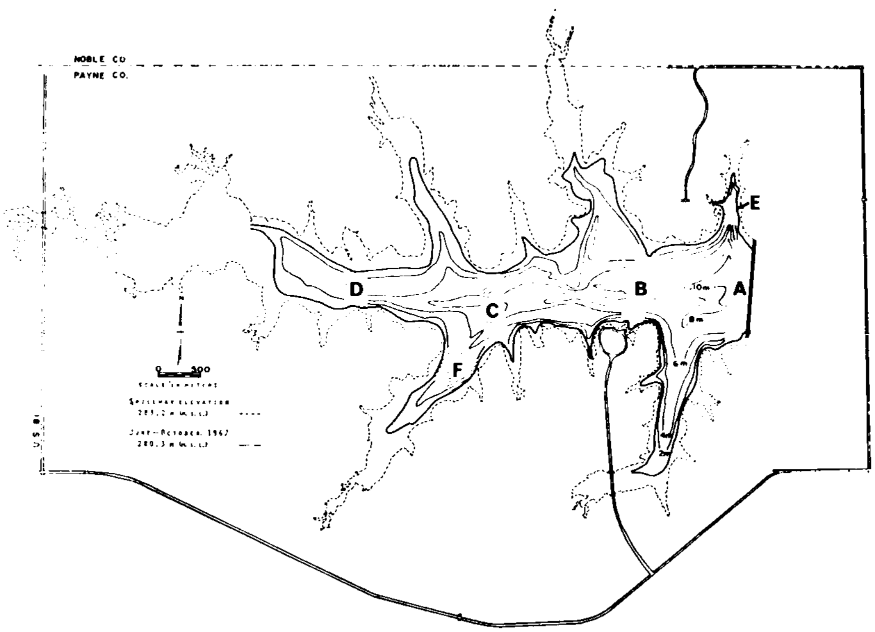

FIGURE 1. *Lake Carl Blackwell, Oklahoma showing two meter depth contours and collection sites (stipped and lettered A-F).*

Male crappie had a statistically higher incidence of infection than females in the summer, fall and winter samples (Table 2) ($X^2 = 6.45$, where $X^2_{.05, 1 d.f.} = 3.84$; Siegel, 1956: 107). In the spring samples, a higher percentage of females were infected than males but this difference was not significant ($X^2_{.05}$). However, when the crappie data for the entire year were analyzed after stratifying the fish by age, season (Table 2), and site of capture, no significant variation between the sexes could be detected (5% level, Fisher exact probability test)[21]. Apparently, interaction in the prevalence of *P. minimum* occurs between the sex of the host and some other variable.

The average numbers of metacercariae in white crappie (both sexes combined) was greater in the summer months than in the other seasons (Fig. 2). The maximum monthly averages reached 80.5 in August, 1967 and dropped to a low of 6.2 in January, 1968. The rise in numbers of metacerariae observed in the spring and summer samples coincided with the expected increase in numbers of infected snails[22] and the development and release of cercariae. Hoffman[13] found that snails did not release cercariae when changed from 22-28 C to 15 C. Cercariae did not infect fish at 15 C but did above 18 C.

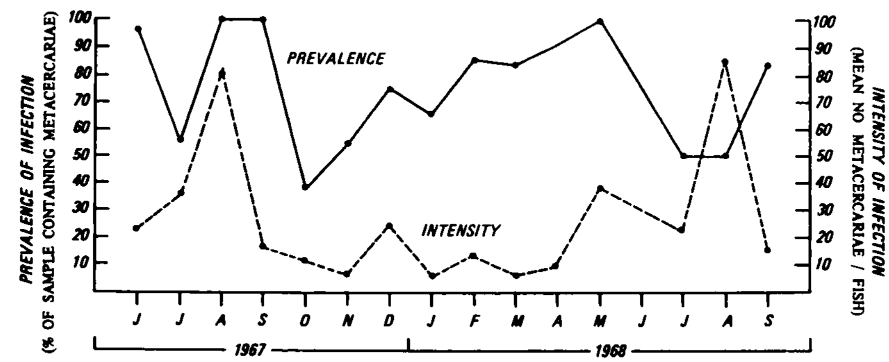

FIGURE 2. *Prevalence and intensity of* Posthodiplostomum minimum *metacercariae in white crappie from Lake Carl Blackwell, Oklahoma, 1967-68.*

TABLE 2. *Prevalence of infection with* Posthodiplostomum minimum *metacercariae in four age groups of white crappie (June, 1967 through May, 1968)*

	Percent Infected (Number of Fish)				
	I and II	III	IV and V	VI and Older	All Ages
			Summer		
Males	75.0 (4)	100.0 (7)	100.0 (5)	—	93.7 (16)
Females	72.7 (11)	69.1 (13)	50.0 (2)	100.0 (2)	71.4 (28)
Combined	73.4 (15)	80.0 (20)	85.7 (7)	100.0 (2)	79.5 (44)
			Fall		
Males	50.0 (2)	83.3 (6)	80.0 (5)	—	76.9 (13)
Females	37.5 (8)	60.0 (5)	50.0 (6)	100.0 (1)	50.0 (20)
Combined	40.0 (10)	72.7 (11)	63.6 (11)	100.0 (1)	60.6 (33)
			Winter		
Males	66.7 (6)	100.0 (6)	87.5 (8)	100.0 (1)	85.7 (21)
Females	50.0 (4)	87.5 (8)	33.3 (6)	100.0 (2)	65.0 (20)
Combined	60.0 (10)	92.8 (14)	64.3 (14)	100.0 (3)	75.6 (41)
			Spring		
Males	—	72.7 (11)	92.3 (13)	100.0 (2)	84.6 (26)
Females	87.5 (8)	85.7 (14)	100.0 (6)	100.0 (4)	90.6 (32)
Combined	87.5 (8)	80.0 (25)	94.7 (19)	100.0 (6)	87.9 (58)
			All seasons		
Males	66.7 (12)	86.7 (30)	90.4 (31)	100.0 (3)	85.5 (76)
Females	64.5 (31)	77.5 (40)	60.0 (20)	100.0 (9)	72.0 (100)
Combined	65.2 (43)	81.5 (70)	78.4 (51)	100.0 (12)	77.8 (176)

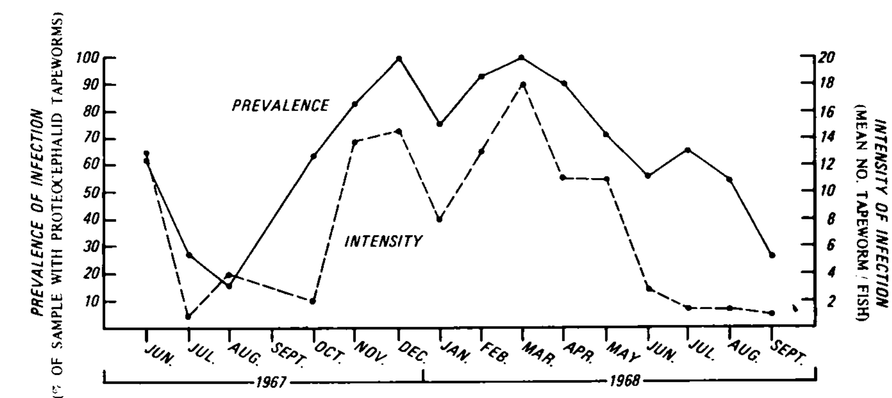

FIGURE 3. *Prevalence and intensity of proteocephalid tapeworms in channel catfish from Lake Carl Blackwell, Oklahoma, 1967-68.*

The death of crappie with a heavy infection with *P. minimum* might account for the decrease in the average intensity of infection observed during the summer. This implies that host mortality is proportional to the number of invading cercariae. Meade and Bedinger[21] suggested, on the basis of laboratory observations, that significant mortality of the host might occur in natural waters due to infection with *P. minimum*. Starrett and Fritz (1957), as reported by Bennett [1], found that most of the annual natural mortality of crappie in Chautauga Lake, Illinois, occurred in the summer months.

A similar sharp decline in the prevalence of infection occurred during the early fall, although a month later than the decline observed in the average intensity of infection. Unlike the latter, the drop in prevalence was followed by a gradual increase through the late fall, winter and spring (Fig. 3). This seasonal pattern may have resulted from summer mortality of the host followed by a gradual rise in the incidence of infection due to the presence of low numbers of cercariae throughout the year. The establishment of an equilibrium between the numbers of successful invasive cercariae and degenerating metcercariae was indicated by the stability found in the average intensity through the fall and winter.

The viability as well as numbers of metacercariae appeared to decrease during the winter. Cysts from fish collected during this period appeared to be smaller in size, more opaque and the larvae less active when compared with those collected during the summer and fall. Presence of both old and degenerated, and fresh and viable cysts in the livers of crappie from the late spring collections indicates a recurring seasonal infection.

The prevalence of infection in white crappie increased with increasing age (Table 2). The differences among the age groups of crappie were significant ($X^2 = 8.20$; where $X^2_{.05, 3d.f.} = 7.81$). Thus, previous exposure apparently did not inhibit reinfection, and older fish, by reason of their longevity, had an increasingly greater prevalence of infection. However, since the average numbers of metacercariae remained fairly constant with respect to increasing age, it appears that an equilibrium is reached where the numbers of new metacercariae encysting in the fish equals those dying or being destroyed by the host. Hoffman[14] reported that *P. minimum* metacercariae persisted at least 4 years in the tissues of fish at 12 C.

Variations in the prevalence of *P. minimum* in white crappie from the six collection sites were from 71.0% to 88.8%. The differences among collection sites were not significant ($X^2_{.05}$). Pooling data from the three deeper *(A, B* and *E)* and more shallow *(C. D* and *F)* areas also revealed no significant differences between them. The average intensity of infection among the collection sites ranged from 9.0 to 36.2 worms per fish.

Phyllodistomum lacustri (Loewen, 1929) is apparently host specific and only infects the catfishes of North America. The life cycle for *P. lacustri* is unknown. It is presumed that an arthropod second intermediate host is utilized and the route of infection into definitive host is *per os*. It primarily inhabits the urinary bladder but has also been reported from the hepatic bile dust (Meyer, 1959: cited by Hoffman[14]). It has previously been reported by Harms[11] from the southcentral U.S.

P. lacustri was found in 27.5% of the channel catfish examined (Table 1). The numbers of worms per fish varied from one to five but one or two was the usual number. Sexually mature worms appeared throughout the sampling period. Immature worms occured only in the samples from February through May, 1968, and in June, 1967. The average number of immature worms (3.7) was slightly higher than the overall average (1.2) indicating some mortality, possibly due to crowding and competition for nutrients in the urinary bladder.

The differences in the rate of infection between the sexes was not significant (i.e., the computed probability in the Fisher test was greater than .05). The data did show considerable differences among the different age groups (Table 3). The immature fish (I and II) were negative for *P. lacustri;* the maturing and newly matured fish (III and IV) were 17.0% infected; older fish (V and VI) were 37.8% infected; and the oldest group (over VI) were 30.0% infected. The differences among the latter three groups were not significant ($X^2_{.05}$). The youngest age group could not be included because of insufficient sample size. When the data for the one through four-year-old fish was pooled, the age differences were significant at the 10% level for the two-tailed test ($X^2 = 6.18$; where $X^2_{.05, 2d.f.} = 5.99$).

The difference in prevalence of *P. lacustri* among age groups may be dependent on the ontogenetic variation observed in the utilization of those larger arthropods, such as dragonflies and mayflies, which may serve as second intermediate host in the life cycle of the parasite. Increasing number of *Hexagenia* larvae appeared in the diets with increasing size of these fish until a length of about 35 cm was reached. Fish 35 cm and larger characteristically changed to piscivorous feeding habits, although not exclusive of invertebrate food items, until a very large size (several kilograms) was attained.

No significant differences could be detected to indicate any seasonal changes in infection rate. The higher values for the spring samples corresponds to the period when immature worms were observed in greatest numbers (Table 3).

The hypothesis of a difference in incidence of infection between fishes captured from the three upper, shallow areas and the lower, deeper parts of the lake was also tested for *P. lacustri* but the difference observed was not significant ($X^2_{.05}$).

Crepidostomum ictaluri (Surber, 1928) are small distome flukes which were rare in occurrence (Table 1). It has previously been reported only in channel catfish and black bullheads *(Ictalurus melas)* from the southcentral United States[11]. In the present study, these flukes were found only in channel catfish. They appeared to show a preference for male fish as seven of 67 males were infected while only 1 of 82 females harbored this parasite. The mean intensity of infection was only three flukes per fish. It is difficult to explain the low infection rate of this parasite since both the first (sphaerid clams) and second intermediate hosts (mayfly naiads *Hexagenia)*[16] are probably present in most areas of the lake. This parasite occurred in catfish collected during all four seasons and no variation among the seasons was apparent.

TABLE 3. *Prevalence of infection with* Phyllodistomum lacustri *in four age groups of channel catfish (June, 1967 through May, 1968)*

		Percent Infected (Number of Fish)				
Season	Sex	I, II	III, IV	V, VI	Over VI	All Ages
Summer	M	—	50.0 (2)	33.3 (3)	0 (4)	22.2 (9)
	F	0 (2)	0 (5)	44.5 (9)	20.0 (5)	23.8 (21)
	T	0 (2)	14.3 (7)	41.7 (12)	11.1 (9)	23.3 (30)
Fall	M	—	22.2 (9)	0 (1)	0 (4)	14.3 (14)
	F	0 (1)	28.6 (7)	40.0 (5)	0 (1)	28.6 (14)
	T	0 (1)	25.0 (16)	33.3 (6)	0 (5)	21.4 (28)
Winter	M	—	33.3 (6)	25.0 (4)	33.3 (9)	31.6 (19)
	F	—	0 (6)	16.7 (6)	25.0 (8)	15.0 (20)
	T	—	16.7 (12)	20.0 (10)	29.4 (17)	23.2 (39)
Spring	M	—	21.4 (14)	40.0 (5)	50.0 (6)	32.0 (25)
	F	—	0 (10)	75.0 (4)	45.2 (13)	33.3 (27)
	T	—	12.5 (24)	55.5 (9)	47.4 (19)	32.7 (52)
All Seasons	M	—	25.8 (31)	30.8 (13)	26.1 (23)	26.9 (67)
	F	0 (3)	7.1 (28)	41.7 (24)	33.3 (27)	25.6 (82)
	T	0 (3)	17.0 (59)	37.8 (37)	30.0 (50)	26.2 (149)

Aside from 11 worms recovered from 2 male catfish in shallow water (Area *D*) during April, these parasites were limited to fishes collected from the deeper areas of the lake (Areas *A* and *B*; Fig. 1). The two infected fish collected in the shallow, upper portion of the lake may have migrated there after becoming infected in deeper water.

Alloglossidium corti (Lamont, 1921) was found during only one necropsy. Eleven worms were recovered from the hindgut of a four-year-old female channel catfish from Area *A* during the winter. It has previously been reported from two separate studies in this region in the black and yellow bullheads *(I. natalis)* by Harms[11] and in channel catfish and yellow bullheads by Houghton[17].

A. corti may be limited in Lake Carl Blackwell by the scarcity or absence of the pondsnail, *Helisoma,* the first intermediate host[6]. This mollusc has not been collected in the lake proper although several recoveries have been made from storage ponds in the watershed above the lake. Dragonfly and mayfly naiads, crayfish, and other "small arthropods" may serve as second intermediate host[6,20].

Eucestoda

Adult and maturing proteocephalid tapeworms (Proteocephalidea Mola, 1928) were common in occurrence in the intestine of channel catfish (78.5%) and, as plerocercoid larvae, were less commonly found encysted in the viscera of white crappie (6.3%). The dominant species in catfish were *Corallobothrium giganteum* and *C. fimbriatum* Essex (1928) (71.6% for adult worms). *Proteocephalus* spp. were also recovered from catfish, but their occurrence was only 26.8%. The dominant species found in white crappie was *P. ambloplitis* (Leidy, 1887). *Corallobothrium* spp. have previously been reported from catfishes from the southcentral U.S. by several workers. Likewise, *P. ambloplites* is apparently also common in occurrence in centrarchids from this region[25]. The first intermediate hosts for proteocephalid tapeworms are cyclopoid crustacea; small fish serve as second intermediate hosts.

For purposes of analysis, data for *Corallobothrium* spp. and *Proteocephalus* spp. were pooled because they occurred together in the same host and in the same portion of the alimentary canal; they showed the same seasonal variation in abundance; they have similar life cycles; newly established, immature worms were difficult to identify to the generic level; and they are closely related genera.

No significant differences in the prevalence of proteocephalids occurred between the sexes of either catfish or crappie after stratifying the data for size, season and locality (Fisher test). Likewise, the prevalence of these tapeworms did not vary significantly among fishes from the six collection sites ($X^2_{.05}$). The prevalence of infection also did not vary significantly among four selected age groups of either host (Table 4). The intensity of infection in catfish did vary with the age of the host; however, one and two-year-old fish had a mean of 3.5 worms per host, three and four-year-old fish had 7.8, five and six-year-old fish had 6.4 and seven-year-old and older fish had 22.2.

TABLE 4. *Prevalence of proteocephalid tapeworm, chiefly* Corallobothrium *spp., in four age groups of channel catfish (June, 1967 through May, 1968)*

	Percent infected (Number of Fish Examined)				
Sex	I and II	III and IV	V and VI	VII and Older	All Ages
		Summer			
Males	—	50.0 (2)	0 (3)	25.0 (4)	22.2 (9)
Females	50.0 (2)	60.0 (5)	44.4 (9)	40.0 (5)	47.6 (21)
Combined	50.0 (2)	57.1 (7)	33.3 (12)	33.3 (9)	40.0 (30)
		Fall			
Males	—	77.8 (9)	100.0 (1)	75.0 (4)	78.6 (14)
Females	100.0 (1)	71.4 (7)	100.0 (5)	0 (1)	78.6 (14)
Combined	100.0 (1)	75.0 (16)	100.0 (6)	60.0 (5)	78.6 (28)
		Winter			
Males	—	66.7 (6)	100.0 (4)	100.0 (9)	89.5 (19)
Females	—	100.0 (6)	83.3 (6)	87.5 (8)	90.0 (20)
Combined	—	83.3 (12)	90.0 (10)	94.1 (17)	89.7 (39)
		Spring			
Males	—	78.6 (14)	100.0 (5)	100.0 (6)	88.0 (25)
Females	—	90.0 (10)	100.0 (4)	100.0 (13)	96.3 (27)
Combined	—	83.3 (24)	100.0 (9)	100.0 (19)	92.3 (52)
		All seasons			
Males	—	74.2 (31)	76.9 (13)	82.6 (23)	77.6 (67)
Females	66.7 (3)	82.1 (28)	75.0 (24)	81.5 (27)	79.3 (82)
Combined	66.7 (3)	78.0 (59)	75.7 (37)	82.0 (50)	78.5 (149)

Considerable seasonal variation in the prevalence of intestinal proteocephalids was found in channel catfish (Table 4; Fig. 3). This variation was highly significant ($X^2 = 35.5$; where $X^2_{.01,3d.f.} = 11.3$). Seasonal changes in the prevalence paralleled changes in the extent of strobilization and maturation of these helminths and also reflected changes in the intensity of infection. Thus, the increased prevalence during the fall and winter corresponded to an increase in the average parasite load (Fig. 3) and to an increase in the average size of each worm. These results support the hypothesis of an annual life cycle for proteocephalid tapeworms. Fragmentation of fully mature worms was observed throughout the late winter and spring. During the same period, reduction in occurrence indicated the passage or loss of worms from the host. Nonsegmented, immature worms occurred throughout the year but were most common during the fall months. Contrary to the present findings, Essex[9] reported that adult *Corallobothrium* spp. were more abundant from spring through fall in channel catfish from the upper Mississippi, Illinois and Rock Rivers.

Nematoda

Contracaecum spiculigerum (Rudolphi, 1809) is a relatively large ascarid found as larvae encysted within the mesenteries or beneath the serosa surrounding the gut of both the catfish and crappie. It was also found in other fishes from the lake [25] and has been shown to possess little host specificity, although host preference was evident as seen by the wide difference in the prevalence and intensity of infection among fishes included in that study. Many workers have found *C. spiculigerum* in fishes from the southcentral U.S.[25].

C. spiculigerum is a cosmopolitan species and adults have been reported in many piscivorus birds including gulls, mergansers, pelicans and cormorants[14]. According to Thomas[26], small fish are the first and apparently the only intermediate hosts, although larger predatory fishes may serve as transfer hosts.

A positive correlation between the rate and severity of infection and the size or age of the host was found in both white crappie and channel catfish. The prevalence of infection increased substantially in older white crappie and channel catfish. The difference observed in the rate of infection among age classes was not significant for white crappie but was highly significant for channel catfish ($X^2 = 15.2$; where $X^2_{.01, 3 d.f.} = 11.3$). The crappie and channel catfish do not begin eating small fishes until their fourth and fifth years of life and appropriately the data show that few fish of either species less than four years are infected with *C. spiculigerum*.

The prevalence of infection did not increase in a similar fashion for largemouth bass *(Micropterus salmoides)* and flathead catfish *(Pylodictis olivaris)*, collected at the same time, as in crappie and channel catfish[25]. In the largemouth bass and flathead catfish the prevalence was high for all age classes reflecting a change to piscivorous food habits at a very young age. However, Spall[25] did find a positive correlation with increasing host size and number of *C. spicularum* in the bass and flathead.

The higher incidence of *C. spiculigerum* in large piscivorous fish appears to reflect a transfer of infective larvae through the food chain of these predatory fishes. Large, non-piscivorous fish such as the carp or carpsucker were only rarely infected or not at all[25]. The accumulation of high numbers of this nematode in older fish appears to indicate that it is long-lived in the fish intermediate host.

The size and appearance of cysts, and the viability of encysted worms appeared to greatly differ within and between the various hosts, indicating a degree of senility in older infections. Some were observed to be only weakly encysted and contained very active worms; others were heavily covered with a dark, nodular, fibrous capsule and contained lifeless worms much reduced in size. This latter condition was particularly evident in older fish.

The hypothesis of a difference in the prevalence of infection between the sexes was tested (Fisher test) for *C. spiculigerum* in channel catfish after stratifying the fish by age and season. No significant differences could be detected, although data in the younger age groups were scanty because, as shown above, this worm rarely occurred in the smaller fish. Chi-square analysis did not reveal any sigificant differences in the incidence of infection among the different sampling area. Also, no significant seasonal differences in prevalence could be detected at the 5% level.

Camallanus oxycephalus (Ward and Magath, 1916) are small-to-medium sized ovoviviparous spirurids. They were collected as both adult and immature worms in channel catfish and white crappie. The parasites were found free in the lumen of the gut or attached to the mucosa. Sexually mature, larvae-bearing females were generally recovered more posterior in the alimentary tract than immature or male worms. Some mature females were observed protruding from the anus. Female worms appeared to outnumber males in all hosts examined which suggests either a differential or an earlier mortality such as seen with the nematode *Trichinella spiralis* in mammals. *C. oxycephalus* has been commonly reported from this region[25].

C. oxycephalus appears to have an annual life cycle. In crappie, although maturation was rarely completely uniform in any population or season, the majority of mature females occurred during the spring and early summer. Those individuals recovered during the fall and winter were largely immature. This majority coincided somewhat with the sexual cycle of the host; female worms were observed to gradually increase in size through the spring, the uteri becoming filled with eggs during April, and these eggs hatching *in utero* during May. Larvated females were observed to remain throughout the summer but their numbers became fewer after July. In channel catfish, *C. oxycephalus* were absent from the June, 1967, samples and from the May and June, 1968, collections. Tornquist (1931; cited by Dogiel` reported an annual life cycle for the related species, *C. lacustris*.

The difference in prevalence between the sexes was not significant in crappie and channel catfish, after stratifying the fish collections by age, locality and season (Table 5).

The prevalence of *C. oxycephalus* in fishes collected from the upper, shallow areas did not vary sigificantly from those caught from the deeper parts of the lake when the variables of age and season were held constant. Data from both sexes and all areas was combined and the influence of the host's age or size on the prevalence of infection was tested for both white crappie and channel catfish (Table 5). No significant differences could be found for white crappie but the prevalence of *C. oxycephalus* in channel catfish did vary sigificantly among three selected age groups (X^2 = 10.01; where $X^2_{.01, 2 d.f.}$ = 9.21). The percent infection for these age groups of catfish was 6.5%, 18.9% and 30.0% for IV and younger, V and VI and over VI, respectively. The winter and spring samples (combined) seemingly contributed the greatest amount to this significance ($X^2 = 9.37$). Catfish sampled during the summer and fall (combined) showed no significant difference due to increasing age in the rate of *C. oxycephalus* infections.

The reasons for an increase in the infection rate in older catfish, but not in the crappie was apparently due to differences in their food habits. Hoffman[14] lists copepods and possibly other crustacea as intermediate hosts. White crappie through age IV, were observed to utilize copepods to a high degree, especially in the colder months, whereas, the catfish apparently fed little on these micro-crustacea. The diets of one through four-year-old catfish consisted primarily of macroinvertebrates, whereas catfish in the older age classes were piscivorous. If *C. oxycephalus* is aided in its transmission by a paratenic host, as has been suggested for *Camallanus* spp. by Kupriyanova (1954: in Dogiel, et al[8]), then crappie probably become infected by eating infected copepods (the first intermediate host). and catfish by eating small fish (the paratenic host).

These fishes were tested for differences in the infection rate for *C. oxycephalus* due to season. A greater percentage of winter caught catfish were infected than those caught during other seasons (due to the December sample). These differences were not significant, however. Catfish collected in June, 1967, and May and most of June, 1968, were not infected at all (Fig. 4).

TABLE 5. *Prevalence and intensity of infection with* Camallanus oxycephalus *in various age groups of white crappie and channel catfish*

Season	Percent and No. of Fish Examined (Mean No. Parasites)			
	White Crappie			
	I and II	III	IV and Older	All Ages
Summer-Fall	68.0 of 25 (3.1)	61.3 of 31 (2.7)	57.1 of 21 (4.0)	62.3 of 77 (3.2)
Winter-Spring	50.0 of 18 (2.1)	61.6 of 39 (2.6)	76.2 of 42 (5.4)	65.7 of 99 (2.6)
All Seasons	60.4 of 43 (2.8)	61.5 of 70 (2.6)	69.8 of 63 (5.0)	64.2 of 176 (2.8)
	Channel Catfish			
	IV and Younger	V and VI	Over VI	All Ages
Summer-Fall	7.7 of 26 (1.0)	5.6 of 18 (3.0)	21.4 of 14 (2.0)	10.3 of 58 (2.0)
Winter-Spring	5.6 of 36 (2.0)	31.6 of 19 (1.3)	33.3 of 36 (2.3)	22.0 of 91 (2.1)
All Seasons	6.5 of 62 (1.7)	18.9 of 37 (1.6)	30.0 of 50 (2.9)	17.5 of 149 (2.4)

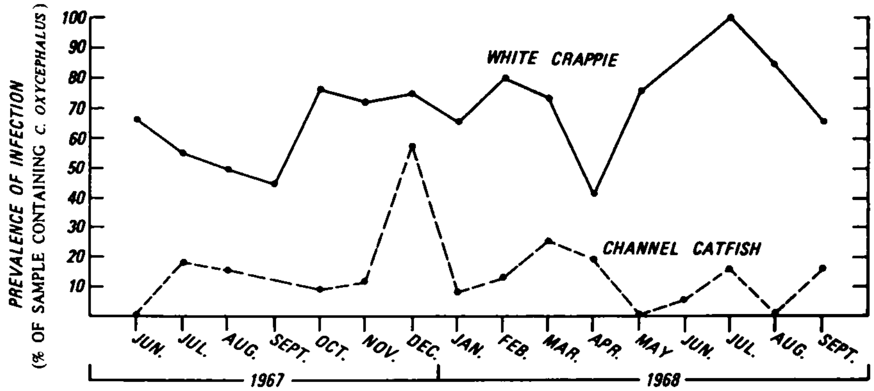

FIGURE 4. *Prevalence of* Camallanus oxycephalus *in white crappie and channel catfish from Lake Carl Blackwell, Oklahoma, 1967-68.*

The decrease and absence of *C. oxycephalus* in catfish corresponds exactly with an increase in occurrence of another intestinal nematode, *Dacnitoides robusta,* which suggests a possible antagonistic relationship between these two helminths. In no case were these two worms found together in the same host.

Rhabdochona cascadilla (Wigdor, 1918) and *R. decaturensis* (Gustafson, 1949) showed a higher occurrence in channel catfish than crappie. This inter-species difference may be due to the higher utilization of mayflies, the intermediate hosts, by catfish than by the white crappie. Only *R. cascadilla* has been previously found in this region where it occurred in white bass *(Roccus chrysops)*[25].

After combining data for both species, hereinafter referred to as *Rhabdochona* spp., and stratifying the fish for age or size and season, the hypothesis of a difference in infection rate between the sexes of both white crappie and channel catfish was tested (Fisher). A single significant value ($p = .049$) was obtained for the cell containing catfish older than age VI collected during the spring months. In this particular case females showed the higher incidence of infection. This disparity probably should be ignored as no other significant cells could be detected.

The effects of the hosts' habitat on the incidence of infection were also tested ($X^2_{.05}$). To increase sample size, the three upper areas *(C. D. F)* were grouped together as were the three lower areas *(A. B. E)*. No significant values between upper and lower were found for either channel catfish or white crappie. Fish collected from coves *(E. F)* also did not vary significantly in the rate of infection with *Rhabdochona* spp. from those collected from the central pool of the reservoir *(A, B, C, D).*

It appears that the overall effects of season on the establishment of *Rhabdochona* spp. in fishes of this lake was negligible. No significant seasonal changes were detected in either catfish or crappie. However, in channel catfish the incidence decreased with increasing host size, and differences were significant for the one-tailed test ($X^2 = 6.65$; where $X^2_{.05,2d.f.} = 5.99$). This difference was most evident during the winter and spring months ($X^2 = 7.62$); the summer and fall collections (combined) were non-significant. The data does not show a similar decrease is white crappie (Table 6).

The inverse relationship between prevalence of infection and host size may be explained by considering the feeding habits of channel catfish. Mayfly nymphs *(Hexagenia* sp.) have been described by Gustafson[10] as the intermediate hosts of *Rhabdochona* spp. Smaller catfish are largely benthophagous and feed heavily on these forms, whereas, fish larger than 35 cm are primarily piscivorous. Burrowing mayfly larvae are widespread throughout the lake in the bottom sediments although less abundant in deeper water[23].

Dacnitoides (Neocucullanus) robusta (Van Cleave and Mueller, 1932) is a short, relatively stout spirurid which was found in channel catfish. Except for a single specimen recovered in October, 1967, all the worms were found in June, July and early August in both 1967 and 1968. The disappearance of this worm after the summer months is difficult to explain. The life cycle is unknown but presumably an arthropod intermediate host is required. Because of its limited nature, no analysis could be made concerning differences in intensity or rate of infection due to age or sex. No apparent differences were noted.

TABLE 6. *Prevalence and intensity of infection with* Rhabdochona *spp. in various age classes of white crappie and channel catfish*

Season	Percent and No. of Fish Examined (Mean No. Parasites)				
	White Crappie				
	I and II	III	IV and V	VI and Older	All Ages
Summer-Fall	12.0 of 25 (1.3)	6.5 of 31 (1.0)	5.6 of 18 (1.0)	33.3 of 3 (3.0)	9.1 of 77 (1.5)
Winter-Spring	16.7 of 18 (2.3)	7.7 of 39 (2.0)	18.2 of 33 (3.3)	33.3 of 9 (1.7)	15.2 of 99 (2.6)
Combined	13.9 of 43 (1.8)	7.1 of 70 (1.8)	13.7 of 51 (3.0)	33.3 of 12 (2.0)	12.5 of 176 (2.1)
	Channel Catfish				
	I and II	III and IV	V and VI	Over VI	All Ages
Summer-Fall	66.7 of 3 (4.1)	52.2 of 23 (9.2)	55.6 of 18 (3.4)	42.8 of 14 (4.0)	51.7 of 58 (5.9)
Winter-Spring	—	66.7 of 36 (4.7)	63.2 of 19 (3.3)	36.1 of 36 (2.7)	53.8 of 91 (3.8)
Combined	66.7 of 3 (4.1)	61.0 of 59 (6.2)	59.5 of 37 (3.4)	38.0 of 50 (3.1)	53.0 of 149 (4.6)

This species has been previously reported twice (as *Dichelyne robusta)* from the southcentral U.S.[11,19]. Both reports were from channel catfish. In addition, Chandler[3] reported this species from fish of the Texas Gulf Coast.

Spinitectus carolini Holl, 1928 and *S. gracilis* Ward and Magath, 1916 were collected from channel catfish and white crappie, respectively. They were also found in a variety of other Lake Carl Blackwell fishes[25]. *Spinitectus* spp. were recovered primarily from the lumen of the gut but occasionally they were found in the parenchyma of the liver. Like *Rhabdochona,* the intermediate hosts are mayfly larvae[14].

S. carolini has previously been reported in a number of studies from this region while *S. gracilis* has been less commonly found[25]. This is a locality record for *S. gracilis* in the white crappie.

The incidence of infection did not vary significantly with sex in either the channel or white crappie. Similarly, the analysis showed no significant differences in the incidence of infection between the upper and lower areas of the lake, or among the various age groups, or among the seasons in either of these fishes.

Spiroxys sp. Schneider, 1866 were only rarely recovered, as larvae, from the intestinal serosa and mesenteries of the channel catfish and white crappie; only males were infected. *Spiroxys* sp. may be more widespread than this study indicates because, owing to its small size and location in the host, it may be frequently overlooked. The definitive hosts are turtles *(Pseudemys, Crysemys);* the first intermediate hosts (experimental) are given as the copepod *(Cyclops* spp. and others). Amphibians *(Rana, Trituris),* dragonfly naiads and others may serve as alternate second intermediate hosts for *S. contortus*[12]. *Spiroxys* sp. has not previously been reported from the southcentral United States.

Acanthocephala

A single specimen of an acanthocephalan was found in this study; this specimen, *Leptorhynchoides thecatus,* was found in a male channel catfish from Area *A*. It was also absent from the nine other species studied by Spall[25]. The variety of fishes and suitable intermediate hosts (copepods, amphipods, ostracods) in the reservoir would seem to favor the success of the Acanthocephala.

Summary

Habitat

The variation in abundance of helminths with a high prevalence, such as *Posthodiplostomum minimum, Contracaecum spiculigerum,* and the proteocephalid tapeworms was not related to characteristics of the habitat. Reservoir collection site did not have appreciable effect on the helminthocenoses of the fishes collected from six sites in spite of conspicuous differences in turbidity and water depth between the sites. Channel catfish and white crappie were apparently sufficiently mobile to mask any habitat differences which may actually occur. Van Cleave and Mueller[27] also found proteocephalids *(Corallobothrium fimbriatum)* to have a general distribution in Oneida Lake, New York. The local distribution of intermediate hosts probably has an added influence on the success and range of helminth parasites. The habitat of many of the intermediate hosts may be more homogeneous than one might expect from looking at the gross habitat differences. Their chances of success may be nearly equal throughout the lake, thus, assuring a relatively uniform distribution of many of the helminths.

Certain habitat features common to the lake such as high turbidity and the absence of aquatic macrophytes probably limited many species of trematodes by reducing the variety and numbers of snails. The greater diversity and abundance of nematodes may be related to enhanced environmental conditions in the profundal substrate, important to their aerobic arthropod intermediate hosts, resulting from continuous circulation of the water column. Constant circulation may also aid continuing success of planktonic crustacea, and consequently proteocephalid tapeworms, by transporting a constant supply of nutrients to the euphotic zone at all times, rather than seasonally as seen in dimictic lakes of temperate North America. Pearse (1924, as reported by Holl[15]) found that a stratified Wisconsin lake, Lake Mendota, had fewer species of parasites than Lake Pepin, a sandy bottomed, warm-water lake which did not stratify. Pearse also reported that greater diversity in habitats in Lake Michigan resulted in a greater overall percentage of helminth parasitism in its fishes.

Age and Food Habits

The age of the host appeared to have far-reaching effects on the prevalence of most parasites. Parasites which mirrored the greatest increases in abundance due to increasing age or size of the host were *Contracaecum spiculigerum* and the proteocephalid tapeworms. *C. spiculigerum* typically increased in both rate and intensity of infection, whereas, the proteocephalids were most significantly different with respect to prevalence only. Both parasites are found as larvae in small fishes and the change in their infectivity is believed correlated with a change in the food habits of the host. It should be noted that older fish not only consume different food items but an increased amount as well. The most striking changes in the abundance of helminth parasites occurred in the catfish which changed from an invertebrate to a vertebrate (fish) diet.

Other helminths, such as *Phyllodistomum lacustri* and *Posthodiplostomum minimum* appeared to increase in larger fish but not significantly. The last named species infects its host through the skin and presumably does not discriminate either to size or species of host. Therefore, the increases observed are probably due only to an accumulation of metacercariae in older fish. Hoffman[14] had observed that these metacercariae may persist in fish for four years under laboratory conditions.

The incidence and severity of infections with *Rhabdochona* spp. were negatively correlated with size in the channel catfish. This was thought to be due to a lessening of the dependence on mayfly larvae (the intermediate host) in the diet of larger catfish. Large non-predatory fish such as the carp, which do not change their insectivorous food habits, did not display a similar decrease in susceptibility to this helminth[25].

Gorbunova (1936; cited by Dogiel, et al[8].) classified parasites of *Esox lucius* and *Rutilis rutilis* as being (1) independent of the age of the host, (2) as increasing with the age of the host, and (3) as decreasing with the age of the host. The majority of the parasites of that study fell into the second group.

Adopting this classification for the parasites of white crappie and channel catfish from Lake Carl Blackwell, the occurrence of *Camallanus oxycephalus* and *Rhabdochona* spp. in white crappie and *Spinitectus* spp. in both fishes appear to be independent of the host's age. Proteocephalid tapeworms, especially *Corallobothrium* spp., and *Contracaecum spiculigerum* in the channel catfish and *Posthodiplostomum minimum* in the white crappie increased with the age of the host. *Rhabdochona decaturensis* in the catfish exhibited the characteristics of the last case. Its success was inversely correlated with aging in channel catfish. Other species of helminths reported in the present survey were generally not numerous enough to classify.

Sex

Except for *Posthodiplostomum minimum* in sunfishes, the occurrence of parasitism did not differ significantly between the sexes of the hosts. Higher incidences and intensities of *P. minimum* were found in the male crappie and other sunfishes[25].

Consideration of differential growth or dietary factors between the sexes seems of little importance with *P. minimum* since the route of infection is through the skin. Possibly the different sex steroid hormones have a dichotomous effect on the establishment of *P. minimum* in male and female sunfishes. Also, differences in spawning behavior between the sexes may account for an increase in strigeid metacercariae in mature males. Males are first to arrive to the inshore spawning areas in the spring, and since they alone guard the nests after egg deposition, they are consequently the last to leave. If, as is supposed in Lake Carl Blackwell, snails are restricted to the narrow perimeter of the lake, then males would be exposed to more cercariae by virtue of their close proximity to the intermediate host.

Seasonal Changes

The present study indicated that changes in season result in many demonstrable changes in the composition of the helminthocenoses of fishes. *Dacnitoides robusta* is abundant in channel catfish only during the summer. Significant age differences in *Rhabdochona* spp. were most evident in the winter months, and so interaction between age and season probably existed with this parasite. The highest incidence and intensity of infection with *P. minimum* in white crappie was in the late spring and summer months. Conversely, *Camallanus oxycephalus* was not found in the June, 1967, and May and June, 1968, channel catfish samples. Highly significant seasonal variations were observed in the prevalence of proteocephalid tapeworms from the channel catfish. The highest infection rate was observed in the winter collections of catfish.

Seasonal variation in incidence and severity of helminth parasitism in fishes, especially those utilizing fish as definitive hosts, was probably influenced by the annual life cycle of the parasite. Observations made in this study and those by Essex[9], Dogiel, et al.[8], and others support this view. Cross[7] and others have shown that the annual maturation of sex cells of helminths is temperature dependent. Somatic maturity, as shown by strobilization in tapeworms, would also seem to be temperature dependent. Hoffman[13] found that release of cercariae from snails and their infectivity was temperature dependent.

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