BULLETIN NO. 95

A Review of the Triaenophorus Problem in Canadian Lakes

BY

R. B. MILLER
University of Alberta, Edmonton

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ABSTRACT

Triaenophorus crassus is a tapeworm which, in one of its immature stages, is very common in the flesh of whitefishes in Canadian lakes. Here it appears as a yellowish cyst about a half-inch long, filled with a viscous yellow fluid and a long, coiled, thin worm. These cysts, while harmless to man and animals, are objectionable in appearance and, when numerous, render the fish unmarketable.

The adult tapeworm lives in the intestine of the northern pike. Here it matures and releases its eggs in the spring. The eggs hatch in the water and infect minute crustaceans called *Cyclops*. Infected *Cyclops*, when eaten by whitefish or lake herrings (ciscoes), carry the parasites to these fish, where they develop into the cysts. The life-cycle is completed when a pike swallows a fish containing one or more of the cysts. Certain details of the life-cycle remain to be thoroughly worked out.

A search for methods of control of this parasite is being conducted by the Central Fisheries Research Station and also by the governments of Ontario and the Prairie Provinces. Reduction or elimination of the final host, the pike, has proven to be too expensive to be practical. Reduction of ciscoes has brought good results in one lake in Alberta, but it is uncertain if the method provides a lasting cure or that it will work in other lakes. Control of the short-lived, free-swimming tapeworm larvae, immediately after hatching, is being studied in laboratory cultures, and two field tests of this method have been made. It has become obvious that control, if it ever comes, will be only after a period of long and patient research on the life-history of the parasite, its relationship to the environment and its hosts and the interrelationships of the various hosts. Meanwhile the Dominion Department of Fisheries operates a Canada-wide whitefish inspection designed to control the production of infected fish.

I. INTRODUCTION

THE TAPEWORMS, or Cestoda, are a group of wholly parasitic animals which belong to one of the major groups of the animal kingdom, the flatworms or Platyhelminthes. Tapeworms are long, flat and ribbon-shaped; they occur as adults in the intestines of all varieties of vertebrate animals. A single, mature specimen has a very small head or scolex at one end; this is buried in the intestinal lining of the host and serves to anchor the worm and prevent it from being swept out by the muscular action of the intestine. To aid in this function, the scolex is provided with suckers and often with small hooks as well. Holding on is the only function of the scolex; no food is taken through it and, indeed, there is no mouth or digestive tract in the whole worm. The rest of the body, called the strobila, consists of a series of similar segments, attached together end to end and each containing a set of male and female reproductive organs. Other organs are but poorly represented; there is a nervous system of sorts, a weakly developed muscular system, an excretory system and no circulatory or digestive systems at all. Food is absorbed through the body surface from the contents of the host's intestine.

Perhaps the most remarkable thing about tapeworms is their life-cycle. This always involves two hosts and often three. The tapeworms of beef and pork which infect man are of the two-host type; a number of the tapeworms of fishes are of the three-host type. One of the latter group, known to zoologists as *Triaenophorus crassus*, is the subject of this review. The worm has for its first larval stage a copepod; the copepods are tiny crustaceans abundant in our lakes. The copepod is called the first intermediate host of the tapeworm. The second intermediate host is one of several kinds of fishes which may eat an infected copepod. The final or definitive host, in which the worm reaches sexual maturity, is the pike; the pike becomes infected by eating the parasitized second intermediate host.

The genus *Triaenophorus* (Order Pseudophyllidea) contains at least three species common in Canadian fishes. Only one of these, *T. crassus* Forel, is of great economic importance; one of its larval stages, the plerocercoid, occurs encysted in the flesh of fishes of the whitefish family (coregonine fishes), the second intermediate where its presence is aesthetically objectionable. So numerous are these cysts that they have seriously interfered with the whitefish industry. Many lakes, potential producers of large quantities of whitefish, are not fished at all, or, at best, only lightly so, because the fish are too heavily parasitized to be acceptable on the American market. A great many other lakes are regularly fished but elaborate and expensive processing and inspection are carried out to prevent the infected fraction of the catch from reaching the export market. In fact, the *Triaenophorus* parasites are so numerous that Dominion inspectors are employed across Canada to examine all shipments of whitefish.

Although the cysts of this tapeworm have undoubtedly existed in our whitefishes since time immemorial, their presence was not widely recognized until about 1932 when inspectors of the U.S. Food and Drug Administration began to refuse to allow heavily infected fish to enter the United States. This action at first affected the Lake Winnipeg cisco fishery but, within a few years, the whitefish industry in the three Prairie Provinces was suffering from rejection of shipments. These rejections led to all manner of unfortunate trade practices designed to get infected fish past American inspection. Official and unofficial attempts were made to persuade the U.S. Food and Drug Administration to adopt a more tolerant attitude to the worms, but that organization remained adamant. For a decade, the situation worsened; then, in 1944, the Dominion Government, at the request and with the co-operation of the Prairie Provinces, appointed the Prairie Provinces Fisheries Investigation Committee. This committee, headed by Professor J. R. Dymond, was instructed to investigate the *Triaenophorus* situation and make recommendations for a solution of the problem. The two more important results of the Committee's report were the establishment of the Central Station of the Fisheries Research Board of Canada at Winnipeg and the setting up of a whitefish inspection system under the Department of Fisheries, both in 1944. The Committee was reconvened in 1947, principally to report on the efficacy of the inspection system.

There also grew out of the Committee's report a standing committee, the Advisory Committee on the Control of Whitefish Infestation, on which sat representatives of Ontario and the Prairie Provinces. This Committee named a standing technical subcommittee composed of men working on the biological aspects of *Triaenophorus*.

All this interest in *Triaenophorus* has produced a considerable amount of information. In Alberta, life-history and control research has proceeded since 1940; the Central Station began research in 1945; later Saskatchewan, and most recently, Ontario, began work in co-operation with the Central Station and with the support of Dominion funds. It is the purpose of this review to collect all the information that has accumulated to date, including such of the earlier Canadian, American and European literature as may be pertinent. Sections two and three deal with taxonomy and life-history, section four with control problems, section five is a general discussion and section six summarizes the review.

II. TAXONOMY

Three species of the genus *Triaenophorus* are known from Canadian fishes: *T. crassus* Forel, *T. nodulosus* (Pallas) and *T. stizostedionis* Miller. The three are very similar anatomically and overlap in life-history details. In this review it is the intention to discuss only *T. crassus* in detail, but in order to facilitate differentiation of *T. crassus*, brief accounts of the other two are included.

Species of *Triaenophorus* were first recorded from North American fishes by Cooper (1918). He recognized *T. crassus* (which he referred to as *T. robustus*) from the intestine of *Esox lucius* and the muscles of *Leucichthys artedi*. He also found *T. nodulosus* in several species of fishes.

In 1928 Hjortland reported *T. crassus* (referred to as *T. robustus*) from *Esox lucius* (pike) and *Leucichthys tullibee* (tullibee) in Minnesota.

In 1932 Wardle reported on the *Triaenophorus* parasites of Manitoba fishes. He found both *crassus* and *nodulosus*, but referred to both as varieties of *T. tricuspidatus*, *morpha megadentatus* and *morpha microdentatus.*

The somewhat confused situation was clarified in 1935 by Ekbaum. She studied Canadian material and compared it to European descriptions; she also explained the synonomy involved and showed that the North American material studied up to that time consisted of *T. crassus* and *T. nodulosus.* Miller (1943a) confirmed Ekbaum's findings.

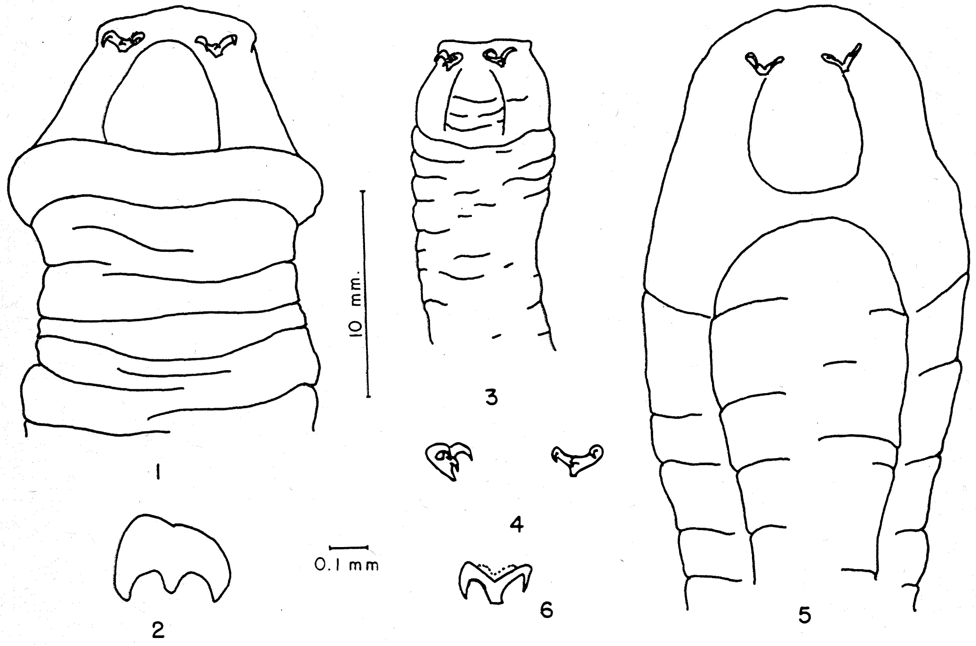


PLATE I

FIGURES 1–6. Camera lucida sketches of scolex and scolex hooks of *Triaenophorus crassus* (figures 1 and 2) *T. nodulosus* (figures 3 and 4) and *T. stizostedionis* (figures 5 and 6). The 10-mm. line refers to the scolices; the 0.1-mm. line to the hooks.

The third species, *T. stizostedionis*, was described by Miller (1945c).

The taxonomic characters and principal life-history details of the three species are as follows:

Triaenophorus crassus. This tapeworm occurs as an adult in the intestine of the pike (*Esox lucius*); the procercoid parasitizes the copepod *Cyclops biscuspidatus* Claus; the plerocercoid may occur in the muscles of any of the whitefish family and their relatives (trout, salmon, inconnu, grayling). The scolex and the characteristic scolex hooks are shown in Plate I, figures 1 and 2, and the anatomy of a mature proglottis (segment) is shown in Plate II, figure 7. Scolex hook measurements are summarized in Table I and cirrus sac length in Table II. *T. crassus* is the largest of the three species and has the largest scolex hooks.

Triaenophorus nodulosus. The adult of this worm also lives in the pike. There is some evidence (Scheuring, 1929; Miller, 1943a) that, on the average, it infects smaller pike than *T. crassus.* The first intermediate host is again *Cyclops biscus-*

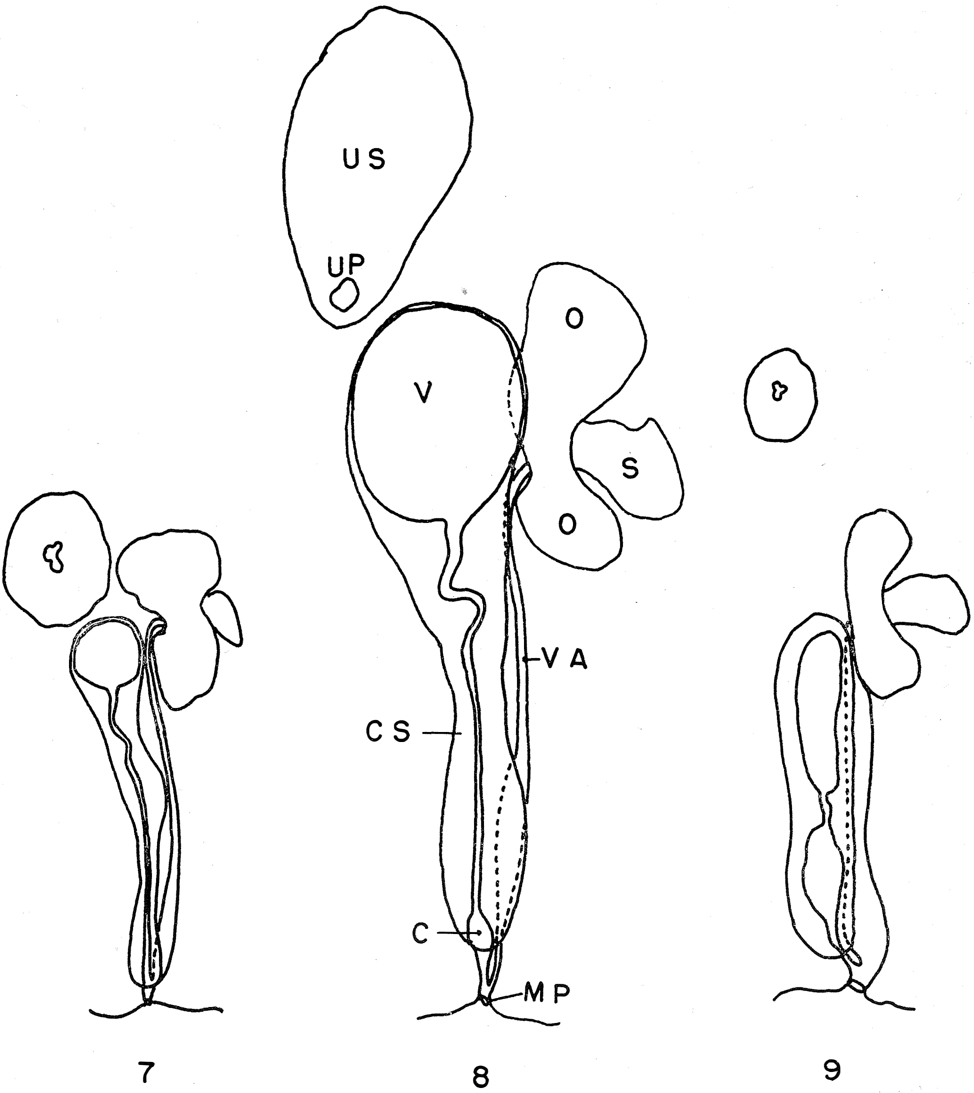


PLATE II

FIGURES 7–9. Camera lucida sketches of the principal genitalia of *T. crassus* (figure 7), *T. nodulosus* (figure 8) and *T. stizostedionis* (figure 9). C, cirrus; CS, cirrus sac; MP, marginal pore; O, ovary; S, shell gland, UP, uterine pore; US, uterine sac; V, internal seminal vesicle; VA, vagina. (X100) *pidatus*; the plerocercoid infects the liver of burbot, *Lota lota maculosa*. Recently, Lawler has reported the plerocercoid from the liver of the perch (*Perca flavescens*) (1950b) and from the sculpin, *Cottus cognatus* (1951a). There is one record from the Arctic grayling of Great Bear Lake (Miller, 1946). Cooper (1918) records *T. nodulosus* cysts from *Micropterus dolomieu*, the smallmouth bass. In Europe, the plerocercoid has been reported from the viscera of over thirty varieties of fresh water fishes. There is some doubt in the author's mind as to the similarity of European *nodulosus* and Canadian *nodulosus*; scolex hook measurements do not agree perfectly and fairly intensive searches have failed to find more than the five mentioned second intermediate hosts in Canada.

Scolex hook measurements of North American *T. nodulosus* are given in Table I and cirrus sac lengths in Table II; scolex and hooks are shown in Plate I, figures 3 and 4, and the anatomy of a mature proglottis is shown in Plate II, figure 8. *T. nodulosus* is smaller than *T. crassus* and has much smaller scolex hooks. The presence of a median prong on the scolex hooks is distinctive.

TABLE I. Dimensions of the scolex hooks of *T. crassus*, *T. nodulosus* and *T. stizostedionis* (μ).

Species	Width of basal plate	Anterior-posterior depth of basal plate	Length of marginal prong
T. crassus	255–300	132–140	245*
T. nodulosus	112–120	20–30	....
T. stizostedionis	123–198	22–33	48–77

*Ekbaum, 1935.

TABLE II. Cirrus sac length (μ) in mature proglottides of *T. crassus*, *T. nodulosus* and *T. stizostedionis*.

Species	Range	Average	Percentage of proglottis width
T. crassus	581–739	704	40–47
T. nodulosus	739–968	827	47–66
T. stizostedionis	493–704	616	32–37

As *T. nodulosus* infects the viscera of its second intermediate host, it is not an economic problem. Further details of this parasite may be found in Miller (1943a, b; 1945a).

Triaenophorus stizostedionis occurs as an adult in the pike-perch, *Stizostedion vitreum*. The first intermediate host is *Cyclops bicuspidatus* and the second, the trout-perch, *Percopsis omiscomaycus*. Like *T. nodulosus* the plerocercoid occurs as a cyst in the viscera of the second intermediate host, so that *T. stizostedionis* is not an economic problem; further, the trout-perch is not used as human food.

The scolex and hooks of this species are shown in Plate I, figures 5 and 6, and the details of the mature proglottis are illustrated in Plate II, figure 9. Tables I and II give scolex hook measurements and cirrus sac lengths.

T. stizostedionis is about the same size as *T. nodulosus*. The scolex hooks are small, lack the middle prong, and each has a distinctive bulge or addition on the basal plate (see figure 6, dotted line).

For easy reference the main anatomical differences of taxonomic value may be listed as follows:

T. crassus: largest scolex hooks; hooks lack median prong; small, round internal seminal vesicle; cirrus sac of intermediate length.

T. nodulosus: smallest scolex hooks with pronounced median prong; large, round internal seminal vesicle; longest cirrus sac.

T. stizostedionis: intermediate scolex hooks, without median prong, but a Y-shaped protuberance visible on each hook in fresh specimens; internal seminal vesicle *elongate oval*; cirrus sac shortest.

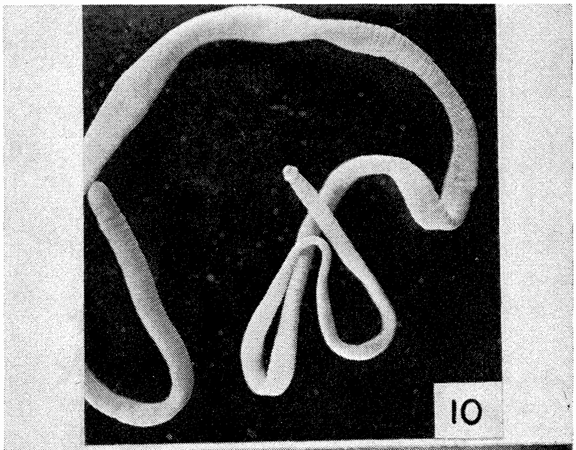
It is evident that the three species are closely related. Anatomically, they are very similar; in life-history, they share the same first intermediate host and two of them the same final host. All are annuals, that is, they die after spawning and leave the host, and all reach maturity in the spring, though not at the same time. *T. crassus* matures first, then, after approximately two weeks, *T. nodulosus* matures and, lastly, after three or four more weeks, *T. stizostedionis* reaches maturity (Miller, 1945c).

III. LIFE-HISTORY OF TRIAENOPHORUS CRASSUS

A. The Adult; Life in the Final Host

The mature adult is a white worm that varies from 130 to 400 mm. in length and 2.0 to 4.2 mm. in breadth at the widest point (see Plate III, figure 10). It occurs in the intestine of the pike (*Esox lucius*) and, less commonly, in muskellunge (*Esox masquinongy*). The latter host was reported by Cooper (1918); in the same paper, Cooper records finding an immature specimen in a burbot (*Lota lota maculosa*). Miller (1945b) has argued that this is a false record as many hundreds of burbot which had fed on parasitized ciscoes in Lesser Slave Lake failed to show established worms. Rawson and Wheaton (1950) in Saskatchewan, and Lawler (1950a) in Manitoba also failed to find *T. crassus* in burbots. Cooper's record was undoubtedly a specimen that was released by digestion from its cyst in a cisco, and, had the burbot lived, would have been itself digested.

In the pike the worms are attached to the intestinal wall in the region just distal to the pylorus. The scolex is deeply buried; at the attachment site the intestinal mucosa is destroyed and a deep pit is excavated in the submucosa which shows considerable hypertrophy in the immediate area (Plate III, figures 11 and 12). In the spring, after the worms have left the host, the empty pits remain and are easily discernible to the unaided eye for a week or so.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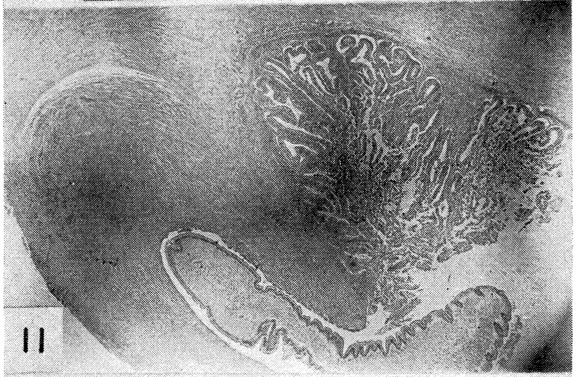
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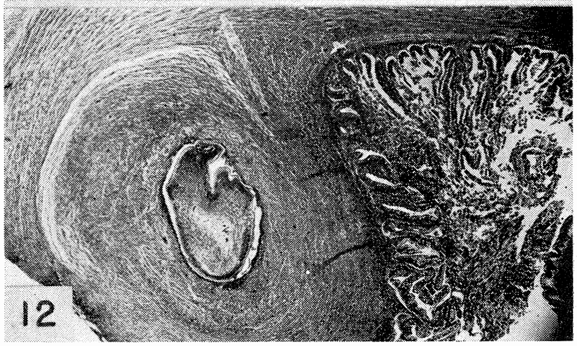
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PLATE III

FIGURE 10. Photograph of a ripe adult *T. crassus* from a pike intestine. (X2)

FIGURE 11. Photomicrograph of a section through a pike intestine at the attachment site of *T. crassus.* (X16)

FIGURE 12. Photomicrograph of the same intestine as figure 11, but sectioned at a different place in order to show the scolex of the worm visible in figure 11; note scolex hook imbedded in pit wall. (X21)

During the summer months, the parasites are small and may escape notice in the copious intestinal slime. In the late fall and winter, they are much larger and may completely fill the intestinal lumen. Normally the strobilae are much kinked and tangled but during spawning time, they extend down the intestine for their full lengths.

In Lesser Slave Lake (Miller, 1943a), the larger pike are the more frequently and heavily infected. Those of three pounds in weight and over were from 90 to 100 per cent infected; those of less than three pounds were from 20 to 45 per cent infected. *T. nodulosus* commonly occurs with *T. crassus* although it is much more abundant in the smaller pike and much less in the larger. Scheuring (1929) found much the same situation in pike from German lakes. Recently Rawson and Wheaton (1950) failed to find any correlation between size of host and number of *T. crassus* in 18 pike from Nesslin Lake.

The number of worms per host varies in Lesser Slave material from 1 to 70, average 12; Rawson and Wheaton (1950) found a range of 5 to 60 ± 5. Miller and Huston (MS) and Libin (1951) found a similar range in pike from Baptiste and Square Lakes, Alberta.

The worms reach maturity in the spring. In Lesser Slave Lake and in Square and Baptiste Lakes the first viable eggs are released toward the end of April. Observations on the development of the genitalia in specimens from Lesser Slave Lake are as follows:

September	No trace of genitalia
October	No trace of genitalia
December	Genitalia well formed, no eggs in uteri
February	Eggs in uteri
March	Eggs in uteri, embryos visible
April	Eggs released in water; some hatching
May 1–14	All worms releasing eggs
May 15–31	Worms mainly spent and dying
June	A few spent worms
July	New generation; all immature

The main spawning period in Lesser Slave Lake is in the first half of May, although some spawning activity extends into June. These data agree with Ekbaum's findings (1937) on Lake Winnipeg, Lake Nipissing and Lake of the Woods. They have been confirmed by Miller (unpublished) in Square Lake, Alberta and by Libin (1951) in Baptiste Lake, Alberta. Rawson and Wheaton (1950) found spawning tapeworms in Nesslin Lake, Saskatchewan, on May 25th and again on June 13th, approximately the same period.

The tapeworms break up when releasing their eggs; pieces of the posterior end break off first and pass out of the host. Most of the eggs are released in the water. This breaking-off process continues until just the scolex remains buried in its pit; finally this too is shed. There follows then a period of approximately one month, from mid-May to mid-June, when the pike are almost free of *T. crassus.* These observations, made on Lesser Slave Lake, have been confirmed by Rawson and Wheaton (1950) on Nesslin Lake, but the period of relative freedom from parasites was from mid-June to the end of July. The loss of worms in the spring and the acquisition of a new generation in early summer have also been observed in European pike (Scheuring, 1929).

B. THE EGGS AND CORACIDIA

Measurements of the eggs and coracidia have been made in Canada by Ekbaum (1937) and Miller (1943b). Observations of hatching have been carried out by the same authors and by Miller and Huston (MS), by Libin (1951) and by Rawson and Wheaton (1950). The eggs accumulate in the worm's uteri; as spawning time nears, the uteri acquire pores to the outside. Through these, the eggs burst when a ripe worm is placed in water; they are produced in such numbers that they appear as a white cloud in a Petri dish in which a worm has been placed. One worm may produce 1,175,000 eggs. The eggs are, of course, not rightly called eggs as they are ready to hatch when released from the worm; they are more properly termed shelled embryos. They are "egg-shaped" and measure from 53 to 68 μ long and 38 to 44 μ in diameter (average 61 by 41 μ). At the small end of each is a minute lid or operculum. The shell is transparent and, under a microscope, the embryo within is clearly visible (Plate IV, figure 13). The eggs are white when first released but turn brown in water in about 45 minutes. They are heavier than water and soon collect on the bottom.

The onchosphere, or embryo within the shell, is very active. It twists and turns about. As hatching approaches, these movements become more violent; the tiny animal contracts itself into a mass at the large end of the shell, then expands violently against the small end, thus battering against the operculum. Finally, this pops open and, in a few seconds, the embryo squeezes through, leaving the empty shell, lid ajar, behind (Plate IV, figure 14).

Miller (1943b), Miller and Huston (MS) and Libin (1951) have observed the hatching of many hundreds of egg cultures. These are made up in Petri dishes and kept at about 40° F. to reduce bacterial action and to simulate natural temperatures. Hatching lasts from ten days to two weeks, but usually half the eggs are hatched by the third day following the beginning of hatching. In most cultures more than 90 per cent of the eggs from one worm prove viable.

The embryos, called coracidia, each consist of an onchosphere with six movable f-shaped hooks, the whole surrounded by a gelatinous layer of large cells bearing cilia (Plate IV, figure 15). At first, they have the same dimensions as the shell and swim very rapidly. In a few hours, the ciliated coat has absorbed considerable water and they measure 73 by 54 μ (average). They are ovate and now swim slowly, the broader, hook-bearing end forward. While moving, they rotate slowly, first one way, and then the other.

The water-absorbing process continues, and, ultimately, the coracidia appear to go into solution. In lake or tap water, they live only two or three days; in distilled water, the life-span is considerably shortened, and in physiological saline, much lengthened. In one experiment (Miller, unpublished), the eggs from one worm were divided into three groups; one group was placed in lake water, one in distilled and one in saline. These cultures were examined daily and the per-

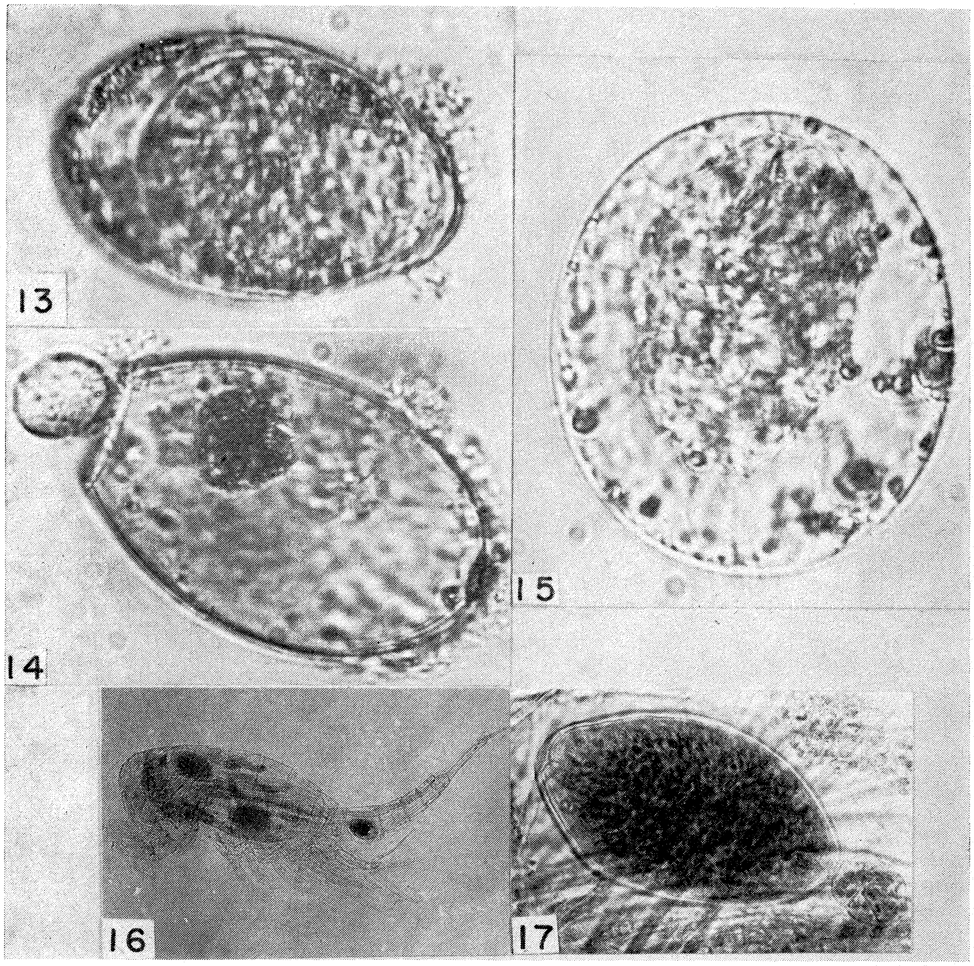


PLATE IV

FIGURE 13. Photomicrograph of a ripe egg of *T. crassus.* (X1250)

FIGURE 14. Photomicrograph of a hatched egg of *T. crassus*; note open operculum. (X1250)

FIGURE 15. Photomicrograph of a recently hatched coracidium of *T. crassus.* (X1250)

FIGURE 16. Photomicrograph of a stained and mounted *Cyclops bicuspidatus*, containing two procercoids of *T. crassus.* (X60)

FIGURE 17. The anterior procercoid of figure 16 photographed through an oil immersion lens. (X390)

centage of the coracidia (relative to the number of hatched eggs) determined. In lake water, 85.5 per cent were alive on the third day and 54 per cent on the fifth; in distilled water, the percentages were 50 and 12 on the same days; in saline, the figures were 93 and 44.3. It was also noted that, owing to imbibition of water, coracidia in the distilled water reached dimensions ten per cent greater than those in lake water and 28 per cent greater than those in saline.

Before the coracidia die, many of them dig their way out of their ciliated coats with the hooks and crawl, briefly and impotently, on the bottom.

C. THE PROCERCOID; LIFE IN THE FIRST INTERMEDIATE HOST

As was seen in the previous section, the coracidium, as a free-living animal, is very short-lived. To survive, it must be swallowed by a suitable host.

In cultures studied by the author, *Cyclops bicuspidatus* Claus proved a suitable first intermediate host. When coracidia were added to a jar containing copepods of this species, they were found in the *Cyclops* stomachs within an hour. The *Cyclops* swallowed them, apparently deliberately, and sometimes as many as thirty were found in the stomach of a single *Cyclops*. Other copepods were also tried; *Cyclops albidus* Jurine and *C. viridis* Jurine ate the coracidia but either digested them or defecated them alive; none was established; *Diaptomus ashlandi* Marsh ate the coracidia which then entered the haemocoele but here they failed to develop. Two Cladocera, *Daphnia pulex* (de Geer) and *D. longispina* (O. F. Müller), were also tried but no infections resulted.

Michajlow (1932) made a study of possible first intermediate hosts of *Triaenophorus nodulosus* and found that only one, *Cyclops strenuus* Fischer, would serve fully. Others he placed in four categories: (1) all coracidia killed by the host digestive juices in stomach; (2) most killed but a few got into body cavity; (3) majority enter the body cavity but fail to develop; and (4) a few get into body cavity and develop normally.

It would appear that *Cyclops bicuspidatus* is the only limnetic species that will serve for *T. crassus*. It would be valuable to test the littoral Copepoda, none of which has been tried. It would seem logical that one of these might serve, as the coracidia are mainly hatched out in shoreward areas. However, Arnason (1948) examined all plankton from Heming Lake during June and found *Triaenophorus* only in *C. bicuspidatus*.

In the stomach of the *Cyclops*, the coracidia dig out of their ciliated coats. Each then uses its hooks to "dissect" a passage through the stomach wall into the haemocoele. This is done by swinging the six hooks together so as to make one point; this is thrust into the stomach wall and the hooks are then spread apart, tearing a hole. The process is repeated until the hole extends completely through the stomach wall. The onchosphere slips through and travels about freely in the haemocoele. Onchospheres penetrate the antennae, caudal rami and thoracic limbs as well as remaining in the stomach area.

Under natural conditions, the number of coracidia entering a single *Cyclops* would rarely exceed one. Arnason (1948) has shown that during June *Cyclops biscuspidatus* from Heming Lake, Manitoba, were from 0 to 50 per cent infected.

He examined 27 naturally infected *Cyclops* and found a total of 30 parasites. In laboratory cultures, as many as 32 may become established in a single host (Miller, 1943b). In such multiple infections, the *Cyclops* give every sign of distress while the parasites are digging through the stomach wall. On one occasion, the author observed violent spasmodic contractions of the stomach which eventually expelled all the parasites through the mouth. Once the onchospheres have reached the body cavity, the host gives no further evidence of distress.

Bathed, as they now are, in the blood of their hosts, the onchospheres begin a period of rapid growth. This lasts approximately eight days and culminates with the formation of the next larval stage, the procercoid. Both the size of the procercoid and the time consumed in its development are influenced by the number per host; where crowding occurs, growth is slower and the final size is less.

The first evidence of procercoid development is increase in size. After a few days, the hook-bearing region begins to pinch off; this process continues until the hooks are isolated in a small blob of protoplasm, connected by a narrow neck to the rest of the body. This blob is called the cercomere. It is posterior in position; at the anterior end a small invagination appears. This is the frontal gland which is used in the second intermediate host. In Lesser Slave experiments, procercoids reached a maximum size of 352 μ; most fully grown procercoids range from 300–350 μ.

Plate IV, figure 16, shows a procercoid in its *Cyclops*; figure 17 shows the same procercoid at a higher magnification; the cercomere with its hooks and the frontal gland may be distinguished.

In the author's work at Lesser Slave Lake, individual *Cyclops* containing procercoids were kept under observation for 22 days. A length of life of procercoids of approximately one month was assumed. Arnason (1948) has confirmed this by his studies of infected *Cyclops* from Heming Lake; he found infected *Cyclops* during early June; infection declined in late June and reached zero in July; absence of infection continued through August. This absence is assumed to be due to the death of *Cyclops* containing procercoids.

The procercoid stage marks the end of development in the first intermediate host. To continue its life, a procercoid, contained in a *Cyclops*, must be swallowed by a suitable second intermediate host.

D. The Plerocercoid; Life in the Second Intermediate Host

THE SECOND INTERMEDIATE HOSTS

Procercoids of *Triaenophorus crassus* will grow into plerocercoids in a considerable variety of hosts. Cooper (1918) found the plerocercoids in the muscle of *Leucichthys artedi* (Le Sueur); Hjortland (1928) recorded them from *L. tullibee* (Richardson); Newton (1932) in Manitoba reported plerocercoids from the flesh of *L. tullibee*, *L. zenithicus* (Jordan and Evermann), *L. nipigon* Koelz, *L. nigripinnis* (Gill) and *Coregonus clupeaformis* (Mitchill); Miller (1945b) found these cysts in *Prosopium williamsoni* (Girard) and in the visceral peritoneum of young *Esox lucius* L. of Lesser Slave Lake. Cysts from the flesh of *Stenodus leucichthys*

(Güldenstadt) and *Cristivomer namaycush* (Walbaum) collected by Dr. D. S. Rawson from Great Slake Lake were reported by Miller (1945b) as plerocercoids of *T. crassus*. Miller (1947) recorded cysts of *T. crassus* from the flesh of *Thymallus signifer* from Great Bear Lake as well as from lake trout and ciscoes. Scheuring records *T. crassus* plerocercoids from three European salmonids in addition to coregonids. Lawler (1950a) has examined *Catostomus commersonni*, *Notropis hudsonius*, *Boleosoma nigrum* and a species of sculpin from Heming Lake without finding plerocercoids of *T. crassus*. Rawson and Wheaton (1950) made similar negative findings in *Stizostedion vitreum*, *Perca flavescens*, *Catostomus commersonni*, *Boleosoma nigrum*, *Pimephales promelas*, *Notropis hudsonius*, *Pungitius pungitius*, *Eucalia inconstans* and *Lota lota maculosa* from Nesslin Lake.

DESCRIPTION OF THE PLEROCERCOID

The plerocercoids of *T. crassus* are the most familiar stage of the worm's life-cycle. Their presence in the flesh of coregonine fishes is the objectionable feature (from a commercial point of view). They have been described by Cooper (1918), Hjortland (1928), Newton (1932) and Miller (1945b) in North America and by numerous European authors. Each plerocercoid is enclosed in a cyst; the cyst is usually yellowish in colour, typically spindle-shaped and from one-quarter of an inch to one inch in length. It is composed of connective tissue formed by the host. Within the cyst is the plerocercoid and a variable quantity of thick yellowish liquid; this liquid is composed of broken-down host tissue, on which the plerocercoid feeds, and excretory products from the worm. The worm itself is a long, coiled, white thread, about 1 mm. in diameter and up to 130 mm. long. At one end is a complete scolex formed as in the adult; the strobila is the same diameter throughout and lacks sex organs. At the posterior end of the strobila, a filament of variable length, termed the cauda, is often present.

The cysts are exceedingly variable in shape (Plate V, figure 18); Newton (1932) believed the more irregular shapes were a result of crowding; the author observed no relation between numbers and shape in Lesser Slave specimens. Usually one cyst contains one worm, but occasionally two plerocercoids are found within a single cyst (lower right of figure 18).

In European fishes it is common to find plerocercoids naked in the flesh, that is, not enclosed in cysts. In North America this is unusual and has been reported only in yearling coregonines. The author has found such plerocercoids in ciscoes from Lake Winnipeg and from Baptiste Lake, Alberta. Recently, Lawler (1950) has found all the plerocercoids to be naked in the infected ciscoes and whitefish of six inches and less from Heming Lake.

LOCATION OF PLEROCERCOID IN HOST

With the exception of a few instances of plerocercoids occurring in the visceral and parietal peritoneum, the cysts are intramuscular. Newton (1932) published a diagram showing cyst distribution in the whitefish. He found 80 per cent in the epaxial muscles between the head and the dorsal fin, 10 per cent in the remaining epaxial muscles and 10 per cent in the hypaxial muscles. On the whole,

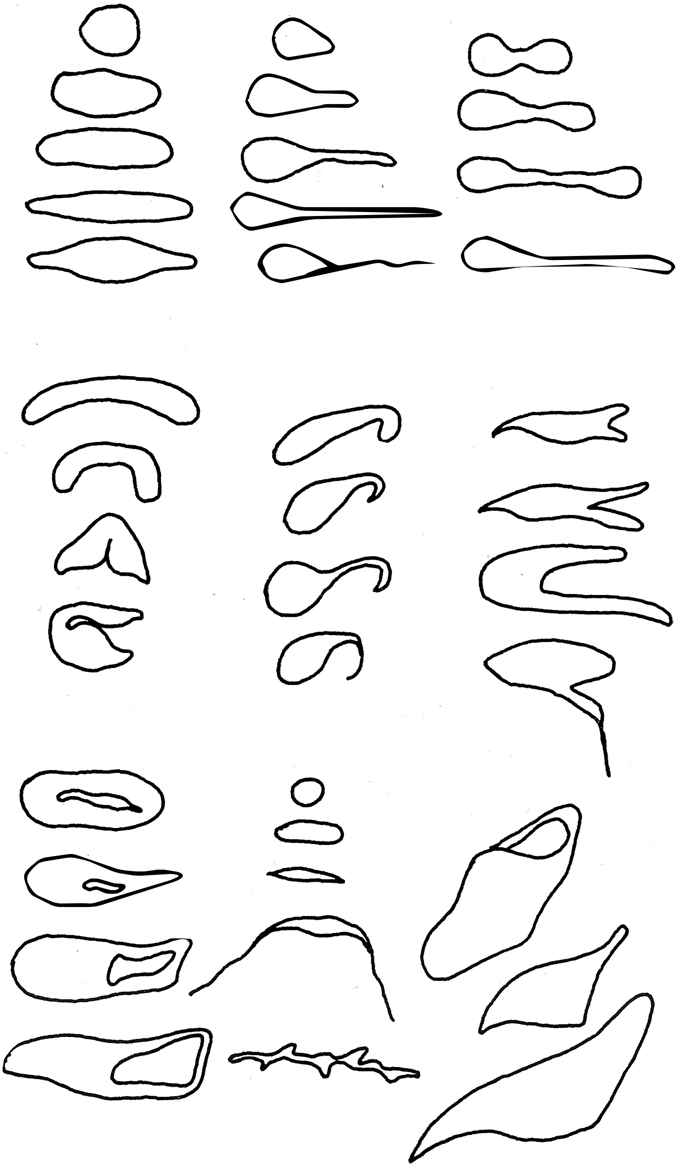


PLATE V

FIGURE 18. Sketches of a variety of encysted plerocercoids of *T. crassus*; the two in the lower right-hand corner each contained two plerocercoids. (Slightly enlarged.)

this distribution has been found to be typical. However, the author has noted that cysts are very rare in the muscles of the tail, that is, distal to the anus. In fact, the cysts are distributed in the flesh bordering the body cavity, from whence they come. A further interesting observation is that the cysts are more numerous on the right side of the body than on the left. Records from 645 ciscoes of Lesser Slave Lake show 2,858 cysts on the right side and 2,149 on the left; from Square Lake, Alberta, 1,032 ciscoes had 5,168 cysts on the right side and 4,191 on the left. The stomach of coregonine fishes lies against the right body wall; this probably accounts for the greater number of cysts on the right side.

MANNER AND TIME OF ARRIVAL IN MUSCULATURE

The question of how the plerocercoid makes its way to the flesh of the second intermediate host must as yet be answered partly by inference. It would appear that the plerocercoids are liberated from the *Cyclops* in the stomach of the host. Here they use their frontal glands to digest a passage through the stomach wall into the coelom. Rosen (1919) has observed this process for *T. nodulosus* in young perch and Miller (1945a) has seen procercoids of the same species invading burbot livers. A few direct observations have been made on *T. crassus*. The author has several times found plerocercoids encysted in the visceral peritoneum of the stomach of ciscoes and also in the parietal peritoneum bordering the stomach. He has also found procercoids resembling those of *T. crassus*, but larger, in scrapings from the outer surfaces of the pyloric caeca. One plerocercoid of *T. crassus* with a fully developed scolex was found protruding from the tip of a pyloric caecum of *L. tullibee.* In a feeding experiment in which *Cyclops* containing procercoids were fed to captive whitefish, one free procercoid was recovered from the stomach. Recently Rawson and Wheaton (1950) examined whitefish stomachs from Nesslin Lake, Saskatchewan, and found procercoids, presumably of *T. crassus*, in various stages of penetration through the stomach during the period July 5th to the last week of August.

Once in the coelom, the procercoids must continue their journey to the muscles by digesting their way through the parietal peritoneum. A period should follow in which procercoids would be found in the flesh in various stages of transition into plerocercoids. In *T. nodulosus* such intermediate stages have been found in the livers of burbot (Miller, 1945a); these were worms, intermediate in size between procercoid and plerocercoid, non-encysted and with scolices beginning to form. No such stages have yet been found for *T. crassus*, although the author and other workers have examined many thousands of fish. All that has been found is the fully formed plerocercoid, naked in the flesh, in young ciscoes and whitefish. However, young plerocercoids are so small relative to the bulk of the host's flesh that they might easily be overlooked and the time it takes them to acquire the scolex may be very short.

The time when the cysts appear in the flesh of the second intermediate host may be quite accurately determined by counting all the cysts in samples of year-classes at monthly or twice-monthly intervals. A time is found when the number suddenly increases, indicating that a new generation of cysts has arrived. In

Lesser Slave Lake ciscoes, this time was found to be during July; in Nesslin Lake whitefish (Rawson and Weaton, 1950) the new crop of cysts arrived the first week in August. In Baptiste Lake ciscoes, Miller and Watkins (1946) have shown that the new crop of cysts arrives sometime between July and October. Lawler (1950a) found fresh plerocercoids in young ciscoes and whitefish between July 21st and August 29th in Heming Lake. Numerous scattered observations on infected whitefish have shown that there is no significant change in numbers of plerocercoids during the period September to June. It is fairly well established, then, that the plerocercoids appear in the flesh each year during July and August, the exact time probably being a function of climate and limnological conditions.

INFLUENCE OF AGE OF HOST ON NUMBER OF PLEROCERCOIDS

At one of its sessions, the Prairie Provinces Fisheries Investigation Committee met Mr. H. J. Hoffman, of the Minnesota Department of Agriculture, Dairy and Food. Mr. Hoffman described his work on Lake-of-the-Woods tullibee; he found that the heavier the fish, the greater the number of plerocercoids it contained. He was able to use this information in separating the tullibee into heavily infected and lightly infected groups; the former group was dyed and used as animal food only. Mr. Hoffman's findings suggested a relationship between the age of host and number of cysts: as fish grow older they become wormier. This possibility is worthy of close examination, because it is of great potential importance in the matter of control. In any population of infected ciscoes or whitefish, it

TABLE III. Cysts per 100 fish in ciscoes (*L. tullibee*) from Lesser Slave Lake. (Number of fish in parentheses.)

Year-class	Age at capture					
	1	2	3	4	5	6
1940	....	....	82(22)	585(27)	....	....
1941	....	....	67(9)	....	....	1200(1)
1942	....	4(50)	....	....	630(1)	....
1943	0(1)	....	....	0(1)	....	....
1944	....	....	4(44)	33(6)	....	....
1945	....	7(151)	46(116)	150(2)	....	..
1946	0(4)	24(374)	62(85)	....	....	....
1947	0(4)	74(413)	181(77)	400(7)	....	....
1948	....	143(423)	274(86)	....	....	....

would be necessary to follow the infection history of each year-class through several years to acquire proof positive that worminess did or did not increase with age. Such data are not plentiful; those available for Lesser Slave Lake ciscoes (*L. tullibee*) are shown in Table III. These data are the result of counting cysts in 2,916 fish over the period 1944–51.

From Table III it is clear that there is an increase in number of cysts with each year of life in each year-class; thus the year-class of 1940 contained 82 cysts per 100 fish as three-year-olds and 585 as four-year-olds; similar increases show for other year-classes.

Table IV gives similar data from 837 Baptiste Lake ciscoes (*L. tullibee*) collected during 1944 and 1945. Three consecutive years in the lives of four year-classes (1940–43) are shown. Each of these shows a regular increase of cysts. By reading the table diagonally from the lower left to upper right, the increase in cyst content with age, without regard to year-classes, may be seen. The build-up of infection with time is then quite impressive.

TABLE IV. Cysts per 100 fish in ciscoes (*L. tullibee*) from Baptiste Lake, Alberta. (Number of fish in parentheses.)

Year-class	Age at capture						
	1	2	3	4	5	6	7
1937	....	....	....	....	....	....	910(11)
1938	....	....	....	....	....	870(78)	....
1939	....	....	....	....	875(153)	....	....
1940	....	....	....	612(146)	715(7)	767(3)	....
1941	....	....	305(18)	465(17)	836(87)	....	....
1942	....	75(4)	103(36)	306(33)	....	....	....
1943	0(3)	44(162)	217(75)	....	....	....	....

Over the period 1947–49 and in 1951 the author also made cyst counts on 1,887 ciscoes (*L. tullibee*) from Square Lake, Alberta. This work was done in connection with a pike-reduction campaign which will be discussed later in this paper. The data on the counts are shown in Table V. Miller (1950) described how the pike-control campaign reduced the average infection of the tullibee. The campaign began in 1947, so that tullibee taken after 1947 were affected. The vertical lines in the table divide the fish affected by the control measures (on the right) from those not affected (on the left). The increase in cysts with age has been partially obscured; there are indications of increases up to the time when control of pike

TABLE V. Cysts per 100 fish in ciscoes (*L. tullibee* ?) from Square Lake, Alberta. (Number of fish in parentheses.)

Year-class	Age at capture							
	1	2	3	4	5	6	7	8
1940	....	....	....	....	....	1230(22)	865(8)	500(1)
1941	....	....	....	....	1240(80)	955(32)	1135(11)	770(24)
1942	....	....	....	1070(210)	1025(121)	1000(41)	790(95)	....
1943	....	....	670(85)	870(200)	830(66)	700(135)	....	....
1944	....	500(1)	616(98)	960(116)	630(139)	....	950(6)	....
1945	....	800(1)	860(76)	486(64)	....	1915(6)	....	....
1946	120(6)	....	413(22)	....	1090(48)	....	....	....
1947	700(1)	200(1)	....	910(109)	....	....	....	....

began; then slight decreases are evident. Control of pike ceased in 1949; in 1951 the cyst count was again high. By reading the table diagonally, the general trend of increase of cysts with age is apparent.

Keleher (1952) has studied the infection of ciscoes of Lake Winnipeg. He examined 500 *L. zenithicus*, 164 *L. nigripinnis*, 176 *L. nipigon* and 38 *L. tullibee*. He concluded that *zenithicus*, *nigripinnis* and *tullibee*, which were infected from 58–62 per cent, were not significantly different in infection rate. *L. nipigon* was much higher, with a rate of 96 per cent. The number of cysts per fish was also much higher in *nipigon*. Table VI presents Keleher's data on infection and age of host for three of the ciscoes.

From Table VI it is evident that *L. zenithicus* and *L. nigripinnis* fail to show accumulation of cysts with age, while *L. nipigon* does show such an accumulation.

Rawson and Wheaton (MS) counted the cysts in, and determined the ages of 214 ciscoes (*Leucichthys* sp.) from Mosher Lake, Saskatchewan. They found a steady increase in number of cysts from age 2 to age 7; thereafter the infection holds steady for two years and then becomes erratic, possibly owing to the smaller numbers of older fish examined.

Lawler (1951c) has worked out the distribution of cysts with age in 142 ciscoes (believed to be *L. tullibee*) from Heming Lake. He reports a general increase in cyst content with age.

The surveys of lakes conducted in connection with whitefish inspection have yielded a vast store of information on the degree of infection of whitefish with cysts of *T. crassus*. However, only a small fraction of this has been analysed for age and cyst accumulation. Some of the analyses available to, or made by, the author are now presented in Table VII.

TABLE VI. Cysts per 100 fish in ciscoes from Lake Winnipeg. (Numbers of fish in parentheses.) Data from Keleher (1952).

	Age at capture						
	3	4	5	6	7	8	9
L. zenithicus							
1947	160(20)	140(31)	150(71)	120(73)	130(54)	150(10)	0(1)
1948	330(3)	130(6)	130(32)	160(47)	160(25)	500(1)	100(1)
1949	200(10)	200(7)	300(11)	220(8)	0(1)	100(2)	
L. nigripinnis							
1947	200(3)	380(7)	280(20)	340(4)	180(13)	90(16)	90(11)
1948	100(1)	0(1)	420(5)	660(3)	1100(1)		0(1)
1949	330(3)	400(3)	60(3)	800(2)	300(1)		100(1)
L. nipigon							
1947		320(7)	530(25)	830(38)	830(28)	1430(3)	1100(1)
1948		520(2)	630(29)	670(16)	800(10)		
1949		400(1)	1000(1)				

TABLE VII. Cysts per 100 whitefish from nine lakes, arranged according to degree of infection. Figures in parentheses are numbers of fish examined.

Age at capture	Lesser Slave 1951 5.2 cysts/100 2.6% infected	Calling Lake 1949 20 cysts/100 15% infected	Utikuma 1944 20 cysts/100 20% infected	La Biche 1944 50 cysts/100 22% infected	Pinehurst 1944 67 cysts/100 40% infected
1	....	....	....	....	....
2	....	....	....	....	....
3	....	....	....	0 (2)	....
4	0 (8)	7(29)	47(83)	37.5(32)	87(63)
5	4.3(117)	27(40)	8(12)	7.9(48)	59(224)
6	2.8(249)	57(7)	0(7)	49 (41)	77(48)
7	10.3(116)	11(9)	0(83)	29.2(65)	50(2)
8	11.1(9)	16(6)	8(13)	73 (11)	....
9	....	0(4)	0(2)	....	....
10	....	20(5)	....	150 (2)	....

TABLE VII (*continued*).

Age at capture	Mosher 1949[1] 71.5 cysts/100	Winnifred 1948 216 cysts/100 80% infected	Lesser Slave 1944 265 cysts/100 31% infected	Muskeg 1950[2] 280 cysts/100 75% infected	Nesslin 1949[3] 1856 cysts/100 100% infected
1	200(1)	....	....	50(12)	124(25)
2	0(1)	....	....	67(18)	360(15)
3	50(2)	300(1)	240(51)	184(58)	569(13)
4	220(13)	160(20)	66(203)	284(130)	966(3)
5	80(11)	240(45)	94(107)	231(54)	1266(6)
6	110(7)	225(28)	260(39)	357(21)	1300(5)
7	160(9)	185(8)	882(34)	687(15)	2742(19)
8	200(36)	....	1156(38)	900(9)	3088(34)
9	110(19)	....	....	733(3)	2718(27)
10	150(14)	....	....	....	2096(29)

[1] Rawson and Wheaton, MS.
[2] Welch, 1950.
[3] Rawson and Wheaton, 1950.

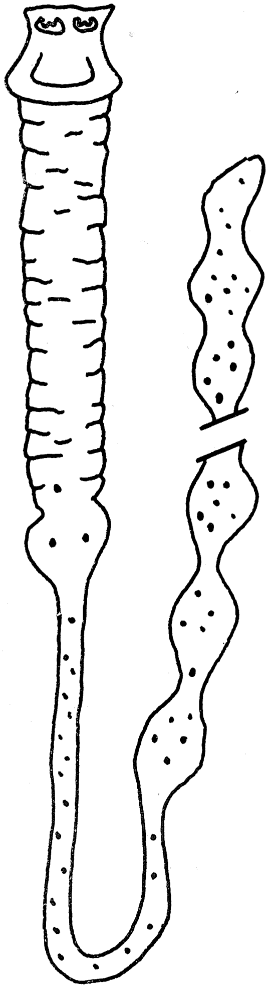
In Table VII the infection of each age-group of whitefish in samples from nine lakes is shown. The lakes are arranged in the order of the degree of infection, lightly infected to the left. A study of this table reveals that an increase of cyst content with age is not apparent in lightly infected populations; up to an infection rate of 71.5 cysts per 100 fish, the degree of infection of each age-group of a sample is of the same order of magnitude. As age-groups 1–3 are not represented in all these samples, this conclusion may be subject to revision. Some of the heavier infections, over 200 cysts per 100 fish, show a significant increase with age. This is well shown in Muskeg Lake, Lesser Slave (1944) and Nesslin Lake data. It is tempting to theorize in this wise: when infection levels are low, whitefish encounter infected *Cyclops* rarely and, consequently, cysts are scattered irregularly through the population more or less at random; when infection levels are high (200 or more cysts per 100 fish), there is a high probability of each whitefish swallowing infected *Cyclops* each summer of its life; as the cysts are cumulative (see p. 16) there is a tendency for them to build up with time and, hence, older whitefish are wormier. In this connection it is instructive to compare Lesser Slave Lake whitefish collected in 1951 with those collected in 1944. The 1951 sample was lightly infected and the degree of infection at different ages was erratic; the 1944 sample was heavily infected, and accumulation of cysts with age was distinct. It is interesting that in Lesser Slave and two other heavily infected lakes, the peak of infection occurred at age 8. Dr. Doan also found that the peak of infection of whitefish of Heming Lake occurred at age 8. Welch (1952) found that maximum infection of whitefish in Lakes Nipigon and Muskeg occurred at age 7 and in Shakespeare Island Lake at age 12. It is probable that in even lightly infected populations a careful statistical study would show some increase of infection with age; Oakland (1949) has shown such an increase in Lake Winnipeg whitefish which are only lightly infected. He has further shown that the degree of infection in Lake Winnipeg varies in locations more than nine miles apart, and in the same place at different times.

Further generalization on cyst content and age is probably futile. Each lake presents its own peculiar ecological conditions; differences in feeding habits of the coregonines and of the pike, and local variations in seasonal movements all contribute to the uniqueness of each lake. It is probably safe to conclude that *Leucichthys tullibee* and *L. nipigon* become wormier with increasing age; that, at the level of infection in Lake Winnipeg, *L. zenithicus* and *L. nigripinnis* do not become more infected as they grow older; and that whitefish may accumulate cysts with age at high infection levels, but not at lower infection levels. The differences in infection levels of the various species of ciscoes point up the necessity of correct cisco identification. This is discussed in a later section.

LENGTH OF LIFE OF PLEROCERCOID

After their arrival in the flesh of the host the plerocercoids remain more or less passive, their development arrested until they are swallowed by a pike and can become adults. How long they remain viable, that is, capable of infecting a pike, is not known; no experiments have been carried out to determine this time. This is very important information when control of the parasite is intended; for if one stage, for example the coracidium, were eliminated, the plerocercoids would remain as a reservoir, capable of infecting pike for an unknown length of time. There are two lines of evidence which enable a guess at the longevity of plerocercoids; the first is provided by the plerocercoids themselves, the second by the manner in which they accumulate in *Leucichthys tullibee.*

Miller (1945b) dissected 243 plerocercoids out of 50 ciscoes (*L. tullibee*); the length, maximum diameter and volume of each cyst was measured and the length of each plerocercoid (unrelaxed) within the cysts; in addition, observations were made on the nature of the contents of the cyst exclusive of the plerocercoid. In general, it developed that large cysts (0.07–0.12 cc. volume) contained large plerocercoids (70–130 mm.); the plerocercoids had very short caudae, or none at all; the fluid in the cysts was pale and non-granular. Smaller cysts (0.03–0.06 cc. volume) contained smaller plerocercoids (36–68 mm.), whose caudae comprised half the total length of the worm; the fluid in the cysts was yellow and contained large calcareous particles. Very small cysts (less than 0.03 cc. volume) often contained no plerocercoids or just the anterior fragments of them, and the cyst contents had become solid and orange-coloured. These observations have been interpreted as changes due to age; the cauda is believed to be the product of the degeneration of the plerocercoid, beginning at the posterior end. Thus one may find young plerocercoids, with no caudae, and very old ones which consist of scolex and cauda only, as well as all intermediate stages. In the final stages of old age, degeneration involves the whole worm and only the scolex hooks may be found within a very small cyst. The cysts are probably completely absorbed after the plerocercoid is dead; a careful search of a parasitized host will usually reveal a number of very small, solid, yellowish or orange bodies in the flesh; these are possibly cysts that are nearly all absorbed. Three stages are shown in



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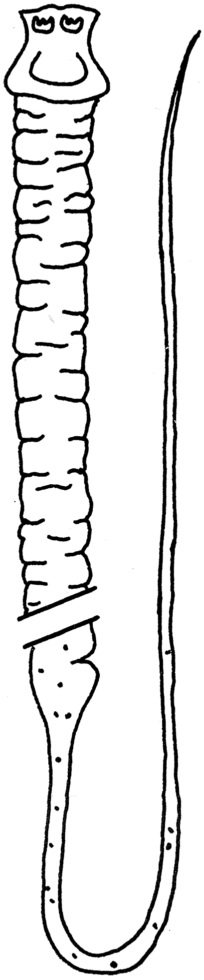

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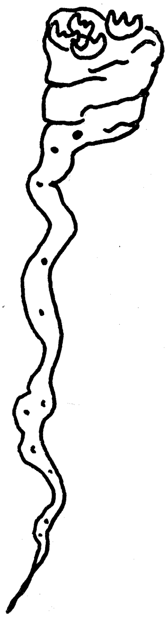

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PLATE VI

FIGURE 19. Sketch of a young plerocercoid of *T. crassus.*
FIGURE 20. Sketch of an older plerocercoid, showing the long cauda.
FIGURE 21. Sketch of a very old plerocercoid in which degeneration has reached the scolex.

Plate VI, figures 19, 20 and 21. This interpretation is supported by the fact that in four-year-old ciscoes, one-third of the cysts showed signs of degeneration, whereas in older fish (5–8 years), half the plerocercoids showed such signs. The fact that degenerate plerocercoids occur in four-year-old fish indicates that some of them, at least, do not live beyond four years.

In a previous section, the relationship between cyst content and age of host was discussed, and the infection of various age-groups of ciscoes was shown in Tables III, IV and V. A study of these tables shows that the cysts do not increase indefinitely as the fish grow older; a maximum is reached after which the number remains roughly constant or may decrease. Only such data as show the infection history of year-classes are reliable for the purpose of estimating the plerocercoid's life span; the data for Square and Baptiste Lakes allow an estimate of the age at which cyst numbers reach a maximum for five year-classes. In two of these, this age is five years, in one six years, and in two either five or six years. Certain other data, notably Keleher's Lake Winnipeg *L. nipigon* (Table VI), suggest a maximum at age 6 when considered by year-classes, but at a greater age when age-groups in a single sample are used; age-groups within a sample, however, are unreliable as the various degrees of infection they show may reflect unequal availability of worms in different years. As a reasonably conservative estimate, we may select six years as the age when maximum infection occurs in ciscoes. After six years, the rate of death and disappearance of plerocercoids equals or exceeds the rate of acquisition of new ones. Young ciscoes, in their first summer, will eat many fewer copepods than the adults do; their chances of infection are, therefore, less. Consequently, of the total cysts found in a six-year fish, very few would be cysts acquired in the first summer (even if still alive); we may, then discount the first summer. Now by combining this estimate with the information obtained by direct observation of plerocercoids, namely, that half the cysts in fish five years or more in age show signs of degeneration, we arrive at four or five years as the length of life of a plerocercoid.

E. COMPLETION OF LIFE-CYCLE

Miller (1945b) fed 39 captive pike pieces of tullibee flesh containing plerocercoids; the pike were caught during late May and early June, a period when they are known to be relatively free of *Triaenophorus*. Fifteen of the pike failed to digest their meal; captivity interfered with their digestive systems. Recoveries of newly established worms were made in eight pike; the plerocercoids were firmly embedded in the gut wall three days after arrival. They were very short—15–20 mm.—only about a third of their length at time of swallowing. A large portion is evidently sloughed off; ragged ends on the worms gave support to this supposition.

Nicholson (1932) fed plerocercoids of *T. crassus* to dogs and proved they were incapable of infecting them. Literally millions have been fed to mink without any evidence of infection. Other fish which feed on ciscoes, for example burbot and pikeperch, do not become infected. Apparently *Esox* spp. are the only hosts for the adult tapeworm.

F. SUMMARY OF LIFE-HISTORY OF *T. crassus*

For easy reference the major life-history details that have been described in the preceding sections are here summarized in tabular form (Table VIII).

TABLE VIII. Summary of the life-history of *T. crassus*.

Stage	Dimensions	Host	Length of life	Season
Egg	61 by 41 μ	None		Late April to early June
Coracidium	73 by 54 μ	None	2–3 days	Late April to early June
Procercoid	300 to 350 μ	*Cyclops bicuspidatus*	30 days	Early June to mid-July
Plerocercoid	35 to 130 mm.	*Leucichthys* spp. *Prosopium* spp. *Coregonus* *Cristivomer* *Stenodus* *Esox* *Thymallus*	4 or 5 years (?)	Arrive in host during July and August
Adult	130 to 400 mm.	*Esox lucius* *Esox masquinongy*	June to April or May	Mature from late April to early June

IV. CONTROL RESEARCH AND PROBLEMS

The great expense, loss and inconvenience caused by the infection of fishes with cysts of *T. crassus* demand that some measure of control be found and applied. The knowledge of the parasite's life-cycle, reported in the previous sections, must, of course, form the basis of any control programme. There are two aspects of control: the first is the immediate, or administrative, problem of what may be done now to alleviate the situation but not necessarily to provide a cure; the second is the research that must be done to find a permanent control measure.

A. SHORT-TERM MEASURES

SELECTION BY WEIGHT

In a previous section, the Lake-of-the-Woods cisco (*L. tullibee*) selection was described. The ciscoes are weighed, the larger and more heavily infected are used for animal food; the smaller and cleaner are used for human food. This method is practical only in a few places; there are no lakes where the whitefish may profitably be selected in this way. In most lakes ciscoes small enough to be acceptable from the parasite viewpoint are too small for the market.

SELECTION BY AREAS

In some large lakes it has been noted that whitefish taken in onshore areas are very much more heavily infected than offshore fish. The onshore fish are also darker in colour. It is possible to select the cleaner fish by taking those caught well offshore and of a light colour. In a few lakes certain bays show greater infection (for example, Lake Nipigon: Welch, 1952) and fishing may be prohibited in these areas. This method is also of very limited application.

CANDLING

Early in the 1940's some of the Alberta whitefish exporters began to candle whitefish. The whole fish were slid around on a glass plate over a light in a dark room. The cysts showed up as shadows. Exports from Lesser Slave Lake were very materially increased by this method. However, efforts to apply the method in other lakes met with indifferent success and it was finally concluded that only fish from certain lakes could be candled.

The peculiar nature of the infection in Lesser Slave Lake explains the success with candling: a small percentage of fish contained a large number of cysts, so that when the candler revealed no worms the fish was probably clean, and when it revealed any worms (one or more) the fish was probably heavily infected.

The candling method was next applied to whitefish fillets; here it is a very effective practice. It is often developed into a regular routine in which fish are filleted, the fillets passed to a candler, who cuts the cysts out of the moderately infected fillets and discards the heavily infected ones. This method has proven economical where infection is not heavy enough to cause high wastage of fillets. At the present time, filleting and candling is the only practical method of handling moderately infected fish.

Some research has been done by the Fisheries Research Board on X-raying of whole fish (McMurtie and Carter, 1948). While it was shown to be possible to reveal cysts by X-ray, no practical or economical method of doing it on a commercial scale could be found. The author tried candlers using polarized light, various coloured lights and different condenser systems without finding anything better than is now in use.

PRE-INSPECTION

When, in 1944, the Canadian Government officially assumed responsibility for the inspection of fishes infected with *T. crassus*, the method used was lake inspection. The whitefish-producing lakes in the Prairie Provinces were visited by survey crews who cut samples of fish and determined the cyst content. Whitefish from such inspected lakes were then handled according to the survey findings; those from lakes where infection was absent or small were granted an "A" inspection certificate and could be exported without processing; those from more heavily infected lakes were required to be processed in some way to remove the cysts, for example, by filleting or candling or both; such processed fish were granted a "B" certificate. This practice proved unsatisfactory in several respects;

it was not always possible to be certain from what lake whitefish had come; whitefish from different lakes could be mixed in one shipment; and, most important, the level of infection established by the survey was not always that found in subsequent samples of fish from the same lakes. These difficulties led the Department of Fisheries to institute the practice of pre-inspection. This switched the emphasis from lake inspection to inspection of actual shipments of fish. In order to reduce the numbers of fish needed to establish the degree of infection of a shipment to the absolute minimum, a considerable amount of research was conducted by the Central Station of the Fisheries Research Board. This work has been reported by Kennedy (1948) and Oakland (1950). As a result of these statistical studies a method of sequential analysis was developed whereby the number of cysts found by an inspector in the first one or few fish he examines determines how many, if any, more he needs to examine to establish a reliable verdict. This method gave the smallest reliable sample. However, in actual practice it proved to be too much trouble to keep returning to a car of fish for further samples. Oakland, therefore, devised a method in which a sample of a certain number of fish is taken, the number being based on the size of the shipment, lake of origin, size of fish, and the condition of the fish (filleted, round or dressed).

ANIMAL FOOD

Large quantities of highly infected ciscoes have been fed to mink in the Prairie Provinces. This is a satisfactory method of making good use of an otherwise unusable product. Bell and Thompson (1951) have made a survey of mink ranches and report that a very high proportion of such infected ciscoes in the diet apparently leads to no untoward results, provided adequate vegetables and other protective foods are also fed.

B. LONG-TERM CONTROL

Research on the control of *Triaenophorus crassus* is necessarily aimed at the destruction of one phase of its life-cycle; if one stage is eliminated or seriously checked, the worm in all its phases must disappear. There are, therefore, four approaches: the destruction of the adult, which may be accomplished by control of the adult host, the pike; the destruction of the plerocercoid, which is sought through reduction of the second intermediate hosts, the ciscoes and whitefish; the destruction of the procercoid, which would involve control of *Cyclops bicuspidatus*; and, finally, the destruction of the eggs or coracidia. A discussion of each of these possibilities may be found in a paper on the subject by Miller (1944). Up to the present time, research has been carried out on pike control, cisco control and elimination of coracidia. No work has been done on the control of *Cyclops*, as this animal is so widespread that were a method of control to be found, it would appear impossible to prevent its rapid re-entry into any lake. Further, *Cyclops* and its relatives (which would surely be killed as well) are essential in the food-chain of lakes, and their destruction would bring disaster greater than the tapeworms.

The three methods on which work has been done are now reported.

PIKE CONTROL

HEMING LAKE. Heming Lake is a 588-acre lake lying in Precambrian country about 80 miles north of The Pas, Manitoba. Dr. K. H. Doan of the Central Fisheries Research Station of the Fisheries Research Board of Canada has worked at pike control at Heming Lake since 1945, and his work has been continued by Mr. G. H. Lawler since 1950. Hoop nets have been operated each spring to capture pike, and use has also been made of gill-nets, trammel nets, poison, and a combination of the last two. In seven years of fishing, about two pounds of pike per acre were removed annually. However, the supply of pike did not diminish; while it became more and more difficult to catch them, this was due to a shift in the average size. Thus in 1945, four-fifths were 18 inches or over in length; in later years only a half exceeded 18 inches. As Heming Lake pike mature at 12 inches, the netting was not cutting down the brood stock, as fish of this size were not effectively exploited by the hoop nets.

The removal of two pounds of pike per acre for four successive years seemed to cause some decrease in the infection of whitefish. In 1946 only half as many cysts were found in the whitefish as in 1945; but after this initial decrease, the number of worms did not materially change. It was concluded that significant pike reduction by netting was practically impossible. The details of the pike removed and the infection of the whitefish are shown in Table IX.

TABLE IX. Pike removed and infection of whitefish with *T. crassus*; Heming Lake, Manitoba. (Data from Lawler, 1951b.)

Year	Number pike caught	Size (% 18″ and over)	Cysts per 100 whitefish
1945	563	82	528
1946	571	58	327
1947	931	48	322
1948	705	53	353
1949	490	59	350
1950	1071	39	333
1951	1075	47	314

In view of the discouraging results obtained by hoop-netting, it was decided to attempt to kill pike by poisoning. In the spring of 1949, 416 pike were caught, marked by fin-clipping and released. Then, in July, "Fish-Tox", a rotenone poison, was applied at the rate of 2.34 pounds per acre. A total of 694 pike was recovered; the marked pike included in the kill enabled a calculation of the proportion of pike over $15\frac{1}{2}$ inches which had been destroyed. This proportion was only 9 per cent of the population. Of course, many pike may have been killed and not recovered, but even allowing for an equal number lost in this way, the results were not encouraging. The experiment proved the impracticability of poisoning pike in large lakes, especially when the cost of the poison ($540 for Heming Lake) is considered.

In the fall of 1949, and again in the spring and summer of 1950, a trammel net was used at Heming Lake (Kennedy and Doan, 1949; Lawler, 1950c). This is a 100-yard net which is set parallel to the shore. The water between net and shore is disturbed and pike are driven into the net. It was soon discovered that the net did not take all the pike; a second attempt, immediately following the first, yielded about as many fish. It was also found that good catches could be made day after day along the same stretch of shore, that is, pike move in to favoured localities. Sandy bottom marshy bays were favoured at Heming Lake. As the trammel failed to take all the fish present between it and shore at one set, poison (emulsifiable rotenone) was used in combination. The net was set as usual, the areas beaten and the pike in the net removed. Then poison was added and the pike again removed from the net. Finally all dead pike between the net and the shore were counted. It was found that one-third of the pike was recovered each time, that is, one-third was taken by the trammel net, one-third blundered into the net trying to escape the poison, and one-third died inside the area. Altogether, 360 pike were taken in 39 sets. As with poison alone, the returns are not great in relation to the cost and effort. However, the trammel net plus poison seems a very effective if expensive way to kill pike.

SQUARE LAKE. This little lake has an area of 2.5 square miles. It lies in rolling wooded country near Lac La Biche, Alberta. It was selected for an experiment in pike control to be financed and carried out by the Fishery Branch of the Alberta Government. An account of the experiment has been published (Miller, 1950), and a brief summary is sufficient for this review. The purpose of the experiment was to kill pike with a rotenone poison during the early spring when pike were concentrated on their spawning grounds. In this way it was hoped to cut down on the amount of poison needed, and also avoid killing other species of fish.

In each of the springs of 1947, 1948 and 1949, pike were caught by netting, marked by clipping fins and released. Poison was then applied. The recovery of marked fish was very poor; in 1947, 21 of the 436 marked pike were recovered; in 1948, 11 of the 162 were recaptured; and in 1949, 48 of 330 were picked up after poisoning. These figures do not indicate the percentage kill, as many fish were killed and not recovered.

By using the 1948 and 1949 recaptures of fish marked in previous years, it was possible to calculate the probable total mortality each year. The results of these calculations are shown in Table X.

The effect of killing the pike on the tapeworms was measured by cutting up samples of ciscoes each year and counting the cysts in them. Altogether 1,687 ciscoes (*L. tullibee* ?) were examined. The results of the cuttings are shown in Table XI.

TABLE X. Pike populations and mortalities caused by poisoning in Square Lake.

Date	Pike population	Observed kill	Calculated kill
1947	1,456	225	495 (34%)
1948	1,076	430	538 (50%)
1949	3,190	1,617	2,740 (86%)

Table XI shows that a reduction in worminess of 39 per cent occurred during the experiment. Presumably this was caused by pike reduction. The cost of the experiment was more than $5,000; it is quite clear that pike reduction by poisoning is futile. The reduction in worminess achieved is not large enough to justify the expense, nor is there any indication that, given limitless money, pike could be reduced to the point where infection of ciscoes would be eliminated.

TABLE XI. Infection of ciscoes (*L.tullibee* ?) of each age with cysts of *T. crassus* in samples taken from Square Lake during the pike reduction experiment.

Date	No. fish cut	Ages and cysts/100 fish						Averages, all ages
		3	4	5	6	7	8	
Nov. 1946	302	668(81)	1053(180)	1291(34)	....	....	....	970
May 1947	100	....	1180(30)	1201(46)	1301(19)	....	....	1,200
Combined	..	....	....	....	....	....	....	1,080
FIRST POISONING—Calculated pike reduction of 34%								
July 1947	200	653(42)	925(51)	1066(62)	954(30)	....	....	890
Oct. 1947	201	592(41)	845(113)	950(45)	....	....	....	820
May 1948	72	....	580(15)	885(43)	1090(14)	....	....	860
Combined	..	....	....	....	....	....	....	856
SECOND POISONING—Calculated pike reduction of 50%								
Aug. 1948	200	525(41)	728(50)	730(56)	1005(41)	1135(11)	....	760
May 1949	112	1255(35)	1139(66)	1370(10)	....	....	....	1,190
Combined	..	....	....	....	....	....	....	890
THIRD POISONING—Calculated pike reduction of 86%								
Aug. 1949	500	413(22)	486(64)	630(139)	700(135)	790(95)	770(24)	657
	1,687							

Work at Heming Lake and at Square Lake, although carried out in different ways, led to the same conclusion: by present methods, pike reduction is not practical.

CISCO CONTROL

GENERAL CONSIDERATIONS. The reduction of cisco populations offers, theoretically at least, a method of *Triaenophorus* control. With few exceptions (Nesslin Lake, Saskatchewan; Siebert Lake, Alberta; Shakespeare Island Lake, Ontario: Welch, 1951), all lakes containing infected whitefish also contain infected ciscoes. The ciscoes are often *tullibee.* It is significant, in addition, that these ciscoes are more heavily infected than the whitefish. A considerable number of lakes contain pike, *Cyclops bicuspidatus* and whitefish, but no ciscoes. These lakes (with the three exceptions noted above) are free of *Triaenophorus.* In Alberta, Wabamum, Ste. Anne, Pigeon, Buck, Newall, Muriel, McGregor, Chin, Battle and other smaller lakes belong in this category; in Ontario, one such lake, Onaman Lake, and in Manitoba, Home Lake, have been investigated. These observations suggest that, in most lakes, the cisco is essential to the life-cycle of *Triaenophorus.* This conclusion is strengthened by the finding that infected Lesser Slave Lake whitefish grow more slowly than the non-infected, while infected *tullibee* scarcely differ in growth rate from the clean (Miller, 1945d). It would seem that ciscoes are the more natural hosts because well-adjusted parasites have little effect on their benefactors. This is all the more probable when one considers the feeding habits of ciscoes and whitefish; ciscoes are primarily plankton-eaters and, as a result, *Cyclops* forms a normal part of their diet; whitefish, although they do eat plankton, feed more consistently on bottom fauna. Thus one would expect to find ciscoes regularly infected with *Triaenophorus* and whitefish irregularly so. It is tempting to regard the infection of whitefish as an accidental "spill-over" from the ciscoes, and indeed, most of our lakes indicate that this is the case. However, there are exceptions and these will receive full discussion in a later section.

THE TAXONOMIC PROBLEM IN CISCOES. From the foregoing discussion it is evident that ciscoe reduction offers a plausible possibility of controlling *T. crassus.* There is, however, one important difficulty: ciscoes of different species exhibit different degrees of infection with *T. crassus*, even though occupying the same lake. This is well shown in Keleher's data from Lake Winnipeg (Table VI) which have already been discussed. In Lake Winnipeg two levels of infection were found; one in *Leucichthys zenithicus*, *L. nigripinnis* and *L. tullibee* and the other, higher level, in *L. nipigon.* Thus, to deal intelligently with ciscoes as hosts for *Triaenophorus*, it is necessary to identify them specifically. The determination of species of the genus *Leucichthys* is a difficult and highly specialized task, and problems have been encountered which are yet unsolved. (See, for example, the discussion of the *Leucichthys* problem in Dymond, 1943.) Mr. J. J. Keleher, of the Central Station of the Fisheries Research Board, is currently engaged in this cisco taxonomy problem. It is possible that a thorough knowledge of the taxonomy of the ciscoes will provide the key to their ecology which will, in turn, explain the different infection levels of different species.

Experiments on the reduction of ciscoes for purposes of controlling *T. crassus* infections have been carried out on two lakes, Lesser Slave Lake, Alberta, and Mosher Lake, Saskatchewan. In both these lakes the most abundant (perhaps the only) cisco is *L. tullibee.*

THE LESSER SLAVE LAKE EXPERIMENT. More or less unrestricted cisco (*L. tullibee*) fishing has been permitted in Lesser Slave Lake since 1941. The ciscoes are used for mink feed. Catches rose from a pre-1941 annual average of 60,000 pounds to an annual take of over four million pounds. The age composition of the ciscoes, as determined by annual samples, has changed tremendously. In 1941, samples taken with $2\frac{3}{4}$-inch nets contained fish up to eight years old; six-year-olds were the largest age group. By 1947, there were only a few fish over three years and nearly eighty per cent were two-year-olds. This age composition has continued to the present time. This large removal of all the older ciscoes has taken a tremendous reservoir of *Triaenophorus* cysts out of the lake. This appears to have a very great influence on the infection of the whitefish. Cyst counts of whitefish and ciscoes from 1944 to the present time are shown in Table XII.

Cyst content of ciscoes reached a minimum of 22.6 cysts per 100 in 1947, having decreased from 890 cysts per 100 in 1944. The whitefish cyst count decreased in the same way from 265 in 1944 to 26 in 1947. The whitefish infection increased in 1948 and then decreased to the present lowest value of 5.20. The ciscoes, on the contrary, began, after 1947, to get more wormy; age analyses (Table III) have shown that, at the present time, the two-year-olds are wormier than they have ever been. There are no data which explain this phenomenon; possibly the enormous population of two-year-olds, which has arisen as a result

TABLE XII. Infection of ciscoes and whitefish in Lesser Slave Lake. (Figures in parentheses show number of fish examined.)

Year	Cysts per 100 fish		Per cent infected	
	ciscoes	whitefish	ciscoes	whitefish
1944	890 (332)	265 (490)	93	30.8
1945	591 (100)	185 (500)	75	17.4
1946	....	....	....	....
1947	22.6(301)	26 (601)	10.9	6.8
1948	28.6(500)	81.6(500)	21	13.4
1949	72.6(500)	49.6(500)	39.8	12.4
1950	155.4(500)	20 (500)	62	3.4
1951	243.6(500)	5.2(500)	72.8	2.6

of the depletion of the older age-groups, has enabled the re-establishment of a normal tapeworm life-cycle—a cycle which came near to breaking with the sudden cisco depletion which reached its greatest point in 1947. Thereafter, the increasing abundance of young ciscoes restored the normal cisco-tapeworm relationship.

The dramatic reduction of whitefish infection in Lesser Slave Lake may be due to a peculiarity of the Lesser Slave infection. In figure 22 the per cent infection of whitefish is plotted against the average number of cysts per fish for 33 lakes selected at random from the three Prairie Provinces. A smooth curve is drawn through the points, which lie along it reasonably well. The same data for Lesser Slave Lake are also plotted; the points represent the different degrees of infection during the years 1944–51. It is clear that Lesser Slave differs materially from the other lakes; it is characterized by a much higher number of cysts per fish for any given percentage infection; that is, a small number of fish contained a much larger than normal number of cysts. This condition may be the explanation of the rapid decrease in infection observed during the ciscoe removal experiment.

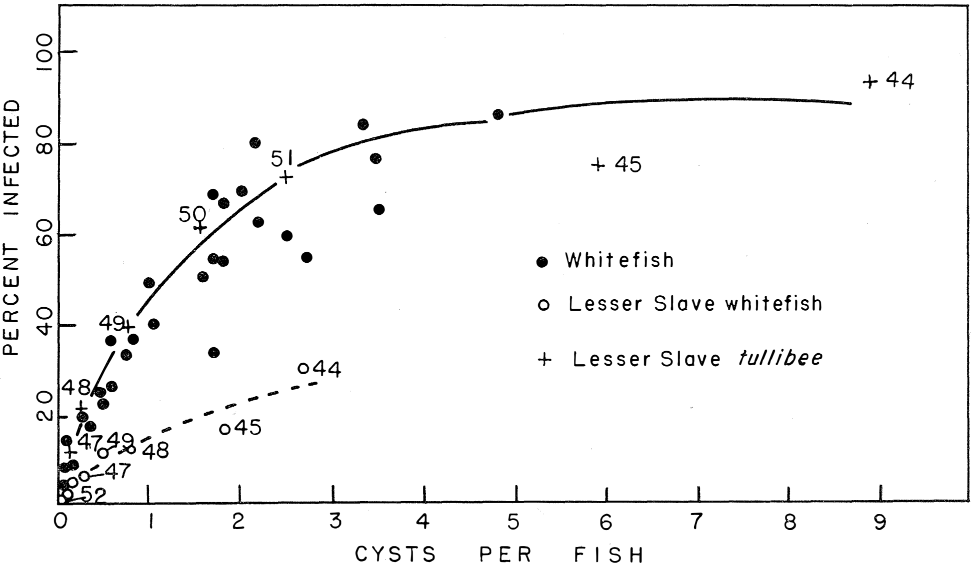

FIGURE 22. Relation between cyst content and per cent infection in whitefish from 33 Prairie Province lakes; the same relation in *L. tullibee* from Lesser Slave Lake, 1944–52, is also shown.

In conclusion, the Lesser Slave Lake data suggest that cisco reduction has been effective in controlling *Triaenophorus* infestation in whitefish; they also indicate that such control will remain operative as long as the cisco population is kept very young by intensive fishing. Thus accumulation of a large cyst population and subsequent large-scale "spill-over" into whitefish may be avoided. A separate account of the Lesser Slave experiment has been published (Miller, 1948).

MOSHER LAKE. This is a small lake in Saskatchewan; it has an area of 0.83 square miles and lies close to Amisk Lake into which it drains. Tests in 1948 revealed heavily infected populations of ciscoes and whitefish. In the summers of 1948 and 1949, under the direction of Dr. D. S. Rawson, with financial support of the Fisheries Research Board, a campaign of cisco removal was carried on. In 1948, 2,900 pounds were taken and 4,532 in 1949. Whitefish infestation stood at 97 cysts per 100 pounds in 1948; in 1949 it dropped to 71.5 and in 1950 to 48.5 cysts per 100 pounds. This experiment has not continued far enough to either substantiate or disprove the general application of the Lesser Slave Lake results. Cisco reduction has not been severe, as the age-composition of the 1949 samples shows a high percentage of fish five to eight years old.

CONTROL OF CORACIDIA

GENERAL CONSIDERATIONS. The eggs and coracidia of *Triaenophorus* are the only stages in the life-cycle which are not parasitic, that is, not contained in the body of some host. They are, therefore, vulnerable to direct attack. About ten years ago the author began introducing chemicals to cultures of eggs and coracidia of *T. crassus* and other species of *Triaenophorus*. The idea was to find some chemical which would either prevent the eggs from hatching, or kill the coracidia or a combination of both. To be satisfactory, the chemical should be harmless to humans and to aquatic creatures and, also, to be useful on a large scale, cheap. Early work with laboratory cultures showed that increasing the acidity of the medium to pH 5.0 would kill the coracidia. Accordingly, in 1945, a field experiment based on this discovery was conducted at Baptiste Lake (Miller and Watkins, 1946).

THE BAPTISTE LAKE EXPERIMENT. Baptiste Lake, near the town of Athabaska, Alberta, has an area of approximately eight square miles. It contains pike and a fairly heavily infected population of ciscoes (*L. tullibee*). The pike spawning areas are confined to a number of bays which aggregate about eight miles of shore line with an average depth of three feet. This area was treated with 20 tons of concentrated sulphuric acid during May 14–17 and May 22–29, the main pike spawning periods. It was hoped that, since the pike and tapeworm spawning periods coincided, most of the tapeworm eggs would be exposed to acid. The quantity of acid added was more than enough to reduce the known alkalinity (175 p.p.m.) of the lake water. However, it was found the surface waters regained their usual pH of 8.0 within a half hour and the bottom mud returned to pH 8.0 within approximately twelve hours.

The effect of the experiment on *Triaenophorus* was assessed by counting the cysts in, and determining the age of, 637 *tullibee* during March to July and 200 during October. The first lot established the infection rate existing prior to the experiment, that is, before the 1945 crop had invaded the *tullibee*; the second lot showed whether this 1945 crop had or had not materialized. The second lot revealed that a normal crop of cysts had developed; the experiment was, then, a failure. The reserve of buffer in the bottom deposits of the lake evidently neutralized the acid before any effect on eggs or coracidia could take place.

THE SEARCH FOR CHEMICALS. One result of the Baptiste Lake experiment was to demonstrate that any chemical, to be satisfactory, must be stable in lake water. Accordingly, substances, for example copper sulphate, which react with the carbonates in the water, are ruled out. The author sought the help of Dr. M. J. Huston, Director of Pharmacy at the University of Alberta. With his advice and participation, tests were carried out on laboratory cultures of eggs and coracidia during the springs of 1946, 1947 and 1948. Altogether 46 chemicals were tested over a series of concentrations. Several of the inorganic dyes were found to be particularly effective in reducing hatching and in killing coracidia. However, these were too expensive for field use. Most of the chemicals tested, were ineffective at low concentrations; others were poisonous and, therefore, dangerous; no really satisfactory material was found. In 1949, Mr. M. L. Libin, a graduate student at the University of Alberta, was employed by the Fisheries Research Board to continue the search for a suitable chemical. Mr. Libin worked under the direction of Dr. Huston and the author. The Alberta Government provided a supply of pike.

Mr. Libin gave very thorough tests to another 15 chemicals. The fifteenth, Dow K604, proved highly effective. Most of the spring of 1950 was devoted to extensive tests of this chemical. It proved wholly effective in killing coracidia at a concentration of 0.35 p.p.m. Tests were run on goldfish at this concentration; the goldfish lost some colour, but were not killed. A complete account of the chemical research may be found in Mr. Libin's M.Sc. thesis in the University of Alberta library, or at the Central Fisheries Research Station, Winnipeg.

TEST OF DOW K604 IN SQUARE LAKE. The encouraging laboratory tests of Dow K604 led to a field test in Square Lake during the spring of 1952. The Fisheries Research Board purchased 2000 pounds of the chemical. Alberta Fisheries employees, under the author's direction, introduced this into the three main pike spawning areas of Square Lake, Alberta, on May 7th and 8th. The Dow K604 was mixed with water, in barrels, to form a batter, which was then poured into the wake of a slowly moving outboard. Samples of the treated water, taken 24 hours after treatment, proved toxic to laboratory cultures of coracidia; but samples taken 48 hours after treatment were not toxic. It was not surprising, therefore, to find that the treatment failed to reduce *tullibee* infection. The degree of infection of 300 *tullibee* taken in October 1951 was 8.03 cysts per fish; in October 1952, 391 *tullibee* contained an average of 8.75 cysts per fish.

It would seem not feasible to treat a portion of a lake. The rate of exchange of shoreward and lakeward water is too rapid and the chemical is soon diluted below effective concentration.

EFFECT OF ELECTRICITY. Part of Mr. Libin's work was a test of the effect of electricity on coracidia. Professor J. A. Harle, Department of Electrical Engineering, University of Alberta, designed a suitable cell in which to test the effect of A.C. current. Experiments with this cell were run using voltages of 2–120 and times of exposures from 5–30 seconds. While the results are not consistent, they do show that coracidia are resistant to sufficiently large doses of electricity to render field use impracticable.

V. DISCUSSION

The *Triaenophorus* problem is fundamentally an ecological problem. The presence or absence of *Triaenophorus* infection in a particular lake is determined by the interrelationships of the pike, coregonine fishes and *Cyclops* in that lake. Clearly, if the tapeworm is to be successful, *Cyclops* must be available for the coracidia in April and May; this means that pike and *Cyclops* must be together at that time of the year, in most lakes the period when the former spawn. Not more than one month later, coregonine fish must be available to eat the procercoids contained in the infected *Cyclops*; this is accomplished by ciscoes in almost all lakes, by ciscoes and whitefish together in many lakes and by whitefish alone in a very few lakes. As it seems improbable that individual *Cyclops* range very far within any one lake, it follows that the coregonine fish, to become infected, must come to the same part of the lake where the pike released the tapeworm eggs and where the *Cyclops* became infected; in almost all lakes this will be an inshore area used by pike for spawning purposes. Finally, to complete the cycle, pike must feed on these same coregonines at some time during the year. The gist of all this is that pike and coregonines must occupy the same niche of a lake at least part of the year; and this part-year must be made up of one period in the spring or early summer. The tapeworm's success is wholly dependent on this intermixing of pike and coregonines at the right times; this appears to be the weakest link in the chain joining the parasite to its several hosts. The absence of parasites in coregonines in many lakes or parts of larger lakes may be explained as a failure of this link. The link may fail for a variety of reasons; some of these are now discussed.

TEMPERATURE; KENNEDY'S LINE

Dr. W. A. Kennedy, of the Central Station of the Fisheries Research Board, has made a very interesting observation on the distribution of *Triaenophorus*. He has sketched a line on the map of Canada in such a way that infected lakes lie north of it, clean lakes south of it. The line obviously resembles an isotherm and follows the same path as an isotherm, that is, its bends north and south coincide with the bends of isotherms. Dr. Kennedy was struck with the resemblance which led him to postulate that temperature was involved. From Fry's work on the seasonal movement of ciscoes (Fry, 1937), and some work of his own of a similar nature, he reasoned that north of the line, the water warms slowly and the coregonines linger in the richer, shallow water until well into the summer; south of the line the more rapidly warming water drives the coregonines into deep water much earlier in the year, *too early to contact infected Cyclops*. Here we have a simple, logical explanation of the northern preference of *Triaenophorus* and of its southward extension only in large lakes which warm slowly in the spring.

There are, of course, exceptions; some infected lakes lie south of Kennedy's line. It is probable that individual lake morphometry is playing a major rôle in these; thus, if a lake is very deep or very well protected from wind action (small lakes) or a combination of both, the slowly-warming feature, essential for the parasite, will be present.

ABUNDANCE OF FISH HOSTS

In the previous section it was shown how temperature, particularly speed of warming in the spring, may either separate or bring together *Cyclops* bearing procercoids and suitable second intermediate hosts. Temperature characteristics may, therefore, act as a barrier of an ecological kind between two or more successive stages of the parasite's life-cycle. In some lakes, however, where temperature characteristics appear the same as in infected lakes, the parasite is absent. These lakes may be explained by assuming that the abundance of fish hosts is not suitable for *Triaenophorus*. The two extremes of this condition are (1) absence of suitable second intermediate host and, (2) absence of primary host. It is unlikely that either extreme is required to eliminate the parasite; more probably there is a critical abundance of pike and a critical abundance of coregonines, that is, populations, which if any smaller, would destroy the life-cycle chain. It is also probable that these critical populations affect each other; the parasite may survive a smaller cisco population when pike are unusually numerous than when they are not. As coregonines are lower in the food-chain than pike, they are normally more numerous. The tapeworm life-cycle is adjusted to this arrangement; thus, the absolute coregonine minimum will be a much larger population (about five times as great) as the absolute pike minimum. This argument is strengthened by this consideration: in a lake of average infection level, a pike may acquire five to ten parasites from eating one cisco; one cisco has to consume many *Cyclops* to acquire one plerocercoid; the tapeworm life-cycle seems to require a relatively larger coregonine than pike population.

The foregoing theoretical considerations should be corroborated by field data; unfortunately information on absolute and/or relative size of pike and coregonine populations is almost completely lacking. Also it is not usually possible to completely divorce temperature effects from relative abundance effects. In spite of these limitations, there are a few examples which seem to illustrate the argument:

(1) LAKES WITH NO CISCOES. The majority of such lakes are free of *Triaenophorus*. They are examples of lakes whose coregonine population *available to Triaenophorus* is too small. The whitefish in these lakes fail to support the parasite because they eat too few parasitized *Cyclops*; this may be due to their total consumption of plankton being too small or it may be that temperature barriers are operating to keep the whitefish in deep water at a critical time of the year (when infected *Cyclops* are available). Nesslin Lake and Shakespeare Island Lake are notable exceptions: though lacking ciscoes, their whitefish support a heavy *Triaenophorus* population. This seems to be due to one or more or a mixture of several things: the lakes are very small, their whitefish grow very slowly and are extremely abundant, and plankton forms a significant part of the whitefish diet. The small size of the lakes ensures that whitefish remain within "range" of *Cyclops*; the slow growth makes them small and readily edible for pike; abundance and a plankton-feeding habit complete the picture.

(2) ALL HOSTS PRESENT. These lakes contain ciscoes, whitefish and pike and a widely varying amount of *Triaenophorus* infection. These different amounts of infection are no doubt partly caused by differences in latitude, shape of lake basin

and other factors which influence rate of warming during open season; but they are also caused partly, if not largely, by differences in numbers of pike, ciscoes and whitefish. Because of differences in availability and seasonal distribution, gill-net returns are very unreliable for assessing relative numbers of different species of fish. Consequently, we have no accurate data on pike: coregonine numbers in any lakes. There are, however, some very suggestive approximate data. Muskeg Lake, with a very high level of infection has an approximate 1: 1 pike: coregonine ratio (Welch, 1950). Lac La Biche has abundant pike and coregonines; in 1944 the whitefish were 22 per cent infected and contained 50 cysts per hundred fish. In 1947 a severe winter-kill drastically reduced the whitefish and ciscoes and the fishery collapsed. The infection level dropped, by 1951, to 5.7 per cent of the whitefish, infected with 9.5 cysts per hundred. The experiment on Lesser Slave Lake illustrates the same thing. We have evidence, therefore, that abundance of coregonines is a necessity for parasite success. There is little or no evidence that abundance of pike is required. The experiments on Square and Heming Lakes show that a relatively small pike population can keep a large *Triaenophorus* population in existence.

OTHER FACTORS

Temperature-caused ecological barriers and relative abundances are not the only factors which determine presence or absence of *Triaenophorus* infection, though they are probably the principal ones. Two others could be operative: pike spawning migration out of the main lake, and peculiar feeding habits. Where two lakes are connected, pike may spawn in the smaller and shallower and leave *Triaenophorus* behind when they return to the larger, deeper lake where the coregonines live. Such a situation is believed to exist in Alberta, but it has not been investigated. Owing to unusual local conditions, populations of coregonines may have feeding habits which exclude *Cyclops* from the diet. No such situation has been found.

SUMMARY OF VARIOUS LAKE TYPES

The points brought out in this discussion are readily fitted into a summation scheme as follows:

A. CLEAN LAKES

I. Absence of definitive host, the pike.
II. Absence of any suitable second intermediate host (no such lake known).
III. Absence of ciscoes; whitefish present but failing to function in the life-cycle.
    (1) The whitefish do not eat sufficient *Cyclops*.
    (2) The pike fail to eat sufficient whitefish.
    (3) Ecological separation of whitefish and pike or whitefish and *Cyclops*.
IV. All usual hosts present.
    (1) Coregonines move to deep water before *Cyclops* become infected; warmer, southern lakes.
    (2) Pike leave lake in spring at spawning time.
    (3) Too few second intermediate hosts.
    (4) Chemistry of lake waters unfavourable for coracidia.

B. INFECTED LAKES

I. All usual hosts present; majority of our whitefish-producing lakes.
  (1) Conditions borderline for parasite; coregonines with less than one cyst per fish and fewer than ten per cent infected.
  (2) Infections of 1 to 1.5 cysts per whitefish; up to fifty per cent infected.
  (3) Very heavy infections of 1.5–10 cysts per whitefish and 50 to 100 per cent of the fish infected.
  (4) Inshore coregonines heavily infected; offshore coregonines less heavily infected, sometimes clean. Large lakes where at least two non-mixing coregonine populations exist.

II. Ciscoes absent; small lakes in which whitefish serve as sole second intermediate host.

VI. SUMMARY

The tapeworm, *Triaenophorus crassus*, in one of its larval stages (the plerocercoid), infects the flesh of all fishes of the whitefish family as well as lake trout, the arctic grayling and the inconnu. The presence of these cysts in the flesh of the common whitefish and ciscoes is a serious drawback to the Canadian inland fishing industry. Producers have been forced to stop fishing lakes whose whitefish are heavily infected; many have begun filleting the catch and passing the fillets over a candler which reveals the cysts so that they may be removed. The Canadian Government has set up an inspection system for whitefish and the Fisheries Research Board has developed a statistical procedure for the inspectors to follow in deciding the number of fish needed to establish a reliable judgment of infection level. The object of this review has been to bring together all the pertinent information on the parasite, not only regarding the details of its life-cycle, but also the various possibilities of control.

The tapeworm lives as an adult in the intestine of the great northern pike or jackfish; here it reaches maturity in the spring, releases its embryos and dies. The embryos pass into the water where they soon hatch from the shell enclosing them. The free-swimming larva which emerges, called a coracidium, must be swallowed by a minute crustacean, *Cyclops*, to survive and develop. In the body cavity of the *Cyclops* the parasite grows into a stage called the procercoid. This, within its *Cyclops*, must be eaten by a suitable fish in order to grow further. Such fishes are the whitefish and ciscoes. In the fish the procercoid passes to the flesh where it develops into a long slender worm, called a plerocercoid, enclosed in a yellowish capsule. These capsules are the cysts whose presence is so objectionable in the flesh of food fishes. When a pike swallows a fish infected with these cysts, the contained plerocercoids develop into adult worms in the pike's intestine and the life-cycle is completed.

Several aspects of this life-cycle are incompletely known; full details are lacking on how the procercoid proceeds from the stomach to the flesh of a fish which has swallowed it; nor is it known how long they require, having reached the flesh, to transform to plerocercoids and become enclosed in cysts; and finally the period of years during which plerocercoids remain capable of infecting pike has not been determined by direct observation but only by inference.

The problem of control is still very far from solution. Theoretically four approaches are possible: the reduction or elimination of pike; of coracidia; of

Cyclops; and of ciscoes (the principal hosts of the plerocercoids). Research has proceeded on all these lines except the reduction or elimination of *Cyclops*. Each line of research has turned up secondary problems which have required attention before the work could be completed. Attempts to reduce infection by reduction of pike have been made in Manitoba at Heming Lake and in Alberta at Square Lake; netting of various kinds and poisoning were employed. The general conclusion reached is that the method is too costly and inefficient unless better means of killing pike are discovered.

Killing of coracidia has been unsuccessfully attempted by acidifying a lake; considerable laboratory work with coracidia has turned up one chemical very effective in laboratory cultures; this chemical has not had a field test. The effects of electricity on coracidia have also been investigated; it was found that the coracidia were too resistant to allow economical control with electricity. This work on coracidial control is still in progress.

Control through reduction of ciscoes has been attempted on Lesser Slave Lake in Alberta and Mosher Lake in Saskatchewan. The results of the latter experiment are inconclusive; in the former considerable success has been achieved. The infection of ciscoes and whitefish in Lesser Slave Lake was very materially reduced by catching so many ciscoes that few beyond the age of two years existed in the lake. It is not clear at the present time if this is a permanent cure; trends of infection in the ciscoes are currently upwards.

The cisco of Lesser Slave Lake is *Leucichthys tullibee.* In this fish cysts build up with age, that is, they accumulate with time and it is this feature which probably explains the success of the Lesser Slave work. Researches on the ciscoes of Lake Winnipeg have shown that this accumulation with age does not occur in all ciscoes; thus the taxonomy of ciscoes has become an essential part of control research.

Surveys of many different lakes, whose fish range all the way from no infection to heavy infection, have revealed that infection levels depend on the complex interactions of environmental and biological factors. For example, rapid warming of lake waters in the spring may drive whitefish and ciscoes to deep water before they have eaten *Cyclops* infected with procercoids (available only in the shallows); such lakes would be free of infection. Again it has been argued that many clean lakes are so because of absence of ciscoes; the relative importance of ciscoes and whitefish in the parasite's life-cycle is another problem under investigation.

The research which has been carried out thus far has served to emphasize that the *Triaenophorus* problem is not capable of easy or quick solution. It is fundamentally an ecological problem which will require long and patient work before any effective control may be expected.

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VIII. LITERATURE CITED

ARNASON, I. G. 1948. Infestation of *Cyclops bicuspidatus* with *Triaenophorus* at Heming Lake, Manitoba, during the summer of 1948. *Fish. Res. Bd. Canada, Ann. Rept. of the Central Fisheries Research Station for 1948*, App. 16, pp. 26–27. (Mimeo.)

BELL, J. M. AND C. THOMPSON. 1951. Freshwater fish as an ingredient of mink rations. *Bull. Fish. Res. Bd. Canada*, No. 92, pp. 1–13.

COOPER, A. R. 1918. North American Pseudophyllidean cestodes from fishes. *Illinois Biol. Monogr.*, **4**, 289–541.

DYMOND, J. R. 1943. The coregonine fishes of northwestern Canada. *Trans. Royal Canadian Inst.*, **24**(2), 171–231.

EKBAUM, E. 1935. Notes on the species of *Triaenophorus* in Canada. *J. Parasitol.*, **21**(4), 260–263.

1937. On the maturation and hatching of the eggs of the cestode, *Triaenophorus crassus* Forel, from Canadian fish. *Ibid.*, **23**(3), 293–295.

FRY, F. E. J. 1937. The summer migration of the cisco, *Leucichthys artedi* (Le Sueur), in Lake Nipissing, Ontario. *Univ. Toronto Studies, Biol. Ser.*, No. 44 (*Pub. Ontario Fish. Res. Lab.*, No. 55).

HJORTLAND, A. L. 1928. On the structure and life history of an adult *Triaenophorus*. *J. Parasitol.*, **14**, 38–44.

KELEHER, J. J. 1952. Growth, maturity and *Triaenophorus* parasitism in relation to taxonomy of Lake Winnipeg ciscoes. *J. Fish. Res. Bd. Canada*, **8**(7), 469–478.

KENNEDY, W. A. 1948. Sufficient samples for quality control in whitefish. *Bull. Fish. Res. Bd. Canada*, No. 76, pp. 3–11.

KENNEDY, W. A., AND K. H. DOAN. 1949. Tests of a trammel net as a means of destroying pike. *Fish. Res. Bd. Canada, Ann. Rept. of the Central Fisheries Research Station for 1949*, App. 7, p. 29. (Mimeo.)

LAWLER, G. H. 1950a. *Triaenophorus* studies at Heming Lake. *Fish. Res. Bd. Canada, Ann.Rept. of the Central Fisheries Research Station for 1950*, App. 7, pp. 24–28. (Mimeo.)

1950b. Notes on *Triaenophorus nodulosus* in Heming Lake. *Ibid.*, App. 8, pp. 28–30. (Mimeo.)

1950c. Trammel netting for pike at Heming Lake. *Ibid.*, App. 11, pp. 31–34. (Mimeo.)

1951a. Observations on *Triaenophorus* at Heming Lake and vicinity. *Fish. Res. Bd. Canada, Ann. Rept. of the Central Fisheries Research Station for 1951*, App. 1, pp. 14–15. (Mimeo.)

1951b. Pike control and whitefish infestation, Heming Lake. *Ibid.*, App. 3, pp. 16–19. (Mimeo.)

1951c. The identification of Heming Lake ciscoes, and parasitism with *T. crassus*. *Ibid.*, App. 5, pp. 20–21. (Mimeo.)

Libin, M. L. 1951. Laboratory experiments on the control of the tapeworm, *Triaenophorus crassus.* (Unpublished M.Sc. thesis, University of Alberta, April, 1951.)

McMurtrie, G. E., and N. M. Carter. 1948. The inspection of whitefish flesh for parasitic worms. *Fish. Res. Bd. Canada, Progress Reports (Pacific)*, No. 77, pp. 95–97.

Michajlow, W. 1932. Les adaptations graduelles des copépodes comme premier hôtes intermediaire de *Triaenophorus nodulosus* (Pallas). *Ann. Parasitol. Humaine et Comp.*, **10**(4), 334–344.

1933. Les stades larvaire de *Triaenophorus nodulosus* (Pallas). I. Le coracidium. *Ibid.*, **11**(5), 339–358.

Miller, R. B. 1943a. Studies on cestodes of the genus *Triaenophorus* from fish of Lesser Slave Lake, Alberta. I. Introduction and the life of *Triaenophorus crassus* Forel and *T. nodulosus* (Pallas) in the definitive host, *Esox lucius. Canadian J. Res.*, D, **21**, 160–170.

1943b. Studies on cestodes of the genus *Triaenophorus* from fish of Lesser Slave Lake, Alberta. II. The eggs, coracidia and life in the first intermediate host of *Triaenophorus crassus* Forel and *T. nodulosus* (Pallas). *Ibid.*, 284–291.

1944. Suggestions for experiments in the control of the pike-whitefish tapeworm, *Triaenophorus crassus. Pub. Alberta Dept. Lands & Mines, Fisheries Service*, 15 pp., Edmonton.

1945a. Studies on cestodes of the genus *Triaenophorus* from fish of Lesser Slave Lake, Alberta. III. Notes on *Triaenophorus nodulosus* (Pallas) in the second intermediate host. *Canadian J. Res.*, D, **23**, 1–5.

1945b. Studies on cestodes of the genus *Triaenophorus* from fish of Lesser Slave Lake, Alberta. IV. The life of *Triaenophorus crassus* Forel in the second intermediate host. *Ibid.*, 105–115.

1945c. Studies on cestodes of the genus *Triaenophorus* from fish of Lesser Slave Lake, Alberta. V. Description and life history of *Triaenophorus stizostedionis* n. sp. *Ibid.*, 117–127.

1945d. Effect of *Triaenophorus* on growth of two fishes. *J. Fish. Res. Bd. Canada*, **6**(4), 334–337.

1946. Notes on the Arctic grayling, *Thymallus signifer* Richardson, from Great Bear Lake. *Copeia*, **1946**(4), 227–236.

1947. Great Bear Lake. *Bull. Fish. Res. Bd. Canada*, No. 72, pp. 31–44.

1948. Reduction of *Triaenophorus* infestation in whitefish by depletion of the cisco population. *Canadian J. Res.*, D, **26**, 67–72.

1950. The Square Lake experiment: An attempt to control *Triaenophorus crassus* by poisoning pike. *Canadian Fish Culturist*, **7**, 3–18.

Miller, R. B., and H. B. Watkins. 1946. An experiment on the control of the cestode, *Triaenophorus crassus* Forel. *Canadian J. Res.*, D, **24**, 175–179.

Miller, R. B., and M. J. Huston. MS. Effect of certain chemicals on the eggs and coracidia of *Triaenophorus crassus.* (An address to the Science Association, University of Alberta, 1948.)

Newton, M. V. 1932. The biology of *Triaenophorus tricuspidatus* (Bloch 1779) in western Canada. *Contrib. Canadian Biol. and Fish.*, **7**, 343–360.

Nicholson, D. 1932. The *Triaenophorus* parasite in the flesh of the tullibee (*Leucichthys*). *Canadian J. Res.*, D, **6**, 162–164.

Oakland, G. B. 1949. Statistical studies of whitefish infestation. *Fish. Res. Bd. Canada, Ann. Rept. of the Central Fisheries Research Station for 1949*, App. 9, pp. 30–31. (Mimeo.)

1950. An application of sequential analysis to whitefish sampling. *Biometrics*, **6**(1), 59–67.

Rawson, D. S., and R. R. Wheaton. 1950. Studies of *Triaenophorus crassus* in Nesslin Lake, Saskatchewan, 1950. *Fish. Res. Bd. Canada, Ann. Rept. of the Central Fisheries Research Station for 1950*, App. 4, pp. 18–21. (Mimeo.)

MS. Whitefish-*Triaenophorus* investigations on Mosher Lake, Saskatchewan, 1949. (Typewritten manuscript, 8 pp. May, 1950.)

Rosen, F. 1919. Récherches sur le développement des cestodes. I. Le cycle evolutif des Bothriocephales. Etude sur l'origine des cestodes et leur états larvaires. *Bull. Société Neuchâtiloise des Sciences Naturelles,* **43, 241–300.**

SCHEURING, L. 1929. Beobachtungen zur Biologie des Genus *Triaenophorus* und Betrachtungen über das jahrezeitliche Auftreten von Bandwürmern. *Z. f. Parasitenkunde*, **2**, 157–177.

WARDLE, R. A. 1932. The Cestoda of Canadian fishes. II. The Hudson Bay drainage system. *Contrib. Canadian Biol. and Fish.*, **7**, 379–403.

WELCH, H. E. 1950. *Triaenophorus* investigations in the Thunder Bay district, Ontario. *Fish. Res. Bd. Canada, Ann. Rept. of the Central Fisheries Research Station for 1950*, App. 6, pp. 22–23. (Mimeo.)

1951. *Triaenophorus* investigations in the Thunder Bay district, Ontario, in 1951. *Fish. Res. Bd. Canada, Ann. Rept. of the Central Fisheries Research Station for 1951*, App. 8, pp. 23–26. (Mimeo.)

1952. Factors affecting the infection of the whitefish, *Coregonus clupeaformis* (Mitchill), by the tapeworm, *Triaenophorus crassus* Forel, in the Thunder Bay district of Ontario. (Unpublished M.A. thesis, University of Toronto, 1952.)