STUDIES OF THE BIOLOGY OF SWIM BLADDER NEMATODES, *Cystidicola* spp. (HABRONEMATOIDEA)

by

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ABSTRACT

The life cycle and larval development of swim bladder nematodes, *Cystidicola* spp., have been elucidated. *C. farionis* developed in three species of amphipod. Naturally infected amphipods have been found previously but one well known report was not valid. *C. cristivomeri* developed in *Mysis relicta* but not in amphipods. Naturally infected mysids were found. The third-stage larva of *Cystidicola* spp. and other cystidicolids undergoes considerable growth and development, but not the third moult, in the intermediate host.

C. cristivomeri was found in lake trout, brook trout, a new host record, and lake whitefish, probably an abnormal host. The intensity of infection of *C. cristivomeri* in lake trout in northwestern Ontario lakes was very high where the trout may be planktonivorous throughout their life. *C. cristivomeri* may have disappeared from the Great Lakes when lake trout populations declined severely. *C. farionis* was found in a variety of salmonids including introduced species in Lakes Huron and Superior. Eggs of *C. farionis* had mostly lateral filaments in lake whitefish and mostly polar filaments in other fish hosts. The number of filaments was variable. Changes in the intensity of infection in lake whitefish with age likely relate to changes in amount and kind of food eaten and growth rate of the fish. The movements and feeding habits of the fish hosts determine which amphipods are important in natural transmission of the parasite.

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INTRODUCTION

Nematodes of the genus *Cystidicola* Fischer, 1798 (Habronematoidea: Cystidicolidae) are parasitic in the swim bladder of physostomous fishes. Numerous host species, primarily of the family Salmonidae, are infected in Asia, Europe and North America (Skrjabin *et al* 1967; Ko and Anderson 1969; Lawler 1970).

In spite of the widespread occurrence of these parasites little is known about their biology. Until recently the confused systematics of *Cystidicola* may have discouraged studies. More than 20 species of nematodes from the swim bladder and intestine of various fishes have been included in *Cystidicola*. Many were poorly described. After critical review, Ko and Anderson (1969) restricted *Cystidicola* to parasites of the swim bladder and recognized three species. One of these, *C. stigmatura* (Leidy, 1886) Ward and Magath, 1917, has been made a synonym of *C. farionis* Fischer, 1798, elsewhere (Campana-Rouget 1955; Moravec and Ergens 1970; Arthur *et al* 1976). Thus there are now two valid species in *Cystidicola*: *C. farionis* from a variety of salmonids in Asia, Europe and North America, and *C. cristivomeri* White, 1941, occurring only in North America in char, *Salvelinus* spp. The broader classification of *Cystidicola* has been revised by Chabaud (1975a,b). The sub-family Cystidicolinae Skrjabin, 1946, was given family status and was placed in the new super-family Habronematoidea. The family Cystidicolidae presently comprises 12 genera parasitic in the alimentary tract and tissues

of freshwater and marine fishes.

The life cycle of *Cystidicola* spp. has not been determined. The intermediate hosts must be known to understand the natural transmission of the parasites and to experimentally infect fish. Experimental infections are necessary to evaluate suspected pathogenic effects of the parasites (Drew 1908; Shipley 1908; MacLulich 1943; Awachie 1973) and to determine the route of migration of the worms to the swim bladder. With knowledge of the life cycle the parasites may be an indicator of movements and feeding habits of the fish hosts (Eddy and Lankester *in press*). Previous authors have suggested that nematode larvae from amphipods were *Cystidicola* sp. (Baylis 1931; Bauer and Nikolskaya 1952; Mamayev 1971; Awachie 1973). Only two of the reports contain even a brief description of the nematodes. The identification of these larvae cannot be confirmed until the intermediate hosts have been demonstrated experimentally and *Cystidicola* spp. larvae have been accurately described.

This research was designed to determine the required intermediate hosts of *Cystidicola* spp., describe the developing larvae and attempt to understand the transmission of the parasites in wild fish populations.

MATERIALS AND METHODS

In the summer of 1976, a variety of fishes from Lake Huron was examined for swim bladder nematodes. The fish were collected by the Ontario Ministry of Natural Resources (MNR) and by commercial fishermen near Manitoulin Island. Lake whitefish, *Coregonus clupeaformis* (Mitchill), were sampled from Burnt Island, near the western end of Manitoulin Island and from the outer and inner basins of South Bay. Lake whitefish in the outer basin migrate into Lake Huron in early summer (Budd 1957), while those in the inner basin form a discrete resident group (Reckahn 1970). Other fishes examined included bloater, *C. hoyi* (Gill), from the inner basin of South Bay and Burnt Island; lake trout, *Salvelinus namaycush* (Walbaum), and splake, *S. fontinalis* (Mitchill) x *S. namaycush*, from Burnt Island; and lake trout taken by anglers from Lake Manitou on Manitoulin Island. The lake whitefish from South Bay were aged by MNR personnel.

During 1977, swim bladder nematodes were collected from bloater, lake herring, *C. artedii* Le Sueur, and rainbow trout, *Salmo gairdneri* Richardson, taken in Lake Superior by commercial and sport fishermen at Black Bay, Thunder Bay, and Rossport. These worms and others from the swim bladder of lake whitefish in Black Sturgeon Lake provided eggs for morphological study and experimental infections. In addition, swim bladder worms were collected from lake trout taken by sport fishermen on numerous lakes north and west of the city of Thunder Bay. The stomach

contents of lake trout were examined when possible. Nomenclature of fishes follows Scott and Crossman (1973).

Preserved swim bladder nematodes from brook trout, *S. fontinalis* (Mitchill), in White Partridge Lake and from lake whitefish in Hogan Lake were obtained for examination from Dr. R.C. Anderson (Dept. of Zoology, University of Guelph). Both lakes are in Algonquin Park, Ontario.

Swim bladders were removed from the fish, opened, and nematodes present were collected in saline (0.7% NaCl). Some of the bladders from whitefish were pressed between glass plates and examined under a dissecting microscope for larvae. Worms were fixed in hot 10% glycerine in 70% ethanol for identification. Females with shelled eggs in their uteri, and males with the tail coiled at least 540^{o} were designated mature; all others were considered immature. Nematode eggs used to infect crustaceans were obtained from unfixed female worms chopped in a blender.

The eggs of nematodes inhabiting the swim bladder probably leave infected fish *via* the pneumatic duct and gastro-intestinal tract. This was investigated by opening and washing the intestines of infected lake herring in sodium bicarbonate solution. The resulting sediment was decanted and examined for eggs directly, and after zinc sulphate flotation.

The variation in number and location of filaments on eggs from worms infecting different fish hosts was also investigated. For

each host species, live worms from 10 to 50 fish were pooled, and a sample of 10 undamaged females were put into a settling flask. Mature eggs released by the worms were pipetted from the bottom of the flask and 30 were examined at 400X.

Three species of amphipods, *Gammarus fasciatus* Say, *G. pseudolimnaeus* Bousefield, and *Hyalella azteca* (Saussure) were collected with a long-handled dip net among vegetation in shallow water at South Bay, Pine Bay (Lake Superior), and a marshy pond near the city of Thunder Bay. Another amphipod, *Pontoporeia affinis* Lindstrom, was taken with an Ekman dredge at depths up to 35-m in South Bay and at 15-m at the mouth of Pine Bay. Opossum shrimp, *Mysis relicta* Loven, were collected at night from deep areas of Sunset and Burchell Lakes in northwestern Ontario using a conical net, 0.8-m diameter and 2-m long, made of 1.7-mm mesh fibreglass screen, with a 4-litre beaker at the tapered end. The net was towed horizontally just below the thermocline. Mysids were transported with ice in aerated lake water. Live *M. relicta* from Burchell Lake were examined for nematodes under a dissecting microscope.

The crustaceans were kept in aerated, dechlorinated water in 4 and 20-litre aquaria. About half of the water was replaced weekly. The shallow-water amphipods were fed dried maple leaves, lettuce, and Tetra-Min Krill Flakes, and were given a substrate of dead maple leaves or aquarium gravel, with glass wool for shelter. Fine bottom sediment from the collecting site was provided as substrate and food for *P. affinis*. Mysids were kept

on fine sand and fed Krill Flakes.

Amphipods were held in the laboratory for up to 10 weeks prior to infection. During later examination any nematode larvae present from natural infections would have been recognized from their advanced development.. Amphipods were experimentally infected by exposing them to nematode eggs for periods of 0.3 - 4 h in small amounts of water in finger bowls or 4-litre jars. Mysids were exposed in aerated water 10-cm deep in a 20-litre aquarium for periods of 4 - 50 h. The exposure time was increased after initial dissections revealed low intensities of infection.

Infected crustaceans were held at various temperatures to determine the effects of temperature on development of the parasite. *P. affinis* were kept at 5 - 7°C with about 8-h of artificial light daily which was unavoidable. *Gammarus* spp. and *H. azteca* were held at temperatures between 5 and 18°C, with 11 - 11 - 14 h of artificial light daily. *M. relicta* were kept in darkness in a refrigerator at 4 - 5°C; one group was held at 9 - 11°C.

Crustaceans were dissected at various intervals after infection and developing nematodes were collected in saline. Heat-relaxed larvae and *en face* preparations (Anderson 1958) were drawn and measured at 400X or 1000X, using a *camera lucida*.

RESULTS

Identification of swim bladder worms

All swim bladder nematodes from fishes of Lake Huron, Lake Manitou, Lake Superior, and Black Sturgeon Lake were identified as *Cystidicola farionis* (= *C. stigmatura*). Worms from swim bladders of lake trout in northwestern Ontario lakes, from brook trout in White Partridge Lake and from lake whitefish in Hogan Lake were identified as *C. cristivomeri*. The morphology of the eggs most readily distinguishes these two species. Eggs of *C. farionis* possess numerous filaments, while those of *C. cristivomeri* have large lateral mamillations or "floats". As well, the uteri of gravid *C. farionis* are convoluted and distended with numerous eggs and occupy most of the pseudocoel. The uteri of *C. cristivomeri* are slender and contain relatively few eggs. In the absence of mature female worms, distinguishing features can be seen in *en face* preparations. In *C. cristivomeri* a rounded shelf-like inflation of the cuticle projects into the oral opening from beneath each lateral pseudolabium. These structures are not prominent in *C. farionis*.

Examination of naturally infected fishes

C. farionis was common in lake whitefish in Lake Huron while bloater and splake were not frequently infected (Table 1). Only immature *C. farionis* were found in splake. Lake trout from Lake Huron were not infected, but one of seven lake trout from Lake

TABLE 1. Lake Huron fish examined for *Cystidicola farionis*, June - September, 1976

Fish species	Location	Sample size	No. (%) infected	No. worms	Mean no. (%) mature worms per infected fish	No. (%) infected fish with mature worms
Coregonus clupeaformis	South Bay, outer basin	42	26 (62)	8* (1-43)	6 (67)	23 (88)
	South Bay, inner basin	73	52 (71)	11 (1-136)	6 (42)	39 (75)
	Burnt Island		5 (71)	8 (1-13)	5 (46)	4 (80)
Coregonus hoyi	South Bay, inner basin	12	0	--	--	--
	Burnt Island	1	1 (100)	3	3 (100)	1 (100)
Salvelinus namaycush	Burnt Island	4	0		-	-
Salvelinus namaycush X Salvelinus fontinalis	Burnt Island	9	1 (11)	26	0	0

* Mean, and (range).

Manitou contained three female *C. farionis*. These worms had unshelled eggs with only a few very short filaments.

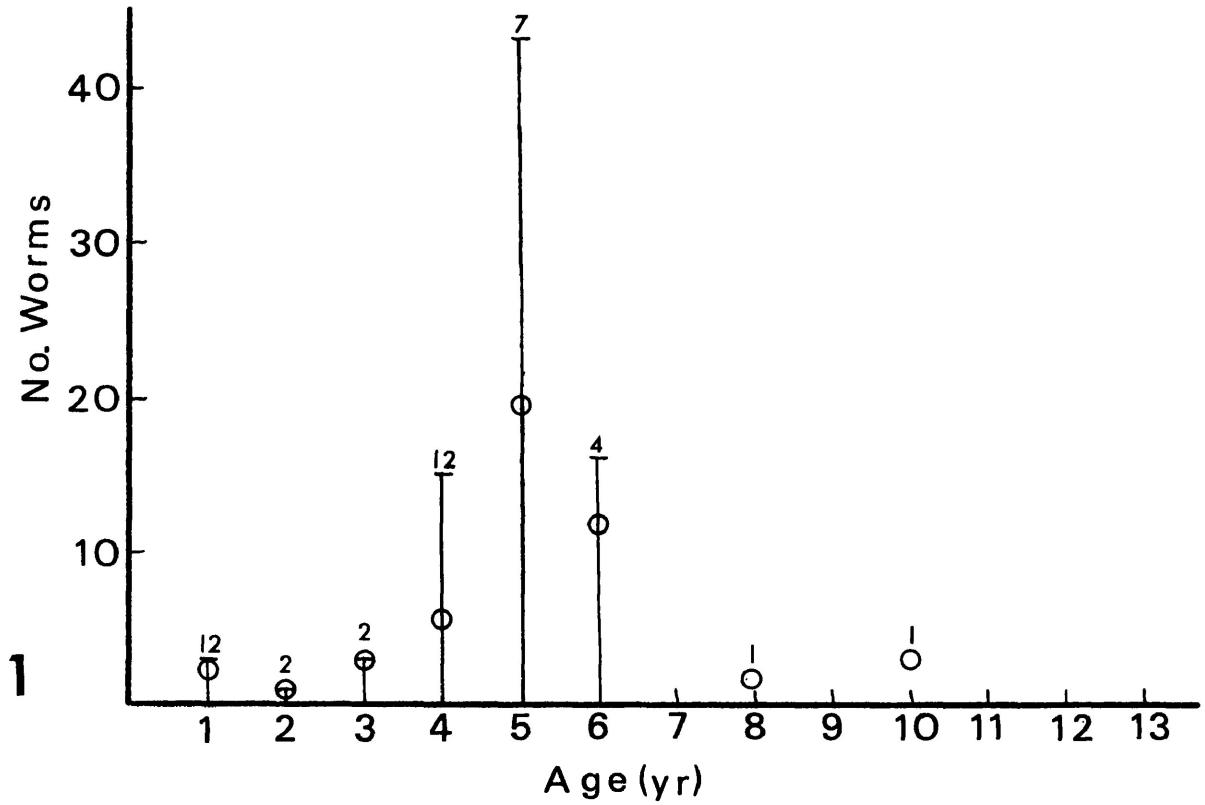
The prevalence (% infected) and intensity (mean number of worms per infected fish) of *C. farionis* were similar in lake whitefish from the three areas sampled (Table 1). Fish were taken in the outer basin of South Bay in June, and in the inner basin from July through September, 1976, but no seasonal changes were seen in prevalence, intensity, or proportion of mature worms present.

Young lake whitefish (<4 yr) from the outer basin of South Bay had few *C. farionis* (one to three) but the intensity of infection increased in fish four years of age and older (Fig. 1). Similarly, the intensity of infection increased in older lake whitefish from the inner basin but not until they were seven years old (Fig. 2). Lake whitefish from the inner basin were smaller and grew more slowly than those from the outer basin (Fig. 3).

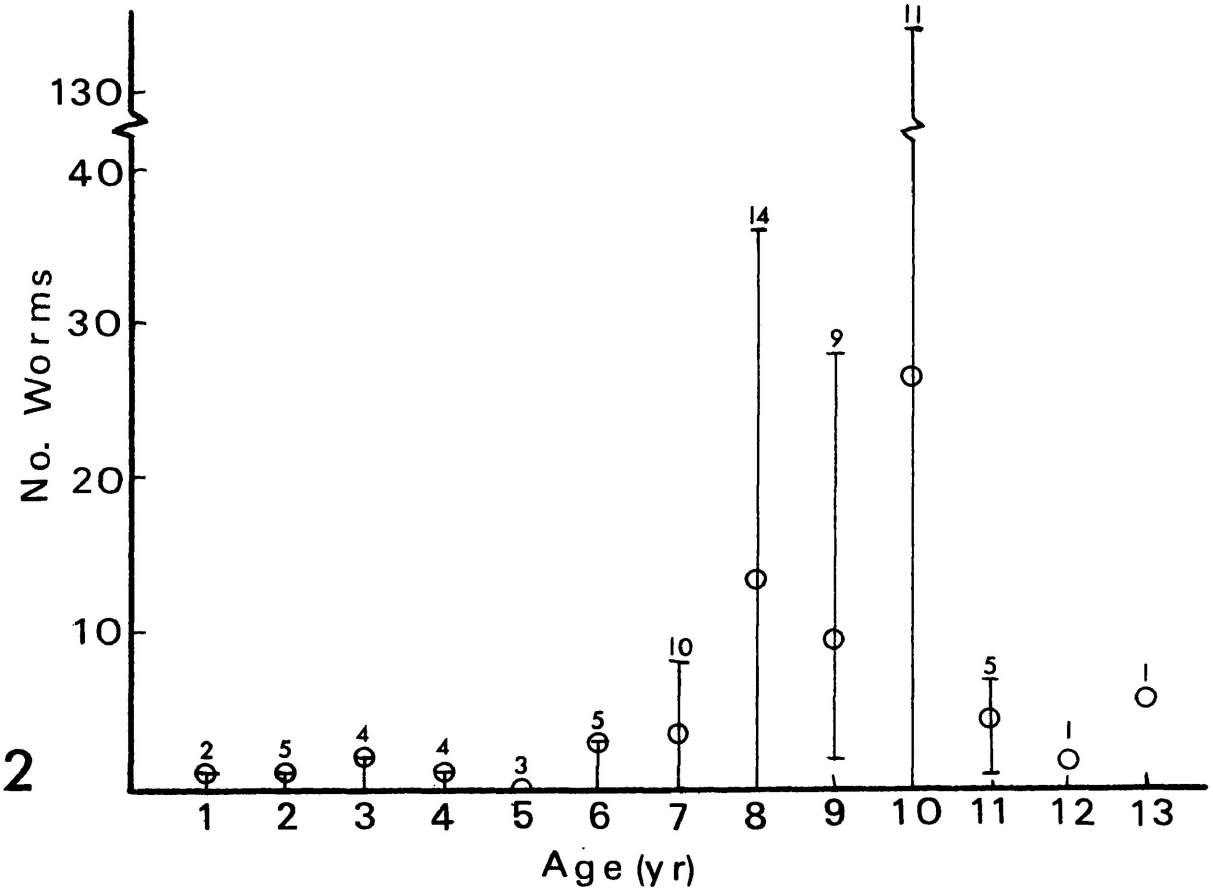
Two *C. farionis* larvae were found in the wall of the swim bladder in each of 2 of 62 lake whitefish. Forty-eight of these fish were infected with a total of 544 worms (mean 11.3, range 1 - 136). Those with larvae in the swim bladder wall had 16 and 136 worms.

In Lake Superior, *C. farionis* was found in 18 of 30 lake herring (60%), 42 of 43 bloater (98%) and 17 of 24 rainbow trout (71%) examined in 1977. The intensity of infection was highest in bloater (225, range 1 - 807) and lowest in rainbow trout (19, range 2 - 50). All samples contained both mature and immature worms.

Figures 1 and 2. Number of *Cystidicola farionis* in known-age lake whitefish from South Bay, Lake Huron. Fig. 1. Outer basin. Fig. 2. Inner basin. (O = mean; I = range; sample size is shown for each age).

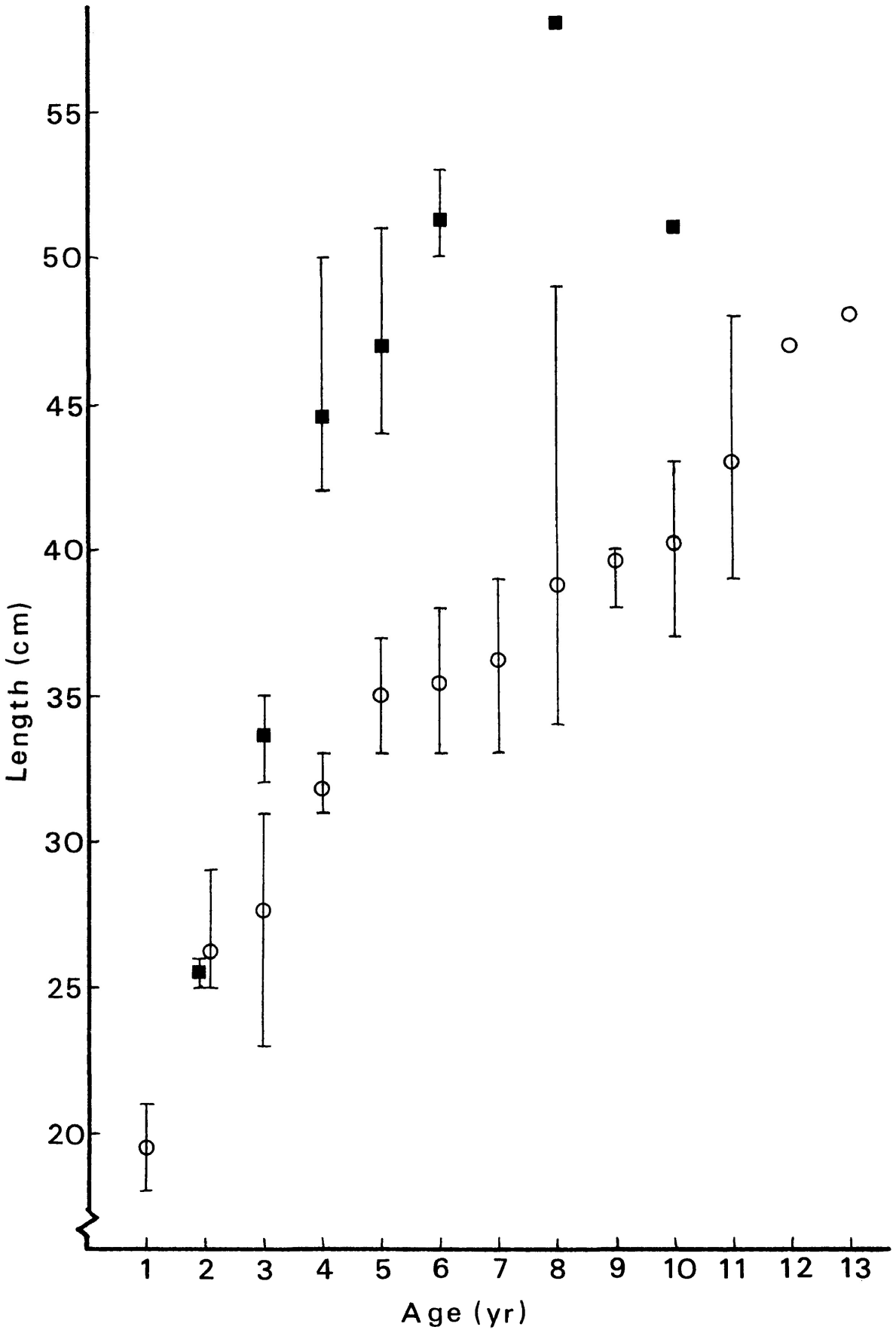

No. Worms
40
30
20
10
12
2
2
12
7
4
1
1
1 2 3 4 5 6 7 8 9 10 11 12 13
Age (yr)

1


No. Worms
130
40
30
20
10
2
5
4
4
3
5
10
14
9
11
5
1
1
1 2 3 4 5 6 7 8 9 10 11 12 13
Age (yr)

2

Figure 3. Fork length of known-age lake whitefish examined for *Cystidicola farionis* from South Bay, Lake Huron.
(■ = mean length of outer basin fish; O = mean length of inner basin fish; I = range; lengths of one year old fish from the outer basin were not available; sample sizes are as shown in Figs. 1 and 2).



3

Lake trout from 14 of 21 lakes in northwestern Ontario were infected with *C. cristivomeri*. In the lakes where the parasite was present, 97% of 87 fish examined were infected, with up to 3000 worms per fish. Food was found in 66 of 88 stomachs examined, and *M. relicta* occurred in stomachs of lake trout from 7 of 11 lakes where *C. cristivomeri* was present. Mysids were not found in stomachs of lake trout from six of seven lakes where swim bladder worms were absent. One fish from Sunset Lake was not infected with *C. cristivomeri*, but the stomach was full of *M. relicta*.

The two samples of *C. cristivomeri* from brook trout in White Partridge Lake comprised a small number of mature and immature worms. Only a few immature *C. cristivomeri* (4 - 5) were present in samples from three lake whitefish in Hogan Lake.

During collection of *Cystidicola* spp. larvated eggs of the nematodes were seen in mucus in the swim bladder. Eggs were also found in washings from the intestines of lake herring infected with *C. farionis*.

Variation in morphology of *C. farionis* eggs

Filaments on *C. farionis* eggs usually arise from a small knob at each pole, and from two lateral fields on opposite sides of the egg. Polar filaments were up to 300-μ long and were longer than lateral filaments. The number of filaments on individual eggs varied widely (Table 2).

Almost all eggs from worms in bloater, lake herring and rainbow trout had polar filaments, while less than half had lateral

TABLE 2. Arrangement of filaments on 30 eggs of *Cystidicola farionis* from different fish hosts

Host	Eggs with polar filaments		Eggs with lateral filaments	
	No. (%)	No. filaments†	No. (%)	No. filaments
Coregonus clupeaformis (Black Sturgeon Lake)	8 (27)	2±1.6* (1-5)	30 (100)	26±16.2 (2-50)
Coregonus clupeaformis (South Bay, Lake Huron)	22 (73)	5±4.2 (1-19)	30 (100)	20±10.2 (1-50)
Coregonus hoyi (Rossport, Lake Superior)	29 (97)	16±5.7 (5-30)	13 (43)	4±3.7 (1-10)
Coregonus artedii (Black Bay, Lake Superior)	30 (100)	18±5.4 (8-30)	4 (13)	2±1.0 (1-3)
Salmo gairdneri (Lake Superior)	30 (100)	15±6.0 (5-27)	8 (27)	4±3.6 (1-10)

† Total number on both poles.

* Mean ± one standard deviation, and (range).

filaments (Table 2). Polar filaments were always more numerous than lateral filaments. The opposite arrangement of filaments was seen on eggs from worms in lake whitefish. Lateral filaments were present on all eggs and were generally more numerous than polar filaments. Polar filaments occurred more frequently on eggs from whitefish in Lake Huron than on eggs from this fish host in Black Sturgeon Lake.

Infection of crustaceans with *C. farionis*

C. farionis larvae hatched from ingested eggs and developed to the third-stage in *Gammarus fasciatus*, *Pontoporeia affinis* and *Hyalella azteca* (Table 3). No developing larvae were recovered from *G. pseudolimnaeus*. Infected amphipods generally contained several larvae and one *G. fasciatus* had 161 larvae up to 1.5-mm long. Prevalence and intensity of infection varied among the amphipod species but there was also much variation within the species. For example, only 9% of 44 *H. azteca* exposed at one time became infected. The remaining 38 *H. azteca* were exposed for the same duration, but in a smaller volume of water, and 66% became infected. Prevalence and intensity of infection in *H. azteca* held at 12 - 14^{o}C was higher than in those similarly exposed but held at 5 - 7^{o}C.

Larvae were found free in the haemocoel of the amphipods, generally in the thorax, but also in the abdomen, head and pereiopods. Occasionally, they were found in muscle or other tissue, but did not become encapsulated. The penetration into the haemocoel by

TABLE 3. *Cystidicola farionis* larvae in experimentally infected amphipods

Amphipod	No. examined	No. (%) infected	No. larvae recovered	Source of nematode eggs
Gammarus fasciatus	27	19 (70)	19† (1-161)	lake herring, whitefish
Gammarus pseudolimnaeus	17	0		lake herring
Hyalella azteca	82	29 (35)	8 (1-37)	bloater, lake herring, rainbow trout
Pontoporeia affinis	93	41 (44)	3 (1-14)	lake herring, whitefish

† Mean, and (range).

first-stage larvae was slower in amphipods held at low temperatures. First-stage larvae were found in the haemocoel of *H. azteca* held at 19°C one day after eggs were ingested. In *G. fasciatus* at 15°C some first-stage larvae were still in the lumen of the intestine, and others were in the haemocoel, at eight days after infection. In *P. affinis* at 5 - 7°C larvated eggs were still present in the intestine at 10 days. After 20 days some eggs had hatched and first-stage larvae were present in the haemocoel.

Host tissue reaction around larvae was observed only in one *G. fasciatus*, which had died just prior to examination (19 weeks post-infection at 12 - 14°C). Ten larvae up to 3.9-mm long were recovered from this amphipod. Two of the smaller larvae (925 and 1220-μ) from the head region of the amphipod were inactive and enclosed in a rough brown material, possibly melanin.

Mortality of amphipods was high both before and after infection. Up to 78% of *H. azteca* and *Gammarus* spp. died during four weeks prior to infection. Mortality of amphipods after infection was often over 70%, and as high as 96%. High mortality occurred among the *P. affinis* that were unavoidably exposed to periods of light. A small number of *P. affinis* infected in an initial experiment were kept in the dark and very few died.

M. relicta exposed to eggs of *C. farionis* for 48-h were held at 4 - 5°C. Three mysids examined immediately after exposure each had 50 - 100 eggs in the stomach and intestine. A few eggs had hatched and one larva had penetrated into the haemocoel. Mortality of the exposed *M. relicta* was high; 21 of 23 died over three weeks. The two remaining mysids examined 1.5 and 3 weeks after infection contained

four and five first-stage larvae respectively, 156 - 195 μ long. The larvae were free in the haemocoel in the ventral thorax and the pereiopods.

Morphogenesis and rate of development of *C. farionis* in amphipods

First-stage *C. farionis* larvae were 130 - 256 μ long, second-stage larvae were 240 - 469-μ long and third-stage larvae were 437-μ to 4.9-mm long (Tables 4 - 8). Each of the three larval stages are easily distinguished by the appearance of the buccal cavity and oral opening.

First-stage larva

The first-stage larva has a rounded anterior end and a pointed tail (Fig. 4). The buccal cavity is long and narrow, and somewhat obscured by surrounding tissue. The round excretory cell lies slightly behind the nerve ring and ventral to the midpoint of the oesophagus. A short excretory duct leads anteriorly to the excretory pore. The oesophagus widens slightly at its posterior end. A lumen is initially present only in the anterior half of the intestine, and an anal opening is not visible. By the time of the first moult, however, the complete intestinal lumen, the rectum containing a plug of clear material, and the anus are present. The genital primordium is not easily seen prior to the first moult which occurs at about 250-μ.

Second-stage larva

The second-stage larva remains ensheathed in the cuticle of the first-stage larva. The buccal cavity is funnel-shaped anteriorly,

TABLE 4. Dimensions (μ) of *Cystidicola farionis* first-stage larvae in *Hyalella azteca* at 17°-18°C

Sample size (n)	10
Length	203±16.9† (169-229)
Width at nerve ring	11±1.2 (10-13)
Buccal cavity	31±5.2 (23-36)
Oesophagus	60±8.9 (49-79)
% of body length	30±3.3 (25-34)
Nerve ring‡	51±7.1 (39-61)
Excretory pore‡	59±7.9 (45-68)

† Mean ± one standard deviation, and (range).

‡ Distance from anterior end.

TABLE 5. Dimensions (μ) of *Cystidicola farionis* larvae in *Hyalella azteca* at 12°-14°C

	Larval stage		
	First	Second	Third*
Sample size (n)	4	18	16
Length	204±25.4† (176-229)	329±43.6 (240-413)	614±106.2 (461-757)
Width at nerve ring	11±3.1 (8-15)	26±3.6 (21-31)	33±4.3 (27-40)
Buccal cavity	25±2.5[a] (22-27)	40±6.5 (29-50)	35±4.9 (29-45)
Oesophagus	52±3.1[a] (49-55)	69±11.1 (58-94)	147±29.0 (103-192)
% body length	27±1.8[a] (25-28)	21±2.1 (17-25)	24±4.2 (15-32)
Nerve ring‡	46±5.7 (42-54)	64±9.7 (44-79)	62±11.0 (50-85)
Excretory pore‡	50±4.2[a] (47-55)	80±12.1 (50-98)	84±14.6 (68-114)
Genital primordium‡		198±30.7 (127-249)	381±58.9 (286-485)
% body length		60±4.3 (53-68)	62±4.1 (56-74)
Tail		53±7.8 (40-64)	50±9.1 (38-66)

* Recently moulted, ensheathed in second-stage cuticle.

† Mean ± one standard deviation, and (range).

‡ Distance from anterior end.

[a] n = 3.

TABLE 6. Dimensions (μ) of *Cystidicola farionis* larvae in *Hyalella azteca* at 5°-7°C

	Larval stage		
	First	Second	Third*
Sample size (n)	6	12	3
Length	190±35.5† (131-236)	284±41.0 (240-360)	631±102.2 (513-690)
Width at nerve ring	14±3.9 (10-19)	53±10.1 (40-71)	72±15.5 (55-85)
Buccal cavity	27±10.9 (15-42)	35±6.3 (21-43)	34±2.5 (31-36)
Oesophagus	51±7.5[a] (42-60)	55±10.6 (34-69)	163±41.4 (118-199)
% body length	27±2.1[a] (24-29)	19±3.7 (14-28)	26±3.0 (23-29)
Nerve ring‡	43±15.1 (21-62)	53±10.1 (40-71)	72±15.5 (55-85)
Excretory pore‡	54±19.5 (25-75)	63±11.9[b] (50-90)	93±22.5 (70-115)
Genital primordium		171±30.8[c] (140-223)	401±71.4 (320-455)
% body length		57±3.3[c] (53-62)	63±2.2 (62-66)
Tail		41±9.2 (22-59)	51±8.6 (43-60)

* Recently moulted, ensheathed in second-stage cuticle.

† Mean ± one standard deviation, and (range).

‡ Distance from anterior end.

[a] n = 4.

[b] n = 11.

[c] n = 7.

TABLE 7. Dimensions (μ) of *Cystidicola farionis* larvae in *Pontoporeia affinis* at 5°-7°C

	Larval stage		
	First	Second	Third*
Sample size (n)	8	7	6
Length	212±8.0† (188-228)	392±38.7 (351-449)	674±65.4 (571-729)
Width at nerve ring	11±3.3 (9-19)	29±6.1 (20-35)	34±3.3 (30-39)
Buccal cavity		40±9.4 (25-50)	43±7.5 (38-54)
Oesophagus		94±12.8 (79-119)	166±15.5 (139-184)
% body length		24±3.2 (19-28)	25±1.8 (23-28)
Nerve ring‡	49±8.0 (36-57)	58±9.7 (45-69)	82±9.9 (68-96)
Excretory pore‡	63±5.9[a] (56-72)	80±8.7[b] (66-89)	117±16.6 (90-133)
Genital primordium‡	-	236±23.1[b] (215-276)	410±42.9 (343-466)
% body length		59±5.1[b] (51-64)	61±2.4 (57-64)
Tail		55±5.2 (48-62)	61±10.7 (44-75)

* Recently moulted, ensheathed in second-stage cuticle.

† Mean ± one standard deviation, and (range).

‡ Distance from anterior end.

[a] n = 7.

[b] n = 6.

TABLE 8. Dimensions (μ) of *Cystidicola farionis* larvae in *Gammarus fasciatus* at 12°-14°C

	Larval stage			
	First[§]	Second	Third*	Third**
Sample size (n)	7	9	11	7
Length	230±15.0† (210-256)	401±41.6 (342-466)	668±105.8 (437-792)	2061±219.0 (1720-2347)
Width at nerve ring		27±1.6 (25-30)	34±2.8 (30-38)	54±4.4 (49-61)
Buccal cavity		43±2.3[a] (40-46)	32±6.2[c] (20-43)	66±10.0 (49-78)
Oesophagus		81±7.2[a] (69-93)	148±29.7[c] (103-191)	559±43.4 (508-620)
% body length		21±2.0[a] (19-25)	22±3.0[c] (16-27)	27±3.5 (23-32)
Nerve ring‡		75±5.4 (66-82)	75±24.1 (49-134)	135±16.5 (111-158)
Excretory pore‡		96±7.9 (82-108)	101±30.3[c] (65-162)	193±27.3 (152-229)
Genital primoridum‡		241±36.3[b] (185-282)	429±87.6 (289-561)	
% body length		58±6.5[b] (47-65)	64±5.7 (57-74)	
Tail		64±4.0 (60-71)	51±13.0 (30-70)	75±14.9 (59-100)

§ At 16 -18 C.

* Recently moulted, ensheathed in second-stage cuticle.

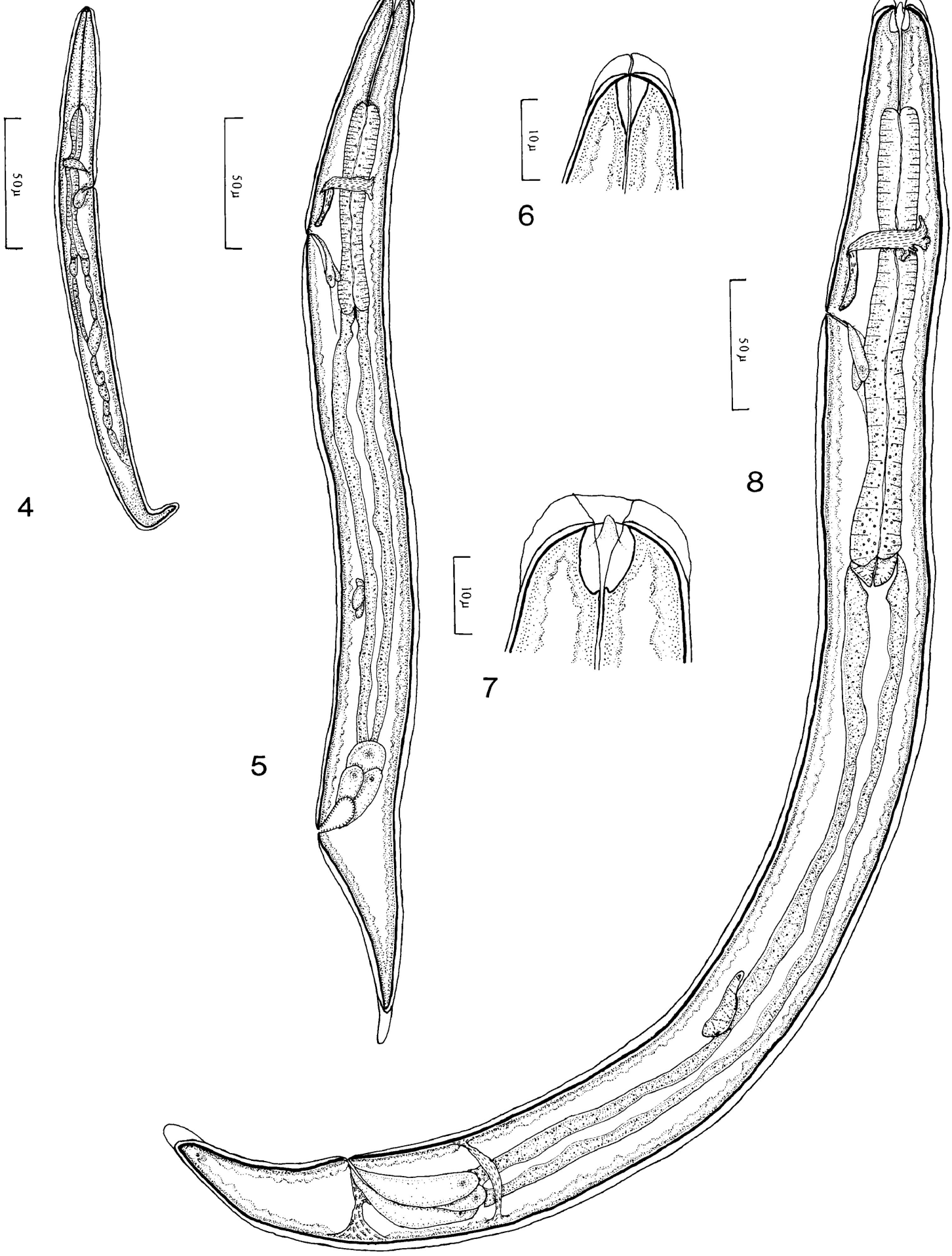
** Second-stage cuticle recently cast.

† Mean ± one standard deviation, and (range).

‡ Distance from anterior end.

[a] n = 8; [b] n = 6; [c] n = 10.

Figures 4 - 8. Larvae of *Cystidicola farionis* from experimentally infected amphipods. Fig. 4. First-stage larva. Fig. 5. Second-stage larva within loosened cuticle of first-stage larva. Fig. 6. Anterior end of second-stage larva (lateral view). Fig. 7. Anterior end of third-stage larva (lateral view) showing lateral pseudolabia and loosened cuticle of second-stage larva. Fig. 8. Third-stage larva.


50µ
4
50µ
5
10µ
6
10µ
7
50µ
8

narrowing to a straight tube lined with thicker cuticle (Fig. 6). The oesophagus is shorter, relative to body length, than in the first-stage larva (Tables 5 - 8). The elongate excretory cell now lies slightly behind the midpoint of the oesophagus (Fig. 5). The ventral ganglion of the nerve ring is prominent and extends posteriorly almost to the excretory duct. The intestine has a narrow lumen where it joins the oesophagus. The genital primordium with two conspicuous nuclei lies ventral to the intestine, slightly behind the midpoint of the larva. Three large cells surround the rectum. The rectal plug remains until the cuticle of the first-stage larva is lost, near the time of the second moult which occurs at about 450-μ.

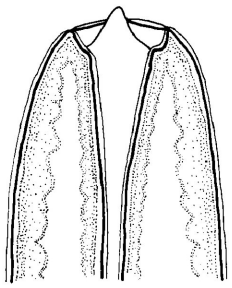
Third-stage larva

The third-stage larva is ensheathed in the cuticle of the second-stage larva up to a length of about 1.9-mm. Lateral pseudolabia are first present in the third-stage larva (Fig. 7, 9 - 11). Two amphids, lateral to the pseudolabia, and four sub-lateral papillae are visible in *en face* view (Fig. 11). No teeth are visible along the inner margin of the oral opening.

The buccal cavity, lined with thick cuticle, is elliptical dorsoventrally behind the oral opening, and narrows gradually to a straight cylinder (Figs. 9, 10, 14). The buccal cavity of third-stage larvae shorter than 1.9-mm is distorted while the second-stage cuticle loosens and draws away (Fig. 7).

Division of the oesophagus into anterior muscular and posterior glandular portions begins in recently-moulted third-stage larvae and

Figures 9 - 14. Advanced third-stage larva of *Cystidicola farionis* from experimentally infected amphipods. Fig. 9. Anterior end (lateral view). Fig. 10. Anterior end (dorsal view). Fig. 11. *En face* view. Fig. 12. Mid-region showing developing gonad. Fig. 13. Posterior end. Fig. 14. Anterior region with oesophagus divided into muscular and glandular portions.



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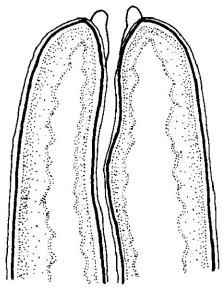

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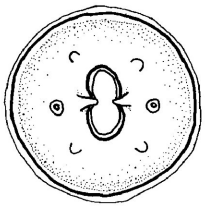

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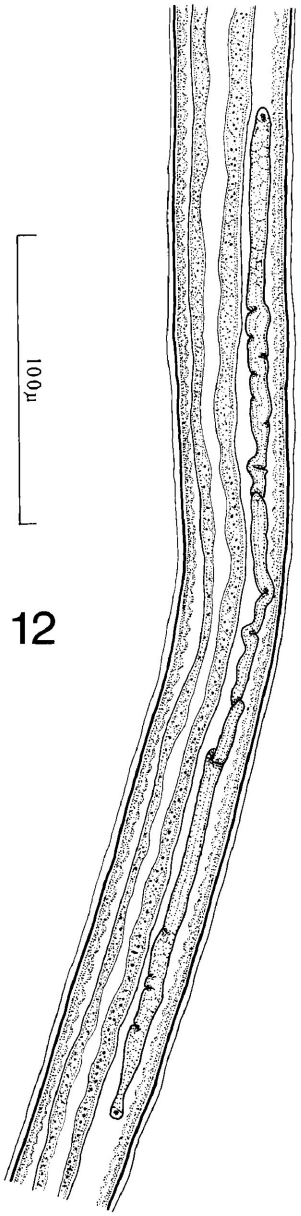

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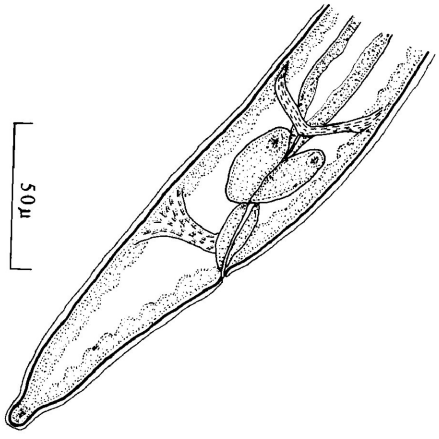

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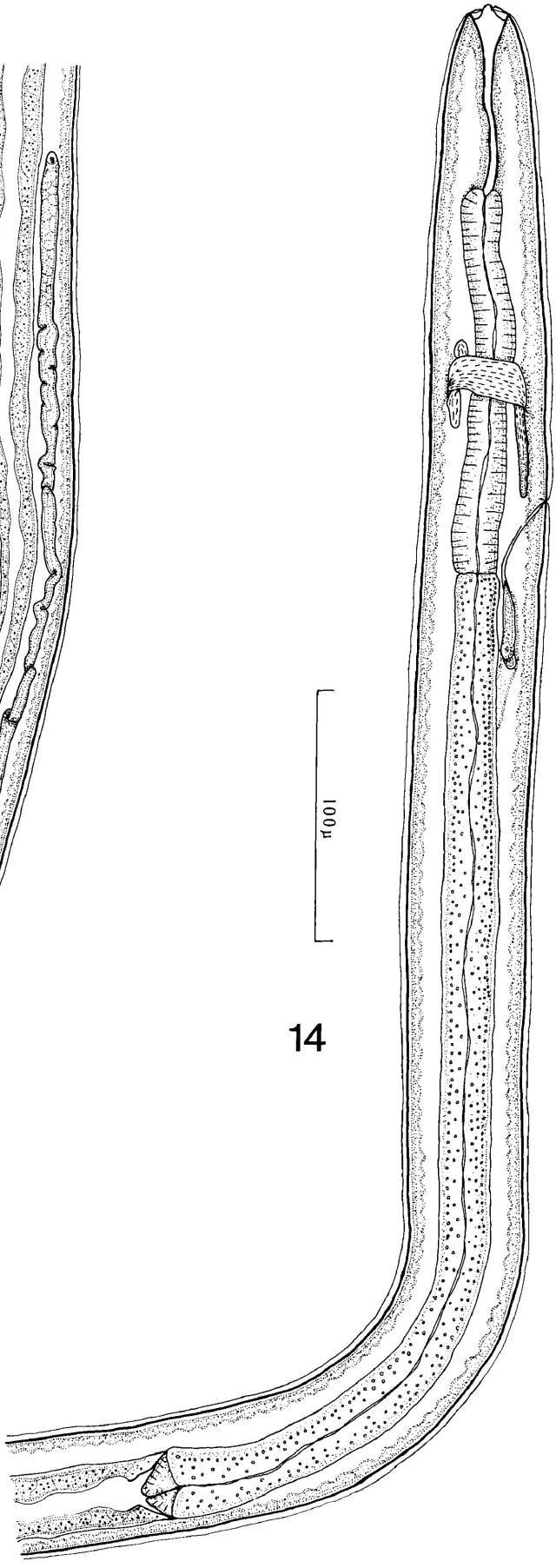

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is distinct in most larvae longer than 1.5-mm. The nerve ring encircles the muscular oesophagus, and the glandular portion begins at the level of the excretory cell. The ratio of lengths of the two portions was 1:2.3 - 1:4.7 in the larvae examined. The conical oesophageo-intestinal valve has a tri-radiate lumen in cross-section.

The ovoid genital primordium in recently-moulted larvae comprises several cells (Fig. 8), but loses the ovoid shape as it grows anteriorly and posteriorly. The elongating gonad is slightly convoluted in the middle region, and has a prominent nucleus at each end (Fig. 12). The gonad reached 0.9-mm, or 18% of body length, in the longest larva.

A dorso-ventral nerve commissure encircles the intestine just anterior to the rectal cells (Fig. 13). The *ani depressor* muscle attaches to the dorsal wall of the rectum behind the rectal cells. An apparent terminal protruberance on the tail is formed by a constriction 7 - 10 μ from the tip, but is poorly-developed or absent in some larvae.

The rate of larval development was influenced by temperature and the species of amphipod host (Table 9). Larvae in both *G. fasciatus* and *H. azteca* developed faster at the higher of two temperatures. Development was slowest in the amphipods held at 5 - 7°C. Larvae developed faster in *G. fasciatus* at 12 - 14°C and in *P. affinis* at 5 - 7°C than in *H. azteca* at those same temperatures respectively. The size ranges of the larvae indicate

TABLE 9. Rate of development of *Cystidicola farionis* in amphipods (sampled weekly)

Host	Temperature	First Sample (wks)	First recovery of larval stage (wks)		
			Second	Third	Third free of 2nd-stage cuticle
G. fasciatus	16-18°C	1	2.5	3	
	12-14°C	3	3	5	8-13†
H. azteca	12-14°C	5	5	6	10
	5-7°C	6	7	8	
P. affinis	5-7°C	3	6	7	14-17†

† Larva present at end of interval; no samples during interval

that the length at the moults did not vary with temperature or the host (Tables 4 - 8).

In many infected amphipods, the larvae recovered had not all reached the same stage of development. First-stage and second-stage larvae were usually still present when third-stage larvae were initially found. The small larvae were often dead or degenerating in later samples.

Infection of *M. relicta* with *C. cristivomeri*

C. cristivomeri larvae hatched from ingested eggs and developed to the third-stage in *M. relicta*. Larvae were recovered from 39 of 60 (65%) mysids exposed to eggs for 19 - 50 h and held at 4 - 5°C. Infected mysids contained 1 - 11 larvae (mean 2.9).

Even at 4 - 5°C larvae hatched and rapidly penetrated into the haemocoel. Two mysids examined immediately after exposure to eggs for 16-h had larvae in the stomach, the intestine and the haemocoel. First-stage and second-stage larvae were generally free in the haemocoel inside pereiopods or near thoracic muscles at the bases of appendages. A few were found among muscle fibres, but were active and not encapsulated. Third-stage larvae were coiled within thin capsules in muscles of pereiopods but were active when dissected free. No melanization of larvae was seen but small larvae were found degenerating inside thin capsules in pereiopod muscles after 10 weeks post-infection.

High mortality of *M. relicta* occurred but was not quantified

prior to exposure to eggs. After exposure there were 64 - 192 mysids per 20-litre aquarium. Within seven weeks 87% had died. Over the next 12 weeks only 40% of the remainder died. During this period the density of mysids was reduced and feeding was more frequent.

Morphogenesis and rate of development of *C. cristivomeri* in *M. relicta*

First-stage larvae of *C. cristivomeri* were 140 - 308 µ long, second-stage larvae were 270 - 731 µ long and third-stage larvae were 715-µ to 5.7-mm long (Table 10). The three larval stages are easily distinguished by the appearance of the buccal cavity and oral opening. Morphogenesis of the larvae is essentially the same as for *C. farionis*.

First-stage and second-stage larvae (Figs. 15, 16, 20)

An intestinal lumen is not seen in first-stage larvae shorter than 200-µ, but a complete lumen and anal opening are present in larvae longer than 250-µ. The first moult occurs at about 300-µ. The oesophagus of the second-stage larva is shorter than in *C. farionis*, and terminates at the level of the excretory cell. The larva remains ensheathed in the cuticle of the first-stage larva until the second moult which occurs at about 720-µ.

Third-stage larva (Fig. 17-19, 21-22)

The third-stage larva is usually ensheathed in the cuticle of

TABLE 10 Dimensions (μ) of *Cystidicola cristivomeri* larvae in experimentally infected *Mysis relicta*

	Larval stage		
	First	Second	Third*
Sample size	11	10	8
Length	220±39.9** (160-282)	425±80.0 (302-545)	1937±735.0 (882-2576)
Width at nerve ring	18±6.1 (7-24)	30±4.6 (23-37)	46±6.0 (40-57)
Buccal cavity	28±7.4 (18-38)	45±4.4 (35-50)	49±7.4 (40-65)
Oesophagus	53±9.4 (39-74)	73±11.3 (51-81)	290±81.9 (159-370)
% body length	25±8.8 (18-45)	17±1.2 (15-19)	16±2.5 (14-21)
Nerve ring†	43±8.7 (26-54)	74±10.3 (55-89)	126±19.2 (99-151)
Excretory pore†	58±12.9 (30-71)	96±14.8 (68-118)	80±35.8 (124-223)
Genital primordium†‡	--	263±49.2 (186-323)	1123±425.5 (513-1570)
% body length		62±3.6 (58-71)	58±3.1 (53-62)
Tail		61±10.4 (46-83)	78±7.6 (65-91)

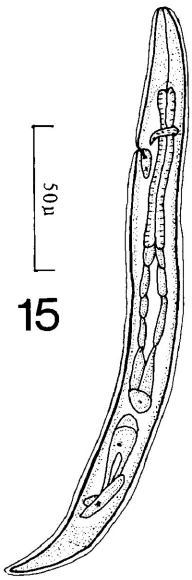
* Ensheathed in second-stage cuticle, distorting buccal capsule (see text).

** Mean ± one standard deviation, and (range).

† Distance from anterior end.

‡ Midpoint of genital primordium or developing gonad.

Figures 15 - 22. Larvae of *Cystidicola cristivomeri* from experimentally infected *Mysis relicta*. Fig. 15. First-stage larva. Fig. 16. Second-stage larva within loosened cuticle of first-stage larva. Fig. 17. Anterior region of third-stage larva showing loosened cuticle of second-stage larva and division of oesophagus into muscular and glandular portions. Fig. 18. Posterior end of third-stage larva. Fig. 19. Mid-region of third-stage larva showing genital primordium. Fig. 20. Anterior end of second-stage larva (lateral view) showing buccal cavity. Fig. 21. Anterior end of third-stage larva (lateral view) showing lateral pseudolabia and distorted buccal cavity during separation of second-stage cuticle. Fig. 22. Anterior end of third-stage larva (lateral view) after separation of second-stage cuticle.



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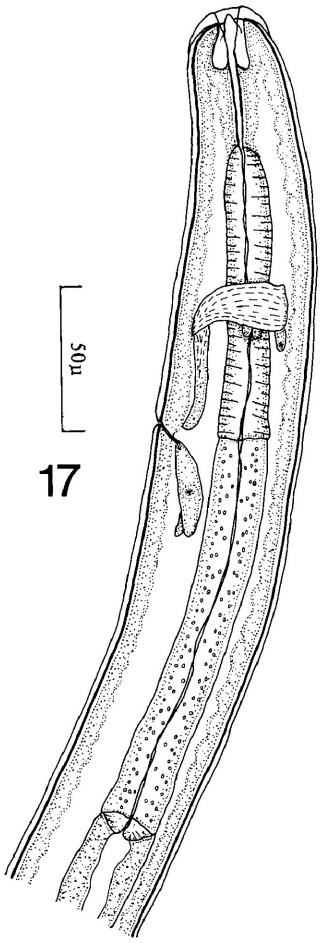

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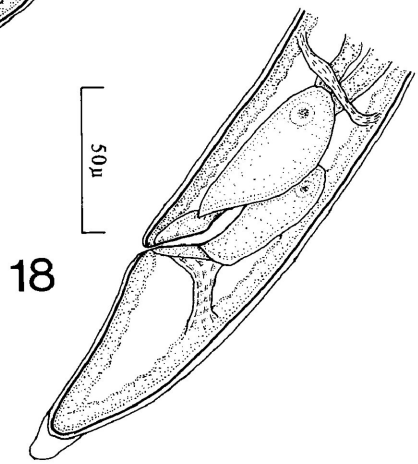

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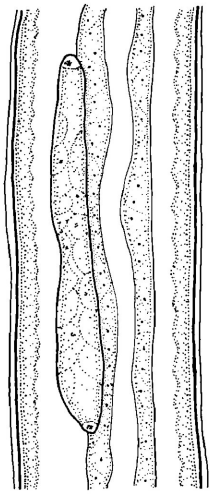

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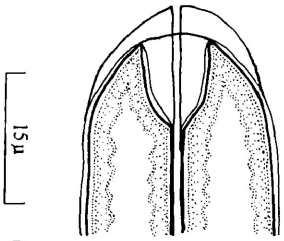

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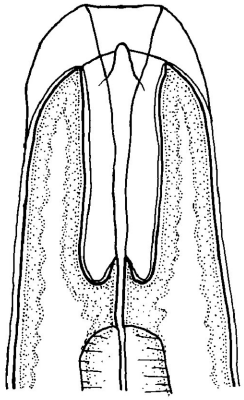

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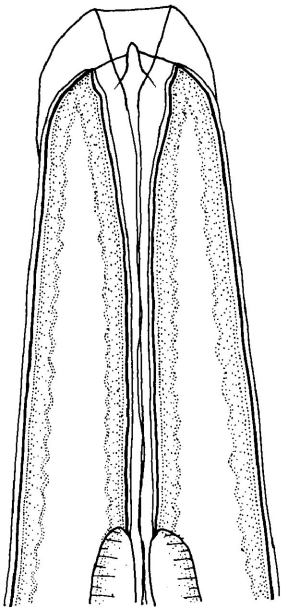

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the second-stage. In one instance, third-stage larvae from a mysid that had recently died were no longer encapsulated and were free of the second-stage cuticle.

In *en face* view, a rounded shelf-like inflation of the cuticle projects medially from beneath each pseudolabium, giving the oral opening a dumb-bell shape. These structures are not seen in *C. farionis*. During separation of the second-stage cuticle the buccal cavity is distorted and appears to be much shorter than the undistorted buccal cavity (cf. Fig. 21, 22). The division between muscular and glandular oesophagus is distinct in most larvae longer than 1.6-mm. The ratio of lengths of the two portions was 1:2.0 - 1:3.5 in the larvae examined. The oesophageo-intestinal valve is smaller than in *C. farionis*. In some larvae, the lengthening gonad becomes convoluted in the middle region, while the gonad of others remains straight and a few large cells begin growing ventrally from the midpoint. The longest gonad found, one of the latter type, was 1.3-mm (26% of body length).

At 4 - 5^{o}C, larvae developed to the second-stage in 10 weeks and to the third-stage in 17 weeks post-infection. Rate of development was temperature dependent, and at 9 - 11^{o}C second-stage larvae were present at three weeks and third-stage larvae at eight weeks post-infection. In some infected mysids, the larvae recovered had not all reached the same stage of development. First-stage larvae were present when second-stage larvae were found, but many were degenerating. Second-stage larvae were still present when third-stage larvae were found.

C. cristivomeri from naturally-infected *M. relicta*

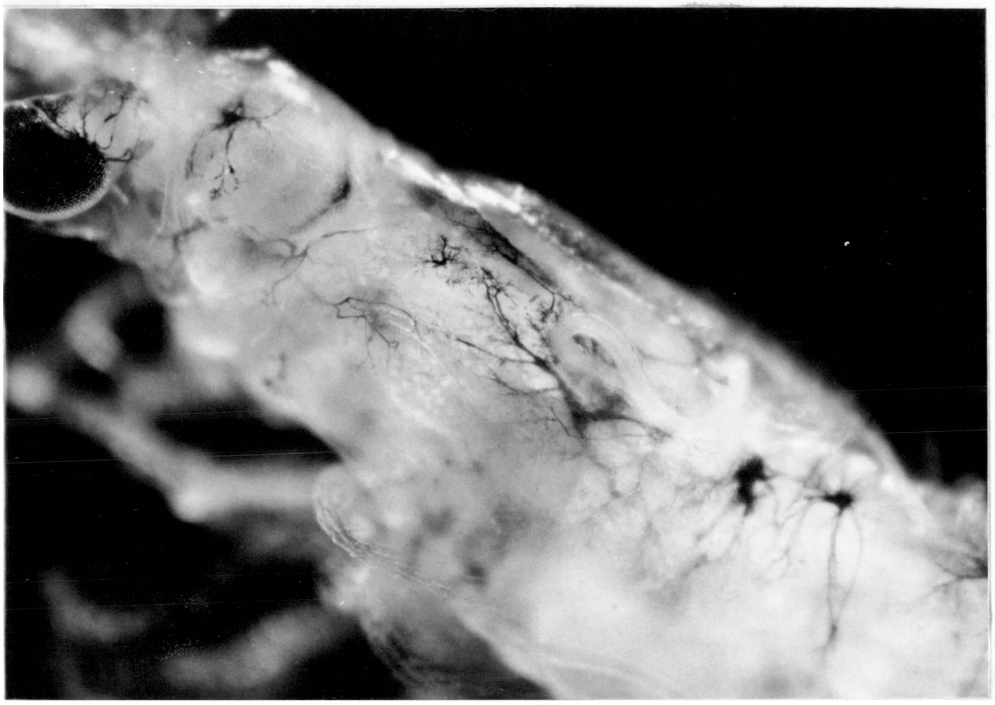
Third-stage *C. cristivomeri* larvae, 5.9 - 10.8 mm long, were found in 6 of 753 (0.8%) *M. relicta* from Burchell Lake in mid-October, 1977 (Fig. 25-31; Table 11). The larvae, one in each infected mysid, were free in the haemocoel, lateral or dorsal to the thoracic viscera, and were visible in whole mysids (Figs. 23, 24). The larvae were not ensheathed in the cuticle of the second-stage larva.

The gonads were longer than those in the third-stage larvae from experimental infections. The two morphological types differed in position and length (Fig. 29,30; Table 11). The convoluted gonad lay entirely posterior to the midpoint of the larva. The straight gonad was longer, and was almost equally extended anterior and posterior from the midpoint of the larva. The convoluted and posteriorly situated gonad is likely that of a male. The longer gonad in the mid-region is likely that of a female. The group of large cells at the midpoint of the female gonad probably forms the vaginal primordium. Flattened cells surround the mid-region of the female gonad, and a narrow lumen is present in the mid-region of both the male and female gonads.

Infection of amphipods with *C. cristivomeri*

P. affinis exposed to eggs of *C. cristivomeri* for 3.5-h were held at 7 - 10°C. Four examined immediately after exposure had larvated eggs in the gut, but only 1 of 22 examined four and nine weeks later was infected. This amphipod contained a single first-

Figures 23 and 24. *Mysis relicta* from Burchell Lake naturally infected with *Cystidicola cristivomeri*. Fig. 23. Dorso-lateral view of thorax containing a third-stage larva. Fig. 24. Close-up of third-stage larva in *M. relicta*.



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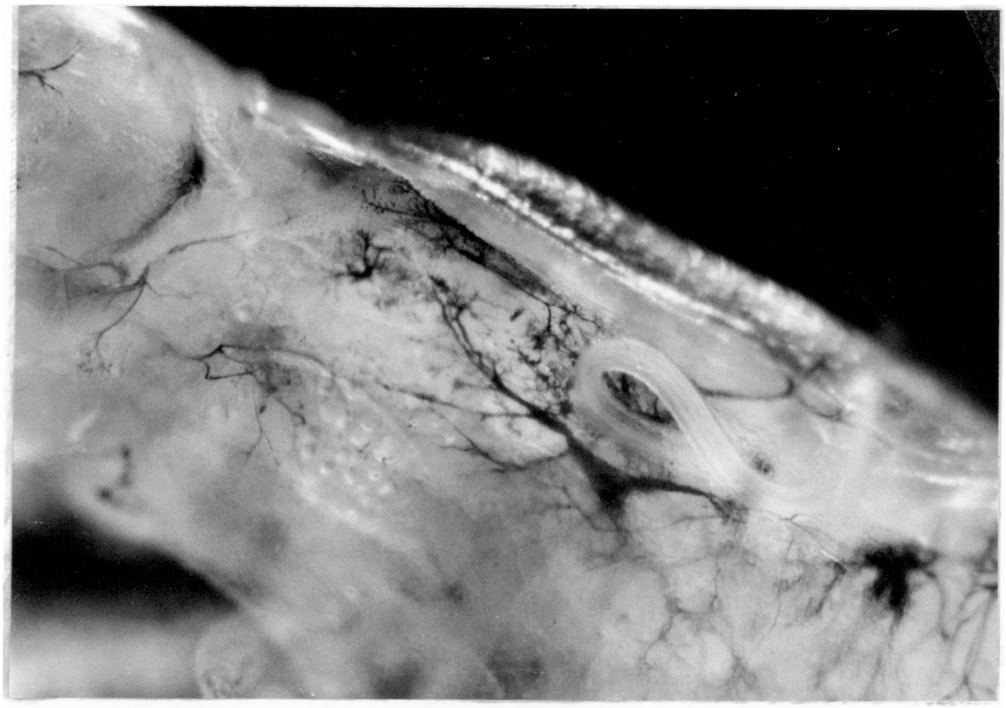

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Figures 25 - 31. Third-stage larvae of *Cystidicola cristivomeri* from naturally infected *Mysis relicta* in Burchell Lake. Fig. 25. Anterior end (lateral view). Fig. 26. Anterior end (dorsal view). Fig. 27. *En face* view. Fig. 28. Mid-region of female larva showing anterior half of gonad and the group of cells forming the vaginal primordium. Fig. 29. Mid-region of male larva showing gonad. Fig. 30. Anterior region. Fig. 31. Posterior end.

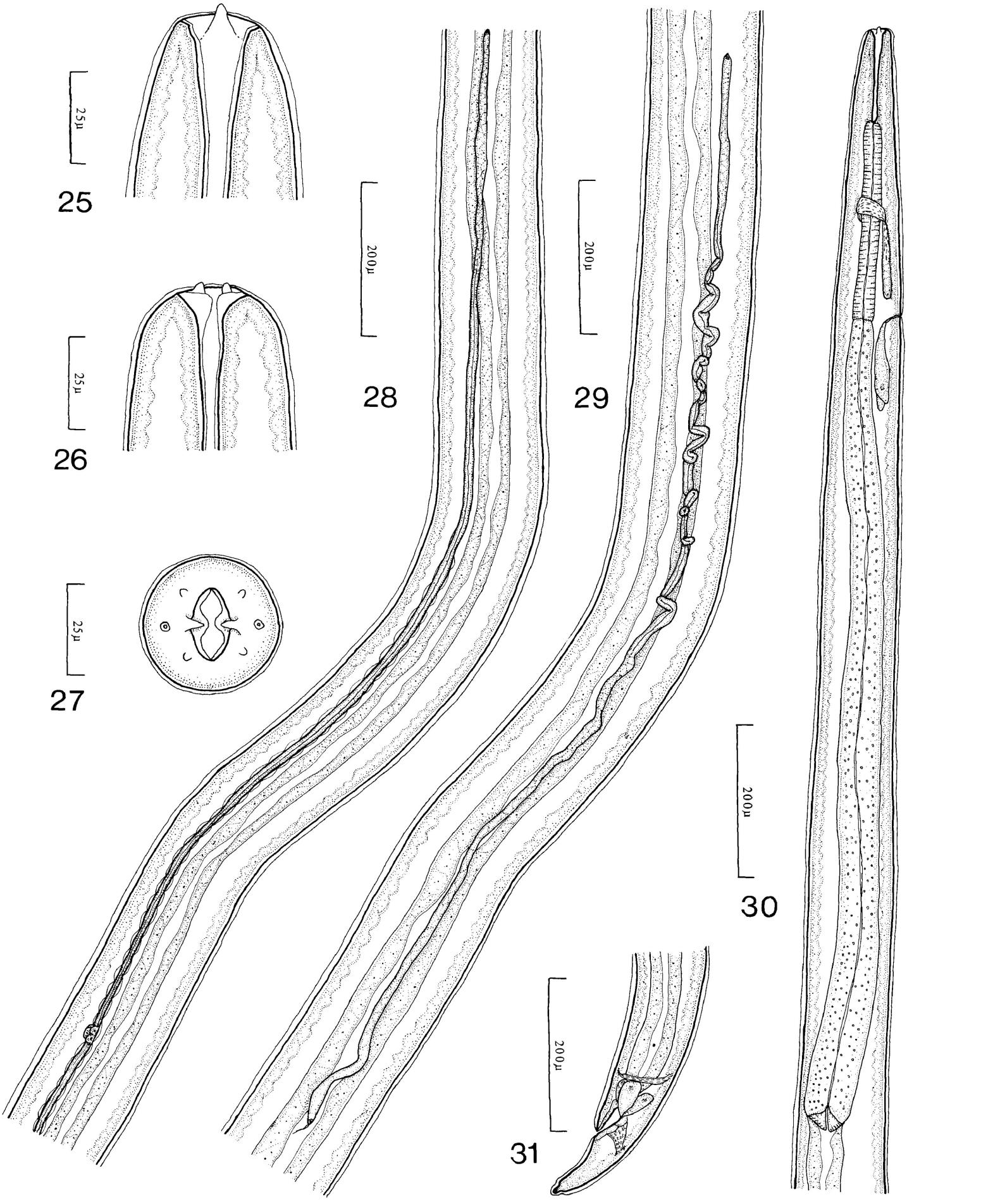

25µ
25
25µ
26
25µ
27
200µ
28
200µ
29
200µ
30
200µ
31

TABLE 11 Dimensions (μ, unless otherwise specified) of *Cystidicola cristivomeri* third-stage larvae in *Mysis relicta* from Burchell Lake

Sample size	4 ♂♂, 2 ♀♀	
Length (mm)	8.5±2.0	(5.5-10.8)†
Width at nerve ring	67±6.5	(57-74)
Buccal cavity	119±10.2	(104-130)
Oesophagus	1110±218.5	(806-1318)
% body length	13±0.8	(12-14)
Nerve ring‡	214±20.9	(188-245)
Excretory pore‡	311±34.5	(248-346)
Gonad: Length (mm)♂	1.3±0.4	(0.9-1.7)
♀	3.8±1.4	(2.8-4.8)
% body length♂	16±1.4	(15-18)
♀	41±5.7	(37-45)
Anterior end‡ (mm)♂	4.3±1.2	(2.9-5.3)
♀	3.4±0.6	(3.0-3.8)
% body length♂	53±2.1	(50-55)
♀	38±3.5	(35-40)
Tail	84±15.9	(59-99)

† Mean ± one standard deviation (range).

‡ Distance from anterior end of larva.

stage larva, 290-μ long, free in the haemocoel nine weeks after infection.

H. azteca exposed to eggs of *C. cristivomeri* for 96-h were held at 17 - 18°C. Three of nine examined immediately after exposure had larvated eggs, and some hatched larvae, in the gut. Single larvae were found free in the haemocoel of 3 of 26 *H. azteca* examined 4 - 10 weeks later. First-stage larvae, 200 and 211-μ long, were found at four and seven weeks respectively. Each had an abnormally enlarged excretory cell, and the larva found at seven weeks contained many vacuoles and refractile granules and was apparently degenerating. A third-stage larva, 685-μ long, with an abnormally enlarged rectum and a contracted tail, was recovered after seven weeks.

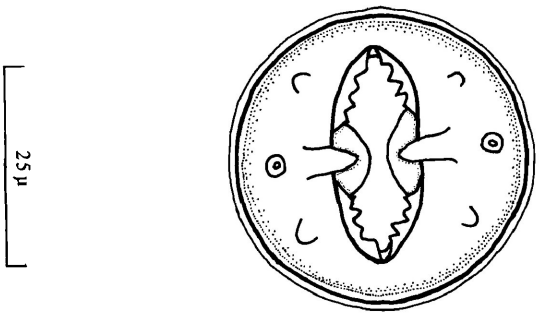
C. cristivomeri larvae in lake trout

Larvae believed to be third-stage and fourth-stage were found among a sample of *C. cristivomeri* from lake trout from Killala Lake. All worms were free in the lumen of the swim bladder.

Male larvae, 10.3 and 12.6-mm long, were apparently developed beyond the third-stage. Small teeth were present around the inner margin of the oral opening (Fig. 32). The gonad extended almost to the rectum and cells forming the spicule primordia were visible (Fig. 33). No sclerotized spicules could be seen, however, and no caudal alae were present as they are in adult males. These worms are thought to be fourth-stage larvae.

Two female worms, 7.7 and 8.5-mm long, lacked circumoral teeth.

Figures 32 - 33. Larva of *Cystidicola cristivomeri* (probably fourth-stage) from the swim bladder of lake trout. Fig. 32. *En face* view showing small teeth around inner margin of oral opening. Fig. 33. Posterior end of male larva (large rectal cells omitted) showing posterior end of gonad and spicule primordia.



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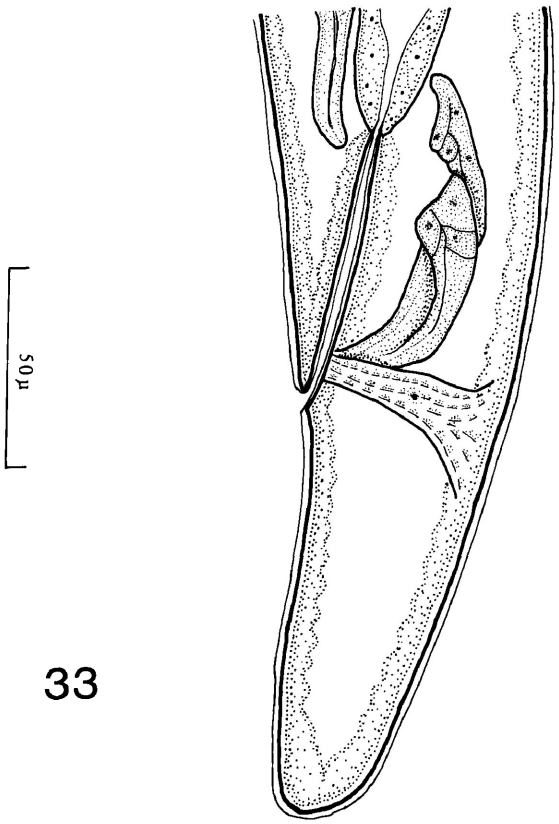

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The vaginal primordium protruded slightly into the body wall but the worms were otherwise identical to third-stage larvae from *M. relicta*. Several other female worms, 12 - 16 mm long, had a vulva, a vagina and circumoral teeth.

DISCUSSION

The larval development of *Cystidicola* spp. is described for the first time from experimentally infected intermediate hosts. Larvae of *C. cristivomeri* developed in *M. relicta* but amphipods apparently are not suitable hosts. The few larvae of *C. cristivomeri* recovered from experimentally infected *H. azteca* and *P. affinis* were abnormal in appearance and had undergone little development compared to those in *M. relicta*. Larvae of *C. farionis*, however, developed in the amphipods *G. fasciatus*, *H. azteca* and *P. affinis*. The failure to infect *G. pseudolimnaeus* is curious but further trials ensuring that eggs are ingested may show that this species is also a suitable host. Larvae of *C. farionis* developed more slowly in *H. azteca* than in the other amphipods, perhaps indicating a slight difference in host suitability. Neither the prevalence and intensity of infection nor the mortality of the amphipods is indicative of host suitability: the number of eggs ingested by the amphipods was not kept constant and mortality was high both before and after infection. Mortality may have resulted from an inadequate food source and, in the case of *P. affinis*, the exposure to light. It is not known if *C. farionis* can develop in *M. relicta*. Eggs ingested by mysids hatched and some first-stage larvae penetrated into the haemocoel but most of the mysids died shortly after infection.

The validity of previous descriptions of nematode larvae thought to be *C. farionis* can now be determined. Larvae found by

Baylis (1931) in *Gammarus pulex* (Linnaeus) were morphologically similar to *C. farionis* from experimentally infected amphipods but were generally longer (4 - 7.9 mm). This is not a critical difference however, as there was no indication that the smaller larvae recovered in experimental infections had reached their maximum size. On the other hand, a larva 7-mm long from *P. affinis* in Lake Ladoga USSR (Bauer and Nikolskaya 1952) apparently was incorrectly identified as *C. farionis*. The oesophagus was 2.1-mm long and the ratio of lengths of muscular to glandular portions was 1: 1.3. This ratio was never less than 1: 2.3 in *C. farionis* larvae from experimentally infected amphipods and increased with the length of the worm up to 1: 4.7. The same ratio was about 1: 4 in *C. farionis* larvae found by Baylis (1931). Other features of the larva found by Bauer and Nikolskaya (1952) were poorly described. One of a few nematode larvae collected from *Gammarus* sp. in South Bay and thought to be *Cystidicola* sp. (pers. comm., D. Cone, Dept. of Biology, Univ. New Brunswick, Fredericton) has been examined. This larva also has obvious differences from *C. farionis*.

The larvae of some other cystidicolid nematodes are known. The morphogenesis of *Cystidicola* spp. resembles that of *Cystidicoloides tenuissima* (Zeder, 1800) Rasheed, 1965, in experimentally infected mayfly nymphs (Moravec 1971). The buccal cavity is straight and narrow in the first-stage larva and funnel-shaped anteriorly in the second-stage larva. The second-stage and third-stage larvae remain ensheathed in the moulted cuticle of the previous stage for lengthy periods. Moravec (1971)

refers to these larvae ensheathed in a moulted cuticle as "transitive stage larvae" but such terminology is needlessly confusing. Lateral pseudolabia and a buccal cavity similar to that of the adult are first present in *Cystidicoloides tenuissima* in the third-stage larva (Moravec 1971). This larva grew from a length of 1.6-mm to 4.1-mm in experimental infections and was up to 8-mm long in naturally infected mayflies (Choquette 1955; Moravec 1971). The gonad becomes elongate and well-developed. In *Cystidicola* spp., the buccal cavity of the third-stage larva differs from that of the adult only in lacking small teeth along the inner margin of the oral opening. Considerable growth of *Cystidicola* spp. occurs after the second moult. The well-developed gonad distinguishes the sexes in third-stage larvae of *C. cristivomeri* and in the *C. farionis* larvae found by Baylis (1931).

Similar features are found in the third-stage larva of other cystidicolid nematodes. The third-stage larva of *Spinitectus micracanthus* Christian, 1972, has a buccal cavity similar to that of the adult (Christian 1972) and an elongate genital primordium by which the sexes can be distinguished (Keppner 1975). This larva grew from 1.2-mm at the second moult to 2.4-mm in experimentally infected mayflies. Larvae of *Ascarophis* spp. from naturally infected marine decapods and amphipods have lateral pseudolabia, a buccal cavity like the adult (Dollfus and Campana-Rouget 1956; Petter 1970) and, in some, a well-developed gonad that distinguishes the sexes (Uspenskaya 1953; Petter 1970; Tsimbalyuk *et al* 1970; Poinar and Kuris 1975; Poinar and Thomas 1976). Thus considerable

growth and development of the third-stage larva in the intermediate host is characteristic of the family Cystidicolidae.

There is confusion in the literature regarding the number of moults undergone by cystidicolid nematodes in their intermediate hosts. Baylis (1931) reported that *Cystidicola farionis* from *G. pulex* were fourth-stage larvae. Noting the well-developed gonads of *Cystidicoloides tenuissima* larvae in mayflies, Moravec (1971) speculated that the third moult to the fourth-stage larva may have occurred in the intermediate host. Only the fourth moult was observed in the definitive host. Keppner (1975) failed to see *S. micracanthus* moult twice in the fish host and speculated that the third moult may occur in mayflies. Both third-stage and fourth-stage larvae of *Cystidicola cristivomeri* were found in the definitive host, however, and Choquette (1955) observed two moults of *Cystidicoloides tenuissima* in fish. The third moult of larval cystidicolids has not been observed in the intermediate host and the worms found by Baylis (1931), Moravec (1971) and Keppner (1975) were probably third-stage larvae. The advanced development characteristic of these larvae likely is responsible for much of the confusion. Apparently, however, the actual third moult of larvae of *Rhabdochona* spp. (Thelazioidea: Rhabdochonidae) has been observed in the intermediate host (Moravec 1972, 1976).

Larvae of *Cystidicola* spp. develop more slowly than other cystidicolids. Third-stage larvae of *C. cristivomeri* were recovered after eight weeks at 9 - 11^{o}C and after 17 weeks at 4 - 5^{o}C. *C. farionis* develops to the third-stage larva in five

to six weeks at 12 - 14°C. Larvae of *Cystidicoloides tenuissima* develop to the third-stage in about three weeks at 13 - 15°C and are infective to fish after 24 days (Moravec 1971). At 21 - 23°C, *Spinitectus micracanthus* develops to the third-stage larva in 20 days (Keppner 1975).

Encapsulation in the intermediate host does not occur consistently among members of the Cystidicolidae. Developing larvae of *Cystidicola farionis* are free in the haemocoel of amphipods and are not normally encapsulated. Third-stage larvae of *C. cristivomeri* in experimentally infected *M. relicta* were enclosed in thin capsules in muscles of pereiopods but larvae 5-10 mm long in naturally infected mysids were free in the haemocoel. Presumably the larvae break free of the capsules as a result of their great increase in size. Larvae of *Ascarophis* spp. are found within capsules in decapod crustaceans (Uzmann 1967, Poinar and Kuris 1975, Poinar and Thomas 1976). The capsules vary from being thin and fragile to thick and granular and are associated with various tissues including muscles of the thorax and legs, digestive organs and carapace. A larva of *Spinitectus* sp. described by Johnson (1966) from a decapod was not encapsulated. Larvae of *S. micracanthus* and *S. gracilis* Ward and Magath, 1917, in mayfly nymphs, on the other hand, do become encapsulated (Keppner 1975). The first-stage larva penetrates an abdominal muscle cell. After the cell ruptures, a thin fibrous capsule forms and increases in size as the larva grows. Larvae of *Cystidicoloides tenuissima*, also in mayfly nymphs, are not

encapsulated (Choquette 1955, Moravec 1971).

After being ingested by fish, *Cystidicola* spp. apparently migrate to the swim bladder as third-stage larvae. The larvae may migrate *via* the oesophagus and the pneumatic duct or may penetrate into the swim bladder after a direct migration through the wall of the gastro-intestinal tract. Larvae of *C. farionis* have been found both in the oesophagus of infected fish (Shipley 1908; Mueller 1940) and in the wall of the swim bladder (this study). The few larvae found in the bladder wall in lake whitefish may have been migrating directly from the digestive tract or may have penetrated the wall after arriving in the bladder *via* the pneumatic duct. The migration route followed by larvae to swim bladder remains unknown.

Pathological changes in the swim bladder have been associated with the presence of *Cystidicola* spp. Damage could result from worms feeding on tissues and fluids of the bladder wall. Margolis (1967a) found red blood cells in the intestine of *Salvelinema walkeri* (Ekbaum, 1935) Margolis, 1967, a cystidicolid nematode from the swim bladder of coho salmon, *Oncorhynchus kisutch* (Walbaum). Mucus is sometimes abundant in infected fish and could possibly impair the gas exchange involved in swim bladder function. Drew (1908) found inflammation and bacterial infection in the swim bladder of rainbow trout infected with *C. farionis*. A few lake trout infected with swim bladder worms had some haemorrhage from the bladder wall (MacLulich 1943). Awachie (1973) reported that the swim bladder of two brown trout, *Salmo trutta* Linnaeus,

infected with 15 and 21 *C. farionis* were "almost completely destroyed". Much heavier worm burdens have been found in many fish without evident pathology. Ulcerations of the swim bladder of Lake Superior fishes were seen most often in rainbow trout (Lankester, unpublished). Few lesions were seen in lake trout even though many fish were heavily infected with *C. cristivomeri*. However, ulcerations of the bladder wall were found in all 21 lake trout from Killala Lake. Some of the trout were heavily infected with *C. cristivomeri* but others had relatively few worms. It is interesting that these fish and most rainbow trout examined were taken near spawning time in shallow water. The role of the parasites in causing such lesions and the significance to the health of the fish must be examined under controlled experimental conditions.

Filaments occur on the eggs of *C. farionis* and other cystidicolid nematodes in the genera *Ascarophis*, *Metabronema*, *Pseudoproleptus*, *Salvelinema* and *Spinitectoides* (Rasheed 1965; Margolis 1967b; Petter 1969; Sey 1970). The filaments on *C. farionis* eggs and the floats on *C. cristivomeri* eggs are made of the same electron dense material, likely protein, as the outer layer of the shell, and are deposited on the surface of the egg as it moves down the uterus (Seabrook 1977). The number of filaments on *C. farionis* eggs is highly variable and consequently Ko and Anderson (1969) concluded that they are not a useful taxonomic character. Curiously, eggs of *C. farionis* have predominantly lateral filaments in lake whitefish and mainly

polar filaments in other hosts. This variation may reflect a genetic difference in the worms or may depend on the host species. The source of the variation could be investigated experimentally by infecting another fish host with larvae grown from whitefish material to determine if the arrangement of filaments changed. There is little information on the variation in filament number and arrangement on eggs of other cystidicolids.

The eggs are released from mature female worms in the swim bladder. They were found in mucus scraped from the inside of the swim bladder and in the intestine of infected fish (this study; Mueller 1940). Mueller suggested that many eggs remain in the bladder and are released upon death and disintegration of the fish. While this may not be an important means of transmission, any intermediate hosts that scavenged upon the fish remains could become heavily infected. Ordinarily, the eggs probably leave the swim bladder *via* the pneumatic duct and are voided with the faeces.

The function of the filaments and floats is open to speculation but they may facilitate consumption of the egg by the intermediate host. Filaments may prevent the eggs from sinking into soft bottom mud (Mueller 1940) or may attach them to vegetation, thus keeping them available to the intermediate host. The setose feeding appendages of crustaceans may more easily pick up eggs with filaments. The term "floats" for the structures on *C. cristivomeri* eggs is perhaps inappropriate as they do not provide flotation (Seabrook 1977). The presence of these structures rather than filaments is possibly related to differences in the

feeding habits of the intermediate hosts that transmit the two parasites to fish.

Brook trout and lake whitefish are new host records for *C. cristivomeri*. The parasite has been found previously only in lake trout (White 1941; White and Cable 1942; Ko and Anderson 1969; Dechtiar 1972) and arctic char, *Salvelinus alpinus* (Linnaeus) (Jamieson 1972; Beverly-Burton 1978; Eddy and Lankester *in press*). Lake whitefish are probably not a suitable host however, as only immature worms were found. Normal development of *C. cristivomeri* in fish apparently occurs only in *Salvelinus* spp.

The opossum shrimp, *M. relicta*, is a suitable experimental intermediate host for *C. cristivomeri* and it is naturally infected in a lake where the parasite is common in lake trout. In northwestern Ontario, *M. relicta* was present in the stomach of lake trout in many of the lakes where *C. cristivomeri* occurred but was not found in stomach samples where the parasite was absent. One exception was Sunset Lake where lake trout fed on *M. relicta* but *C. cristivomeri* was absent. Trout were not present in the lake prior to being stocked, however (pers. comm., R. Hamilton, Ministry of Natural Resources, Thunder Bay) and there are no connecting lakes with infected lake trout. *M. relicta* is present in all of the lakes in central Ontario from which Ko and Anderson (1969) reported *C. cristivomeri* in lake trout (Martin and Chapman 1965) and is absent from Opeongo Lake (Dadswell 1974) where the parasite was not found (Ko and Anderson 1969). Mysids are present in White Partridge Lake (Martin and Chapman 1965) where brook

trout have *C. cristivomeri*, and in Char Lake and Stanwell-Fletcher Lake, Northwest Territories, where arctic char are infected (Lasenby and Langford 1972; Beverly-Burton 1978; Eddy and Lankester *in press*). It would appear therefore, that *M. relicta* is the source of *C. cristivomeri* infection in fish in nature.

M. relicta inhabits deep cold lakes. They are usually within a few metres of the bottom during the day and migrate upward at night, often to the thermocline (Beeton 1960). Mysids consume a wide range of material depending on availability but tend to feed on benthic detritus in the daytime and on zooplankton and some algae at night (Lasenby and Langford 1973). Particles up to 70-μ in size are ingested. The eggs of *C. cristivomeri* measure 40-45 μ (White and Cable 1942; Ko and Anderson 1969) and are presumably ingested with bottom detritus. Reynolds and DeGraeve (1972) found most *M. relicta* at temperatures of 1 - 6°C. Larvae of *C. cristivomeri* develop slowly at these temperatures. The life span of *M. relicta*, often up to two years (Larkin 1948; Lasenby and Langford 1972; Carpenter *et al* 1974), is long enough however, to accommodate the slow development of the parasite. Mysids have been transplanted into several lakes as a food source for fish (Sparrow *et al* 1964; Linn and Frantz 1965; Schumacher 1966; Stringer 1967). The consequences of accidentally introducing *C. cristivomeri* with such transplants are not known, but pathogenicity may be more severe in fish not previously exposed to the parasite.

Infection of lake trout with *C. cristivomeri* obviously

depends upon the extent to which *M. relicta* is consumed. Several studies indicate that mysids are a common food of young lake trout smaller than about 30-cm, while older trout become piscivorous (Eschmeyer 1956; Rawson 1961; Dryer *et al* 1965; Wright 1968; Anderson and Smith 1971; Smith 1972). The intensity of *C. cristivomeri* in lake trout was very high in some northwestern Ontario lakes indicating extensive use of *M. relicta* in the diet. Eight trout from Wolotka Lake had 30-3000 *C. cristivomeri* with a mean of about 900 worms. By contrast 11 trout from Northern Light Lake had 2 - 10 *C. cristivomeri*. Anglers indicated that lake trout in Wolotka Lake were small but fairly abundant. The fish sampled were 0.2 - 0.6 kg in weight and 28 - 30 cm long. Only invertebrates including many mysids were found in the stomach. Lake trout from Northern Light Lake on the other hand, were larger (0.5 - 2.4 kg and 45 - 64 cm) and had fish in the stomach. Martin (1952, 1966) studied lakes in which the lake trout were small, slow growing and readily taken by anglers. Suitable forage fish were unavailable at crucial times in these lakes and the trout remained largely planktonivorous throughout their life. Presumably, if *M. relicta* is present where lake trout are largely planktonivorous, fish of all ages would consume mysids extensively. The very high intensities of *C. cristivomeri* such as found in Wolotka Lake would result. Lake trout in Flack Lake, the type locality of *C. cristivomeri*, are predominantly planktonivorous and fairly small (Purych 1977). White (1941) reported that all of 40 trout from this lake were heavily infected with up to 900 worms. Confirmation

that planktonivorous trout typically have high intensities of *C. cristivomeri* requires further data, especially relating intensity of infection to age of lake trout. If such information is available, *C. cristivomeri* may be a useful indicator of the feeding habits and size composition of lake trout populations.

Despite the presence of *M. relicta* in the Great Lakes (Carpenter *et al* 1974), *C. cristivomeri* has not been reported. No swim bladder worms were found in lake trout from South Bay and Lake Huron (this study; Bangham 1955). Lake trout from Lake Superior, most over 2-kg in weight, had only a few immature *C. farionis* (Lankester, unpublished). Since *M. relicta* is eaten extensively only by young lake trout (Dryer *et al* 1965; Anderson and Smith 1971), further sampling of smaller fish is required to firmly establish the absence of *C. cristivomeri* from the Great Lakes. It would be interesting to examine the "humper" lake trout from off-shore shoals in Lake Superior. These fish are small, slow growing and feed mainly on invertebrates including *M. relicta* (Lawrie and Rahrer 1973).

If *C. cristivomeri* is indeed absent from the Great Lakes, an explanation is not obvious. There is no indication that post-glacial dispersal could have excluded the parasite from these waters. Both *M. relicta* and lake trout colonized the Great Lakes area from southern refugia as the ice receded (Ricker 1959; Lindsey 1964; Khan and Qadri 1972; Dadswell 1974). The glacial immigrant fauna in Lake Huron and lakes in the Algonquin Park area originated from glacial Lake Algonquin during this time

(Martin and Chapman 1965). Lake Algonquin and other glacial lakes preceding the Great Lakes must have contained *C. cristivomeri* as the parasite is now present in many locations in the basins of these former lakes.

Lake trout populations in the Great Lakes were severely depleted after 1940 by lamprey predation and fishing pressure (Eschmeyer 1957; Berst and Spangler 1972; Smith 1972; Pycha and King 1975). If *C. cristivomeri* was present in original lake trout stocks it may have disappeared as the trout population declined nearly to extinction. Although lake trout in Lake Superior now contain only a few immature and inconspicuous *C. farionis*, Leidy (1886) found a large number of swim bladder nematodes in these fish prior to their decline. The worms had distinct characters "even generic" distinguishing them from *Ancyracanthus cystidicola*, a synonym of *C. farionis*, but these characters were not described. The presence of filaments on the eggs was not mentioned. It is tempting to speculate that the distinct characters to which Leidy (1886) referred were eggs with lateral floats rather than filaments, and that the worms were in fact *C. cristivomeri*.

Amphipods have generally been regarded as the intermediate host of *C. farionis*. This belief was based in part on the report by Bauer and Nikolskaya (1952) of a *C. farionis* larva in *P. affinis*, but their identification has now been rejected. Other reports of *C. farionis* larvae in amphipods seem to be correct however, and several species are suitable experimental hosts. Baylis (1931)

found larvae of *C. farionis* in 8 of over 130 *G. pulex* in a stream in Britain. Larvae also found in *G. pulex* in Britain by Rumpus (1973) were similar to *C. farionis* described by Baylis (1931) (pers. comm., A. Rumpus, Polytechnic of Central London, England). Awachie (1973) reported *C. farionis* larvae in *G. pulex* in Wales. These larvae were not described but likely were *C. farionis* since brown trout in the same section of stream had the parasite. Mamayev (1971) reported *C. farionis* larvae in *Anisogammarus* sp. in the Soviet Union but the identification cannot be confirmed since the larvae were not described.

Although several species of amphipods are suitable intermediate hosts for *C.farionis* all may not be equally important in the natural transmission of the parasite. Feeding habits and behaviour may make some amphipods more prone to ingesting the nematode eggs than others. The abundance and distribution of the various intermediate and definitive hosts will also determine which amphipods are exposed to nematode eggs voided from fish, and which amphipods are the important source of infection. Generally *Gammarus* spp. and *H. azteca* occur in shallow water and *P. affinis* in deep water. In South Bay *H. azteca* is most abundant at depths of 5 - 10 m and *G. fasciatus* to depths of 13-m (Cooper 1964). *P. affinis* is abundant from 10-m to the deepest part of South Bay. These amphipods are found at similar depths elsewhere in Lake Huron (Teter 1960) and in Lake Superior (Eddy 1943; Thomas 1966; Freitag *et al* 1976 and unpublished data).

The distribution of deep-water and shallow-water amphipods may overlap but *P. affinis* is most abundant beyond the depths of *Gammarus* spp. and *H. azteca*. Peak densities of *P. affinis* often occur at intermediate depths in its distribution (30 - 50 m) (Eggleton 1937; Eddy 1943; Henson 1966; Alley 1968).

The shallow water amphipods are generally associated with vegetation (Cooper 1964). The omnivorous *G. fasciatus* ingests living and dead plant and animal matter (Clemens 1950). *H. azteca* feeds on epiphytic growth on rooted plants, algae and detritus (Cooper 1965). These amphipods generally breed in the late spring and summer, are most abundant in summer and early fall and decline in numbers through the winter (Clemens 1950; Biette 1969; Bousefield 1973). The life span is about one year but those born early in the summer may mature, breed and die before winter. Cooper (1965) found two generations of *H. azteca* per year. Since these shallow-water amphipods have a life span of one year or less, the prevalence of *C. farionis* might be expected to fluctuate seasonally. Fluctuations in prevalence would also be expected in fish that become infected primarily from these amphipods. Prevalence of *C. farionis* in *G. pulex* examined by Awachie (1973) fluctuated seasonally, reaching highest levels in the winter. Prevalence in both the amphipod and brown trout in the stream was lowest during the summer.

P. affinis is the dominant benthic organism in the Great Lakes and has been found at densities up to 14,000/m^2 (Marzolf

1965a; Cook and Johnson 1974). In shallow water, *P. affinis* has a one year life cycle but lives two to three years in colder water at depths greater than about 20-m (Cooper 1964; Alley 1968). Seasonal fluctuations in the prevalence of *C. farionis* would not be expected. The amphipod presumably acquires eggs of *C. farionis* while ingesting material from the substrate in which it burrows (Marzolf 1965a). The diurnal vertical migration of *P. affinis* (Marzolf 1965b; Alley 1968) may be important in making infected amphipods available to pelagic fish. Only a small proportion of the amphipods may migrate on any night (Marzolf 1965b) but they occur at such high densities that substantial numbers may be available in the water column. The prevalence of *C. farionis* should be greater among the adults and sub-adults that migrate (Marzolf 1965b) than among younger *P. affinis*.

Bloater inhabit the Great Lakes at depths of 18 - 165 m and are most abundant deeper than 50-m (Dryer 1966; Lawrie and Rahrer 1973). Swim bladder worms were not found in bloater from South Bay (this study; Bangham 1955) but those from Lake Superior were heavily infected with *C. farionis*. Since bloater rarely, if ever, move into the depths inhabited by the shallow-water amphipods, the parasite is likely acquired solely from *P. affinis*. This amphipod appears in the diet of bloater longer than 18 - 20 cm when the fish becomes a bottom feeder and increases in importance in the diet of larger fish (Bersamin 1958; Wells and Beeton 1963; Dryer and Beil 1968; Anderson and Smith 1971).

Infected bloater from Lake Superior were 24 - 31 cm long. The one uninfected bloater, 20-cm long, was probably too small to consume *P. affinis* extensively.

Lake herring from Lake Superior were commonly infected with *C. farionis*. Warren (1951) found 114 of 200 (57%) lake herring also from Lake Superior infected with 1 - 632 *C. farionis* (mean 35.2).[1] The parasite was found in a small proportion of lake herring from Lake Huron (Bangham 1955; Ko and Anderson 1969). Lake herring are pelagic in midwater depths for much of the year but collect in dense schools at depths of 5 - 11 m in mid-October prior to spawning (Dryer and Beil 1964; Lawrie and Rahrer 1973; Scott and Crossman 1973). Their food consists largely of plankton although many items including amphipods are consumed. Approximately similar proportions of immature worms are present in lake herring from Lake Superior in May and June as in the fall (Lankester, unpublished). Thus, recruitment of *C. farionis* does not appear to occur exclusively in the fall from shallow-water amphipods. The majority of worms is likely acquired from *P. affinis* taken as plankton during their vertical migration. Alternatively, lake herring may consume more benthos than is commonly believed and ingest infected *P. affinis* near the bottom.

Lake whitefish from South Bay and Lake Huron were frequently infected with *C. farionis* although Bangham (1955) found the parasite

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[1] Warren (1951) reports in text that 144 lake herring were infected but raw data given in an appendix indicate that 114 were infected.

in only 12 of 61 (20%) lake whitefich from South Bay. Lankester (unpublished) has found *C. farionis* in whitefish in Lake Superior. Lake whitefish are found in water as shallow as 3 - 9 m in the spring and before spawning in the fall but move into deeper water in the summer (Koelz 1929; Spangler 1970; Scott and Crossman 1973). The diet of the bottom-feeding lake whitefish depends on the availability of food items. Amphipods, especially *P. affinis*, are often used heavily Koelz 1929; Hart 1931; Anderson and Smith 1971). The movements of the fish are such that both *P. affinis* and shallow-water amphipods may be involved in the transmission of *C. farionis*. The proportion of immature *C. farionis* in lake whitefish taken in both deep and shallow water of South Bay and Lake Huron did not vary appreciably from June through September. Only immature worms were found in lake whitefish from Lake Superior during the spring. The worms may be acquired from shallow-water amphipods at that time. Fish examined in November had some mature worms, suggesting that a seasonal cycle of infection occurs. Leong (1975) and Watson (1977) speculated that seasonal cycles of *C. farionis* in lake whitefish in Cold Lake, Alberta and Southern Indian Lake, Manitoba resulted from lowered resistance of the fish hosts at low temperatures. Abundance of the parasite (defined as prevalence x intensity) was highest in winter and lowest in summer.

Changes in the intensity of *C. farionis* with age in lake whitefish in South Bay likely reflect changes in the diet of the host. Young-of-the-year whitefish are primarily planktonivorous, ingesting copepods and cladocerans, but gradually switch to a diet of small benthic organisms (Reckahn 1970). Larger organisms

such as *P. affinis* are included in the diet as the fish grows. The *P. affinis* first eaten are smaller and represent a younger age class than those eaten by older fish (Cooper 1964; Reckahn 1970). Thus the intensity of *C. farionis* in lake whitefish increases as the diet gradually changes to include the older amphipods that likely are more frequently infected with larvae. As well, larger fish will eat greater numbers of amphipods. Changes in the diet likely depend on the size of the fish rather than the age. In the smaller lake whitefish in the inner basin of South Bay, the changes in the diet and the corresponding increase in intensity of *C. farionis* occurs at a later age than in fish from the outer basin. In Cold Lake and Southern Indian Lake, both the prevalence and intensity of *C. farionis* and the comsumption of amphipods increased with age of lake whitefish (Leong 1975; Watson 1977). The parasite fauna of *Coregonus lavaretus* (Linnaeus) in Lake Ladoga, USSR also changed with age and diet (Bauer and Nikolskaya 1957). Parasites transmitted by copepods were dominant in fish up to two years old. After that age parasites transmitted by amphipods were gradually acquired. A few *C. lavaretus* two and three years old were infected with *C. farionis* and the parasite was common in older fish.

Many of the salmonids introduced into the Great Lakes have become infected with *C. farionis* including the hybrid splake (this study; Collins and Dechtiar 1974). Rainbow trout in Lake Superior usually have mature *C. farionis* but Ko and Anderson (1969)

found only immature worms in this host in Lake Huron. The parasite also occurs in Pacific salmon in the Great Lakes including coho, chinook, *O. tshawytscha* (Walbaum), and pink salmon, *O. gorbuscha* (Walbaum), in Lake Superior (Lankester, unpublished) and kokanee salmon, *O. nerka* (Walbaum), in Lake Huron (Collins and Dechtiar 1974). Another introduced fish,rainbow smelt, *Osmerus mordax* (Mitchill), is infected with *C. farionis* in the Great Lakes (Fischthal 1952; Nordlie 1960; Collins and Dechtiar 1974) but few mature worms have been found (Lankester, unpublished). Rainbow smelt is one of the few non-salmonid hosts of *C. farionis*.

The distribution and food habits of the exotic salmonids are not well known. The presence of *C. farionis*, sometimes in large numbers, suggests that amphipods are important in the diet. Rainbow trout consume a wide variety of food, switching as they grow from plankton to benthic invertebrates and to fish (Scott and Crossman 1973). Larger crustaceans such as amphipods are a main part of the benthic diet. Rainbow trout in Lake Superior do not move far into deep water (Eddy 1943) and probably become infected at least in part from shallow-water amphipods. The small size of pink salmon in Lake Superior and their absence from bottom nets indicate that they are pelagic and planktonivorous (Lawrie and Rahrer 1973). These fish are potential competitors with lake herring and similarly would acquire *C. farionis* from *P. affinis* in the water column. Kokanee salmon are also pelagic but may consume significant amounts of benthic organisms (Scott and

Crossman 1973). A large part of the diet of coho salmon in the Great Lakes consists of alewife and smelt (Harney and Norden 1972; Scott and Crossman 1973) but coho smaller than 30-cm in Lake Superior feed mainly on insects and crustaceans (McKnight and Serns 1974). Some larvae could presumably be acquired by salmon from infected amphipods in the stomach of prey fish. Smelt eaten by the salmon are infected largely with immature *C. farionis*. It is not known if these worms would still be capable of migrating to the swim bladder in the salmon.

Ideally, the infections of *C. farionis* in all definitive hosts from a particular location should be considered when determining the amphipod of importance in natural transmission. The studies of parasites of fishes of Cold Lake (Leong 1975) and Southern Indian Lake (Watson 1977) provide such information. Leong (1975) suggests that *Gammarus lacustris* Sars acts as the intermediate host for *C. farionis* in Cold Lake. Lake herring had only a few immature *C. farionis* and the worms in lake whitefish apparently matured in the spring and the summer. According to Leong, *G. lacustris* would become infected at this time. The parasites would develop in the intermediate host during the summer and re-infect lake whitefish in the fall. Larvae of *C. farionis* were present in whitefish throughout the year, however, and likely were not acquired exclusively in the fall from *G. lacustris*. Stomach contents of lake whitefish and lake herring contained approximately similar proportions of *G. lacustris*, but lake

whitefish consumed more *P. affinis* and were more frequently infected with *C. farionis*. Coho salmon had been introduced into Cold Lake. Two year old fish had no *C. farionis* but some three year old fish were infected (Leong 1975). Stomach contents of coho indicated that the consumption of *P. affinis* increased over that age interval while the consumption of *G. lacustris* declined. Thus *P. affinis* may be more important than *G. lacustris* in the transmission of *C. farionis* in Cold Lake.

Watson (1977) suggests that *Gammarus* sp. is the intermediate host for *C. farionis* in Southern Indian Lake. The parasite was found in lake whitefish but not in lake herring. Both fishes had eaten *H. azteca* and *P. affinis* but only whitefish had eaten *Gammarus* sp. Less than 1% of lake herring stomachs contained any amphipod, however, and the abundance of other parasites with amphipod intermediate hosts was low. The absence of *C. farionis* from lake herring could result from the low consumption of all amphipods and not just *Gammarus* sp. Thus none of the amphipods can be ruled out as a source of *C. farionis* for lake whitefish in Southern Indian Lake.

In many cases the prevalence of *C. farionis* in lake whitefish seems to have no relation to that in other definitive hosts. Lake whitefish are commonly infected in South Bay but no swim bladder worms were found in bloater. Many species of fish in Lake Superior are infected with fairly large numbers of *C. farionis* but lake whitefish have few worms and mature worms

are not common. Lake whitefish in Cold Lake and Southern Indian Lake are infected with *C. farionis* but only a few immature worms are found in lake herring in Cold Lake and none in Southern Indian Lake. *C. farionis* in lake whitefish is also distinguished by the arrangement of filaments on the eggs. There is insufficient evidence, however, to suggest that the worms in lake whitefish are a separate species. The differences in prevalence of *C. farionis* in the various fishes are probably best explained through feeding habits. The infectivity of *C. farionis* to various amphipods did not seem to depend on the source of the eggs. The possibility that the worms in lake whitefish are genetically distinct should nevertheless be recognized in future work.

More information from both field and laboratory study is required to completely understand the natural transmission of *Cystidicola* spp. and to justify certain assumptions. Amphipods are suitable intermediate hosts for *C. farionis* and *M. relicta* for *C. cristivomeri*. The distribution of these crustaceans will potentially expose them to eggs of *Cystidicola* spp. and natural infections have been found. The diets of the definitive hosts of *Cystidicoa* spp. include these crustaceans. Almost certainly these crustaceans act as intermediate hosts for the parasites in the wild. Larval development of *C. farionis* and *C. cristivomeri* is likely restricted to amphipods and mysids respectively but this host specificity remains to be tested.

Data on the prevalence of infection in the intermediate

hosts is needed. Seasonal fluctuations in prevalence should be considered in relation to movements and feeding habits of the definitive host, especially for *C. farionis*. The shallow-water amphipods seem to have a more definite seasonal association with definitive hosts than does *P. affinis*, and may have a more pronounced seasonal cycle of infection with *C. farionis*. Similar fluctuations would probably be found in fish that become infected primarily from these amphipods. Lake whitefish have more contact with the shallow-water amphipods than other fish hosts and often exhibit seasonal cycles of *C. farionis*. The prevalence of infection in amphipods is expected to increase with age. Prevalence in *P. affinis* may differ between the older amphipods in the water column that are available to pelagic fish and those on the bottom that are exploited by benthic feeders. It would be interesting to compare the prevalence of infection of *C. cristivomeri* in *M. relicta* between lakes with piscivorous lake trout and those with planktonivorous trout.

Development of the parasites in the definitive hosts must be studied in order to accurately assess data from natural infections. The presence of immature worms in fish is interpreted here as indicating recent infection. This conclusion will not be valid if the worms develop slowly, mature on a seasonal basis or if development is delayed when many worms are present (a "crowding effect"). The life span of *Cystidicola* spp. in fish must also be determined. Margolis (1967b) found the related swim

bladder nematode *Salvelinema salmonicola* (Ishii,1916) Margolis,1966, in a sockeye salmon, *O. nerka*, that had been at sea for almost three years. The worms were acquired in fresh water and thus were at least three years old. Apparent annual cycles of *C. farionis* in some fish suggest that the life span is one year or less. The rate of development and life span of the worms may vary in different fish.

When several species of hosts are present, as in the Great Lakes, analysis of the transmission of the parasite should consider the community of hosts. A particular species of fish can become infected from one or several species of amphipods. These in turn may have ingested nematode eggs released from several fish species. Thus the infection found in one host species will be dependent on the infections in other hosts. Leong (1975) provides this kind of community analysis of the transmission of *Metechinorhynchus salmonis* (Muller) (Acanthocephala) among fishes in Cold Lake.

LITERATURE CITED

Alley, W. P. 1968. Ecology of the burrowing amphipod *Pontoporeia affinis* in Lake Michigan. Univ. Mich. Great Lakes Res. Div. Spec. Rep. 36. Ann Arbor.

Anderson, E. D. and L. L. Smith, Jr. 1971. A synoptic study of food habits of 30 fish species from western Lake Superior. Univ. Minn. Agric. Exp. Stn. Tech. Bull. 279.

Anderson, R. C. 1958. Methode pour l'examen des nematodes en vue apicale. Ann. Parasitol. Hum. Comp. 33: 171-172.

Arthur, J. R., L. Margolis and H. P. Arai. 1976. Parasites of fishes of Aishihik and Stevens Lakes, Yukon Territory, and potential consequences of their interlake transfer through a proposed water diversion for hydroelectrical purposes. J. Fish. Res. Board Can. 33: 2489-2499.

Awachie, J. B. E. 1973. Ecological observations on *Metabronema truttae* Baylis, 1935, and *Cystidicola farionis* Fischer v. Waldheim, 1798 (Nematoda, Spiruroidea) in their intermediate and definitive hosts, in Afon Terrig. Acta Parasitol. Pol. 21: 661-670.

Bangham, R. V. 1955. Studies on fish parasites of Lake Huron and Manitoulin Island. Am. Midl. Nat. 53: 184-194.

Bauer, O. N. and N. P. Nikolskaya. 1952. New data on the intermediate hosts of parasites of whitefish. (In Russian). Dokl. Akad. Nauk SSSR 84: 1109-1112. (Partial transl. by E. Jermolajev, in J. Budd Mem. Libr., Min. Nat. Res. Fish. Res. Stn., South Baymouth Ont.)

Bauer, O. N. and N. P. Nikolskaya. 1957. Dynamics of the parasitofauna of the whitefish *Coregonus lavaretus* from Lake Ladoga and its epizootic importance. Bull. All-Union Sci. Res. Inst. Fresh-Water Fish. 42. Parasites and diseases of fish. Transl. Isr. Prog. Sci. Transl., 1961. pp 224-238.

Baylis, H. A. 1931. *Gammarus pulex* as an intermediate host for trout-parasites. Ann. Mag. Nat. Hist. 7: 431-435.

Beeton, A. M. 1960. The vertical migration of *Mysis relicta* in Lakes Huron and Michigan. J. Fish. Res. Board Can. 17: 517-539.

Bersamin, S. V. 1958. A preliminary study of the nutritional ecology and food habits of the chubs (*Leucichthys* spp.) and their relation to the ecology of Lake Michigan. Pap. Mich. Acad. Sci. Arts Lett. 43: 107-118.

Berst, A. H. and G. R. Spangler. 1972. Lake Huron: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 877-887.

Beverly-Burton, M. 1978. Metazoan parasites of arctic char (*Salvelinus alpinus* L.) in a high arctic landlocked lake in Canada. Can. J. Zool. 56: 365-368.

Biette, R. M. 1969. Life history and habitat differences between *Gammarus lacustris lacustris* Sars and *Hyalella azteca* (Saussure) in West Blue Lake, Manitoba. M. Sc. thesis, University of Manitoba, Winnipeg.

Bousefield, E. L. 1973. Shallow-water gammaridean amphipods of New England. Cornell University Press, Ithaca N.Y.

Budd, J. 1957. Movements of tagged whitefish in northern Lake Huron and Georgian Bay. Trans. Am. Fish Soc. 86: 128-134.

Campana-Rouget, Y. 1955. Sur deux nouveaux genres de spirurides parasites de poissons; discussion systematique des genres voisins. Ann. Parasitol. Hum. Comp. 30: 346-362.

Carpenter, G. F., E. L. Mansey and N. H. F. Watson. 1974. Abundance and life history of *Mysis relicta* in the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 319-325.

Chabaud, A. G. 1975a. Keys to the genera of the Order Spirurida. Part 1. Camallanoidea, Dracunculoidea, Gnathostamatoidea, Physalopteroidea, Rictularioidea and Thelazioidea. *In* CIH keys to the nematode parasites of vertebrates. *Edited by* R. C. Anderson, A. G. Chabaud and S. Wilmott. Commonwealth Agricultural Bureaux, Farnham Royal, Bucks, England. No. 3: 1-28.

Chabaud, A. G. 1975b. Keys to the genera of the Order Spirurida. Part 2. Spiruroidea, Habronematoidea and Acuarioidea. *In* CIH keys to the nematode parasites of vertebrates. *Edited by* R. C. Anderson, A. G. Chabaud and S. Wilmott. Commonwealth Agricultural Bureaux, Farnham Royal, Bucks, England. No. 3: 29-58.

Choquette, L. P. E. 1955. The life history of the nematode *Metabronema salvelini* (Fujita, 1920) parasitic in the speckled trout, *Salvelinus fontinalis* (Mitchill), in Quebec. Can. J. Zool. 33: 1-4.

Christian, F. A. 1972. *Spinitectus micracanthus* sp. n. (Nematoda: Rhabdochonidae) from the bluegill, *Lepomis macrochirus* Rafinesque, in Ohio. Proc. Helminthol Soc. Wash. 39: 51-54.

Clemens, H. P. 1950. Life cycle and ecology of *Gammarus fasciatus* Say. Stone Inst. Hydrobiol. Contr. 12. Ohio State University.

Collins, J. J. and A. O. Dechtiar. 1974. Parasite fauna of kokanee salmon (*Oncorhynchus nerka*) introduced into Lake Huron. J. Fish. Res. Board Can. 31: 1818-1821.

Cook, D. G. and M. G. Johnson. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 763-782.

Cooper, J. E. K. 1964. The bottom fauna of South Bay, Lake Huron. M.A. thesis, University of Toronto, Toronto.

Cooper, W. E. 1965. Dynamics and production of a natural population of a fresh-water amphipod, *Hyalella azteca*. Ecol. Monogr. 35: 377-394.

Dadswell, M. J. 1974. Distribution, ecology, and postglacial dispersal of certain crustaceans and fishes in eastern North America. Nation. Mus. Nat. Sci. Publ. Zool. 11. National Museums of Canada, Ottawa.

Dechtiar, A. O. 1972. Parasites of fish from Lake of the Woods, Ontario. J. Fish. Res. Board Can. 29: 275-283.

Dollfus, R. P. and Y. Campana-Rouget. 1956. Une nouvelle espece d'*Ascarophis* (Nematoda, Spirurinae) chez *Gadus luscus* L. Revision du genre. Ann. Parasitol. Hum. Comp. 31: 385-404.

Drew, G. H. 1908. Some notes on parasitic and other diseases of fish. Parasitology 2: 195-197.

Dryer, W. R. 1966. Bathymetric distribution of fish in the Apostle Islands region, Lake Superior. Trans. Am. Fish. Soc. 95: 248-259.

Dryer, W. R. and J. Beil. 1964. Life history of lake herring in Lake Superior. U.S. Fish Wildl. Serv. Fish. Bull. 63: 493-530.

Dryder, W. R. and J. Beil. 1968. Growth changes of the bloater (*Coregonus hoyi*) of the Apostle Islands region of Lake Superior. Trans. Am. Fish. Soc. 97: 146-158.

Dryder, W. R., L. F. Erkkila and C. L. Tetzloff. 1965. Food of lake trout in Lake Superior. Trans. Am. Fish. Soc. 94: 169-176.

Eddy, S. 1943. Limnological notes on Lake Superior. Proc. Minn. Acad. Sci. 11: 34-39.

Eddy, S. B. and M. W. Lankester. Feeding and migratory habits of Arctic char indicated by the presence of the swim bladder nematode, *Cystidicola cristivomeri* White, 1941. J. Fish. Res. Board Can. *in press*.

Eggleton, F. E. 1937. Productivity of the profundal benthic zone in Lake Michigan. Pap. Mich. Acad. Sci. Arts Lett. 21: 593-612.

Eschmeyer, P. H. 1956. The early life history of lake trout in Lake Superior. Mich. Dept. Conserv. Inst. Fish. Res. Misc. Publ. 10. Ann Arbor.

Eschmeyer, P. H. 1957. The near extinction of lake trout in Lake Michigan. Trans. Am. Fish. Soc. 85: 102-119.

Fischthal, J. H. 1952. Parasites of northwest Wisconsin fishes. III. The 1946 survey. Trans. Wisc. Acad. Sci. Arts Lett. 41: 17-58.

Freitag, R., P. Fung, J. S. Mothersill and G. K. Prouty. 1976. Distribution of benthic macroinvertebrates in Canadian waters of northern Lake Superior. J. Great Lakes Res. 2: 177-192.

Harney, M. A. and C. R. Norden. 1972. Food habits of the coho salmon, *Oncorhynchus kisutch*, in Lake Michigan. Trans. Wisc. Acad. Sci. Arts Lett. 60: 79-85.

Hart, J. L. 1931. The food of the whitefish *Coregonus clupeaformis* (Mitchill) in Ontario waters, with a note on the parasites. Contr. Can. Biol. Fish. 6(21): 445-454.

Henson, E. B. 1966. A review of Great Lakes benthos research. Univ. Mich. Great Lakes Res. Div. Publ. 14: 37-54.

Jamieson, J. L. 1972. Parasites of *Salvelinus alpinus* (Salmonidae) in the northern Foxe Basin, Northwest Territories, with emphasis on those of medical importance. M. Sc. thesis, University of Toronto, Toronto.

Johnson, S. 1966. On a *Spinitectus* larva (Spiruroidea: Nematoda) from a shrimp (Crustacea) in India. Ind. J. Helminthol. 18: 49-52.

Keppner, E. J. 1975. Life cycle of *Spinitectus micracanthus* Christian, 1972 (Nematoda: Rhabdochonidae) from the bluegill, *Lepomis macrochirus* Rafinesque, in Missouri with a note on *Spinitectus gracilis* Ward and Magath, 1917. Am. Midl. Nat. 93: 411-423.

Khan, N. Y. and S. U. Qadri. 1971. Intraspecific variations and postglacial distribution of lake char (*Salvelinus namaycush*). J. Fish. Res. Board Can. 28: 465-476.

Ko, R. C. and R. C. Anderson. 1969. A revision of the genus *Cystidicola* Fischer, 1798 (Nematoda: Spiruroidea) of the swim bladder of fishes. J. Fish. Res. Board Can. 26: 849-864.

Koelz, W. 1929. Coregonid fishes of the Great Lakes. Bull. U.S. Bur. Fish. 43 (1927), doc. 10: 297-643.

Larkin, P. A. 1948. *Pontoporeia* and *Mysis* in Athabaska, Great Bear and Great Slave Lakes. Bull. Fish. Res. Board Can. 88: 1-33.

Lasenby, D. C. and R. R. Langford. 1972. Growth, life history, and respiration of *Mysis relicta* in an arctic and temperate lake. J. Fish. Res. Board Can. 29: 1701-1708.

Lasenby, D. C. and R. R. Langford. 1973. Feeding and assimilation of *Mysis relicta*. Limnol. Oceanogr. 18: 280-285.

Lawler, G. H. 1970. Parasites of coregonid fishes. *In* Biology of coregonid fishes. *Edited by* C. C. Lindsey and C. S. Woods. University of Manitoba Press, Winnipeg. pp. 279-309.

Lawrie, A. H. and J. F. Rahrer. 1973. Lake Superior. A case history of the lake and its fisheries. Great Lakes Fish. Comm. Tech. Rep. 19. Ann Arbor.

Leidy, J. 1886. Notices of nematoid worms. Proc. Acad. Nat. Sci. Phil. 38: 308-313.

Leong, R. T. S. 1975. Metazoan parasites of fishes of Cold Lake, Alberta: a community analysis. Ph.D. thesis, University of Alberta, Edmonton.

Lindsey, C. C. 1964. Problems in zoogeography of the lake trout, *Salvelinus namaycush*. J. Fish. Res. Board Can. 21: 977-994.

Linn, J. D. and T. C. Frantz. 1965. Introduction of the opossum shrimp (*Mysis relicta* Loven) into California and Nevada. Calif. Fish Game 51: 48-51.

MacLulich, D. A. 1943. Parasites of trout in Algonquin Provincial Park, Ontario. Can. J. Res., Sect. D 21: 405-412.

Mamayev, Y. L. 1971. Helminth larvae in fresh-water crustaceans in the Primorsk Region. (In Russian). *In* Parazity zhivotnykh i rastenii dal'nego vostoka. Dal'nevostochnoe knizhnoe Izdatel'stro, Vladivostok USSR. pp. 120-132.

Margolis, L. 1967a. Blood feeding in *Salvelinema walkeri* (Nematoda: Cystidicolinae), a parasite of coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 45: 1295-1296.

Margolis, L. 1967b. The swim bladder nematodes (Cystidicolinae) of Pacific salmons (genus *Oncorhynchus*). Can. J. Zool. 45: 1183-1199.

Martin, N. V. 1952. A study of the lake trout, *Salvelinus namaycush*, in two Algonquin Park, Ontario, lakes. Trans. Am. Fish. Soc. 81: 111-137.

Martin, N. V. 1966. The significance of food habits in the biology, exploitation, and management of Algonquin Park, Ontario, lake trout. Trans. Am. Fish. Soc. 95: 415-422.

Martin, N. V. and L. J. Chapman. 1965. Distribution of certain crustaceans and fishes in the region of Algonquin Park, Ontario. J. Fish. Res. Board Can. 22: 969-976.

Marzolf, G. R. 1965a. Substrate relations of the burrowing amphipod *Pontoporeia affinis* in Lake Michigan. Ecology 46: 579-591.

Marzolf, G. R. 1965b. Vertical migration of *Pontoporeia affinis* (Amphipoda) in Lake Michigan. Univ. Mich. Great Lakes Res. Div. Publ. 13: 133-140.

McKnight, T. C. and S. L. Serns. 1974. Food habits of coho salmon (*Oncorhynchus kisutch*) in an inland Wisconsin Lake. Trans. Am. Fish. Soc. 103: 126-130.

Moravec, F. 1971. Studies on the development of the nematode *Cystidicoloides tenuissima* (Zeder, 1800). Vestn. Ceskoslov. Spol. Zool. 35: 43-55.

Moravec, F. 1972. Studies on the development of the nematode *Rhabdochona (Filochona) ergensi* Moravec, 1968. Folia Parasitol. 19: 321-333.

Moravec, F. 1976. Observations on the development of *Rhabdochona phoxini* Moravec, 1968 (Nematoda: Rhabdochonidae). Folia Parasitol. 23: 309-320.

Moravec, F. and R. Ergens. 1970. Nematodes from fishes and cyclostomes of Mongolia. Folia Parasitol. 17: 217-232.

Mueller, J. F. 1940. Parasitism and disease in fishes of the Lake Ontario watershed. *In* A biological survey of the Lake Ontario watershed. N.Y. Conserv. Dept. Ann. Rep. 29 (Supplement): 211-225.

Nordlie, F. 1960. Some ecological aspects of the helminth parasitism of the American smelt, *Osmerus mordax* (Mitchell). Proc. Minn. Acad. Sci. (1957-58) 25-26: 239-241.

Petter, A. J. 1969. Enquete sur les nematodes des poissons de la region nantaise. Ann. Parasitol. Hum. Comp. 45: 559-580.

Petter, A. J. 1970. Quelques spirurides de poissons de la region nantaise. Ann. Parasitol. Hum. Comp. 45: 31-46.

Poinar, Jr., G. O. and A. M. Kuris. 1975. Juvenile *Ascarophis* (Spirurida: Nematoda) parasitizing intertidal decapod crustacea in California: with notes on prevalence and effects on host growth and survival. J. Invert. Pathol. 26: 375-382.

Poinar, Jr., G. O. and G. M. Thomas. 1976. Occurrence of *Ascarophis* (Nematoda: Spiruridea) in *Callianassa californiensis* Dana and other decapod crustaceans. Proc. Helminthol. Soc. Wash. 43: 28-33.

Purych, P. R. 1977. A case against stocking. Ontario Fish Wildl. Rev. 16(2): 3-5.

Pycha, R. L. and G. R. King. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950-70. Great Lakes Fish. Comm. Tech. Rep. 28. Ann Arbor.

Rasheed, S. 1965. Observations on the spiruroid nematodes of fish with a revision of the genus *Metabronema* Yorke and Maplestone, 1926. Zeit. Zool. Syst. Evol. 3: 359-387.

Rawson, D. S. 1961. The lake trout of Lac la Ronge, Saskatchewan. J. Fish. Res. Board Can. 18: 423-462.

Reckahn, J. A. 1970. Ecology of young lake whitefish in Lake Huron. *In* Biology of coregonid fishes. *Edited by* C. C. Lindsey and C. S. Woods. University of Manitoba Press, Winnipeg. 437-460.

Reynolds, J. B. and G. M. DeGraeve. 1972. Seasonal population characteristics of the opossum shrimp, *Mysis relicta*, in southeastern Lake Michigan, 1970-71. Intern. Assoc. Great Lakes Res., Proc. 15th Conf. Great Lakes Res: 117-131.

Ricker, K. E. 1959. The origin of two glacial relict crustaceans in North America, as related to Pleistocene glaciation. Can. J. Zool. 37: 871-893.

Rumpus, A. E. 1973. The ecology of the parasites of *Gammarus pulex* in the River Avon, Hamphire. Ph.D. thesis, University of Exeter, Exeter.

Schumacher, R. E. 1966. Successful introduction of *Mysis relicta* (Loven) into a Minnesota Lake. Trans. Am. Fish. Soc. 95: 216.

Scott, W. B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184. Ottawa.

Seabrook, R. G. 1977. An examination of the eggs of swimbladder nematodes, *Cystidicola* spp. Fischer, 1798, using the transmission and scanning electron microscope. Hon. B.Sc. thesis, Lakehead University, Thunder Bay.

Sey, O. 1970. *Collarinema triglae* gen. et sp. nov. (Nematoda: Rhabdochonidae) from the red gurnard (Trigla lyra L.) in the Adriatic Sea, Yugoslavia. Acta Zool. Acad. Scient. Hungar. 16: 209-214.

Shipley, A. E. 1908. Note on *Cystidicola farionis* Fischer. A threadworm parasitic in the swim bladder of a trout. Parasitology 1: 190-192.

Skrjabin, K. I., A. A. Sobolev and V. M. Ivaskin. 1967. Spirurata of animals and man and the diseases caused by them. Part 4. Thelazioidea. Essentials of nematodology 16. Transl. by Isr. Progr. Sci. Transl. 1971.

Smith, S. H. 1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 717-730.

Spangler, G. 1970. Factors of mortality in an exploited population of whitefish *Coregonus clupeaformis*, in northern Lake Huron. *In* Biology of coregonid fishes. *Edited by* C. C. Lindsey and C. S. Woods. University of Manitoba Press, Winnipeg.

Sparrow, R. A., P. A. Larkin and R. A. Rutherglen. 1964. Successful introduction of *Mysis relicta* in Kootenay Lake, British Columbia. J. Fish. Res. Board Can. 21: 1325-1327.

Stringer, G. E. 1967. Introduction of *Mysis relicta* Loven into Kalamalka and Pinaus Lakes, British Columbia. J. Fish. Res. Board Can. 24: 463-465.

Teter, H. E. 1960. The bottom fauna of Lake Huron. Trans. Am. Fish. Soc. 89: 193-197.

Thomas, M. L. H. 1966. Benthos of four Lake Superior bays. Can. Field-Nat. 80: 200-212.

Tsimbalyuk, E. M., V. V. Kulikov and A. K. Tsimbalyuk. 1970. A contribution to the biology of *Ascarophis pacificus* (Nematoda, Ascarophididae). (In Russian). Zool. Zhurn. 49: 1874-1875.

Uspenskaja, A. V. 1953. Life cycles of nematodes of the genus *Ascarophis* van Beneden (Nematoda - Spirurata). (In Russian). Zool. Zhurn. 32: 828-832.

Uzmann, J. R. 1967. Juvenile *Ascarophis* (Nematoda: Spiruroidea) in the American lobster, *Homarus americanus*. J. Parasitol. 53: 218.

Warren, B. H. 1951. Metazoan parasites of the lake herring, *Leucichthys artedi* Leseuer 1818, from the north shore of Lake Superior. M.Sc. thesis, University of Minnesota, Minneapolis.

Watson, R. A. 1977. Metazoan parasites from whitefish, cisco and pike from Southern Indian Lake, Manitoba: a preimpoundment and diversion analysis. M.Sc. thesis, University of Manitoba, Winnipeg.

Wells, L. and A. M. Beeton. 1963. Food of the bloater, *Coregonus hoyi*, in Lake Michigan. Trans. Am. Fish. Soc. 92: 245-255.

White, F. M. 1941. Studies on the morphology of *Cystidicola cristivomeri* sp. nov. (Nematoda: Thelaziidae), from the swim bladder of the lake trout. Proc. Indiana Acad. Sci. 50: 211.

White, F. M. and R. M. Cable. 1942. Studies on the morphology of *Cystidicola cristivomeri* sp. nov. (Nematoda: Thelaziidae) from the swim bladder of the lake trout, *Cristivomer namaycush* (Walbaum). Am. Midl. Nat. 28. 416-423.

Wright, K. J. 1968. Feeding habits of immature lake trout (*Salvelinus namaycush*) in the Michigan waters of Lake Michigan. M.Sc. thesis, Michigan State University, Ann Arbor.