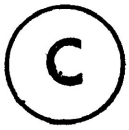
MIGRATION AND DEVELOPMENT OF *CYSTIDICOLA* SPP. (HABRONEMATOIDEA) IN THEIR DEFINITIVE HOSTS AND THE POPULATION BIOLOGY OF *C. CRISTIVOMERI* WHITE, 1941 in *SALVELINUS* SPP.

by



GEOFFREY ALAN BLACK

A thesis
presented in partial fulfillment of the requirements
for the degree of Master of Science

Department of Biology
Lakehead University
Thunder Bay, Ontario
May, 1980

Abstract

The development of *Cystidicola cristivomeri* in lake trout, *Salvelinus namaycush*, and *C. farionis* in rainbow trout, *Salmo gairdneri*, is described. The population biology of *C. cristivomeri* was investigated in lake trout in three lakes in northwestern Ontario and in arctic char, *S. alpinus*, in Gaviafaeces Lake, Northwest Territories.

Young lake trout fed selectively on large *Mysis relicta* which were more frequently infected with *C. cristivomeri* (up to 5.1%) than small mysids. *Pontoporeia affinis* was not a suitable intermediate host in nature and there was no evidence that fish paratenic hosts were important in transmitting this nematode to lake trout.

Third-stage larvae given to lake trout migrated directly *via* the pneumatic duct to the swimbladder. In experimentally infected fishes, at 4-10°C, *C. cristivomeri* were mature after 67 (males) and 210 days (females); *C. farionis* were mature after 112 (males) and 235 days (females). There was no measurable mortality of *C. cristivomeri* after 600 days in experimentally infected lake trout.

Field studies indicated that most *C. cristivomeri* live at least 10 years and some probably live longer. The development of female worms to sexual maturity was retarded and they grew more slowly when large numbers of *C. cristivomeri* were present in the swimbladder. Short female worms produced

eggs at a slower rate than longer females. This density dependent regulation of *C. cristivomeri* at the infrapopulation level may result in long-term stability of the nematode suprapopulation in a lake.

The number of ulcerative lesions on the inner surface of the swimbladder of lake trout was directly dependent upon the number of mature *C. cristivomeri* present in a fish.

Acknowledgements

I would like to express my sincere thanks to Dr. Murray W. Lankester for his support, advice and encouragement throughout this study and especially for his invaluable assistance during the preparation of this thesis.

I am indebted to Dr. Lionel Johnson, of the Freshwater Institute in Winnipeg, Manitoba, and his crew at Nauyuk Lake in 1979 for providing facilities and hospitality while I was in the Arctic, for the use of equipment, and for aging arctic char. I thank Mrs. Irene Weir of London, Ontario for aging lake trout scales.

I am grateful to Mrs. M. Jones for her painstaking technical assistance, and also to Mrs. L. Ryder for encouragement and technical assistance throughout this study.

Several people from the Ontario Ministry of Natural Resources were helpful during this study including T. Chisholm, R. Ryder and his crew, D. Sakiyama, C. A. Elsey and R. Hamilton. In addition, I appreciate the cooperation of the numerous anglers who regularly fished the three study lakes in northwestern Ontario and to Kemp Fisheries, Thunder Bay, who provided swimbladders from coregonids.

I wish to thank Drs. W. Momot, R. Freitag and S. Magwood for their editorial assistance, Dr. W. Momot for laboratory facilities and Mrs. B. Salo for typing this manuscript.

Financial support for operating costs was provided from an NSERC Operating Grant to Dr. Lankester.

Table of Contents

List of Figures

List of Tables

Introduction

Nematodes of the genus *Cystidicola* are parasitic in the swimbladder of salmonid fishes. Two species are presently recognized; *C. cristivomeri* White, 1941, reported only from char, *Salvelinus* spp., in North America and *C. farionis* Fischer, 1798, from a variety of salmonids in Eurasia and North America. *Cystidicola cristivomeri* develops to the infective stage in the opossum shrimp, *Mysis relicta* Lovén, and *C. farionis* develops in various amphipods (Smith and Lankester 1979). The development of these worms in their definitive hosts has not been studied.

Cystidicola cristivomeri appears to have a wide distribution in North America but undoubtedly the extent of its distribution is incompletely known. This nematode has been reported from lake trout, *S. namaycush* (Walbaum), from Lac La Marte, Northwest Territories (N.W.T.) and from several inland lakes in Ontario (Ko and Anderson 1969; Dechtiar 1972; Lankester and Smith *in press*). It has also been reported from arctic char, *S. alpinus* (L.), from the N.W.T. in rivers draining the Foxe Basin (Jamieson 1972), Char Lake (Beverly-Burton 1978), Sommerset Island (Eddy and Lankester 1978) and Boothia Peninsula (Lankester unpubl.) and from brook trout, *S. fontinalis* (Mitchill), in Ontario (Lankester and Smith *in press*).

Recently, some parasitologists have begun to examine parasite populations using concepts previously applied only to free-living animals (Crofton 1971b; Anderson 1974a, 1978; Holmes *et al* 1977). This has proven to be an intellectually stimulating and productive approach contributing to a better understanding of mechanisms that regulate growth and stability of parasite populations. However, these populations differ basically from those of free-living species in that two levels of organization rather than one must be recognized (Esch *et al* 1975). In the present paper, infrapopulation refers to the nematodes present in the swimbladder of an individual fish and suprapopulation includes the total of all swimbladder nematodes in all fish and larval stages in all intermediate hosts within a lake.

To date, most studies of parasite populations have been conducted on species with either seasonal or annual life cycles and many are found in a variety of definitive hosts within the same ecosystem. Preliminary investigations suggested that *C. cristivomeri* is long-lived and it frequently infects a single definitive host. In addition, this parasite occurs in oligotrophic lakes providing a relatively simple ecosystem in which to study the dynamics of a parasite population.

This study was undertaken to determine the migration route and to describe the development of *Cystidicola* spp. in their definitive hosts, determine the life span of *C. cristivomeri* and examine its transmission and population biology in nature.

Study Area and Methods

The biology of *Cystidicola cristivomeri* was studied in lake trout from three separate lakes (Burchell, Greenwater and Squeers) within 100 km of Thunder Bay, Ontario, and in arctic char from Gaviafaeces Lake, Kent Peninsula, Northwest Territories (68°20'N, 107°45'W). Burchell Lake (48°35'N, 90°38'W; area = 1027 ha; depth, maximum = 75 m, mean = 24 m) (Fig. 1) and Squeers Lake (48°31'N, 90°33'W; area = 387 ha; depth, maximum = 34 m, mean = 11 m) (Fig. 2) are in the James Bay watershed. Greenwater Lake (48°34'N, 90°26'W; area = 3060 ha; depth, maximum = 55 m, mean = 18 m) (Fig. 3) is in the Lake Superior watershed. The three lakes are 442-488 m above sea level, stratified in summer, usually ice covered from November to April, oligo-mesotrophic and have a potential annual fish production of 0.28-0.37 kg/ha (Ontario Ministry of Natural Resources, Thunder Bay District, unpublished data).

Northern pike, *Esox lucius* L., yellow perch, *Perca flavescens* (Mitchill), white sucker, *Catostomus commersoni* (Lacépede), and deepwater sculpin, *Myoxocephalus quadricornis* (L.), co-habit with lake trout in all three lakes. In addition, Burchell Lake contains walleye, *Stizostedion vitreum* (Mitchill), lake herring, *Coregonus artedii* Lesueur, burbot, *Lota lota* (L.), ninespine stickleback, *Pungitius pungitius* (L.), rock bass, *Ambloplites rupestris* (Rafinesque), two species of darters,

Fig. 1. Map with depth contours (ft.) of Burchell Lake, northwestern Ontario ($48^{o}35'N$, $90^{o}38'W$).

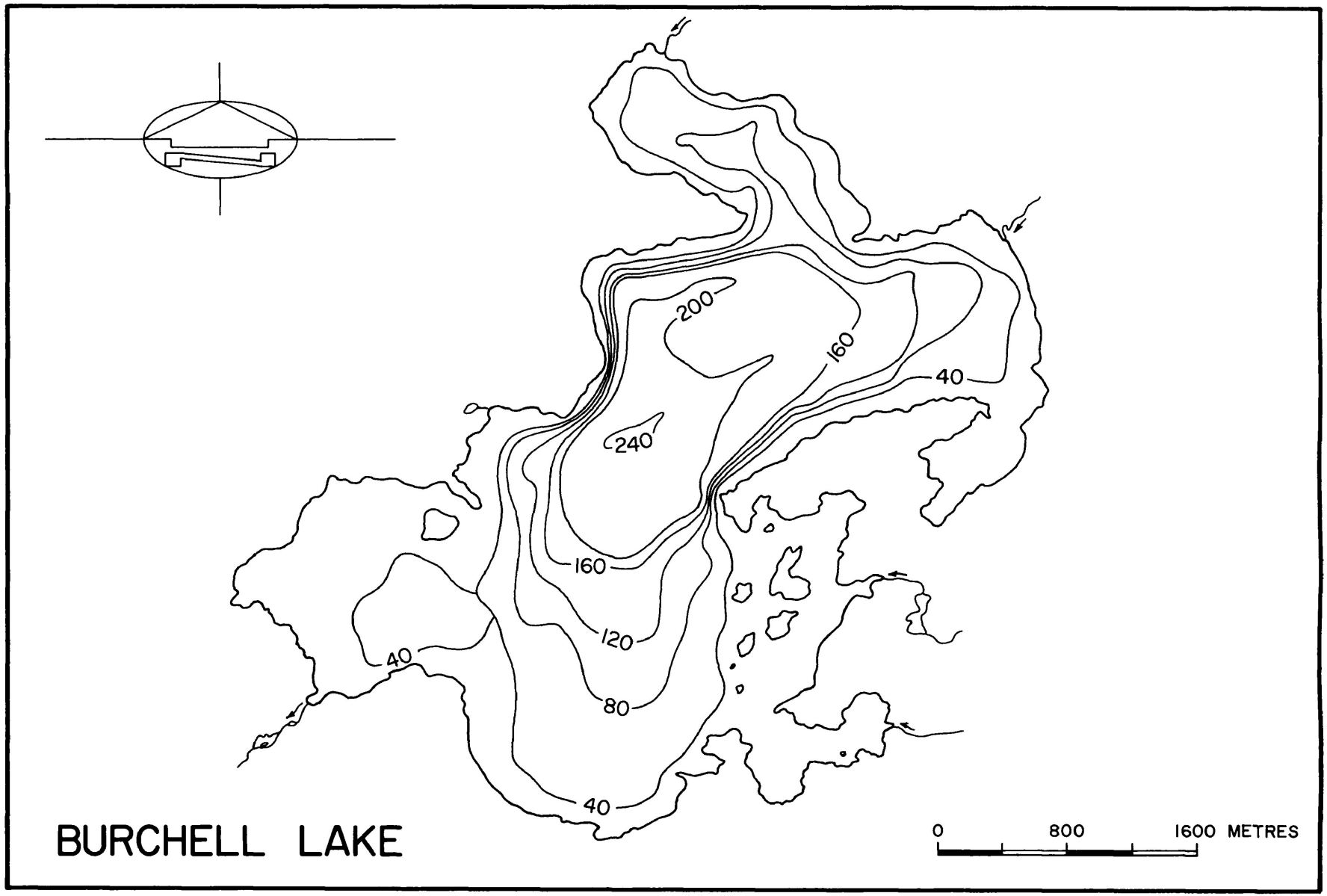

200
160
40
240
160
120
40
80
40
BURCHELL LAKE
0
800
1600 METRES

Fig. 2. Map with depth contours (ft.) of Squeers Lake, northwestern Ontario ($48^{o}31'N$, $90^{o}33'W$).

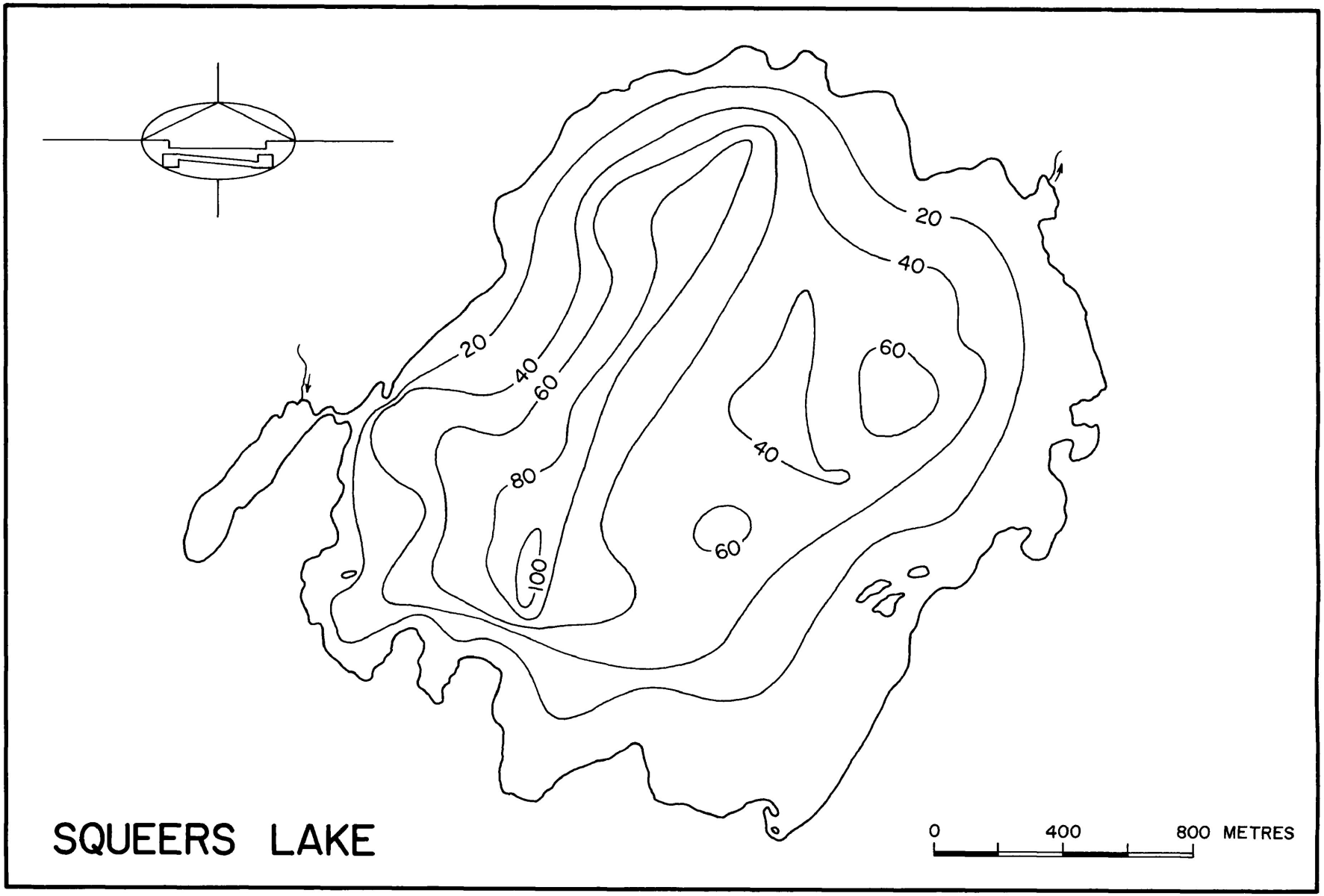
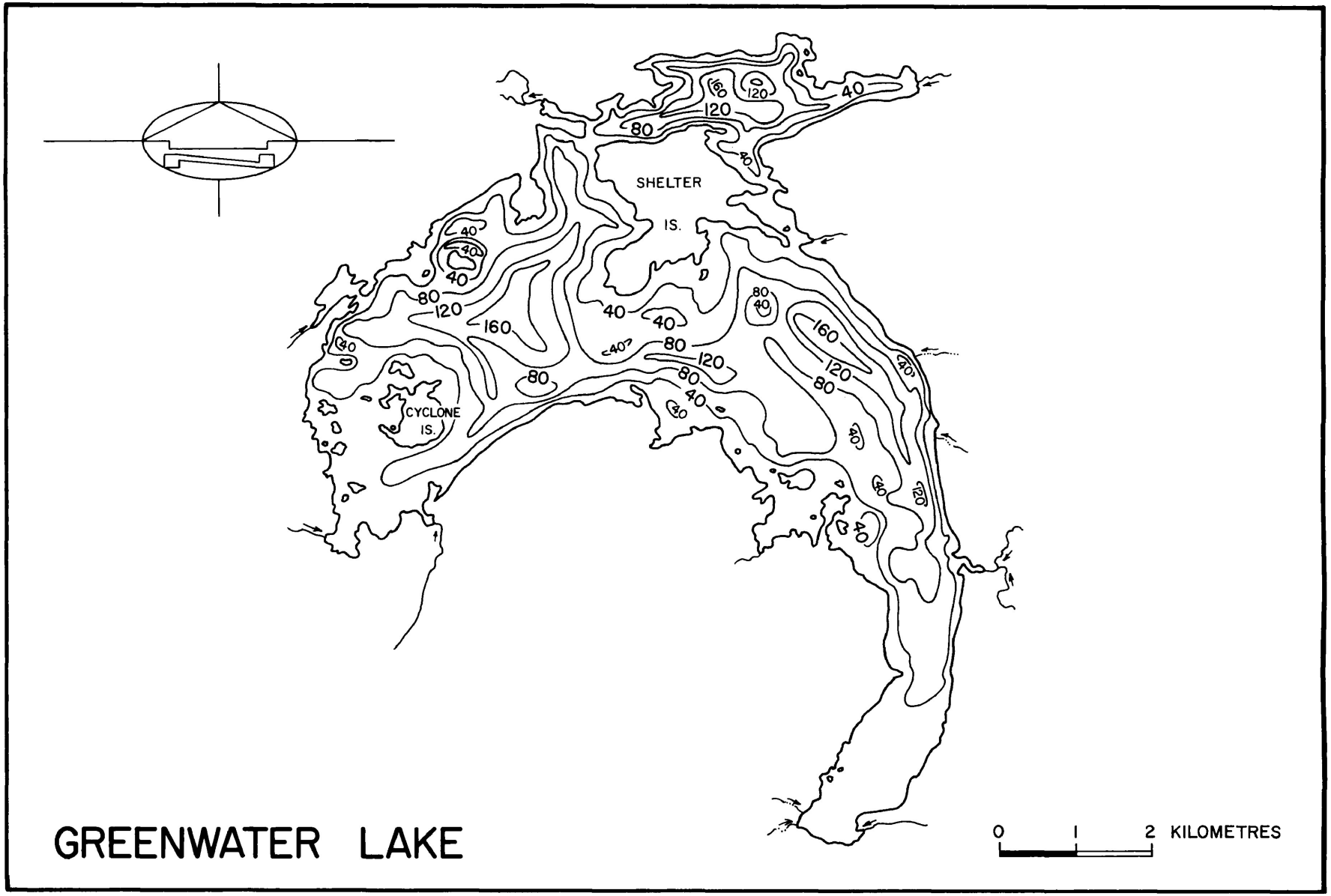

20
40
60
80
100
20
40
60
40
60
SQUEERS LAKE
0
400
800 METRES

Fig. 3. Map with depth contours (ft.) of Greenwater Lake, northwestern Ontario ($48^{o}34'N$, $90^{o}26'W$).



GREENWATER LAKE

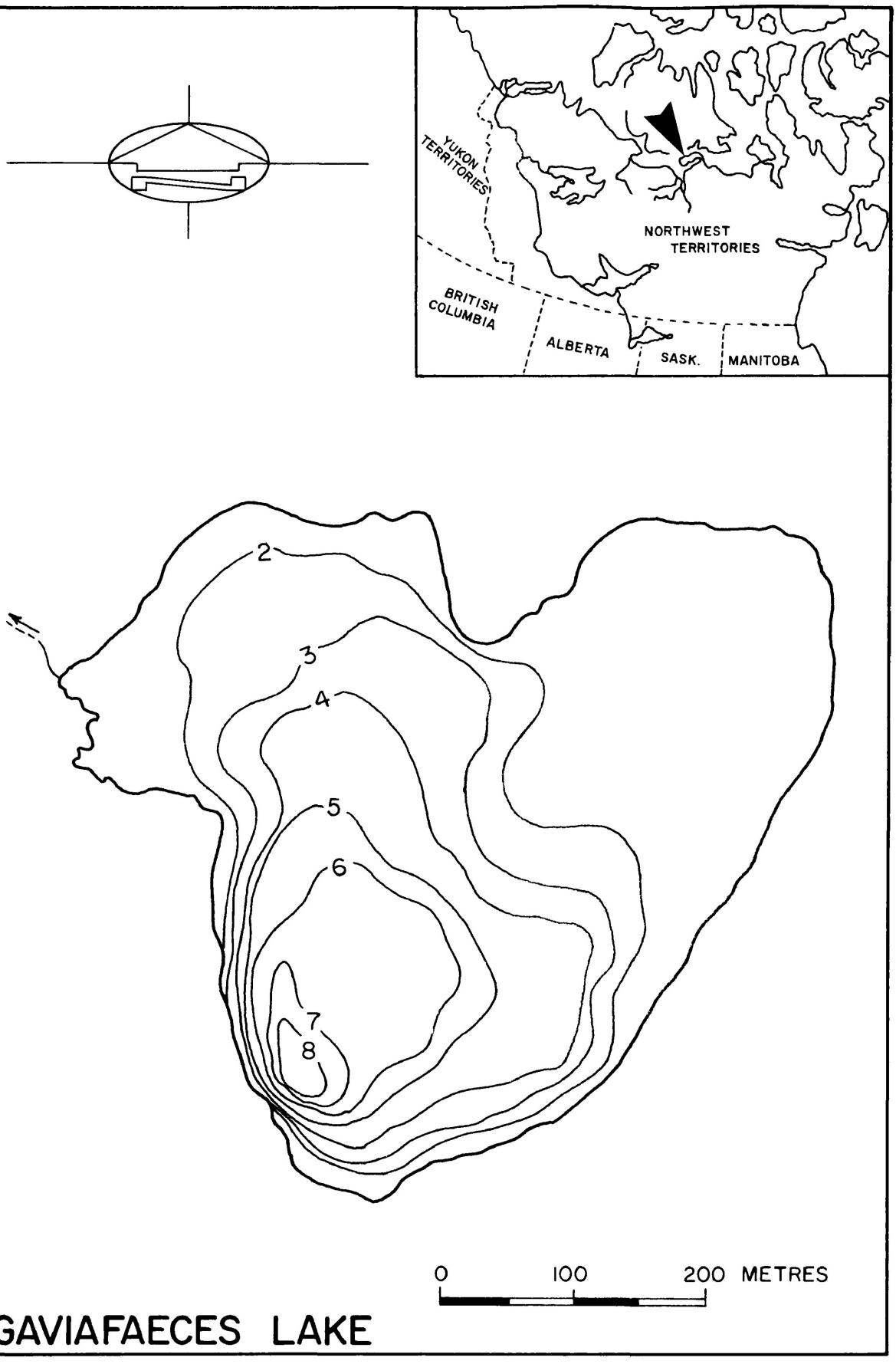
Etheostoma spp., and several species of cyprinids; Squeers Lake contains three species of cyprinids; and Greenwater Lake contains lake herring, lake whitefish, *Coregonus clupeaformis* (Mitchell), ninespine stickleback, burbot and least darter, *E. microperca* Jordan and Gilbert. Nomenclature of fishes follows Scott and Crossman (1973).

Gaviafaeces Lake (area = 17.4 ha; depth, maximum = 8 m, mean = 2.9 m) (Fig. 4) is ice-covered for 10-11 months of the year. Arctic char are land-locked in Gaviafaeces Lake and are the only fish present. Food items consumed by the char in decreasing order of importance are chironomid larvae and pupae, sphaeriid clams and *Mysis relicta* (Dr. L. Johnson, Canada Department of Fisheries and Oceans, Freshwater Institute, Winnipeg, Manitoba, pers. comm. 1979).

Lake trout (generally >30 cm fork length) were examined from anglers' catches from the three study lakes in northwestern Ontario, July-September 1978 and January-July 1979. Smaller lake trout were collected using gill nets (10-25 mm bar mesh) in October 1978, and July and October 1979. Arctic char (>10 cm long) were captured in Gaviafaeces Lake using the same gill nets as above; electrofishing was used to collect smaller specimens.

The swimbladder and stomach from each fish were preserved in 10% formalin. Swimbladders inadvertently ripped during removal from fish were discarded. The ages of fish were

Fig. 4. Map with depth contours (m) of Gaviafaeces Lake, Northwest Territories ($68^{o}20'N$, $107^{o}45'W$).


YUKON TERRITORIES
NORTHWEST TERRITORIES
BRITISH COLUMBIA
ALBERTA
SASK.
MANITOBA
2
3
4
5
6
7
8
0
100
200 METRES
GAVIAFAECES LAKE

determined by examining scales from lake trout and otoliths from arctic char. Otoliths and scales were collected from a few additional lake trout to compare results of the two methods of aging. Data recorded for each fish included fork length, weight and sex. Bladder length and color of the flesh (scale 1 to 5) were recorded for lake trout only.

Swimbladders were cut open and the inner surface examined for lesions. Only the number of discrete lesions were recorded. Nematodes were scraped from the swimbladder into settling flasks and a visual estimate of the number of specimens in each sample was made. All worms were counted in samples estimated to contain less than 200 specimens. Samples of 200-1000 were subsampled by transferring the worms to a graduated cylinder and adding a volume of water (ml) equal to the estimated number of worms in the sample. The cylinder was agitated and 100 ml of the suspension were quickly poured off. The worms in this subsample were counted. Samples estimated to contain 1000-3000 worms were first placed in 1500 ml of water in an Erlenmeyer flask. The flask was agitated and 500 ml of the suspension poured off. This portion of the original sample was then subsampled using a graduated cylinder as described previously. Samples estimated to contain more than 3000 worms were suspended in 1500 ml of water in an Erlenmeyer flask and 500 ml poured off. This decanted volume

was made up to 1500 ml in another flask and the 500 ml of suspension poured off was then subsampled using a graduated cylinder. The number of worms in the subsample was multiplied by the appropriate dilution factor to obtain an estimate of the total number of worms in the original sample. The accuracy of the subsampling method (2 SD < ± 19%) was assessed by counting all worms in 23 samples containing 200-1500 worms.

The subsample of worms was counted and examined in glycerin using a dissecting microscope at 7-45X. Female worms with shelled eggs in their uteri and males with caudal alae and spicules or a tail coiled at least 540^{o} were considered mature; all others were considered immature. The maximum and minimum lengths of immature worms in each sample and the length of the three longest male and female worms were recorded.

Stomach contents were identified, divided into respective groups and measured volumetrically.

Lake herring in Burchell and Greenwater Lakes were examined as potential paratenic hosts of *C. cristivomeri*. The visceral cavity of 71 lake herring (5.0-16.9 cm) were opened and the whole fish immersed in a fish gastric digest solution (Meyer and Olsen 1971) in Baermann funnels. The swimbladder was removed from 27 lake herring (17.0-24.9 cm) and examined for *C. cristivomeri*; the remaining viscera were digested. The

gastro-intestinal tract, swimbladder and remaining viscera from 10 additional lake herring (17.0-24.9 cm) were removed and digested separately. All digests were examined after 2-4 h for *C. cristivomeri*. Stomach contents from many lake herring were identified.

The abundance of third-stage *C. cristivomeri* larvae in naturally infected *M. relicta* was estimated during October, 1979 in each of the three study lakes in northwestern Ontario. Mysids were captured by towing a conical hoop net (1.0 m diam., 3.5 m long, mesh opening = 0.4 mm) beneath the thermocline at night and a small otter trawl (see Dadswell 1975 for details) along the lake bottom during the day. Specimens were measured from the tip of the rostrum to the tip of the uropods and divided into two groups; small (3.0-16.9 mm) and large (17.0-24.0 mm). Mysids, in pepsin solution, were put in a blender for 3 sec and then poured onto tissue paper in a Baermann funnel. Larvae passed through the tissue paper and settled to the bottom of the funnel within 3 h at room temperature.

The suitability of *Pontoporeia affinis* as a natural intermediate host for *C. cristivomeri* was also investigated. Amphipods were captured in Squeers Lake in the fall, 1978, using a small epi-benthic sled and were examined for larvae in the manner described for mysids.

The route of migration and development of *C. cristivomeri* and *C. farionis* in lake trout and rainbow trout, *Salmo gairdneri* Richardson, respectively, were investigated. Trout used in experimental infections had been raised in captivity and were fed a commercially prepared pelleted fish food. Experimentally infected fish were kept in 350 l polyethylene tanks with a continuous supply of dechlorinated water (flow = 2 l/min, 4-10^{o}C). Larvae of *C. cristivomeri* used in experimental infections originated from naturally infected *M. relicta*. *C. farionis* were obtained from the swimbladder of lake whitefish captured in Lake Nipigon in February, 1979. Fishes were anesthetized with ethyl m-aminobenzoate methanesulfonate (MS-222) and given larvae suspended in cold 0.7% NaCl or cold dechlorinated water using a Rusch #8 stomach tube. Infected fish commonly regurgitated larvae while recovering from anesthesia but attempts to collect and count expelled larvae were unsuccessful.

Migrating larvae were recovered from fish at various intervals post-infection by examining separately the lumen of the stomach, esophagus, pneumatic duct and swimbladder. These and all other visceral organs were then pressed between glass plates and examined for larvae using a dissecting microscope. Visceral organs and skeletal muscle were later placed in a pepsin solution for 2-4 h at room temperature in Baermann funnels. Worms recovered were fixed in hot 10% glycerin in 70% alcohol and cleared in glycerin. Drawings and measurements were made

with the aid of a *camera lucida*. *En face* preparations followed Anderson (1958).

The relative number of eggs released by female *C. cristivomeri* of different sizes was investigated using worms from lake trout from Greenwater and Squeers Lakes collected in June and October, respectively. Thirty female worms from individual fish were placed in 0.7% NaCl in a 20 ml test tube sealed with paraffin and kept at $8^{o}C$ for 166-170 h. Worms were then removed from the test tubes, fixed in hot glycerin-alcohol, and measured. Samples containing damaged worms were discarded. Test tubes were centrifuged at 2500 rpm for five minutes and decanted. The remaining fluid was agitated with a magnetic stirrer for 15 min, pipetted onto slides, and examined at 100X. The tubes were rinsed by adding a few drops of water and the procedure repeated until the number of eggs from the last rinse was <10% of the total counted from all previous slides.

Statistical procedures followed Zar (1974) and Nie *et al* (1975). Statistical significance of all analyses was at the 0.05 probability level. Normality of distributions was examined by calculating the third moment statistic (Remington and Schork 1970). Data deviating from normality, not alleviated by appropriate transformations, were analysed with non-parametric statistics whenever possible; otherwise parametric statistics were used in conjunction with ANOVA (Zar 1974).

RESULTS

Migration of *Cystidicola* spp. to the swimbladder

Experimentally infected lake trout (15-25 cm long) and rainbow trout (10-25 cm) frequently regurgitated after larvae were administered. Thirty-two percent of *C. cristivomeri* larvae given to lake trout were recovered; larvae of *C. farionis* given to rainbow trout were not counted. All larvae recovered were third stage (Table 1). Six to eight h after infection, larvae were found only in the stomach of fishes. Shortly thereafter, larvae were found in the lumen of the esophagus and in the short pneumatic duct. Larvae reached the swimbladder as early as 16 h after infection. No larvae were recovered from any of the other tissues examined.

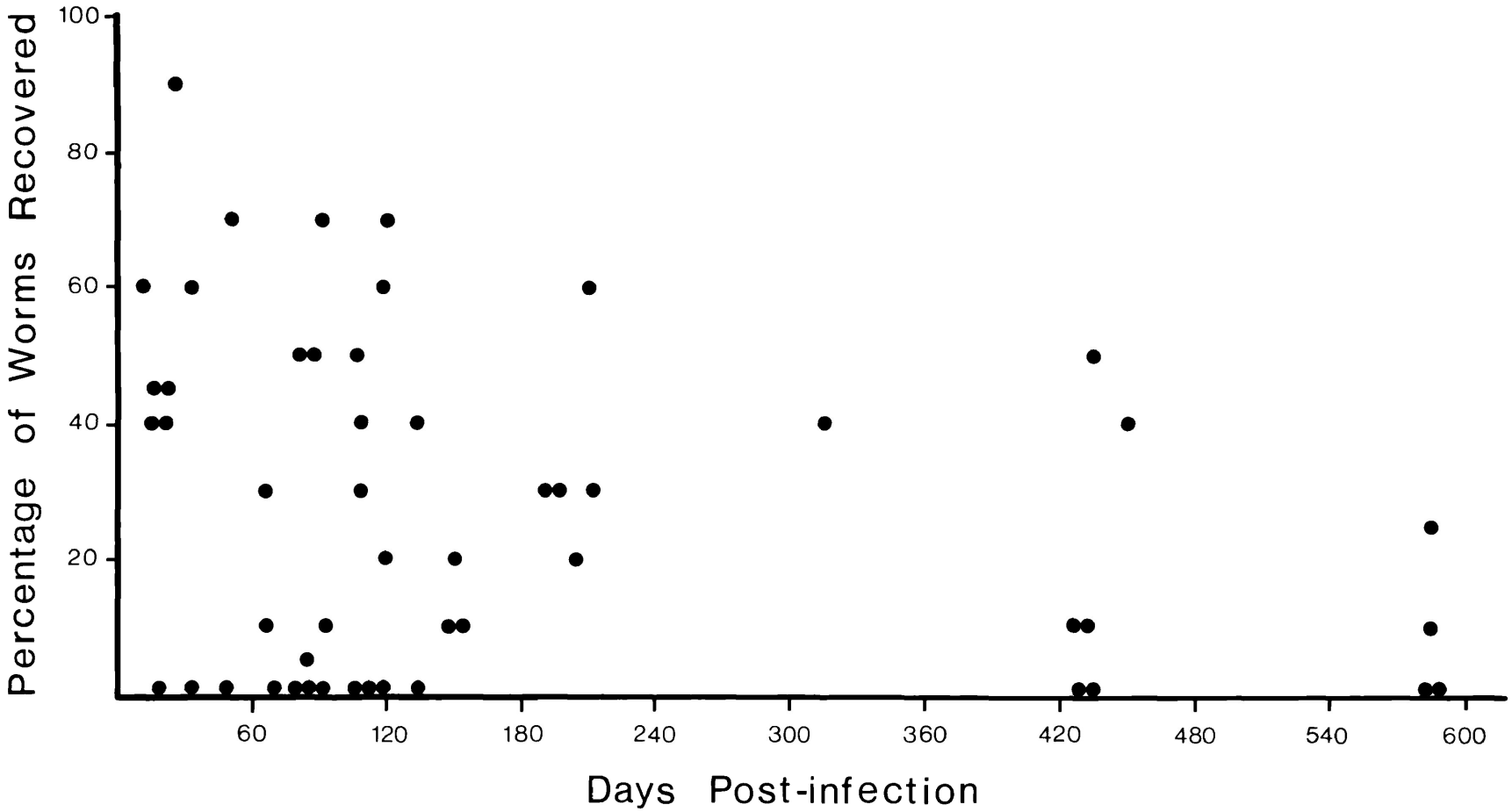
Development of *C. cristivomeri* in experimentally infected lake trout

Infective larvae of *C. cristivomeri* used in this experiment were from naturally infected *M. relicta*. Twenty-six percent of 650 larvae given to 52 lake trout were recovered 14-600 days after infection. There was no significant correlation between the percentage of worms recovered from each fish and time post-infection (Spearman $r=-0.16$, $N=52$) (Fig. 5).

Table 1. Number and location of *Cystidicola cristivomeri* and *C. farionis* recovered from lake trout and rainbow trout, respectively, at various times after infection (4-10°C).

Species	Hours after infection	No. of fish examined/no. with larvae	No. of larvae recovered			
			Stomach	Esophagus	Pneumatic duct	Swimbladder
C. cristivomeri	6-8	2/1	2	0	0	0
	12-17	4/4	12	3	0	0
	18-23	9/8	13	7	0	17
C. farionis	6-8	2/1	1	0	0	0
	16-17	2/1	3	3	0	14
	18	1/1	20	46	1	37

Fig. 5. Percentage of *Cystidicola cristivomeri* recovered from experimentally infected lake trout killed at various intervals post-infection.


Percentage of Worms Recovered
100
80
60
40
20
60
120
180
240
300
360
420
480
540
600
Days Post-infection

Larvae at the third moult were first recovered after 20 days; some had not yet begun to moult after 50 days. Third-stage larvae underwent little growth prior to the moult. Smaller larvae took longer to reach the moult and moulted at a smaller size than larger larvae. However, worms of equal length recovered from different fish infected and killed on the same days, often differed in their state of development. No differences were seen between male and female larvae in the time required to reach the third moult. Male and female larvae undergoing the fourth moult were recovered after 84-104 and 84-203 days, respectively. Only the longest females were moulting at 84 days; some had not yet begun to moult after 455 days. Mature male and female worms were first recovered after 67 and 210 days, respectively. Most males were mature within 100 days of infection. Mature male and female *C. cristivomeri* from lake trout killed within 600 days of infection were 11.4-19.9 mm and 15.5-26.1 mm long, respectively.

Third-stage *C. cristivomeri* larvae from *Mysis relicta*

Considerable variation in length; females usually longer than males (Table 2). Male gonad convoluted, extending anteriorly to middle of body and not extended to the rectum. Female gonad straight, extending into anterior half of body; primordium of *vagina uterina* protruding ventrally (Fig. 17).

Table 2. Major dimensions (μm, unless otherwise specified) of third-stage larvae of *Cystidicola cristivomeri* from *Mysis relicta* and developing larvae from experimentally infected lake trout held at 4-10°C

	Third-stage larvae		Larvae at third moult		Larvae at fourth moult	
	Males	Females	Males	Females	Males	Females
Sample size	10	10	10	10	6	2
Time post-infection			20-21 days		84-104 days	85-203 days
Length (mm)	8.0±2.1* (3.8-10.2)	10.7±2.4 (7.0-15.4)	8.4±2.8 (5.3-14.2)	10.0±2.7 (6.9-14.8)	12.8±1.4 (10.4-14.2)	17.4 (16.9-17.8)
Buccal cavity	119±12 (93-140)	133±12 (116-150)	124±18 (86-157)	134±11 (120-156)	144±10 (136-160)	158 (145-170)
Nerve ring†	196±15 (157-210)	216±14 (192-240)	202±22 (167-243)	216±15 (195-240)	232±12 (220-250)	261 (250-272)
Width at nerve ring	61±9 (45-71)	72±7 (60-83)	69±10 (58-89)	71±9 (62-87)	89±5 (80-94)	110 (100-120)
Excretory pore†	316±31 (247-380)	357±30 (305-412)	327±35 (280-374)	357±36 (306-420)	382±29 (341-410)	410 (380-440)
Esophagus (mm)	0.98±0.17 (0.68-1.24)	1.18±0.10 (0.95-1.34)	1.03±0.16 (0.77-1.34)	1.13±0.15 (0.90-1.37)	1.32±0.07 (1.24-1.39)	1.54 (1.49-1.58)
% body length	13.4±2.7 (9.2-18.1)	11.3±1.7 (8.7-13.9)	12.7±1.9 (9.4-15.4)	11.8±1.7 (8.6-13.5)	10.4±1.1 (9.3-11.9)	8.9 (8.4-9.3)

Cont'd

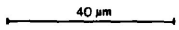
Table 2. (Cont'd)

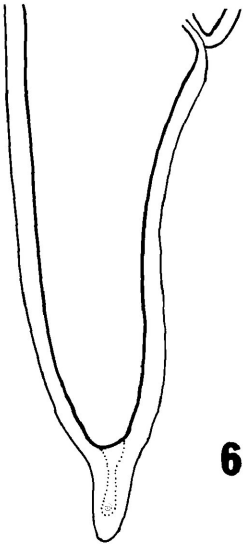
	Third-stage larvae		Larvae at third moult		Larvae at fourth moult	
	Males	Females	Males	Females	Males	Females
Gonad						
Length (mm)	1.12±0.44 (0.33-1.62)	5.03±1.70 (3.00-8.36)	2.43±0.91 (1.44-4.13)	4.70±1.70 (3.16-7.96)	3.72±0.57 (2.92-4.58)	8.91 (8.55-9.26)
% body length	14.1±3.0 (8.8-19.0)	46.3±6.7 (34.0-54.2)	28.9±5.0 (19.3-36.4)	46.4±4.9 (40.6-55.5)	28.9±2.1 (26.1-32.1)	52.0 (49.2-54.8)
Anterior end (mm)†	4.31±1.21 (2.20-5.78)	3.76±0.71 (2.90-5.22)	5.80±1.91 (3.67-9.77)	3.40±0.73 (2.45-4.86)	8.91±1.00 (7.26-10.20)	5.15 (4.59-5.71)
% body length	56.2±4.2 (51.7-63.3)	36.1±6.9 (28.0-50.6)	68.6±4.9 (61.3-76.9)	34.7±3.1 (27.8-39.5)	69.5±2.1 (66.6-72.5)	29.7 (27.2-32.1)
Vulva (mm)†						9.49 (9.25-9.73)
% body length						54.7
Left spicule					569±15 (390-760)	
Right spicule					136±19 (101-153)	
Tail	75±7 (60-87)	77±9 (65-90)	96±11 (80-115)	80±8 (65-93)	141±19 (120-170)	100 -

* Mean ± S.D. subtended by range.

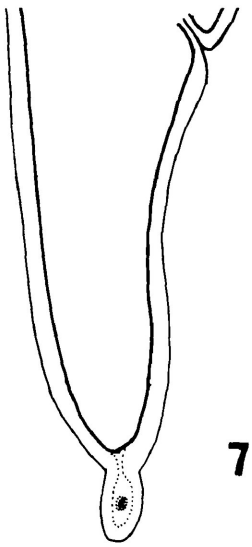
† Distance from anterior end.

Figs. 6-8. Posterior end of third-stage *Cystidicola cristivomeri* larva from *Mysis relicta*. Figs. 9-10. Posterior end of female *C. farionis* fourth-stage larva from rainbow trout. Figs. 11-13. *En face* view of *C. cristivomeri*. Fig. 11. Third-stage larva from *M. relicta*. Fig. 12. Fourth-stage larva from lake trout. Fig. 13. Adult *C. cristivomeri* from lake trout. Figs. 14-16. *En face* view of *C. farionis*. Fig. 14. Third-stage larva from rainbow trout. Fig. 15. Fourth-stage larva from rainbow trout. Fig. 16. Adult *C. farionis* from rainbow trout.

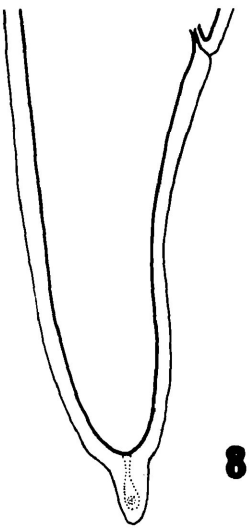




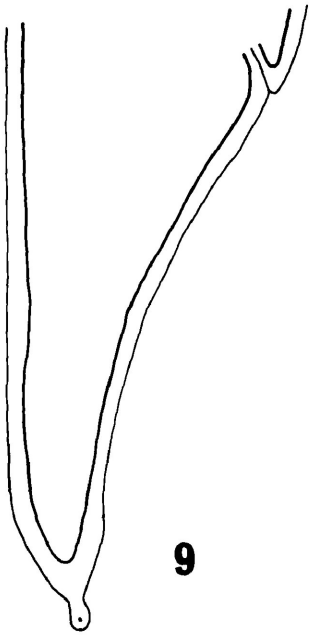
6



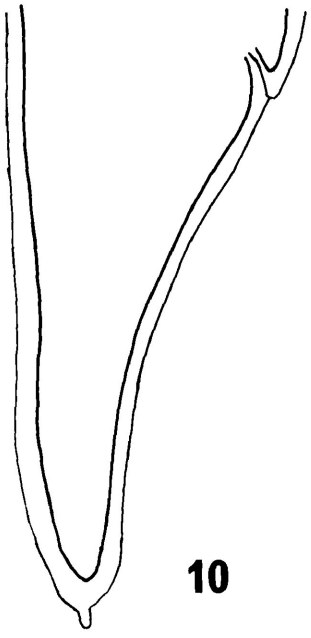
7



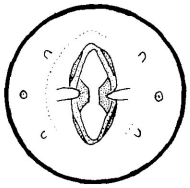
8



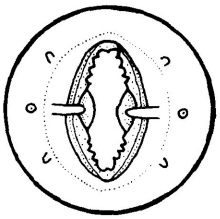
9



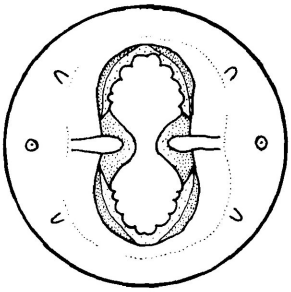
10



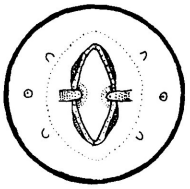
11



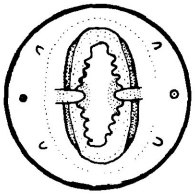
12



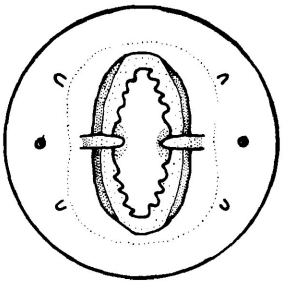
13



14

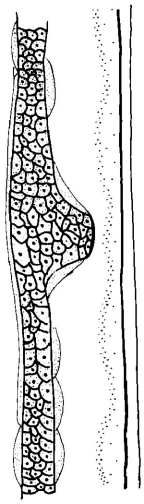


15



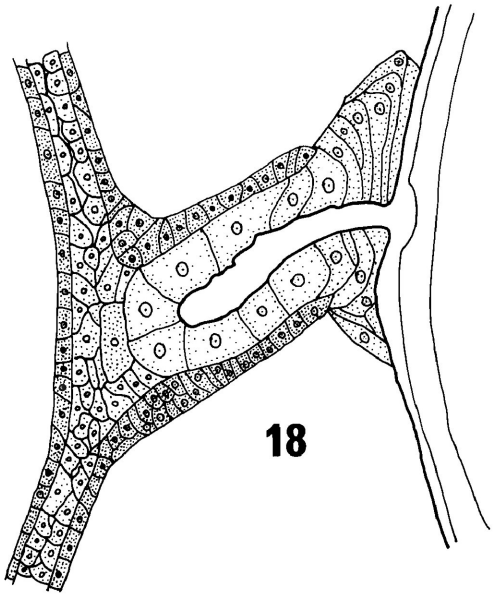
16

Figs. 17-19. Developing vagina of female *Cystidicola cristivomeri*. Fig. 17. Third-stage larva from *Mysis relicta*. Fig. 18. Fourth-stage larva at third moult from lake trout. Fig. 19. Sub-adult at fourth moult from lake trout.

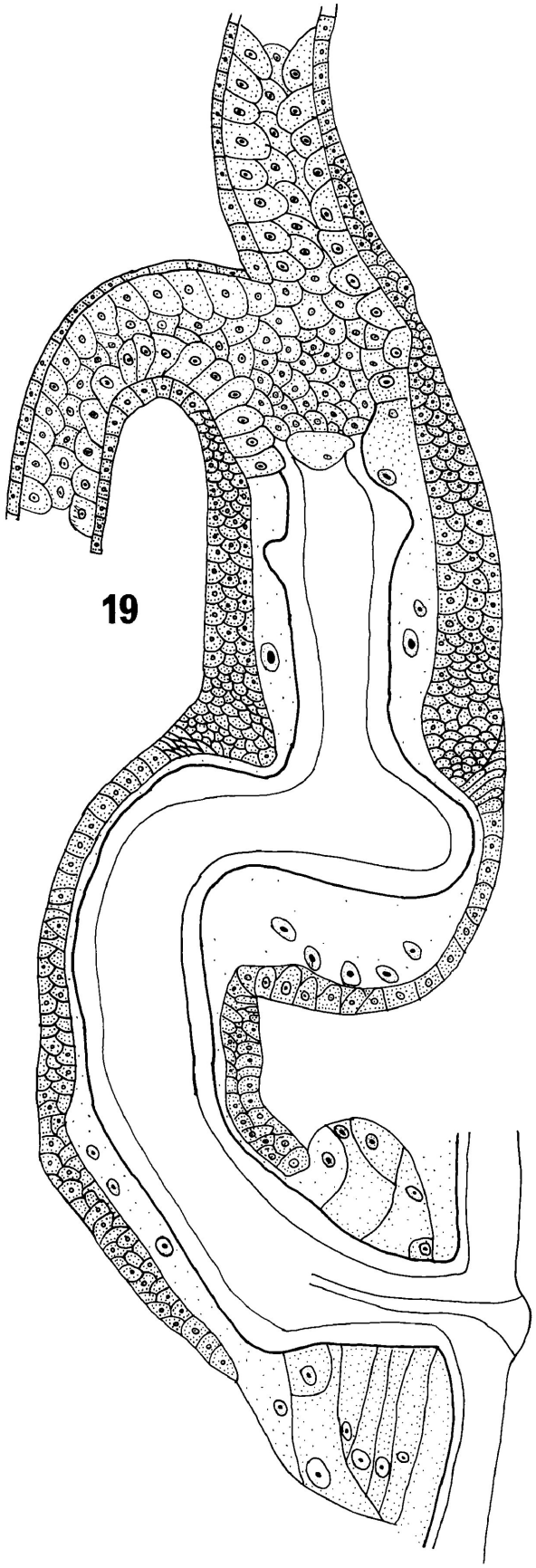


17

40 µm

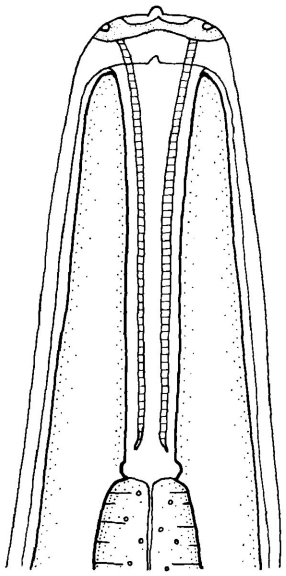


18

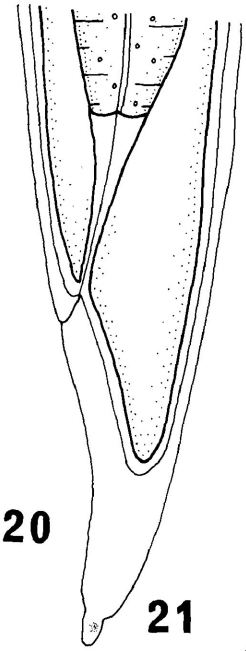


19

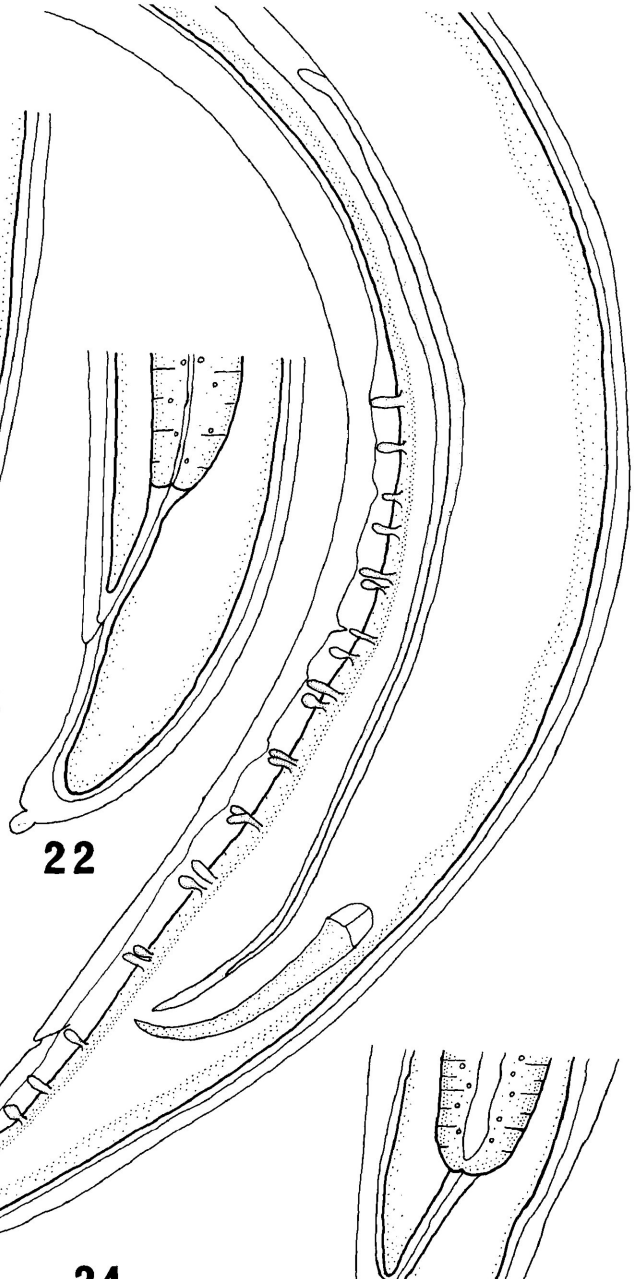
Figs. 20-25. Developing larvae of *Cystidicola cristivomeri* from lake trout. Fig. 20. Anterior end of larva at third moult. Fig. 21. Posterior end of female larva at third moult. Fig. 22. Posterior end of male larva at third moult. Fig. 23. Anterior end of sub-adult at fourth moult. Fig. 24. Posterior end of male at fourth moult. Fig. 25. Posterior end of female at fourth moult.



20



21

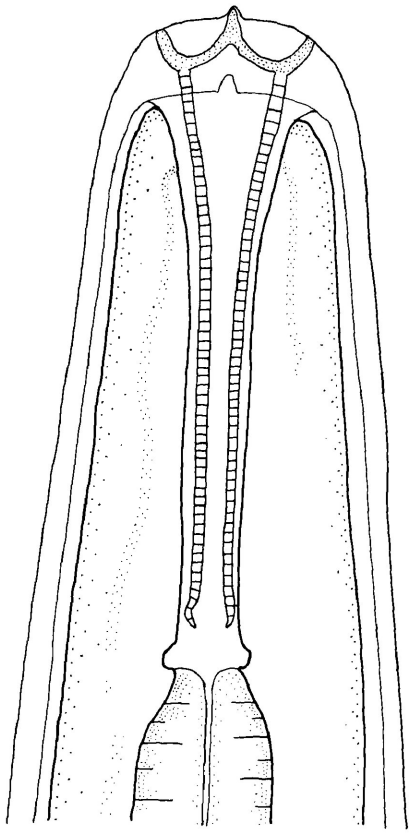


22

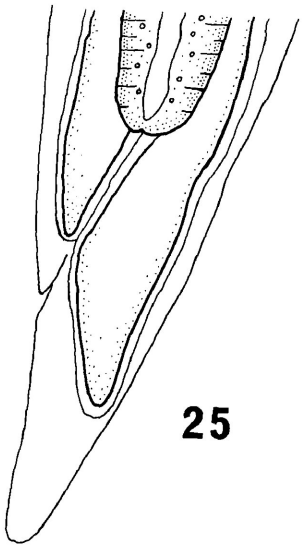
24

40 µm

80 µm



23



25

In *en face* view, two lateral amphids and four submedian papillae present (Fig. 11). Oral opening elliptical dorso-ventrally. Lateral pseudolabia, each extended medially as a lip-like projection continuous posteriorly with lateral wall of buccal capsule. No circumoral teeth. Tip of tail with conspicuous cuticular projection (Figs. 6-8). An apparent lumen in the projection containing a sphere of tissue of varying density.

Larvae at third moult in lake trout

Third-stage cuticle loosened at anterior and posterior ends (Figs. 20, 21, 22). Tail of fourth-stage male more bluntly rounded than female. Male gonad extending to rectum; twice the length and less convoluted than in third-stage larvae. Little change in length of female gonad; *vagina uterina* and *vagina vera* united (Fig. 18). Cuticle thickened over future vaginal opening. Circumoral teeth present in fourth-stage larva (Fig. 12); four teeth in each submedian quadrant projecting from a ridge which originates from the wall of the buccal capsule posterior to margin of oral opening.

Larvae at fourth moult in lake trout

Fourth-stage cuticle loosened at anterior and posterior ends (Figs. 23-25). Spicules of males incompletely sclerotized; caudal papillae present. Female gonad straight,

amphidelphic and didelphic; regions of ovary, oviduct and uterus differentiated. Vagina of female lined with cuticle and open ventrally (Fig. 19). *En face* appearance (Fig. 13) similar to that of fourth-stage larva.

Development of *C. farionis* in experimentally infected rainbow trout

Infective larvae of *C. farionis* used in this experiment were from the swimbladder of lake whitefish. One hundred and ninety-seven worms were recovered for study after 12-235 days from 53% of 36 infected rainbow trout.

Male and female larvae at the third moult were first recovered after one and nineteen days, respectively; some had not yet begun to moult after 97 days. There was no relationship between the time elapsing prior to the third moult and length of larvae. Male and female larvae undergoing the fourth moult were first recovered after 74 and 112 days, respectively. Most males were mature after 112 days. One mature female was recovered after 235 days and was 23.0 mm long. Mature male *C. farionis* from rainbow trout killed within 235 days of infection were 10.6-16.4 mm long. The morphogenesis of *C. farionis* was similar to that of *C. cristivomeri* and only differences are described.

Infective third-stage *C. farionis* larvae from lake whitefish

Larvae described and measured (Table 3) were recovered from the swimbladder of rainbow trout 17 hr after infection. Little variation in length. Male gonad occasionally extending to rectum. *Vagina uterina* and *vagina vera* occasionally united in females. In *en face* view (Fig. 14), lateral wall of buccal capsule beneath pseudolabia not projected as a conspicuous lip-like structure into buccal cavity as in *C. cristivomeri*.

Larvae at the third and fourth moults in rainbow trout

Circumoral teeth present in fourth-stage and fifth-stage worms (Figs. 15, 16); otherwise *en face* view similar to third-stage larvae. Tail with small cuticular projection occasionally present in fourth-stage females (Figs. 9, 10); lumen never apparent; small sphere of tissue rarely present. At the fourth moult, distal end of female uteri reflected.

Prevelance of *C. cristivomeri* in naturally infected *Mysis relicta*

Mysis relicta collected from each of the three lake trout lakes were divided into groups of small (3.0-16.9 mm long) and large (17.0-24.0 mm) individuals and digested in pepsin. Only third-stage larvae were recovered by this method and those from small mysids were 3.6-8.7 ($\bar{X}$=6.1) mm long and those from large mysids 4.7-15.2 ($\bar{X}$=9.4) mm long.

Table 3. Major dimensions (µm, unless otherwise specified) of *Cystidicola farionis* from experimentally infected rainbow trout held at 4-10°C*.

	Third-stage larvae		Larvae at third moult		Larvae at fourth moult	
	Males	Females	Males	Females	Males	Females
Sample size	10	10	6	10	10	6
Time post-infection	17 hours		1-19 days	12-74 days	74-97 days	111-112 days
Length (mm)	5.9±0.7** (4.4-6.7)	6.5±0.8 (5.3-7.9)	6.8±0.7 (5.9-7.5)	8.0±0.9 (6.6-9.2)	10.8±1.0 (8.72-12.2)	14.4±1.6 (11.7-16.7)
Buccal cavity	95±6 (90-105)	97±8 (83-107)	94±6 (89-105)	99±7 (89-110)	114±13 (95-132)	120±5 (111-127)
Nerve ring†	210±17 (190-230)	218±14 (195-235)	217±16 (190-234)	232±9 (214-244)	271±30 (229-310)	281±18 (255-300)
Width at nerve ring	65±9 (50-83)	61±5 (54-70)	63±7 (55-74)	65±4 (57-70)	71±8 (60-82)	83±7 (75-92)
Excretory pore†	341±27 (295-375)	335±19 (310-370)	341±9 (330-353)	361±23 (321-400)	416±37 (360-460)	443±39 (390-483)
Esophagus (mm)	1.33±0.12 (1.11-1.52)	1.41±0.14 (1.24-1.62)	1.40±0.11 (1.22-1.54)	1.58±0.10 (1.38-1.68)	1.97±0.26 (1.55-2.37)	2.25±0.20 (1.94-2.56)
% body length	22.5±2.0 (18.2-25.2)	21.7±2.2 (17.7-25.9)	20.7±1.9 (18.2-22.9)	20.0±1.5 (18.3-22.5)	18.2±1.7 (16.2-20.8)	15.8±1.8 (14.2-19.3)

Cont'd

Table 3. (Cont'd)

	Third-stage larvae		Larvae at third moult		Larvae at fourth moult	
	Males	Females	Males	Females	Males	Females
Gonad						
Length (mm)	1.21±0.37 (0.84-1.87)	3.25±0.77 (1.94-4.76)	2.07±0.39 (1.65-2.57)	4.06±0.61 (3.20-4.81)	4.60±1.17 (2.89-6.52)	9.71±1.29 (8.00-11.90)
% body length	20.3±5.5 (15.0-30.8)	49.3±6.6 (36.7-60.9)	30.4±3.5 (24.6-34.3)	50.9±4.4 (46.6-59.7)	42.0±7.4 (32.9-53.4)	67.6±3.6 (61.2-71.5)
Anterior end (mm)†	3.46±0.74 (2.32-4.20)	2.52±0.24 (2.19-2.94)	4.45±0.38 (4.08-4.90)	2.89±0.33 (2.49-3.57)	5.97±0.64 (5.07-7.26)	3.24±0.57 (2.45-3.89)
% body length	58.3±8.7 (46.5-69.5)	38.8±4.1 (32.0-46.4)	65.6±2.3 (62.6-68.9)	36.3±2.0 (32.4-38.8)	55.3±7.7 (43.6-65.3)	22.5±2.9 (18.0-26.3)
Vulva (mm)†						7.83±1.31 (5.78-9.60)
% body length						54.2±3.4 (49.4-57.6)
Left spicule					614±84 (517-778)	
Right spicule					140±21 (117-188)	
Tail	96±9 (78-110)	82±7 (72-95)	98±18 (63-110)	90±10 (77-104)	182±21 (146-220)	116±8 (103-126)

* Third-stage larvae for experimental infections were from the swimbladders of lake whitefish from Lake Nipigon.
** Mean ± S.D. subtended by range.
† Distance from anterior end.

The prevelance of infection in *M. relicta* was calculated by assuming that only one larva develops to the infective stage in each infected mysid as reported by Smith and Lankester (1979). In Squeers Lake, 0.3% of 700 small and 5.1% of 350 large mysids were infected. In Burchell Lake, the prevelance of infection in three replicate samples of 600 small mysids was 0.0-0.2% ($\overline{X}$=0.1%) and in three samples of 250 large mysids was 1.2-2.0% ($\overline{X}$=1.6%). Similarly, in Greenwater Lake, the prevelance of infection was 0.0-0.2% ($\overline{X}$=0.1%) in small and 0.2-2.8% ($\overline{X}$=1.6%) in large mysids.

No *C. cristivomeri* larvae were recovered from 1500 *Pontoporeia affinis* examined from Squeers Lake.

Potential paratenic hosts of *C. cristivomeri*

Cystidicola cristivomeri was not recovered from 98 lake herring examined from Burchell and Greenwater Lakes. *Mysis relicta* was present in the stomachs of the large lake herring, 17.0-24.0 cm long, but not in those 5.0-16.9 cm.

Incidental laboratory experiments demonstrated that third-stage *C. cristivomeri* removed from the swimbladder of one lake trout could, after being administered by stomach tube, migrate again to the swimbladder of another.

Biology of lake trout and arctic char in the study lakes

The ages of lake trout used in all analyses were determined by counting scale annuli, assumed laid down on May 10. Ages determined by examining both scales and otoliths were the same for six lake trout 7-9 years old from Greenwater Lake and for four fish 6-10 years old from Burchell Lake. However, the scale ages of three other lake trout from Burchell Lake were 8, 9 and 10 while the ages estimated by examining otoliths were 11, 14 and 12, respectively, suggesting that the ages of some older fish from this lake were underestimated.

The growth rate of lake trout up to age 5 was similar in all three lakes (Fig. 26; Tables 4 - 6). Fish increased little in length in Squeers Lake after age 6 and in Burchell Lake after age 8. The mean length of 10-year-old fish from Burchell Lake is probably over-estimated because of small sample size including one unusually large fish (Table 5). The length of lake trout in Greenwater Lake continued to increase throughout the life of the fish (Fig. 26; Table 4). Arctic char in Gaviafaeces Lake increased little in length after age 7 (Fig. 26; Table 7).

The length-weight relationship of lake trout was not significantly different between the three lakes. Therefore, data for all fish were combined. The regression equation was:

Fig. 26. Mean fork length of lake trout and arctic char from northwestern Ontario lakes and Gaviafaeces Lake, respectively.

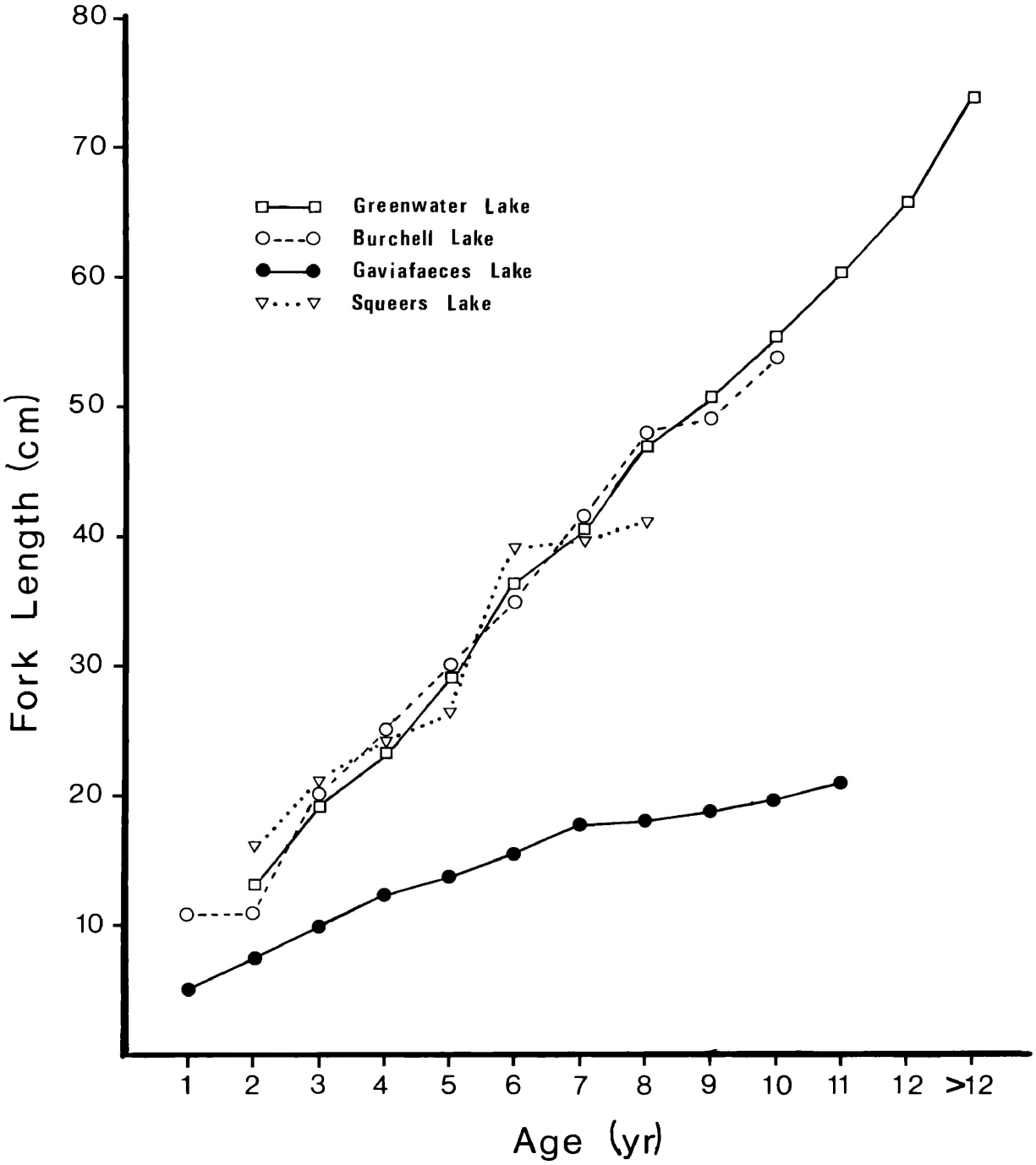

Greenwater Lake
Burchell Lake
Gaviafaeces Lake
Squeers Lake
Fork Length (cm)
80
70
60
50
40
30
20
10
1
2
3
4
5
6
7
8
9
10
11
12
>12
Age (yr)

Table 4. Estimated numbers and measurements of *Cystidicola cristivomeri* in lake trout from Greenwater Lake, 1978 and 1979

	Age											
	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	>XII
Lake trout												
Examined/infected	2/2	16/16	53/53	26/26	9/9	33/33	52/52	49/49	22/22	7/7	8/8	9/7
Length (cm)	13.0±1.0*	19.1±3.2	23.5±2.2	29.3±4.1	36.8±1.7	42.0±2.3	47.5±2.7	51.1±2.3	55.4±3.5	60.8±2.9	66.2±4.5	74.7±7.4
	12.3-13.7	13.4-26.7	19.6-29.6	21.7-39.8	34.6-39.7	37.5-48.4	41.0-52.3	44.2-56.7	49.4-63.0	57.9-66.7	61.0-72.4	65.0-88.1
C. cristivomeri												
Total no.	10.7±0.7	36±22	77±25	115±47	102±58	128±70	113±95	181±124	111±67	130±97	151±103	62±86
	10-11	4-82	27-130	40-226	21-215	40-321	17-481	30-628	6-259	9-306	45-338	0-218
No. females	0.0	2.6±4.2	3.1±2.9	7.9±8.0	21±13	42±28	45±36	88±63	59±39	69±53	84±68	28±38
		0-15	0-14	0-35	2-43	12-147	5-175	11-310	3-159	3-166	22-231	0-96
% females	0.0	5.5±8.3	3.9±3.5	7.0±7.2	25.5±17.9	33.4±12.5	42.2±11.4	48.1±7.3	52.5±8.3	49.9±7.7	53.9±10.2	46.9±9.2
		0.0-31.3	0.0-13.0	0.0-33.3	1.5-57.4	7.1-56.9	9.9-58.8	35.4-69.8	39.1-75.6	33.3-56.0	35.2-68.3	39.3-66.7
No. immatures	9.5±0.7	30±17	66±23	88±39	54±49	31±35	17±36	5.1±8.5	1.1±3.6	0.9±1.2	6.4±8.4	1.1±2.1
	9-10	3-62	27-124	16-157	2-152	0-176	0-187	0-47	0-17	0-3	0-24	0-6
Max. length of males (mm)	15.0±1.4	21.6±3.3	22.9±2.3	24.8±2.2	27.1±1.4	28.5±2.3	28.0±3.0	30.0±3.1	30.3±1.8	33.0±1.2	32.9±5.9	33.6±8.0
	14.0-16.0	16.0-26.3	17.0-26.0	20.5-29.3	26.3-28.7	23.0-33.0	22.3-35.0	24.7-39.0	27.0-32.7	32.0-34.7	28.7-37.0	23.0-45.7
Max. length of females (mm)	17.2±2.6**	23.8±5.8**	27.3±4.4	30.7±4.3	36.4±0.5	35.4±2.3	35.2±3.3	38.7±3.8	38.4±2.8	43.3±2.8	43.5±7.4	42.3±5.7
	15.3-19.0	16.7-32.3	17.0-36.0	19.7-39.3	36.0-37.0	30.7-39.3	29.7-41.7	33.0-49.3	33.0-42.0	39.0-45.0	38.3-48.7	33.7-50.3
Min. length of immatures (mm)	7.0±0.0	6.4±1.7	5.7±1.3	6.7±3.0	10.1±4.1	10.9±4.0	11.7±4.3	13.3±4.0	13.3±3.5	12.0±2.6	12.8±5.7	25.0±2.0
		3-10	3-10	3-16	5-19	5-21	5-21	7-21	9-18	10-15	7-19	23-27

* Mean ± S.D. subtended by range.
** Includes longest immature females when three mature females were not present.

Table 5. Estimated numbers and measurements of *Cystidicola cristivomeri* in lake trout from Burchell Lake, 1978 and 1979

	Age									
	I	II	III	IV	V	VI	VII	VII	IX	X
Lake trout										
Examined/infected	8/8	21/21	22/22	21/21	14/14	12/12	22/22	28/28	25/25	6/6
Length (cm)	11.7±0.5*	11.7±1.0	20.3±2.1	25.4±3.1	30.5±2.8	35.6±2.0	42.8±2.8	48.4±2.6	49.9±1.9	54.1±5.0
	10.7-12.5	10.3-14.6	15.5-24.6	20.9-31.5	26.3-34.8	31.4-39.6	36.5-47.8	44.0-55.2	46.2-53.8	51.0-63.9
C. cristivomeri										
Total no.	32±7	29±12	224±119	261±111	369±226	469±261	1490±1234	1683±869	2361±1555	945±854
	22-46	7-64	86-617	85-601	45-856	85-1000	68-4763	153-3394	437-5968	88-2521
No. females	0.1±0.4	0.6±1.1	1.0±1.7	3.2±7.7	4.1±8.0	57±63	126±141	358±214	549±293	274±222
	0-1	0-4	0-5	0-31	0-24	0-189	0-451	16-710	40-1254	1-618
% females	0.5±1.4	2.5±5.2	0.4±0.8	1.1±2.4	1.1±2.3	10.6±9.8	10.9±9.4	22.9±10.6	26.7±10.0	27.0±16.9
	0-3.8	0-21.1	0-2.8	0-9.0	0-7.8	0-26.7	0-33.3	2.2-38.0	6.5-42.0	1.1-51.2
No. immatures	29±9	26±12	218±115	252±107	349±222	317±225	1107±1132	840±577	1180±1337	310±316
	19-45	6-59	86-596	85-591	45-856	81-821	65-3526	45-2564	151-4902	85-904
Max. length of males (mm)	17.4±2.2	17.5±2.1	18.8±2.7	17.4±1.7	20.7±3.7	21.0±2.1	22.1±3.1	24.1±2.4	24.0±2.3	25.6±4.1
	13.0-20.3	14.0-21.0	14.0-23.0	16.0-19.7	18.0-23.3	17.7-24.3	17.3-26.3	19.3-27.7	19.3-28.0	19.7-29.0
Max. length of females (mm)	17.0±1.4**	19.4±2.4**	19.2±2.5	18.7±2.8	19.6±5.3	25.8±4.0	27.7±3.8	31.4±4.9	32.2±3.4	35.7±4.8
	15.0-19.0	14.7-25.0	15.7-22.7	15.3-23.0	14.0-29.0	18.0-30.7	24.0-35.7	21.7-40.7	25.7-38.0	28.7-39.3
Min. length of immatures (mm)	5.0±0.9	5.4±1.2	6.4±1.6	6.9±2.0	6.8±1.9	8.9±2.2	9.0±2.4	9.3±2.3	9.3±1.9	9.3±1.0
	4-6	3-8	3-10	3-10	4-10	5-12	5-17	4-15	5-12	8-11

* Mean ± S.D. subtended by range.
** Includes longest immature females when 3 mature females were not present.

Table 6. Estimated numbers and measurements of *Cystidicola cristivomeri* in lake trout from Squeers Lake, 1978 and 1979.

	II	III	IV	V	VI	VII	VIII
Lake trout							
Examined/infected	4/4	14/14	6/6	6/6	22/22	12/12	7/7
Length (cm)	15.9±2.4 12.3-17.4	20.8±1.8 17.2-24.2	23.2±2.5 19.4-26.9	26.2±5.2 20.5-32.5	39.5±3.9 34.5-50.1	41.0±3.8 34.4-46.0	42.8±4.3 36.6-49.0
C. cristivomeri							
Total no.	187±119 31-281	442±121 251-654	537±62 441-606	627±229 458-1053	1348±808 409-3180	1355±555 384-2434	1327±442 627-1909
No. females	3.0±0.8 2-4	5.9±7.0 0-25	1.3±2.2 0-5	9.8±12.9 0-34	375±324 47-1546	431±277 25-1034	581±294 168-970
% females	3.4±4.2 1.1-9.7	1.2±1.3 0.0-4.6	2.6±4.1 0.0-8.7	1.3±1.4 0-3.2	28.7±13.7 4.9-49.0	31.2±18.0 6.5-66.1	43.8±14.7 13.1-57.7
No. immatures	179±122 19-278	427±115 245-622	521±63 424-583	578±202 366-931	606±557 59-1809	583±321 0-1085	356±362 46-967
Max. length of males (mm)	20.7±0.0	19.9±1.2 18.7-21.0	19.2±1.1 18.0-20.0	20.4±2.1 18.0-22.7	22.4±2.3 18.3-26.0	23.1±2.4 20.3-27.0	23.8±3.1 20.3-30.0
Max. length of females (mm)	20.2±0.8 19.0-21.0	22.9±1.3 21.0-25.0	21.5±2.0 19.3-23.0	23.7±1.8 22.3-26.0	30.3±3.9 26.0-38.3	33.7±3.5 29.7-39.3	35.0±4.1 30.7-42.7
Min. length of immatures (mm)	6.3±1.7 4-8	5.7±2.4 3-12	5.5±1.8 3-7	6.6±2.7 3-10	8.6±1.8 6-12	8.6±1.0 8-11	9.6±1.3 7-11

* Mean ± S.D. subtended by range.

Table 7. Estimated numbers and measurements of *Cystidicola cristivomeri* in arctic char from Gaviafaeces Lake, 1979

	Age											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XV
Arctic char												
Examined/infected	11/2	10/9	17/17	9/9	9/9	8/8	11/11	4/4	12/12	7/7	2/2	1/1
Length (cm)	5.4±0.4* 4.8-6.1	7.5±0.6 6.6-8.4	10.3±0.9 8.6 12.0	12.7±1.2 11.0-14.9	13.4±1.0 12.0-14.8	16.4±2.0 13.3-20.1	17.9±2.0 14.9-21.3	18.4±3.2 14.2-21.8	19.8±2.2 14.0-21.8	20.5±2.1 18.3-24.6	22.2±3.6 19.6-24.7	28.3
C. cristivomeri												
Total no.	0.3±0.6 0-2	23±26 0-72	55±28 28-133	207±260 79-892	107±58 53-229	242±196 73-677	224±72 124-328	215±161 72-439	340±171 86-677	324±323 95-1018	303±132 209-396	1920
No. females	0.0	0.0	0.4±0.7 0-2	1.0±2.6 0-8	3.2±4.0 0-12	3.3±4.2 0-12	18±17 0-51	26±30 0-69	48±31 10-103	46±30 13-80	50±22 34-65	150
% females	0.0	0.0	1.0±2.1 0.0-7.1	1.2±3.4 0.0-10.1	2.1±2.2 0.0-5.2	3.0±5.6 0.0-16.4	6.8±5.8 0.0-16.9	8.5±6.6 0.0-15.7	16.4±11.7 3.4-38.4	19.9±15.6 6.4-52.1	19.8±15.9 8.6-31.1	7.8
No. immatures	0.3±0.6 0-2	23±26 0-72	52±28 23-131	203±262 59-892	97±45 53-191	225±191 49-642	184±49 120-274	154±107 72-311	242±170 53-578	234±287 12-858	228±160 115-341	1470
Max. length of males (mm)		14.7±2.0 13.0-17.0	15.7±2.1 12.0-20.0	16.4±1.6 14.5-19.0	18.3±2.3 14.0-20.0	19.0±2.2 16.5-21.7	19.4±3.5 15.3-27.0	22.1±1.7 21.0-24.0	21.4±2.5 15.3-24.7	23.9±3.2 17.3-27.3	20.7±4.2 17.7-23.7	26.0
Max. length of females (mm)	11.5±0.7** 11.0-12.0	13.9±1.8** 11.3-17.0	17.2±3.7** 11.7-22.0	24.5±6.4 20.0-29.0	21.2±5.2 13.0-28.0	23.7±3.1 18.3-26.0	28.1±1.8 26.3-31.7	31.7±2.4 29.0-33.7	31.0±3.5 23.0-34.7	34.3±2.4 30.7-37.3	32.0±6.6 27.3-36.7	34.0
Min. length of immatures (mm)	10.5±2.1 9-12	8.6±3.6 6-17	6.3±0.9 5-8	5.8±1.3 4-8	6.6±1.2 5-9	6.5±1.2 5-8	6.3±1.1 4-8	5.8±1.7 4-8	7.0±1.9 4-11	7.0±2.4 4-11	6.5±0.7 6-7	5.0

* Mean ± S.D. subtended by range.
** Includes longest immature females when three mature females were not present.

[1] $\log_e$ Weight = -5.1 + 3.1 $\log_e$ Length

and explained 99% of the variation. The length-weight regression for arctic char from Gaviafaeces Lake was:

[2] $\log_e$ Weight = -3.9 + 2.7 $\log_e$ Length

and explained 99% of the variation.

Mysis relicta was an important item in the diet of lake trout <35 cm long in all three lakes (Tables 8-10). Mysids continued to occur commonly in the stomachs of lake trout >35 cm in Squeers and Burchell Lakes although fishes were also eaten. In Greenwater Lake, *M. relicta* was rarely eaten by lake trout >35 cm long (Table 8). Lake trout 10-25 cm long ate significantly more large than small *M. relicta* at each length class (5 cm) of fish tested (non-parametric sign test, $P < 0.05$). Eighty-one percent of 574 *M. relicta* from the stomachs of 82 lake trout were 17.0-24.0 mm long; the remainder were 3.0-16.9 mm.

Cystidicola cristivomeri in lake trout and arctic char

In Greenwater Lake, the mean total number of worms (TNW) increased almost linearly with age of lake trout up to age 5 and remained fairly constant thereafter (Fig. 27; Table 4). Only nine-year-old fish had significantly higher numbers of worms than lake trout of the other age classes (Duncan's multiple range test F = 3.1 df = 7,195; ages listed in increasing magnitude of

Table 8. Stomach contents of lake trout from Greenwater Lake, July 1978 - October 1979.

	Fish Length (cm)					
	<24.9	25.0-34.9	35.0-49.9		>50.0	
Food Item	July and Oct.	July-Oct.	July-Apr.	May-June	July-Apr.	May-June
Sample size	62	32	50	44	41	58
Mysis relicta	94(91)*	81(33)	6(<1)	0	0	0
Total fish	8(8)	41(67)	64(99)	48(84)	46(100)	54(83)
Lake herring	0	3(36)	18(50)	18(37)	20(72)	19(33)
Other**	3(4)	12(9)	6(5)	4(4)	0	4(34)
Unidentifiable	5(4)	28(22)	50(44)	41(39)	29(28)	28(16)
Mean length (cm)	5.3	8.9	10.8		13.8	
Formicidae	0	0	0	18(11)	0	40(5)
Ephemeroptera	0	0	0	32(7)	0	21(5)
Miscellaneous†	5(<1)	3(<1)	4(<1)	4(<1)	5(<1)	19(6)
Empty	2	9	34	18	51	14
Mean volume (ml)††	0.46	2.26	8.33	9.40	19.0	19.3

* % occurence (% volume).
** Includes: stickleback, sculpin, yellow perch, lake whitefish and lake trout.
† Predominately crayfish and coleoptera larvae.
†† Calculated from stomachs containing food.

Table 9. Stomach contents of lake trout from Burchell Lake, July 1978 - October 1979.

	Fish Length (cm)					
	<24.9	25.0-34.9	35.0-49.9		>50.0	
Food Item	July-Apr.	July-June	July-Apr.	May-June	July-Apr.	May-June
Sample size	55	35	40	45	18	18
Mysis relicta	67(26)*	20(8)	20(3)	49(21)	11(11)	22(2.3)
Total fish	24(73)	49(86)	68(96)	44(14)	67(89)	28(16.8)
Lake herring	4(45)	3(8)	10(22)		22(16)	6(5.2)
Stickleback	2(4)	3(9)	5(1)	9(2)	0	6(<1)
Other**		11(36)	8(8)	4(1)	6(45)	0
Unidentifiable	18(24)	34(33)	53(65)	31(11)	56(28)	22(12)
Mean length (cm)	7.4	6.0	6.8		9.3	
Formicidae	0	3(2)	0	40(11)	0	56(8.3)
Ephemeroptera	2(<1)	6(2)	3(<1)	80(51)	0	89(68)
Miscellaneous†	5(<1)	6(2)	5(<1)	56(3)	0	61(4)
Empty	11	29	18	0	28	0
Mean volume (ml)††	0.68	1.83	3.45	9.69	18.7	15.1

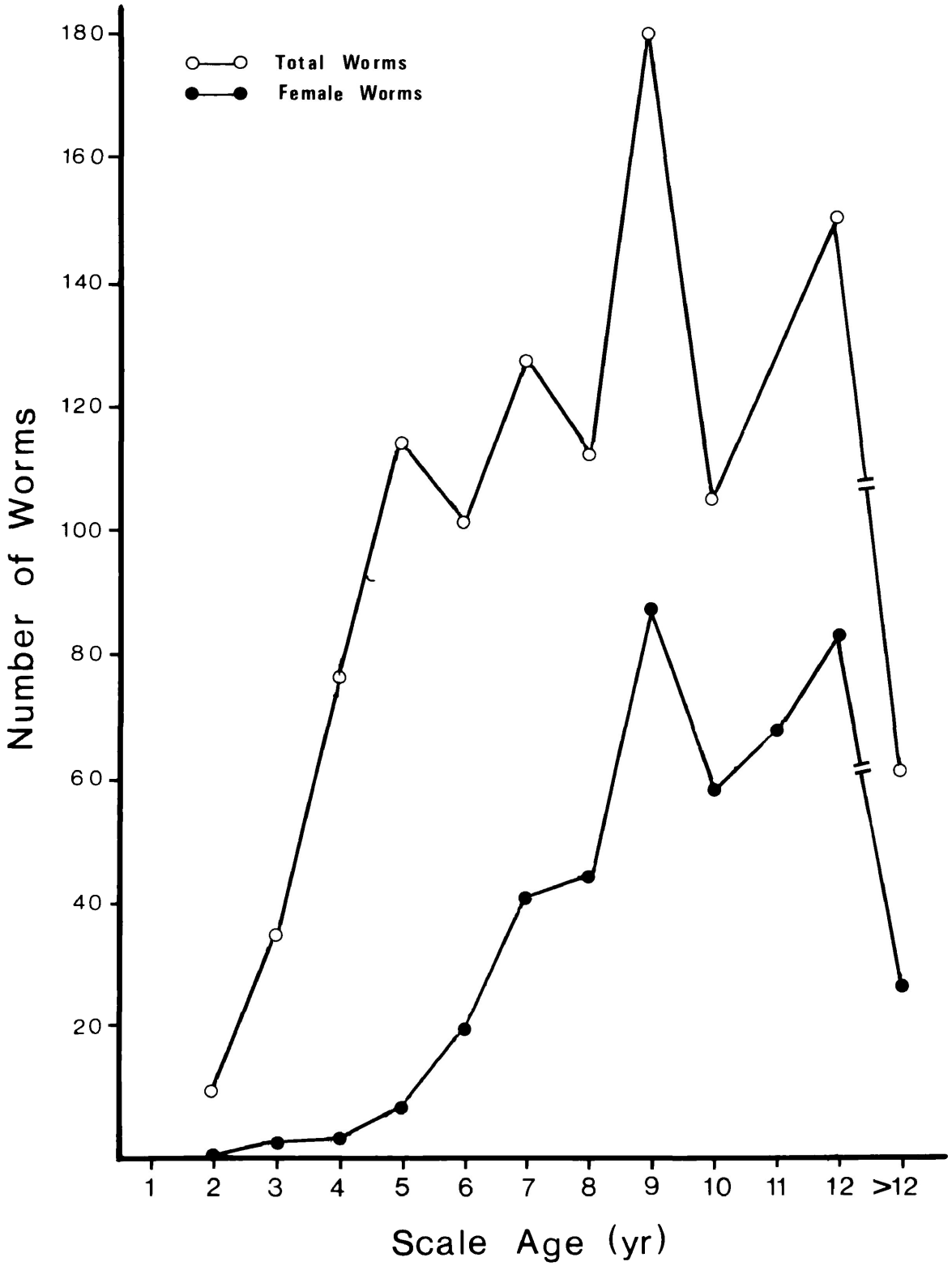
* % occurence (% volume).
** Includes: sculpin, yellow perch and lake trout.
† Predominately coleoptera larvae, chironomid larvae and flying insects.
†† Calculated from stomachs containing food.

Table 10. Stomach contents of lake trout from Squeers Lake, July 1978 - October 1979.

	Fish Length (cm)			
	<24.9	25.0-34.9	>35.0	
Food Item	Oct.	Sept.-Feb.	Sept.-Oct.	Jan.-Feb.
Sample size	26	25	53	49
Mysis relicta	96(69)*	44(19)	11(30)	43(8)
Total fish	12(14)	52(50)	17(39)	49(72)
Yellow perch	0	12(16)	2(3)	20(28)
Unidentifiable	12(14)	48(34)	17(36)	43(44)
Mean length (cm)	5.3	4.1	5.3	
Microcrustaceans	4(14)	40(31)	8(25)	18(17)
Miscellaneous†	15(3)	4(<1)	13(6)	8(3)
Empty	0	12	66	6
Mean volume (ml)††	0.62	2.14	1.13	2.16

* % occurence (% volume).
† Predominately flying insects and mayfly nymphs.
†† Calculated from stomachs containing food.

Fig. 27. Mean numbers of *C. cristivomeri* in relation to age of lake trout from Greenwater Lake.


Total Worms
Female Worms
Number of Worms
180
160
140
120
100
80
60
40
20
1
2
3
4
5
6
7
8
9
10
11
12
>12
Scale Age (yr)

TNW; ages underscored by the same line are not significantly different, $P > 0.05$).

[3] 6 10 8 5 7 11 12 9

The mean number of female worms (NFEMW) increased slowly in fish up to age 5 and then increased more rapidly up to age 9 (Fig. 27; Table 4). The mean number of immature worms (NIMMW) reached a maximum in lake trout at age 5 and declined steadily in older fish (Table 4). The mean minimum length of immature worms (MINLEN) increased sharply in fish from age 5 to age 6 (Table 4). There were significantly more mature male worms than females in fish at each age up to age 8 (non-parametric sign test, $P < 0.05$) (Table 4).

In Burchell Lake, the mean TNW in lake trout increased up to age 9 (Fig. 28; Table 5). The mean NFEMW in fish increased slowly up to age 5 and more rapidly in older fish. The mean NIMMW increased in lake trout up to age 7 and remained high in older fish; the mean MINLEN increased slowly with fish age (Table 5).

In Squeers Lake, the mean TNW increased in lake trout up to age 6 and then remained fairly constant (Fig. 29; Table 6). The mean NFEMW was low in fish up to age 5 then increased sharply. The mean NIMMW was high in all age classes of fish; the mean MINLEN increased slowly as fish aged (Table 6).

Fig. 28. Mean numbers of *C. cristivomeri* in relation to age of lake trout from Burchell Lake.

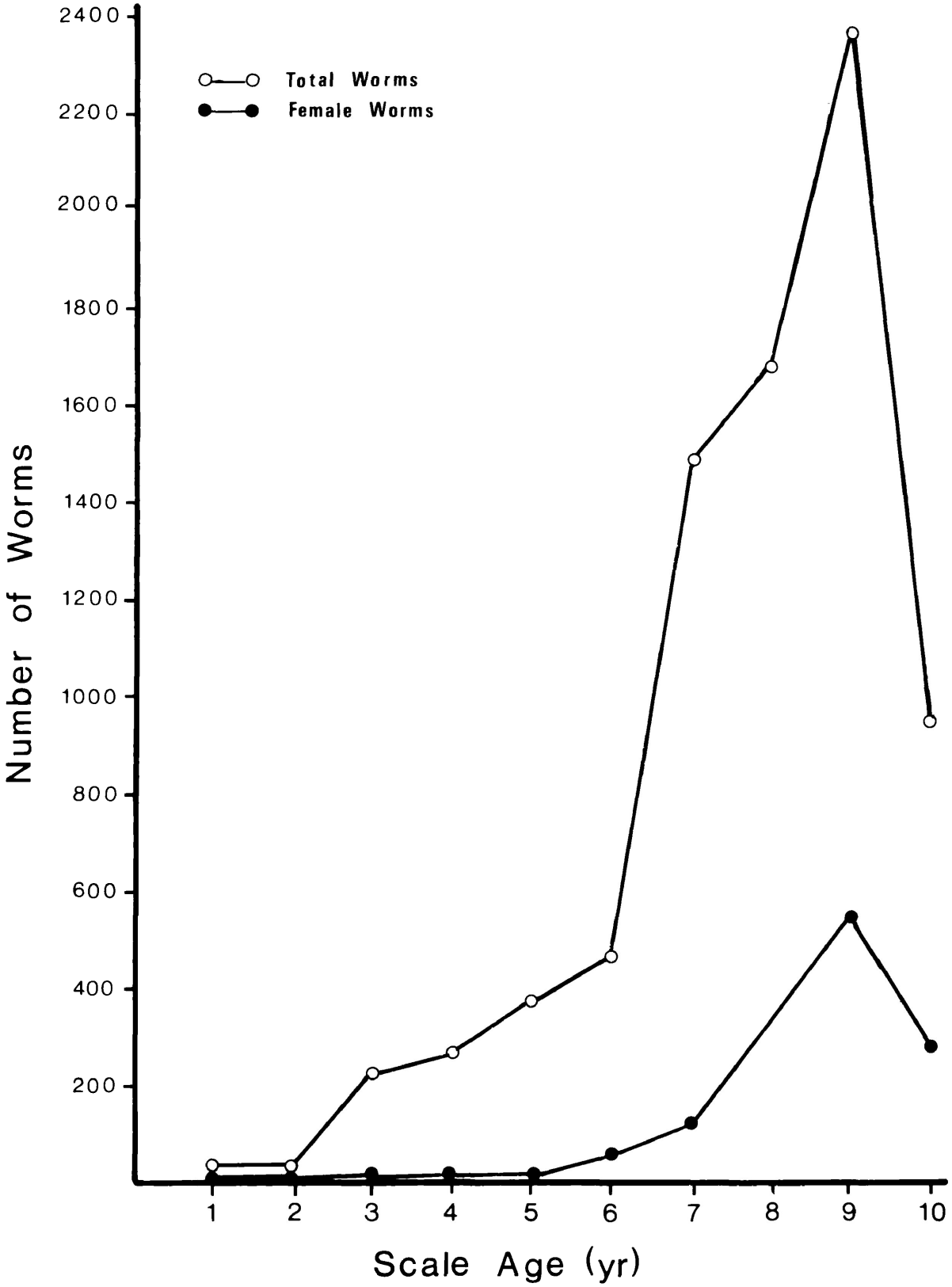
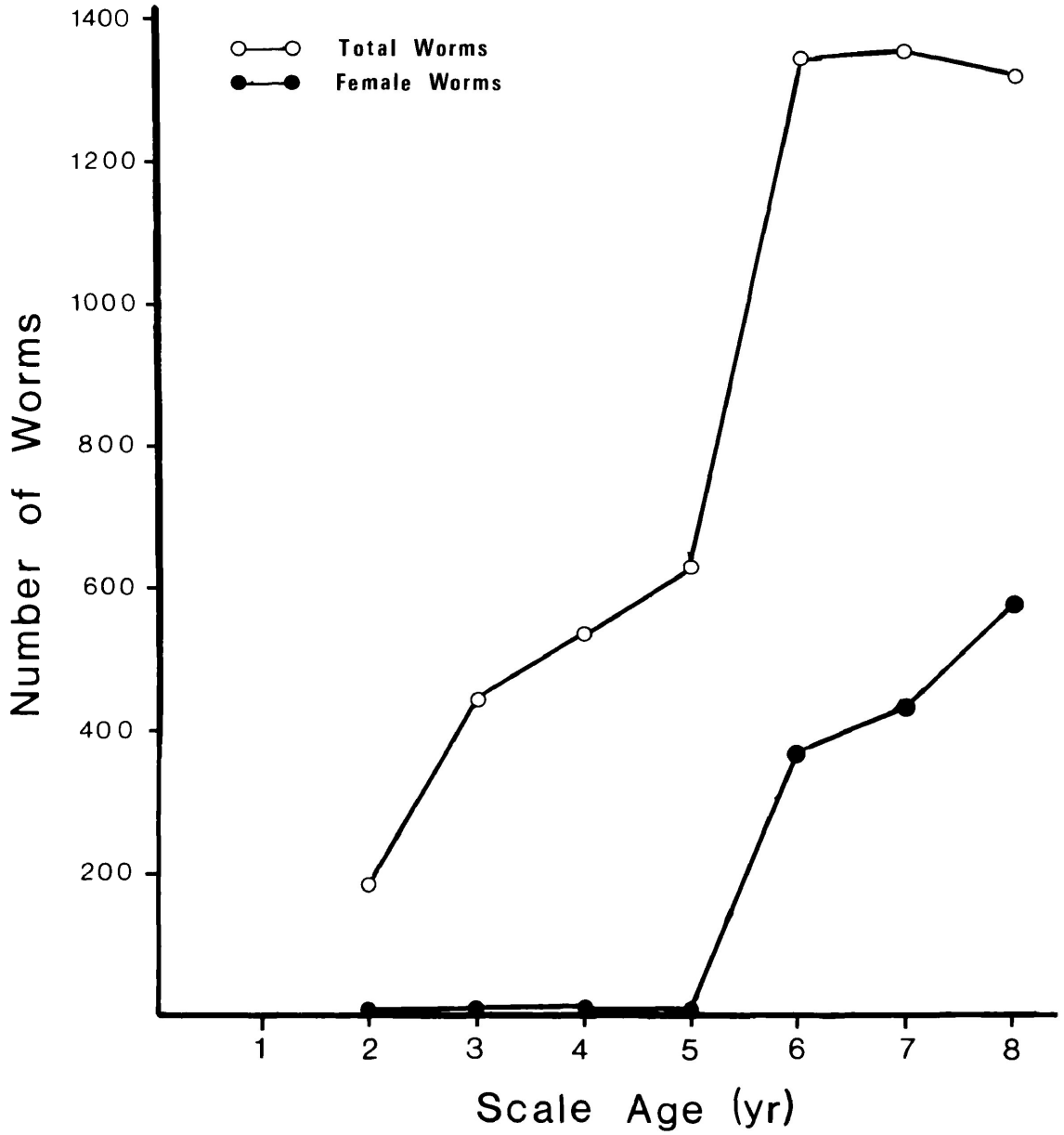

Total Worms
Female Worms
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
Number of Worms
1
2
3
4
5
6
7
8
9
10
Scale Age (yr)

Fig. 29. Mean numbers of *C. cristivomeri* in relation to age of lake trout from Squeers Lake.


Total Worms
Female Worms
1400
1200
1000
800
600
400
200
Number of Worms
1
2
3
4
5
6
7
8
Scale Age (yr)

In Gaviafaeces Lake, the mean TNW and mean NFEMW increased steadily in arctic char up to age 9 and then remained fairly constant (Fig.30; Table 7). The mean TNW in four-year-old fish was probably overestimated by a small sample size including one fish with a very large number of worms (Table 7). The mean NIMMW increased in fish up to age 6 and changed little in older fish; the mean MINLEN remained low at all ages (Table 7).

The effect of season of capture and sex of fish on the TNW, NFEMW and percentage of female worms (PFEMW) were examined at each fish age in Greenwater, Burchell, and Gaviafaeces Lakes and at length classes in Squeers Lake (some fish from Squeers Lake were not aged; see Appendix 1 and 2 for sample sizes at each season). Season of capture had no significant effect on the worm variables except in trout <30 cm long from Squeers Lake (NFEMW in winter 1979 > fall 1978, Mann Whitney U = 68, df = 4,19). Sex of fish had a significant effect in only a few instances (Greenwater Lake, age 4: NFEMW and PFEMW, males > females, t = 3.60, df = 51 and t = 3.66, df = 51, respectively; age 10: NFEMW, females > males, U = 62, df = 7,10; Squeers Lake, fish >40 cm long: TNW, females > males, U = 125, df = 14,11).

There were considerable differences in the numbers of worms in lake trout between the lakes (Figs. 27-30; Tables 4 - 7). The mean NFEMW remained low in fish up to age 5 in all lakes (Fig. 31). The mean NFEMW was not significantly different in

Fig. 30. Mean numbers of *C. cristivomeri* in relation to age of arctic char from Gaviafaeces Lake.

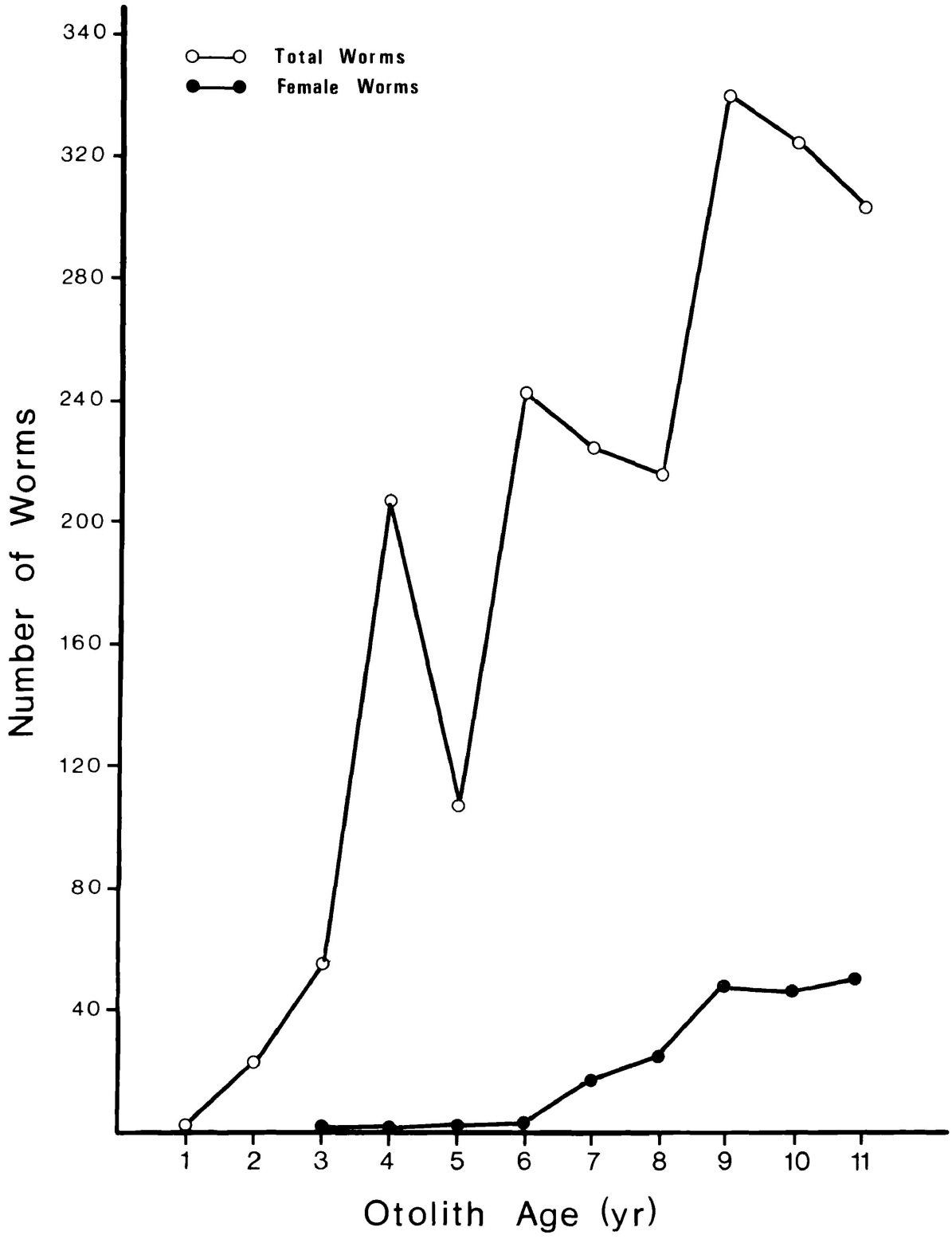
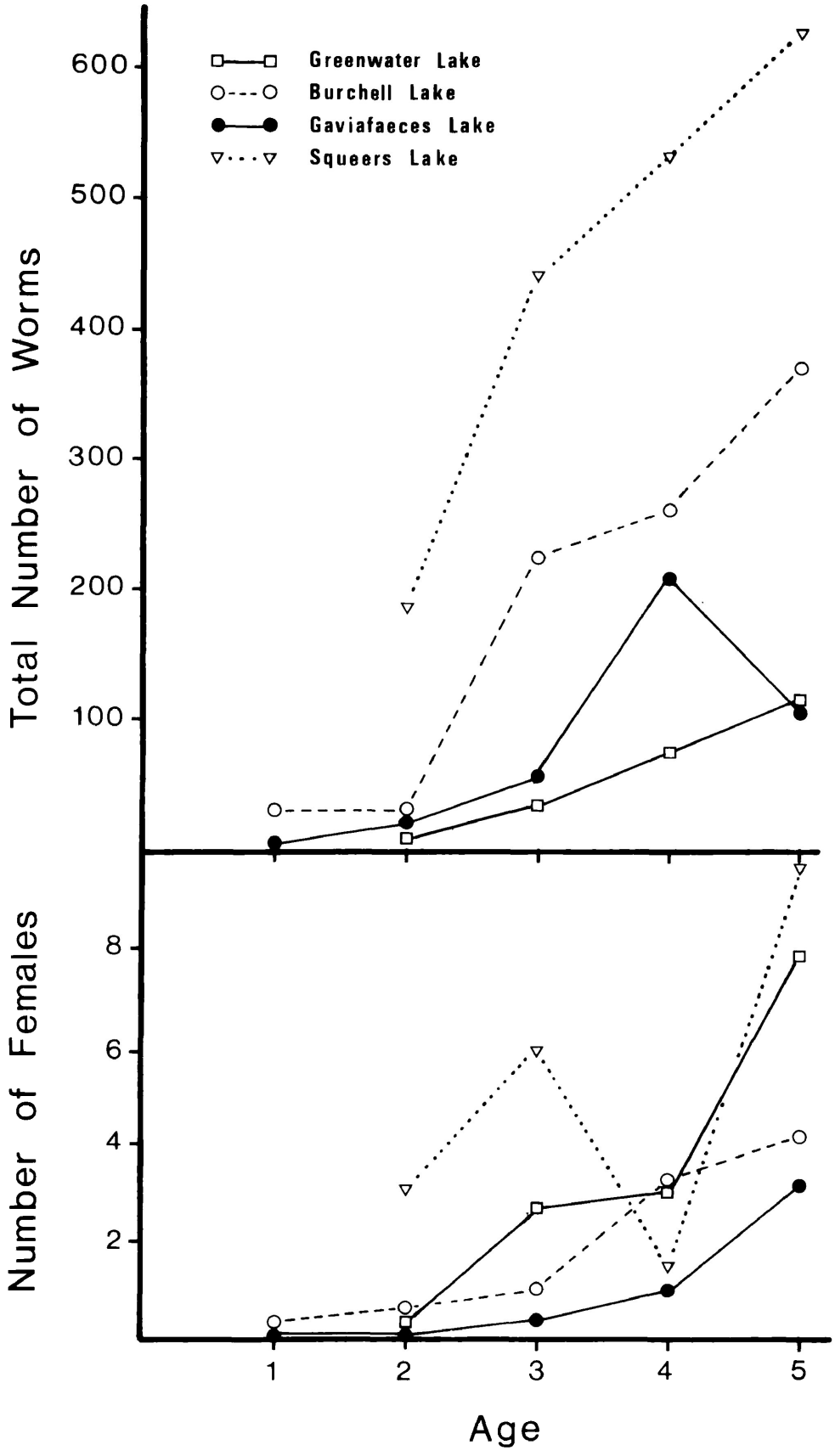

Total Worms
Female Worms
Number of Worms
340
320
280
240
200
160
120
80
40
1
2
3
4
5
6
7
8
9
10
11
Otolith Age (yr)

Fig. 31. Mean numbers of *C. cristivomeri* in lake trout and arctic char 1-5 yr old from lakes in northwestern Ontario and Gaviafaeces Lake, respectively.


Greenwater Lake
Burchell Lake
Gaviafaeces Lake
Squeers Lake
Total Number of Worms
600
500
400
300
200
100
Number of Females
8
6
4
2
1
2
3
4
5
Age

four-year-olds or five-year-olds between the lakes despite significant differences in the mean TNW at each fish age (Table 11).

Cystidicola cristivomeri developed to sexual maturity within two years at 4-10^{o}C in experimentally infected lake trout with a mean of 4.6 worms per fish. However, in wild lake trout with large numbers of *C. cristivomeri*, mature female worms were not abundant until fish were older than five years. These observations suggested that the development of *C. cristivomeri* to sexual maturity may be retarded when large numbers of worms are present in the swimbladder. If *C. cristivomeri* develops more slowly under crowded conditions, the inner surface area of the swimbladder available to individual worms also may have an effect. These hypotheses were tested by combining data for lake trout in all lakes in a stepwise multiple regression analysis to determine the effects of total numbers of worms and length of fish on the percentage of worms present in three-year-old fish that were mature females in five-year-olds ($PFEMW_{3-5}$). This analysis accounts for differences in recruitment rates of immature worms into fish in all lakes. Length of fish was used as an approximation of the swimbladder surface area since swimbladder length was linearly related to fish length ($r=0.99$, $n=368$). A correction factor (cf) was calculated to estimate the number of worms a

Table 11. Comparisons of the mean total number (TNW) of *Cystidicola cristivomeri* in fishes of different age classes from the lakes studied.*

Age	TNW from lakes†				F	df
II	G	Ga	B	S	19.7	3,33
III	G	Ga	B	S	68.1	3,65
IV	G	Ga	B	S	49.9	3,85
V	Ga	G	B	S	28.5	3,51

* Duncan's multiple range test; means listed in increasing order of magnitude and those underscored by the same line are not significantly different ($P > 0.05$).

† G = Greenwater Lake; Ga = Gaviafaeces Lake; B = Burchell Lake; S = Squeers Lake.

fish at age five had when it was three years old. This was calculated by assuming, for example, that individual five-year-old fish with more than the mean number of worms in fish at that age class ($\overline{TNW}_5$) would have had proportionately more worms than the mean ($\overline{TNW}_3$) when it was three-years-old. Therefore:

$$[4] \qquad cf = \frac{\text{TNW in a fish at age five in lake X}}{\overline{TNW}_5 \text{ in fish from lake X}}$$

$$[5] \qquad PFEMW_{3-5} = \frac{\text{NFEMW in a fish at age five in lake X}}{(\overline{TNW}_3 \text{ in lake X}) \times cf}$$

The average number of worms present in a fish from age three to age 5 (TNW_{3-5}) was:

$$[6] \qquad TNW_{3-5} = \frac{(\overline{TNW}_3 + \overline{TNW}_4 + \overline{TNW}_5) \times cf}{3}$$

The $PFEMW_{3-5}$ was significantly related to the TNW_{3-5} and fish length (Table 12). TNW_{3-5} was the most important independent variable and explained 14% of the variance. Fish length was also significant and explained an additional 10% of the variance. The multiple regression equation is:

$$[7] \qquad PFEMW_{3-5} = -23.9 - 0.035\ TNW_{3-5} + 1.5\ \text{Length}$$

and was significant ($F = 6.7$, $df = 2,43$).

Multiple regression analyses were used with data at

Table 12. Spearman correlation coefficients between variables important in analyses of the percentage of female (PFEMW) *Cystidicola cristivomeri* from fishes in the lakes studied.

	Lake trout adjusted Age 5 (n=46)			Greenwater Lake age = 8 (n=52)		
	$PFEMW_{3-5}$	TNW_{3-5}	Fish length	PFEMW	TNW	Fish length
NFEMW[†]	-	-0.01	0.31*	-	0.88*	0.0
TNW_{3-5}	-0.42*		0.16	-0.15		-0.12
Fish length	0.21	0.16	-	0.25*	-0.12	-

	Greenwater Lake age = 9 (n=49)			Burchell Lake age = 6 (n=12)		
	PFEMW	TNW	Fish length	PFEMW	TNW	Fish length
NFEMW		0.96*	0.22		0.58	0.43
TNW	0.07	-	0.15	0.34		0.46
Fish length	0.29*	0.15	-	0.37	0.46	-

	Burchell Lake age = 7 (n=22)			Burchell Lake age = 8 and 9 (n=53)		
	PFEMW	TNW	Fish length	PFEMW	TNW	Fish length
NFEMW	-	0.15	0.09		0.74*	0.03
TNW	-0.27		0.74*	-0.34*	-	0.13
Fish length	-0.24	0.74*	-	-0.36*	0.13	-

	Gaviafaeces Lake all ages (n=91)			
	PFEMW	Age	TNW	Fish length
NFEMW		0.81*	0.73*	0.78*
Age	0.76*		0.85*	0.95*
TNW	0.59*	0.85*		0.88*
Fish length	0.71*	0.95*	0.88*	-

[†] NFEMW = no. of female worms; TNW = total no. of worms; PFEMW = percentage of female worms.

* $P < 0.05$.

individual fish ages in Greenwater and in Burchell Lakes to examine the effect of TNW and fish length on the PFEMW. Variables in the analyses were occasionally interrelated (Table 12). Generally, the analyses illustrated that the PFEMW was related negatively with the TNW and positively with fish length (Table 13). The regressions accounted for differing amounts of the variance in the PFEMW at each age (Table 14). In Gaviafaeces Lake, sample sizes at individual ages were small (Table 7). Therefore, age was included in the multiple regression analysis combining data from all fish. All variables were significantly interrelated (Table 12). Age was the most important independent variable and explained 40% of the variance. TNW also had a significant effect and explained an additional 7% of the variance but fish length had no significant effect. The multiple regression equation is:

[8] PFEMW = -7.3 + 2.8 Age - 0.012 TNW

and was significant ($F = 39.1$, $df = 2,88$). In Squeers Lake, neither the TNW nor fish length had a significant effect on the PFEMW.

In *vitro* studies of *C. cristivomeri* were conducted to investigate any relationship between the length of mature female worms and the number of eggs released. The number of eggs released by female worms in vials of water at $8^{o}C$ was

Table 13. Regression equations of the percentage of female *Cystidicola cristivomeri* (PFEMW) and of the maximum length of female worms (MAXLF) on the total number of worms and fish length at individual fish ages.

Lake	Fish Age	Regression Equation	F value	df
Greenwater	8	PFEMW = -17.8 + 1.3 Length	5.8*	1,50
Greenwater	9	PFEMW = 3.3 + 0.9 Length	4.1*	1,47
Burchell	6	PFEMW = -81.2 + 2.6 Length	4.0	1,10
Burchell	7	PFEMW = 14.6 - 0.003 TNW	2.4	1,20
Burchell	8 and 9†	PFEMW = -48.0 - 0.003 TNW + 1.6 Length	9.3*	2,50
Burchell	8	MAXLF = -36.9 + 1.4 Length	8.5*	1,19
Burchell	9	MAXLF = -14.8 + 0.9 Length	7.5*	1,21

* $P < 0.05$.

† Age, when added into the analysis as a dummy variable, had no significant effect; therefore, data were combined.

Table 14. Percentage of the variance (R^2 X 100) in the percentage of female *Cystidicola cristivomeri* (PFEMW) and in the maximum length of female worms (MAXLF) explained by the total number of worms (TNW) and fish length.

Dependent variable	Lake	Fish Age	R^2 X 100	
			TNW	Length
PFEMW	Greenwater	8	6.0	10.5*
PFEMW	Greenwater	9	0.2	8.0*
PFEMW	Burchell	6	2.0	28.6
PFEMW	Burchell	7	10.7	0.0
PFEMW	Burchell	8 and 9†	12.6*	14.4*
MAXLF	Burchell	8	0.0	30.8*
MAXLF	Burchell	9	8.0	26.3*

* $P < 0.05$.

† Age, when added into the analyses as a dummy variable, had no significant effect; therefore, data were combined.

significantly and positively correlated with length of worms (Spearman r_s = 0.90, n = 16 and r_s = 0.40, n = 42 for worms from lake trout in Squeers and Greenwater Lakes, respectively) (Fig. 32).

The mean maximum length of female *C. cristivomeri* (MAXLF) was greatest in fish from Greenwater Lake (Fig. 33; Tables 4-7, 15). Fish from Greenwater Lake also had fewer worms than fish from the other lakes (Figs. 27-30; Tables 4-7). These observations suggested that the maximum length attained by female worms might be determined by the total number of worms (TNW) present and perhaps, by the space available in the swim-bladder. Since the MAXLF and the MAXLM (Figs. 33-34; Tables 4-7) were significantly and positively correlated with fish age (r_s = 0.83, 0.83, 0.83 and 0.90 for MAXLF and r_s = 0.80, 0.73, 0.49 and 0.76 for MAXLM in Greenwater, Burchell, Squeers and Gaviafaeces Lakes, respectively), subsequent analyses to determine the effect of TNW and fish length on the MAXLF were done, when possible, within individual age classes for each of the lakes.

In Burchell Lake, the variables in the analyses were occasionally interrelated (Table 16). The MAXLF was positively related to fish length and was the only independent variable which explained a significant amount of the variance (Tables 13, 14). In Gaviafaeces Lake, all ages were combined. All variables were significantly interrelated (Table 16).

Fig. 32. Relationship between the number of nematode eggs laid in 24 hr and the length of female *C. cristivomeri* from lake trout from Squeers and Greenwater Lakes.

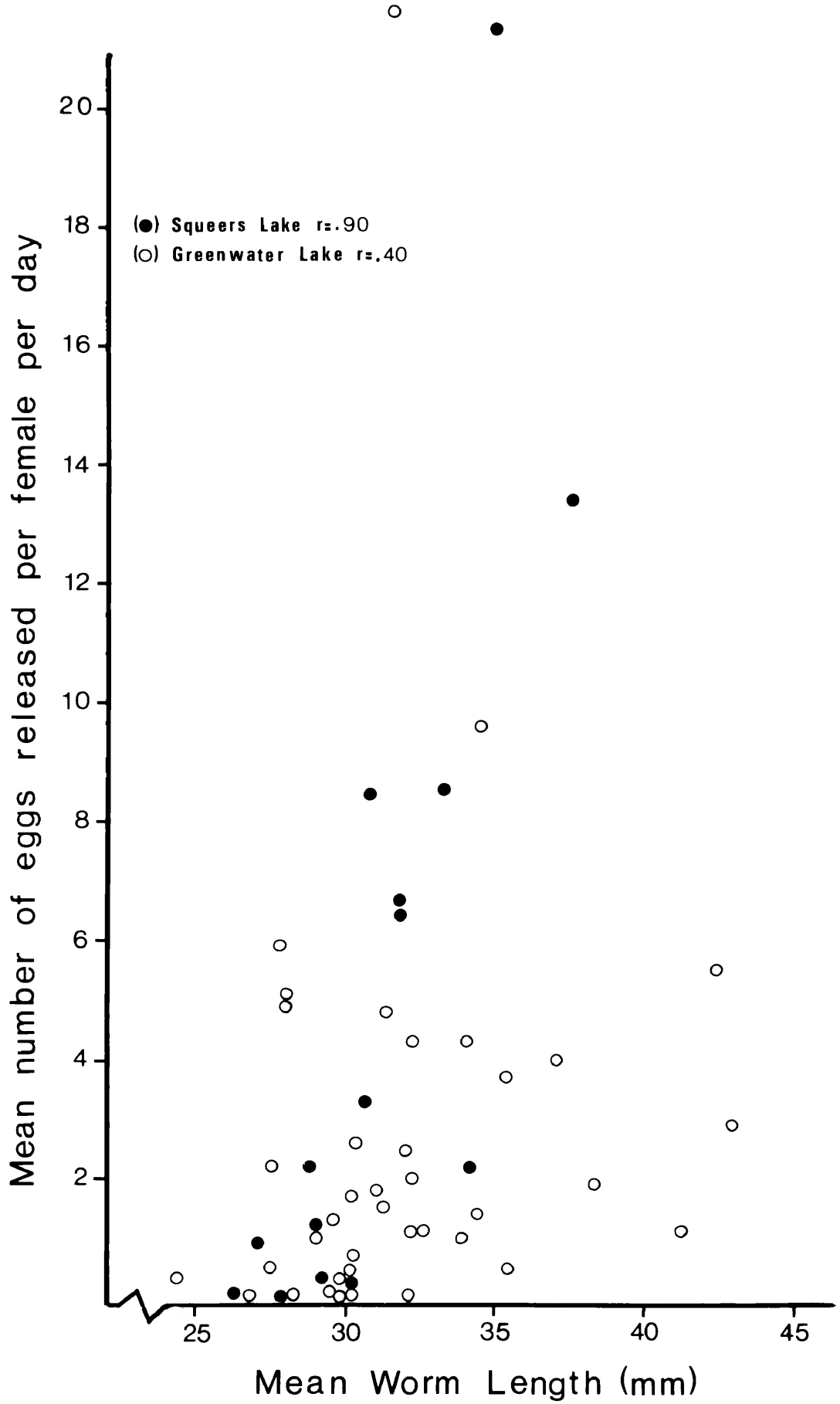

(●) Squeers Lake r=.90
(○) Greenwater Lake r=.40
Mean number of eggs released per female per day
20
18
16
14
12
10
8
6
4
2
25
30
35
40
45
Mean Worm Length (mm)

Fig. 33. Mean maximum length of female *C. cristivomeri* in relation to age of lake trout and arctic char from lakes in northwestern Ontario and Gaviafaeces Lake, respectively.

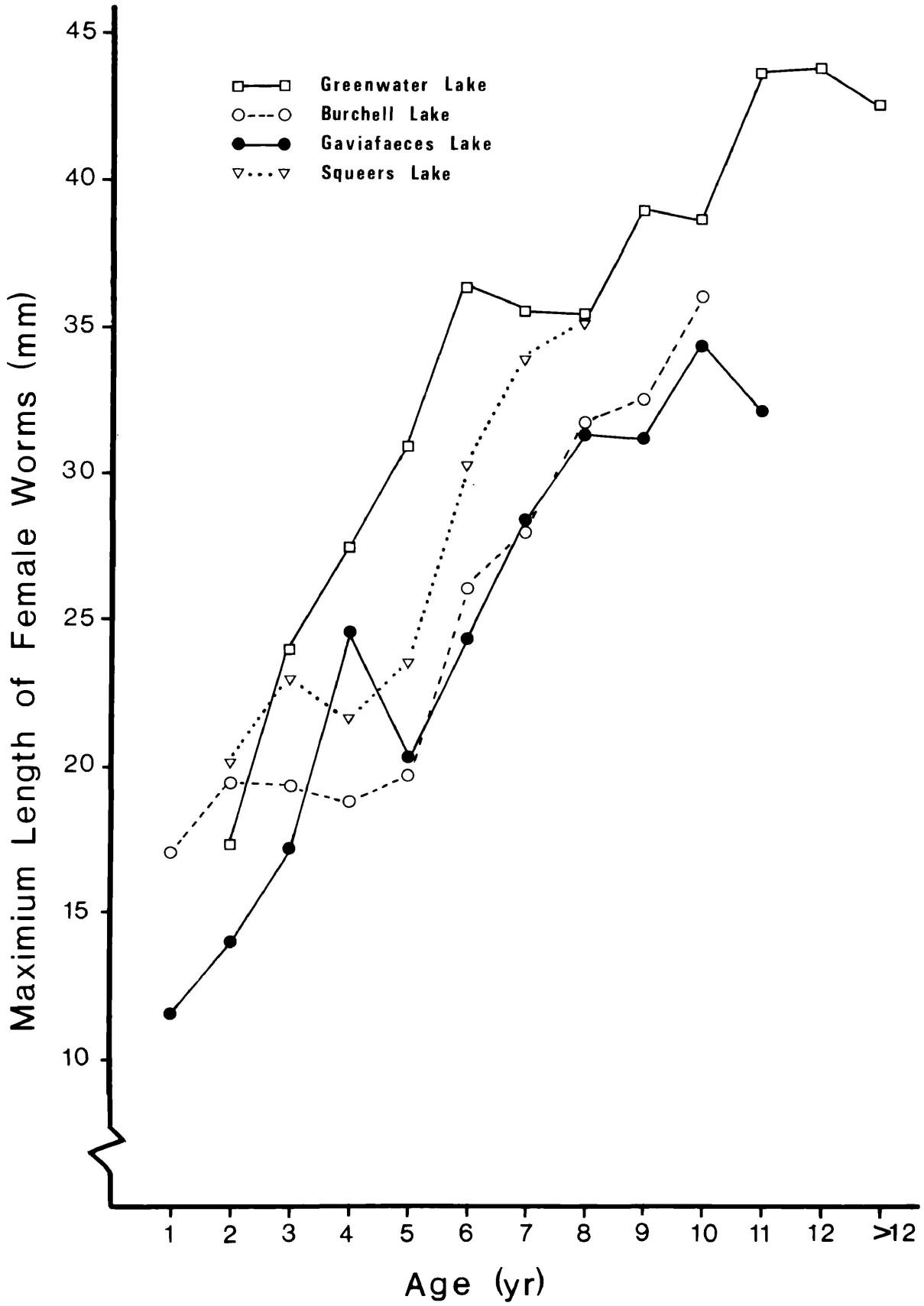

Greenwater Lake
Burchell Lake
Gaviafaeces Lake
Squeers Lake
Maximium Length of Female Worms (mm)
45
40
35
30
25
20
15
10
1
2
3
4
5
6
7
8
9
10
11
12
>12
Age (yr)

Table 15. Comparisons of the mean maximum length of female (MAXLF) *Cystidicola cristivomeri* in fishes of different age classes from the lakes studied*.

Age	MAXLF from Lakes†	F	df
II	Ga G B	18.5	2,29
III	Ga B S G	6.3	3,38
IV	B S Ga G	8.9	3,59
V	B Ga S G	15.5	3,37
VI	Ga B S G	10.1	3,23
VII	Ga B S G	18.7	3,37
VIII	B Ga S G	4.3	3,56
IX	B Ga G	30.1	2,61
X	Ga B G	4.7	2,22

* Duncan's multiple range test; means listed in increasing order of magnitude and those underscored by the same line are not significantly different ($P > 0.05$).

† Ga = Gaviafaeces Lake; G = Greenwater Lake; B = Burchell Lake; S = Squeers Lake.

Fig. 34. Mean maximum length of male *C. cristivomeri* in relation to age of lake trout and arctic char from lakes in northwestern Ontario and Gaviafaeces Lake, respectively.

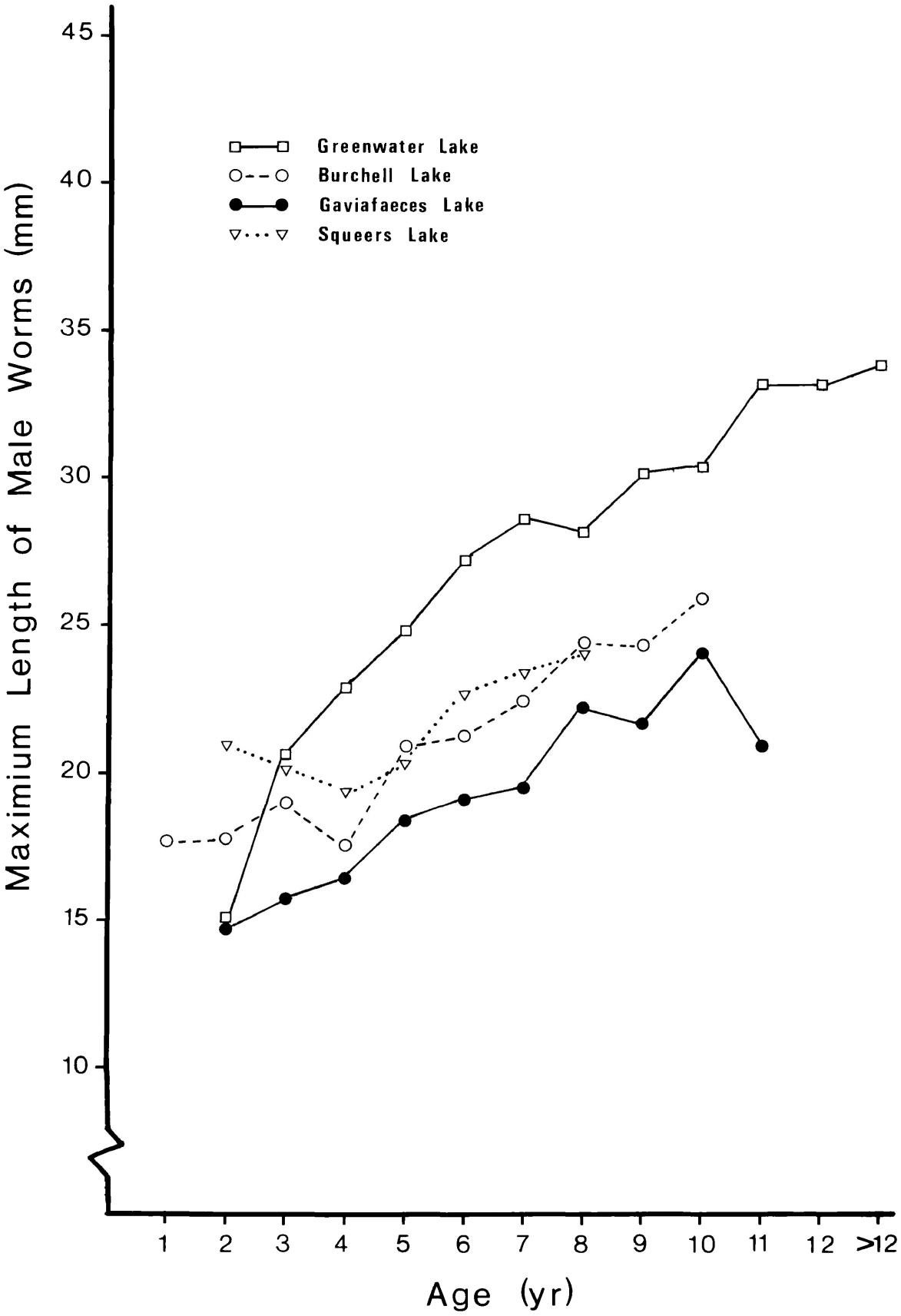

Greenwater Lake
Burchell Lake
Gaviafaeces Lake
Squeers Lake
Maximium Length of Male Worms (mm)
45
40
35
30
25
20
15
10
1
2
3
4
5
6
7
8
9
10
11
12
>12
Age (yr)

Table 16. Spearman correlation coefficients between variables important in analyses of the maximum length of mature female (MAXLF) *Cystidicola cristivomeri* from fishes in the lakes studied.

	Burchell Lake age = 8 (n=21) MAXLF	TNW	Fish length
TNW[†]	-0.03		-0.09
Fish length	0.59*	-0.09	-

	Burchell Lake age = 9 (n=23) MAXLF	TNW	Fish length
TNW	0.53*		0.25
Fish length	0.47*	0.25	-

	Gaviafaeces Lake all ages (n=69) MAXLF	Age	TNW	Fish length
Age	0.90*		0.85*	0.95*
TNW	0.73*	0.85*		0.88*
Fish length	0.87*	0.95*	0.88*	-

[†] TNW = total no. of worms; MAXLF = maximum length of mature female worms

* $P < 0.05$

Age was the most important independent variable and explained 78% of the variance. The effects of the TNW and fish length were also significant and each explained an additional 2% of the variance. The multiple regression equation is:

[9] MAXLF = 6.5 + 1.5 Age - 0.006 TNW + 0.68 Length

and was significant (F = 101.7, df = 3,65). In Greenwater and Squeers Lakes, neither the TNW nor fish length had a significant effect on the MAXLF.

Lesions on the inner surface of the swimbladder appeared as raised ulcers (1-20 mm dia.), sometimes encircled by hyperemic mucosa and occasionally with a hard ochre-colored material covering a central crater (Figs. 35, 36). The mean numbers of lesions were low in lake trout less than six years old (Table 17). The mean number of mature worms (males + females) also remained low in fish less than six-years-old (Tables 4 - 7). The number of lesions was significantly and positively correlated with the number of mature worms (r_s = 0.70, 0.80 and 0.80 in Greenwater, Burchell and Squeers Lakes, respectively).

There was no correlation between the color of fish flesh and the TNW in any of the lake trout lakes. There was no correlation between the condition factor of fish (= Weight X $10^5/(\text{length})^3$) and the TNW or the NFEMW.

Fig. 35-36. Ulcers in the swimbladder of lake trout caused by *Cystidicola cristivomeri*. Fig. 35. Tangled mass of worms adjacent to swimbladder lesion. Fig. 36. Linear arrangement of lesions along the ventral surface of the swimbladder.

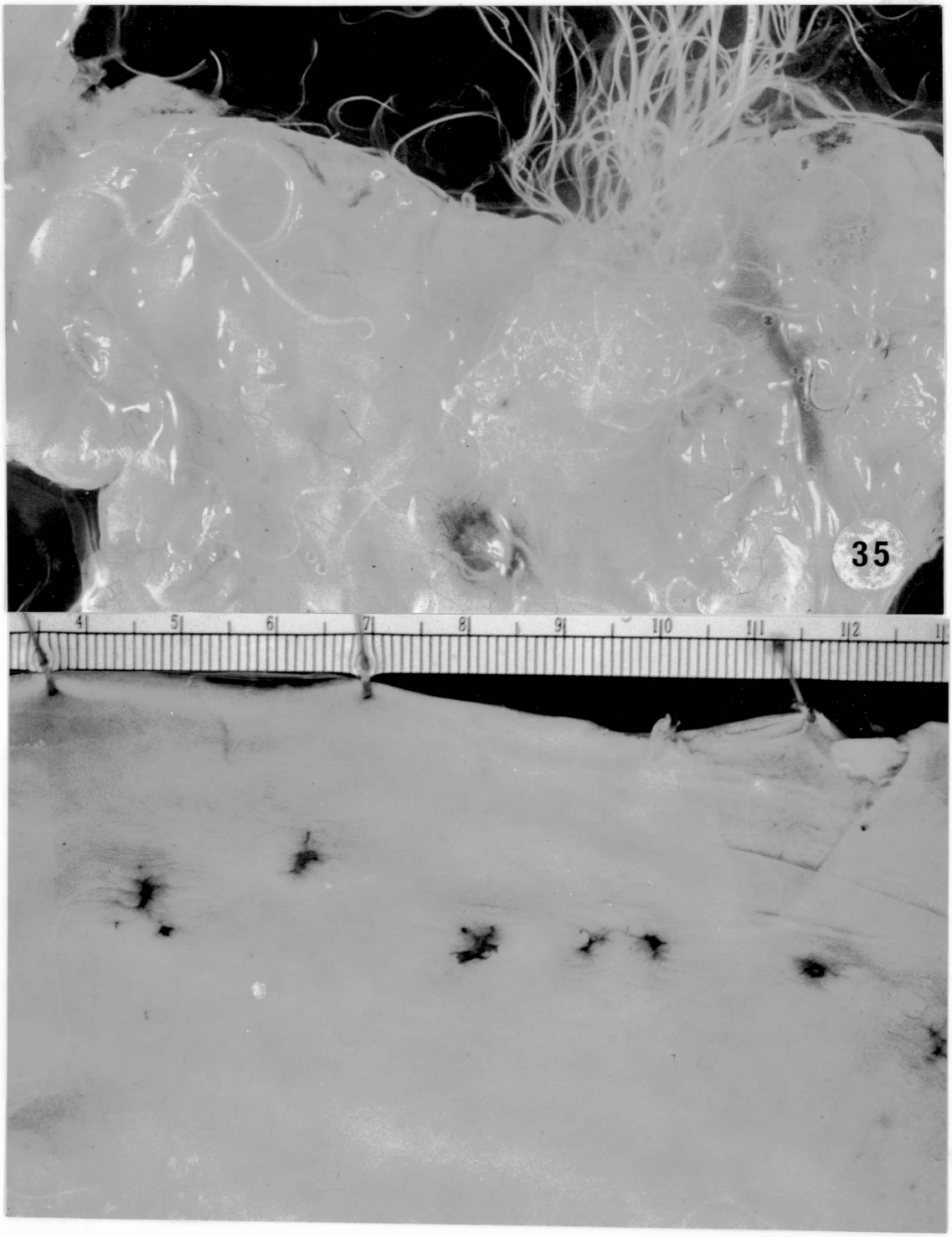

35

Table 17. Number of lesions in the swimbladder of lake trout with *Cystidicola cristivomeri*.

Fish Age	Number of lesions		
	Greenwater Lake	Burchell Lake	Squeers Lake
I		0	
II	0	0	0.3±0.6 (0-1)
III	0.1±0.4 (0-1)*	0	0.4±0.5 (0-1)
IV	0.1±0.3 (0-1)	0.1±0.3 (0-1)	0
V	0.3±0.5 (0-2)	0.5±0.9 (0-3)	0.8±1.0 (0-2)
VI	0.6±0.5 (0-1)	1.0±0.8 (0-2)	3.4±2.5 (0.8)
VII	1.4±1.0 (0-4)	2.4±1.7 (0-5)	3.9±2.2 (0-7)
VIII	1.5±1.2 (0-6)	3.3±2.3 (0-7)	5.7±2.0 (4-9)
IX	2.0±1.3 (0-5)	4.4±2.2 (1-8)	
X	2.3±1.5 (0-5)	2.2±1.5 (0-4)	
XI	2.7±1.9 (0-6)		
XII	3.0±1.1 (0-5)		
>XII	0.8±1.0 (0-3)		

* Mean ± S.D. (range)

Discussion

Cystidicola spp. migrate as third-stage larvae to the swimbladder of their fish hosts *via* the pneumatic duct. Several authors have speculated that these nematodes migrate directly to the swimbladder (Shipley 1908; Mueller 1940; White and Cable 1942; Smith 1978) but evidence has been lacking. Drew (1909), on finding nematodes identified as *C. farionis* in the intestine and associated mesentery of brown trout (*Salmo trutta* L.), suggested that this parasite undergoes a tissue migration to the swimbladder. However, in view of findings presented here, worms recovered by Drew (1909) probably were not *C. farionis*.

Protuberances, similar to the posterior cuticular projection on the tail of third-stage larvae of *Cystidicola* spp., have also been reported on third-stage larvae of other closely related nematodes. Choquette (1955) reported that female *Cystidicoloides tenuissima* Zeder, 1800 could be distinguished by a knob-like appendage on the tail which was absent on males. However, Moravec (1971) found exceptions in both sexes. Presumably, the material of varying density enclosed within the tail projection of *Cystidicola* spp. is an extension of the hypodermis but a connection was not visible. This material is shed with the third-stage cuticle and if it is an extension of hypodermis, it must be pinched off from the worm at the time of the moult.

Several authors have suggested that some nematodes of the family Cystidicolidae moult to the fourth stage in the intermediate host. Moravec (1971) speculated that well developed larvae of *C. tenuissima* in mayflies were fourth stage and that both third-stage and presumptive fourth-stage larvae were capable of development in the definitive host. Keppner (1975) did not observe the third moult of *Spinitectus micracanthus* (Christian, 1972) in bluegills (*Lepomis macrochirus* Rafinesque) and suggested it occurs in the intermediate host. Baylis (1931) reported that *C. farionis* from *Gammarus pulex* (L.) were fourth stage larvae. None of the above mentioned authors observed the third moult in the intermediate host. *Cystidicola cristivomeri* undergoes considerable growth in *M. relicta* after the second moult but does not develop beyond the third stage. The worms described by Baylis (1931), Moravec (1971) and Keppner (1975) likely were third stage. Continued growth of larvae in the intermediate host after the second moult appears to be common in this family (Baylis 1931; Choquette 1955; Uzmann 1967; Moravec 1971; Keppner 1975; Smith and Lankester 1979) and has probably led to the confusion.

The size of third-stage cystidicolid larvae may influence the length of time required to reach sexual maturity after being ingested by the definitive host. Long larvae of *C. cristivomeri* in lake trout moulted sooner than shorter larvae.

Some cystidicolid nematodes, such as *C. tenuissima* in brown trout and *C. farionis* in lake whitefish, may be expelled from their fish host at certain times of the year (Leong 1975; Pellitero 1976; Watson 1977; Watson and Dick 1979). Presumably, small larvae picked up late in the season would have less chance of developing to maturity than longer larvae.

Cystidicola spp. take longer to reach maturity than species of closely related genera . *Cystidicoloides tenuissima*, in brook trout (*Salvelinus fontinalis* Mitchill), matured after 60-70 days (Choquette 1955); in brown trout, at 18°C, mature male and fifth stage females were recovered after 12 and 20 days, respectively (Moravec 1971). Mature male and fifth stage female *Spinitectus micracanthus* were recovered from bluegills after 26 and 36 days, respectively (Keppner 1975). Neither Choquette (1955) nor Keppner (1975) reported the temperature at which their experiments were conducted. Mature male and female *C. cristivomeri* were first recovered after 67 and 210 days, respectively. Mature male and female *C. farionis* were first recovered after 110 and 235 days, respectively. However, female *C. farionis* may have reached maturity earlier than found since infected rainbow trout had not been sampled between 112 and 235 days, post-infection.

The swimbladder nematode that reaches sexual maturity in lake whitefish in North America is referred to *C. farionis*

but the validity of this identification recently has been questioned (Lankester and Smith *in press*). Certain biological and morphological features seem to distinguish the nematode in lake whitefish from *C. farionis* in other salmonids. In some lakes, mature swimbladder nematodes are found in lake whitefish but not in lake herring while the opposite is found in other lakes. In lakes in western Canada, the swimbladder worm in lake whitefish appears to mature seasonally (Leong 1975; Watson 1977; Watson and Dick 1979) while little evidence was found of seasonal changes in the intensity of immature swimbladder nematodes in lake whitefish in Lakes Superior and Nipigon (Lankester and Smith *in press*). The eggs from swimbladder nematodes in lake whitefish are also distinctive in having predominantly lateral rather than polar filaments (Smith 1978). Evidence reported here further suggests that the swimbladder nematode that matures in lake whitefish is different from that which matures in other salmonids. Third-stage larvae used to infect rainbow trout originated from lake whitefish from Lake Nipigon. In Lake Nipigon, lake herring were commonly infected with mature *C. farionis* yet lake whitefish have only third and early fourth-stage larvae in the swimbladder (up to 2500) (Black unpubl.). However, when these apparently arrested larvae from lake whitefish were put into rainbow trout, they became sexually mature and were identical to *C. farionis*. Further studies

are required to substantiate the suggestion that the swim-bladder nematode which matures in lake whitefish is a distinct species.

Immature lake trout captured in October fed almost exclusively on large mysids (>17 mm long). Large mysids were more heavily infected with *C. cristivomeri* than small mysids. Although the size composition of the mysid population was not determined in the study lakes, large shrimp (considered $\geq$ one year old) constituted less than 10% of the autumn population in lakes in eastern North America (Brownell 1970; Lasenby and Langford 1972; Reynolds and DeGraeve 1972; Carpenter *et al* 1974). *Mysis relicta*, when present in a lake, is a very common forage of young lake trout (Eschmeyer 1956; Rawson 1961; Dryer *et al* 1965; Wright 1968; Anderson and Smith 1971; this study). This dependence on mysids in conjunction with selective feeding on large shrimp ensures that most, if not all, lake trout will become infected with *C. cristivomeri* in lakes where *M. relicta* is abundant. Smith and Lankester (1979) observed limited development of *C. cristivomeri* in experimentally infected *Pontoporeia affinis* Lindstrom but results reported here suggest that *P. affinis* is not a suitable intermediate host of this parasite in nature.

The prevelance of *C. cristivomeri* was similar in *M. relicta* from both Burchell and Greenwater Lakes yet young

lake trout from Burchell Lake were more heavily infected with swimbladder nematodes than those from Greenwater Lake. Analysis of trout stomachs indicated that young fish in both lakes fed predominantly on mysids but most samples from Greenwater Lake were taken in the fall while samples from Burchell Lake were taken throughout the year. Small lake trout frequently utilize a piscine forage when readily available (Eschmeyer 1956; Wright 1968; Frantz and Cordone 1970; Martin 1970) and their diet may change with season (Dryer *et al* 1965; Wright 1968; Frantz and Cordone 1970; Anderson and Smith 1971). Possibly, lake trout in Greenwater Lake consume fewer mysids at certain times of the year than lake trout in Burchell Lake.

There is no evidence that a paratenic host is important in the transmission of *C. cristivomeri* to lake trout. No infective larvae were recovered from lake herring from the study lakes and large piscivorous lake trout (>50 cm long) in Greenwater Lake had few immature worms that would indicate recent infection. However, the possibility that paratenic hosts are involved in the transmission of *Cystidicola* spp. cannot be excluded entirely. Work reported here and that by Opie (1980), who experimentally infected rainbow trout with *C. farionis* larvae from rainbow smelt (*Osmerus mordax* Mitchill), indicate that larvae removed from the swimbladder

of one fish can reach the swimbladder of another. Feeding experiments in the laboratory would determine whether cystidicolid larvae could escape from the carcass of a fish eaten and migrate to the swimbladder of a piscivorous salmonid. Since paratenic hosts apparently play no role in transmitting *C. cristivomeri* in Greenwater Lake and lake trout greater than 35 cm long rarely consumed *M. relicta*, there is essentially no recruitment of larvae to fish older than five years (mean length = 29.3 cm) in this lake. This conclusion is also supported by the observation that the number of immature worms were highest in five year old fish and the size of immature worms increased sharply in fish after age five.

Swimbladder lesions associated with the presence of *Cystidicola* spp. have been described by several authors (Drew 1909; MacLulich 1943; Awachie 1973; Lankester and Smith *in press*) but how the lesions develop and whether they cause fish mortality is presently unknown. The number of lesions in the swimbladder of lake trout with *C. cristivomeri* was most highly correlated with the number of mature worms present. The number of lesions also appeared related to the size of mature worms. There were more lesions in fish from Greenwater Lake with large mature worms than in lake trout from the other lakes with similar numbers, but smaller mature worms.

Salvelinema walkeri (Ekbaum, 1935) Margolis, 1967 in the swimbladder of coho salmon, *Oncorhynchus kisutch* (Walbaum), feeds on blood (Margolis 1967b). Whether *Cystidicola* spp. feed in a similar way is unknown but it should be noted that worms were never found attached to the wall of the swimbladder at necropsy of infected fish. Lankester and Smith (*in press*) found tangled masses of *C. farionis* closely associated with ulcerative lesions in the swimbladder of rainbow trout. Since similar lesions in lake trout appear dependent on the number of mature *C. cristivomeri* present, they may result when adult worms aggregate, possibly to mate. *Mysis relicta* has been introduced into a large number of lakes where shrimp formerly were absent (Gosho 1975). In view of the potential for *C. cristivomeri* to cause disease, mysids might be transported, when practical, only from lakes where the parasite is absent.

Evidence indicates that *C. cristivomeri* is particularly long-lived in lake trout. There was no measurable mortality of worms after 600 days in experimentally infected lake trout. In Greenwater Lake, the maximum length of mature worms increased with increasing fish age (ages 2 to 12) suggesting that worms present in young fish keep growing and are still present when fish are much older. Also, the number of worms remained essentially constant in fish from age five until after age 12 as would be expected if worms were long-lived

and there was no recruitment during this period. Therefore, most *C. cristivomeri* in lake trout from Greenwater Lake appear to live at least 10 years and some probably live longer. Worms likely are similarly long-lived in the other lakes where fish were more heavily infected since the maximum length of mature worms continued to increase with fish age.

There is reason to suspect that worms may live even longer than suggested. The number of worms in age classes greater than 12 years cannot be compared to that in younger age classes because of small sample sizes and because ages may have been underestimated. Although scale ages of fish less than 10 years old agreed with otolith ages, scales have frequently been reported to underestimate the age of old lake trout (Bulkley 1957; Dubois and Langueux 1968; Simard and Magnin 1972; Johnson 1976; Power 1978). Also, the stunted growth of lake trout in Squeers Lake and to a lesser extent in Burchell Lake, is not uncommon in this species (Martin 1952, 1966; Kerr 1971), but probably resulted in underestimates of the ages of some of the older lake trout in these lakes.

The longevity of *C. cristivomeri* is rather unique for a parasite of fishes. Most fish parasites have seasonal or annual life cycles (Kennedy 1975). Only a few fish parasites have been reported to live longer than one year in their definitive host including the monogeneans *Discocotyle sagittata* (Leuckart, 1842)

Diesing, 1850 and *Diplozoon paradoxum* Nordmann, 1832; the digenean *Tubulovesicula lindbergi* (Layman, 1930) Yamaguti, 1934; the cestode *Eubothrium salvelini* Nybelin, 1922; and two nematodes *Cucullanus truttae* Fabricius, 1794 (=*Dacnitis truttae*) and *Salvelinema salmonicola* (Ishii, 1916) Margolis, 1966 (Paling 1965; Anderson 1974b; Margolis and Boyce 1969; Hoffman 1967; Margolis 1965; Margolis 1967a, respectively). The longevity of *C. cristivomeri* makes detection of any seasonal recruitment or maturation that may exist difficult. Also, a long life span is an important consideration when examining parasite population dynamics.

Female *C. cristivomeri* appeared to mature more slowly in heavily infected fish than in those with fewer worms suggesting a density-dependent regulation of maturation. This is apparent upon casual examination of data for five-year-old fishes where the mean numbers of mature females were essentially the same in fishes from each of the four lakes despite significant differences between total number of worms present. Analysis of data from five-year-old lake trout indicated that the percentage of female *C. cristivomeri* in individual fish was inversely related to the total numbers of worms and positively related to fish length. The effect of fish length likely reflects the space available for worms in the swimbladder. The same variables affecting the percentage of mature females

were important with reasonable consistency when data for older lake trout from Burchell and Greenwater Lakes and when data from all ages from Gaviafaeces Lake were analyzed. The failure to demonstrate a density-dependent relationship at individual fish ages in Squeers Lake may not be surprising. The ages of many of the older fish were almost certainly underestimated and would result in considerable unaccountable variation in the analyses.

It might be argued that the inverse relationship between the percentage of mature females and total numbers of worms resulted from density-dependent mortality of *C. cristivomeri* rather than retarded growth of female worms. Several parasites appear to experience density-dependent mortality (Hasselberg and Andreasson 1975; Anderson and Michel 1977; Mills *et al* 1979) but most of these examples are thought to be mediated by host immune responses. However, it has not been demonstrated that the immune system of fishes responds effectively to endoparasitic helminths (Harris 1973) and there is general agreement that it plays no role in the regulation of fish parasite infrapopulations (Kennedy 1975, 1977). Mills *et al* (1979) observed density-dependent mortality of the ectoparasitic digenean, *Transversotrema patialensis* (Soparker, 1924), on its fish host *Branchydanio rerio* (Hamilton-Buchanan) which apparently resulted from intraspecific competition for space; an immune response was not thought to

be involved. Density-dependent mortality is an unlikely explanation for the observed relationship between the percentage of mature females and total numbers of *C. cristivomeri* since dead worms were never found in swim-bladders or being expelled from fish through the stomach, and larvae of all developmental stages were found in the most heavily infected fishes. There was no detectable mortality of worms in experimentally infected lake trout up to 600 days nor was there evidence that many worms died over a long period of time in lake trout from Greenwater Lake.

Mature female *C. cristivomeri* may not grow as rapidly in heavily infected fish as in fish with fewer worms. In Gaviafaeces Lake, the maximum length of females was related negatively with total number of worms and positively with fish length. In Burchell Lake, fish length was the only variable significantly affecting the maximum length of female worms and no significant effects on female length were seen in fish from the other lakes. However, in Greenwater Lake where the intensity of infection was low, the maximum length of females was consistently higher than that in the more heavily infected fish from Burchell Lake. The magnitude of the differences between these lakes may be somewhat exaggerated. The probability of measuring the longest worms in fish from Greenwater Lake was high since absolute counts of worms were

made from most fish. However, the subsampling technique used on worms from Burchell Lake fish probably decreased the chances of measuring the longest females. Failure to demonstrate a negative relationship between total number of worms and maximum length of females at individual fish ages in these two lakes may not be surprising. In Greenwater Lake, the variation in numbers of worms in fish of the same age may have been insufficent to reveal any effect of worm numbers on the maximum size attained by females. In Burchell Lake, the subsampling technique and the suspected problem of aging older fish probably resulted in additional unaccountable variation in the analyses. Consequently, any relationship between numbers of worms and maximum length of females may have been masked.

If the maximum length attained by female worms is determined in a density dependent way then the laboratory observation that short worms lay eggs at a slower rate than larger worms is of obvious significance. In comparing the egg-output of worms from Squeers and Greenwater Lakes it is apparent that female worms of the same length, whether from fish with heavy or light infections, deposit similar numbers of eggs under laboratory conditions. There was a higher correlation between egg output and worm length with worms from Squeers Lake than with those from Greenwater. This may

be explained by the ways in which worms from the two lakes were collected. Those from Squeers Lake were placed in test tubes within 24 hours of being taken from freshly caught fish. However, those from Greenwater Lake were removed from fish taken by anglers and up to 60 hours elapsed before most were put in tubes in the laboratory.

An estimate cannot be made of relative output of eggs from infrapopulations in lake trout because all mature female worms were not measured. However, other studies indicated that the resultant effect of density-dependent egg output at the infrapopulation level may be impossible to predict for any particular parasite without measuring it directly. The total egg production by an infrapopulation may either increase (Boray 1969), remain constant (Michel 1967), or even decrease (Hasselberg and Andreassen 1975) with increasing number of worms. It is apparent that the total egg output by an infrapopulation of *C. cristivomeri* is dependent upon the number and length of female worms present. The length of female worms, in turn, is dependent upon the length of time a fish has been infected and probably the size of the infrapopulation during this time.

All organisms have a reproductive potential capable of increasing population size. Obviously, some form of control must exist to restrain that increase. The controls

may be effective equally over the entire range of population densities in which case they are density-independent and not regulatory in the sense of the word used here. On the other hand constraints may operate with increasing severity as population size increases in which case they are density-dependent. The latter situation results in a negative feedback control of population growth and is the form of regulation demonstrated here for *C. cristivomeri*. Density-dependent controls, when in operation, usually affect an infrapopulation in the following way: as recruitment increases the proportion of worms establishing and maturing decreases as does the growth rate and egg output per female (Holmes *et al* 1977). This statement is an accurate description of the negative feedback controls acting on *C. cristivomeri* in its definitive hosts, except there is no evidence that fewer recruits successfully establish as infrapopulations increase in size.

Bradley (1972, 1974) outlined three ways in which the size of suprapopulations may be determined (not necessarily regulated). The first (Type I) is parasite numbers determined by factors such as feeding preferences that influence rates of transmission. The result of different levels of transmission is readily visible by comparing worm burdens in fish from Burchell and Greenwater Lakes. However, parasite number determined by transmission is density-independent (Holmes *et al*

1977; Kennedy 1977) and is not regulation in the sense used here. Bradley's Type II is regulation at the level of the host population either by the death of the most heavily infected hosts of an overdispersed parasite population or by an effective immune response which rids the host of parasites and results in permanent immunity. Type III is regulation at the level of the host individual either by some form of partial immunity or, as recognized by Holmes *et al* (1977), by other mechanisms such as intraspecific competition which is known to regulate populations of free-living organisms.

Bradley's Type II regulation has received considerable attention. Overdispersion as a characteristic of various parasite populations has frequently been described (Esch *et al* 1977). Crofton (1971a, 1971b) recognized and described mathematically that overdispersion of parasites in their host population with death of the most heavily infected individuals can lead to regulation of the parasite suprapopulation. May (1977) subsequently re-examined Crofton's model and substituted more realistic assumptions but generally came to similar conclusions. Bradley's Type II regulation is unlikely to play an important role in the population regulation of *C. cristivomeri*. Lesions in the swimbladder appear to be caused by adult worms and density dependent restraints prevent the maturation of large numbers of worms except in a few very old fish. However,

C. cristivomeri may demonstrate another way in which the size of a parasite suprapopulation is affected at the host population level. The long development time required and the low reproductive output, probably for several years after maturation, results in considerable loss from the system with the natural death of the host. Adult lake trout suffer up to 50% annual natural mortality (Sakagawa and Pycha 1971) and presumably higher mortality in earlier life. Other fishes also experience high annual mortality but most parasites have seasonal or annual life cycles (Kennedy 1975). Consequently, a reasonable percentage of these parasites would establish in their definitive host and reproduce before the host dies. The loss of reproductive potential in a long-lived parasite like *C. cristivomeri* clearly does not act in a negative feedback manner and hence is not regulatory.

Bradley's Type III regulation at the level of the host individual, although well known in homeotherms (see Bradley 1972, 1974; Kennedy 1975; Grundmann *et al* 1976; Schad 1977), seems rare in poikilotherms. Leong (1975) found *Metechinorhynchus salmonis* (Müller, 1784) infecting ten species of fishes in Cold Lake, Alberta. The maturation of female acanthocephalans was strongly regulated in lake whitefish. The mean numbers of gravid females were not

significantly different between age classes in spite of significant differences in the mean total numbers of worms. Holmes *et al* (1977) modelled this system and found that regulation at the infrapopulation level in lake whitefish was sufficient to regulate the levels of the whole suprapopulation. Kennedy (1977) summarizing his own work and that of his associates on *Pomporhynchus laevis* (Müller, 1776) in the River Avon concluded that this acanthocephalan was regulated in a manner similar to that of *M. salmonis* in lake whitefish. However, this conclusion was based on studies conducted with fish in which *P. laevis* did not mature. Apparently, evidence has since been found for density-dependent regulation in the suitable hosts of *P. laevis* (Holmes *et al* 1977). It may be significant that the population levels of both *M. salmonis* and *P. laevis* were high in the two localities mentioned. Kennedy (1977) suggested that density-dependent regulation may only occur in very crowded populations. Mills *et al* (1979) reported that the ectoparasitic digenean *T. patialensis* exhibits density-dependent natality and mortality on its fish host, *B. derio*. However, their findings were based on laboratory experiments and the infrapopulation levels at which density dependent natality occurred probably do not exist in nature (Mills *et al* 1979). A few additional studies have suggested density-dependent regulation of fish parasites

but the means by which this occurs remain obscure (Kennedy 1977). *Cystidicola cristivomeri* is characterized by density-dependent growth before and after maturation and consequently, density-dependent reproductive output. This is another example of a fish parasite whose infrapopulations are regulated.

Density-dependent regulatory processes minimize fluctuations in the size of parasite suprapopulations. Many authors have modelled host-parasite systems in an attempt to examine factors important in affecting this stability (Anderson 1976; Holmes *et al* 1977; May 1977; Anderson and May 1978; May and Anderson 1978). Most models were based on the assumption that parasites are overdispersed in their host populations and some hosts may die as a result of heavy infection. However, this form of regulation seldom occurs if regulation at the level of the host individual is strong (Anderson 1978). A long term study is necessary to establish whether population levels of *C. cristivomeri* are stable but evidence presented here suggests that they are. The numbers of worms in older trout from Greenwater Lake appear to have remained stable over the last seven years.

The biology of *Cystidicola* spp. remains incompletely known. Experimental examination is needed to determine whether the swimbladder nematode which matures in lake whitefish is the same species which matures in other salmonids in North America.

Experimental examination of the delayed development of *C. cristivomeri* under crowded conditions would provide a more precise understanding of this regulatory mechanism. This experiment could also include an examination of host immune response associated with increased worm burdens and changes in egg output by infrapopulations in infected fish. A long term study of *C. cristivomeri* in nature is needed to confirm that population levels of this nematode are indeed stable. Comparison of egg output between *C. cristivomeri* and *C. farionis* may provide an appreciation of any ecological differences between these two nematodes. Finally, experimental infection of fish in the laboratory would demonstrate whether *C. cristivomeri* is more pathogenic in lake trout from unexposed populations than in fish from lakes where the parasite already exists.

Literature Cited

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

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

Anderson, R. M. 1974a. Population dynamics of the cestode *Caryophyllaeus laticeps* (Pallus, 1781) in the bream (*Abramis brama* L.). J. Anim. Ecol. 43: 305-321.

Anderson, R. M. 1974b. An analysis of the influence of host morphometric features upon the population dynamics of *Diplozoon paradoxum* (Nordmann, 1832). J. Anim. Ecol. 43: 873-887.

Anderson, R. M. 1976. Dynamic aspects of parasite population ecology. *In* Ecological aspects of parasitology. *Edited by* C. R. Kennedy. North Holland Publishing Co., Amsterdam.

Anderson, R. M. 1978. The regulation of host population growth by parasite species. Parasitology 76: 119-157.

Anderson, R. M. and R. M. May. 1978. Regulation and stability of host-parasite population interactions: I. Regulatory processes. J. Anim. Ecol. 47: 219-247.

Anderson, R. M. and J. F. Michel. 1977. Density-dependent survival in populations of *Ostertagia ostertagi*. Int. J. Parasitol. 7: 321-329.

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

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

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

Boray, J. C. 1969. Experimental fascioliasis in Australia. Adv. Parasitol. 7: 96-210.

Bradley, D. J. 1972. Regulation of parasite populations: A general theory of the epidemiology and control of parasitic infections. Trans. Roy. Soc. Trop. Med. Hyg. 66: 697-708.

Bradley, D. J. 1974. Stability in host-parasite systems. *In*: Ecological stability. *Edited by* M. B. Usher and M. H. Williamson. Chapman and Hall, London.

Brownell, W. N. 1970. Studies on the ecology of *Mysis relicta* in Cayuga Lake. M.Sc. thesis. Cornell Univ., Ithaca, New York.

Bulkley, R. V. 1957. The use of branchiostegal rays to determine age of lake trout *Salvelinus namaycush* Walbaum. M.Sc. thesis. Utah State Agricultural College, Logan, Utah.

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

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

Crofton, H. D. 1971a. A quantitative approach to parasitism. Parasitology 62: 179-193.

Crofton, H. D. 1971b. A model of the host-parasite relationships. Parasitology 63: 343-364.

Dadswell, M. J. 1975. A small-boat otter trawl for limnological studies. J. Fish. Res. Board Can. 32: 2535-2538.

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

Drew, G. H. 1909. Some notes on parasitic and other diseases of fish. Parasitology 2: 193-201.

Dubois, A. and R. Lagueux. 1968. Étude comparée de l'âge scalaire et de l'âge otolithique de la toulade (*Salvelinus namaycush*) Lac Mistassini, Quebec. Naturaliste can. 95: 907-928.

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

Eddy, S. B. and M. W. Lankester. 1978. Feeding and migratory habits of Arctic char, *Salvelinus alpinus*, indicated by the presence of the swimbladder nematode *Cystidicola cristivomeri* White. J. Fish. Res. Board Can. 35: 1488-1491.

Esch, G. W., J. W. Gibbons and J. E. Bourque. 1975. An analysis of the relationship between stress and parasitism. Amer. Mid. Nat. 93: 339-353.

Esch, G. W., T. C. Hazen and J. M. Aho. 1977. Parasitism and r- and k- selection. *In* Regulation of parasite populations. *Edited by* G. W. Esch. Academic Press, New York.

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

Frantz, T. C. and A. J. Cordone. 1970. Food of lake trout in Lake Tahoe. Calif. Fish and Game. 56: 21-35.

Gosho, M. E. 1975. The introduction of *Mysis relicta* into freshwater lakes (a literature survey). Fish. Res. Inst. College Fish. Univ. Wash. Circular No. 75-2.

Grundmann, A. W., R. G. Warnock and D. L. Wassom. 1976. Some mechanisms of natural regulation of parasitic helminth populations. Am. Midl. Nat. 95: 347-360.

Harris, J. E. 1973. The immune responses of dace *Leuciscus leuciscus* (L.) to injected antigenic materials. J. Fish. Biol. 5: 261-276.

Hasselberg, C. A. and J. Andreassen. 1975. Some influences of population density on *Hymenolepis diminuta* in rats. Parasitology 71: 517-523.

Hoffman, G. L. 1967. Parasites of North American freshwater fishes. University of California Press, Berkley and Los Angeles.

Holmes, J. C., R. P. Hobbs and T. S. Leong. 1977. Populations in perspective: Community organization and regulation of parasite populations. *In* Regulation of parasite populations. *Edited by* G. W. Esch. Academic Press, New York.

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

Johnson, L. 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board. Can. 33: 2459-2488.

Kennedy, C. R. 1975. Ecological animal parasitology. John Wiley & Sons, New York.

Kennedy, C. R. 1977. The regulation of fish parasite populations. *In* Regulation of parasite populations. *Edited by* G. W. Esch. Academic Press, New York.

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

Kerr, S. R. 1971. A simulation model of lake trout growth. J. Fish. Res. Board Can. 28: 815-819.

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

Lankester, M. W. and J. D. Smith. Host specificity and distribution of the swimbladder nematodes, *Cystidicola farionis* Fischer, 1798 and *C. cristivomeri* White, 1941 (Habronematoidea), in salmonid fishes in Ontario. Can. J. Zool. *in press*.

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

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

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

Margolis, L. 1965. Parasites as an auxillary source of information about the biology of Pacific salmons (genus *Oncorhynchus*). J. Fish. Res. Board Can. 22: 1387-1395.

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

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

Margolis, L. and N. P. Boyce. 1969. Life span, maturation, and growth of two hemiurid trematodes, *Tubulovesicula lindbergi* and *Lecithaster gibbosus*, in Pacific salmon (genus *Oncorhynchus*). J. Fish. Res. Board Can. 26: 893-907.

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

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

Martin, N. V. 1970. Long-term effects of diet on biology of lake trout and fishery in Lake Opeongo, Ontario. J. Fish. Res. Board Can. 27: 125-146.

May, R. M. 1977. Dynamical aspects of host parasite associations: Crofton's model revisited. Parasitology 75: 259-276.

May, R. M. and R. M. Anderson. 1978. Regulation and stability of host-parasite interactions. II. Destabilizing processes. J. Anim. Ecol. 47: 249-267.

Meyer, M. C. and O. W. Olsen. 1971. Essentials of parasitology. Wm. C. Brown Co., Iowa.

Michel, J. F. 1967. Regulation of egg output of populations of *Ostertagia ostertagi*. Nature 215: 1001-1002.

Mills, C. A., R. M. Anderson and P. J. Whitfield. 1979. Density dependent survival and reproduction within populations of the ectoparasitic digenean *Transversotrema patialense* on the fish host. J. Anim. Ecol. 48: 383-399.

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

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

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sciences, 2nd edition. McGraw-Hill Book Company, New York.

Opie, T. C. 1980. Studies on the swimbladder nematode *Cystidicola farionis* Fischer, 1798 in rainbow smelt, *Osmerus mordax*. H.B.Sc. thesis. Lakehead University, Thunder Bay, Ontario.

Paling, J. E. 1965. The population dynamics of the gill monogenean gill parasite *Discocotyle sagittata* Leuckart on Windemere trout, *Salmo trutta* L. Parasitology 55: 667-694.

Pellitero, M. P. A. 1976. Variaciones estacionales de las infestaciones por *Cystidicoloides teniussima* en truchas (*Salmo trutta* m. Fario) de los rios de la Provincia de Leon. Anales Facultad Vet. de Leon 22: 155-167.

Power, G. 1978. Fish population structure in arctic lakes. J. Fish. Res. Board Can. 35: 53-59.

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

Remington, R. D. and M. A. Schork. 1970. Statistics with applications to the biological and health sciences. Prentice-Hall, New Jersey.

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

Sakagawa, G. T. and R. L. Pycha. 1971. Population biology of lake trout (*Salvelinus namaycush*) of Lake Superior before 1950. J. Fish. Res. Board Can. 28: 65-71.

Schad, G. A. 1977. The role of arrested development in the regulation of nematode populations. *In* Regulation of parasite populations. *Edited by* G. W. Esch. Academic Press, New York.

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

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

Simard, A. and E. Magnin. 1972. Methode de determination de l'âge et croissance du touladi, *Salvelinus namaycush* Walbaum, du Lac L'Assomption et du Lac Tremblant, Quebec. Naturaliste can. 99: 561-578.

Smith, J. D. 1978. Studies on the biology of swim bladder nematodes, *Cystidicola* spp. (Habronematoidea). M.Sc. thesis. Lakehead Univ., Thunder Bay, Ontario.

Smith, J. D. and M. W. Lankester. 1979. Development of swimbladder nematodes (*Cystidicola* spp.) in their intermediate hosts. Can. J. Zool. 57: 1736-1744.

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

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

Watson, R. A. and T. A. Dick. 1979. Metazoan parasites of whitefish *Coregonus clupeaformis* (Mitchill) and cisco, *C. artedii* Lesueur from Southern Indian Lake, Manitoba. J. Fish. Biol. 15: 579-587.

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

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

Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, New Jersey.

Appendix 1. Number and age of lake trout examined from Greenwater and Burchell Lakes, 1978-79.

Lake	Season	Age (yr.)												
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	>XII
Greenwater	July-Oct. 1978	0	0	0	0	2	6	15	19	11	3	1	4	2
	Jan.-Apr. 1979	0	0	0	0	0	0	1	2	5	4	2	2	1
	May-June 1979	0	0	0	0	0	1	13	29	33	12	4	2	5
	July-Oct. 1979	0	2	16	53	24	2	4	2	0	3	0	0	1
Burchell	July-Oct. 1978	0	0	1	6	7	1	10	7	2	1	0	0	0
	Jan.-Apr. 1979	0	0	12	8	1	2	1	0	0	1	0	0	0
	May-June 1979	0	0	0	0	0	5	9	19	21	4	0	0	0
	July-Oct. 1979	8	21	9	7	6	4	2	2	2	0	0	0	0

Appendix 2. Number and length of lake trout examined from Squeers Lake, 1978-79.

	Length (cm)		
Season	< 30	30 - 40	> 40
Fall 1978 and 1979	27	24	24
Winter 1978	4	14	9