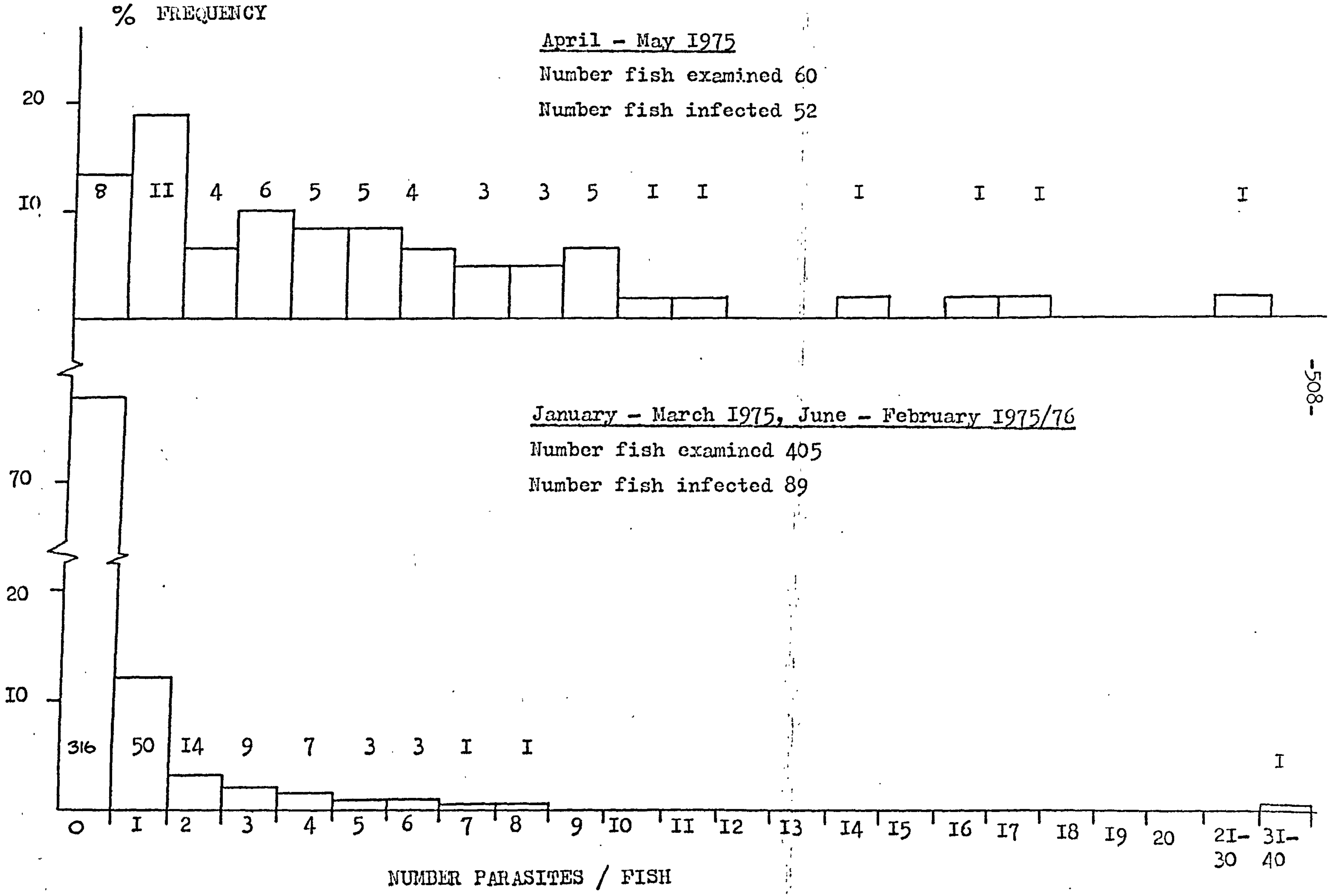


Fig. I. Seasonal changes in the frequency distribution of *Acanthocephalus clavula*. Gill net samples.

CHAPTER VIII

THE TAPEWORM (CESTODA) PARASITES OF PERCH (*Perca fluviatilis* L.) FROM LLYN TEGID

INTRODUCTION

The tapeworm parasites recorded from perch in the British Isles were listed in Chapter IV, Table I.

In this study the following pseudophyllidean tapeworms were recorded from perch: *Diphyllobothrium* sp. (pleroceroids), *Triaenophorus nodulosus* (pleroceroids) and *Eubothrium* sp./ *Bothriocephalus* sp. (plerocerciform juveniles). In addition, the proteocephalid tapeworm *Proteocephalus* sp., *Coregonus lavaratus* type (plerocerciform juveniles) were also found in perch.

VIII.1 ORDER Pseudophyllidae Carus, 1863

FAMILY Diphyllobothriidae Lühe, 1910

GENUS *Diphyllobothrium* Cobbold, 1858

Diphyllobothrium sp.

VIII.~~21~~ II INTRODUCTION

A certain degree of confusion still exists with regard to the identity of the *Diphyllobothrium* species in Britain, north west Europe and on a world wide basis (Chubb, 1976). According to Chubb (1966, 1968, 1976) three species of the genus *Diphyllobothrium* have been found as plerocercoids in the freshwater fish of the British Isles.

Diphyllobothrium latum (L., 1758) plerocercoids were found unencapsulated in the muscles of pike (*Esox lucius*), perch (*Perca fluviatilus*) and certain other predatory coarse fish. The adult worm infects man, and possibly certain other mammals (Chubb, 1968). *D. latum* has been recorded from perch in the British Isles at Garradice Lough (Ireland) (H~~u~~ikey & Harris, 1945) and trout (*Salmo trutta*) from South Wales (Dug~~o~~uid & Sheppard, 1944), and pike at Lake Windermere (Rawson, 1952; Chubb, 1965). This species may be endemic to Ireland, though it's occurrence in the remainder of the British Isles remains dubious (Chubb, 1976). *D. latum* has been more frequently recorded from perch in continental Europe and U.S.S.R. (Bykhovskaya-P~~e[illegible]~~avlovskaya, 1940; Scolari, 1955; Barysheva & Bauer, 1957; Nagibina, 1957; Kozicka, 1959; Kosheva, 1960; Tallquist, 1965; Tell, 1971; Borroni & Grimaldi, 1973, 1974; etc).

Diphyllobothrium dendriticum (Nitzsch, 1824) plerocercoids are princi~~apply~~pally parasitic in salmonoid fish in the British Isles, and have been less frequently recorded in sticklebacks (*Gasterosteus aculeatus*). They are usually encapsulated on the stomach and viscera (Chubb, 1976). In Llyn Tegid this species has been recorded from trout (*Salmo trutta*) and grayling (*Thymallus thymallus* (Chubb, 1963a, 1976; Aderounmu, 1965). Adult worms may be found in gulls (Laridae), as well as certain fish eating mammals and experimentally in man (Chubb, 1968). Chubb (1968, 1976) considered that *D. medium* (Fahnig, 1954) and *D. norvegicum* Vik, 1957 are synonyms of *D. dendriticum*, a view which is held by other works, including Halvorsen (1970) and Bylund (1975a).

Diphyllobothrium ditremum (Creplin, 1825) plerocercoids are parasitic in salmonid fish and sticklebacks (*Gasterosteus aculeatus*) in the British Isles. They are usually encapsulated on the stomach and viscera (Chubb, 1976). This species is the commoner of the two *Diphyllobothrium* species present in Llyn Tegid and is recorded from trout (*S. trutta*), grayling and gwyniad (*Coregonus lavaratus*) (Chubb, 1963a, 1976; Aderounmu, 1965). The adult worms of this species may be found in birds of the families Phalacrocoracidae, Ardeidae, Colynebidae and Anatidae (Chubb, 1968). *D. osmeri* (Linstow, 1878) and *D. vogeli* Kuhlow, 1953 are considered by Chubb (1968, 1976) to be synonyms of *D. ditremum*. However, Bylund (1975b) considered that on the morphological and histological characters of the plerocercoid and adult worm, *D. vogeli* is a separate species. *D. dentriticum* and *D. ditremum* have a wide distribution in the British Isles, continental Europe and U.S.S.R. (Bykhovskaya-Pavlovskaya *et al.* 1962; Halvorsen, 1970; Kennedy, 1974). Neither species has previously been recorded from perch in the British Isles.

However, *Diphyllobothrium* sp. (plerocercoid in the intestinal lumen) was recorded from perch by Rawson (1952) at Lake Windermere, and *Diphyllobothrium* sp. (plerocercoids) have been found in perch from Ireland (Kare, 1966).

In addition to the work of Chubb (1966, 1968, 1976) and Bylund (1975b), other recent taxonomic studies on this genus include Halvorsen (1970) and Bylund (1969, 1973, 1975a).

VIII. 12 ~~22~~. ADDITIONAL MATERIALS AND METHODS

The majority of the specimens of *Diphyllobothrium* sp. from perch were of poor quality primarily as a result of deep freezing of the material prior to detailed examination (see Chapter II). The usual low incidence of this parasite in perch made the examination of large numbers of fresh (or histologically treated) specimens difficult. However, the incidence of infection rose during the latter months of this study (January and February, 1976) and observations were then made on a small number of fresh, living plerocercoids in tapwater and 0.85% sodium chloride solution. No histological studies were performed.

VIII. 13 ~~23~~ RESULTS

Observations on the identification of the *Diphyllobothrium* sp. present in perch.

Observations on frozen and fresh material permitted the tentative identification of *D. dendriticum* on a number of occasions. Large (20 - 40mm long by 3 - 5mm wide, after deep freezing and thawing) plerocercoids were found at various visceral sites. They were encapsulated in thin walled capsules of white, host connective tissue. Live specimens were active in saline solution, and remained alive for over one hour in cold tapwater. When relaxed in cold tapwater these plerocercoids were smooth, ribbon-like with a small, flattened extended scolex with two bothria. After relaxation in tapwater they measured approximately 3cm. In addition, small (10 - 15mm long by 3 - 5mm wide) plerocercoids were found, similarly encapsulated. These parasites appeared rather degenerate and had a very poorly defined scolex. No observations were made on fresh, living specimens of this type.

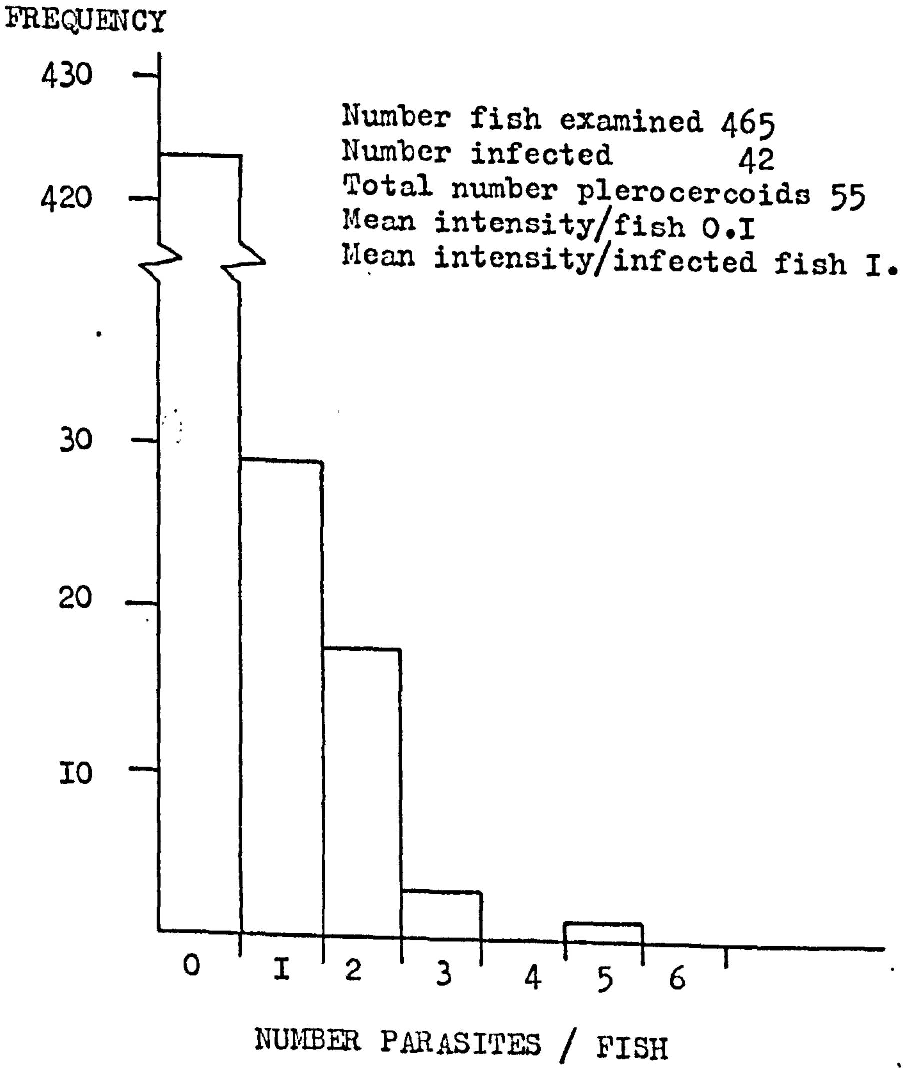
Until further specific determination can be made these two "types" of plerocercoid will be referred to collectively as <u>Diphyllobothrium</u> sp.

Gill net samples

Forty-two of 465 fish (9.0%) were infected with a total of 55 plerocercoids. The mean intensity /infected fish was 1.3 (maximum 5) . The mean intensity/fish was 0.1. The frequency distribution of <u>Diphyllobothrium</u> sp. from the gill net samples of adult perch is shown in Fig. 1. Of these infected over half (29 fish) harboured only one plerocercoid.

Table I shows the distribution of this parasite in the viscera of perch. Approximately equal numbers of plerocercoids were found encapsulated on the gonads, swimbladder and liver. Over half of the 55 parasites (52.7%) were found encapsulated on the ~~in the liver~~ wall of the intestine. Capsules always contained one plerocercoid each.

Fig. I. Frequency distribution of Diphyllobothrium sp. Gill net samples. January 1975 - February 1976.



Number fish examined 465
Number infected 42
Total number plerocercoids 55
Mean intensity/fish 0.I
Mean intensity/infected fish I.3

No plerocercoids were found associated with the stomach or pyloric caeca.

Trawl sample

Three of 64 fish (4.7%) were infected in March (1976), with a total of three plerocercoids. The mean intensity/infected fish was (1.0) (maximum 1). The mean intensity/fish was 0.05.

Purse seine sample

None of 30 0+ perch fry examined in July (1976) were infected.

Table I. Distribution of the plerocercoids of *Diphyllobothrium* sp. within the viscera of perch.

	Number of plerocercoids	% of total
Liver	9	16.4
Stomach wall and wall of pyloric caeca	0	-
Wall of intestine	29	52.7
Wall of swimbladder	9	16.4
Wall of gonads	8	14.5
Total	55	-

Seasonal aspects of the Diphyllobothrium sp. infection

The results from the gill net samples are presented in Table II. There were no apparent seasonal changes in incidence or the mean intensity/infected fish. However, during January and February (1976) the incidence of infection rose from 8.6% (December 1975) to 20.0% (January 1976) and 38.1% (February 1976). The mean intensity/infected fish did not rise markedly over this period (Table II).

Effect of host age and length on the Diphyllobothrium sp. infection

None of 30 0+ perch fry (mean length 2.3 cm, maximum 2.7 cm) examined in July (1976) were infected. However, the parasite was recorded from one of 36 (2.8%) 0++ fish (length 3.0 - 8.9cm) in March (1976) (Table IV).

The results from the gill net samples are presented in Tables III & V. There appeared to be a higher incidence in younger, smaller perch (aged 2-2++ years, length 9.0 - 11.9cm). In older, larger perch the incidence fell and then remained constant, except perhaps in the oldest age group (Table III & V). The mean intensity/infected fish was usually low. There may be a rise in intensity with increasing age and length of the fish, to a peak in perch aged 5-5++ years and 15.0 - 17.9 cm (Tables III & V). In older, larger perch the intensity of infection appeared to fall (Tables III & V).

These results are represanted graphically in Figs. 2 & 3.

Table II. Seasonal aspects of the Diphyllobothrium sp. infection.

Gill net samples. January 1975-February 1976

Month	Number fish examined	Number fish infected	% incidence	Number parasites	Mean/infected fish	Maximum
J	6	1	16.6	1	1.0	1
F	30	2	6.7	2	1.0	1
M	30	2	6.7	2	1.0	1
A	30	0	-			
M	30	0	-			
J	39	2	5.1	3	1.5	2
J	40	4	10.0	4	1.0	2
A	30	2	6.7	3	1.5	2
S	30	1	3.3	1	1.0	2
O	60	5	8.3	8	1.6	2
N	54	6	11.1	7	1.2	2
D	35	3	8.6	5	1.7	2
J	30	6	20.0	11	1.8	5
F	21	8	38.1	8	1.0	1
Total	465	42	9.0	55	1.3	5

Table III. Effect of host age on the Diphyllobothrium sp. infection. Gill net samples. January 1975 - February 1976.

Age (yrs)	Number fish examined	Number fish infected	% incidence	Number of parasites	Mean/ infected fish	Maximum
2-2++	4	1	25.0	1	1.0	1
3-3++	138	14	10.1	16	1.1	3
4-4++	164	16	9.8	22	1.4	3
5-5++	78	5	6.4	10	2.0	5
6-6++	43	5	11.6	5	1.0	2
$\geqslant 7$	38	1	2.6	1	1.0	1

Table IV. Effect of host age on the Diphyllobothrium sp. infection. Trawl sample. March 1976

Age (yrs)	Number fish examined	Number fish infected	% incidence	Number parasites	Mean/ infected fish	Maximum
0++	36	1	2.8	1	1.0	1
1++-4++	28	2	7.1	2	1.0	1
Total	64	3	4.7	3	1.0	1

Table V. Effect of host length on the Diphyllobothrium sp. infection. Gill net samples. January 1975 - February 1976

Length (cm)	Number fish examined	Number fish infected	% incidence	Number parasites	Mean/ infected fish	Maximum
9.0-11.9	56	9	16.1	10	1.1	2
12.0-14.9	321	28	8.7	36	1.3	3
15.0-17.9	60	3	5.0	7	2.3	5
⩾18.0	29	2	6.9	2	1.0	1

Fig. 2. Effect of host age on Diphyllobothrium sp. infection. Gill net and trawl samples. January 1975 - March 1976.

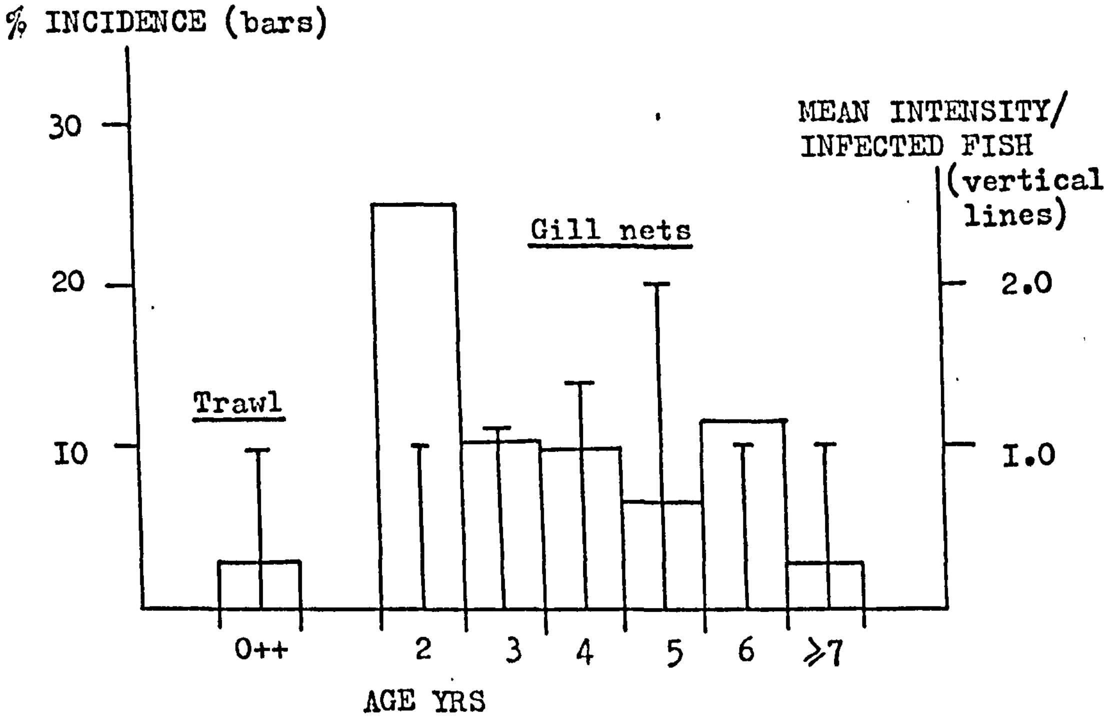


Fig. 3. Effect of host length on Diphyllobothrium sp. infection. Gill net samples. January 1975 - February 1976.

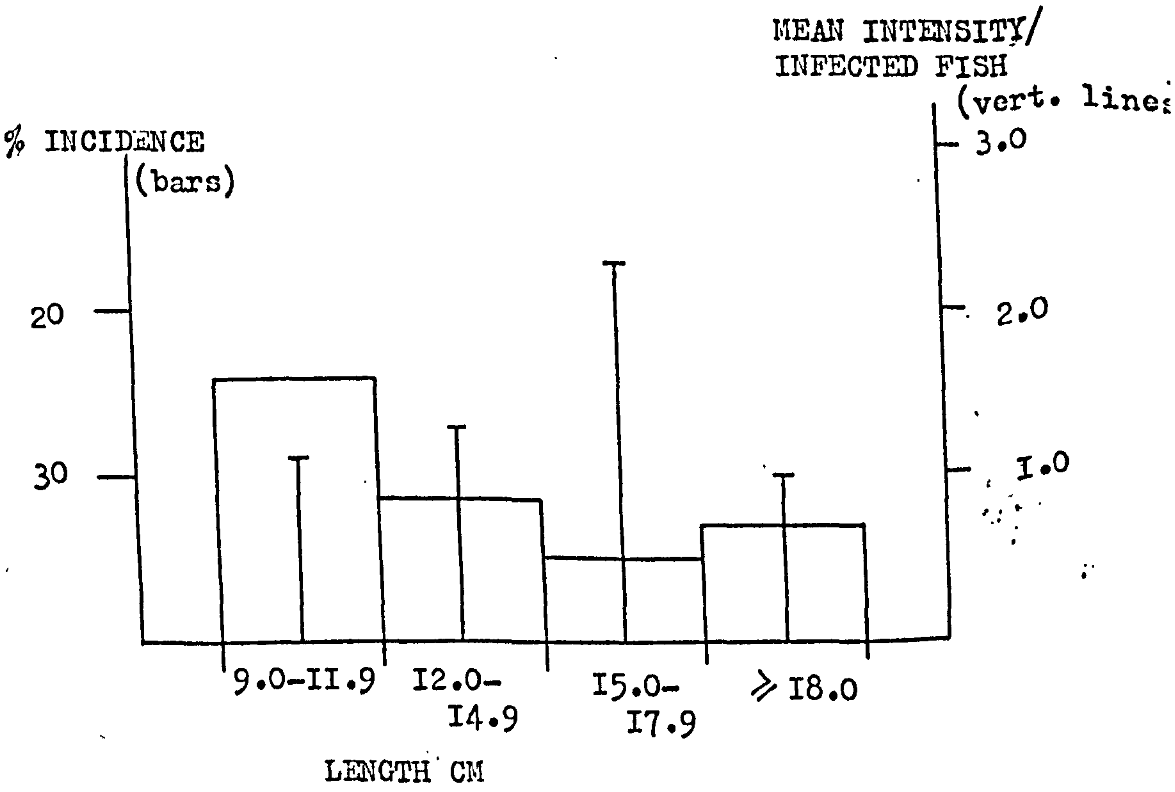


Table VI. Effect of host sex on the Diphyllobothrium sp. infection. Gill net samples. January 1975 - February 1976

	Male	Female
Number fish examined	183	282
Number fish infected	18	24
% incidence	9.8	8.5
Number parasites	25	30
Mean/infected fish	1.4	1.3
Maximum	5	3

Effect of host sex

From the gill net samples taken between January 1975- February 1976, the incidence and mean intensity/infected fish was very similar in male and female perch (Table VI).

VIII.~~24~~14 DISCUSSION

The life cycles of D. latum, D. dendriticum and D. ditremum all involve a copepod first intermediate host, a piscine second intermediate host, and a warm blooded piscivorous definitive host.

The Diphyllobothrium sp. in this study was found in 9.0% of the adult perch examined from the gill net samples. The parasites showed a predilection for the wall of the intestine, where they were most commonly found. However, the wall of the swimbladder, gonads and liver were other sites that were infected. Because of the relatively low occurrence of this parasite in perch, any competitive relationship that may exist between these plerocercoids and the plerocercoids of Triaenophorus nodulosus could not be demonstrated. In addition, the two "types" of Diphyllobothrium plerocercoids recorded in this study showed no individual preferences for site of encapsulation in perch. Halvorsen (1970) stated that the relative abundance of the plerocercoids of Diphyllobothrium spp. in a given site will vary with the host species, the size of the host and the intensity of infection. Therefore, he concluded that the site of infestation of these parasites is of little taxonomic value. Chubb (1963a) recorded plerocercoids of D. ditremum and D. dentriticum from the stomach serosa of salmonoid fish in Llyn Tegid. Clearly this site is not favoured by Diphyllobothrium sp. in perch.

Kennedy (1970) suggested that in fish (intermediate) host-parasite systems where the (larval) parasite is long-lived there may be no regular seasonal fluctuations in parasite occurrence. Whilst perch seasonally ingest large numbers of planktonic crustaceans during the summer-autumn months of June-October (see

Chapter III), there were no seasonal fluctuations in the incidence and mean intensity/infected fish of *Diphyllobothrium* sp. However, during the winter months of November (1975)-February (1976) cyclopoid crustaceans were found in the stomachs of perch. During January and February (1976) there was a rise in the incidence of the *Diphyllobothrium* sp. infection. The significance of this rise is not known though a comparable rise did not occur in January-February (1975), when cyclopoid crustaceans were not recorded from perch stomachs until March. Powell & Chubb (1966) and Campbell (1974) have reported short-term changes in the occurrence of *Diphyllobothrium* spp. in trout (*Salmo trutta*) at Llyn Padarn and Loch Leven respectively.

Perch may acquire the infection during their first year of life in Llyn Tegid. However, Hynes (1950) and Halvorsen (1970) have shown that young sticklebacks (*Gasterosteus aculeatus*) are not suitable hosts to *D. dendriticum*, even though they ingest large quantities of copepods. The plerocercoid infection only occurred in sticklebacks over 3.0 cm in length.

The incidence of *Diphyllobothrium* sp. in perch from Llyn Tegid appeared to be highest in fish aged 2-2++ years and length 9.0-11.9 cm. This may be related to the feeding habits of perch of this size, who probably feed extensively on planktonic crustaceans. In older, larger perch the incidence of infection fell, and then remained constant except in the very oldest fish.

The intensity of infection appears to reach a peak in perch aged 5-5++ years and length 15.0-17.9 cm. Observations on the feeding habits of perch at Llyn Tegid indicated that plankton feeding was most prevalent in perch smaller/younger than this, though larger fish were markedly cannabilistic in diet (see Chapter III). The rise in the intensity of infection may be a result of either selective plankton feeding by certain larger perch, or secondary infection of large perch from smaller, infected prey fish. This latter method of infection is known to occur in D. dendriticum, where trout acquire the infection secondarily from infected sticklebacks (Hickey & Harris, 1947; Kuhlow, 1953; Vik, 1957; Halvorsen, 1970) and also in D. latum (Baer, 1925; Hobmaier, 1927; Pavlovski & Gnezdilov, 1939) and T. nodulosus (Bauer, 1959; Vik, 1959; Kuperman, 1973). This does not appear to be the most likely explanation for the rise in intensity in Llyn Tegid perch, since the incidence of infection did not rise, and in still older, larger perch the mean intensity/infected fish fell. Therefore, it seems that the observed rise in intensity in perch aged 5-5++ years (length 15.0-17.9 cm) is a result of selective plankton feeding by certain fish. In fact, in the age group 5-5++ and the length group 15.0-17.9 cm, the same fish harbouring 5 plerocercoids was responsible for the rise in intensity. It is, therefore, likely that the rise in intensity of infection is simply a result of the heavy infection of a single fish.

The definitive hosts of D. dendriticum are principally gulls (Laridae). Halvorsen (1970) suggested that if gulls are incapable of catching live trout,the importance of other non-salmonoid fish in the life history of this tapeworm may be great. Halvorsen concluded that the occurrence of D. dendriticum in Norway may be dependent on the presence of small, infected fish in shallow water. Normally, sticklebacks (Gasterosteus aculeatus) will fulfill the requirements of acting as the second intermediate host to this species, and its importance in this respect has been indicated by

Unsworth (1944) and Kuhlow (1953). In the absence of sticklebacks, other fish (e.g. small burbot, *Lota lota*) which live in shallow water may function as intermediate host (Halvorsen, 1970). Sticklebacks are absent from Llyn Tegid, and not recorded as host to *D. dendriticum* in the River Dee system (Chubb, 1976). Therefore, hearing in mind the low incidence of this parasite in trout and grayling at Llyn Tegid, and also that perch are probably inshore from June-September, small perch may fill a role in the life history of *D. dendriticum* that is occupied in other localities by sticklebacks or small burbot. However, the identity and viability of the plerocercoids from perch at Llyn Tegid requires further study.

VIII. ~~25~~ 15 SUMMARY

The occurrence of *Diphyllobothrium* sp. in perch is a new host record for Llyn Tegid.

The plerocercoids were found encapsulated on the wall of the intestine, gonads, swimbladder and in the liver.

There was no seasonal fluctuation in incidence or intensity of infection, though a rise in incidence was noted at the end of the study period.

There was a peak in incidence of infection in perch aged 2-2++ years and length 9.0-11.9 cm. There may be no change in the mean intensity/infected fish with host age and length.

There was no difference in the incidence or intensity of infection in male and female adult perch.

The possible role of perch in the life history of *D. dendriticum* at Llyn Tegid is suggested. However, there is a need for the specific determination of the *Diphyllobothrium* sp. in perch, and the viability of the plerocercoids should be investigated.

VIII.~~3~~ 2 ORDER Pseudophyllidea Carus, 1863

FAMILY Triaenophoridae Lömberg, 1889

GENUS Triaenophorus Rud., 1793

Triaenophorus nodulosus (Pallas, 1781)

VIII. ~~31~~ 21 INTRODUCTION

Triaenophorus nodulosus was among the first parasitic organisms to be described. Sche~~r~~uring (1930) (in Kuperman, 1973) cited what was probably the earliest reference to this tapeworm when, in 1688, "nests of worms" were described from the intestine of pike and the liver of perch.

T. nodulosus is widely distributed in the north and central part of the Holarctic, including North America, Europe (including British Isles, though not Ireland) and the U.S.S.R. (Michajlow, 1962; Kane, 1966; Kuperman, 1973; Kennedy, 1974). Other species in the genus include T. crassus (Forel, 1868) which has a similar distribution to T. nodulosus, and T. stizostedionis Miller, 1945 which is only found in North America.

Kuperman (1973) has summarised the knowledge on the genus Triaenophorus.

VIII.~~32~~ 22 ADDITIONAL MATERIALS AND METHODS

Examination of the purse seine, trawl and gill net samples

The dissection of perch for parasites has been described in detail in Chapter II. In addition, gross observations on the T. nodulosus infection were recorded. Capsules containing the plerocercoids were then punctured and the number of parasites counted. Their development was assessed in the manner of Chubb (1964):

developing plerocercoids: small, unencapsulated plerocercoids in visceral tissues;

mature plerocercoids: plercercoids encapsulated in a thin walled capsule. (Later stages in the development were mature plerocercoids with a well defined posterior cauda. These parasites were normally found within capsules with thicker walls.)

Degenerating plerocercoids: dead, degenerate plerocercoids within hardened capsules.

This system represents a continuum with newly acquired developing plerocercoids at one end, and dead degenerate plerocercoids at the other.

Host encapsulation of *T. nodulosus*

In order to study the host encapsulation of this parasite, perch were gill netted or caught using a mid-water trawl from Llyn Tegid (during 1975 and early 1976). The perch were killed by a blow to the head and immediately dissected at the lakeside. Infected and uninfected perch livers were carefully removed and fixed in a good excess of 10% neutral buffered formalin (Bucke, 1971). To aid penetration of the fixative, large livers were cut into "steaks" several millimetres thick, prior to fixation. After 24 hours the fixative was decanted and replaced with fresh. This was then left for at least 48 hours, though usually much longer. All tissues were processed, as follows, within 6 months of initial fixation (see Appendix II).

Whole livers or liver steaks were washed overnight in running tap water. They were then dehydrated using ascending grades of ethyl alcohol, with two short washes in absolute alcohol. The tissues were cleared in methyl benzoate and benzene, and embedded in "Paraplast". Methyl benzoate was found to produce more satisfactory results than chloroform. Prior to dehydration, a number of tissue samples were treated with a commercial decalcifying agent, RDC (RDC Bethlehem Instrument Ltd, Hemel Hempstead, Herts).

Serial sections were cut at 6-8um on a rotary microtome. The following stains were used on both infected and ininfected tissues.

Haematoxylin and Eosin (H & E)
Modified Mallory-Heidenhain (Casson, 1950)
Von Kossa (Lillie, 1965)
Fite-Faraco (Parisot & Decker, 1960)
Ziehl-Neelsen (Amlacher, 1970; Lillie, 1965)
Gram (Lillie, 1965).

The sections were examined using standard light and phase microscopy, and photographed using a Leitz photo-microscope.

VIII. ~~35~~ 23 RESULTS

Gill net samples

Four hundred and twenty of 465 (90.3%) perch were infected with a total of 1418 plerocercoids of *T. nodulosus*. The mean intensity/infected fish was 3.4 (maximum 20). The mean intensity/fish was 3.0.

The parasite population consisted of approximately equal numbers of encapsulated mature and encapsulated degenerating plerocercoids. Unencapsulated developing plerocercoids were rare. Out of 1418 plerocercoids, 51.4% were degenerating, 48.5% mature and 0.1% developing. Mature plerocercoids were contained within capsules with thin, white walls, and the plerocercoid was surrounded by a clear, albuminous fluid. In older capsules the walls may become thickened and hardened, and the contents caseous and finely granular. In such capsules degenerating plerocercoids were often found. Capsules were commonly found containing two or more plerocercoids.

In addition to the capsules of *T. nodulosus*, another type of capsule was found within the viscera of perch. The liver, swimbladder and mesenteries were the common sites of infection. These capsules were small (up to 3mm in diameter) and yellow/brown in colour. There was usually a core of dark, necrotic material. These capsules were often found in small clusters, not infrequently associated with the capsules of *T. nodulosus*. Whilst these capsules were common in perch at Llyn Tegid, chronically infected fish were not seen. The squashing of fresh material revealed the absence of microsporidian or myxosporidian spores.

In connection with the plerocercoid infection with T. nodulosus, extensive fibrosis was seen in a number of heavily infected fish, and peritoneal adhesions observed once. These were no signs of extensive haemorrhage in infected livers.

Table VII shows the distribution of the plerocercoids in the viscera of perch. 93.4% were found in the liver, with smaller numbers elsewhere. Table VII also shows the percentage of plerocercoids at each site that were mature. At all sites (except one) there were approximately equal numbers of mature and degenerating plerocercoids. Of those found encapsulated onto the outer wall of the gonads, 81.0% were mature (Table VII).

Trawl sample

Thirty-five of 65 (54.7%) perch were infected with a total of 152 plerocercoids of T. nodulosus. The mean intensity/infected fish was 4.3 (maximum 28). The mean intensity/fish was 2.4

Purse seine sample

No T. nodulosus plerocercoids were recovered from 30 perch fry, examined in July 1976.

Seasonal aspects of the Triaenophorus nodulosus infection

The monthly incidence and mean intensity/infected fish from the gill net samples of perch are shown in Table VIII. There appears to be no seasonal change in the incidence or intensity of infection.

The monthly incidence and mean intensity/infected fish of

Table VII. Distribution of the plerocercoids of Triaenophorus nodulosus in the viscera of perch. Gill net samples. January 1975 - February 1976.

	% of total number of pleroceroids	% mature
Liver	93.4	47.8
Stomach wall, wall of pyloric caeca	0.8	50.0
Wall of intestine	3.4	45.8
Wall of swimbladder, urinary bladder	0.8	50.0
Outer wall of gonad(s)	1.4	81.0

Total number of plerocercoids 1418

Table VIII. Seasonal aspects of the Triaenophorus nodulosus infection. Gill net samples. January 1975 - February 1976.

Month	Number fish examined	Number fish infected	% incidence	Mean intensity/ infected fish	Maximum
J	6	5	83.3	3.6	5
F	30	28	93.3	4.1	13
M	30	30	100.0	4.2	10
A	30	26	86.7	3.1	6
M	30	28	93.3	3.2	9
J	39	31	79.5	3.0	9
J	40	34	85.0	3.5	18
A	30	29	96.7	2.6	13
S	30	27	90.0	2.8	20
O	60	51	85.0	3.2	9
N	54	50	92.6	3.5	13
D	35	34	97.1	3.4	9
J	30	26	86.7	3.7	8
F	21	21	100.0	3.3	12
Total	465	420	90.3	3.4	20

Table IX. Seasonal changes in the abundance of developing, mature and degenerating plerocercoids. Gill net samples. January 1975-February 1976

Month	Developing				Mature				Degenerating			
	1	2	3	4	1	2	3	4	1	2	3	4
J	0				4	66.7	8	2.0(3)	4	66.7	10	2.5(4)
F	0				20	66.7	62	3.1(9)	24	80.0	50	2.1(5)
M	0	3.3	1	1.0(1)	26	86.7	70	2.7(7)	23	76.7	53	2.3(5)
A	0				21	70.0	46	2.2(4)	17	56.7	35	2.1(4)
M	0				23	76.7	56	2.4(7)	18	60.0	34	1.9(7)
J	1	3.3	1	1.0(1)	20	51.3	49	2.5(7)	23	59.0	42	1.8(5)
J	0				21	52.5	50	2.4(6)	23	57.5	70	3.0(8)
A	0				22	73.3	48	2.2(6)	16	53.3	28	1.8(4)
S	0				27	90.0	34	1.3(10)	19	63.3	41	2.2(10)
O	0				29	48.3	55	1.9(6)	46	76.7	107	2.3(6)
N	0				27	50.0	57	2.1(9)	43	79.6	119	2.8(7)
D	0				19	54.3	54	2.8(7)	28	80.0	63	2.3(6)
J	0				19	63.3	51	2.7(8)	18	60.0	44	2.4(5)
F	0				18	85.7	43	2.4(6)	12	57.1	28	2.3(5)
Total	2	0.4	2	1.0(1)	296	63.7	683	2.3(10)	314	67.5	724	2.3(10)

N.B.

1 = number fish infected

2 = % incidence

3 = number parasites

4 = mean intensity/infected fish; figures in parentheses are the maximum number parasites/fish

Table X. X^2 test (variance to mean ratio) on monthly *Triaenophorus nodulosus* counts. Gill net samples. January 1975-February 1976

Month	Mean intensity/ fish	Variance	X^2	d	Agreement with Poisson series
J	3.0	4.00	6.67		$P > 0.050$*
F	3.7	7.48	58.60		$P < 0.001$
M	4.2	5.59	38.59		$P > 0.050$*
A	2.7	3.94	42.32		$P > 0.050$*
M	3.0	4.76	46.01		$P > 0.010$
J	2.4	4.18	66.18	+2.85	$P < 0.010$
J	3.0	9.51	123.63	+6.95	$P < 0.001$
A	2.5	6.12	70.99		$P < 0.001$
S	2.5	16.95	196.62		$P < 0.001$
O	2.7	4.19	91.56	+2.72	$P < 0.010$
N	3.3	5.44	87.37	+2.97	$P < 0.010$
D	3.3	6.00	61.82	+2.93	$P < 0.010$
J	3.2	4.42	40.06		$P > 0.050$*
F	3.4	7.35	43.25		$P < 0.001$

N.B.

Agreement with a Poisson series accepted when $P > 0.05$(*) (Elliot, 1971).

degenerating, mature and developing plerocercoids are shown in Table IX. Degenerating and mature plerocercoids were present in all months, and their occurrence shows no regular fluctuations. Developing plerocercoids were only found in two fish; one in March and one in June. These two fish also harboured mature and degenerating plerocercoids.

A X^2 test (variance to mean ratio) (Elliot, 1971) was performed on the monthly counts of T. nodulosus. The results are summarised in Table X. The variance was greater than the mean in all months. Agreement with a Poisson series was accepted ($P > 0.05$) in only 4 of the 14 monthly samples. The results suggest that the parasite population is overdispersed.

The effect of host sex upon the incidence and intensity of infection

The male and female fish caught by gill nets were divided into two age groups (2-5++ years, and $\geqslant$ 6 years).

Out of 159 male perch between age 2-5++ years, 147 (92.5%) were infected with a mean intensity/infected fish of 3.7. Twenty out of 24 (83.3%) male perch of age $\geqslant$ 6 years were infected with a mean intensity/infected fish of 2.9.

Out of 225 female perch between age 2-5++ years, 207 (92.0%) were infected with a mean intensity/infected fish of 3.3. Forty-three of 57 (75.4%) female perch of age $\geqslant$ 6 years were infected with a mean intensity/infected fish of 2.7.

The mean intensity/infected male and female fish from each age group was compared. The results are summarised in Table XI. Within both age groups there is no significant difference ($P > 0.05 > 0.100$)

in the mean intensity in male and female fish. The effects of host age and length upon the T. nodulosus infection have been considered below.

Table XI. Effect of host sex on the intensity of the T. nodulosus infection in two age groups of adult perch. Gill net samples. January 1975-February 1976

	AGE (yrs)	
	2-5++	≥6
mean intensity/infected male perch	3.7	2.9
variance	7.13	5.39
mean intensity/infected female perch	3.3	2.7
variance	5.74	2.65
F	1.24	2.03
V_1	146	19
V_2	206	42
value of P	>0.05	>0.05
d/t	+1.61	0.21
value of P	>0.05 > 0.10	>0.05 > 0.10

Effect of host age and length on the Triaenophorus nodulosus infection

The results from the purse seine, trawl and gill net samples are shown in Tables XII to XV. These results indicate that there is a change in the incidence of infection with host age and length. None of 30 0+ perch fry (mean length 2.3 cm, maximum 2.7 cm) examined in July (1976) were infected. Of 36 0++ fish (3.0 - 8.9 cm) examined in March (1976), 19.4% were infected. The incidence is highest in both male and female perch between age 1++ - 5++ years, and length 9.0 - 14.9 cm. In older, larger perch the incidence falls (Tables XII to XV).

The mean intensity/infected fish is highest in perch aged 1++ years or above, and length 9.0 cm or above. To investigate the effects of host age and length on the mean intensity/infected fish in more detail, the adult fish caught by gill nets were used. A one way analysis of variance was applied to the log (x + 1) transformed parasite counts from fish of separate age classes. Male and female fish were treated separately; the age classes 3, 4, 5, 6 and $\geqslant 7$ of male fish were used, and the age classes 3, 4, 5, 6, 7 and $\geqslant 8$ of female fish were used. In both male and female fish there is no significant change in the mean intensity/infected fish with host age (male perch: $F = 2.02$, $v_1 = 5$, $v_2 = 160$, $P > 0.05$; female perch: $F = 1.34$, $v_1 = 5$, $v_2 = 244$, $P > 0.05$). The adequacy of the transformation was checked by graphical means (Elliot, 1971). Similarly, a one way analysis of variance was applied to the log (x + 1) transformed parasite counts from the fish in the four length groups in Table XV. Male and female fish were treated separately, and in both instances there was no significant change in the mean intensity/infected fish with increasing host length (male perch: $F = 0.43$, $v_1 = 3$, $v_2 = 163$, $P > 0.05$; female perch: $F = 1.70$, $v_1 = 3$, $v_2 = 248$, $P > 0.05$). The adequacy of the transformation was again checked by graphical means.

With increasing host age and length the occurrence of mature plerocercoids falls (Fig. 4 & 5). The occurrence of degenerating plerocercoids may reach a peak in perch between age 4-5++ years, followed by a slight decline in older, larger perch. However, degenerating plerocercoids were common, even in the oldest and largest fish (Fig. 4 & 5). The high incidence of mature <u>and</u> degenerating plerocercoids in male perch of 18.0cm or above may be a reflection upon the small number of fish (3) of that size examined.

Changes in the parasite distribution pattern with host age and sex

The trawl caught fish were divided into perch of age 0++ and those between age 1++ - 4++ years. In the 0++ fish there was a large zero class in the frequency distribution, and the variance was approximately equal to the mean (Fig. 6). In the older fish from this sample the zero class was missing, the variance very much greater than the mean, and the parasite population appeared markedly overdispersed. A X^2 test (variance to mean ratio) (Elliot, 1971) showed that in the 0++ fish the variance was not significantly different from the mean, and agreement with a Poisson series was accepted at $P > 0.10$ (Table XVI). In the fish from the older age group, agreement with a Poisson series

Fig. 4. Effect of host age on the incidence of mature and degenerating plerocercoids of <u>Triaenophorus nodulosus</u>. Gill net samples. January 1975 - February 1976.

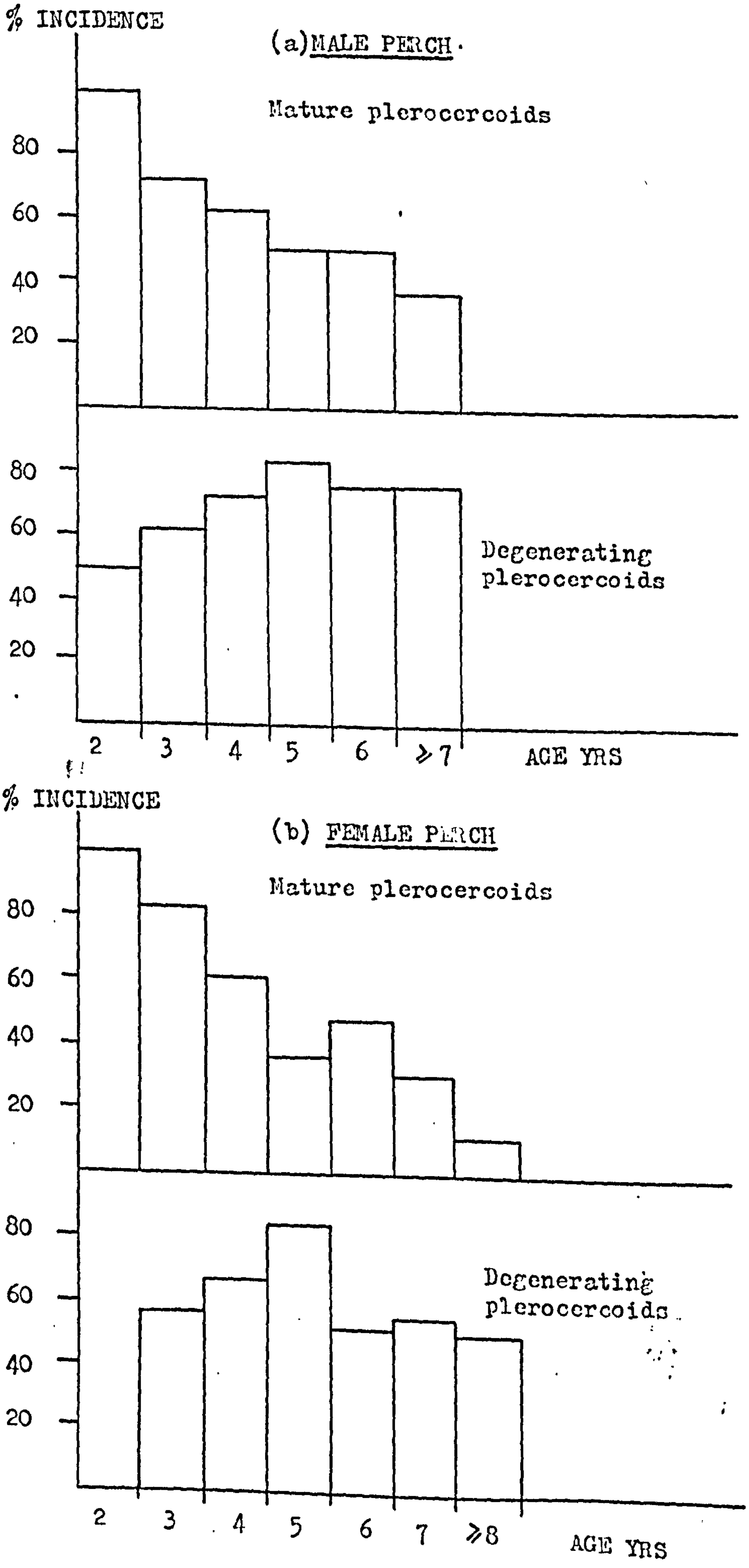
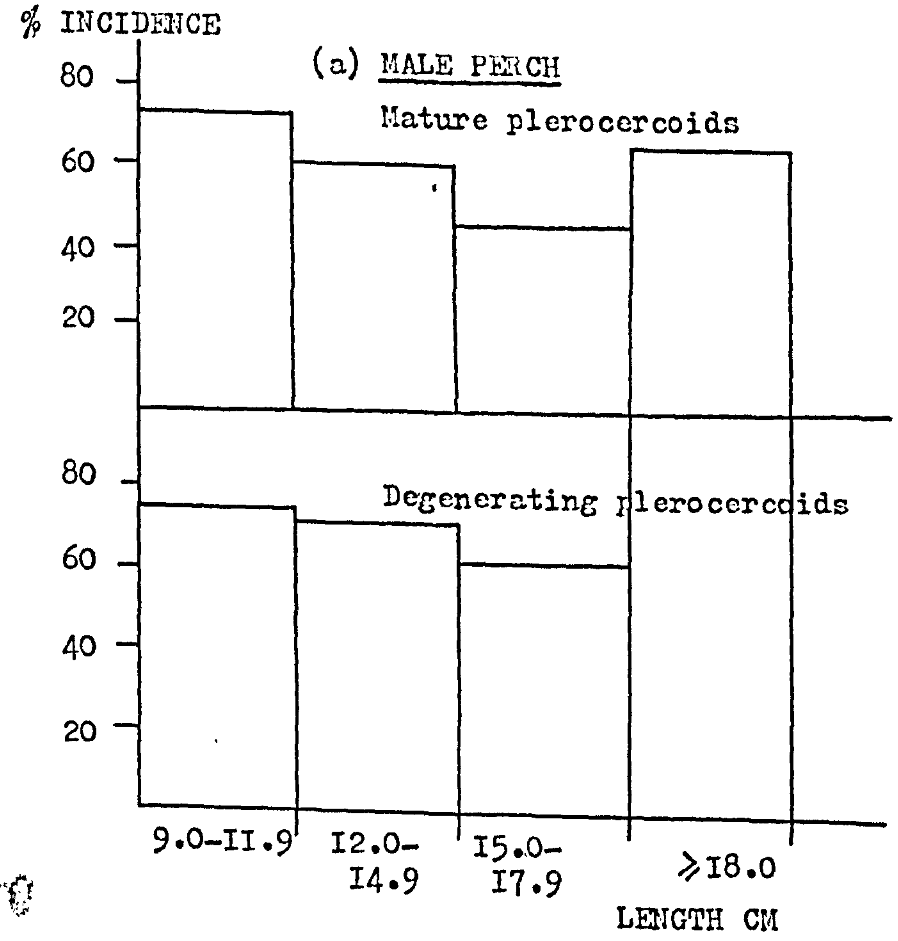


Fig. 5. Effect of host length on the incidence of mature and degenerating plerocercoids of Triaenophorus nodulosus. Gill net samples. January 1975 - February 1976.



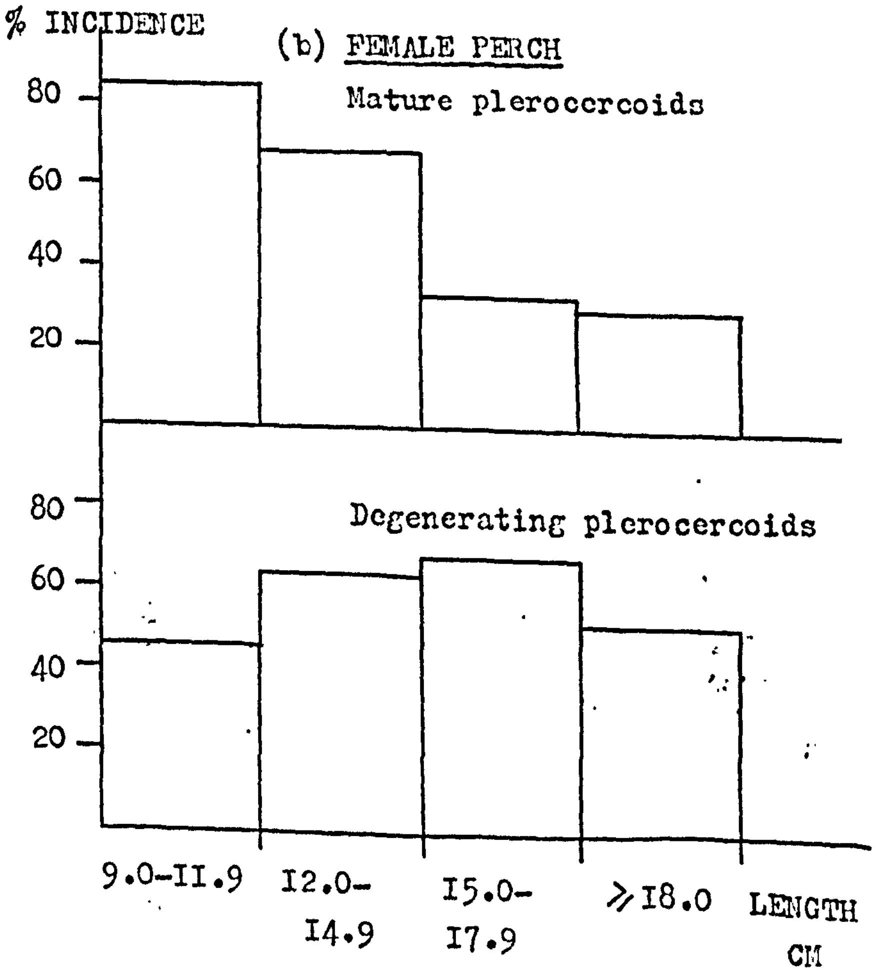


Table XII. Effect of host age on the Triaenophorus nodulosus infection. Trawl and purse seine samples. March and July 1976.

Age (yrs)	Unsexed			Male			Female		
	1	2	3	1	2	3	1	2	3
0+	30	0.0	-						
0++	36	19.4	1.1(2)						
1++				1	100.0	11.0(11)	1	100.0	3.0(3)
2++				7	100.0	3.6 (7)	3	100.0	3.0(4)
3++				9	100.0	7.4(28)	6	100.0	3.8(5)
4++				1	100.0	7.0 (7)			

N.B.

1 = number fish examined

2 = % incidence

3 = mean intensity/infected fish; figures in parentheses are the maximum number plerocercoids/fish.

Table XIII. Effect of host age on the Triaenophorus nodulosus infection. Gill net samples. January 1975 - February 1976.

Age (yrs)	MALE			FEMALE		
	1	2	3	1	2	3
2-2++	2	100.0	6.5 (7)	2	100.0	2.0 (2)
3-3++	51	88.2	4.2(13)	87	93.1	3.4 (9)
4-4++	66	93.9	3.2 (9)	98	92.9	3.4(23)
5-5++	40	95.0	3.9(18)	38	92.1	2.7 (9)
6-6++	16	87.5	2.9 (7)	27	81.5	2.7 (6)
7-7++	8	75.0	2.8 (9)	20	75.0	2.7 (6)
≥8				10	60.0	2.2 (4)

N.B.

1 = number fish examined

2 = % incidence

3 = mean intensity/infected fish; figures in parentheses are the maximum number of plerocercoids/fish

Table XIV. Effects of host length on the Triaenophorus nodulosus infection. Trawl and purse seine samples. March and July 1976.

Length (cm)	Unsexed			Male			Female		
	1	2	3	1	2	3	1	2	3
3.0	30	0.0	-						
3.0-5.9	29	24.1	1.1(2)						
6.0-8.9	7	0.0	-						
9.0-11.9				18	100.0	6.0(28)	10	100.0	3.5(11)

N.B.

1 = number fish examined

2 = % incidence

3 = mean intensity/infected fish; figures in parentheses are the maximum number of plerocercoids/fish

Table XV. Effects of host length on the Triaenophorus nodulosus infection. Gill net samples. January 1975 - February 1976.

Length (cm)	Male			Female		
	1	2	3	1	2	3
9.0-11.9	43	97.7	3.4 (13)	13	92.3	2.5 (7)
12.0-14.9	124	91.1	3.7 (18)	197	93.9	3.3(23)
15.0-17.9	13	69.2	2.8 (7)	47	80.9	3.2 (9)
≥18.0	3	100.0	5.0 (13)	26	65.4	2.4 (9)

N.B.

1 = number of fish examined

2 = % incidence

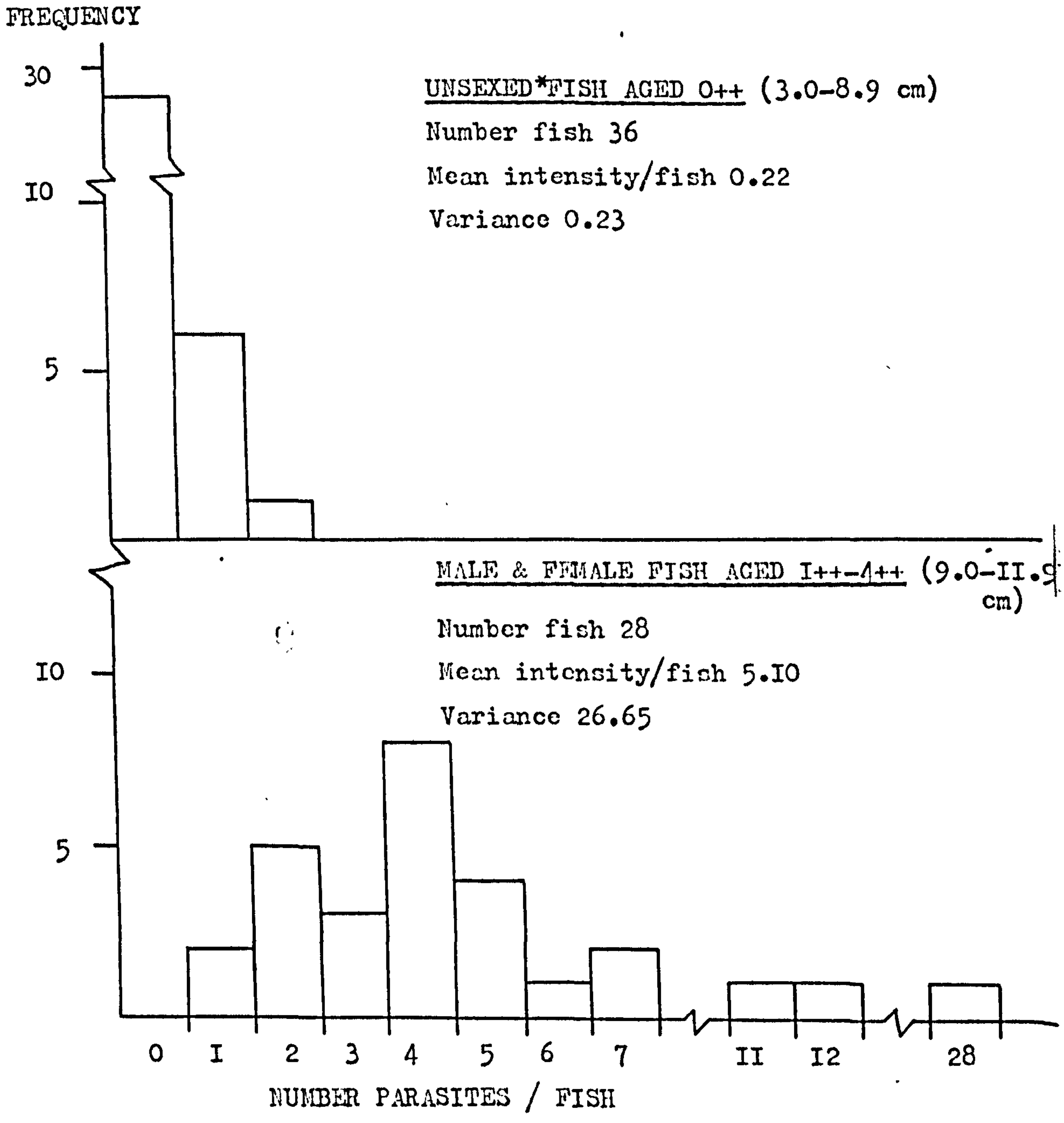
3 = mean intensity/infected fish; figures in parentheses are maximum number of plerocercoids/fish

was rejected and the results strongly suggest that the parasite population was overdispersed (Fig. 6; Table XVI).

The samples of the adult perch caught by gill nets were divided into those fish between age 2-5++ years, and those $\geqslant 6$ years. The frequency distributions of T. nodulosus within male and female perch at different ages are shown in Figs. 7 & 8. The distribution pattern of T. nodulosus in both male and female perch aged 2-5++ years was very similar (Fig. 7). However, in the older age groups of fish there may be a difference in the distribution pattern between the sexes (Fig. 8). Analysis by a X^2 test (variance to mean ratio) indicated that in all instances, the parasite population in the adult perch of both sexes was overdispersed (Table XVII). In male fish there was no significant difference in the variance or mean intensity/fish in either age group ($F = 1.35$, $v_1 = 158$, $v_2 = 23$, $P > 0.05$; $t = 0.45$, $v = 181$, $P > 0.05 > 0.10$). However, in female fish there <u>was</u> a significant difference in the variance in the two age groups ($F = 1.79$, $v_1 = 224$, $v_2 = 56$, $P < 0.05$). The fish in the older age group have a smaller variance; no heavily infected fish are present and there is a large zero class in the frequency distribution (Fig. 8). Transformation of the parasite counts using a log (x+1) transformation equalised the variances, and the mean intensity/fish from each age group was then found to be not significantly different ($d = +0.37$, $P > 0.05 > 0.100$).

These results suggest that in older female fish there may be a decrease in the degree of overdispersion, with a large zero class in the frequency distribution, and heavily infected fish absent.

Fig. 6. Frequency distribution of Triaenophorus nodulosus. Trawl sample. March 1976.



(NB. *...sex not distinguishable to the naked eye)

Fig. 7. Frequency distribution of Triaenophorus nodulosus. Gill net samples. January I975 - February I976.

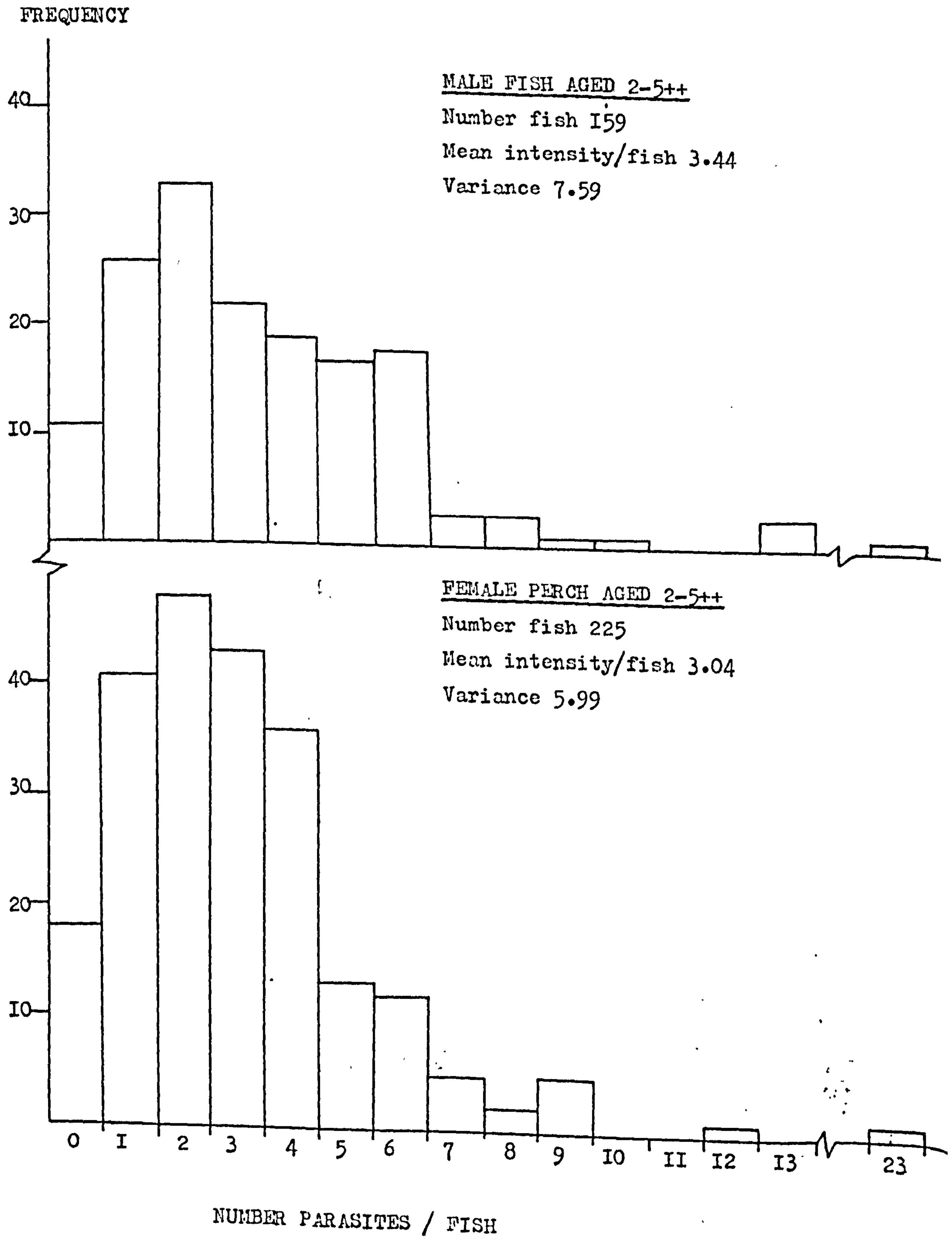


Fig. 8. Frequency distribution of <u>Triaenophorus nodulosus</u>.
Gill net samples. January 1975 - February 1976.

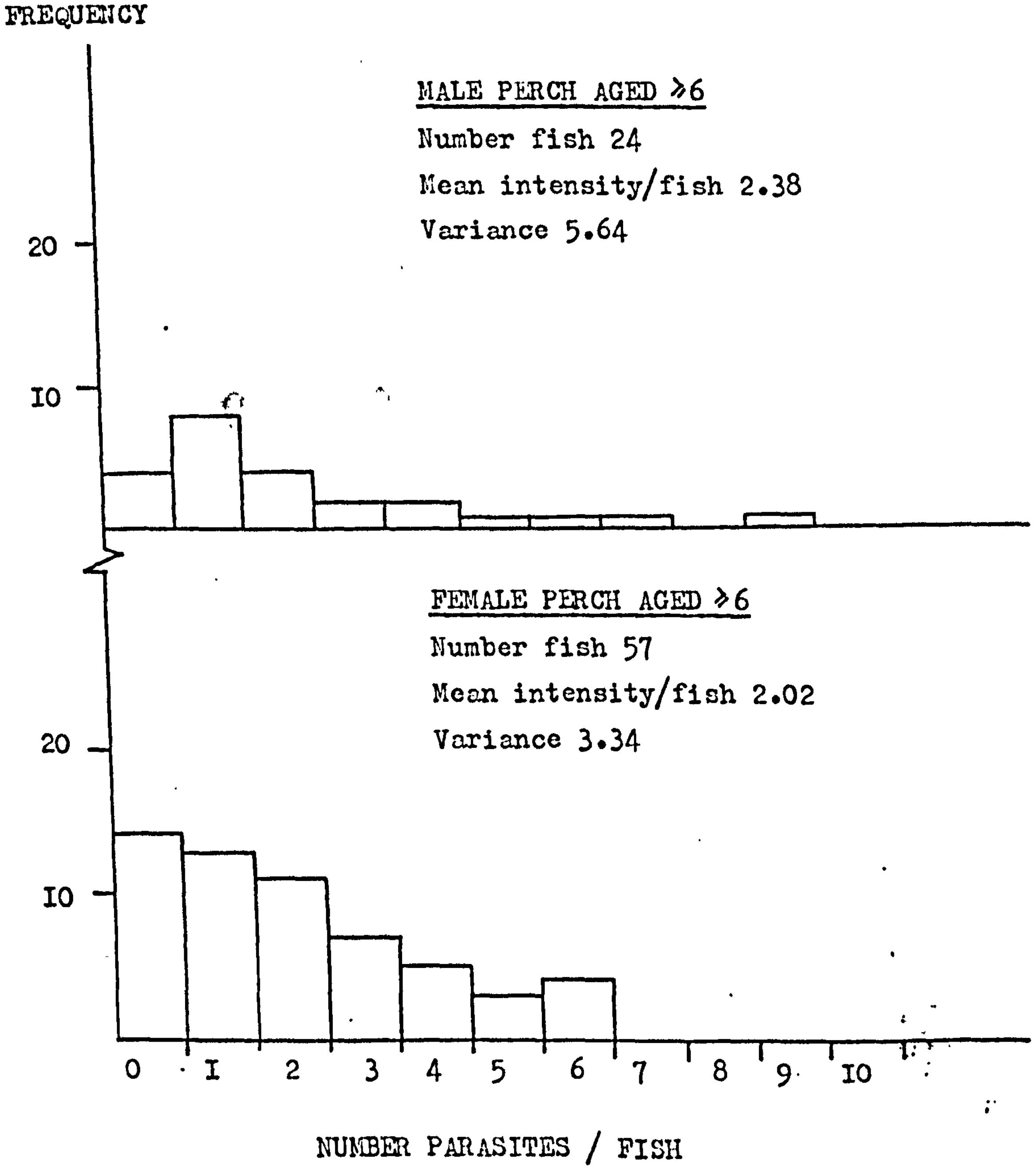


Table XVI. X^2 test (variance to mean ratio) on the Triaenophorus nodulosus infection in the trawl sample. March 1976

Age (yrs)	X^2	d	Value of P
0++	36.59	+0.13	> 0.100 *
1++ - 4++	141.09	-	< 0.001

N.B. Agreement with a Poisson series accepted when $P > 0.05$ (*) (Elliot, 1971).

Table XVII. X^2 test (variance to mean ratio) on the Triaenophorus nodulosus infection in the gill net samples. January 1975-February 1976

Age (yrs)	X^2	d	Value of P
Male fish			
2-5++	348.61	+8.68	< 0.001
$\geqslant 6$	54.50	-	< 0.001
Female fish			
2-5++	441.37	+8.57	< 0.001
$\geqslant 6$	92.59	+3.07	< 0.050

N.B. Agreement with a Poisson series accepted when $P > 0.05$ (Elliot, 1971).

Comparison of the Triaenophorus nodulosus infection at different sites in Llyn Tegid

Site B (12m) and Site D (12m)

Data from the gill net samples taken in October 1975-February 1976 are shown in Table XVIII. Of 22 fish caught at site B, 90.9% were infected. Of 38 fish caught at site D, 94.7% were infected. An F-test revealed no significant difference in the variance of the parasite counts/infected fish at each site ($F = 1.18$, $v_1 = 35$, $v_2 = 110$, $P > 0.05$); a d-test showed that there was no significant differences in the mean intensity/infected fish ($d = +1.11$, $P > 0.05 > 0.100$).

Site A (6m) and Site B (12m)

Data from the gill net samples taken between May-July 1975 are presented in Table XIX. Of 60 fish from site A, 83.3% were infected, while 85.7% of 49 fish from site B were infected. An F-test revealed a highly significant difference between the variances of the parasite counts/infected fish ($F = 2.59$, $v_1 = 41$, $v_2 = 49$, $P < 0.05 < 0.01$). Consequently, the parasite counts were transformed using a log (x+1) transformation. An F-test on the variances showed that there was now no significant difference ($F = 1.39$, $v_1 = 41$, $v_2 = 49$, $P > 0.05$). A d-test on the transformed counts showed that there is no significant difference in the mean intensity/infected fish at either site ($d = +0.58$, $P > 0.05 > 0.10$).

Table XVIII. Comparison of the infection with *Triaenophorus nodulosus* at site B and D. Gill net samples. October 1975 - February 1976

	Site B	Site D
Number fish examined	122	38
Number infected fish	111	36
Mean intensity/infected fish	3.4	3.9
Variance	4.88	5.77

Table XIX. Comparison of the infection with *Triaenophorus nodulosus* at site A and B. Gill net samples. May-July 1975

	Site A	Site B
Number fish examined	60	49
Number fish infected	50	42
Mean intensity/infected fish	3.1 (0.57)	3.5 (0.59)
Variance	3.32 (0.03)	0.59 (0.04)

N.B. Figures in parentheses are mean and variance of transformed log (x+1) counts.

Effect of crowding on the development of *Triaenophorus nodulosus* within the liver of perch

The percentage of mature plerocercoids was calculated for livers harbouring three levels of infection of *T. nodulosus*. Male and female fish were treated separately. Because of the changes in the structure of the parasite population with increasing host age, the various age classes of perch were also treated separately. The results are shown in Table XX and XXI. It would appear that even in livers containing over 8 plerocercoids there is no decrease in the occurrence of mature parasites.

Observations on the histology of the host reaction to *Triaenophorus nodulosus*

All observations were made on the encapsulated plerocercoid associated with hepatic tissue. Because of the small numbers of developing parasites encountered, no histological study was made of unencpasulated plerocercoids.

Sections of encapsulated plerocercoids showed the capsule to consist of a chronic inflammatory host reaction, with little evidence of cellular exudation. The wall of the capsule can be divided into three layers (Plate 1).

a. Innermost layer. This thin layer stained bright red with Mallory's and dull pink with H + E. It was acellular, or contained cells with degenerating nuclei. In some areas this layer was

Table XX. Percent of Triaenophorus nodulosus plerocercoids 'mature' in livers of male perch harbouring varying levels of infection. Gill net samples. January 1975 - February 1976

Age of fish (yrs)	Number fish examined	Number plerocercoids/liver		
		1-3	4-8	8
3-3++	51	54.9	57.1	66.7
4-4++	66	40.5	33.8	81.8
5-5++	40	28.2	13.6	69.2

Table XXI. Percent of Triaenophorus nodulosus plerocercoids 'mature' in livers of female perch harbouring varying levels of infection. Gill net samples. January 1975 - February 1976

Age of fish (yrs)	Number fish examined	Number plerocercoids/liver		
		1-3	4-8	8
3-3++	87	74.6	61.9	77.8
4-4++	98	41.7	53.2	52.5
5-5++	38	22.4	23.1	66.6
6-6++	27	46.7	81.1	-

seen to be sloughing off from the surrounding layer, and was frequently discontinuous. A positive result with the Von Kossa reaction suggested that calcification had occurred in this layer. Small calcium deposits were frequently found between this layer and the next (Plate II). These deposits were removed by treatment with a commercial decalcifying agent, RDC.

b. Middle layer. This layer was a cellular, basophilic layer, and contained large numbers of fibroblasts. The flattened nuclei were arranged concentrically around the capsule. Staining with Mallory's revealed the presence of collagenous connective tissue.

c. Outer layer. This layer was distinctly different from the middle layer. It consisted of loose connective tissue, distinctly fibrous in form. The outer layer stained blue with Mallory's and pink with H + E. There was evidence of vascularisation in this layer, and also in the middle layer. Small capillaries were seen along with nucleated red blood cells. There was little leucocytic cellular exudation between the capsule and the liver tissue, and adjacent hepatic cells appeared normal.

The presence of another type of capsule within the viscera of perch has been noted. Sections of these capsules in hepatic tissue revealed that they consisted of a layered fibroblastic outer wall, enclosing inner necrotic layers and a necrotic core (Plate 3). With Mallory's, the outer parts of the wall stained blue, whilst the inner layers and core stained bright red. Calcium deposits were frequently found within the inner layers and core of these capsules (Plate 2). Staining of tissue sections of these capsules with Ziehl-Neelsen and Fite-Faraco techniques did not demonstrate the presence of acid fast bacilli. Similarly, a Gram stain did not indicate the presence of Gram positive or negative bacteria within these capsules. Critical observations on H + E stained serial sections revealed the absence of helminth material, including the chitinous hooks from the scolex of T. nodulosus. There was no cellular exudative material around this capsule, and adjacent liver cells appeared normal.

Observations on the influence of Triaenophorus nodulosus on the growth rate and condition factor of perch

The high incidence and intensity of infection, along with the occurrence of hepatic fibrosis, and on one occasion peritoneal adhesions, have been noted.

(i) Growth rate

The effect of T. nodulosus on the growth rate of 0++ and 4++ fish was examined.

The 0++ fish were caught using a trawl in March 1976. The mean length of infected and uninfected fish is shown in Table XXII. From this small sample there appears to be no reduction in the growth of 0++ perch infected with a mean intensity of 1.1 plerocercoids/infected fish.

The infection of T. nodulosus is prevalent in fish of both sexes of age 4-4++ years. The mean length of perch of age 4++

PLATES

Histology of capsule of Triaenophorus nodulosus

Plate I. Capsule wall showing layers (a), (b) and (c). H & E stained

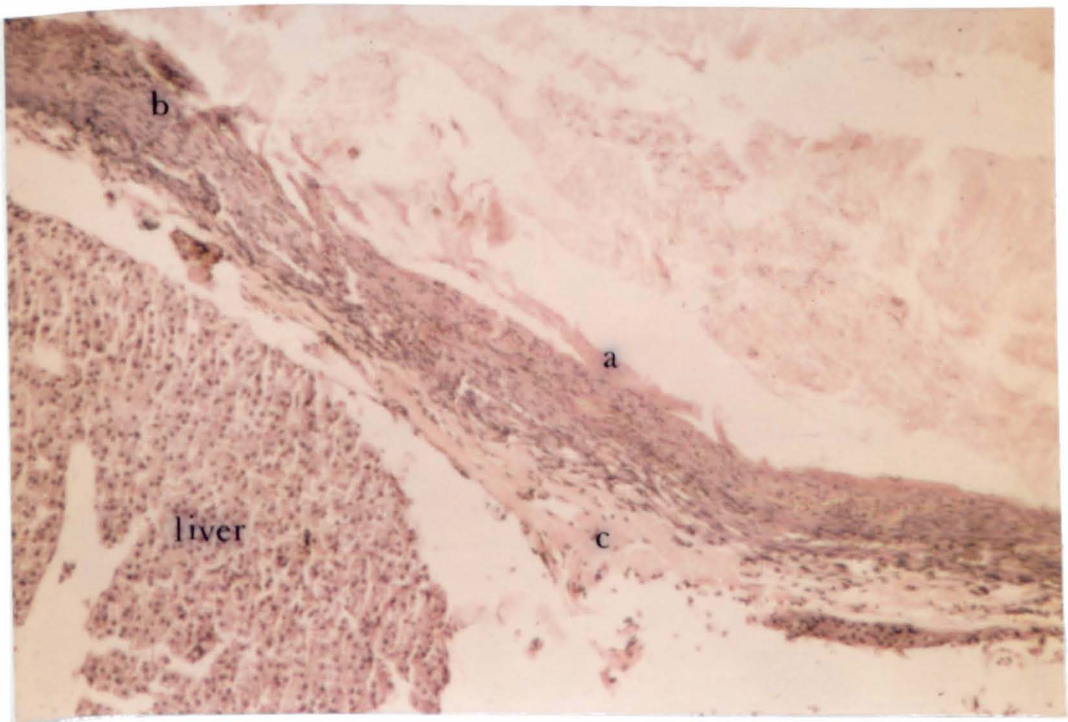
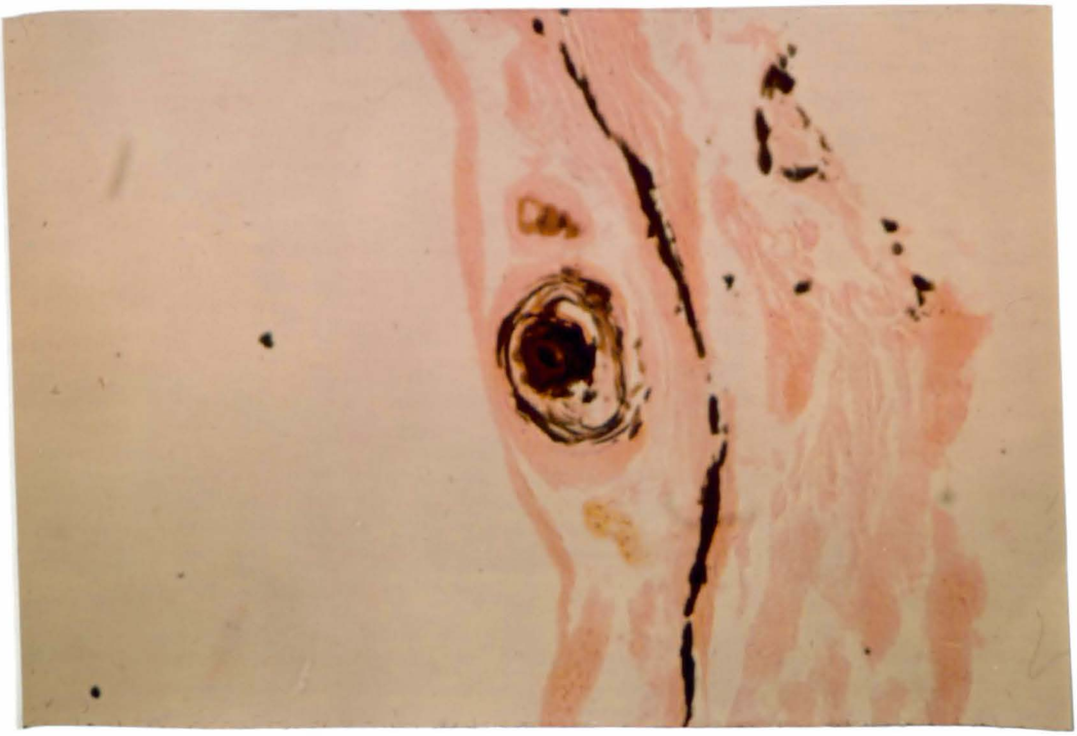
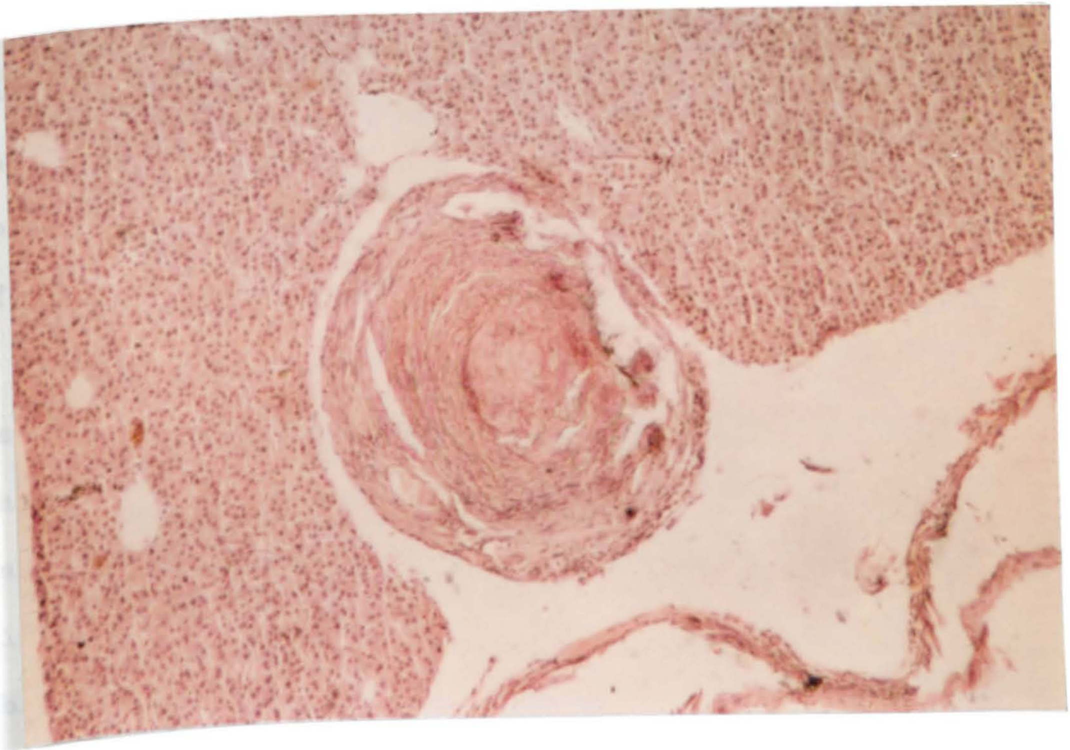


Plate 2. Capsule wall, plus additional capsule of undetermined origin. Von Kossa stained



PLATES (cont.)

Plate 3. Capsule of undetermined origin, seated in liver tissue.
H & E stained



Scale for Plates I, 2 & 3:

IOOum

years caught between January-March 1975 and October 1975-February 1976 (gill net samples) was calculated for fish harbouring no *T. nodulosus*, less than 4 plerocercoids, 4-8 plerocercoids, and over 8 plerocercoids (Table XXIII). Because of the high incidence of infection, few fish with no plerocercoids were available. Therefore it is difficult to assess the effect of the parasite on the growth of infected and uninfected fish. However, at the three remaining levels of infection there appears to be no decrease in the growth rate of male or female fish with increasing intensity of infection (Table XXIII).

To avoid unnecessary errors, only perch caught during the essentially non-growing months of October-March were used (see Chapter ~~3~~ III). Nonetheless, because of small sample sizes of perch aged 4++, fish from *two* growing seasons were grouped together. Since the growth of fish may vary from one season to the next, this may have influenced the results.

(ii) Condition Factor (K)

The effect of *T. nodulosus* on the condition factor of the 0++ trawl caught fish was examined. The condition factor was calculated as described in Chapter ~~3~~ III, after Graham & Jones (1962). The mean K value of the 7 infected fish was 156.9 (± 95% confidence limits 17.2), while the mean K value of the 29 uninfected fish was 146.9 (± 6.8). There appears to be no marked effect by *T. nodulosus* on the condition factor of 0++ perch infected with a mean intensity/infected fish of 1.1.

Because of the inaccuracy of the routine methods of weighing of the fish from the gill net samples, no K values could be calculated for these fish.

Table XXII. Effect of Triaenophorus nodulosus on the growth rate of O++ perch

	Mean length (cm)
Uninfected fish	5.38 ± 0.28 (29)
Infected fish	5.59 ± 0.16 (7)
Total number fish 36	

N.B. Mean length ± 95% confidence limits

Figures in parentheses are number of fish examined.

Table XXIII. Effect of Triaenophorus nodulosus on the mean length of adult perch aged 4++. Gill net samples. January - March, 1975, October - February 1975/76 (grouped)

	Mean length (cm)	
	Male fish	Female fish
Uninfected fish	- (0)	15.37 ± 2.07 (3)
Fish harbouring:		
1-3 plerocercoids	12.50 ± 0.23 (28)	13.40 ± 0.63 (34)
4-8 plerocercoids	12.58 ± 0.32 (16)	13.70 ± 0.56 (21)
8 plerocercoids	12.10 (2)	16.70 (2)
Total (overall)	12.52 ± 0.19	13.74 ± 0.50

N.B. Mean length ± 95% confidence limits

Figures in parentheses are number of fish examined.

VIII. ~~34~~ 24 DISCUSSION

The life cycle of *T. nodulosus* involves three hosts. Whilst several species of predatory fish may harbour the adult worm, pike (*Esox lucius*) is the most important definitive host. At Llyn Tegid mature, egg-producing *T. nodulosus* have only been recorded from pike (Chubb, 1963b, 1976). The procercoid of this parasite may occur within a range of copepod crustacean, first intermediate host species. Different species of copepod may act as host in different localities, illustrating the phenomenon of "parasitological vicarition', as described by Gottowa (1961) and Michajlow (1962). *Cyclops stennus*, *C. vicinus* and *Eudiaptomus gracilis* are all important planktonic hosts to *T. nodulosus* in Europe (Michajlow, 1962; Halvorsen, 1968; Kuperman, 1973), whilst in North America *Cyclops bicuspidatus* is the most important host (Miller, 1943; Watson & Price, 1960; Watson & Lawler, 1965; Kuperman, 1973). There are no published records on the crustacean hosts of *T. nodulosus* in the British Isles. Thomas (195~~8~~9) and Mills (in prep.) recorded the following species of Copepoda from Llyn Tegid: *Cyclops strennus abyssorum*, *C. agilis* (s.str.), *C. agilis* v. *speratus*, *C. albidus*, *C. viridis* and *Diaptomus gracilis*. Mills (Pers. comm.) considered that the *C. strennus abyssorum* identified by Thomas (195~~8~~9) should be assigned to *C. abyssorum* (v. *prealpinus*?). On completion of his work, Mills (pers. comm.) hopes to add a number of other species to this list. Michjalow (1962) has listed the plerocercoid of *T. nodulosus* from 57 species of fish, though Kuperman (1973) has pointed out that cyprinids are not commonly infected. Kuperman's experimental investigations indicate that cyprinid fish may be morphologically and/or physiologically unsuitable as second intermediate hosts to *T. nodulosus*. In the British Isles, the plerocercoid has been recorded from perch, pike, brown trout (*Salmo trutta*), eel (*Anguilla anguilla*), bullhead (*Cottus gobio*), loach (*Noemachielus barbatula*) and a flatfish (*Platichthys flescus*) (Kennedy, 1974; Chubb, 1976). At Llyn Tegid the plerocercoid is commonly associated with perch, though pike and brown trout have been infrequently recorded as infected. In many lakes a single species of fish appears to be the most important second intermediate host (Chubb, 1964), though in some instances (e.g. Lawler, 1969b) at least two species of fish may harbour high levels of the infection.

The incidence of infection may vary from one study to the next, though the intensity/infected fish is usually low. Rizvi (1964) studied the *T. nodulosus* plerocercoid infection of perch from Rostherne Mere, where 25.1% of 343 fish were infected. The mean intensity/infected fish was 1.5. Mishra (1966) working on the perch from the Shropshire Union Canal found 9.4% of 201 fish infected, with a mean intensity/infected fish of 1-3.3. A low level of infection was found in bullhead (*Cottus gobio*) and loach (*Noemachielus barbatula*) from the River Avon (Rumpus, 1975). In a previous study at Llyn Tegid Chubb (1964) found 57.5% of 497 perch infected with a mean intensity/infected fish of 1.5. There have been several continental European studies on this parasite. Bykhovskaya-Pavlovskaya (1940) found 27.4% of 226 perch infected, and the range of intensity was 1-18. Kozicka (1959) found only 3.5% of 58 perch infected, and the intensity of infection was also very low. Lawler (1969b) recorded *T. nodulosus* from 69% of

111 perch and 58% of 169 smelt (*Osmerus esperlanus*), and the intensity of infection was usually low. Tell (1971) found 52.0% of 250 perch infected and the range of intensity was 1-9. Burbot (*Lota lota*) and pike were also infected in this study. Wierzbicki (1970) examined 504 perch and found that 63.5% were infected. The range of infection was 1-8.

The infection of the second intermediate host is markedly influenced by its' feeding habits in relation to the availability of infective plankton (Chubb, 1964; Kuperman, 1973). The low intensity of infection in most studies may also be a reflection upon the fact that only a small proportion of the ingested procercoids become established as plerocercoids. Vogt (1938) found that only 1-2% of the ingested procercoids survive to become plerocercoids. Kuperman (1973) reported similar results, and found that the number of established plerocercoids could not be increased by the experimental feeding of large numbers of infected copepods. He suggested that large numbers of procercoids may invoke a defence mechanism in the fish, limiting the number of plerocercoids that may develop. Chubb (1964) suggested that an immunity effect might influence the level of the infection in perch. Sche~~v~~uring (1919) found that trout could not be infected with *T. nodulosus* if they had previous experience of the parasite. Vogt (1938) concluded that there was no acquired immunity to this parasite in rainbow trout (*Salmo gairdneri*). The possible immune response by perch to this parasite is discussed further below. However, superinfection with *T. nodulosus* may occur (Sche~~v~~uring, 1923), and in this study several perch were found harbouring high levels of superimposed infections.

Bogatova (1936) and Shulman (1961) (cited by Kuperman, 1973), and Vik (1959) have found high levels of infection of *T. nodulosus* in large orfe, loach and burbot (*Lota vulgaris* (= *lota*) respectively. Since these fish do not ingest appreciable numbers of plankton, these results have been taken to indicate re-encapsulation, or the secondary infection of fish from infected prey fish (Bauer, 1959; Vik, 1959; Kuperman, 1973). Plerocercoids present in the prey fish migrate from the alimentary tract of the predator and become re-encapsulated. A similar process has been established for *Diphyllobothrium latum* (Baer, 1925; Hobmaier, 1927; Pavlovski & Gnezdilov, 1939), and for *D. dendriticum* (Hickey & Harris, 1947; Kuhlow, 1953; Vik, 1957, Halvorsen, 1970). At Llyn Tegid, plankton feeding was predominant amongst fish below ~~16.0~~ 15.0 cm and aged less than 6 years. Cannibalism primarily occurred in perch larger and older than this. The fall in incidence of *T. nodulosus*, along with the increase in the occurrence of degenerating plerocercoids with increasing host age /length, supports the views of Lien (1970), who concluded that secondary infection with this parasite does not occur in perch.

Kennedy (1970) suggested that in fish (intermediate) host-parasite systems where the parasite is longlived, there may be no regular seasonal fluctuations in parasite occurrence. In agreement with the observations of Chubb (1964), Rizvi (1964), Mishra (1966), Lien (1970) and Rumpus (1975), the *T. nodulosus* infection of perch at Llyn Tegid shows no marked seasonal fluctuations. The occurrence of mature and degenerating plerocercoids varied irregularly from month to month. The recruitment of *T. nodulosus* from the planktonic intermediate host(s) occurs during the spring-summer, (Miller, 1945a;

Lawler, 1969a; Lien, 1970), primarily between March-June at Llyn Tegid (Chubb, 1964). Developing plerocercoids were only recorded twice during this present study: once during March and once during June.

Lien (1970) reported that a crowding effect was responsible for the occurrence of relatively fewer non-degenerate plerocercoids in perch harbouring over 10 plerocercoids. Within individual age classes of perch at Llyn Tegid, there was found to be no such decrease in the occurrence of mature plerocercoids, even at the infection level of 8 plerocercoids/liver. The greater occurrence of mature plerocercoids encapsulated onto the gonads of perch at Llyn Tegid has been indicated.

Referring to the infection of tench (*Tinca tinca*) by *T, nodulosus*, Aisa & Gattaponi (1971) found a slightly higher incidence of infection in fish from the centre of Lake Traisemo (Italy), as compared to the incidence in fish from the littoral zone (52.5% compared to 43.7%). Wierzbicki (1971) reported that *T. nodulosus* were "the most numerous dominant plerocercoids" in the deepest part of Lake Dargin (Poland). The intensity of infection was found to be higher in this region, than in either of two shallower areas. During the months that they were compared at Llyn Tegid the incidence and mean intensity/infected fish was similar at sites B and D, and at sites A and B. However, only the infection in adult perch was compared and only from a relatively restricted area within the lake (see Chapter II). Further information is required on the local variations in the infection of young perch, and variations in the infection of adult perch from a wider area in Llyn Tegid. Chubb (1964) suggested that as perch do not move extensively within the lake, focal points of infection may exist.

Whilst the incidence and mean intensity/infected fish were similar in male and female perch, there were detectable changes in the T. nodulosus infection with host age and length. However, it should be noted that since the plerocercoid of this parasite is long-lived (2-3 years: Chubb, 1964; Lien, 1970), and the remains of the degenerate capsule may persist for longer still, interpretations on the effects of host age (and length) on the infection may be complicated by variations in recruitment in previous years.

None of 30 0+ perch fry examined in July were infected. Watson & Lawler (1965) found that infective plankton were available in Heming Lake (Canada) for about 8-10 weeks, from mid-May until late July. The availability of infective plankton may follow a similar pattern in Llyn Tegid. The presence of mature, encapsulated plerocercoids from the previous summers infection, in 0++ perch caught in March, illustrates that infection can occur during the first summer that perch spend in Llyn Tegid. The infection of young of the year fish with T. nodulosus has been reported by several authors, including Markevich (1943) studying perch, Miller (1945a) studying burbot (Lota lota maculosa) and Lawler (1969a) studying yellow perch (Perca flavesceus). However, this process is markedly influenced by the timing of egg release by adult T. nodulosus in pike, and the ingestion of infected copepods by perch fry not more than one month after the plankton become infected (Lawler, 1969a). In addition, since pike probably release the majority of T. nodulosus eggs whilst they are inshore spawning, and since copepods do not possess great mobility, infected pike containing mature cestodes and perch fry must be spatially and temporally coexistent. A change in this timing could result in a serious disruption of the cycle (Lawler, 1969a).

At Llyn Tegid the infection with T. nodulosus was prevalent in perch aged 1++ years or above. The incidence of infection was highest in fish between 1++ - 5++ years (and length 9.0 - 14.9 cm). In older, larger perch the incidence of infection fell, but there was no significant fall in the mean intensity/infected fish. The observed fall in incidence may be explained by any one of a combination of factors.

Arme & Owen (1968) found a fall in the occurrence of Ligula intestinalis in older roach (Rutilus rutilus), and suggested that this might be a result of the reduced longevity of infected fish.

With increasing age and length perch exhibited a detectable change in their feeding habits. Copepoda were only rarely eaten by fish aged over 4-5 years (and larger than 1~~5~~7.9 cm). Concurrent with this observed change was a change in the occurrence of mature and degenerating plerocercoids. Mature plerocercoids were prevalent in smaller, younger perch, while degenerating plerocercoids were more common in slightly older, larger perch. Lien (1970) found similar results in perch from Lake Bogstad (Norway). Lien considered that the observed change in feeding habits with host size was the most plausible explanation for the observed decrease in non-degenerate plerocercoids in larger perch. In younger, smaller perch that are feeding to a greater extent on plankton, the infection is in a dynamic state, with the gain of procercoids from infected copepods and the loss of plerocercoids by degeneration (Chubb, 1964). The fall in the occurrence of mature plerocercoids in fish aged 3 years or above, suggests that in these fish degeneration may be proceeding at a faster rate than recruitment. In perch older than 4-5 years recruitment may cease, and the parasite population gradually degenerates. The fall in incidence in older perch may therefore be explained by a cessation in recruitment in conjunction with the gradual degeneration and absorption of the parasite by the host. This is discussed further below.

Parasites often have an overdispersed, contagious or clumped distribution in their host population (e.g. Kennedy, 1968, 1970, 1972; Kennedy & Hine, 1969; Crofton, 1971 a, b; Pennyquick, 1971b; Anderson, 1974; Boxshall, 1974; Hine & Kennedy, 1974; Kennedy & Rumpus, 1977; etc). The overdispersed nature of the *T. nodulosus* infection in perch at Llyn Tegid has been indicated. In perch that have spent one summer in the lake (age 0++) the incidence and intensity of infection is low, and the distribution of *T. nodulosus* appears random. However, Iwao (1970) and Boxshall (1974) have shown that departures from randomness may be difficult to detect at low mean densities. In all of the older age groups the frequency distribution of *T. nodulosus* was clearly overdispersed.

Watson & Lawler (1965) found that the distribution of infected copepods (*Cyclops bicuspidatus thomasi*) in Heming Lake (Canada) were non-random, and that aggregations of infected plankton occurred in littoral regions. In such areas the incidence of infection with procercoids of *T. nodulosus* reached 5-10% in some samples taken during the summer. Watson & Lawler pointed out that such clumping would result in either zero or multiple infections in the second intermediate host. Jarecka (1958) also noted the focal nature of the infection of plankton with the procercoids of certain cestodes occurring in Lake Druzno (Poland).

Under present conditions, perch that have spent one summer in the lake will have been exposed to a limited number of procercoids. This is a result of their low intensity of plankton feeding, and as a result of the availability of infected plankton in relation to perch spawning and the onset of plankton feeding in perch fry. Hence, the incidence and intensity of infection in young of the year fish is (at present) low in Llyn Tegid, and marked overdispersion of the parasite population in these fish unlikely. Further details are required on the nature of the infection in fish that have spent two and three summers in the lake (age 1+ and 2+ years). However, it would appear that these fish probably feed heavily on plankton and are exposed to a greater number of procercoids over successive years. Hence, the incidence and intensity of infection rises, and the frequency distribution of the parasite develops into its marked overdispersed form. Crofton (1971a) and Elliot (1971) have discussed the factors which favour overdispersion, with special reference to the negative binomial. Kennedy (1970) summarised some of our knowledge on the factors producing aggregated distributions in the parasites of fish in particular. At Llyn Tegid, the overdispersed nature of the T. nodulosus infection of perch may be influenced by a number of factors including the non-random distribution of infected copepods (e.g. Watson & Lawler, 1969; Crofton, 1971a), variations in the feeding habits of perch with age and between individual fish (e.g. Kennedy, 1970; Crofton, 1971a, Hine & Kennedy, 1974), and differences in the physiological suitability of individual fish (e.g. Kennedy, 1970; Crofton, 1971a), or a combination of these. Whilst the infection is markedly overdispersed in adult fish of all ages, there may be a reduction in the degree of overdispersion in older female fish. In these fish there is a fall in incidence of infections (and a significant zero class in the frequency distribution). Heavily infected fish are apparently absent.

These results could be produced in a number of ways. It should be noted that in male and female perch aged 2-5++ years the frequency distribution of the parasite was very similar (Fig. 7).

Observations on overdispersed populations, such as T. nodulosus, are dependent upon adequate sample sizes. Whilst only a relatively small number (24) of male fish aged ≥6 years were available, a significant number (57) of female fish of the same age were examined.

A low rate of recruitment in previous years could affect the observed level of infection in the older fish in this study. However, no similar change in the infection in a small sample of older male fish was observed. In addition, it seems likely that the mean intensity/infected fish would also be affected by a low rate of recruitment in previous years. No change in the intensity of T. nodulosus was observed with the age of adult perch.

The observed change in the feeding habits of perch with age (and length) could influence the infection in older fish, and this has already been discussed. Whilst we have little information on the persistence of degenerate capsules in perch viscera, a reduction in plankton feeding with age (and length) of the fish, along with the continued degeneration of the parasite and capsule might lead to a fall in incidence. This might also result in older fish harbouring a light infection of small degenerate capsules, being recorded as uninfected. This would cause a reduction in the incidence of infection though only marginally influence the mean intensity/infected fish. Similarly, in older, more heavily infected fish, small degenerate capsules might remain unobserved. This would not affect the incidence of infection, only marginally influence the mean intensity/fish and lead to the effective disappearance of heavily infected fish from the parasite frequency distribution. The dynamic nature of the infection in smaller, younger fish has been described. In male and female fish aged ≥6 years there is a fall in incidence of infection though mean intensity/infected fish is not significantly affected. Whilst only a small number of male fish of this age were observed, there is a greater fall in incidence in female fish, a rise in the zero class of the frequency distribution and the apparent disappearance of heavily infected female fish. This might also be explained by an increased rate of degeneration and absorption in female fish, or the greater physiological suitability of older male fish. However, supporting evidence is lacking.

There is a substantial body of evidence that illustrates that certain parasites may reduce the longevity of their piscine hosts, and so contribute to fish population "natural mortality" (Oppenheimer & Kesteven, 1953; Bauer, 1958; Markov, 1958; Williams, 1967; Sinderman, 1970; Paperna & Zwerner, 1976; etc). Several workers have noted that Ligula intestinalis may subject fish infected with the plerocercoid stage to increased predation by host and non-host predators (Van Dobben, 1952; Arme & Owen, 1968; Harris & Wheeler, 1974; Sweeting, 1976). Similar effects have been attributed to Diplostomum gasterostei (metacercariae), Schistocephalus solidus (plerocercoid) and Acanthocephalus clavula (adult worm) in sticklebacks (Gasterosteus aculeatus (Pennyquick, 1971a), Triaenophorus crassus (plerocercoids) in sockeye salmon (Oncorhynchus nerka) (Rogers, et al. 1972) and Dactylogyrus sp.on large mouth bass (Micropterus salmoides) (Herting & Witt, 1967). These effects may be limited to heavily infected fish, and are often associated with parasites that rely on the death of their piscine intermediate host for the continuation of their life cycle (e.g. cestode plerocercoids, strigeid metacercariae) (Crofton, 1971a; Pennyquick, 1971a). However, Coble (1970) found that fathead minnow (Pinephales promelas) infected with metacercariae of Clinostomum marginatum were not more susceptable to predation by large mouth bass (M. salmoides). Similarly, Vaughan & Coble (1975) reported that fathead minnow (P. promelas) infected with Lernaea cyprinacaea, brook trout (Salvelinus fontinalis) infected with Salmincola edwardsii, and yellow perch (Perca flavesceus) infected with Neascus sp. (of Crassiphiala bulboglossa) were not more vulnerable to predation by three piscine predators.

The disappearance of older female perch heavily infected with T. nodulosus may be a result of their reduced longevity, and possible increased vulnerability to predation. In addition, heavily infected fish may be more likely to succumb deterioration in environmental conditions, or stress associated diseases. In summary, the observed change in the distribution pattern of T. nodulosus in older female perch may be a result of inadequate sample size. However, similar results could be produced by the observed change in feeding habits of perch with age along with the continued degeneration of the parasite and capsule, and/or the reduced longevity of heavily infected fish. It seems unlikely that variations in the rate of recruitment in previous years, the increased rate of degeneration in female fish (or the greater physiological suitability of male fish) might explain these results.

A similar study was performed at Llyn Tegid in 1957/58 (Chubb, 1964). A comparison of the results from the 1957/58 and the 1975/76 (present) studies are presented in Table XXIV and Fig. 9 (a & b). The length frequencies of the fish examined in both studies were similar, except that slightly more larger perch were examined in the earlier study. In each instance the feeding habits of the fish and the sites of capture were similar. Chubb (1964) was unable to demonstrate a detectable change in the feeding habits or nature of the infection with host age or length. In the 1975/76 study there was a higher incidence and mean intensity of infection, along with a greater occurrence of degenerating plerocercoids (Table XXIV). In addition, there was a greater occurrence of developing plerocercoids in the earlier study, indicating a higher rate of recruitment. The greater occurrence of degenerating plerocercoids in the later study may only be explained in part by variations in the assessment of the development of parasites by the two workers.

Between the two studies there has been a significant change in the frequency distribution of T. nodulosus (Fig. 9 a & b). In both instances the variance was greater than the mean, and a X^2 test (variance to mean ratio) (Elliot, 1971) strongly suggested that the parasite populations were overdispersed (Table XXIV). The overdispersion was especially pronouned in the 1975/76 study (Fig. 9b). In 1957/58 there was a large zero class in the distribution and no perch were found to harbour more than 5 plerocercoids (Fig. 9a). In the present study, the zero class was small and 13.6% of the fish (63 out of 465) harboured over 5 plerocercoids (Fig. 9b). Chubb (1964) normally recorded one plerocercoid/capsule, while in 1975/76 capsules were commonly found containing 2 or more plerocercoids.

Between the two studies there has been a distinct change in the nature of the T. nodulosus infection of perch. Lawler (1969a) examined the T. nodulosus infection in 22,696 yellow perch (Perca flavesceus) from Heming Lake (Canada) between 1954 and 1967. He found

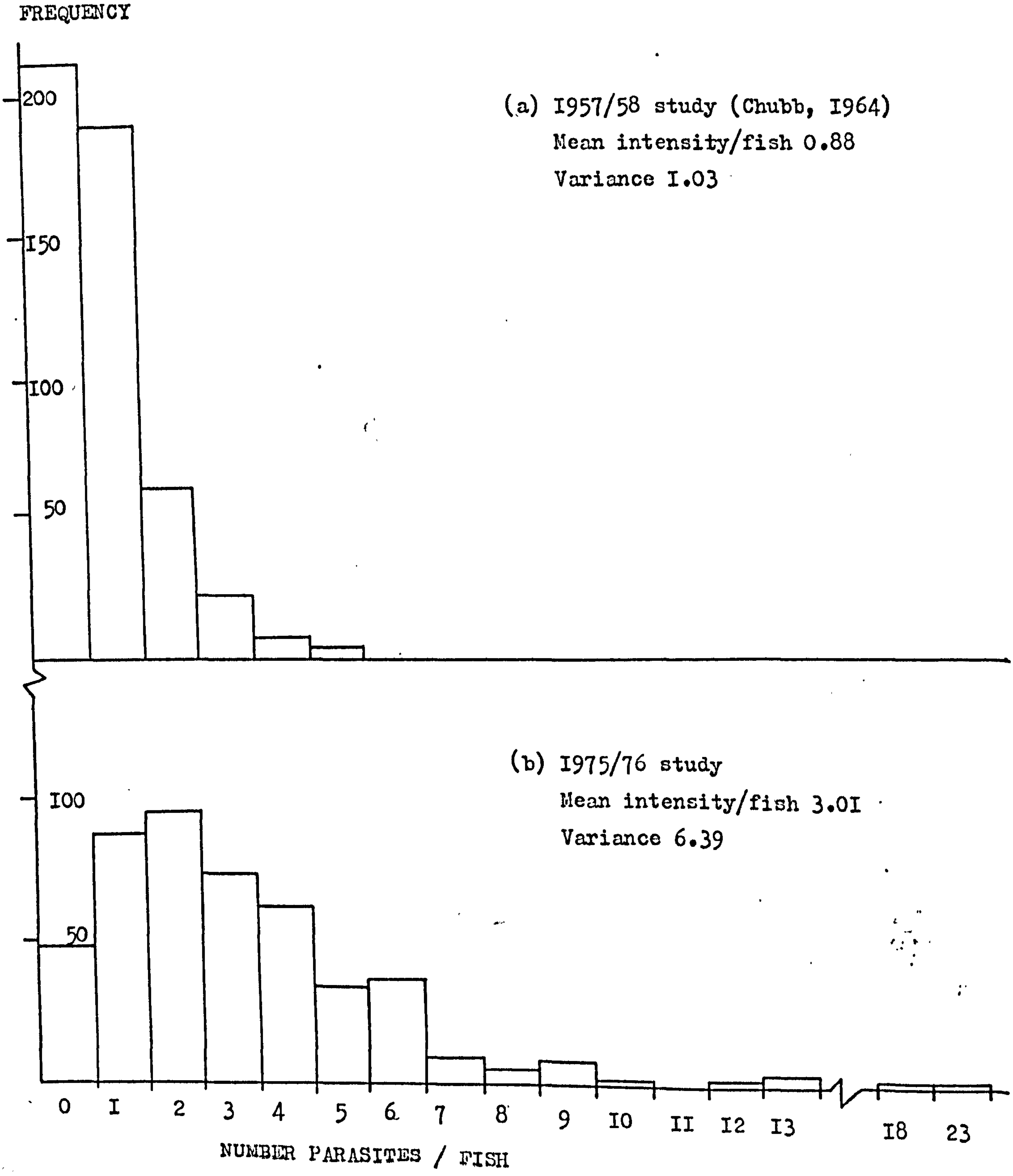
Table XXIV. Comparison of two studies on the <u>Triaenophorus nodulosus</u> plerocercoid infection of perch from Llyn Tegid

	1957/58	1975/76
Number fish examined	497	465*
% incidence	57.5	90.3
Mean intensity/infected fish	1.5	3.4
% incidence developing plerocercoids	4.9	0.4
% incidence degenerating plerocercoids	10.7	67.5
X^2 (variance to mean ratio)	580.55	985.04
d	+ 2.59	+ 13.94
Data from:	Chubb (1964)	Present study

N.B.

* Gill net samples only

Fig. 9. Comparison of the frequency distributions of the Triaenophorus nodulosus infection of perch in two studies at Llyn Tegid.



that the infection level in perch declined when intensive fishing reduced the average length of pike in the lake below 25.0 cm. There is no evidence to suggest a change in populations of pike definitive or plankton intermediate host(s) in Llyn Tegid, though detailed investigations have not been made.

Diphyllobothrium ditremum and *D. dendriticum* may have been introduced into Llyn Padarn around 1959 (Powell & Chubb, 1966). Powell & Chubb recorded a fall in the occurrence of the plerocercoids of these cestodes in trout (*Salmo trutta*) between 1963-1965. Evidence suggested that during this time the trout had developed an increasing immunity to the plerocercoids, and the result was the observed fall in parasite occurrence (Powell & Chubb, 1966). Campbell (1974) observed the *Diphyllobothrium* spp. (plerocercoid) infection of trout (*S. trutta*) in Loch Leven between 1967-72. The incidence of infection increased from the winter of 1~~8~~967/68 to a maximum in the winter of 1968/69. This decreased during 1970 and remained constant until the end of the study. The mean intensity/fish was 0.5 between April 1967-October 1968, and then increased to 1.0 during the winter of 1968/69 until March 1972 (Campbell, 1974). Dogiel (1958) described some long-term observations on the parasite fauna of the fish from Lakes B. Chan and Sartlan (U.S.S.R.). The observations were made in 1934, 1944 and 1947, during which time the incidence of *T. nodulosus* plerocercoids in perch at Lake Sartlan fell from 52.0% in 1934 to 14.2-20.0% between 1944/47. The changes in the parasite fauna were attributed to long-term climatic changes superimposed upon the increasing salinity of the lakes, or long-term changes in some unknown factor(s) (Dogiel, 1958). Bauer *et al.*(1969) and Kuperman (1973) state that the development of the eggs of *T. nodulosus* will proceed normally in fresh or brackish waters with a salinity not exceeding 5-6% .

From the above observations it is clear that fluctuations may occur in fish parasite populations over a period of years. However, Kennedy & Rumpus (1977) have found that the Pomphorhynchus laevis population of the River Avon has remained constant over a 9 year period (1966-74). Kennedy & Rumpus state that, with a number of exceptions, fish-parasite systems are inherently unstable and do not appear to be regulated by feedback controls. They suggested that the observed long-term constancy of the P. laevis infection may be attributed to constant prevailing climatic and ecological conditions, or because of the presence of (as yet) undetermined feedback controls (Kennedy & Rumpus, 1977).

Crofton (1971a) proposed the lethal level concept that stated that the majority of parasite species are capable of killing their hosts if present in large enough numbers. Crofton (1971a & b) stated that the death of a single heavily infected host in the "tail" of an overdispersed parasite population will result in the removal of a large number of parasites from the system. However, Anderson (1976b) stated that the form of the distribution was unimportant and that the lethal level concept may operate in a regulatory role in both underdispersed and overdispersed parasite populations. Regulation of the T. nodulosus parasite population size may exist by parasite induced mortalities of perch. However, the population size of T. nodulosus in perch may also be influenced by the host reactions to the newly acquired procercoid (Vogt, 1938; Kuperman, 1973). The balance between the various regulatory effects in a host-parasite system (whether resulting from parasite induced host mortality, density dependent regulation in bothhost and parasite populations via intra-specific competition, or host generated immunological effects) will undoubtedly vary between different types of parasite life cycles (Anderson, 1976b). The rate of flow of parasites through a life cycle system may be markedly effected by time lags, primarily as a result of developmental processes (Anderson, 1976a). The life cycles of fish helminths may contain many such developmental time lags (e.g. in egg, larval, and adult phases). Theoretical studies have shown that the inclusion of time lags in certain simple models of population growth leads to the oscillation of population size because of the delayed form of the regulation (Wangersky & Cunningham, 1956; Anderson, 1976a). The significance of these results on the long-term aspects of the *T. nodulosus* infection at Llyn Tegid remain to be elucidated. Clearly there has been a change with time in the nature of the infection in perch. The results suggest that in 1975/6 the parasite population is at a peak, though with reduced recruitment and the greater occurrence in degenerating plerocercoids, about to decline. Andrews (1977) indicated the need for frequent, regularly spaced surveys along with controlled laboratory investigations, in order to elucidate the factors controlling the epidemiology and long-term occurrence of this parasite.

The results from a brief study on the host reactions to *T. nodulosus* by perch at Llyn Tegid have been presented. A host inflammatory response are the reactions of the tissues to injury. In broad terms this response can be divided into three stages: early circulatory changes; exudation of protective cells and fluids; and the repair and regeneration of tissues (Runnels *et al*, 1965).

Larval helminths in their intermediate or reservoir hosts may elicit an initial phase of host exudative inflammation, but this decreases after encapsulation. This type of reaction has been observed in a number of instances, concerning the larval helminths of fish. For example, Arme & Owen (1970) reported a massive cellular exudate around the plerocercoids of *Ligula intestinalis* infecting the fry of roach (*Rutilus rutilus*). In infections of longer standing, the number of cells participating decreases, and sheets of connective tissue predominated. Stromberg & Crites (1974) observed a distinct cellular response around some plerocercoids of *T. nodulosus* infecting the liver of bass (*Morone chrysops*). Larger plerocercoids were encapsulated in a connective tissue capsule. Bauer (1959) noted a similar exudative response to this parasite, prior to encapsulation. However, Stromberg & Crites (1974) found that not all plerocercoids invoked a similar exudative response. Silverman & Hulland (1961) have reported that the rate of development of *Cysticercous bovis* in experimentally infected calves was influenced by the degree of host inflammatory response, and varied considerably from one individual to the next.

Hunter & Dalton (1939) divided the cyst walls of larval helminths into two types. The first type are those that consist of a layer of host origin and a layer of parasite origin (e.g. cyst of *Posthodiplostomum minimum*). The other type are capsules that consist of material of solely host origin (e.g. capsule of *Clinostomum marginatum*). Clearly the capsule of *T. nodulosus* belongs to this second category. Berenzantsev (1975) considered that the process of capsule formation around helminth larvae in host tissues can be regarded as a specific proliferative reaction. The capsule wall serves to maintain a relative equilibrium between parasite and host. Such a capsule may function in a similar fashion to other biological membranes in tissue-blood barriers, in maintaining homeostasis in individual systems or organs. The capsules of Trichinella larvae are permeable to glucose, amino acids and certain ions, though high molecular weight compounds (including host antibodies) do not pass through (Berenzantsev, 1975).

The capsules of T. nodulosus observed in this study were comprised of three layers. The inner layer was thought to be produced by degeneration of the middle, fibroblastic layer, and further loose connective tissue may be laid down in the outermost layer. Mikailova et al. (1964) described a two layered capsule surrounding the larvae of certain helminths parasitic in fish. There was an inner dead layer that was surrounded by an outer connective tissue layer. Sche~~y~~uring (1929) (cited by Amlacher, 1970) described a two layered capsule surrounding the plerocercoid of Triaenophorus sp. Sche~~y~~uring suggest~~ing~~ed that the inner layer is continually attacked by the enzymes of the enclosed parasite, and the inner layers suffer continual neoformation. The products of this enzymic attack may be used by the parasite for nutritive purposes.

Calcification was seen within the inner layer, and between this layer and the middle layer, of the capsule. Calcium deposits were found in the majority of capsules that were sectioned, though they were usually light. Prior et al. (1968), Amlacher (1970) and Arme & Owen (1970) have all reported calcification in fish tissues, associated with larval helminths. Dystrophic calcification may occur in any devitalised area. It appears to be a result of local changes in the tissues, though the exact mechanisms are not understood (Anderson, 1966).

The pathology of this parasite in its' second intermediate host has been noted by many workers. Sche~~y~~uring (1922) (cited by Miller (1945a) suggested that the plerocercoids may release substances that destroy liver tissue, providing a source of nutrients for the parasite. This was largely confirmed by Stromberg & Crites (1974) who reported the production of haemorrhagic streaks, necrosis of hepatic cells, squamous metaplasia and fibrosis in the liver of infected bass (Morone chrysops). It was further suggested by Stromberg & Crites that there may be a serious obstructive disease associated with the growing plerocercoids within the liver of these fish. Hoeppli (1953) cited examples of certain larval cyclophyllidean cestodes in their mammalian intermediate hosts damaging adjacent tissues as a result of their growth and consequent pressure necrosis. In addition, Bauer et al (1969) state that the connective tissue capsule of T. nodulosus may displace large numbers of parenchymetous cells in the liver of trout, causing irreparable damage and eventual death of the fish. Infected trout fry may have a distended abdomen with almost transparent walls (Bauer et al, 1969).

Lopukhina (1961) found that young, infected rainbow trout (Salmo gairdneri) had a reduced mean weight and length, and their blood values of percentage monocytes was higher and percentage lymphocytes lower, than in uninfected fish. Their haemoglobin content was within normal limits. Whilst Lopukhina (1966) found that the glycogen content of the livers of perch, trout and smelt were not affected by infection with T. nodulosus, Amlacher (1970) states that heavily infected fish livers may suffer cirrhosis and a total loss of glycogen. Rizvi (1964) recorded the occurrence of a single plerocercoid from within the ovary of 1 out of 343 perch examined at Rostherne Mere, Cheshire. The ovary was exceptionally swollen and showed signs of internal infection. This site of infection is atypical for T. nodulosus.

Petrushevski & Shulman (1958) stated that infection with T. nodulosus may cause enlargement of the liver, and that a heavy infection may lead to the total destruction of hepatic tissue. Epizootics of this parasite have been recorded from perch during May-June in some Russian lakes. Matthay (1963) reported the death of large numbers of perch from massive infections with this parasite in May (1957) and January (1958), at Lake Zug (Switzerland).

Lawler (1969a) studied the infection in young yellow perch (Perca flavescens) from Heming Lake, Canada. Infected livers were markedly swollen, and in some instances scarcely any hepatic tissue was unaffected. In one infected fish the liver was completely destroyed. Based on his observations, Lawler concluded that the presence of this parasite in such a vitally important organ as the liver, must be a major factor in controlling mortality in natural populations of yellow perch.

It should be noted that in continental Europe and North America, the plerocercoid of T. crassus is a serious problem where it infects the flesh of commercially valuable coregonine fish (Miller, 1945a, 1952; Vik, 1959; Riechenbach-Klinke & Negele, 1971; Hoffman, 1973; etc).

During this study at Llyn Tegid no observations were made on the tunnelling unencapsulated plerocercoids, though the reports of several other workers indicate that heavy infestations with this stage, particularly in young fish, may be pathogenic (Lopukhina, 1961; Petrushevski & Shulman, 1958; Lawler, 1969a; Stromberg & Crites, 1974).

The encapsulated plerocercoids in perch from Llyn Tegid appeared to produce little pathology within the hepatic tissues that were examined histologically. However, in heavily infected perch, extensive fibrosis was observed in a number of instances, and peritoneal adhesions recorded once. The presence of T. nodulosus within the liver of 0++ perch did not markedly affect their growth rate or condition factor. Similarly the growth rate of 4++ fish was not reduced by increasing levels of infection.

Therefore, whilst a sudden, large infection with tunnelling, unencapsulated plerocercoids may be harmful, especially in young fish, substantial numbers of encapsulated plerocercoids may be harboured with little apparent harm. Vogt (1938), Chubb (1964) and Kuperman (1973) have all suggested mechanisms by which superinfestation may be prevented. Clearly, under natural conditions, processes exist for the circumnavigation of these mechanisms. Since this parasite is long lived in its second intermediate host, the infection may accumulate in fish during successive years. The present status of T. nodulosus in Llyn Tegid suggests that massive infections of young of the year fish are unlikely. However, the low rate of recruitment observed in 1975/76 may change with time, as illustrated by the comparison of the observations of Chubb (1964). Nonetheless, the infection appears to spread rapidly through the perch population during their second, third and perhaps fourth summers in the lake. High levels of infection, built up over successive years, may be harmful to these fish. The possible disappearance of heavily infected, older, female fish has been noted. Assuming this disappearance, of heavily infected older female fish, it is possible to postulate that younger heavily infected perch might also suffer from reduced longevity. However, the continued recruitment of the parasite into these fish might obscure this effect

The etiology of the other capsules encountered within the viscera of perch remain obscure. Using Ziehl-Neelsen, Fite-Faraco and Gram stains, the presence of bacteria in tissue sections could not be demonstrated. The absence of chitinous hooks (from the scolex of *T. nodulosus*) suggested that these capsules were not degenerate *T. nodulosus* capsules. However, the attachment apparatus on the scolex of *T. nodulosus* is not completely formed until about day 40 post infection (Miller, 1945a; Kuperman, 1973). Nonetheless, it seems unlikely that the large numbers of these capsules that were observed in some fish are the result of the host encapsulation of the very young plerocercoid stage, and its death before the hooks of the scolex were formed. The similarity of these lesions to those produced by acid fast bacteria, flavobacteria and *Ichthyophonus hoferi* (a fungus) (Amlacher, 1970; Ghittino, 1971; Reichenbach-Klinke, 1971; and Wolke, 1975) is noted.

VIII.25
~~8.35~~

SUMMARY

The plerocercoid of *T. nodulosus* is a common parasite of perch in Llyn Tegid. In adult perch there is a high incidence and mean intensity/infected fish, and the parasite population is markedly overdispersed.

There were no seasonal changes in the incidence or intensity of infection, or in the occurrence of mature or degenerating plerocercoids. Developing plerocercoids were rare, though their seasonal occurrence was similar to that seen in a previous study.

Host sex appears to have little affect on the incidence and intensity of infection in adult fish.

The parasite is prevalent in perch that have spent at least two summers in the lake. In older, larger perch there is a fall in the incidence of infection, though the intensity remains unaffected.

In older perch degenerating plerocercoids were usually more abundant than mature plerocercoids.

The feeding habits of perch and their seasonal changes, and changes with host age and length, are crucial in any consideration of the epizootiology of this parasite. There was no secondary infection of large perch from infected, smaller perch.

The parasite did not reduce the growth rate of condition factor of certain perch that were investigated. There was no extensive histopathology in the tissue sections that were examined. Nonetheless, it is suggested that high intensities of infection may reduce the longevity of perch.

Crowding within perch livers did not result in a greater occurrence of degenerate plerocercoids.

Results suggest that there may be no significant variation in the incidence or intensity of infection in adult perch between sites within a restricted area of the lake.

There has been a significant change in the size and structure of the parasite population in perch since 1957/58.

The presence of an additional type of capsule in the viscera of perch is noted.

ADDITIONAL NOTE TO CHAPTER VIII

Re. Long-term observations on *Triaenophorus nodulosus*

Stromberg & Crites (1975). Analysis of the changes in the prevalence of *Camallanus oxycephalus* (Nematoda: Cam~~m~~allanidae) in western Lake Erie. *Ohio J. Sci*. 75, 1-6.

The prevalence of *C. oxycephalus* in the fish of western Lake Erie during 1927, 1957 and 1972 was compared. The prevalence had increased between 1957-1972, which was related to changes in plankton, benthos and fish communities of the western basin. It appeared that the rise in the number of gizzard shad (*Dorosoma copedianum*) was a principal factor in the increased prevalence of this parasite. Young gizzard shad consumed large numbers of cyclopoid copepods, which concentrated the nematode larvae, and delivered a larger number of parasites to the piscivorous fish which feed upon the shad. When the numbers of shad increased, piscivorous fish began to consume more shad and contacted the parasite more frequently (Stromberg & Crites, 1975).

VIII.3 ORDER Pseudophyllidea Carus, 1863

FAMILY Amphicotyle Ariola, 1899
GENUS *Eubothrium* Nybelin, 1922
Eubothrium sp.

FAMILY Bothriocephalidae Blanchard, 1849
GENUS *Bothriocephalus* Rud., 1808
Bothriocephalus sp.

VIII.~~41~~31 INTRODUCTION

Tapeworms of the family Bothriocephalidae are chiefly parasitic as adults in the intestines of marine, migratory and freshwater fish, and amphibians and birds, whilst members of the genus *Bothriocephalus* principally parasitise marine fish (Bykhovskaya-Pavlovskaya *et al.*, 1962). According to Kennedy (1974) only *Bothriocephalus claviceps* Goeze, 1782 has been recorded from the freshwater fish of the British Isles, along with a number of undetermined records of *Bothriocephalus* sp. It is likely that in most instances, records of *Bothriocephalus* sp. refer to *B. claviceps*. *B. claviceps* matures in the intestines of eel (*Anguilla anguilla*), and the life history has been studied by Jarecka (1959). In common with the studies on the life cycle of many other members of the genus (e.g. *B. cuspidatus* Cooper, 1917 by Essex, 1928; *B. scorpii* Müller, 1776 by Markowski, 1935; *B. formosus* Müller and Van Cleave, 1932 by Hunter and Mackenthun, 1940; *Bothriocephalus* sp. (from carp, *Cyprinus carpio*) by Korting, 1975) development of the procercoid occurs in a copepod crustacean intermediate host. Jarecka (1959) lists *Macrocyclops albidus*, *M. fuscus*, *Eucyclops macruroides* and *E. macrurus* as the copepod hosts of *B. claviceps*. Chubb (1961, 1963a) has recorded adult *B. claviceps* from 10 of 54 eels in Llyn Tegid, and from 7 of 151 eels from the streams following into Llyn Tegid.

Adult tapeworms of the family Amphicotylidae parasitise the intestines of fish, and members of the genus *Eubothrium* appear to chiefly parasitise migratory (and occasionally freshwater) fish (Bykhovskaya-Pavlovskaya *et al.*, 1962). According to Kennedy (1974) two species of this genus occur in the freshwater fish of the British Isles: *Eubothrium crassum* Bloch, 1779 and *Eubothrium salvelini* (Schrank, 1790). In addition, there are a number of records of *Eubothrium* sp. Kennedy (1969) suggested that there are two races of *E. crassum*, with a freshwater and marine life cycle respectively. Observations on the gross morphology of adult specimens of *E. crassum* from trout (*Salmo trutta*) and salmon (*S. salar*) supported this hypothesis (Chubb, 1961, 1976). The freshwater form of this parasite is a common parasite of trout in Llyn Tegid (Ball, 1957; Chubb, 1961, 1963a, 1976; Aderounmu, 1965). *E. crassum* utilises a copepod crustacean intermediate host, though in some situations an additional piscine intermediate host maybe involved, in which the plerocercoid develops (Rosen, 1918; Vik, 1963).

Bothriocephalus sp. has previously been recorded from perch in the British Isles at Shropshire Union Canal (Cheshire)(Mishra and Chubb, 1969) and at Ockendon Moat (Essex) (Shillcock, 1972). *E. crassum* has been recorded from perch in the British Isles in Ireland (Kane, 1966) and Loch Leven (Scotland) (Campbell, 1974), while *Eubothrium* sp. have been similarly recorded at Lake Windermere (Rawson, 1952).

VIII.~~42~~32 RESULTS

Plerocerciform, juvenile, pseudophyllidean tapeworms were found within the lumen of the alimentary tract of perch. The tapeworms were found in the stomach, pyloric caeca and intestine (Table XXV). However, the most posterior portion of the intestine (81-100%) harboured the majority (71.5%) of these parasites.

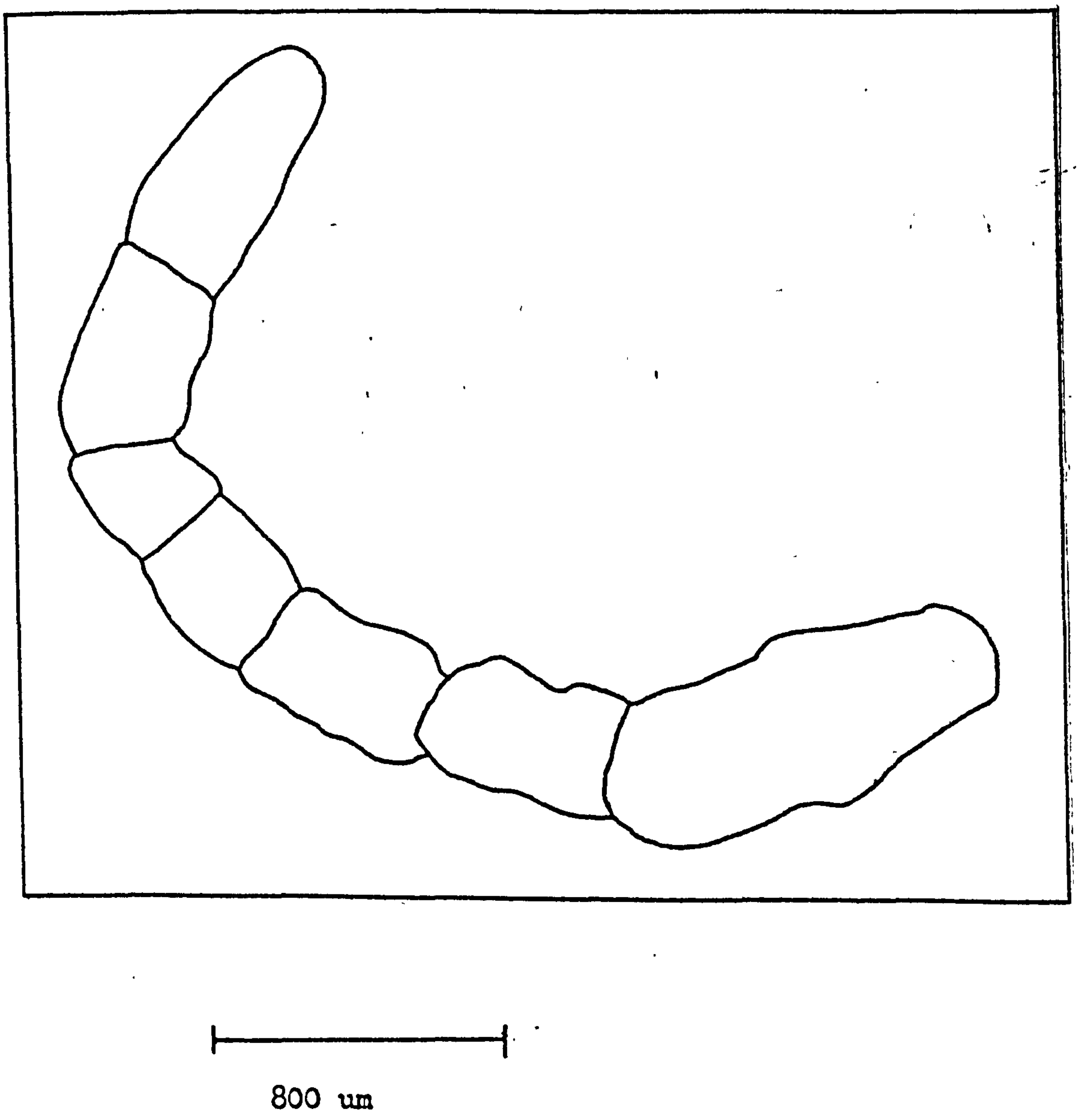
The tapeworms were usually elongated, tear-drop shaped, and measured 2-3 mm long. At the blunt, rounded anterior end there were two poorly defined bothria. Segmentation was usually absent, though observed in a small number of specimens. The gonadal developments associated with adult worms were not seen. Specimens identified as *Bothriocephalus* sp. were found on a few occasions (Fig. ~~8~~10). However in the majority of instances it was impossible to distinguish between *Eubothrium* sp. and *Bothriocephalus* sp. with any degree of certainty. Since *E. crassum* and *B. claviceps* parasitise fish in Llyn Tegid, it is possible that both may infect perch. Therefore because of the difficutly experienced in separating the plerocerciform juveniles of both species, the infection was treated as *Eubothrium* sp./*Bothriocephalus* sp.

Eubothrium sp./*Bothriocephalus* sp. were recorded from 14 of 465 adult perch (3.0%) examined from the gill net samples from January 1975-February 1976. The total number of tapeworms was 21, and the mean intensity/infected fish was 1.5 (maximum 5). In addition, these tapeworm were recorded from 8 of 30 perch fry (26.7%) examined in July 1976. The total number of tapeworms in these fish were 13, and the mean intensity/infected fish was 1.6 (maximum 5). None of 65 perch examined from the trawl sample in March 1976, including 36 0++ fish, were infected.

Seasonal aspects of the infection with *Eubothrium* sp./*Bothriocephalus* sp.

The results from the gill net samples of fish are shown in Table XXVI. Whilst the incidence and mean intensity/infected fish was always low, there is an indication of the seasonal occurrence of these parasites. These tapeworms were present in March, April, July-November (1975), though absent for the winter months of January, February (1975)

Fig. 10. Bothriocephalus sp. from intestine of perch at Llyn Tegid. Formalin fixed, stained in Horen's Trichrome (see Chapter II). Camera lucida drawing at x100.



and December-February (1975/76) and the spring-summer months of May and June (1975). The mean intensity/infected fish was usually between 1.0-2.0. The higher value of the intensity of infection in August (1975) was a result of the presence of a single perch harbouring 5 parasites (Table XXVI).

Effect of host age and length on the *Eubothrium* sp./*Bothriocephalus* sp. infection

Perch of all ages and sizes may harbour the infection (Tables XXVII and XXVIII). Out of 30 perch fry (aged 4-6 weeks (0+), mean length 2.3 cm, maximum 2.7 cm) examined in July (1976), 8 were infected. None of 30 0++ perch (aged 8-9 months, length 3.0 - 8.9 cm) examined in March (1976) were infected (Tables XXVII and XXVIII).

The incidence of infection was low in the adult perch aged 2-5++ and length 9.0-14.9 cm examined from the gill nets (Tables XXVII and XXVIII). In older, larger perch the incidence of infection may rise slightly.

In fish of all ages and sizes the mean intensity/infected fish was usually between 1.0-2.0 (Tables XXVII and XXVIII).

Effect of host sex on the *Eubothrium* sp./*Bothriocephalus* sp. infection

There was no difference in the incidence or mean intensity infected fish between the adult male and female perch examined from the gill nets between January 1975-February 1976 (Table XXIX).

Table XXV. Site of infection of *Eubothrium* sp./*Bothriocephalus* sp. Gill net samples. January 1975-February 1976.

Site	Number parasites	% of total
Stomach	2	9.5
Pyloric caeca	2	9.5
Intestine (0-20%) (anterior)	2	9.5
(21-40%)	-	
(41-60%)	-	
(61-80%)	-	
(81-100%) (posterior)	15	71.5
Total number parasites	21	-

Table XXVI. Seasonal aspects of the Eubothrium sp./Bothriocephalus sp. infection. Gill net samples. January 1975 - February 1976.

Month	Number fish examined	Number fish infected	% incidence	Number of parasites	Mean/ infected fish	Maximum
J	6	-				
F	30	-				
M	30	3	10.0	5	1.7	3
A	30	1	3.3	1	1.0	1
M	30	-				
J	39	-				
J	40	3	7.5	3	1.0	1
A	30	1	3.3	5	5.0	5
S	30	2	6.7	2	1.0	1
O	60	3	5.0	3	1.0	1
N	54	1	1.9	2	2.0	2
D	35	-				
J	30	-				
F	21	-				
Total	465	14	3.0	21	1.5	5

Table XXVII. Effect of host age on the Eubothrium sp./Bothriocephalus sp. infection. Purse seine, trawl and gill net samples. January 1975 - March 1976, July 1976.

Age (yrs.)	Number fish examined	Number fish infected	% incidence	Number parasites	Mean/ infected fish	Maximum
PURSE SEINE (JULY 1976)						
0+	30	8	26.7	13	1.6	5
TRAWL (MARCH 1976)						
0++	36	0	-			
GILL NETS (JANUARY 1975 - FEBRUARY 1976)						
2-2++	4	0	-			
3-3++	138	3	2.2	3	1.0	1
4-4++	164	3	1.8	5	1.7	2
5-5++	78	2	2.7	4	2.0	3
6-6++	43	3	6.9	3	1.0	1
7-7++	38	2	5.3	6	3.0	5

Table XXVIII. Effect of host length on the <u>Eubothrium</u> sp./ <u>Bothriocephalus</u> sp. infection. Gill net samples. January 1975 - February 1976.

Length (cm)	Number fish examined	Number fish infected	% incidence	Number parasites	Mean/ infected fish	Maximum
9.0-11.9	56	2	3.6	2	1.0	1
12.0-14.9	321	7	2.2	10	1.4	3
15.0-17.9	60	3	5.0	3	1.0	1
≥18.0	29	2	6.9	6	3.0	5

Table XXIX. Effect of host sex on the <u>Eubothrium</u> sp./<u>Bothriocephalus</u> sp. infection. Gill net samples. January 1975 - February 1976.

	Male	Female
Number fish examined	183	282
Number fish infected	6	8
% incidence	3.3	2.8
Number parasites	9	12
Mean intensity/infected fish	1.5	1.5
Maximum	3	5

VIII.33 DISCUSSION

E. crassum and *B. claviceps* both occur in Llyn Tegid. The former species matures in brown trout (*Salmo trutta*), whilst the latter matures in eel (*Anguilla anguilla*). Since both species of tapeworm utilise a planktonic crustacean intermediate host, any plankton feeding species of fish is exposed to infection. Of the juvenile specimens recovered from perch, differentiation between *Eubothrium* sp. and *Bothriocephalus* sp. was found difficult. Therefore, the results of the infection have been treated jointly as *Eubothrium* sp./*Bothriocephalus* sp.

Van Cleave and Mueller (1934) found that juvenile *B. claviceps* occurred in a range of fish hosts in Lake Oneida (U.S.A.) that were unsuited to bring them to maturity. In an environment containing eels infected with *B. claviceps*, perch may become infected with juvenile worms. *Bothriocephalus* sp. juveniles have been previously recorded from perch in the British Isles at Shropshire Union Canal (Cheshire) (Mishra and Chubb, 1969) and at Ockendon Moat (Essex) (Shillcock, 1972). Since these parasites do not mature in perch, this host must have little biological significance for the parasite species. Infection may be of short duration and of a seasonal nature, and related to the feeding habits of the fish and/or the availability of infective plankton. Jarecka (1959) has shown that juvenile *B. claviceps* in small fish do not penetrate the gut wall, but remain in the intestinal lumen. Nonetheless, the possibility exists of eels acquiring the infection from parasitised perch.

Rosen (1918) found that the life cycle of *E. crassum* may involve two intermediate hosts, the copepods *Cyclops strenuus* and *C. serrulatus* (≡ *C. agilis*), and perch. He suggested that the plerocercoid develops within the intestinal lumen of perch, or more rarely the abdominal cavity. Trout become infected by feeding upon parasitised perch.

Vik (1963) found that sticklebacks (Gasterosteus aculeatus) could act as a second intermediate host to E. crassum, with the plerocercoid encapsulated within the abdominal cavity of the fish. However, Vik also suggested that transmission of the parasite might also occur directly from copepod to trout, with the plerocercoid phase in the intestine of trout. Wootten (1972) found that the life cycle of E. crassum at Hanningfield Reservoir (Essex) may involve a single copepod intermediate host, and the definitive hosts brown trout (Salmo trutta) and rainbow trout (S. gairdneri). Perch are found within the same environment but were not infected. However, 9 out of 165 (5.5%) ruffe (Gymnocephalus cernua) were infected with young, adult worms. Because of the low incidence of the parasite in ruffe, and because ruffe constituted only a small part of the diet of brown trout and rainbow trout, it is unlikely that ruffe provide more than a minor source of infection for trout at Hanningfield Reservoir (Wootten, 1972).

At Llyn Tegid, adult E. crassum is a common parasite of brown trout (Ball, 1957; Chubb, 1961, 1963a, 1976; Aderounmu, 1965). In a sample of perch fry (aged 4-6 weeks) examined in July (1976) there was an incidence of infection of 8 out of 30 (26.7%). Whilst this was only a small sample, it illustrates that during certain months of the year, perch fry may serve as a source of infection for the trout that feed upon them. Nonetheless, the transmission of E. crassum to trout via infected copepods is highly likely.

In the adult perch examined the incidence of infection was low, and may follow a seasonal pattern. The spring-autumn occurrence of Eubothrium sp./Bothriocephalus sp. in perch may be a result of the seasonal availability of infective plankton and/or the seasonal changes in feeding habits of perch (see Chapter III). Copepods were ingested by perch during March and April (1975) and between June-February (1975/76), though there was a peak in their occurrence in perch stomachs during July and September (1975). Campbell (1974) reported the occurrence of the plerocercoids of E. crassum from the intestinal lumen of perch at Loch Leven (Scotland). This parasite was most common in perch during the period August-October (1971), when the juvenile stages were most common in trout (Salmo trutta). In addition, in the perch at Llyn Tegid there was seen to be a slight increase in the incidence of infection of these parasites in perch aged over 5++ years and above 14.9 cm. Since perch of this size do not feed to any great extent upon plankton but are noticeably cannabilistic, larger perch may acquire the infection from smaller, infected ~~perch~~ fish ingested as food. The fact that the mean intensity/infected fish does not rise in these larger perch may be an indication of the short duration of the infection in perch.

VIII.~~44~~ 34 SUMMARY

The infection of perch with Eubothrium sp./Bothriocephalus sp. is a new host record for Llyn Tegid.

The incidence of infection may follow a seasonal pattern.

The incidence of infection was highest in perch fry, during July (1976). The incidence of infection was low in adult perch aged between 2-5++ years and 9.0-14.9 cm. In larger, older perch there may be a rise in the incidence.

The intensity of infection was low. There was no difference in the incidence or intensity of infection in male and female perch.

The biological significance of the occurrence of these parasites in perch was discussed.

VIII.4 ORDER Proteocephalidea Mola, 1928

FAMILY Proteocephalidae La Rue, 1911

GENUS *Proteocephalus* Weinland, 1858

Proteocephalus sp., *Coregonus lavaratus* type

VIII.41 INTRODUCTION

Tapeworms of the genus *Proteocephalus* often have a two host life cycle, involving the development of the procercoid and plerocercoid in certain copepod crustaceans (e.g. *Cyclops* sp., *Mesocyclops* sp., *Eudiaptomus gracilis*, etc.), and the occurrence of the plerocercoid and adult worm in the intestines of certain freshwater fish. Reptiles and amphibians are less commonly recorded as definitive host to this genus (Bykhovskaya-Pavlovskaya *et al*., 1962). However, certain proteocephalid life cycles may involve a second intermediate host. Rees (1963) suggested that *Proteocephalus nilotius* (Beddard, 1913) may have a three host life cycle, involving copepod and amphibian intermediate hosts, and a varanid lizard definitive host. *Proteocephalus ambloplitis* (Leidy, 1887) has a planktonic first intermediate host, with the occurrence of the plerocercoid in small bass (*Ambloplitis*, *Micropterus*). Larger, predatory bass are the definitive host, and acquire the infection as a result of their piscivorus habits (Wardle and McCleod, 1952). However, Fischer and Freeman (1969, 1973) have shown that at Lake Opeongo (Canada) plerocercoids commonly enter the gut of bass by direct entry from parenteral sites in the same fish, and only rarely following the ingestion of infected bass (since cannibalism is rare in this lake). Nonetheless, the importance of the plerocercoid infection in fish other than bass in Lake Opeongo was stressed (Fischer and Freeman, 1973). The life cycles of certain other, closely related tapeworms (e.g. *Ophiotaenia filaroides* (La Rue, 1909)) may follow more than one developmental pattern (La Rue, 1909; Mead and Olsen, 1971), and the migration of plerocercoids from parenteral sites into the gut lumen of the same host may be more common than previously realised (Fischer and Freeman, 1969).

Proteocephalus percae Müller, 1780 is a common parasite of perch and its North American counterpart, the yellow perch (*Perca flavescens*) (Bykhovskaya-Pavlovskaya *et al.*, 1962; Hoffman, 1967; Kennedy, 1974). The life history ond development of this species was recently studied by Wootten (1974). *P. percae* does not occur in Llyn Tegid. The species recorded from perch in this study is undoubtedly the same species that matures in the gwyniad (*Coregonus lavaratus*). This tapeworm is similar to *Proteocephalus pollanicola* Gresson, 1952, but differs from it in a number of features (Chubb, 1961, 1970, 1976; Farenden, 1976). *P. pollanicola* occurs in *Coregonus pollan* (a close relative of the gwyniad) that is found in an isolated lake in Ireland. *P. pollanicola* was studied by Gresson (1952) and Gresson and Corbett (1954).

VIII.~~52~~42 RESULTS

Proteocephalus sp. was not recorded from the adult perch from the gill net samples taken between January 1975-February 1976, or from the sample of 30 0+ perch fry examined in July 1976.

Juvenile, plerocerciform specimens were found in the alimentary tract lumen of 6 of 36 (16.7%) 0++ (length 4.0-6.9 cm) perch examined in March 1976. None of the larger,older perch from this sample were infected. The results are summarised in Table XXX. The mean intensity/ infected fish was 2.0 (maximum 3). The most common site of infection was the anterior half of the intestine, though specimens also occurred in the pyloric caeca and the posterior half of the intestine. The juvenile tapeworms measured 2-3 mm after relaxation by deep freezing.

Table XXX. Data on perch infection with Proteocephalus sp.

Trawl sample. March 1976.

HOST DATA			SITE OF INFESTATION	Intestine	
Length (cm)	Age (yrs.)	Number worms	Pyloric caeca	Anterior	Posterior
5.1	0++	2	-	2	-
5.6	0++	2	-	-	2
4.1	0++	1	-	1	-
5.5	0++	3	-	3	-
4.8	0++	2	1	-	1
4.1	0++	2	-	1	1
6 fish	0++	12	1	7	4

N.B. Average length infected fish 4.9 cm

Mean intensity/infected fish 2.0 (maximum 3)

VIII.43 DISCUSSION

Farenden (1976) studied the overwintering of *Proteocephalus* sp. at Llyn Tegid in the gwyniad, between October 1975 - March 1976. The occurrence was highest in October (13.3%), November (12.0%) and March (19.4%), and low in December (4.5%), January (2.8%) and February (no infections). The incidence is probably higher during the summer months (Chubb, 1976). Gravid worms were found in October and March. It was concluded that seasonal variations in the availability of infected copepods in relation to the feeding habits of the host, along with seasonal variations in environmental temperature and the physiological resistance of the host, influence the overwintering of *Proteocephalus* sp. in gwyniad (Farenden, 1976).

Proteocephalus sp. were recorded from 0++ perch in March, that were feeding to a large extent on copepods (cyclopoids, but especially calanoid Copepoda) (see Chapter III). Therefore, the occurrence of this tapeworm in perch is clearly related to their feeding habits. However, adult perch ingest appreciable numbers of copepods at certain times of the year, yet *Proteocephalus* sp. was not recorded from these fish, or from the perch fry examined in July (1976). However, the perch fry had been feeding extensively on Cladocera, and Copepoda were rare in the stomachs of these fish (see Chapter III). The absence of *Proteocephalus* sp. from the adult perch may be a result of their occurrence being overlooked, in the intestine which often contains substantial amounts of mucous, food remains and debris. Any plankton feeding fish is liable to infection though mature *Proteocephalus* sp. have only been recorded from gwyniad. Juvenile tapeworms have also been recorded from pike (*Esox lucius*), salmon smolt (*Salmo salar*), trout (*S. trutta*) and grayling (*Thymallus thymallus*) at Llyn Tegid (Chubb, 1963a, 1976). The infection in pike may have been acquired secondarily from gwyniad taken as food.

However, seasonal variations in feeding habits of perch in relation to the availability of infected plankton, as well as seasonal or age related resistance phenomena may also influence the infection of perch with Proteocephalus sp.

VIII.~~54~~44 SUMMARY

The occurrence of Proteocephalus sp., Coregonus lavaratus type from perch is a new host record for Llyn Tegid and the British Isles.

The infection was only found in juvenile fish. This may be a result of their unrecorded occurrence in older perch, or the influence of availability of infected plankton, host feeding habits, and variations in host resistance phenomena.

Proteocephalus sp. does not mature in perch, and hence this host has little biological significance for the species.

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CHAPTER IX

THE NEMATODE PARASITES OF PERCH (*Perca fluviatilis* L.) FROM LLYN TEGID

INTRODUCTION

Three species of nematodes were recorded from the perch at Llyn Tegid: *Camallanus lacustris*, *Cucullanus truttae* and *Raphidascaris cristata* (juveniles).

X.I FAMILY Camallanidae Railliet & Henry, 1915

GENUS Camallanus Railliet & Henry, 1915

Camallanus lacustris (Zoega, 1776)

X.I.I INTRODUCTION

The family Camallanidae is comprised of six genera, which are divided into two subfamilies (Yeh, 1960; Stromberg & Crites, 1974a). The Procamallaninae (Yeh, 1960) comprises of two genera: Procamallanus Baylis, 1928, and Spirocamallanus Olsen, 1952; while the Camallaninae Yeh, 1960 comprises of the genera Camallanides Baylis & Daubney, 1922, Camallanus Railliet & Henry, 1915, Paracamallanus York & Maplestone, 1926, and Zeylanema Yeh, 1960. Approximately three quarters of the 130 species have been described from piscine hosts, with 77 species from freshwater fish and 19 species from marine fish. The remaining 34 species occurred in reptilian (15 species) or amphibian (19 species) hosts (Stromberg & Crites, 1974a). Stromberg & Crites (1974a) reviewed the origin, dispersal and distribution of camallanid nematodes. Only Camallanus lacustris has been recorded from the freshwater fish of the British Isles (Kennedy, 1974). The parasite fauna of the British herpetofauna is poorly studied.

The life histories of camallanid nematodes have been studied by Li (1935), Pereira et al. (1936), Moorthy (1938), Kupriyanova (1954), Campana-Rouget (1960), Moravec (1969a, b, c), Stromberg & Crites (1974b, c), Stumpp (1975), and Crites (1976).

Petter et al. (1974) described Camallanus moraveci n.sp. in the rectum of the cyprinodonts Mollienisia latipinna and Xiphophorus helleri from Singapore.

X.I.2 ADDITIONAL MATERIALS AND METHODS

Camallanus lacustris from the alimentary tract of perch were categorised into the following stages: larvae (third and fourth stage larvae), males, and females. Female nematodes were further divided into pre-larvigerous and larvigerous (containing active first stage larvae) worms.

X.I.3 RESULTS

Two hundred and fifty-nine of the 465 (55.7%) gill netted perch that were sampled between January 1975 - February 1976 were infected. The mean intensity/infected fish was 4.2 (maximum 41). The mean intensity/fish was 2.3.

From the trawl sample of 65 perch taken in March 1976, 12 fish (18.8%) were infected with a mean intensity/infected fish of 3.8 (maximum 16). The mean intensity/fish was < 1.

The purse seine sample of perch fry examined in July 1976 were uninfected.

Seasonal aspects of the infection

The results from the gill net samples of adult perch are shown in Table I and II. The parasite was present in all months of the year. However, the incidence of infection was at its lowest in January, and July-September 1975, though the low value of incidence in January may have been a reflection on the small number of fish examined. During all other months of the year the incidence fluctuated between 46.7 - 70.4% (Table I). The mean intensity/infected fish fluctuated from month to month and showed no marked seasonal pattern. Heavily infected fish were present in most months (Table I).

Male and female worms were present in all months, though there were detectable changes in sex ratio. The results in Table II suggest that during January - May (excluding March) 1975 and October - February 1975/76, the sex ratio was approximately 1:1. The number of male and female C. lacustris for this period were summed, and no significant difference from 1:1 ratio found ($X^2 = 2.62$, DF = 1, $P > 0.05$). In March 1975 there were markedly more female than male parasites (Table II). The results suggest that during June - September 1975 there was also a greater proportion of female worms. The number of male and female worms present during June - September were summed, and a very highly significant departure from a 1:1 ratio found ($X^2 = 12.83$, DF = 1, $P < 0.001$). During this period a total of 69 males and 118 females were recovered (Table II).

The seasonal occurrence of larval C. lacustris is shown in Fig. 1. Larvae were present in all months, with no marked seasonal pattern. However, their incidence was low during July - September, when a total of 22 larvae were recorded from 100 perch (Fig. 1, Table I and II). The incidence of larval worms was highest during February, October and December 1975 and February 1976 (Fig. 1).

Larvigerous females were present in all months (Fig. 1, Table II). Whilst the precise data for January - May 1975 was lacking the results suggest that larvigerous females were most abundant during July and September 1975. There was a marked fall in the occurrence of larvigerous females in August 1975, and over the autumn-winter of 1975/76 (October onwards), their incidence appeared to steadily decline (Fig. 1).

Effect of host sex

One hundred and fifty-four of 282 (54.6%) of the adult female gill netted perch were infected. From the same samples of fish, 105

Table I. Seasonal aspects of the Camallanus lacustris infection.

Gill net samples. January 1975 - February 1976

	Number Fish Examined	% Incidence	Total Number Parasites	Mean intensity/ infected fish	Maximum
J	6	33.3	10	5.0	7
F	30	70.0	120	5.8	18
M	30	53.3	49	3.1	11
A	30	56.7	108	6.4	41
M	30	46.7	39	2.8	13
J	39	60.0	113	3.9	27
J	40	42.5	52	3.1	10
A	30	36.7	45	4.1	17
S	30	43.3	45	3.5	14
O	60	58.3	153	4.4	22
N	54	70.4	141	3.7	20
D	35	65.7	110	4.8	31
J	30	53.3	38	2.4	7
F	21	66.7	62	4.4	18
TOTAL	465	55.7	1085	4.2	41

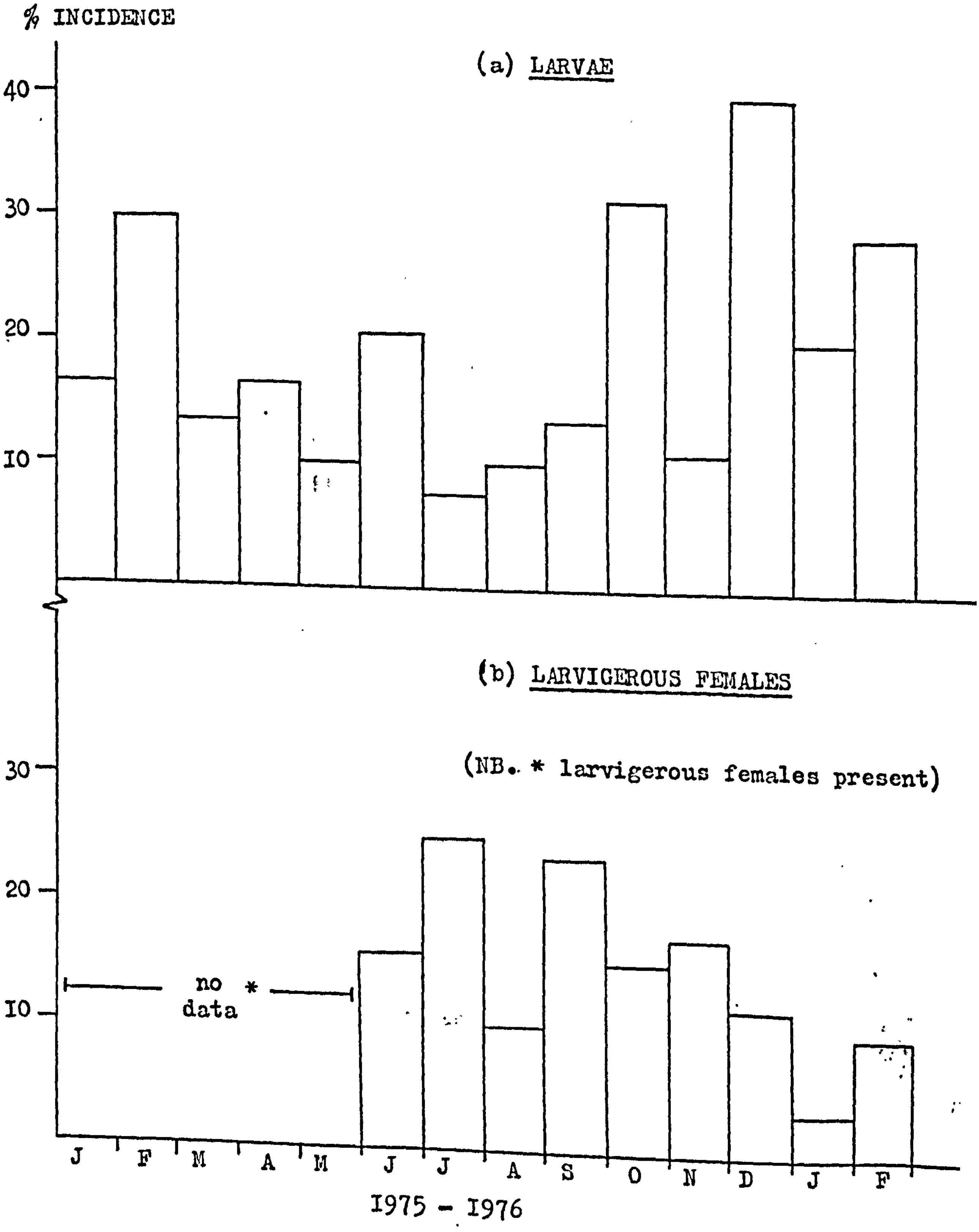
Table II. Seasonal composition of Camallanus lacustris population.

Gill net sample. January 1975 - February 1976

Month	Total Number Larvae	Total Number Males	Total Number Females	% Adults Female	% Females Larvigerous
J	3	5	2	28.6	*
F	48	36	36	50.0	*
M	6	12	31	72.0	*
A	27	44	36	45.0	*
M	11	14	14	50.0	*
J	46	23	44	65.7	20.5
J	3	19	30	61.2	63.3
A	4	17	24	58.5	16.7
S	15	10	20	66.7	50.0
O	61	48	44	47.8	31.1
N	45	50	46	47.9	39.1
D	24	50	37	42.5	30.3
J	13	14	11	44.0	27.3
F	26	19	17	47.2	23.5
TOTAL	332	365	388	51.5	33.5

NB * data not available, though larvigerous females present

Fig. I. Seasonal occurrence of Camallanus lacustris. Gill net samples. January 1975 - February 1976.



of 183 (57.4%) adult male perch were infected. The frequency distribution of the parasite counts in male and female fish are shown in Fig. 2. In both instances the frequency distribution was similar, and the parasite population overdispersed (Fig. 2).

The mean intensity/infected fish was: male perch, 3.9 (maximum 23), variance 14.86; female perch, 4.4 (maximum 41), variance 21.79. An F-test revealed a significant difference in the variances ($F = 1.59$, $v_1 = 153$, $v_2 = 104$, $P < 0.05$). A log (x+1) transformation equalised the variances ($F = 1.13$, $P > 0.05$), and a d-test found no significant difference in the mean intensity/infected male and female perch ($d = +0.75$, $P > 0.05$).

Further aspects of the effect of host sex on the infection are considered in the following section.

Effect of host age and length

The sample of perch fry aged 0+ (approximately 4-6 weeks, length 2.0 - 2.7 cm) was uninfected. In the perch aged 0++ (8-9 months, length 3.0 - 8.9 cm) the incidence of infection was 11.1% and the mean intensity/infected fish was 1.5 (maximum 3). In the fish aged 1++ - 4++ (length 9.0 - 11.9 cm) from the trawl sample, the incidence was 28.6%), and the mean intensity/infected fish was 4.8 (maximum 16) (Table III and IV).

The incidence of infection increased with age and length of the adult fish from the gill net samples (Table III and IV). However, in female fish the incidence increased steadily with length, while in male fish the incidence appeared to reach a peak in perch between 12.0 - 14.9 cm, and remained fairly constant thereafter (Table IV).

The results suggest that in female perch the mean intensity increased with host age and length. However, in male perch the mean

Fig. 2. Frequency distribution of <u>Camallanus lacustris</u> in adult male & female perch. Gill net samples. January 1975 - February 1976.

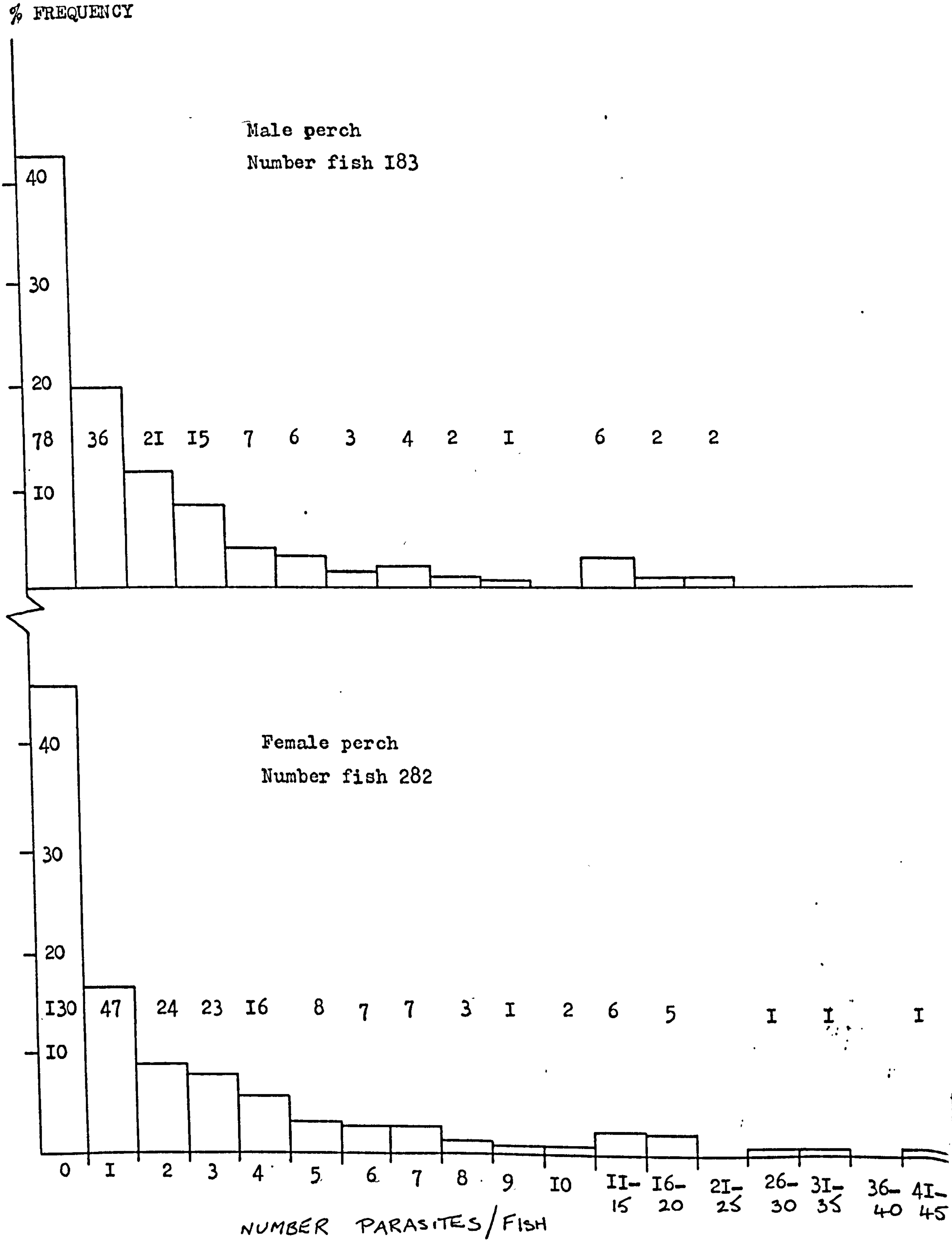


Table III. Effect of host age on the occurrence of <u>Camallanus lacustris</u>. Purse seine, trawl and gill net samples.

Age (yrs)	Number fish examined	% incidence	Mean intensity/ infected fish	Maximum
Purse seine sample July 1976				
0+	30	-		
Trawl sample March 1976				
0++	36	11.1	1.5	3
1++-4++	28	28.6	4.8	16
Gill net samples January 1975-February 1976				
Male Fish				
2-2++	2	50.0	(1.0)	(1)
3-3++	51	43.1	2.3	10
4-4++	66	57.6	4.3	23
5-5++	40	65.0	4.5	14
6-6++	16	68.8	4.0	18
≥7	8	87.5	4.4	8
Female Fish				
2-2++	2	-		
3-3++	87	35.6	3.3	15
4-4++	98	51.0	3.8	41
5-5++	38	68.4	5.2	27
6-6++	27	81.5	4.4	10
≥7	30	83.3	6.4	31

Table IV. Effect of host length on the occurrence of Camallanus lacustris. Purse seine, trawl and gill net samples.

Length (cm)	Number fish Examined	% incidence	Mean intensity/ infected fish	Maximum
Purse seine sample July 1976				
2.2-2.7	30	-		
Trawl sample March 1976				
3.0-8.9	36	11.1	1.5	3
9.0-11.9	28	28.6	4.8	16
Gill net samples January 1975 - February 1976				
Male Fish				
9.0-11.9	43	39.5	3.1	22
12.0-14.9	124	62.1	3.9	23
15.0-17.9	13	69.2	3.7	8
⩾ 18.0	3	66.7	(5.0)	(5)
Female Fish				
9.0-11.9	13	23.1	(1.0)	(1)
12.0-14.9	197	46.7	3.9	41
15.0-17.9	46	82.6	4.1	20
⩾ 18.0	26	84.6	7.6	31

intensity reached a peak in fish aged 4-4++ and length 12.0 - 14.9 cm, and then remained fairly constant (Table III and IV).

Nonetheless, it should be noted that relatively few large, old male perch were examined in this study.

In order to investigate the effects of host age further, the fish were divided into two age groups (2-4++ and $\geqslant 5$), and the sexes kept separate. The results are shown in Fig. 3 and Fig. 4. There was a fall in the zero class of the frequency distribution (indicating an increase in incidence) in the older age groups of both sexes (Fig. 3 and 4). However, whilst this fall was very highly significant in female fish ($X^2 = 26.08$, DF = 1, $P < 0.001$), in male fish the difference was significant, though not highly significant ($X^2 = 4.51$, DF = 1, $P < 0.05 > 0.01$).

In female perch there was a marked change in the nature of the frequency distribution with an increase in age (Fig. 4). This resulted in an increase in the mean intensity/infected fish and an increase in the occurrence of heavily infected fish. In male perch this change in the distribution pattern was not so marked, and the infection appeared similar in male fish of both age groups.

Distribution of Camallanus lacustris in the alimentary tract of perch

There were no marked seasonal trends in the distribution of larval, adult male or adult female (pre-larvigerous and larvigerous) worms in the alimentary tract of perch. Consequently the results of the 14 monthly samples of gill netted perch were summed.

C. lacustris was most abundant in intestine I and II, and to a lesser extent the pyloric caeca and intestine III (Fig. 5). Relatively few worms were found in the stomach and the more posterior regions of the intestine (Fig. 5). Larval, adult male and adult

Fig. 3. Effect of host age on the Camallanus lacustris infection. Gill net samples. January 1975 - February 1976. Male perch only.

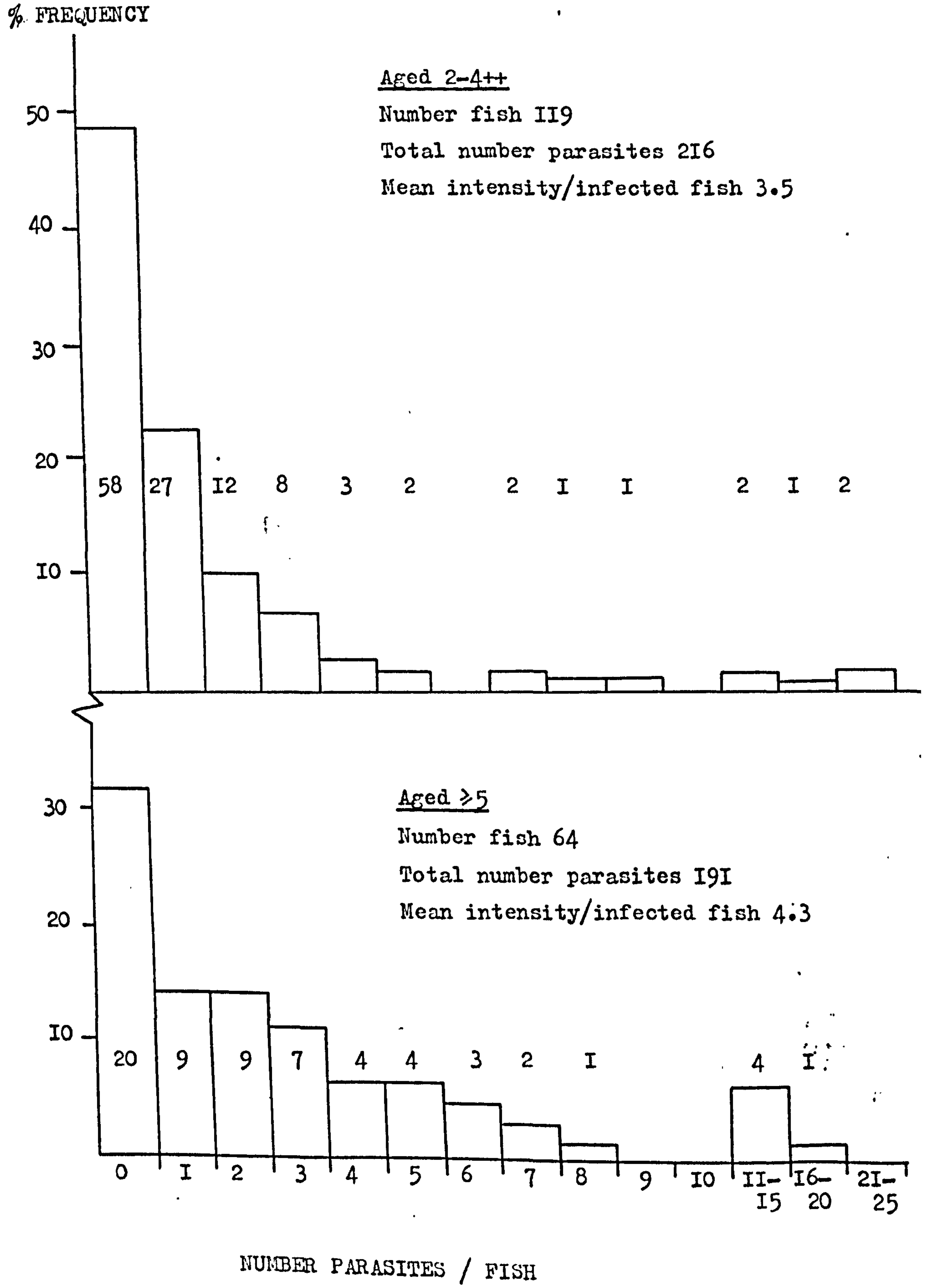


Fig. 4. Effect of host age on _Camallanus lacustris_ infection. Gill net samples. January 1975 - February 1976. Female perch only.

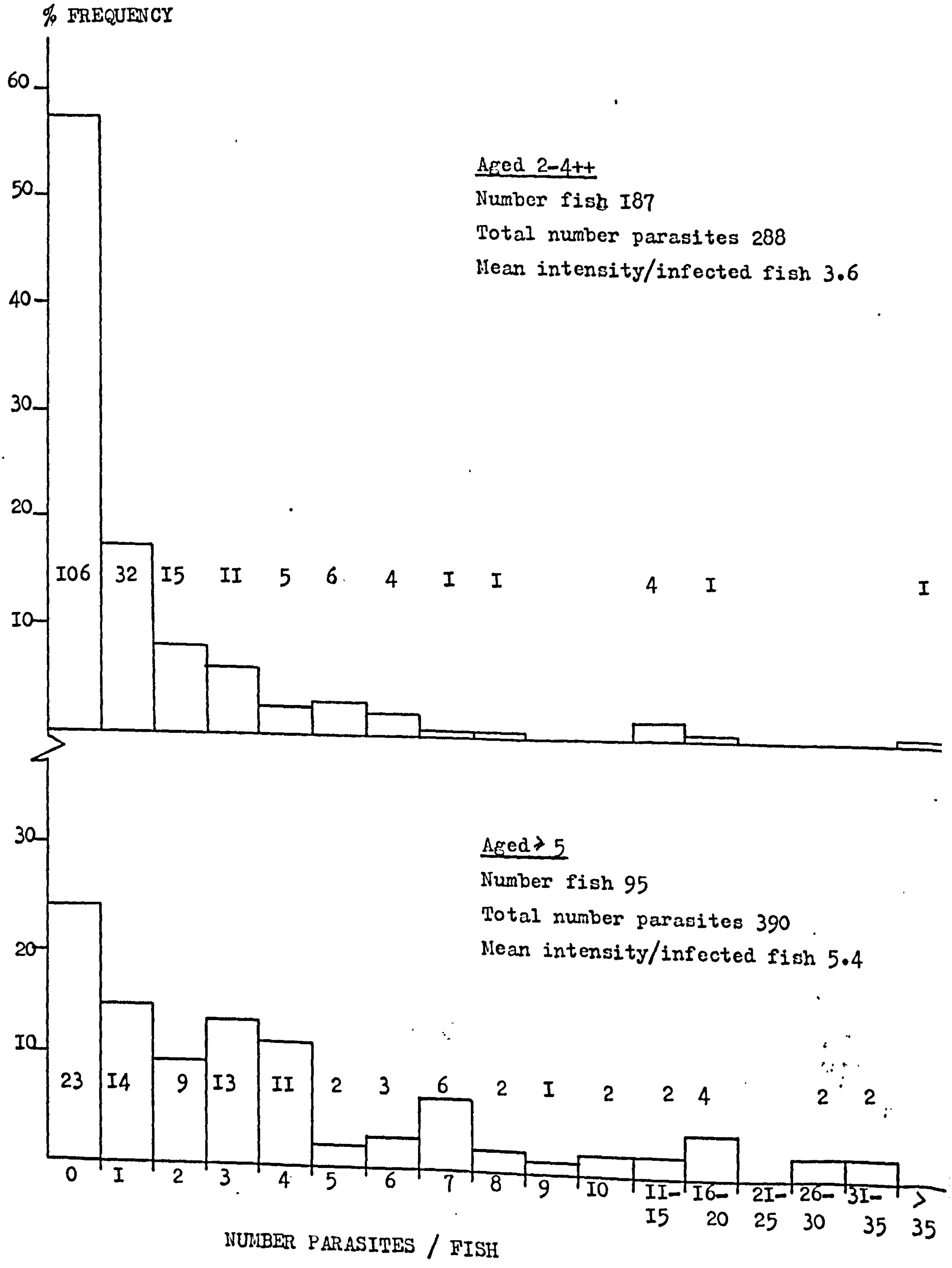


Fig. 5. Percentage distribution of *Camallanus lacustris* in intestinal tract of perch; ~~percentage~~ composition of parasite population at each site. Gill net samples. January 1975 - February 1976.

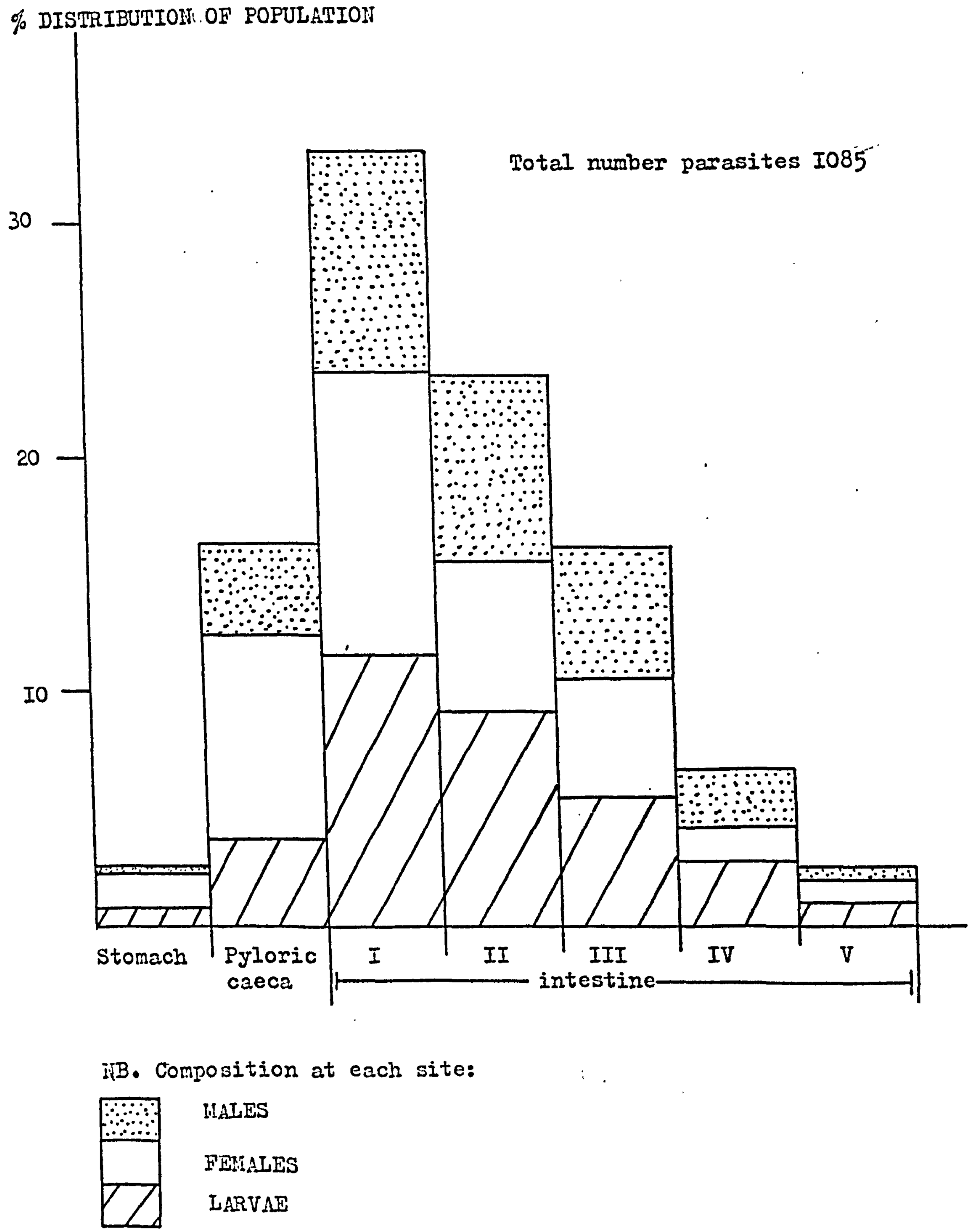


Fig. 6. Distribution of Camallanus lacustris in alimentary tract of perch at three levels of intensity. Gill net samples.

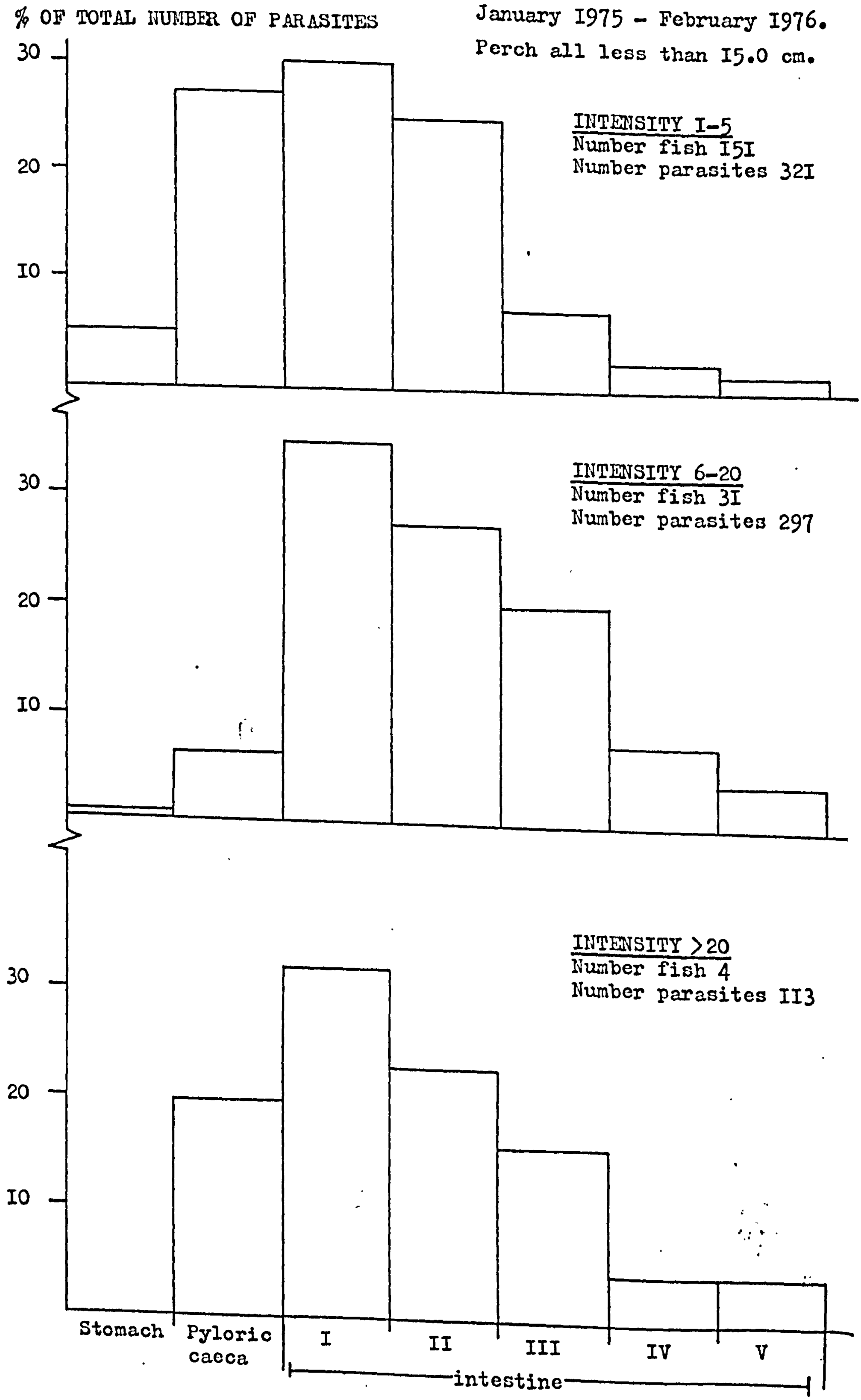


Fig. 7. Distribution of Camallanus lacustris in alimentary tract of perch at three levels of intensity. Gill net samples. January 1975 - February 1976. Perch all greater than or equal to 15.0 cm.

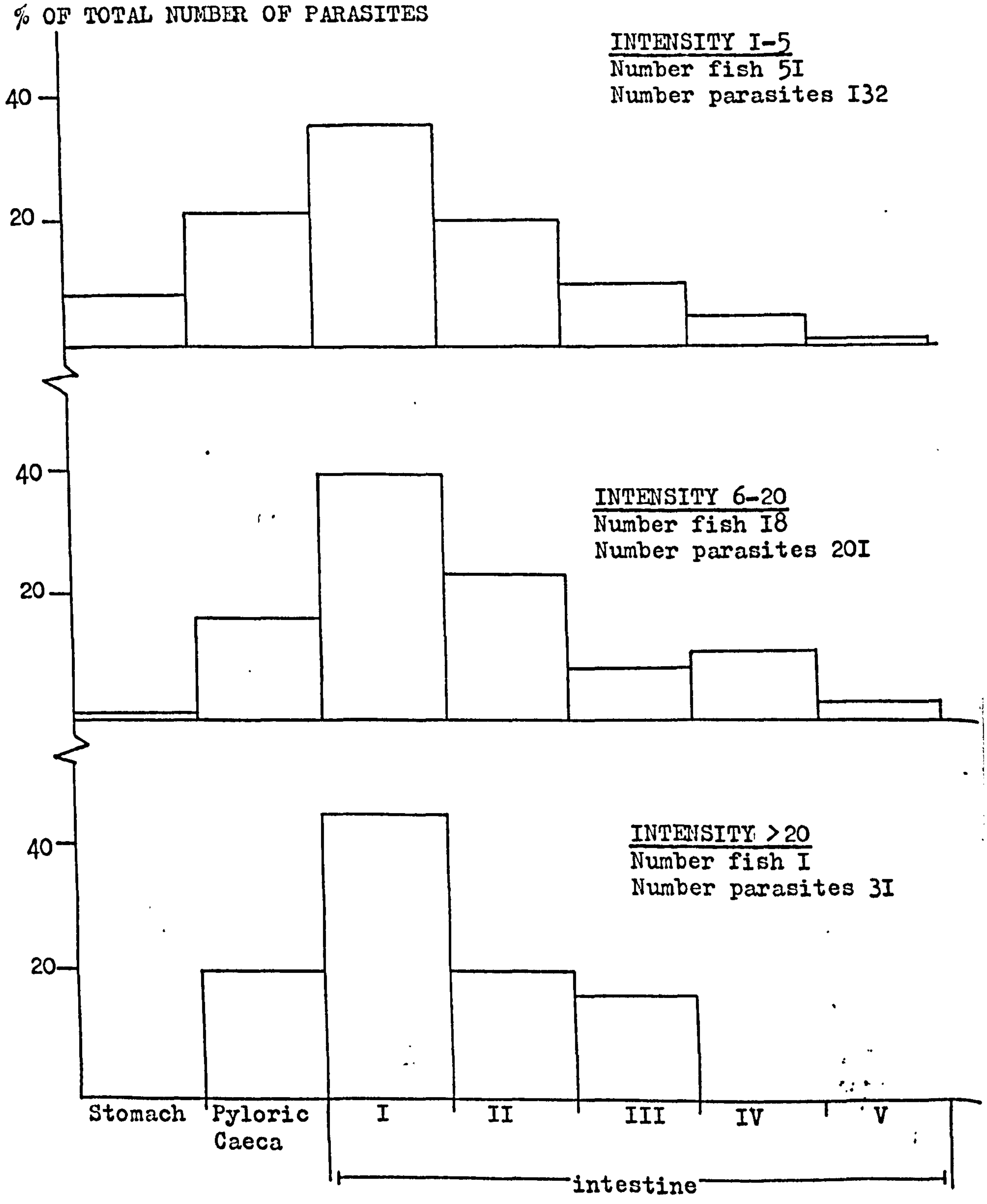
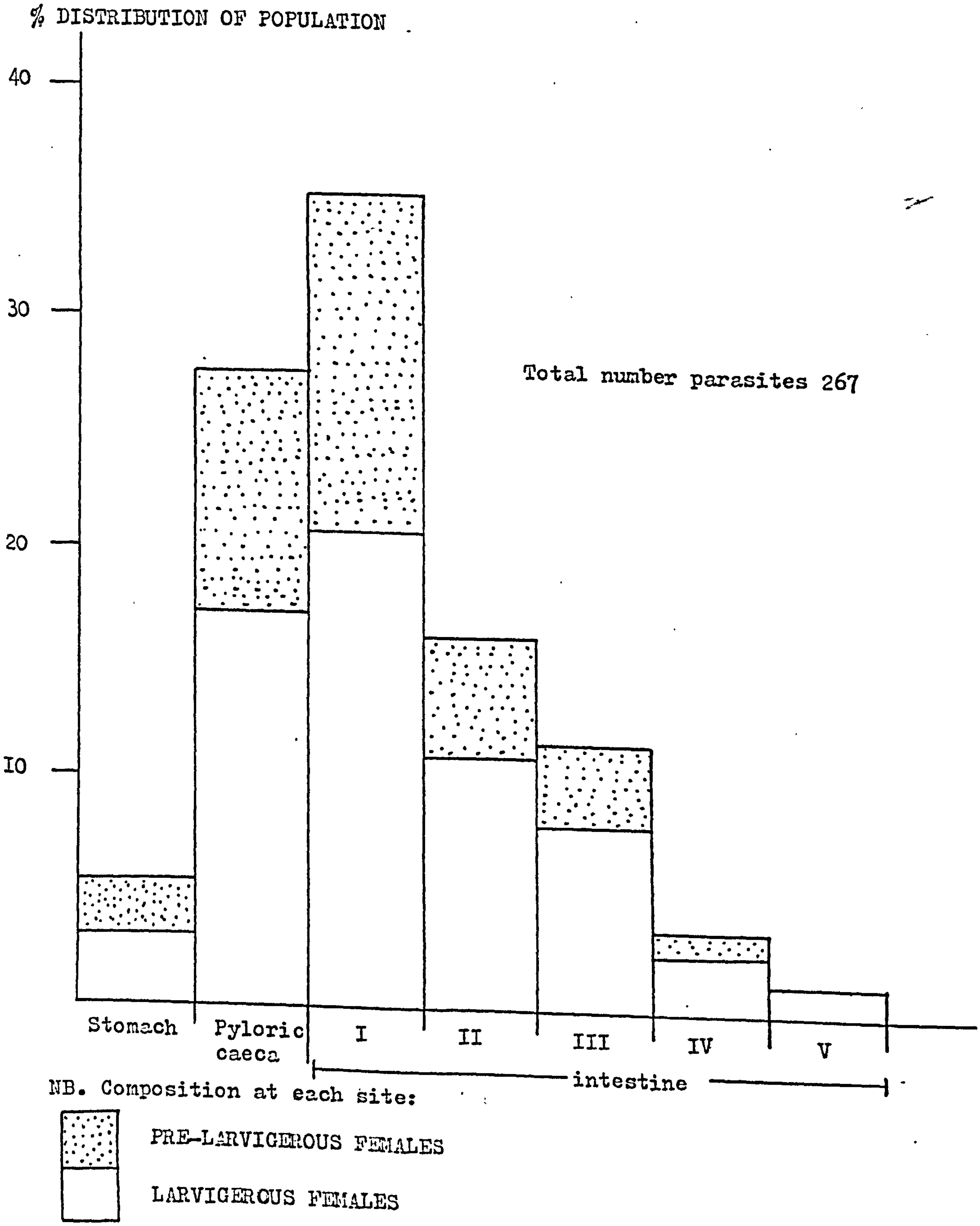


Fig. 8. Percentage distribution of female *Camallanus lacustris*; composition at each site. Gill net samples. June 1975 - February 1976.



female worms did not exhibit any differential preference for their site of occurrence, and the proportion of each stage at each alimentary site was approximately the same (Fig. 5). Larvigerous females were found throughout the alimentary tract, though none were found in the most posterior region of the intestine (Fig. 8). This may have been a reflection on the relatively few C. lacustris that were found at this site. The proportion of pre-larvigerous and larvigerous females at each alimentary site was approximately the same (Fig. 8).

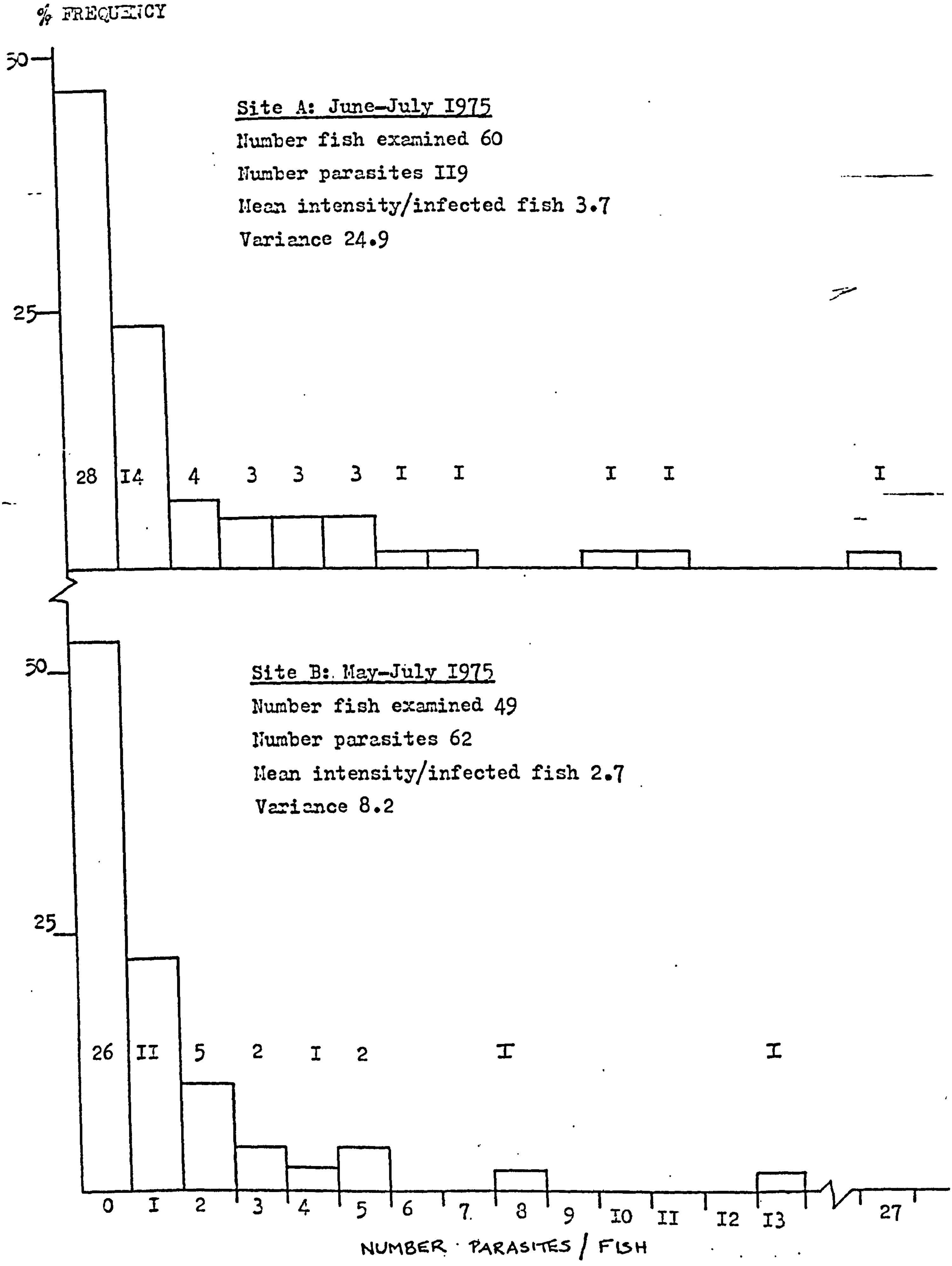
The influence of intensity of infection on the distribution of C. lacustris is shown in Fig. 6 and 7. To reduce any effects of host size, the perch were divided into two length groups: 9.0 - 14.9 cm and ⩾15.0 cm. The distribution of C. lacustris at three levels of intensity was calculated (Fig. 6 and 7). The distribution of the parasite was similar in fish of both length groups, and the distribution was not markedly effected by increasing levels of intensity. However, relatively few heavily infected fish (>20 parasites) were encountered. It is noted that in perch of length 9.0 - 14.9 cm at intensity 6-20 (Fig. 6), there was a smaller proportion (and absolute number) of parasites in the pyloric caeca. The significance of this results remains undetermined, since the proportion of parasites in the pyloric caeca of these perch at intensity >20 was similar to that at intensity 1-5 (Fig. 6). In addition, a similar result was not obtained in the larger perch at intensity 6-20 (Fig. 7).

Effect of site of capture in Llyn Tegid

Comparison of site A (6m) and site B (12m)

The infection at these two sites was compared during May-July 1975. The results are shown in Fig. 9, and suggest that the infection at the

Fig. 9. Occurrence of <u>Camallanus lacustris</u> at site A (6m) and site B (I2m). Gill net samples. May – July I975.



<u>Site A: June–July I975</u>
Number fish examined 60
Number parasites II9
Mean intensity/infected fish 3.7
Variance 24.9

<u>Site B: May–July I975</u>
Number fish examined 49
Number parasites 62
Mean intensity/infected fish 2.7
Variance 8.2

two sites was similar. At site A, 32 of 60 (53.5%) fish were infected, while at site B, 23 of 49 (46.9%) were infected. An F-test revealed a significant difference between the variance of the mean intensity/infected fish at each site ($F = 3.04$, $v_1 = 31$, $v_2 = 22$, $P < 0.05$). The parasite counts were transformed using a log(x+1) transformation, and the variances then found to be equal ($F = 1.50$, $P > 0.05$). Consequently, a t-test on the log (x+1) transformed counts found no significant difference in the mean intensity/infected fish at site A and site B ($t = 0.83$, $DF = 53$, $P > 0.05$).

Because of the low incidence of larval nematodes during the summer months, the effect of the seasonal migration of perch into shallow water on nematode recruitment could not be investigated. Nonetheless, during these months larval C. lacustris were found at both site A (6m) and site B (12m).

Comparison of site B (12m) with site D (12m)

The infection at these two sites was compared during the spring (February-April 1975) and the autumn-winter (October-December 1975). February-April. At site B 39 of 59 (66.1%) fish were infected, while at site D only 10 of 26 (38.5%) fish were infected. This result indicated a significant, though not highly significant, difference in the incidence of infection at each site ($X^2 = 4.57$, $DF = 1$, $P < 0.05 > 0.01$). The frequency distribution of the infection at each site is shown in Fig. 10. Whilst only relatively few fish were caught at site D during this period the overdispersed nature of the infection at both sites was clear. An F-test showed that there was no significant difference between the variance of the mean intensity/infected fish at each site ($F = 2.10$, $v_1 = 38$, $v_2 = 9$, $P > 0.05$). A t-test on the log (x+1) transformed parasite counts found no significant difference in the mean intensity/infected fish at site B and site D

Fig. 10. Occurrence of *Camallanus lacustris* at site B and site D (both 12m). Gill net samples. February 1975 - April 1975.

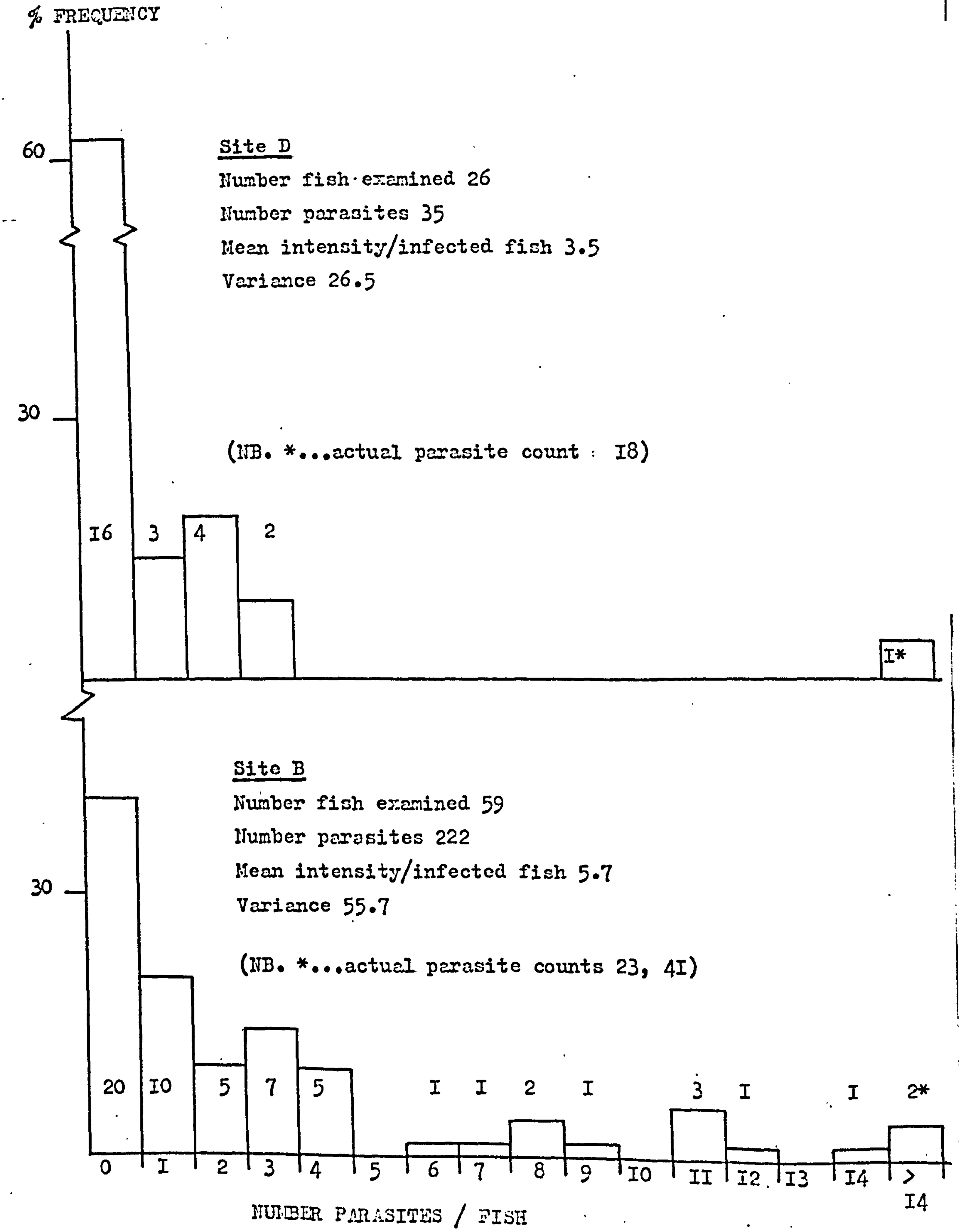
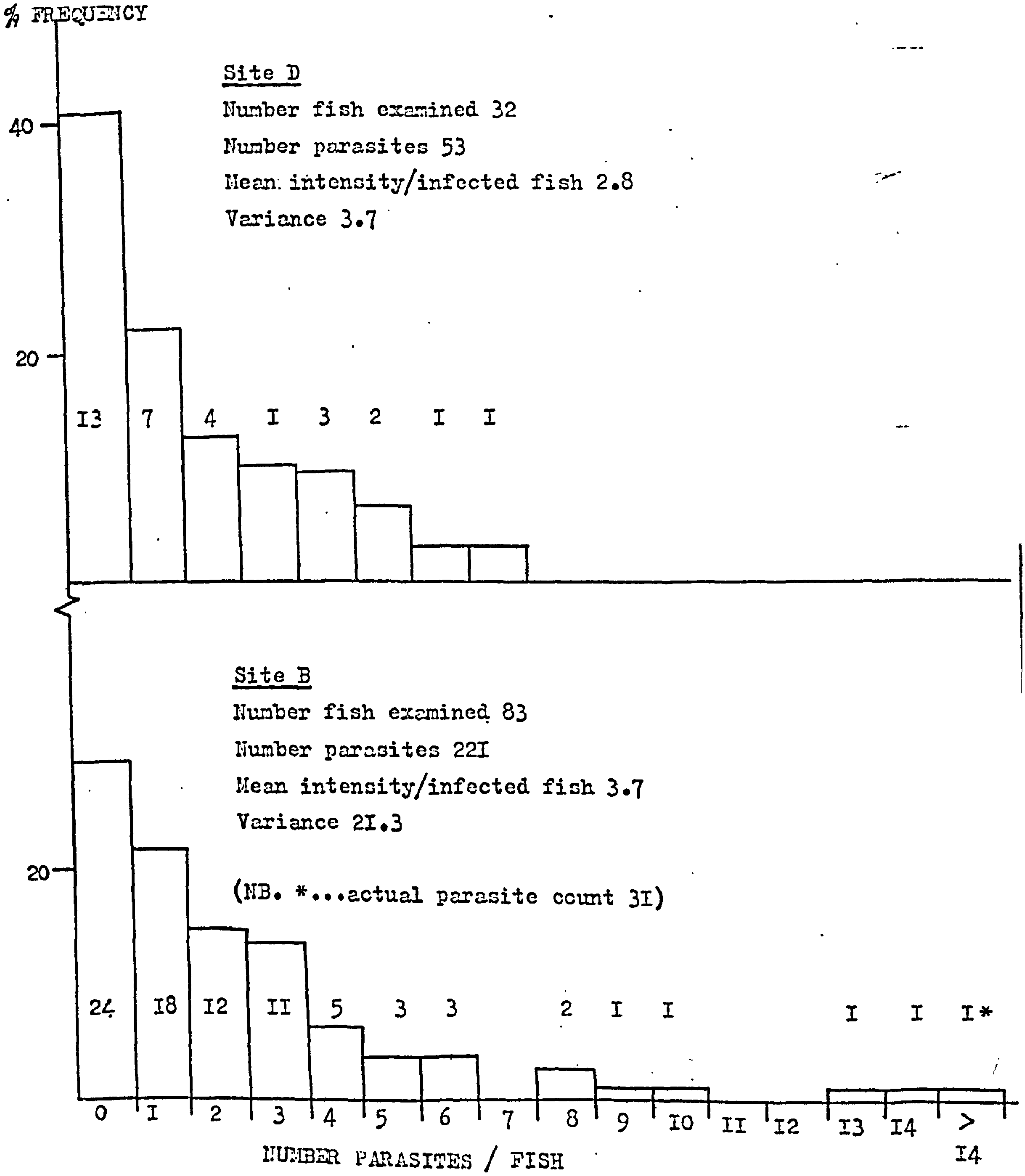


Fig. II. Occurrence of Camallanus lacustris at site B and site D (both I2m). Gill net samples. October 1975 - December 1975.



($t = 1.24$, DF = 47, $P > 0.05$).

October-December. At site B, 59 of 83 (71.1%) fish were infected, while at site D, 19 of 32 (59.4%) were infected. This result was not significant ($X^2 = 0.97$, DF = 1, $P > 0.05$). The frequency distribution of the infection at each site is shown in Fig. 11. The infection appeared similar at the two sites, though fewer heavily infected fish were caught at site D. This may have been a reflection of sampling deficiencies in relation to the overdispersed nature of the parasite distribution. An F-test found a significant difference between the variance of the mean intensity (infected fish at each site ($F = 5.80$, $v_1 = 52$, $v_2 = 18$, $P < 0.05$). Consequently, the variances were equalised by the use of a log (x+1) transformation ($F = 2.24$, $P > 0.05$) and a t-test found no significant difference in the mean intensity/infected fish at each site ($t = 0.70$, DF = 76, $P > 0.05$).

IX.I.4 DISCUSSION

Camallanus lacustris is mainly a parasite of perch-like fish, though it has been frequently recorded from members of the Anguillidae, Esocidae, Gadidae, Gacterosteidae, Pleuronectidae, Salmonidae, and Siluridae, and to a lesser extent from the Cyprinidae (Moravec, 1971). Kennedy (1974) reviewed the occurrence of this parasite in the freshwater fish of the British Isles, and its occurrence in the fish of the River Dee System was summarised by Chubb (1976). The records of this parasite from perch (Perca fluviatilis) in the British Isles were given in Chapter IV, Table I.

Whilst this parasite may occur in a range of piscine hosts, perch can be considered as the principal definitive host (Moravec, 1971).

The results from the present study found that *C. lacustris* was a relatively common parasite of perch at Llyn Tegid, though no other fish species has been found infected (Chubb, 1963a; 1976). Mishra (1966) and Mishra & Chubb (1969) performed the only other detailed study on this parasite in the British Isles. At the Shropshire Union Canal (Cheshire) perch and pike (*Esox lucius*) were infected, though the incidence and mean intensity of the infection was much higher in perch (Mishra & Chubb, 1969). There have been a number of continental European studies on this parasite. For example, Barysheva & Bauer (1957) recorded *C. lacustris* from nine species of fish (including two varieties of *Coregonus lavaratus*) from Lake Ladoga (U.S.S.R.). The parasite was most prevalent in perch, though catfish (*Siluris glanis*), ruffe (*Gymnocephalus cernua* and burlot (*Lota lota*) also harboured a high incidence and mean intensity of infection. Nagibina (1957) recorded *C. lacustris* from several species of fish from Lakes Onega and Konchezero (U.S.S.R.), though the "most seriously infected" host was always perch. Kozicka (1959) found *C. lacustris* in the alimentary tract of perch, pike-perch (*Lucioperca luciperca*), ruffe and rudd (*Scardinius erythrophthalmus*) from Lake Druzno (Poland). Whilst perch was the most heavily invaded fish, the parasite was also recorded from one year old cyprinid fry. Rauckis (1970a, b) studied the infection of perch and pike at Lake Dusia (U.S.S.R.). Perch was the most heavily infected fish (see later). Tell (1971) studied the parasite fauna of the predatory fish perch, pike, pike-perch and burbot from Lake Võrtzjarv (U.S.S.R.). *C. lacustris* was found in all four species, though the incidence of infection varied as follows: perch (74.0%), pike-perch (52.5%), burbot (50.0%) and pike (35.0%). The maximum intensity of infection (60) was recorded from perch. In comparison to these observations it is of interest to note the findings of Wootten (1973), who studied the parasite fauna of the fish of Hanningfield Reservoir (Essex). Perch and ruffe both commonly occurred in the lake, though *C. lacustris* was only recorded from 50% of 181 perch (with a maximum intensity of 2). In addition, the parasite was also recorded from 25.0% of 4 eels (*Anguilla anguilla*), with an intensity of 3.

The life cycle of *C. lacustris* has been studied by Kupriyanova (1954), Campana-Rouget (1961) and Moravec (1969a, b, c). First stage larvae were shed by female worms and developed through two moults into infective third stage larvae in a number of cyclopoid copepods (including *Cyclops strenuus*). Calanoid copepods, cladocerans, and a variety of other freshwater arthropods and molluscs were all unsuitable intermediate hosts (Kupriyanova, 1954; Moravec, 1969a). In suitable cyclopoid copepods infective third stage larvae occurred in the haemocoel after 12 days post invasion (Moravec, 1969a). When eaten by a fish the development of the larvae may follow one of three courses (Moravec, 1969b). In predatory fish of the Percidae, Esocidae, Gadidae, Salmonidae and Siluridae the development of the larva proceeds normally. In perch, the third stage larva moulted after 13-15 days post invasion (Moravec, 1969a). Worms destined to become males moulted for the last time after 35 days, while prospective female worms took 65-69 days to reach their final moult. Females were found with first stage larvae in their uterus three months after their initial invasion by third stage larvae (Moravec, 1969a). In non-predatory fish such as certain members of the Cyprinidae, development did not proceed beyond the third stage larva (Moravec, 1969b). In predatory cyprinids (e.g. chub, *Leuciscus cephalus*), Moravec (1969b) found that development continued as normal, but at a slower rate. Thus cyprinid fish may form a reservoir of infection, and pass on the parasites to larger predatory fish when eaten. In addition, the accumulation of infective larvae in small forage fish provides contact between the nematodes and frogs, turtles and snakes which do not normally feed on copepods (Stromberg & Crites, 1974a). Ergens (1966) considered that the parasite fauna of pike at Lipno Reservoir (Czechoslovakia) was influenced by the parasite fauna of its prey fish, who acted as reservoir hosts to certain parasites. Mishra & Chubb (1969) suggested that pike acquired *C. lacustris* and *Bunodera luciopercae* (Digenea) from the ingestion of infected perch at Shropshire Union Canal (Cheshire) (see later).

Copepod (intermediate host) - fish (definitive host) life cycles have been reported for a number of other camallanid nematodes, including *Spirocamallanus fulvidraconis* (Li, 1935), *S. cearensis* (Pereira *et al.* 1936), *Paracamallanus sweeti* (Moorthy, 1938), and *Camallanus oxycephalus* (Stromberg & Crites, 1974b). The existence of additional piscine intermediate hosts or transport hosts has been suggested in a number of these life cycles. Pereira *et al.* (1936) considered that the characin *Curimatus elegans* was a transport host for *S. cearensis*. Development in *C. elegans* continued to the fourth stage larva, but did not proceed further. However, completion of the life cycle from copepod to definitive host was not attempted. Moorthy (1938) believed that small planktivorous fish carrying the third stage larvae of *P. sweeti* were true intermediate hosts, since some larval development occurred. Moorthy considered that most of the worms reached the definitive host (snake-head, *Ophiocephalus gachua*) through them feeding on infected forage fish, Lepidocephalichthys thermalis. C. oxycephalus developed to maturity in some species of fish, but did not develop beyond fourth stage larvae in the alimentary tract of others (Stromberg & Crites, 1974b, 1975). Stromberg & Crites (1974b) considered that the life cycle of C. oxycephalus may be completed either directly from the copepod intermediate host, or from the copepod, through a forage fish transport host, to the definitive host. In addition, Crites (1976) found that C. oxycephalus larvae penetrated through the intestinal wall of freshwater drum (Aplodinotus grunniens) from Lake Erie (North America) and became encapsulated amongst the mesenteries. This was suggested as an alternative pathway to the life cycle of C. oxycephalus, which may lead to the infection of predatory fish (Crites, 1976).

Such alternative pathways are relatively common in the life histories of parasitic nematodes. For example, Moravec (1970a, b) studied the life history of Raphidascaris acus. The definitive hosts were predatory fish (e.g. pike, trout Salmo trutta), from which female nematodes liberated eggs into the external environment. Invertebrates (e.g. Chironomidae larvae) and various fish (e.g. bullhead Cottus gobio, loach Noemacheilus barbatulus) ingested either the eggs containing second stage larvae, or free-swimming larvae that had hatched from the eggs. In invertebrates, the larvae entered the haemocoel where they grew but did not moult for a second time (Moravec, 1970a). When infected invertebrates, or eggs or free-swimming larvae, were eaten by a suitable fish intermediary, the larvae penetrated the intestinal wall and entered the liver or became encapsulated amongst the viscera. Here the nematode moulted for the second time, and developed into infective third stage larvae (Moravec, 1970a). The definitive host became infected when fish intermediaries containing infective larvae were eaten (Moravec, 1970a, b). In addition, Sprent (1953, 1955, 1959, 1962, 1963 a, b, 1970a, b, c; etc) and Sprent & McKeown (1967) studied the life history and development of certain ascaridoid nematodes of pythons (Pythonidae). The results indicated that the life history pattern of many of these parasites exhibited a considerable degree of flexibility. Sprent (1962, 1963b, 1970a) considered that the term "life-pyramid" was more suitable than "life-cycle" when considering the development of these nematodes. The pyramid possessed a broad base, where a range of invertebrate and vertebrate host may ingest the eggs. Here the second stage larva may develop and exist for an indefinite period of time, though without further development. These animals may be ingested by a range of other animals, and the second stage larva may survive for a succession of predatory episodes. Eventually an animal (usually mammal or bird) is reached where further development may occur. The specificity of the pyramid becomes narrower, as the requirements of the third stage larva were more strigent than for the survival of the preceeding stage. The requirements for sexual differentiation and maturation exhibited the highest degree of specificity, and may only be met by genera within the Pythonidae (<u>Python</u>, <u>Liasis</u>, <u>Morelia</u>, etc.) (Sprent, 1970a). Returning to the camallanid nematodes of fish, it is also interesting to note that <u>Camallanus cotti</u> may survive for three generations in the absence of a copepod intermediary. However, transfers past the third generation were unsuccessful (Stumpp, 1975).

At Llyn Tegid perch acquired the infection of <u>C. lacustris</u> during their first year in the lake. However, the incidence and mean (and maximum) intensity of infection in perch aged 0++ (8-9 months) was low. The absence of <u>C. lacustris</u> from perch fry aged 0+ (4-6 weeks) may have been a result of the relatively small number of fish examined. However, recruitment into adult perch (see later) appeared reduced at this time of the year, and the fry examined were feeding on Cladocera (see Chapter III), which are not satisfactory intermediate hosts to C. lacustris (Kupriyanova, 1954; Moravec, 1969a).

The results indicated that there was an increase in the incidence of infection with increasing host age and length, in adult fish of both sexes. However, relatively few male perch over 14.9 cm were examined. In female perch the mean intensity increased with host age and length, and when these fish were divided into two age groups (2-4++, $\geqslant 5$), there was a greater occurrence of heavily infected fish amongst the older female perch. In male perch the mean intensity reached a peak in fish aged 4-4++, and length 12.0 - 14.9 cm. It then appeared to remain fairly constant in older, larger male perch. Once again it is important to stress that only relatively small numbers of older, larger male fish were examined. When the male perch were divided into the above two age groups there was no marked increase in the number of heavily infected, older fish, and the infection appeared similar in both age groups.

Plankton feeding was most prevalent in smaller, younger perch (see Chapter III), and cyclopoid copepods were not often recorded from the stomachs of perch aged over 5 years. Thus in perch aged 5 years or less, the number of copepods eaten increased as the fish grew older and larger. This increased the chances of infection, and resulted in a rise in the incidence and intensity. However, whilst C. lacustris has lived for 14 months in laboratory perch (Chubb, pers. comm.), it is considered that this parasite does not accumulate with age (as, for example, with the long-lived Diplostomum gasterostei (Digenea), Chapter VII). The occurrence of this nematode in a particular age/length group of perch was seen as a reflection of their intensity of copepod ingestion, in relation to the constant turn-over of parasites (see later).

The incidence of infection (and in female fish the intensity too) continued to increase in fish that had effectively ceased plankton feeding. Since *C. lacustris* was only recorded from perch at Llyn Tegid (Chubb, 1963a, 1976), and since perch aged 6 years or above are known to be cannibalistic, larger older perch must have acquired their infection from smaller plantivorous perch eaten as prey. This phenomenon has been discussed in relation to the *Bunodera luciopercae* infection in Chapter VII. However, in older male perch the intensity of the *C. lacustris* infection did not increase to the same extent as in female perch. Therefore this result may have been influenced by a number of factors, including the small number of older male perch examined, or the fact that male perch may have ingested fewer infected perch than female fish. However, fish of both sexes exhibited cannibalistic tendencies (see Chapter III). In addition, older male perch may be physiologically more resistent, or less physiologically suited to heavily infestations, or might have suffered a selective mortality. The epizootiological factors that influenced the infection in older male perch require further investigation.

The infestation of adult perch at Llyn Tegid was overdispersed. The factors influencing overdispersion in parasite populations were discussed in Chapter VII (re. *Diplostomum gasterostei* and *Bunodera luciopercae* (Digenea)) and in Chapter VIII (re. *Triaenophorus nodulosus* (Cestoda)).

At Llyn Tegid the mean intensity of infection was fairly low (especially in small, young perch), and few heavily infected fish were encountered. The *C. lacustris* infection did not induce any marked adverse effects on the perch at Llyn Tegid, though the possibility of increased mortality of heavily infected older male fish was noted. However, camallanid nematodes are known to the pathogenic in some species of tropical fish (Schbert, 1972, 1976; Petter et al. 1974; Stumpp, 1975; Dulin, 1977). The parasites take a plug of host alimentary tract into their buccal capsule, and the mucosa may become completely destroyed (Petter et al., 1974). These camallanids feed on blood and inter-cellular fluids, and even relatively light infestations with these large nematodes may lead to the death of small piscine hosts (Petter et al., 1974; Stumpp, 1975; Dulin, 1977). The intensity of infection of young of the year perch at Llyn Tegid was low.

C. lacustris was found throughout the alimentary tract of perch, but occurred predominantly in the pyloric caeca and intestine I-III. This distribution was not influenced by any seasonal factors, or by increasing levels of intensity (up to >20 parasites per fish). Larval, adult male and adult pre-larvigerous and larvigerous female worms did not exhibit any site preference (seasonal or otherwise), and the proportion of each stage at each site was approximately the same. Stromberg & Crites (1975) found that C. oxycephalus showed a marked seasonal maturational migration within the intestine of white bass (Morone chrysops). In July when the new generation of worms entered the fish, the parasites were found along the entire length of the intestinal tract. During this time, third and fourth stage larva occurred in the intestine, and adults in the rectum. Shortly thereafter the adult parasites were lost and the population was restricted to the intestine. By August a maturational migration had begun, which resulted in the worm population inhabiting the rectum by October.

Here they remained until their death the following July. During April and May female C. oxycephalus were seen protruding from the rectum of infected fish. No such migration was seen within the intestine of perch at Llyn Tegid, and larvigerous female C. lacustris were found at all sites in the alimentary tract during all months of the year. Inter-specific relationships within the intestinal helminth fauna of perch at Llyn Tegid are discussed in Chapter XI.

At Llyn Tegid the incidence and mean intensity of the infection of perch did not exhibit any marked seasonal changes. Mishra (1966) noted a similar lack of seasonality in perch from the Shropshire Union Canal (Cheshire). Rauckis (1970a, b) examined small numbers of perch and pike from Lake Dusia (U.S.S.R.). The incidence and range of intensity was: perch; January-March, 100.0%, 1-31; April-May, 76.9%. 1-14; June-July, 60.0%, 1-26; October-November, 93.3%, 1-48; pike; January-March, 54.5%, 1-5; April-May, 31.2%, 1-8; June-July, 74.4%, 1-4; October-November, 46.6%, 1-9. It is important not to place too much emphasis on the seasonal aspects of this study, since only 58 perch and 57 pike were examined. Nonetheless, C. lacustris was present in perch and pike during all seasons with apparently no marked seasonal changes in incidence or intensity. In contrast, Ergens (1966) reported the pronounced seasonal occurrence of C. lacustris in 181 pike from the Lipno Reservoir (Czechoslovakia), that were examined over a period of three years. The incidence and intensity of infection reached a minimum each winter, and a maximum each summer. Izyumova (1960) (cited by Ergens, 1966) found similar results from the Rybinsk Reservoir (U.S.S.R.).

Since small perch were found infected at Llyn Tegid during the whole year, recruitment of C. lacustris into larger, cannibalistic perch may have occurred at anytime. However, this was most likely to have occurred during July-September 1975 and December-February 1975/76, when small peaks in cannibalism were observed (see Chapter III).

Recruitment into smaller perch was determined by the availability of infective plankton, and the feeding habits of the fish.

The seasonal cycle of some cyclopoid copepods (e.g. *Cyclops strenuus strenuus*) may be variable (Young, 1974), though studies in the British Isles have found that nauplii, copepodid and adult stages of this species were present for the whole year, with a mid-winter minimum (Elbourn, 1966; Young, 1974). At Llyn Tegid, Thomas (1959) found that *C. strennuus abyssorum* (= *C. abysorrum*, Mills, in prep.) was present for the whole year, with a monocyclic breeding cycle. Reproduction took place in the late summer and autumn, with some females remaining ovigerous until the early January. Adult copepods were found in most months, though this species appeared to overwinter primarily as nauplii. Copepodites were present from March to July, with adults most abundant from June-July to October-November (Thomas, 1959). It should be noted that Thomas based these observations on samples that consisted of three vertical hauls at a single site (35-40m) in Llyn Tegid. Approximately two samples per month were taken during late 1954 until mid-1956. In addition, Mills (in prep) has also recorded *Cyclops agilis*, *C. agilis v. speratus*, *C. albidus* and *C. viridis* from Llyn Tegid.

First stage larval *C. lacustris* may have been liberated during much of the year (see below), and can survive for 80 days at 7°C (Moravec, 1969a). This, along with the fact that cyclopoid copepoda were thought to be available for the whole year, may indicate that the availability of infective plankton was not restricted to a particular season. Nonetheless, the rate of recruitment into perch would depend on the relative intensity of ingestion of cyclopoids and the incidence of infective third stage larvae contained therein.

Cyclopoid copepods were not dominant plankton in the diet of perch at Llyn Tegid, though they were apparently ingested in all months (except March, 1975) (see Chapter III). However there was a peak in cyclopoid ingestion in September and appreciable numbers of these crustaceans were thought to have been eaten during the winter (October onwards) of 1975/76. Whilst the availability of third stage larval C. lacustris in the plankton was not determined, it is likely that recruitment occurred at all times of the year. Third and fourth stage larval nematodes were found in perch during all months of the year, though their presence was not necessarily indicative of recent recruitment. The transition from third stage larva to adult worm at 20-25°C took 35 days in males and 65-69 days in females (Moravec, 1969a), and may take even longer at lower temperatures. The occurrence of larval worms varied from month to month, and it is not known whether these changes were a result of actual recruitment of third stage larvae, the loss of larval worms because of their failure to establish or their moulting to adult worms, or perhaps sampling deficiencies. Nonetheless, it is interesting to note that the occurrence of larval nematodes was low during some months (e.g. September) when the ingestion of cyclopoid copepods was prevalent. This may have indicated a spatial or temporal separation of the fish from infective copepods.

Stromberg & Crites (1975) found that recruitment of C. oxycephalus into whitebass at Lake Erie (North America) was restricted to July-August. This was probably a reflection on the marked seasonal release of first stage larvae by this parasite, in relation to the feeding habits of the fish. Stromberg & Crites stated that while there was little change in the incidence of infection during the year, there was a marked decrease in mean intensity between July and the following June. The infection increased rapidly in July, but a net loss of worms occurred as early as September. The results suggested that the *C. oxycephalus* population remained fairly stable in fish with a mean summer intensity of 10 worms or less. Stromberg & Crites (1975) considered that a density dependent mechanism (related to host size) might have regulated the size of the nematode population in fish harbouring more than 10 worms. The relatively high intensity during the months when recruitment was in progress, followed by a gradual decline in the intensity once recruitment has ceased, suggests that during the summer months the infection was in a dynamic state (with input and output of worms from the system). Similar conditions have been noted on several occasions with reference to the parasitic infestations of fish (e.g. Hopkins, 1959; Chubb, 1963b; Chubb *et al.*, 1964; Kennedy, 1968; Hine & Kennedy, 1974b; etc.), and this was discussed in relation to the *Bunodera luciopercae* infection of perch in Chapter VII. A similar dynamic condition may have existed in the *C. lacustris* infection, since recruitment may have occurred in most months, yet the incidence and mean intensity of infection remained constant.

Spall & Summerfelt (1969) found that in the fish from Lake Carl Blackwell (North America), the sex ratio of *C. oxycephalus* favoured females, and suggested that this might have been the result of a differential or earlier mortality of male worms. At Lake Erie, the sex ratio of *C. oxycephalus* was 2:1 in favour of males during August, but changed to 1:1 by September. The sex ratio then remained 1:1 until the following July, when it returned briefly to 2:1 before all the old worms died (Stromberg & Crites, 1975). This was attributed to the difference in the timing of the final moult between the sexes, since male nematodes moult ahead of females (Stromberg & Crites, 1974b, 1975). Therefore, male nematodes were recruited into the adult population ahead of females, and this produced the initial sex ratio of 2:1. When all the larvae had moulted for the last time, the ratio became 1:1. The following summer when the females died before males, the ratio returned briefly to 2:1 (Stromberg & Crites, 1975). Stromberg & Crites considered that the male persistence over the winter served to maximise the probability that all females were mated.

Bykhovskaya-Pavlovskaya (1940) and Mishra (1966) both noted that the sex ratio of C. lacustris favoured females. However, Mishra (1966) reported that during certain months (December, January), the number of male worms slightly exceeded the number of females. A somewhat similar difference in the sex ratio was observed at Llyn Tegid. During the autumn to spring period of October-May (excluding March 1975), there was a 1:1 sex ratio. However, during March and June-September 1975, the sex ratio markedly favoured females. The interpretation of these results proved difficult, and was complicated by the suggested dynamic condition with the nematode population (with recruitment and loss of worms in most months), and the fact that male C. lacustris moult for the last time considerably in advance of females (Moravec, 1969a), the relative timing of which may be influenced by seasonal changes in temperature.

A critical point in the life history of any parasite is the contact of suitable host(s) by infective agents (Stromberg & Crites, 1974a). Such contact may be influenced by climatic conditions, and may be favoured by the production of prodigious numbers of young, and/or the timing of the release of dispersal stages to coincide with an abundance of intermediate hosts. Stromberg & Crites went on to consider the reproduction strategies of camallanid nematodes in tropical and temperature climates. They suggested that large numbers of young were produced and released continously by tropical species, for the entire reproductive life of the female. Since populations of copepods in tropical regions do not fluctuate on a markedly seasonal basis, reproduction in tropical camallanids may continue throughout the year with a high likelihood that some larvae will complete the life cycle (Stromberg & Crites, 1974a). However, in temperate regions where copepod populations often fluctuate seasonally, the continuous production of larvae would be a waste of resources, since the chances of contacting a suitable intermediate host during most of the year would be small (Stromberg & Crites, 1974a).

In Lake Erie (North America), Stromberg & Crites (1975) found a marked seasonal cycle of development in C. oxycephalus infecting white bass. Copulation occurred in October-November, and sperm cells were carried through the winter. Fertilisation occurred in April. Larvae began to appear by mid-June, and the uterus was completely filled with first stage larvae by late June. There was a synchronous release of larvae (through the prolapsed uterus of the adult female) during late June-early July. This coincided with the maximum abundance of cyclopoid copepods at Lake Erie (Stromberg & Crites, 1975). Spall & Summerfelt (1969) found a similar developmental cycle of C. oxycephalus in Lake Carl Blackwell (North America), in channel catfish (Ictalurus punctatus) and white crappie (Pomoxis annularis).

With the exception of C. oxycephalus and C. lacustris there have been few seasonal studies on the occurrence and maturation of camallanid nematodes in temperate regions. Tornquist (1931) noted seasonal cycle similar to that observed for *C. oxycephalus* by Spall & Summerfelt (1969) and Stromberg & Crites (1975), in *C. lacustris* in Sweden. Infection of fish occurred in the summer, and growth and maturation followed in the autumn and winter. Larvae accumulated in the female nematodes during the spring, and were expelled during the summer. Subsequently the female worms perished. Mishra (1966) studied the *C. lacustris* infection of perch at Shropshire Union Canal. He found that female worms containing larvae were present in all seasons of the year, though the proportion was lowest in January-March (13.1% of 11 female worms) and highest in October-December (65.3% of 36 female worms). Mishra (1966) considered that apart from a late spring-early summer rise in larval discharge, *C. lacustris* exhibited no seasonal cycle of development. In accordance with these observations, Wierzbicki (1970) reported that different developmental stages of *C. lacustris* in perch at Lake Dargin (Poland) showed "nearly equal abundance" in all seasons of the year. Malahova (1961) (cited by Wierzbicki, 1970) found similar results in the U.S.S.R.

At Llyn Tegid larvigerous female *C. lacustris* were present in all months, this may be taken to indicate larval release during the whole year. However, since larvigerous females did not exhibit any marked cycle of occurrence, laboratory observations are required to elucidate this phenomenon. Stromberg & Crites (1974a) stated that many camallanid nematodes from temperate regions may have large body volumes when compared to tropical species, and that this may permit the storage of large numbers of larvae in the former. Between June-February 1975/76 detailed observations were made on the occurrence of larvigerous female *C. lacustris* at Llyn Tegid. There was a marked fall in their occurrence in August, though it is not known whether this was a result of an actual loss of larvigerous (or post-larvigerous) worms in late July, or a sampling deficiency. Over the autumn-winter (from October), the occurrence of larvigerous females steadily fell, and reached a minimum in January. This may have been produced by a loss of larvigerous (or post-larvigerous) females at the end of their reproductive life, perhaps in relation to the cessation in development of pre-larvigerous females. Stromberg & Crites (1975) found that growth of female *C. oxycephalus* was arrested between November-April at Lake Erie.

Let us briefly summarise some of the above information concerning the biology of *C. lacustris*. The incidence and mean intensity at Llyn Tegid did not exhibit any marked seasonal changes. First stage larvae may have been liberated during all months of the year, though a decline in the occurrence of larvigerous females indicated that this liberation may have been restricted during the mid-winter. This is in general agreement with the suggestions of Stromberg & Crites (1974a) concerning the reproductive strategies of camallanid nematodes. However, the seasonal development of *C. lacustris* is not always as marked as that reported from the North American *C. oxycephalus*. The developmental cycle of *C. lacustris* may vary from locality to locality (e.g. compare Tornquist, 1931 to Mishra, 1966; Wierzbicki, 1970; present study), which is likely to reflect seasonal variations in prevailing ecological conditions at each locality, and/or seasonal variations in recruitment of the parasite. Many authors (e.g. Dogiel, 1958, 1962; Bauer, 1959; Hopkins, 1959; Chubb, 1964, 1967, 1977; Walkey, 1967; Tedla & Fernando, 1970; etc.) have suggested that seasonal variations in temperature may produce the observed seasonal maturation of many parasites in temperate regions. Nonetheless, the nature of the seasonal cycle of maturation is likely to be influenced by the species of parasite, the degree of local seasonal temperature changes and perhaps other factors. The restriction of recruitment of

C. lacustris to a particular time of year (either by the availability of infective larvae, or host feeding habits) might also result in the appearance of a maturation cycle (Walkey, 1967; Tedla & Fernando, 1970). The environmental influences on the development of *C. lacustris* require further investigation, with additional field and laboratory studies.

Since cyclopoid copepods were available and ingested during the whole year, recruitment at Llyn Tegid was not restricted to a particular season. However, the rate of recruitment was likely to have varied on a seasonal basis, dependent on the intensity of cyclopoid ingestion in relation to the incidence of infective third stage larvae. Nonetheless, recruitment was low during some months when cyclopoid ingestion was prevalent.

The infection of perch with *C. lacustris* was compared at two 12m sites at the south-west end of Llyn Tegid, during February-April and October-December (1975). In both instances the mean intensity/infected fish was similar at both sites, though during the former period there was a significantly lower incidence at site D. During October-December the incidence at the two sites was similar. The low incidence at site D during February-April may have been a reflection on the small number of fish examined.

Wierzbicki (1971) found that *C. lacustris* prevailed in the shallow regions of Lake Dargin, where the mean intensity was higher than from the littoral and deep water regions. At Llyn Tegid, the incidence and intensity of infection of *C. lacustris* was compared at a 6m and 12m site during May-July 1975. Third and fourth stage larval nematodes occurred at both sites, and the overall infection was very similar. Spall & Summerfelt (1969) reported that the incidence of infection of *C. oxycephalus* from shallow and deep water sites at Lake Carl

Blackwell was not significantly different.

IX.I.5.

SUMMARY

The life history of C. lacustris at Llyn Tegid involved a copepod intermediate host and perch as the sole definitive host. C. lacustris has not been recorded from pike in Llyn Tegid. Small perch acquired the infection from infected copepods, while larger perch became infected as a result of their cannibalistic feeding habits.

The parasite population was overdispersed, though very heavily infected fish were relatively uncommon.

Perch acquired the infection during their first year in the lake. The incidence and intensity of infection increased with host age and length. The infection was similar in adult fish of both sexes, though further studies are required to elucidate the factors influencing the infection in older male perch.

There was no marked seasonal change in the incidence and intensity of infection. Seasonal changes in the dynamics of the infection were discussed; the release of first stage larvae and recruitment was thought to have occurred in most months. The factors influencing the rate of recruitment were considered.

C. lacustris occurred within the pyloric caeca and anterior intestine of perch, and to a lesser extent the stomach and posterior intestine. Larval male and female (pre-larvigerous and larvigerous) worms did not exhibit any form of differential site preference.

The effect of site of capture of the perch in Llyn Tegid on the infection was investigated, and no marked differences found.

IX.2. FAMILY Cucullanidae Cobbold, 1864

GENUS Cucullanus Müller, 1777

Cucullanus truttae (Fabricius, 1794)

IX.2.1 INTRODUCTION

Cucullanus truttae is an oviparous nematode of wide occurrence in salmonoid and other fish in the British Isles (Kennedy, 1974; Chubb, 1976). At Llyn Tegid it has been recorded from pike (Esox lucius) and eel (Anguilla anguilla) (Chubb, 1963a). Stranack (1966) has previously recorded this parasite from perch (Perca fluviatilis) from the Rivers Avon, Itchen and Test (Hampshire).

IX.2.2 OBSERVATIONS

Two male and two female (with ova) C. truttae were found in the lumen of the pyloric caeca of a single female perch gill netted in October 1975. The fish was 23.2cm long and aged 8+ yrs.

DISCUSSION

Within the family Cucullanidae it has not yet been established whether the definitive host becomes infected by directly ingesting eggs, or via an intermediate host (Janiszewska, 1970). Whilst either method of transmission may have resulted in the infection of the perch, it is possible that this large fish became infected by the ingestion of an infected prey fish. Pike and eel are known to harbour the infection at Llyn Tegid, though trout (Salmo trutta) have not been found infected (Chubb, 1963a; 1976).

IX.2.3 SUMMARY

This is a new host record for Llyn Tegid, though perch is unlikely to be of any biological significance to this parasite.

IX.3. FAMILY Anisakidae Skryabin and Karokhin, 1945

GENUS Raphidascaris Ralliet and Henry, 1915

Raphidascaris cristata (Linstow, 1872)

IX.3.1 INTRODUCTION

According to Davies (1967) Raphidascaris cristata and the North American R. canadensis Smedley, 1933 may be synonyms of R. acus (Bloch, 1779). R. acus is distributed throughout the entire Palaearctic region, in Europe (including British Isles, not Ireland) and Asia (Kane, 1966; Moravec, 1971). With the exception of the original description of R. cristata by Linstow (1872), all records of this species have been from the British Isles. Chubb (1976) accepted the views of Davies (1967) concerning the synonymy of R. cristata with R. acus, and provided a review of the occurrence of these nematodes in the fish of the British Isles. In addition, Rawson (1952) recorded undetermined Raphidascaris sp. from Shropshire Union Canal and Lake Windermere, and Kennedy et al. (1975) reported R. cristata from the River Stour. The records of Raphidascaris nematodes in perch from the British Isles were provided in Chapter IV, Table I. Rauckis (1970a) and Tell (1971) have studied the R. acus infection of perch in continental European waters.

The life history and development of R. acus has been investigated by several workers, including Mozgovoi and Kosinova (1963), Engashev (1964; 1965a, b, c, d; 1966; 1969), Kosinova (1965), Kosinova and Mozgovoi (1965), Davies (1967, 1968) and Moravec (1970a, b).

The pathogenicity of the infection of fish with juvenile R. acus has been described by Osmanov (1953) (in Petrushevskii and Shulman, 1958) and Bauer and Zmerlaja (1972, 1973).

IX.3.2 RESULTS

Raphidascaris cristata was not recorded from the trawl and purse seine samples of fish. From the gill net samples of 465 perch taken between January 1975-February 1976, 21 fish (4.5%) were infected with a total of 31 parasites. The mean intensity/infected fish was 1.5 (maximum 4). The mean intensity/fish was < 1. The frequency distribution of the infection is shown in Fig. 12. The majority of the infected fish harboured one worm.

Site of occurrence in perch

The worms were found encapsulated in the intestinal wall, and amongst the nearby mesenteries. The small, flattened capsules were opaque yellow-white in colour, with the nematode visible inside. The capsules usually contained one parasite. The maximum number of parasites/capsule was two. Over 60.0% of the 31 parasites were found associated with the wall (and mesenteries) of the posterior intestine (intestine V) (Table V).

Seasonal occurrence

The results from the gill net samples are shown in Table VI. These results suggest that there was a seasonal change in the incidence of the infection, with R. cristata present during January-March 1975 and September-February 1975/76. Only one fish was infected during April-August 1975 (Table VI). The mean intensity/infected fish fluctuated between 1.0-2.7.

When the changes in incidence were analysed statistically (Table VII), the results indicated that there was a highly significant difference in the incidence of infection in January-March 1975 and September-February 1975/76, when compared to April-August 1975 ($X^2=8.11$, $P < 0.01$, Table VII).

Effect of host sex, age and length.

Fourteen (7.7%) of 183 male perch were infected with R. cristata, while 7 (2.5%) of 282 female perch harboured the infection. The mean intensity/infected male and female perch was 1.6 and 1.1 respectively

Fig. 12 . Frequency distribution of Raphidascaris cristata. Gill net samples. January 1975-February 1976.

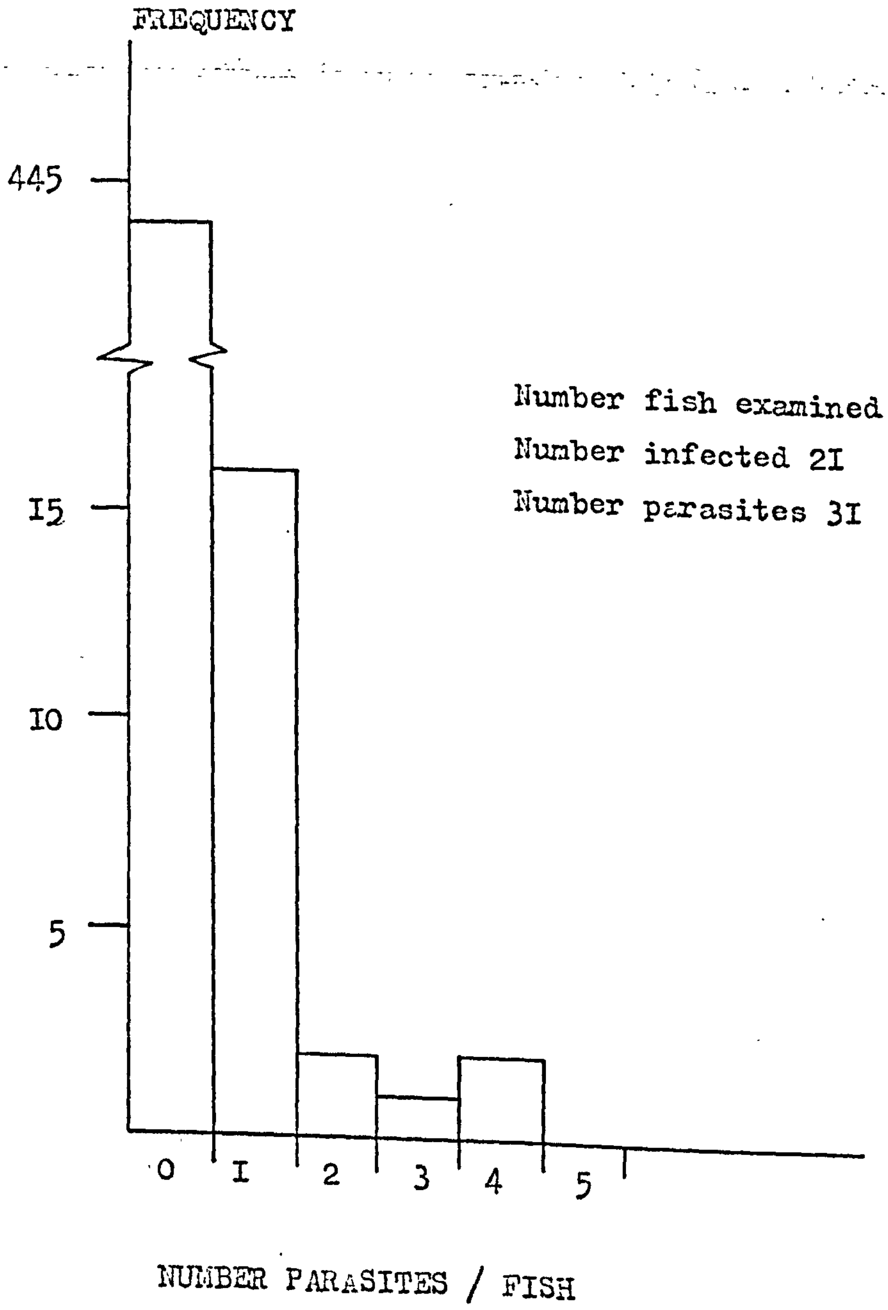


Table V. Site of occurrence of Raphidescaris cristata in perch. Gill net samples. January 1975-February 1976.

SITE	NUMBER PARASITES	% OF TOTAL
INTESTINE II	1	3.2
INTESTINE III	3	9.7
INTESTINE IV	8	25.8
INTESTINE V	19	61.3
TOTAL	31	

Table VI. Seasonal Occurrence of Raphidascaris cristata. Gill net samples. January 1975-February 1976.

MONTH	NUMBER FISH		%	NUMBER	MEAN/INFECTED	MAX.
	EXAMINED	INFECTED	INCIDENCE	PARASITES	FISH	
J	6	1	16.7	2	(2.0)	2
F	30	4	13.3	4	1.0	1
M	30	2	6.7	2	1.0	1
A	30	0				
M	30	0				
J	39	0				
J	40	1	2.5	1	(1.0)	1
A	30	0				
S	30	1	3.3	2	(2.0)	2
O	60	3	5.0	8	2.7	4
N	54	4	7.4	7	1.8	4
D	35	2	5.7	2	1.0	1
J	30	1	3.3	1	(1.0)	1
F	21	2	9.5	2	1.0	1
TOTAL	465	21	4.5	31	1.5	4

Table VII. Analysis of seasonal occurrence of _Raphidascaris cristata_ by 2 x 2 contingency table (Elliot, 1971). Gill net samples. January 1975-February 1976.

	Raphidascaris cristata Number fish infected	_Raphidascaris cristata_ Number fish uninfected	Total
January-March 1975 September-February 1975/6	20	276	296
April-August 1975	1	168	169
Total	21	444	n = 465

$$X^2 = 8.11 \ (df = 1)$$

$$P < 0.01 > 0.001$$

Table VIII. Effect of host age and sex on the occurrence of <u>Raphidascaris cristata</u>. Gill net samples. January 1975-February 1976.

AGE (yrs.)	NUMBER FISH		%	NUMBER	MEAN/INFECTED	MAX.
	EXAMINED	INFECTED	INCIDENCE	PARASITES	FISH	
MALES						
2-2++	2	-				
3-3++	51	2	3.9	5	2.5	4
4-4++	66	7	10.6	8	1.1	2
5-5++	40	4	10.0	9	2.3	4
6-6++	16	1	6.3	1	(1.0)	(1)
	8	-				
TOTAL	183	14	7.7	23	1.6	4
FEMALES						
2-2++	2	-				
3-3++	87	1	1.1	1	(1.0)	(1)
4-4++	98	4	4.1	5	1.3	2
5-5++	38	-				
6-6++	27	2	7.4	2	1.0	1
	30	-				
TOTAL	282	7	2.5	8	1.1	2

Table IX. Analysis of effect of host sex on the occurrence of <u>Raphidascaris cristata</u> using 2 x 2 contingency table (Elliot, 1971). Gill net samples. January 1975 - February 1976.

	<u>Raphidascaris cristata</u> Number fish infected	 uninfected	Total
Male	14	169	183
Female	7	275	282
Total	21	444	n = 465

$X^2 = 5.73$ (df = 1)

$P < 0.05 > 0.01$

Table X. Effect of host length on occurrence of Raphidascaris cristata. Gill net samples. January 1975-February 1976.

LENGTH (cm)	NUMBER FISH EXAMINED	NUMBER FISH INFECTED	% INCIDENCE	NUMBER PARASITES	MEAN/INFECTED FISH
9.0-11.9	377	20	5.3	30	1.5
$\geqslant$ 15.0	88	1	1.1	1	(1.0)
TOTAL	465	21	4.5	31	1.5

(N.B. Analysis by 2 x 2 contingency table (Elliot, 1971): $X^2 = 1.99$, $df = 1$, $P > 0.05$).

Table XI. Effect of site of capture on occurrence of Raphidascaris cristata. Gill net samples. January 1975-February 1976.

	NUMBER FISH EXAMINED	NUMBER FISH INFECTED	% INCIDENCE	NUMBER PARASITES	MEAN/INFECTED FISH
Site A (6m)	115	4	3.4	6	1.5
Site B (12m)	260	13	5.0	19	1.5
Site C (18m)	21	-			
Site D (12m)	69	4	5.8	6	1.5
TOTAL	465	21	4.5	31	1.5

(Table VIII). The influence of host sex on the incidence of infection was analysed statistically (Table IX). The results of this analysis suggest that there was a significant (though not highly significant) difference in the incidence in male and female perch (X^2=5.73, $P < 0.05$ > 0.01, Table IX).

Adult perch of a range of ages and sizes were infected (Table VIII and X). The incidence of infection in perch aged 3-3++ was lower than that in most other age groups, though few perch aged 2-2++ and > 6 were examined. When the perch of both sexes were divided into two length groups (Table X), there was found to be no significant difference in the incidence of infection in perch 9.0-11.9cm when compared to perch $\geqslant$15.0cm (X^2=1.99, $P > 0.05$, Table X).

Effect of site of capture in Llyn Tegid

There was no marked variation in the incidence and mean intensity/infected fish at sites A, B and D. Whilst the infection was apparently absent from site C, only 21 perch were examined from this depth (Table XI).

IX.3.3 DISCUSSION

Nematodes identified as *R. cristata* were first recorded from Llyn Tegid by Chubb (1961, 1963a), though the likelihood of synonymy of this species with *R. acus* has been noted.

The life history and development of *R. acus* was most recently studied by Moravec (1970a, b). In common with the life history of some other parasitic nematodes (see section X.14), the life history of *R. acus* may follow more than one pattern. The adult parasite lives in the pyloric caeca and intestine of certain predatory fish (including pike *Esox lucius*, brown trout *Salmo trutta*, and rainbow trout *S. gairdneri*). Eggs are released into the water with definitive host faeces. The eggs or newly hatched second stage larvae may be eaten by a range of freshwater invertebrates, though larval Chironomidae were found to be the most suitable hosts (Moravec, 1970a). Within the body cavity of the chironomid larvae, and perhaps certain other invertebrates, the larval nematodes increased slightly in size but did not develop further (Moravec, 1970a, b). The invertebrates form a reservoir of infection from which the intermediate hosts may become infected. The intermediate hosts of R. acus may be any one of a range of small fish, including bullhead (Cottus gobio, sculpin (Cottus poecilopus) and loach (Noemachielus barbatulus) (Moravec, 1970a, b). As well as acquiring the parasite from infected invertebrate reservoir hosts, these fish may become infected by the ingestion of eggs or free swimming (second stage) larvae of R. acus. Within these fish the second stage larvae became encapsulated in the intestinal wall, mesenteries or the liver (Moravec, 1970a). The larvae then grow and moulted to third stage infective juveniles. The definitive host becomes infected by the ingestion of infected piscine intermediaries. The completion of the life cycle was impossible without the intervention of a fish intermediate host (Moravec, 1970a). Thomas (1937) studied the life cycle of R. canadensis and found that the definitive host (pike) became infected by feeding on fish (minnows Phoxinus spp., perch, Perca flavescens), harbouring nematodes encapsulated in the mesenteries and liver. The fish intermediate hosts became infected by feeding on eggs containing second stage larvae.

At Llyn Tegid adult R. cristata have been recorded from eel Anguilla anguilla and brown trout,while juvenile nematodes have been found in the intestinal lumen of perch (Chubb, 1976). In this present study only encapsulated juvenile nematodes were found. Perch may acquire the infection either by the direct ingestion of parasite eggs or free second stage larvae, or via an infected invertebrate reservoir host. Benthic invertebrates (e.g. chironomid larvae) are important items in the diet of perch at certain times of the year (Chapter III), and may be a source of infection. Encapsulated juvenile nematodes have only been recorded from perch at Llyn Tegid, though the parasite fauna of other possible intermediate hosts (e.g. bullhead, loach) has not been examined in detail.

The results suggest that there may have been a relationship between the incidence of the infection in male and female perch, and the seasonal occurrence of this parasite. The incidence was very low during April-August 1975, and this result was highly significant when compared to the incidence during January-March 1975 and September-February 1975/76. However, whilst more female perch were examined during the first part of this study, the sex ratio approached 1:1 during September-February 1975/76 (see Chapter III). The lower incidence of infection in female fish may reflect undetermined differences in the biology, or physiological susceptability to infection, in male and female perch. However, this result may also be influenced by the fact that more females were examined during April-August, when there was a very low incidence of infection. In addition, whilst the seasonal occurrence of R. cristata may represent a real change in the level of infection in the perch population, the fall in the incidence during April-August may have been produced by the greater number of female fish (perhaps with a lower incidence of infection) that were examined during that period. Clearly this aspect of the infection of perch with R. cristata requires further investigation. Moravec (1970b) found that juvenile R. acus were present in bullhead and sculpin throughout the year at the River Bystřice (Czechoslovakia). Nonetheless, it is interesting to note that Davies (1967), who studied the seasonal occurrence of encapsulated juvenile R. acus in roach (Rutilus rutilus), chub (Leuciscus cephalus) and dace (Leuciscus leuciscus) at the River Lugg (Hereford), found a slight decrease in the incidence of infection in all three fish species during the summer months.

Because of the small sample sizes the occurrence of R. cristata in perch aged 2-2++ (or less) requires further study. Within the samples of adult gill netted perch, fish at a range of ages and sizes harboured the infection. There was no marked increase in the incidence or intensity of infection with host age and size. Davies (1967) found that juvenile R. acus either died, or were killed, after a period of encapsulation in a cyprinid intermediate host, while Moravec (1970a) reported that these nematodes may live for at least 153 days in the liver of loach. The life span of R. cristata in perch is not known. However, even if long-lived, the accumulation of this parasite with host age/size may have been precluded by the low incidence of infection making successive superimposed infections unlikely.

Bearing in mind that perch were not caught in equal numbers at all sites in Llyn Tegid at all times of the year, there were no marked differences in the infection at sites A (6m), B (12m) and D (12m). Few perch were examined from site C (18m). Moravec (1970b) found that brown trout in the lower reaches of the River Bystřice (Czechoslovakia) carried a much higher intensity of infection than in the trout zone of the river. This was attributed to variations in the infestation of the piscine intermediate hosts at each locality (Moravec, 1970b).

IX.3.4 SUMMARY

Encapsulated, juvenile R. cristata were recorded from Llyn Tegid for the first time, from the intestinal wall and mesenteries of perch.

The incidence and mean intensity/infected fish was low. Male fish had a significantly higher incidence of infection than female fish, which was discussed in relation to an apparent seasonal change in the incidence of infection.

Whilst the infection was absent from perch aged 2-2++ (or less), fish of a range of ages older than this harboured the parasite. There was no marked change in the incidence and mean intensity/infected fish with increasing age and length of adult gill netted perch.

There was no marked variation in the incidence or mean intensity/infected fish at sites A, B and D. The infection was apparently absent from site C.

The likelihood of synonymy of R. cristata with R. acus was briefly noted.

References

The references to chapter IX are listed at the end of chapter XI.

CHAPTER X

THE ACANTHOCEPHALAN PARASITE OF PERCH (*Perca fluviatilis* L.) FROM LLYN TEGID

A single species of acanthocephalan was found infecting perch at Llyn Tegid: *Acanthocephalus clavula*.

Family Echinorhynchidae (Cobbold, 1879) Hamann, 1892

Genus *Acanthocephalus* Koelretuer, 1771

Acanthocephalus clavula (Dujardin, 1845)

X.1 INTRODUCTION

Nicholas (1967, 1973) reviewed the literature on the biology of the Acanthocephala. Rojanapaibul (1977) studied the life history and biology of *Acanthocephalus clavula* at Llyn Tegid, and provided a review of the relevant literature.

The name *Echinorhynchus clavula* (Dujardin, 1845, nec Hamann, 1892) has been used for two quite distinct spceies. The name was originally given to the species at Rennes (France) by Dujardin (1845). Subsequently Lühe (1911) used the same name for another species which he mistakenly identified as *E. clavula*. Several authors accepted Lühe's interpretation. Petrochenko (1956) used Lühe's description of *E. clavula* Duj., 1845, and furthermore he transferred the species to the genus *Pseudoechinorhynchus* nov. gen. Grabda-Kazubska & Chubb (1968) regarded *E. clavula* sensu Lühe, 1911 to be *Echinorhynchus borealis* Linstow, 1901. In addition, they demonstrated that *E. clavula* Duj., 1845 belonged to the genus *Acanthocephalus* Koelreuter, 1771. In summary, *A. clavula* (Duj., 1845) Grabda-Kazubska & Chubb, 1968 has the synonym: *Echinorhynchus clavula* Duj., 1845, and *Pseudoechinorhynchus clavula* (Duj., 1845) Petrochenko, 1958 (all from Rojanapaibul, 1977).

X.2 ADDITIONAL MATERIALS AND METHODS

A proportion of the *Acanthocephalus clavula* that were recovered from the alimentary tract of perch were fixed and stained as described in Chapter II, and examined at low and high power. The majority were dissected in tapwater without fixation or staining, and divided into the following categories with the aid of a dissecting (binocular) microscope: males, females with ovarian balls only, and females with shelled acanthors. Three female parasites were considered spent because of the presence of small numbers of ovarian balls and shelled acanthors in the otherwise depleted body cavity of large adult worms.

X.3 RESULTS

Out of 465 perch that were gill netted between January 1975 - February 1976, 141 (30.3%) were infected. The mean intensity/infected fish was 3.7 (maximum 35), while the mean intensity/fish was 1.1 From the trawl sample of 64 perch taken in March, 1976, 17 (26.6%) were infected with a mean intensity/infected fish of 2.2 (maximum 7). The mean intensity/fish was <1. None of the purse seined sample of perch fry examined in July 1976 were infected.

Seasonal aspects of the infection

The incidence and mean intensity/infected fish showed marked seasonal variations (Table I). The absence of the infection from the January 1975 sample, may be a reflection on the small number (6) of fish examined that month (Table I). During February-March 1975 the incidence rose, and reached a peak in April-May 1975. From June 1975 onwards the incidence fell and reached 13.3% in August 1975 (Table 1). Between September-November 1975 the incidence fluctuated between 20.0-23.3%, before reaching a minimum of 2.9% in December 1975. During January and February 1976 the incidence of the infection began to rise (Table I).

The mean intensity/infected fish followed a similar pattern.

Table I. Seasonal occurrence of Acanthocephalus clavula. Gill net samples. January 1975 - February 1976

Month	Number fish examined	% incidence	Number parasites	Mean/infected Fish	Maximum
J	6	-			
F	30	20.0	13	2.2	6
M	30	50.0	38	2.5	11
A	30	90.0	132	4.9	14
M	30	83.3	154	6.2	22
J	39	33.3	36	2.8	8
J	40	22.5	53	5.9	35
A	30	13.3	4	1.0	1
S	30	23.3	11	1.6	4
O	60	20.0	27	2.3	6
N	54	20.4	30	2.7	5
D	35	2.9	1	(1.0)	1
J	30	13.3	4	1.0	1
F	21	33.3	12	1.7	3
TOTAL	465	30.3	515	3.7	35

There was a spring-summer peak in April-May 1975, though the mean intensity remained low for the remainder of the year. The significance of the small autumn-winter peak of mean intensity in October-November 1975 remains undetermined (Table I). The high value of mean intensity in July 1975 was the result of a single heavily infected fish harbouring 35 A. clavula (Table I).

The seasonal changes and the frequency distribution are illustrated in Fig. 1. During April-May 1975 the incidence and intensity of infection was high, and heavily infected fish were relatively common. During the remainder of the study period, the incidence and intensity of infection was much lower and, with the exception of a single perch harbouring 35 A. clavula taken in July, heavily infected fish were absent (Fig. 1).

The monthly totals of male and female worms are given in Table II. With the exception of August-October 1975 and January 1976, female A. clavula out numbered males. Over the 14 month period a total of 216 males and 299 females were recovered, a result which was very highly significantly different from a 1:1 ratio ($X^2 = 13.70$, DF = 1, $P < 0.001$). Inspection of the monthly totals in Table II suggested that during March-June females markedly outnumbered males, though during the remaining months this was not so. During March-June 148 male and 212 female A. clavula were recovered, which indicated a very highly significant difference from a 1:1 ratio ($X^2 = 11.37$, DF = 1, $P < 0.001$). During February 1975 and July-February 1975/76, 68 male and 87 female worms were present. This result did not significantly differ from a 1:1 ratio ($X^2 = 2.33$, DF = 1, $P > 0.05$).

There was a marked spring-summer peak of shelled acanthor production in April-June 1975 (Table II). Female worms containing

Table II. Seasonal changes in sex ratio and maturation of *Acanthocephalus clavula*. Gill net samples. January 1975-February 1976

Month	Number parasites			Females with shelled acanthors	
	Total	Male	Female	Number	Percent
J	-				
F	13	5	8	1	12.5
M	38	12	26	5	19.2
A	132	56	76*	17	22.4
M	154	69	85	39	45.8
J	36	11	25*	11	44.0
J	53	22	31	2	6.5
A	4	3	1	-	
S	11	6	5	-	
O	27	14	13*	1	7.7
N	30	11	19	2	10.5
D	1	-	1	-	
J	4	2	2	-	
F	12	5	7	-	
Total	515	216	299	78	26.1

N.B. * A single spent female *A. clavula* was observed in April, June and October 1975 shelled acanthors were absent during August, September and December 1975, and January, February 1976. The results suggest that in addition to the spring-summer peak of acanthor production, there was also an autumn-winter occurrence of shelled acanthors in October-November 1975 (Table II).

Effect of host sex

The frequency distribution of the infection in adult male and female perch is shown in Fig. 2. The results from the gill net samples taken between January 1975-February 1976 are presented. The incidence and mean intensity/infected fish was similar in male and female perch. The small number of heavily infected female fish may be a reflection on the greater number of female perch examined, in relation to the overdispersed nature of the infection. It should be noted that whilst there was no regular increase of mean intensity with host age and length (see below), the female gill netted perch were on average larger than the males, and exhibited a greater variation in standard length (see Chapter III; male perch, mean length 12.8 cm, variance 1.93; female perch, mean length 14.2 cm, variance 7.24).

Effect of host age and length

In an attempt to minimise the influence of seasonal fluctuations in the infection on this aspect of the study, only the gill net samples of perch taken during March-June 1975 were used. The purse seine sample of perch fry (aged 4-6 weeks, length 2.0 - 2.7 cm) were uninfected in July 1976. The absence of the infection from the sample of trawled perch aged 0++ (8-9 month, length 3.0-8.9 cm) suggests that perch did not acquire the infection during their first year in the lake. Perch appeared to acquire the infection for the first time during their second year in the lake, as indicated

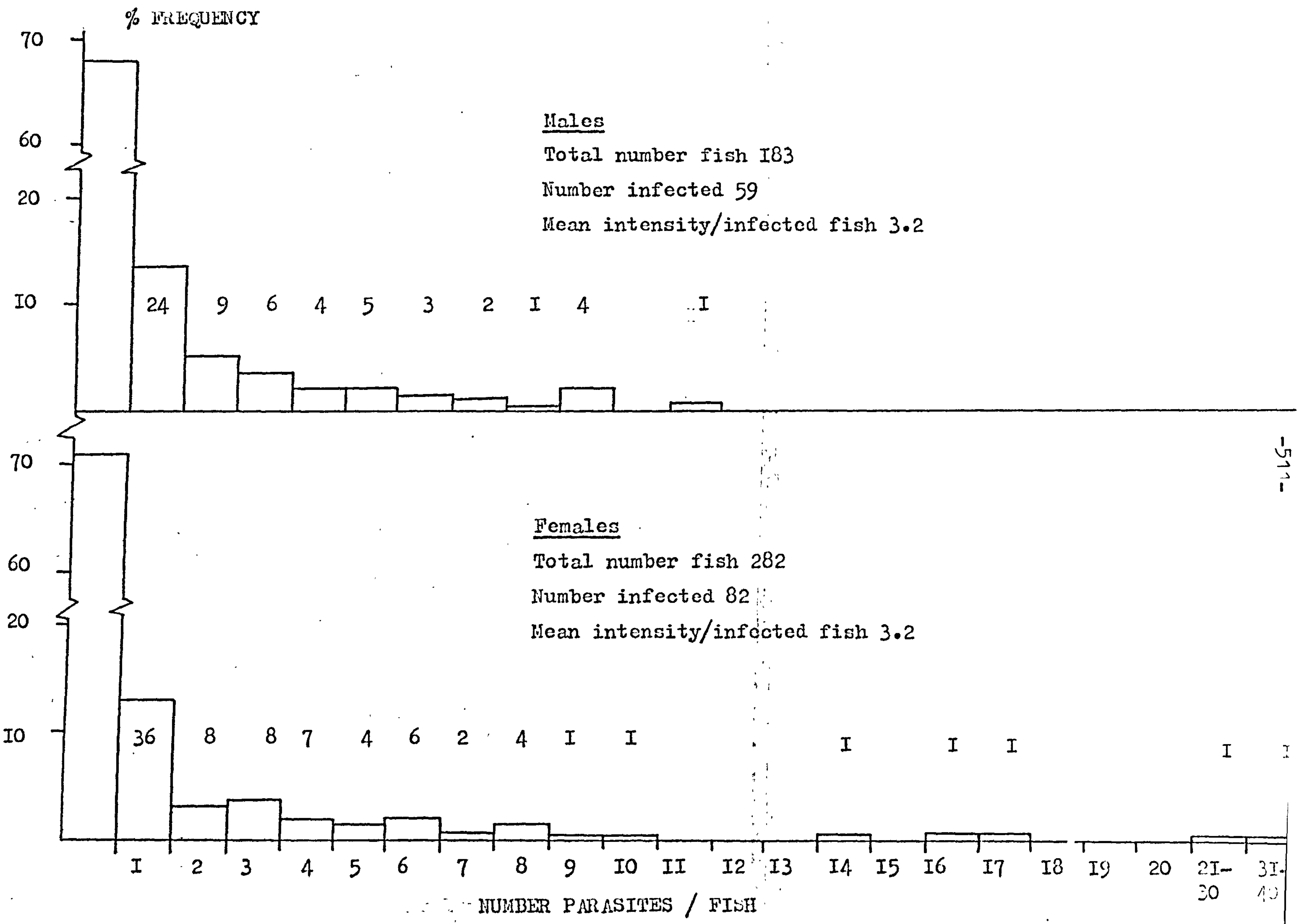


Fig. 2. Frequency distribution of *Acanthocephalus clavula* in male and female perch. Gill net samples. January 1975 - February 1976.

Table III. Effect of host age on the occurrence of *Acanthocephalus clavula*. Purse seine, trawl and gill net samples.

Age (yrs)	Number fish examined	% incidence	Number parasites	Mean/infected fish	Maximum
Purse seine sample. July 1976					
0+	30	-			
Trawl sample. March 1976					
0++	36	-			
1++ - 4++	28	60.7	37	2.2	7
Gill net samples. March-June 1975					
2-2++	1	(100.0)	9	(9.0)	9
3-3++	61	52.5	149	4.7	17
4-4++	20	80.0	48	3.0	10
5-5++	26	76.9	120	6.0	22
≥ 6	21	52.4	34	3.1	8

Table IV. Effect of host length on the occurrence of *Acanthocephalus clavula*. Purse seine, trawl and gill net samples.

Length (cm)	Number fish examined	% incidence	Number parasites	Mean/infected fish	Maximum
Purse seine sample. July 1976					
2.0-2.7	30	-			
Trawl sample. March 1976					
3.0-8.9	36	-			
9.0-11.9	28	60.7	37	2.2	7
Gill net samples. March-June 1975					
9.0-11.9	12	75.0	31	3.4	9
12.0-14.9	96	60.4	282	4.9	22
⩾15.0	21	61.9	47	3.6	14

by the presence of A. clavula in trawled perch aged 1++. However, relatively few perch aged 1-2++ were examined. The infection was prevalent in adult gill netted perch of all length groups (Table IV). However, while the mean intensity/infected fish appeared to fluctuate irregularly with host age, the incidence reached a peak in perch aged 4-5++. In fish younger, and older, than this the incidence of infection was lower (Table III).

Effect of site of capture in Llyn Tegid

As a result of the seasonal occurrence of this parasite, in relation to the size of gill net catches at the four sites in Llyn Tegid (see Chapter III), the infection at different sites could only be compared during October-November 1975. The results are summarised in Table V.

At this time of the year the infection was absent from site A (6m), though only 13 fish were examined. At site B, C and D (12m, 18m and 12m respectively), the mean intensity/infected fish (and range of intensity) was similar (Table V). However, the results suggest that the incidence of infection at site B was lower than that at both site C and D. A X^2 analysis revealed that this difference was highly significant ($X^2 = 12.34$, DF = 2, $P < 0.010 > 0.001$).

Distribution of Acanthocephalus clavula within the alimentary tract of perch

The results from the perch examined during March-June 1975 and shown in Fig. 3. A. clavula was most common at the anterior end of the intestine of perch (intestine I, II), and to a lesser extent in intestine III. Relatively few worms were found in the stomach,

Table V. Effect of site of capture on *Acanthocephalus clavula* infection. Gill net samples. October-November 1975

Site	Depth	Number fish examined	Number fish infected	% incidence	Mean intensity/ infected fish	Maximum
A	6m	13	0	-	-	-
B	12m	54	6	11.1	2.0	6
C	18m	21	8	38.1	2.7	5
D	12m	26	9	28.9	2.7	4

Fig. 3. Distribution of _Acanthocephalus clavula_ along the alimentary tract of perch. Gill net samples. March – June 1975.

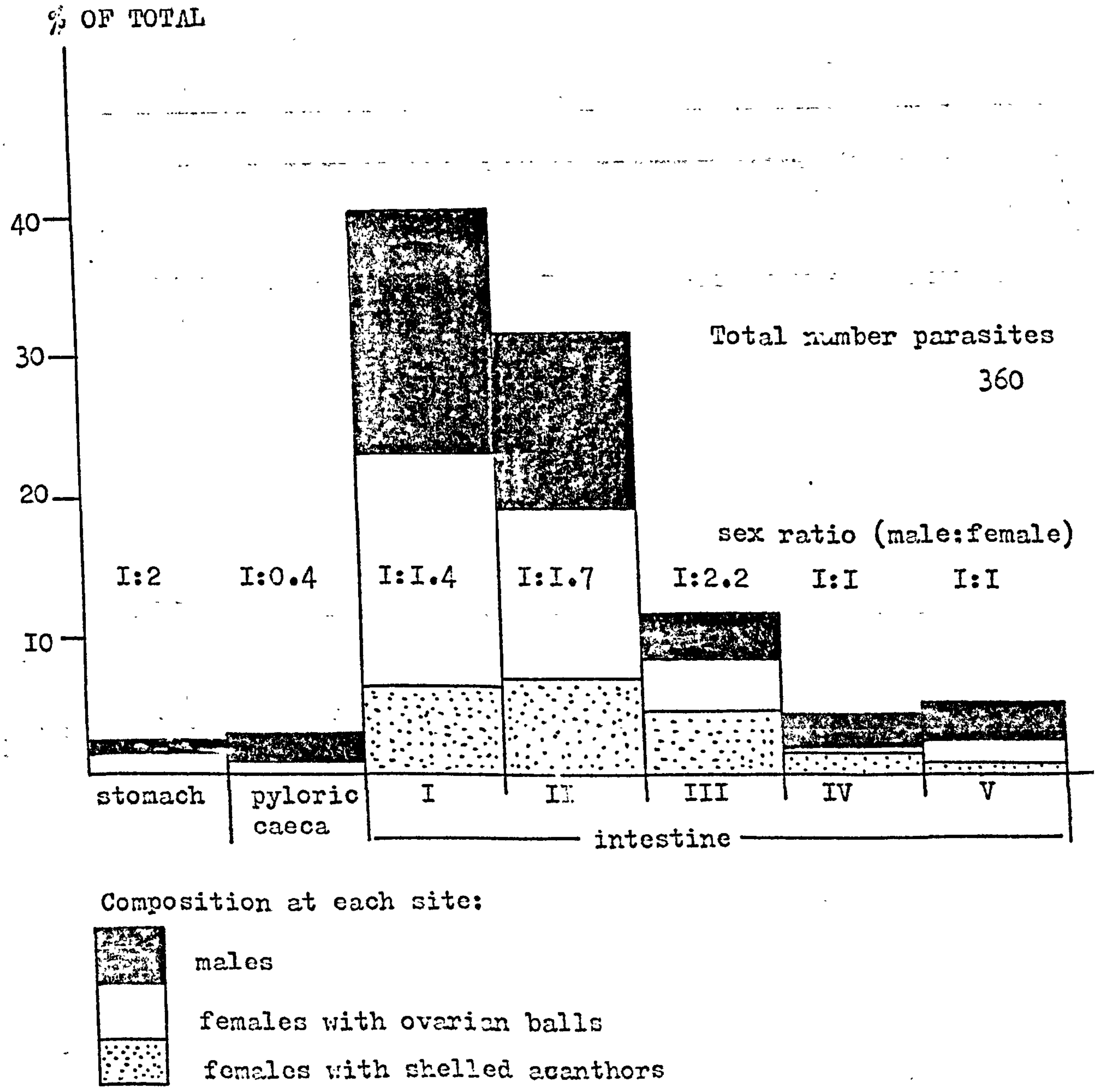
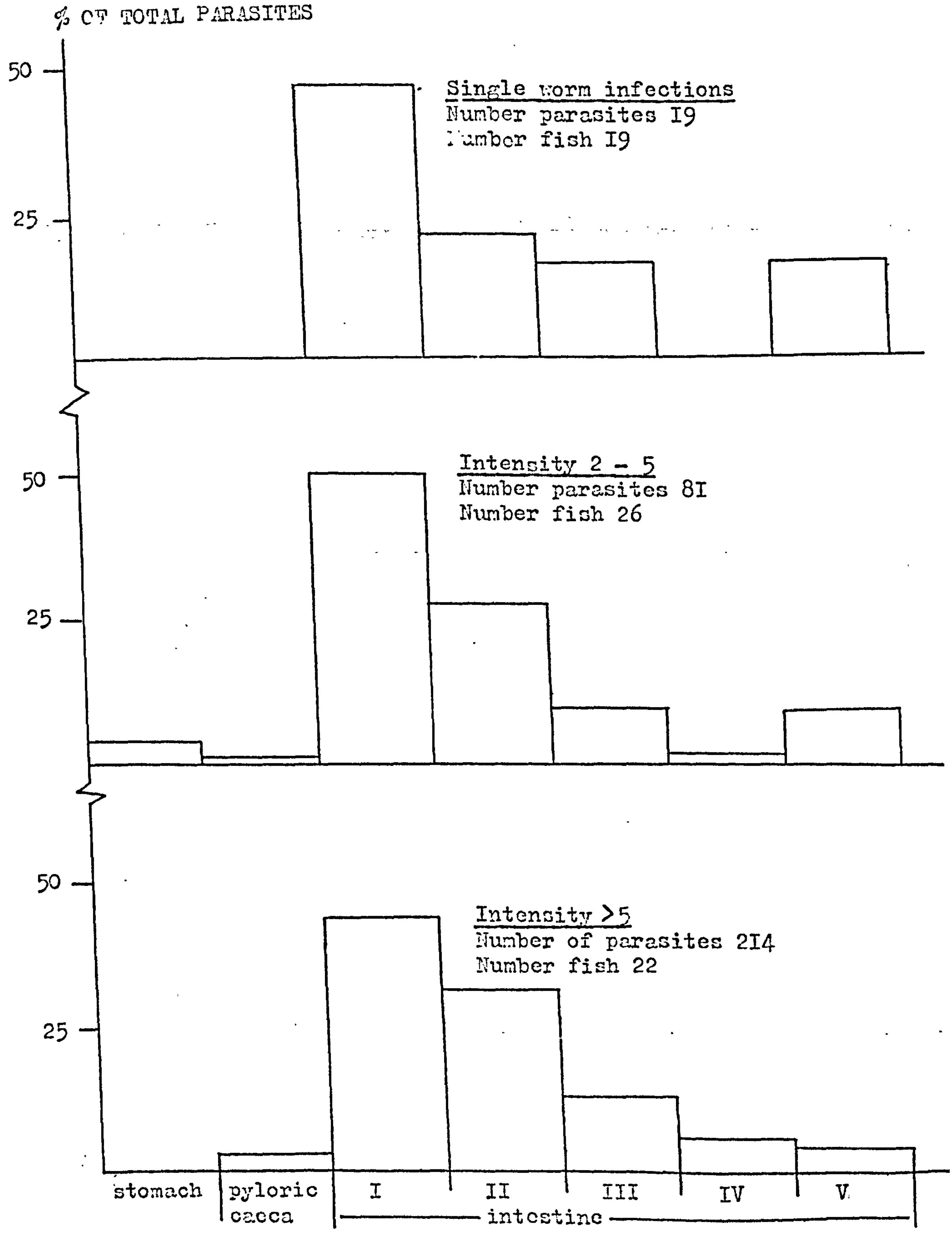


Fig. 4. Distribution of Acanthocephalus clavula along the alimentary tract of perch. Gill net samples. March - June 1975. All fish less than 15.0 cm.

TOTAL NUMBER OF FISH 67



pyloric caecae and the posterior intestine (Fig. 3).

The percentage composition of the A. clavula population at each site is shown in Fig. 3. Females containing shelled acanthors were only found in the intestine, and were most abundant in intestine I-III. The sex ratio (male:female) in the stomach and pyloric caeca was 1:2 and 1:0.4 respectively. At intestine I-III the sex ratio favoured females, while males and females were present in approximately equal numbers in intestine IV and V (Fig. 3).

During March-June 1975, the influence of intensity of infection on the distribution of A. clavula was investigated. To reduce the influence of host size on this aspect of the study, only perch less than 15.0 cm were used. The results are summarised in Fig. 4. The distribution of the parasite was similar in infections of single, 2-5 and >5 parasites (Fig. 4).

X.4 DISCUSSION

The life cycle of Acanthocephalus clavula was studied by Rojanapaibul (1977), and summarised by Rojanapaibul (1976). When eaten by the intermediate host Asellus meridianus, mature shelled acanthors hatched and released the acanthor. The acanthor penetrated the intestinal wall of the isopod, and remained for some time within the intestinal tissues. Later the parasite migrated to the haemocoel of the intermediate host, but still remained attached to the intestinal wall. Following growth and development, the acanthor changed through acanthella to cystacanth. No additional growth or development occurred in the cystacanth stage (Rojanapaibul, 1977). At 8-13°C development to cystacanth took 12 weeks (Rojanapaibul, 1976). In a suitable piscine definitive host the young acanthocephalan excysted and attached to the host intestinal wall by proboscis penetration. At 8-13°C in bullhead (Cottus gobio), copulation occurred after 7 days post infection. Development of the shelled acanthors to maturity took 45 days, and shelled acanthors were recovered from the bottom of experimental aquaria after 48 days (Rojanapaibul, 1976, 1977).

A. clavula has been recorded from 11 species of fish in the British Isles (Kennedy, 1974; Rojanapaibul, 1977). The records of this parasite from perch in the British Isles are summarised in Chapter IV, Table I. At Llyn Tegid this parasite has been recorded from the following species of fish: perch (Perca fluviatilis), pike (Esox lucius), roach (Rutilus rutilus), bullhead, eels (Anguilla anguilla), brown trout (Salmo trutta), grayling (Thymallus thymallus) and gwyniad (Coregonus lavaratus), (Chubb, 1961, 1964, 1976; Andrews & Rojanapaibul, 1976; Rojanapaibul, 1977).

Chubb (1968) considered that the distribution of some acanthocephalan parasites of fish may be related to the ability of acanthors to develop only in a specific crustacean intermediate host. A. clavula may mature in a range of definitive hosts (e.g. Chubb, 1964; Andrews & Rojanapaibul, 1976) though Asellus meridianus may be the only suitable intermediate host (Rojanapaibul, 1977). Nonetheless, the possible role of other, related crustaceans (e.g. Asellus aquaticus) in the life-history of A. clavula requires investigations. Chubb (1968) went on to note that many fish Acanthocephala may be more specific to their definitive hosts than was apparent from the literature, and that precise limits of specificity may exist outside of which the parasites may be able to exist temporarily, but not become sexually mature. Hine & Kennedy (1974a) found that Pomphorhynchus laevis reached maximum size and development in chub (Leuciscus cephalus) and barbel (Barbus barbus) in the River Avon (Hants.), and considered that the local population of this parasite was maintained from acanthors released from parasites contained within these two definitive hosts. Although the scarcity of P. laevis from the two most upstream stations may have been related to the scarcity of G. pulex (the crustacean intermediary), the distribution of P. laevis in the River Avon was related primarily to the relative abundance of the referred definitive hosts (chub, barbel) (Hine & Kennedy, 1974a). However, the distribution of P. laevis in the British Isles as a whole is less readily explicable, and cannot be simply explained by the lack of investigations, or the distribution of G. pulex and the preferred definitive hosts, chub and barbel (Hine & Kennedy, 1974a).

Van Cleave (1916) made some of the earliest observations on the seasonal occurrence of fish acanthocephalans, concerning the Gracilisentis gracilisentis and Tanaorhamphus longirostris infections of gizzard shad (Dorosoma cepidianum) in North America. He concluded that the main factors influencing seasonal changes in the infection were the length of life of the parasite in the definitive host and the feeding habits of the latter, and the length of the development in the intermediate host.

The seasonality of the infection of fish with Neoechinorhynchus rutili has been studied by Steinstrasser (1936), Walkey (1967), Chappell (1969a), Bibby (1972) and Halvorsen (1972). Steinstrasser (1936) reported the seasonal occurrence of N. rutili in rainbow trout (Salmo gairdneri). He suggested that fish were infected in the middle of November, and then the parasite took three months to produce shelled acanthors. Chappell (1969a) found that the N. rutili infection of three-spined sticklebacks (Gasterosteus aculeatus) from Yorkshire did not exhibit any seasonal pattern, though the incidence of infection decreased during the autumn as a result of sampling deficiences. However, Walkey (1967) studied the *N. rutili* infection of three-spined sticklebacks from County Durham, and found that although the parasite did not exhibit any cycle of incidence, there was a maturation cycle. From February-May the proportion of immature *N. rutili* dropped, with a corresponding rise in the percentage of mature worms. Gravid worms were found in greatest numbers during the spring-early summer, which was followed by a decline in their occurrence during the autumn to attain a minimum winter value. Walkey (1967) concluded that the maturation cycle of *N. rutili* was initiated by seasonal changes in temperature, though the overall size of the parasite population was largely determined by the availability of infected intermediate hosts. Irregularities in the seasonal occurrence of the ostracod intermediary led to irregular fluctuations in the size of the parasite population, which masked any tendency towards a seasonal cycle of incidence (Walkey, 1967). In comparison, Bibby (1972) suggested that the observed seasonal cycle of incidence of *N. rutili* in minnow (*Phoxinus phoxinus*) from Frongoch Lake (Wales) was a result of decreased feeding during the winter months. The observed fall in incidence during November-April was attributed to a fall in lake temperature lowering the metabolic demands of the fish, hence resulting in a fall in food consumption (Bibby, 1972). Halvorsen (1972) studied the *N. rutili* infection of roach at the River Glomma (Norway), and found that the parasite occurred with a low frequency throughout the study period (May-August, May-December). The length of female worms increased from May to August, followed by an apparent decrease. Halvorsen concluded that *N. rutili* exhibited seasonal maturation, with a possible generation gap during August-November.

De Guisti (1949) studied the seasonal periodicity of *Leptorhynchus thecatus* in bass (*Huro salmoides*, *Micropterus dolomien* and *Ambloplites rupestris*) in North America. In northern areas the fish harboured the greatest number of immature worms in May-June. As the season progressed, the number of immature acanthocephalans decreased, and the majority of the worms became mature adults. During July-September there was a peak in the infection, though the number of parasites present during October-November remained fairly constant. During December-February the intensity of infection decreased, and by late February this parasite was only occasionally found.

Shulman & Shulman-Albova (1953) studied the infection of *Echinorhynchus gadi* in the fish of the White Sea. Shelled acanthors were produced at the end of July. Following the death of the mature worms, the incidence of the infection decreased in August. Recruitment of the new generation began in September, which resulted in an increase in incidence. However, Polyanski (1955) found that *E. gadi* in the fish of the Barents Sea (which does not freeze over in winter) developed uniformly throughout the year, with no cyclical fluctuations.

Bauer & Nikolskaya (1957) examined the occurrence of *E. salmonis* in white fish (*Coregonus lavaratus*) from Lake Ladoga (U.S.S.R.) during July-November. The incidence and intensity of infection was high in all months. Tedla & Fernando (1969, 1970) studied the seasonal occurrence and maturation of *E. salmonis* in yellow perch (*Perca flavescens*) from Lake Ontario (North America). The incidence of infection fell from 43% in May to zero in August. There was a gradual increase in incidence from September, to a peak of 75% in February-March. The intensity followed a similar pattern (Tedla & Fernando, 1969). The new generation was acquired during the autumn-early winter, and the production of mature shelled acanthors occurred during the following spring-early summer (Tedla & Fernando, 1970).

Awachie (1965) found no seasonal cycle of incidence of *E. truttae* in brown trout from the Afon Terrig (North Wales). Cystacanths were present in *G. pulex*, and acanthors in brown trout, throughout the year. However, the intensity of the infection in the intermediate and definitive hosts exhibited seasonal changes, and bore an inverse relationship to each other. In trout the intensity of infection was greatest in June-September, and this was correlated to the feeding activity of the fish (Awachie, 1965).

Hine & Kennedy (1974b) studied the population biology of *Pomphorhynchus laevis* in the River Avon (Hants.). There was no cycle in incidence or development in the intermediate host, *G. pulex*. Cystacanths were available throughout the year. Fish ingested *G. pulex* and acquired *P. laevis* in all months, and there were no marked seasonal changes in incidence and intensity of the infection in the definitive hosts. In dace (*Leuciscus leuciscus*) and grayling, *P. laevis* grew little and matured only in the summer, but in chub and barbel the parasite grew and produced acanthors during the whole year (Hine & Kennedy, 1974b). Rumpus (1973, 1975) found no seasonal changes in incidence and intensity of the *P. laevis* infection of *G. pulex* and bullhead at the River Avon. It is interesting to note that over a 9 year period, this parasite has maintained a similar pattern of distribution along the river, and the level of incidence and intensity in dace and *G. pulex* at one site has remained fairly constant (Kennedy & Rumpus, 1977) (see Chapter VIII, *re*. *Triaenophorus nodulosus*).

Komarova (1950) reported the seasonal occurrence of *Acanthocephalus lucii* in the percid fish of the River Dnepr (U.S.S.R.). *A. lucii* deposited shelled acanthors in the summer and then perished, which resulted in a fall in the incidence and intensity of infection in perch from June-September. At the end of the summer, and in the autumn, the development of *A. lucii* occurred in the intermediate host, during which time the parasite was largely absent from perch. Fish became infected with a new generation of worms at the end of the autumn, and there was a sharp rise in the infection in fish during December-January. During the winter-spring the acanthocephalans grew, and by the summer they were sexually mature. Wysocka (1965) studied the seasonal occurrence of *A. lucii* and *A. anguillae* in fish from the Zegrzynski Reservoir (Poland). Unfortunately, these two species of *Acanthocephalus* were treated as one. Rauckis (1970a, b) examined small numbers of perch (58) and pike (57) infected with *A. lucii* from Lake Dusia (U.S.S.R.) during the course of a single year. Apart from a higher incidence of infection in both fish in April-May, there were no marked seasonal changes in the incidence or intensity of the infection. At Lake Dargin (Poland), Wierzbicki (1970) found that the highest incidence and intensity of infection of perch with *A. lucii* was during the spring-summer months, and lowest during the autumn-winter. Stycznska (1958) reported a similar cycle in *A. lucii* from Lake Druzno (Poland), though precise data for this study were lacking. Halvorsen (1972) studied the infection of perch with this parasite at the River Glomma (Norway) during May-August 1966 and May-December 1967. Whilst only small numbers of fish were involved, the parasite was present in June, September and October. Andrews (unpublished observations) recorded female *A. lucii* containing shelled acanthors from perch at Princes Park Lake (Liverpool 8, Merseyside) during April and August 1975, and March 1976. The fish were not examined in any other months.

Amin (1975a) described *Acanthocephalus parksidei* sp. n. from several Wisconsin fish (North America). Amin (1975b) found a considerable seasonal variation in the degree of the infection, and development, of the parasite in its definitive hosts. The frequency of the infection and maturation reached a peak in the spring. Mature worms were eliminated during the summer and a new generation was present during the early autumn. New infections of immature parasites occurred throughout the autumn-spring (Amin, 1975b).

Muzzall & Rabalais (1975) examined the seasonal periodicity of A. jacksoni in five species of fish from Jackson Cutoff (Ohio, North America). The isopod intermediary (Lirceus lineatus) first contained cystacanths of A. jacksoni in October. Adult acanthocephalans were first recorded from fish during November, and female worms with shelled acanthors were present during January-July. There was a high incidence of infection during April-June, though the low values for January-February may have been a result of small sample sizes (Muzzall & Rabalais, 1975). There was a decrease of incidence in July, and the infection was absent during August-October. L. lineatus was absent or unavailable from July-September, and Muzzall & Rabalais suggested that A. jacksoni survived this period in the egg stage.

Previous seasonal studies on the A. clavula infection of fish include Chubb (1964), Jeacock (1969), Pennycuick (1971a), Halvorsen (1972) and Rojanapaibul (1977).

Chubb (1964) examined 104 pike, 390 roach, 54 eels and 76 grayling from Llyn Tegid during October 1957-October 1959. Bearing in mind the relatively small numbers of pike, eel and grayling that were examined, Chubb (1964) found no evidence of any seasonal periodicity, though he noted that the incidence of infection was related to the feeding habits of the fish. Jeacock (1969) found a distinct pattern of seasonal incidence in eels from Afon Cefni (North Wales). There were two peaks of incidence: in early spring, and in late autumn. Halvorsen (1972) studied the A. clavula infection of burbot (Lota lota) from the River Glomma (Norway). Only 28 burbot (mean length 43.6 cm) were examined, primarily between May-August 1966 and May-December 1967. The parasite was present in all months. Pennycuick (1971a) studied the A. clavula infection of three-spined sticklebacks from Priddy Pool (southern England). From October 1966 until April 1968, the parasite was present in all months, though the incidence and intensity reached a minimum in August 1967 and April 1968. Female worms containing shelled acanthors were present in all months except October 1976 and September 1967. It was considered that the fish became infected with the largest numbers of A. clavula during August-September, which corresponded to a peak in feeding activity of the fish, perhaps combined with a peak in the level of infection in (and abundance of) the intermediate host, Asellus sp. (Pennycuick, 1971a).

Rojanapaibul (1977) examined 387 roach, 58 eels, 95 bullhead and 675 gwyniad from Llyn Tegid during an 18 month period in 1974-1976. These results were summarised by Andrews & Rojanapaibul (1976).

Fifty-seven percent of the gwyniad were infected with A. clavula. The incidence and mean intensity/fish increased from 40.4% and 8.3 (respectively) in January to a spring-summer peak of 75.3-92.1% and 8.9-16.5 in May-July. Thereafter the incidence and intensity of infection fell, and during September-December fluctuated between 13.6-27.8% and 0.6-1.3 (respectively). Female worms with shelled acanthors were found during January-August and November-December (Rojanapaibul, 1977).

Rojanapaibul (1977) found that 22.5% of the roach were infected with A. clavula. The incidence of the infection increased from 23.3% in January to a peak of 57.1% in July. In July there was a sharp fall in the incidence of infection, which then fluctuated between 3.3%-18.0% for the remainder of the year. The mean number of parasites/fish was very low, and varied from 0.04 in November to 1.0 in June. Female worms with shelled acanthors were present in February, April-June and October. Vegetable matter (especially algae) and planktonic crustaceans, followed by dipteran larvae and pupae were the most important food items of roach at Llyn Tegid (Ali, 1973). A. meridianus were ingested in relatively small numbers which undoubtedly accounted for the low intensity of infection of A. clavula. The peak of incidence (and to a lesser extent intensity) may have been the result of a small peak in A. meridianus ingestion by roach during the spring-summer. However, Ali (1973) found that there was little seasonal variation in the diet of roach, though more food was eaten during the spring-summer period. The results suggested that increased numbers of A. meridianus may have been eaten during the autumn-winter (Ali, 1973).

Rojanapaibul (1977) found that 28.4% of the bullhead and 53.4% of the eels were infected at Llyn Tegid. Because of the small numbers of fish involved, the data were grouped into three-monthly periods. In bullhead the incidence and mean intensity/fish varied from 17.2% and 0.3 (respectively) in July-September, to 52.6% and 1.1 (respectively) in January-March. Shelled acanthors were found in female worms during the whole year. The low intensity of infection may have been a result of small numbers of A. meridianus ingested by these fish, in relation to the low incidence of the infection in the intermediate host. However, since the low intensity was confined to a much shorter intestine (than, for example, in roach), this may have facilitated intersexual contact and copulation, and permitted all year acanthor production (Andrews & Rojanapaibul, 197~~7~~6).

The incidence of infection in eels fluctuated from 35.7% in April-June to 76.9% in January-March. The mean intensity/fish varied from 1.1 in April-June to 7.7 in January-March. Female worms containing shelled acanthors were present throughout the year.

Chubb (1964) suggested that temperature may play an important role in determining the presence or absence of a well defined seasonal periodicity of development in some Acanthocephala. Extremes of temperature may have been important in producing the seasonal cycle of occurrence and maturation in *E. gadi* from the White Sea (Shulman & Shulman-Albova, 1953), and in *E. salmonis* from Lake Ontario (Tedla & Fernando, 1970), by the restriction of parasite maturation or intermediate host availability (Hine & Kennedy, 1974b). However, a change in host feeding habits that restricts the acquisition of infective stages may also produce a maturation cycle (Walkey, 1967; Tedla & Fernando, 1970). Chubb (1964) considered that the temperature at Llyn Tegid was such that it permitted the uniform development of *A. clavula* throughout the year, and Andrews & Rojanapaibul (1976) stated that lake temperature never fell low enough to prevent the production of shelled acanthors. The seasonal cycle of *A. clavula* in perch at Llyn Tegid is thought to have been elated primarily to seasonal variations in the intake of infective stages, as a result of seasonal changes in host feeding habits. Infected *A. meridianus* were available in all months, and the mean incidence was 2.0% (Andrews & Rojanapaibul, 1976; Rojanapaibul, 1977). During the spring-summer months (March-May 1975) perch ingested large numbers of *A. meridianus* (see Chapter III). Therefore during this period the incidence and intensity of infection increased and reached a peak in April-May. As the intensity of infection increased the chances of inter-sexual contact and copulation were greater. This resulted in an increase in the proportion of female worms containing shelled acanthors. Since few spent females were encountered, it would appear that female A. clavula were either shed while gravid, or pass out shortly after depositing their shelled acanthors. Rojanapaibul (1977) found that fertilised female A. clavula were shed from bullhead after 48-53 days post infection (at 8-13°C), after liberating the majority of their shelled acanthors.

A.meridianus ingestion (and hence recruitment) was low during June-July. With the continued output of worms, the incidence and intensity of infection fell, and female A. clavula containing shelled acanthors were absent during August-September. However, there appeared to be a small peak of A. meridianus ingestion by perch between August-November, which may have resulted in a small peak in incidence and intensity (and the occurrence of female worms containing shelled acanthors) in October-November. The infection fell to a minimum in December, and female worms with shelled acanthors were absent during December-February 1975/76. With an increase in the occurrence of A. meridianus in perch stomachs during January-February 1976, the incidence and, to a lesser extent, the intensity of infection began to rise.

Therefore, the parasite population in the alimentary tract of perch was in a dynamic balance, that is, the resultant point of an equilibrium that was the product of gain and loss of worms from the host. This type of dynamic equilibrium has been noted several times by workers studying fish parasites (e.g. Hopkins, 1959; Chubb, 1963b; Chubb et al, 1964; Kennedy, 1968; Hine & Kennedy, 1974b; etc), and has been discussed in Chapter VII (re. Bunodera luciopercae) and

Chapter IX (re. Camallanus lacustris). Chubb et al. (1964) suggested that this phenomenon was of probable wide occurrence. In systems of this nature the input may be influenced by the availability of infective stages and the host feeding habits, and output may be influenced by the failure of parasites to establish, by the rejection of established parasites, and by natural mortality at the end of the parasite's natural life span (Kennedy, 1970).

It is interesting to note that Haram & Jones (1971) found that A. meridianus ingestion by gwyniad showed a seasonal variation, with these isopods most often recorded from the fish stomachs during February-May (and August). Therefore the seasonal changes in the A. clavula infection of gwyniad may be markedly influenced by seasonal variations in host feeding habits, as was indicated for perch (Andrews & Rojanapaibul, 1976; present study).

During March-June female worms markedly outnumbered males. This may have been a result of the earlier, post-copulatory death of male A. clavula. A similar bias in the sex ratio of acanthocephalans has been noted by several workers, including Bykhovskaya-Pavlovskaya (1940), Burlingame & Chandler (1941), Chubb (1964), Awachie (1965), Pennycuick (1971a), Amin (1975b) and Rojanapaibul (1977). During the remainder of the year at Llyn Tegid, the sex ratio of A. clavula in perch was approximately 1:1. This may have been because of the low intensity of infection at this time of year reducing the chances of copulation, and hence effectively prolonging the life span of the male worm.

Hunt & Jones (1972) found that A. meridianus was abundant in the littoral zone at Llyn Tegid, though it was much less abundant at 6m and 12m. Hunt & Jones stated that A. meridianus was found "regularly, though not abundant" at 20m, and this was attributed to the nearby Afon Glyn washing the isopod from shallower regions (Hunt & Jones, 1972).

Since the 20m site of Hunt & Jones was close to my 18m (C) and 12m (D) sites, this relative abundance of *A. meridianus* in deeper water may explain the higher incidence of *A. clavula* recorded at these two sites during October-November. However, in view of the limited nature of this part of the present study, the occurrence of *A. clavula* in perch from different sites in Llyn Tegid requires further investigation. Wierzbicki (1971) found that the incidence of *A. lucii* in perch at Lake Dargin (Poland) was higher in shallow water. This was attributed to the favourable conditions provided by the shallow water areas for the intermediate host, *Asellus aquaticus* (Wierzbicki, 1971).

The infection of perch with *A. clavula* was overdispersed, though there was a seasonal occurrence of heavily infected fish. High individual intensities were most common during April-May, when the incidence, mean intensity and percentage of female worms with shelled acanthors were all high. Overdispersed distributions are common in fish parasite populations (e.g. Kennedy, 1970; Pennycuick, 1971b; Boxshall, 1974; Hine & Kennedy, 1974b; etc.). Crofton (1971) and Elliot (1971) considered the factors influencing overdispersed distributions with special reference to the Negative Binomial. Dietary differences and differences in physiological resistance to infection have been suggested as important in producing the non-random distribution of fish parasites in their host population (Kennedy, 1972a). Crofton (1971) suggested that parasites may kill heavily infected hosts, and this may result in regulation of the host and parasite populations to their mutual advantage. However, ~~as noted by~~ Boxshall (1974) suggested, in relation to the *Lepeophtheirus pectoralis* infection of plaice (*Pleuronectes platessa*), that overdispersion also resulted in an increase in the probability of a male and female parasites occurring in the same fish.

The results from the 14 monthly samples of adult gill netted fish suggested that the infection in male and female perch was similar. Rojanapaibul (1977) considered the effects of host sex on the A. clavula infection of gwyniad and roach at Llyn Tegid. There was a degree of seasonal variation in the differences between the sexes of the incidence and intensity of infection in gwyniad, and the incidence in roach. The intensity of infection in roach was very low (Rojanapaibul, 1977). Pennycuick (1971c) found that the A. clavula infections of male and female three-spined sticklebacks were similar.

The results from the purse seine and trawl samples of fish suggest that perch did not acquire the infection during their first year in the lake. This may be related to the low occurrence of A. meridianus in the stomachs of these fish (see Chapter III). A. clavula was present in perch aged 1++ and above, though few perch aged 1-2++ were examined. Because of the low incidence and intensity of infection during much of the year only the gill net samples of adult perch examined between March-June were used to investigate the effects of host age and length further. Consequently, perch of a small size range were available and the sample size of some age/length groups was small. Both these factors may have influenced the results. However, the lack of any marked changes in the incidence and intensity of infection with the age and length of these fish was likely to be related to the fact that perch of all ages and sizes may ingest A. meridianus (Ali, 1973; present study, Chapter III). There was no evidence to suggest that larger perch acquired the infection secondarily from infected prey fish, though this may occur in large pike (Chubb, 1964, 1970). Whilst cannibalism was the most common form of fish ingestion by perch at Llyn Tegid (see Chapter III), the incidence and intensity of infection with A. clavula was low for most of the year. This may have reduced the chances of large perch acquiring the infection from smaller perch. The influence of host feeding habits on the parasite fauna of perch is considered in Chapter XI.

Pennycuick (1971c) found that the smallest sticklebacks, and those in their first year of life, were generally not infected with A. clavula at Priddy Pool. The incidence and intensity of infection increased steadily with age and length of the fish, although the largest fish were not the most heavily infested. Since individual worms die and pass out of the fish, the numbers of A. clavula did not accumulate with time. Thus the changes in the incidence and intensity were related to the feeding habits of the fish. Pennycuick (1971c) suggested that the fall in the infection in the oldest, largest fish may have been a result of older fish becoming senile and less able to support large parasite burdens. Rojanapaibul (1977) studied the effect of host age and length on the A. clavula infection of roach and gwyniad at Llyn Tegid. The incidence of infection tended to increase with the length of both fish. While the intensity increased with the length of gwyniad, there was no such increase in the much less heavily infected roach. These conclusions were based on roach 17-21cm, and gwyniad 18-23 cm long.

In this present study no observations were made on the influence of A. clavula on the host. Definitive hosts may harbour large numbers of acanthocephalans. Up to 1000 Polymorphus minutus have been recorded from ducks (Wolffhügel, 1900), and Clark et al. (1958) recovered 610 P. botulus from a dead eider duck. Ball (1930) found 1154 Corynosoma strumosum in a single seal (Phoeca richardii), and Awachie (1963) reported over 200 *Echinorhynchus truttae* from brown trout. Bullock (1963) reported similar high individual intensities of *A. jacksoni* from 4 species of fish, and Chubb (1965) found between 200-500 *Pomphorhynchus laevis* in seven chub (*Le~~y~~uciscus cephalus*). The helminth diseases of fish were reviewed by Williams (1967), and recent publications concerning the Acanthocephala include Logachev & Semenyuk (1971), Pennycuick (1971a), Hine & Kennedy (1974a), Schmidt *et al*. (1974), Paperna & Zwerner (1976) and Parr (1976). In addition, Harris (1970, 1971, 1972) studied the immune response of cyprinid fish to helminth parasites, with particular reference to *Pomphorynchus laevis*.

Parasitologists have known for a long time that individual species of parasites are found only in restricted, specific sites (or micro-habitats) within their hosts, that the habitats occupied by some species are more restricted than others, and that some species move to new microhabitats (or even undergo complex migrations) as they mature (Holmes, 1973). Acanthocephalan parasites may change their site of attachment zone within the alimentary tract of their host during their life span (Crompton, 1970), and reports of this phenomenon in fish Acanthocephala include Bullock (1963), Awachie (1965, 1966), Uglen & Beck (1972) and Kennedy *et al*. (1976). Holmes (1961, 1963) suggested that parasitic helminths select one or more of the physiological conditions along the alimentary tract, and that biochemical changes in the worms during development that enabled or necessitated migration may also be important. Nonetheless, some fish acanthocephalans may remain at their initial site of attachment, including *Neoechinorhynchus cylindratus* and *Leptorhynchus thecatus* in large mouth bass (*Huro* salmoides) (Vernard & Warfel, 1953), Pomphorhynchus laevis in goldfish (Carassius auratus) and rainbow trout (Salmo gairdneri) (Kennedy, 1972b; Kennedy et al., 1976), and Neoechinorhynchus rutili in carp (Tesarcik, 1972).

A. clavula did not appear to undergo any significant migration within the intestine of perch, eel and gwyniad (Rojanapaibul, 1977; present study).

Rojanapaibul (1977) found that A. clavula showed a preference for a particular region of the host intestine, which differed from host species to species. In gwyniad the worms exhibited a preference for the 0-40% (intestine I-II) region of the intestine, whilst in eels they were found more posteriorly at 41-100% (intestine III-V). However, the parasite was able to survive in all regions of the intestine of both fish (Rojanapaibul, 1977). In perch, A. clavula was most common at the anterior end of the intestine (I-II), and to a lesser extent intestine III. Relatively few worms were found in the stomach, pyloric caeca and intestine IV-V. In agreement with the observations of Rojanapaibul (1977) concerning the A. clavula infection in gwyniad, the sex ratio of the parasite favoured females at the anterior region of the intestine, whilst in the more posterior regions it was approximately 1:1. In eel female parasites were always more abundant than males in the preferred, posterior regions of the intestine.

In perch female A. clavula containing shelled acanthors were only found in the intestine, and were most abundant at intestine I-III. However, they also occurred in intestine IV and V. Rojanapaibul (1977) reported that in gwyniad, females with shelled acanthors were found throughout the intestine, though mature acanthors only occurred in intestine I-II. In eels female worms with mature and immature acanthors were found in intestine II-V.

Intra- and inter-specific reactions in populations of intestinal helminths may influence their distribution (Crompton, 1973; Holmes, 1973). Aspects of inter-specific reactions are considered in Chapter XI.

The fact that acanthocephalan parasites may exist at high intensities in their definitive hosts has been noted. Intra-specific reactions have been reported as influencing the site occurrence of Acanthocephala on several occasions (e.g. Burlingame & Chandler, 1941; Holmes, 1961; Awachie, 1966). However, in perch at Llyn Tegid the distribution of A. clavula was similar at levels of intensity of 1, 2-5 and >5 worms.

X.5 SUMMARY

There were spring-summer and autumn-winter peaks of parasite incidence, intensity and maturation, that were related to host feeding habits.

The infection was overdispersed, though similar in adult fish of both sexes.

Perch acquired the infection during their second year in the lake. In adult fish aged 2 years or above (and length 9.0 cm and above) there were no marked changes in incidence and intensity of infection with host age and length. This was related to host feeding habits.

The higher incidence of infection at sites C and D may have been related to a local abundance of A. meridianus.

A. clavula was found predominantly in the anterior intestine of perch. The distribution of the parasite was similar in infections of one, 2-5 and >5 worms.

References

To avoid further repetition, the references for Chapter X are listed at the end of Chapter XI.

CHAPTER XI

SOME HOST, PARASITE AND ENVIRONMENTAL RELATIONSHIPS WITHIN THE PARASITE FAUNA OF PERCH (Perca fluviatilis L.) FROM LLYN TEGID

XI.1 INTRODUCTION

The host specificity of the parasite fauna and the biology of the individual parasite species have been examined in Chapters VI-X. In this final chapter seasonal changes in the total parasite fauna, along with the influence of host age and sex, have been summarised. Literature cited has been kept to a minimum, and comprehensive references on each parasite species may be found in the preceding, relevant chapters. In addition, interspecific competition within the helminth fauna of the alimentary tract has been examined, and the combined effects of Diplostomum gasterostei (Digenea) and Triaenophorus nodulosus (Cestoda) on perch considered.

XI.2. INTER-SPECIFIC COMPETITION WITHIN THE HELMINTH FAUNA OF THE ALIMENTARY TRACT OF PERCH

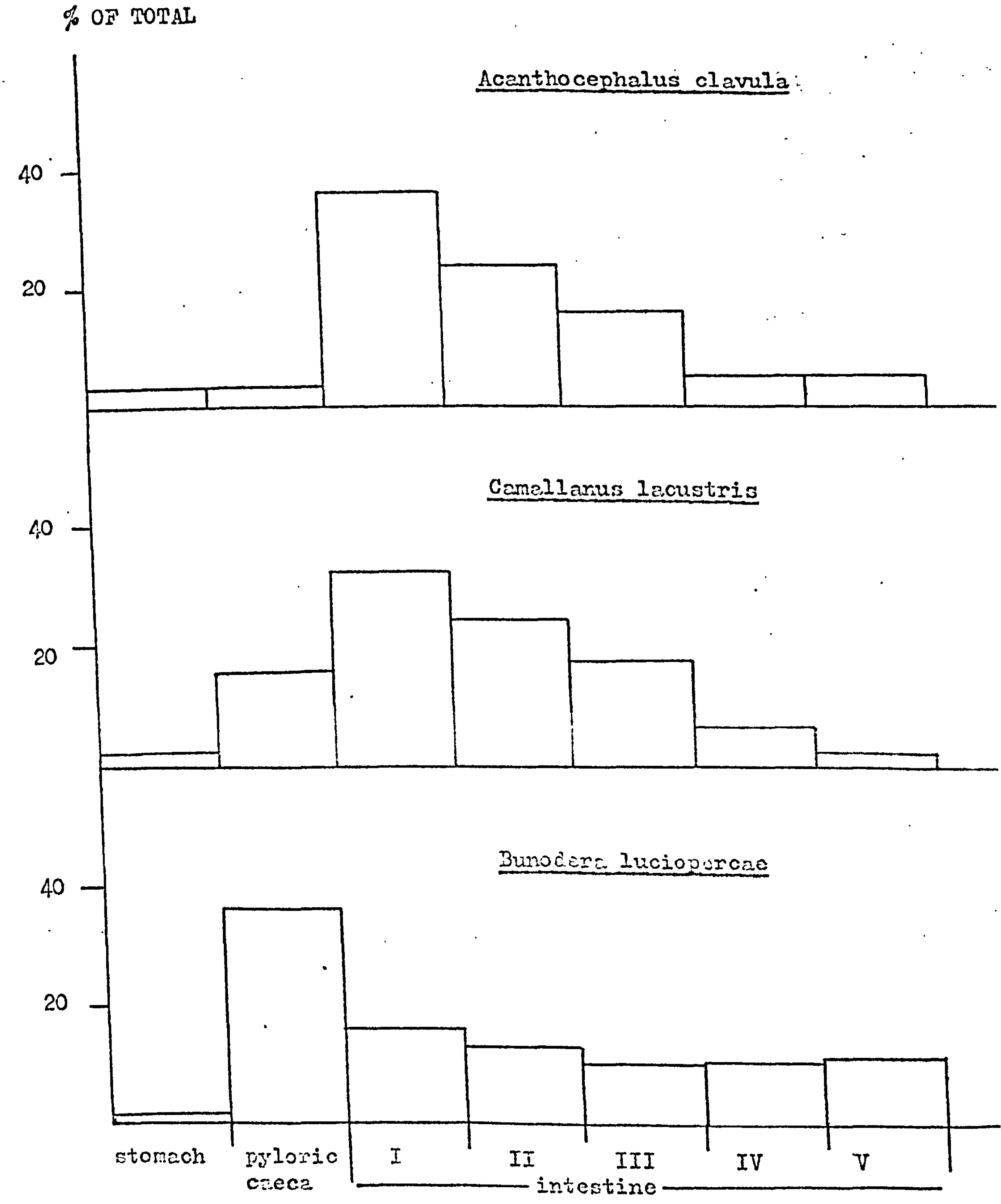
The most common members of the helminth fauna of the alimentary tract of perch were Acanthocephalus clavula (Acanthocephala), Bunodera luciopercae (Digenea) and Camallanus lacustris (Nematoda). During certain months of the year (e.g. March-May), when the incidence of A. clavula, B. luciopercae and to a lesser extent C. lacustris were high, concurrent infections were not uncommon (Table I). The distribution of these helminths in the alimentary tract of perch is shown in Fig. 1. During January 1975-February 1976 all three species were found throughout the alimentary tract. B. luciopercae was most abundant in the pyloric caeca, though appreciable numbers were also found throughout the intestine. A. clavula and C. lacustris exhibited somewhat similar distributions, with both species

Table I. Concurrent infections with Acanthocephalus clavula, Bunodera luciopercae and Camallanus lacustris. Gill net samples. March-May 1975. All fish less than 15.0cm.

	Number Fish	% of Total
Uninfected	0	-
One species:		
A. clavula	1	1.3
B. luciopercae	13	17.3
C. lacustris	0	-
Two species:		
A. clavula and B. luciopercae	30	40.0
A. clavula and C. lacustris	3	4.0
B. luciopercae and C. lacustris	7	9.3
Three species:		
A. clavula and B. luciopercae and C. lacustris	21	28.0

TOTAL NUMBER FISH 75

Fig.I . Distribution of helminths in the alimentary tract of perch.
Gill net samples. January 1975 - February 1976.



most abundant in intestine I, II and to a lesser extent III. In addition, C. lacustris was also present in appreciable numbers in the pyloric caeca. B. lucioperca and C. lacustris did not exhibit any marked seasonal changes in their distribution in the alimentary tract, though A. clavula was seasonally abundant during February/ March-June/July. Intra-specific relationships have been discussed in Chapter VII, IX and X.

Inter-specific competition is the active demand by members of two or more species at the same trophic level for a common resource or requirement that is actually, or potentially, limiting (Miller, 1967). According to Crompton (1973), as a result of inter-specific reactions, some parasitic helminths may change their site (or become confined to one part of their normal site) when another species is present. In addition, several workers have reported a competitive reaction between two species of coexisting helminths, which resulted in a reduction in the intensity of one species when the intensity of the other was high (Holmes, 1973).

Therefore, in order to investigate the existence of any inter-specific competition within the helminth fauna of the alimentary tract of perch, selected data on A. clavula, B. luciopercae and C. lacustris were used. The distribution and abundance of each helminth was examined at increasing levels of intensity of each of the remaining two species. To reduce any possible seasonal influences, several adjacent monthly samples (which showed a high incidence and reasonable range of intensities of each of the helminth species under scrutiny) were used. To reduce any effects of host age/size on the results, only gill netted adult perch between 9.0-14.9 cm were used.

Effect of A. clavula on B. luciopercae

The distribution of B. luciopercae in the alimentary tract of perch during March-May 1975 was not markedly influenced by the presence of A. clavula, or by intensities of the acanthocephalan varying from 1 to > 5 (Fig. 2). At 0, 1, 2-5 and >5 A. clavula/fish, there was no marked difference in the mean intensity of B. luciopercae (Fig. 2).

Effect of A. clavula on C. lacustris

The distribution and abundance of C. lacustris in the alimentary tract of perch during March-June 1975 was not markedly influenced by the presence of A. clavula, or by intensities of the acanthocephalan from 1 to > 5 (Fig. 3). However, the distribution of the nematode vaired rather irregularly, and this was thought to be a result of the overdispersed nature of the infection influencing the distribution of the parasite in the relatively small number of perch available. Many of the peaks of distribution shown in Fig. 3 were the result of a single heavily infected fish markedly influencing the overall percentage distribution of C. lacustris at that intensity of A. clavula. For example, at A. clavula intensity 1, the peak of distribution at intestine II was the result of 5 of 9 nematodes at that site being recovered from a single fish. In addition, the high mean intensity of C. lacustris at A. clavula intensity > 5 was produced by one perch harbouring over 40 nematodes.

Because of the seasonal occurrence of A. clavula (see Chapter X), the influence of this parasite on the distribution and abundance of B. luciopercae and C. lacustris could not be investigated at any other time of the year.

Effect of B. luciopercae on A. clavula

This could not be investigated over a sufficiently large range of intensities of B. luciopercae, since when A. clavula was seasonally abundant (see Chapter X), the range and mean intensity of B. luciopercae was low (see Chapter VII).

Fig. 2. Effect of Acanthocephalus clavula on distribution of Bunodera luciopercae. Gill net samples. March - May 1975.

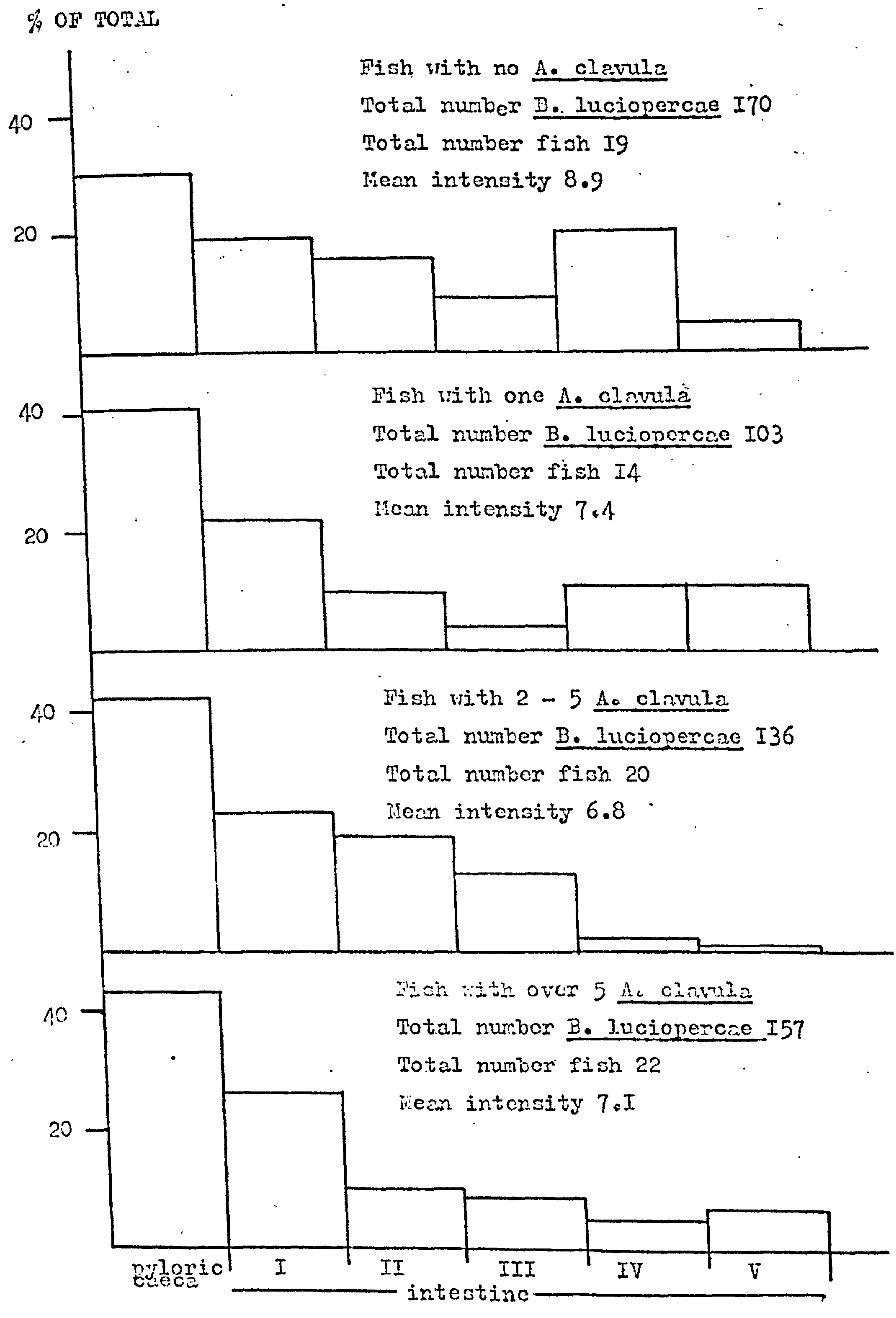
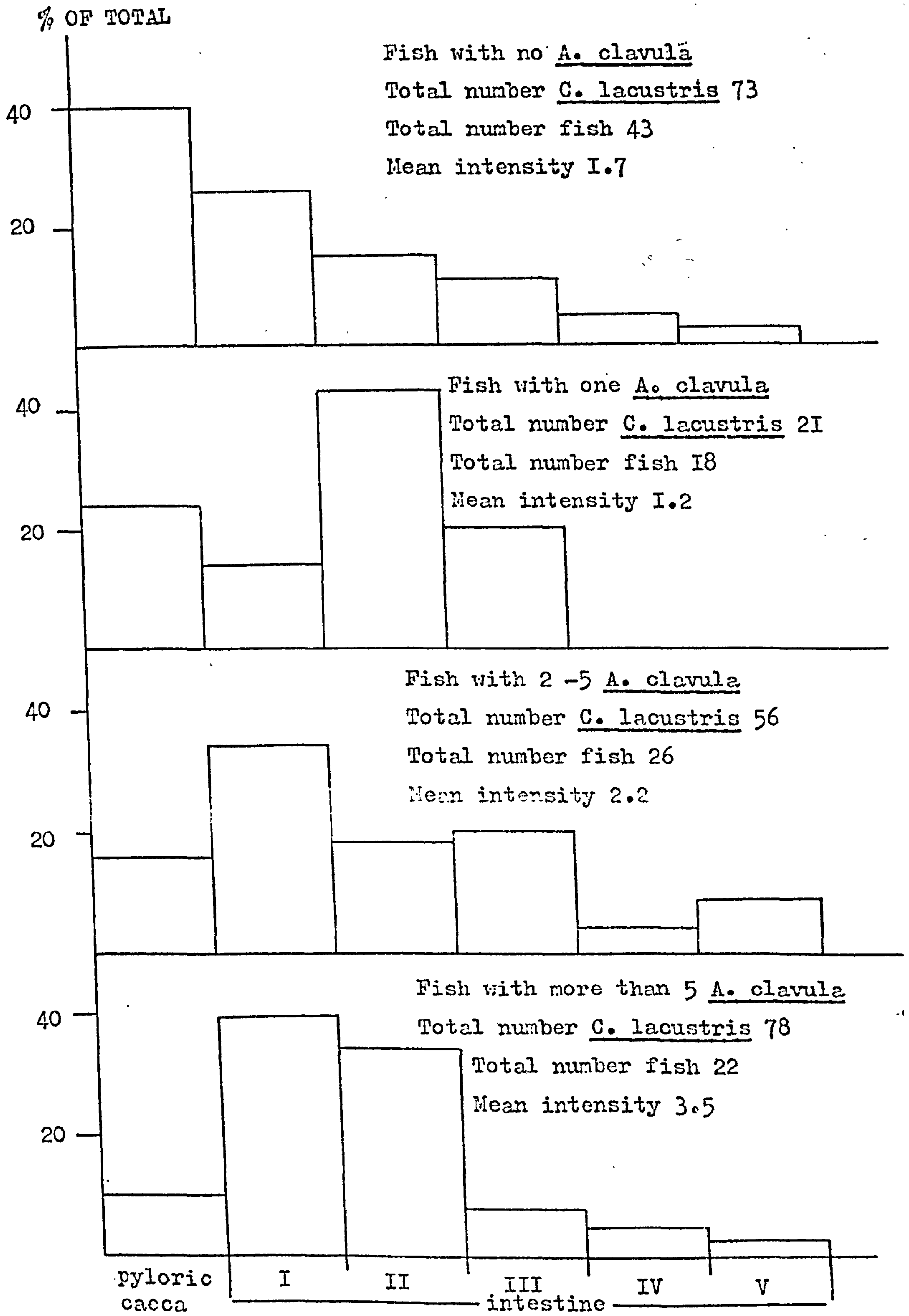


Fig.3. Effect of <u>Acanthocephalus clavula</u> on distribution of <u>Camallanus lacustris</u>. Gill net samples. March - June 1975.



Effect of B. luciopercae on C. lacustris

The distribution of C. lacustris during November-January 1975/76 was not markedly influenced by increasing intensities of B. luciopercae (Fig. 4). The mean intensity of C. lacustris at 1-10, 11-30 and >30 B. luciopercae did not fluctuate markedly (Fig. 4). Because of the high incidence of infection during these months, the distribution of C. lacustris in the absence of the digenean could not be determined. The influence of B. luciopercae on the distribution of C. lacustris during the spring-early summer was not investigated, because of the high incidence of A. clavula (see Chapter X), and relatively small range of intensity of B. luciopercae.

Effect of C. lacustris on A. clavula

The distribution of A. clavula during March-June 1975 was not markedly effected by the presence of C. lacustris, up to an intensity of >5 nematodes/fish (Fig. 5). Similarly, there was no marked change in the mean intensity of A. clavula at intensities of C. lacustris of 300, 1, 1-5 and >5 (Fig. 5). Because of the seasonal occurrence of A. clavula, this part of the study could not be repeated at any other time of the year.

Effect of C. lacustris on B. luciopercae

The distribution of B. luciopercae during November-January 1975/76 was not markedly influenced by the presence of C. lacustris, or by intensities of the nematode up to (and exceeding) 5/fish (Fig. 6). However, there was a fall in the mean intensity of B. luciopercae, from 15.2 when no C. lacustris were present to 10.2 at C. lacustris intensity >5 (Fig. 6). This reduction was analysed statistically using a one way analysis of variance. Since the B. luciopercae population was overdispersed, the counts were transformed using a log (x+1) trans-

Fig. 4. Effect of _Bunodera luciopercae_ on the distribution of _Canallanus lacustris_. Gill net samples. November-January 1975/76.

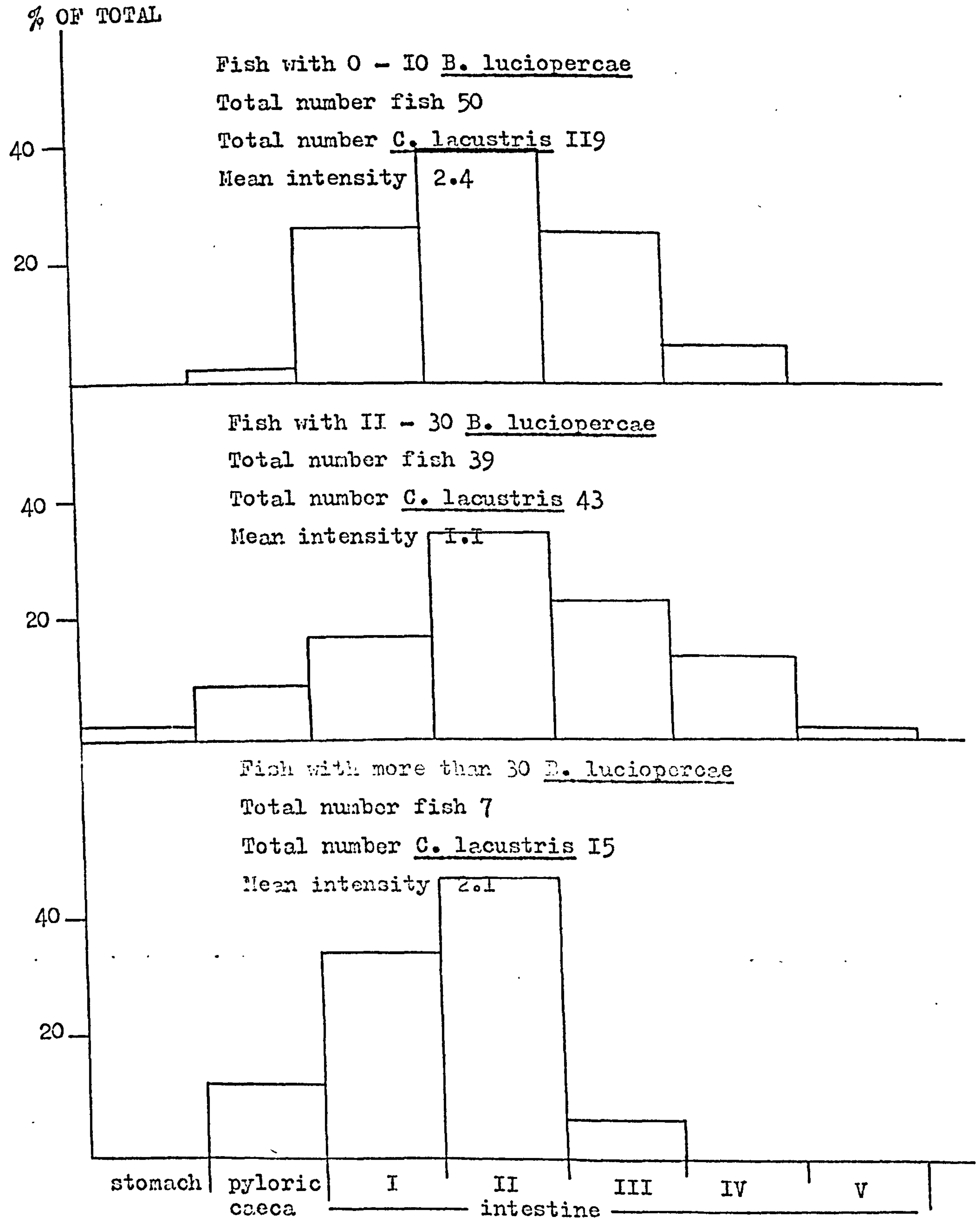


Fig.5. Effect of Camallanus lacustris on distribution of Acanthocephalus clavula. Gill net samples. March - June 1975.

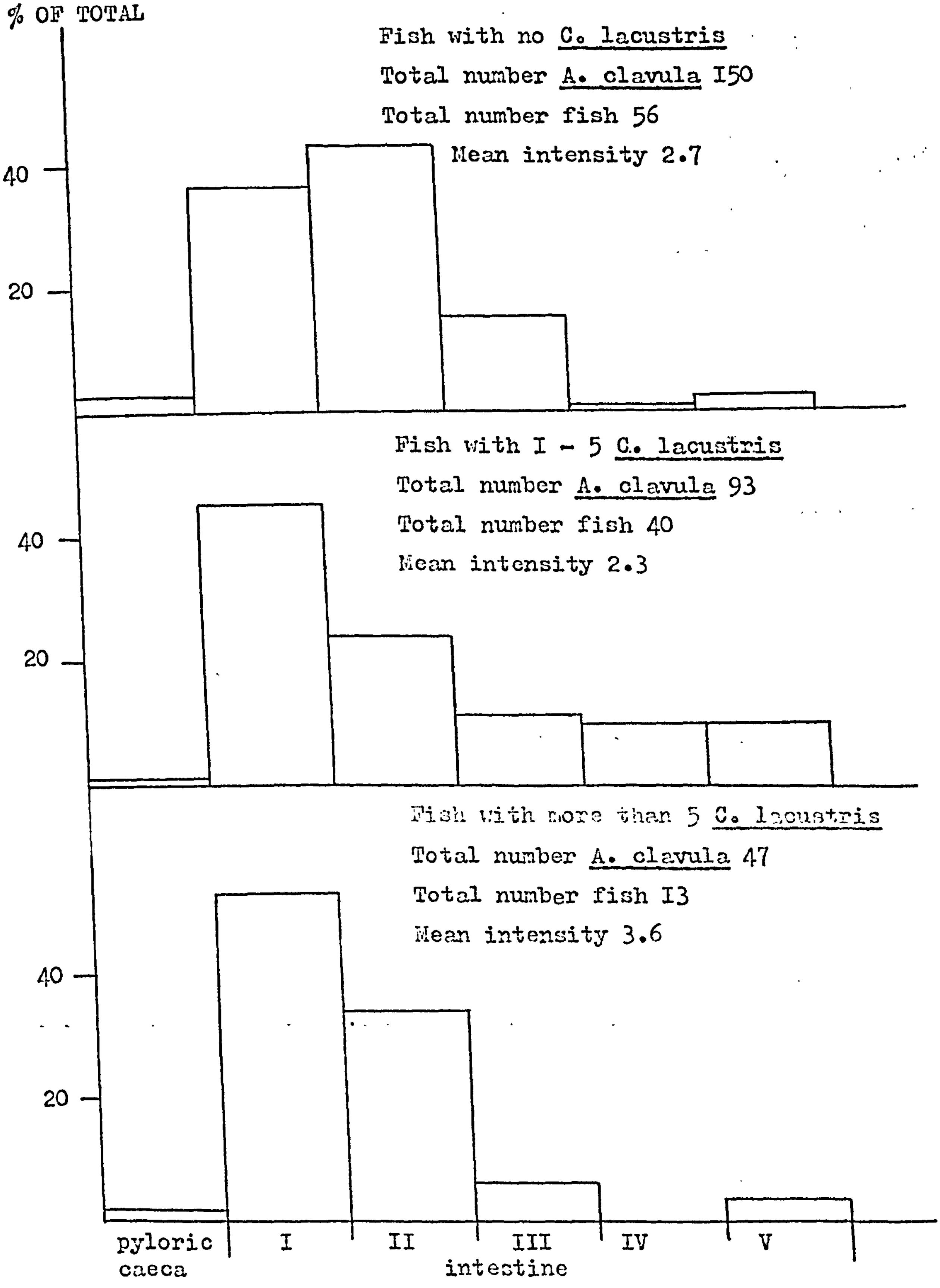
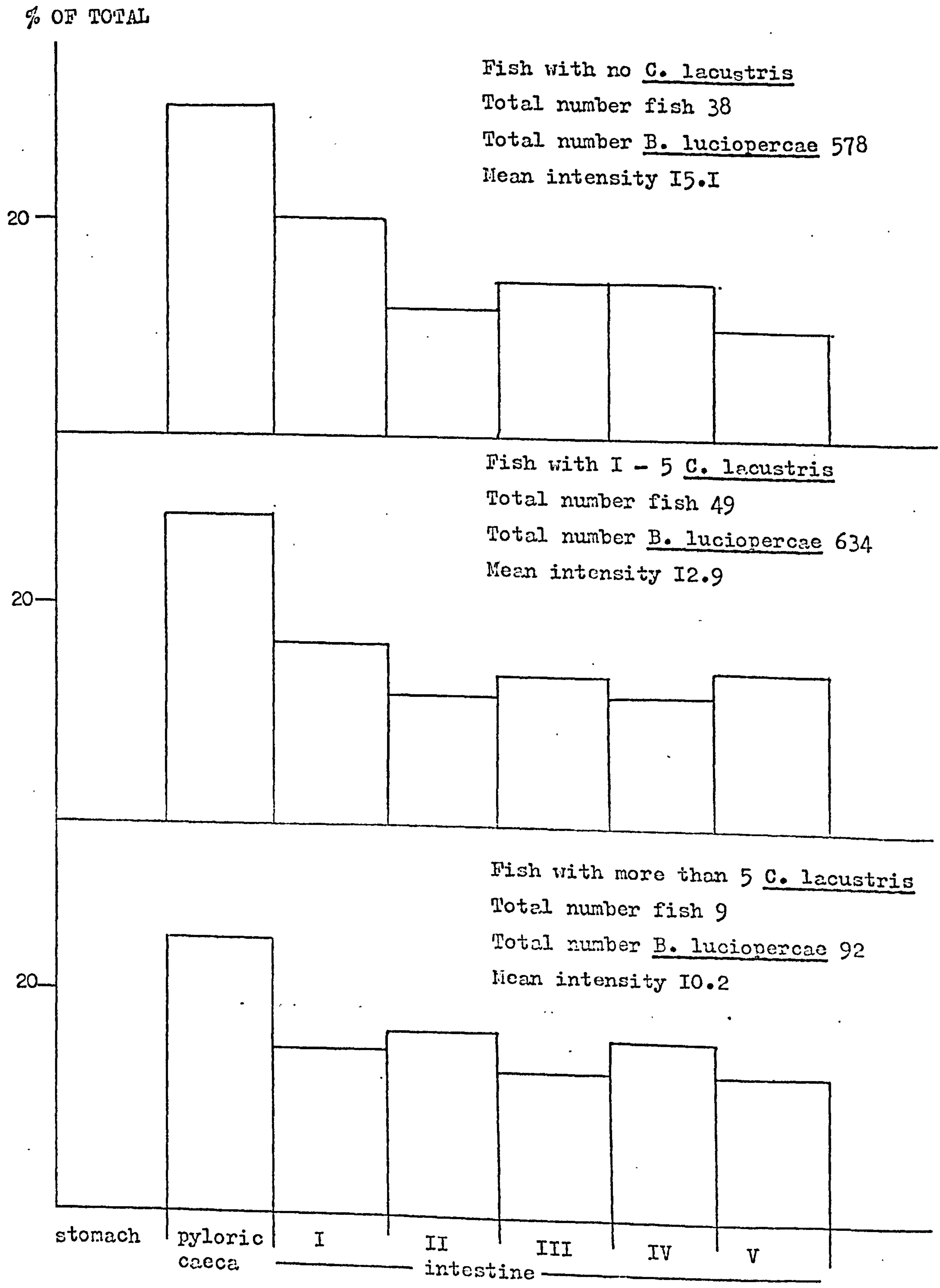


Fig. 6 . Effect of <u>Camallanus lacustris</u> on distribution of <u>Bunodera luciopercae</u>. Gill net samples. November - January 1975/6.



formation. The adequacy of the transformation was checked by a graphical method (Elliot, 1971). The results indicated that there was no significant difference in the intensity of B. luciopercae at increasing levels of intensity of C. lacustris ($F = 1.85$, $V_1 = 2$, $V_2 = 93$, $P > 0.05$).

Because of the high incidence and mean intensity of A. clavula (and possible additional inter-specific reactions), this aspect of the investigation was not repeated during the spring-early summer.

Inter-specific reactions in parasitic helminths have been discussed by Crompton (1973) and Holmes (1973). Similar species (closely related species, or ecological equivalents) coexisting in the same habitat at the same time should either compete, usually to the exclusion of one, or interact so as to specialise and hence segregate their niches (Holmes, 1973). Holmes went on to consider niche specialisation in parasitic helminths, and concluded that they responded to the regular occurrence of competitors in essentially the same way as free-living organisms. Whilst the three helminths commonly found in the alimentary tract of perch at Llyn Tegid were not closely related, there was a considerable degree of overlap in their distribution. Although no detailed observations were made on the specific microhabitat preference of A. clavula, B. luciopercae and C. lacustris within each site, it is known that each species attached (to a greater, or lesser, extent) to the wall of the alimentary tract (Cannon, 1972; Crompton, 1973; Petter et al., 1974; personal observations). However, each of these three helminths are thought to feed by using different mechanisms, and to rely on different nutritional resources. According to Crompton (1973) acanthocephalans feed by the absorption of nutrients that are present in the host alimentary tract lumen, across their tegument. Intestinal flukes often feed by browsing on mucosa or epithelial tissues, and the cellular debris produced during the constant renewal of intestinal epithelium may be a major item in the diet of many trematodes (Smyth, 1966; Crompton, 1973). Many parasitic nematodes which live in close contact with the wall of the host alimentary tract are tissue feeders, and ingest blood, mucosa, contents of lymphatics, products of their own histolytic secretions, or a combination of these (Lee, 1965; Crompton, 1973). Stumpp (1975) stated that Camallanus cotti fed on host blood and intercellular fluids.

Therefore, it was not possible to determine any inter-specific reactions that resulted in a change in the distribution or abundance of one species of helminth, by the presence of a second coexisting species. At the intensities examined the spatial requirements of the three species did not apparently conflict, and the use of different feeding mechanisms and nutritional resources may have been important in limiting inter-specific competition between these helminths.

XI.3. EFFECT OF Diplostomum gasterostei AND Triaenophorus nodulosus ON PERCH

Chubb (1973) considered the influence of parasites on freshwater fish in the British Isles. He pointed out that in nature a fish may be infected by several species of parasites, and a population of fish may be infected by 10, 20 or more species. Each of the parasites contribute to the stress on the fish, and to concentrate on one species without proper regard for the others is wrong (Chubb, 1973). From a review of the salient literature (see Chapter VII and VIII), the potentially most pathogenic parasites infecting perch at Llyn Tegid were Diplostonum gasterostei (Digenea) and Triaenophorus nodulosus (Cestoda). As was noted in Chapter VII and VIII, when the infections of D. gasterostei and T. nodulosus were examined individually they did not markedly effect the growth rate or condition factor (K) of perch. In accordance with the suggestions of Chubb (1973), the influence of combined infections of

D. gasterostei and T. nodulosus on the growth rate of perch was examined (Table II). The age class 4 years was selected because of its abundance in the gill net samples (see Chapter III), and because fish of this age harboured appreciable levels of both parasites, and concurrent infections were common (see Chapter VII and VIII). Perch caught during the essentially non-growing season of October-March (see Chapter III) were used, and the growth rate of male and female fish infected with varying numbers of the two helminths calculated (Table II). Heavy infestations with a single species did not effect the growth rate. Unfortunately, too few fish were heavily infected with both helminths to determine the combined effect of intensities of over 30 D. gasterostei and over 4 T. nodulosus on the growth rate of the fish.

In order to examine any relationship between the intensity of infection with D. gasterostei and the intensity of T. nodulosus, a correlation was applied to the log (x+1) transformed counts. The male and female perch gill netted between January 1975-February 1976 were treated separately. The results indicated that there was no significant correlation between the intensity of the two helminths in male fish ($r = -0.047$, degrees of freedom 181, $P > 0.05$), while there was a very highly significant negative correlation in female fish ($r = -0.214$, degrees of freedom 280, $P < 0.01$). Thus female fish heavily infected with D. gasterostei tended to be lightly infected with T. nodulosus, and vice versa. Cloutman (1975) noted a similar negative correlation between Posthodiplostomum minimum metacercariae and plerocercoids of Proteocephalus ambloplitis infecting large mouth bass (Micropterus salmoides) but did not speculate on the mechanisms involved. Similarly, the significance of the result obtained in this present study, along with the restriction of the phenomenon to female perch, is difficult to interprete. Fish heavily infected with one species may have been physiologically, ecologically and/or behaviorally more resistant/less susceptable to

Table II. Effect of Diplostomum gasterostei and Triaenophorus nodulosus on the growth rate of perch. Gill net samples. January-March 1975, October-February 1976.

MALE FISH

Number Diplostomum gasterostei/ fish	Number Triaenophorus nodulosus/fish 1-4	≥ 5
1-30	12.47±0.24(24)	12.65±0.37(12)
≥31	12.50±0.47(8)	12.40(2)

Total (overall) mean length 12.52±0.19(46)

FEMALE FISH

Number Diplostomum gasterostei/ fish	Number Triaenophorus nodulosus/fish 1-4	≥ 5
1-30	13.60±0.64(32)	12.90±0.77(10)
≥31	14.30±1.42(12)	14.43±0.95(3)

Total (overall) mean length 13.74±0.50(57)

N.B. Mean length ± 95% confidence limits.

Figures in parentheses are number of fish examined.

heavy infestations of the other species. However, it was suggested that female perch heavily infested with T. nodulosus may have suffered a premature mortality (see Chapter VIII). If this was so, female fish that harboured a heavy infestation of T. nodulosus would have died before they could have accumulated a large number of D. gasterostei, since the intensity of the latter parasite tended to increase with host age (see Chapter VII). Therefore, fish heavily infected with D. gasterostei may have largely represented older perch that successfully survived the planktonic phase in their life without acquiring a heavy infestation of T. nodulosus. Those fish that did acquire a heavy burden of the cestode were effectively removed from the population before they could become heavily infected with D. gasterostei. Nonetheless, the occurrence of this phenomenon in other fish-metacercaria-plercercoid systems will lead to a better understanding of the mechanisms involved.

XI.4. INFLUENCE OF HOST AGE ON THE PARASITE FAUNA OF PERCH

Dogiel (cited by Polyanski, 1958) established the following rules concerning the age dynamics of the parasite fauna of freshwater fish:

(1) an increase in incidence and intensity of infestation with host age;

(2) qualitative changes in the composition of the parasite fauna directly proportional to changes in the ecology of the host;

(3) infestation of young fish initially with parasites that have a direct life-cycle or which actively penetrate the fish.

Studies on the effect of host age on the parasite fauna of fish include Gorbunova (1936), Bykhovskaya-Pavlovskaya (1940), Bauer and Nikolskaya (1957), Dogiel (1958), Chappell (1969b), Rumyantsev (1973), Hicks and Threlfall (1973) and Cloutman (1975).

During their first few weeks of life at Llyn Tegid, perch fry were infected by Bunodera luciopercae and Bothriocephalus sp./Eubothrium sp.

(Table III). The occurrence of these two helminths was a result of the planktivorous habits of these fish. Young and older perch were both found at shallow, inshore locations during the summer (June-September). However, the absence of parasites with a direct life-cycle from perch fry may be a reflection on the relatively poor protozoan and monogenean fauna of perch at Llyn Tegid. In addition, the cysts of *Hemeguya psorospermica* were absent from adult perch during June-October, and the data suggested that this may have been a result of increased lake temperatures. The incidence of the only perch monogenean at Llyn Tegid (*Ancyrocephalus percae*) was low during all months.

Juvenile perch aged 8-9 months (examined in March 1976) were infected with 8 species of parasites (*H. psorospermica*, *B. luciopercae*, *Diplostomum gasterostei*, *Tetracotyle* sp. I, *Diphyllobothrium* sp., *Triaenophorus nodulosus*, *Proteocephalus* sp. and *Camallanus lacustris*) (Table III). Juvenile perch were notably planktivorous, and several of these parasite species utilise a planktonic intermediate host. The absence of *Bothriocephalus* sp./*Eubothrium* sp. from these fish may be related to sampling deficiencies, the seasonal availability of infective plankton, or perhaps the fact that perch may feed on different species/groups of plankton at different times of the year, or as they grow older. *Acanthocephalus clavula* was not recorded from the juvenile perch, may be explained by the low occurrence of *Asellus meridianus* in the diet of these fish.

Since the procercoids of *T. nodulosus*, and the free-swimming cercariae of *D. gasterostei* and *Tetracotyle* sp. I, were only available for a few months, it is likely that the juvenile perch acquired these parasites during their early (summer-early autumn) months in the lake.

Unfortunately, insufficient data were available on the parasite fauna of perch aged 1-2++. Adult (gill netted) perch harboured a greater variety of parasite species than the younger fish. In those species that

Table III. Parasite fauna of perch. Purse seine, trawl and gill net samples. January 1975-July 1976.

	I	II	III (i)	III (ii)
H. psorospermica	-	+	+	+
M. muelleri	-	-	+!	-
A. percae	-	-	+	+
B. luciopercae	+	+	+	+
D. gasterostei	-	+	+	+
D. spathaceum	-	-	+	+
Tetracotyle sp. I	-	+	+	+
Tetracotyle sp. II	-	-	+	+
Bothriocephalus/Eubothrium sp.	+	-	+	+
Diphyllobothrium sp.	-	+	+	+
T. nodulosus	-	+	+	+
Proteocephalus sp.	-	+	-	-
C. lacustris	-	+	+	+
C. truttae	-	-	-	+!
R. cristata	-	-	+	+
A. clavula	-	-	+	+
Number species	2(30)	8(36)	14(384)	14(81)

N.B.		
	I	Perch fry, purse seined July 1976, aged 4-6 weeks
	II	Juvenile perch, trawled March 1976, aged 8-9 months
	III	Adult gill netted perch, (i) aged 2-5++, (ii) aged $\geqslant 6$
	-	Absent
	+	Present
	+!	Single infected fish
		Figures in parentheses are number fish examined

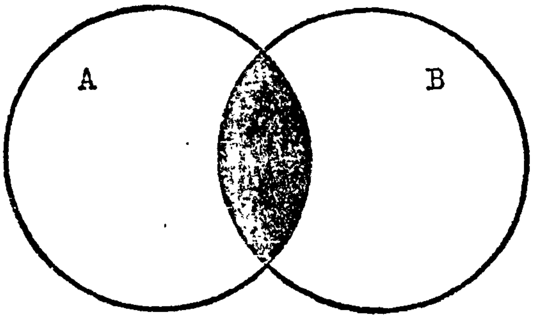
were present in adult and young perch, the adults usually harboured a higher incidence and intensity of infection. However, the cysts of H. psorospermica were most prevalent in juvenile perch, and the occurrence of Proteocephalus sp. was restricted to these fish. This has been discussed in Chapter V and Chapter VIII respectively.

When the adult (gill netted) perch were divided into two age groups (2-5++ and ≥6 years), each harboured a similar collection of 14 species of parasites (Table III). However, there were discrete changes in the quantitative aspects of the infections. It was suggested that the increase in the intensity of B. lucioperca, and the increase in the incidence and intensity of C. lacustris, in older perch was the result of secondary infection from infected prey fish, since plankton feeding was less common amongst older, larger perch. A similar phenomenon may also explain the occurrence of Cucullanus truttae, and the small increase in incidence of Bothriocephalus sp./Eubothrium sp., that was seen in the older age group. A. meridianus was eaten by perch of all ages, and there was no evidence to suggest that older perch acquired A. clavula from infected prey fish.

In addition, the observed fall in the occurrence of plankton in the diet of older perch also caused a change in the nature of the T. nodulosus infection. In young planktivorous perch the state of the infection represented a continuum, with the acquisition of procercoids from infected copepods at one end, and the loss of worms by degeneration and death at the other. Consequently, there was a larger proportion of mature plerocercoids in the younger perch, when compared to the plerocercoids in older fish. In older, largely non-planktivorous perch the recruitment of T. nodulosus effectively ceased and the parasite population gradually degenerated. Because of the relatively long life-span of this cestode (and Diphyllobothrium sp.), the infection was present even in the oldest fish. There was no evidence of secondary establishment of plerocercoids from infected prey fish.

Fig. 7. Effect of host age and feeding habits on the routes of parasitic invasion of perch at Llyn Tegid.

I. Perch less than one year old



NB.

A...parasites with an infective that directly infects perch

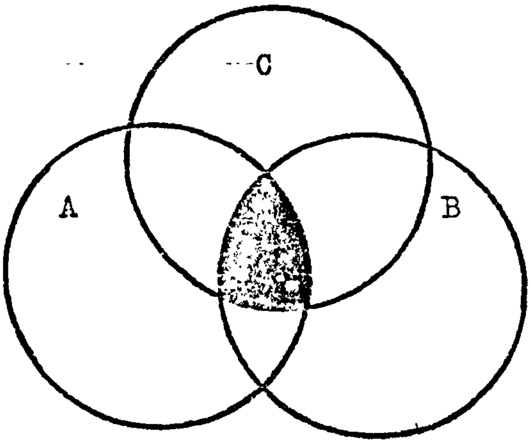
B...parasites with a planktonic intermediate host

C...parasites with a benthic intermediate host

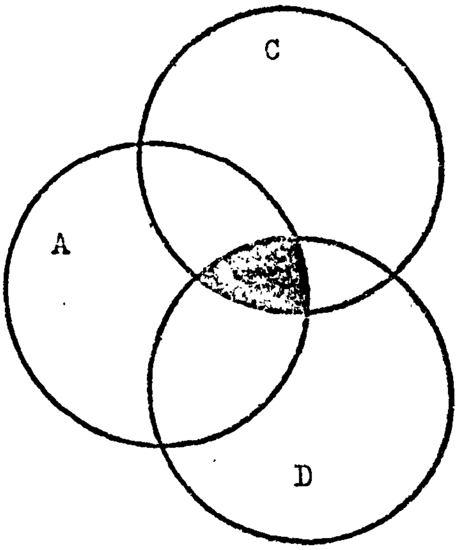
and

D...parasites that may be secondarily acquired

II. Perch aged 2 - 5++



III. Perch aged 6 or over



The incidence of *D. gasterostei* reached a maximum in fish that had spent 2-3 summers in the lake. Since these metacercariae may be long-lived, there was a tendency for the intensity of the infection to increase, as parasites accumulated with host age. Other factors that may have influenced the infection of older perch with *D. gasterostei* were discussed in Chapter VII. Because of the low incidence of *Tetracotyle* spp., superimposed infections were thought to have been unlikely, and the intensity did not increase with host age.

Host feeding habits were a major influence on the parasite fauna of perch of all ages. The relationship betwee host age, feeding habits, and the routes of parasitic invasion are shown in Fig. 7. These results largely support the rules proposed by Dogiel (see start of section), though at Llyn Tegid perch fry were initially infected with parasites that utilised a planktonic intermediate host (e.g. *B. luciopercae*), in addition to those that relied on diet penetration (e.g. *D. gasterostei*).

XI.5. INFLUENCE OF HOST SEX ON THE PARASITE FAUNA OF PERCH

Several studies have revealed that host sex may influence the infection of fish with certain parasites (e.g. Thomas, 1964; Paling, 1965; Kennedy, 1968; Cannon, 1973; Shotter, 1973). Such differences may be produced by variations in physiological, ecological and/or behavioral resistance (Thomas, 1964), including variations in host susceptability or attractiveness, or as a result of differences in the feeding habits, of male and female fish (Kennedy, 1970; Cannon, 1973). However, differences in the parasite infections of fish in relation to host sex have been demonstrated much less often than in relation to (for example) host age (Kennedy, 1970).

Whilst there were discrete differences in the infection of certain parasite species (e.g. Bunodera luciopercae, Tetracotyle sp. I, Triaenophorus nodulosus, Raphidascaris cristata), host sex did not produce any marked influence on the parasite fauna of perch at Llyn Tegid. Chappell (1969b) and Cloutman (1975) reported similar results on the parasite fauna of the fish in their studies. Physiological, ecological and/or behavioral differences between the sexes may have been such that they produced little effect on the parasite fauna of male and female fish. However, Thomas (1964) noted that the influence of host sex may be obscured by seasonal changes in parasite occurrence, and that seasonal reversals in the infestation patterns of the two sexes may be self cancelling. Clearly further studies should be aimed at elucidating the importance of these two factors on the apparent similarity of the parasite fauna of male and female perch at Llyn Tegid.

XI.6. SEASONAL CHANGES IN THE PARASITE FAUNA OF PERCH: "THE YEAR OF THE PERCH"

From the data collected from 465 adult perch gill netted between January 1975-February 1976, the parasite fauna may be divided into the following groups.

(a) Parasite species of low occurrence, where the presence or absence of seasonal occurrence and/or maturation could not be established (i.e. Myxobolus muelleri, Ancyrocephalus percae, Diplostomum spathaceum, Tetracotyle sp. II, Proteocephalus sp., Cucullanus truttae and Raphidascaris cristata).

(b) Parasite species which exhibited seasonal occurrence and/or maturation (i.e. Henneguya psorospermica, Bunodera luciopercae, Bothriocephalus sp./Eubothrium sp. and Acanthocephalus clavula).

(c) Parasite species with no well defined pattern of seasonal occurrence and/or maturation (i.e *Diplostomum gasterostei*, *Tetracotyle* sp. I, *Diphyllobothrium* sp., *Triaenophorus nodulosus*, and *Camallanus lacustris*).

There now follows a general account of the seasonal changes in the biology of perch and its parasite fauna at Llyn Tegid.

January-February. The lake temperature was 5.5°C at the surface and at 10m. Perch were less active during the cooler winter months, as indicated by the poorer gill net catches. At this time of the year perch were found predominantly in approximately 12m of water. Empty stomachs were relatively common, though *Asellus meridianus*, cyclopoid Copepoda, dipteran larvae (and to a lesser extent, pupae) were all eaten. Larger perch were found to have ingested other fish.

The population of *B. luciopercae* was primarily at stages I-II (see Appendix III), and the presence of stage I flukes may have been an indication of recent recruitment. The incidence and mean intensity were relatively stable. *B. luciopercae* containing eggs (stage IV) were present in February, before the spring rise in temperature. Pisidia were found to harbour redia containing immature cercariae. Whilst plankton were ingested, *Bothriocephalus* sp./*Eubothrium* sp. was absent from perch during the winter months of November-February, perhaps as a result of the seasonal availability of infective plankton, in relation to the species (or small numbers) of those crustaceans that were eaten. There may have been a release of first stage larvae of *C. lacustris* during most months, though the results suggested that this may have been restricted during the mid-winter months (December-February). Recruitment of *B. luciopercae* and *C. lacustris* into large perch was most likely to have occurred during December-February (and July-September) when cannibalism was observed.

March-April. According to the thermistor readings the lake temperature (at surface and 10m) was still at 5.5°C. However, the data supplied by the Dee and Clwyd River Division indicated that lake temperature had begun to rise in late March-April (see Chapter II). Gill net catches were larger during these months, indicating increased perch activity. Fewer empty stomachs were found, and there was a peak of *A. meridianus* ingestion. The incidence of cyclopoid copepods in perch stomachs was low, and the incidence of other plankton very low. Dipteran larvae were an important dietary component. Perch were largely restricted to deeper water, and the fall in the percentage of closed opercula indicated the start of the growing season.

There was a fall in the mean intensity of *B. luciopercae*, and stage I flukes were relatively uncommon. Input of flukes was very low, and the fall in intensity may have been produced by the loss of gravid worms as lake temperatures began to rise. Pisidia were infected with redia containing immature cercariae. The maximum egg production of *T. nodulosus* in pike (*Esox lucius*) during April-May (Chubb, 1963b) resulted in the seasonal availability of infective plankton. Recruitment of *T. nodulosus* into perch was restricted to the spring-summer months. Developing plerocercoids were recorded in March and June. Juvenile *Bothriocephalus* sp./*Eubothrium* sp. were recorded in most months that plankton were eaten. *A. meridianus* containing infective stages of *A. clavula* were present in all months, with an approximate incidence of 2.0%. As a result of the prevalence of *A. meridianus* ingestion by perch, the incidence and mean intensity of *A. clavula* reached a peak in April-May. As the intensity increased the chances of inter-sexual contact and copulation were greater, and hence there was a peak in the occurrence of female worms with shelled acanthors. During March-June, as a result of the post-copulatory death of male worms, there was a greater proportion of female *A. clavula*.

May-June. The lake temperature was 9.5-11.5°C at the surface and 8.5-10.5°C at 10m. Perch activity was much increased and gill net catches were very high. There were very few empty stomachs at this time. Whilst there was a fall in the ingestion of *A. meridianus*, the incidence of Cladocera in perch stomachs had increased, and calanoid and cyclopoid Copepoda were also eaten. Dipteran pupae and larvae, and nymphal Plecoptera were all important dietary components. Perch had undergone their shoreward migration, though this fish was still abundant in deeper water. Spawning occurred during June-July. Spent male gonads were found only in these months, and during July all of the female gonads were spent.

The cysts of *H. psorospermica* were absent from perch at all depths in Llyn Tegid during June-October, when lake temperature (at surface and 10m) exceeded 10.0°C. As lake temperatures rose the loss of gravid *B. luciopercae* continued. Since infective plankton was not yet available, few stage I flukes were found and the input was low. Consequently, the incidence and mean intensity fell. Also in response to increased temperatures, pisidia released the cercariae of *B. luciopercae* over a short period of time. With the passage of gravid flukes into the external environment, bivalves became infected with the next generation of *B. luciopercae*. The decrease in the ingestion of *A. meridianus*, along with the post-reproductive loss of male and female *A. clavula*, resulted in a fall in the incidence and mean intensity of the parasite infection. The majority of remaining females contained shelled acanthors.

Cercarial release in *D. gasterostei* and *Tetracotyle* sp. I was likely to have been dependent on an increase in temperature, and the distribution of these infective stages was thought to have been restricted to the inshore littoral habitat of the molluscan intermediary. Perch became infected by these strigeoids whilst in shallow water during the summer months.

July-August. The lake temperature at the surface was approximately 19.5°C, and the temperature at 10m was approximately 13.5°C. Gill net catches were high, and few empty stomachs were found. Plankton feeding was prevalent, and dipteran larvae and pupae, and ephemeropteran and plecopteran nymphs were all important food items. Larger perch appeared to feed on other fish. The perch population was distributed from shallow, littoral regions down to a depth of 12m.

As a result of the availability of plankton containing the metacercaria of B. luciopercae in relation to the prevalence of plankton ingestion by perch, the incidence and mean intensity of this parasite in perch reached a peak in August. The flukes were primarily at stage I, and the infection was considered to be in a dynamic state, with a high input and output of B. luciopercae, perhaps influenced by intra-specific reactions at high intensities. Intra-molluscan development proceeded, with the occurrence of sporocyst and relial stages. The recruitment of C. lacustris into perch was not restricted to a particular season. Whilst the incidence and mean intensity did not exhibit any regular seasonal fluctuations, the incidence of third and fourth larval stages in perch was low during some months (e.g. July-September) when plankton feeding was common. Recruitment of B. luciopercae and C. lacustris into large perch was most likely during July-September (and December-February) when a small peak of cannabilism was observed. Since A. meridianus was not a major food item, the incidence and mean intensity of A. clavula, and the occurrence of females with shelled acanthors, was low.

September-October. The thermocline disappeared in late September-early October. During October the lake temperature at surface and 10m was 11.0°C. Coincident with the disappearance of the thermocline was the autumn return of perch to deeper water. Gill net catches were still large, though there was an increase in the occurrence of empty stomachs. A. meridianus, dipteran larvae and pupae, and Hydracarina were all eaten, though there was a marked fall in the ingestion of plankton during October. From September onwards there was a gradual increase in the size of the female gonads, though maximum size was not attained until February-May. In contrast, male gonads which appeared to have reached their maximum size were present as early as October.

The incidence and mean intensity of B. lucioperca*e* was high in September, but the intensity markedly decreased in October. This was considered to have been a result of a fall in input (as plankton feeding decreased) in relation to the continued output of flukes (because of intra-specific reactions at high intensities). The population of B. luciopercae was at stage I and II, and some of the flukes present in October may have survived to reach maturity the following spring-summer. The slow intra-molluscan development of this parasite continued. A slight increase in the ingestion of A. meridianus may have produced a small autumn increase in the incidence and mean intensity of A. clavula, along with the occurrence of females with shelled acanthors during September-November.

During the summer months, perch from shallow water harboured a higher incidence and intensity of D. gasterostei and Tetracotyle sp. I, than the perch in deeper water. When the perch from shallow water returned to deeper water in the autumn, the seasonal aspects of these infections were obscured as the lightly and more heavily infected fish mixed.

November-December. The lake temperature at surface and 10m was 7.0-8.5°C. Gill net catches indicated that perch activity was reduced, and there was a high incidence of early stomachs. Dipteran larvae and cyclopoid copepods were eaten, though the incidence of A. meridianus and other plankton in the diet of perch was low. The perch population was largely restricted to deeper water, and the increase in the incidence of closed opercula indicated that the growing season had ended.

As the lake water cooled, cysts of H. psorospermica were again found on the gills of perch. The incidence and mean intensity of B. lucioperсae remained fairly constant. The presence of stage I flukes was taken to have indicated recent recruitment, and the population of the parasite was primarily at stage I and II. Falling lake temperatures may have stimulated the production of immature cercariae of B. lucioperсae within pisidia, and adult flukes appeared to require an extended period at low temperatures for their normal development. The incidence of A. meridianus in the diet of perch resulted in a low incidence and mean intensity of A. clavula.

XI.7. CONCLUSIONS AND SUGGESTIONS FOR FURTHER WORK

It was not possible to determine any interspecific reactions that resulted in a change in the distribution or abundance of the three most common members of the alimentary tract fauna (i.e. A. clavula, B. lucioperсae, C. lacustris). There was a very highly significant correlation between the intensity of D. gasterostei and T. nodulosus in female perch. Further studies should be aimed at elucidating the factors responsible for this phenomenon.

Host sex did not have any marked influence on the parasite fauna of perch. However, host feeding habits were a major influence on the parasite fauna of perch of all ages. The results suggested that environmental temperatures, and changes in host distribution and feeding habits, were important influences on seasonal changes in the parasite fauna of perch at Llyn Tegid. High temperatures may have an adverse effect on the early developmental stages of H. psorospermica, and cysts were only recorded from perch when lake temperatures were below 10.0°C. Further studies should include the identification of the infective agent of this parasite, the study of the seasonal occurrence of the early developmental stages of H. psorospermica in perch, and the elucidation of the influence of host biology on the infection process. Increasing temperature was thought to have stimulated cercarial release in *D. gasterostei* and *Tetracotyle* sp. I. Since the cercariae of these two strigeoids do not expand far beyond the restricted littoral habitat of the molluscan intermediary, perch acquired the infection when they were present in shallow water during the summer months. The lower incidence and intensity of the infection at the deeper site during these months suggested that the shallow and deep water perch communities were discrete, and only mixed during the autumn when the thermocline disappeared. This suggestion requires further investigation and the biological characteristics of the shallow and deep water perch communities determined. Whilst an increase in temperature may also have stimulated cercarial release in *B. lucioperсae*, a fall in temperature during the autumn may have initiated the production of immature cercariae. Recruitment of *B. luciopercae* into perch was dependent upon host feeding habits, in relation to the availability of infective plankton. It was considered that an extended period at low temperatures was necessary to allow the normal development of adult flukes, and that gravid *B. luciopercae* were released in response to a rise in temperature. Temperature was clearly a major co-ordinating factor in the life-history of this parasite, and further studies should be aimed at investigating this phenomenon in greater detail under controlled, experimental conditions. Temperature may also be important in stimulating egg release from adult *T. nodulosus* in pike, and the infection of perch with developing plerocercoids was dependent on the spring-summer availability of infective plankton, in relation to perch feeding habits. Host feeding habits were an important influence on the seasonal occurrence and maturation of *A. clavula* in perch, since lake temperatures never fell low enough to prevent parasite maturation. The host and environmental influences on the development of *C. lacustris* in perch require further field (and also laboratory) investigation.

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Appendix I. Course of gonad maturation (after Nikolsky, G.V. (1963) The Ecology of Fishes. Academic Press, London and New York).

STAGE I. Young individuals that have not yet spawned.

STAGE II. Quiescent - gametes have not yet started to develop or have already been discharged. Gonads of a very small size; eggs not visible to the naked eye.

STAGE III. Ripening - eggs visible to the naked eye; the gonads increase weight very rapidly.

STAGE IV. Ripeness - gametes ripe; gonads have reached their maximum size. Gametes do not yet run out when light pressure is applied.

STAGE V. Reproduction - gametes run out on application of light pressure to the thorax. The weight of the gonads rapidly decreases from start to finish of spawning process.

STAGE VI. Spent - gametes extruded, and cavity of gonad swollen. Gonad has the appearance of an empty sac. A few eggs may remain in females, and a few sperms in males.

APPENDIX II

Parafin embedding schedule-manual (clear in methyl benzoate)

		Thickness of tissue	
	4mm	2mm	1mm
	(time in hours)		
50% ethyl alcohol	3	2	1
70% ethyl alcohol (may be left overnight, or stored)	2	1	1
90% ethyl alcohol	2	1	1
95% ethyl alcohol*	2	1	1
Absolute ethyl alcohol* I	2	1	½
II	2	½	¼
Methyl benzoate I (may be left overnight, or stored)	2	1	½
II (may be left overnight, or stored)	1	½	½
Benzene I	1	½	½
II	1	½	½
III	1	½	½
Benzene/wax mixture (optional)	2	1	½
Wax** I	2	1	1
II	2	1	½
III	2	1	½

——— BLOCK ———

N.B. *The use of 95% alcohol may replace absolute alcohol in an alcohol-methyl benzoate schedule, thus preventing excessive tissue hardening.

**By the use of negative pressure during wax baths II and III the total time spent in molten wax may be shortened (to 4-5 hours for tissue 4mm thick)

Appendix III. Scale for the assessment of the state of maturity of *Bunodera luciopercae* (modified from Wootten, 1973c)

Stage (I). Small, juvenile worms. Gonads very small; vitellaria not yet visible.

Stage (II). Gonads starting to develop; vitellaria small or just starting to develop.

Stage (III). Gonads full size; vitellaria large and clearly visible.

Stage (IV). Eggs starting to appear in uterus.

Stage (V). Gravid worms. Eggs fill much of the posterior $\frac{2}{3}$ of the body.

The scale is a continuum with newly acquired flukes (stage (I)) at one end, and gravid flukes (stage (V)) at the other.