THE BIOLOGY OF THE PARASITE FAUNA OF
PERCH (Perca fluviatilis L.) FROM
LLYN TEGID, NORTH WALES

THESIS SUBMITTED IN ACCORDANCE WITH THE
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Abstract

With the aim of studying the biology of the total parasite fauna of perch (<u>Perca fluviatilis</u> L.), 559 fish were examined from Llyn Tegid (North Wales) over a period of 19 months. The fish were caught using gill nets, a mid-water trawl and a purse seine, and examined using dissection and histological techniques. Data on relevant aspects of host biology were collected. The effects of host age, length and sex on the parasite fauna were investigated, and special attention paid to seasonal occurrence and/or maturation.

The parasite fauna of perch may be influenced by several factors, including the diversity and abundance of the ichthyofauna and aquatic invertebrate fauna, the abundance of the local piscivorous avian fauna, and the history and geographical isolation of the environment.

The following species of parasites were recovered.

<u>Myxobolus muelleri</u> was recorded from one fish. The cysts of <u>Henneguya psorospermica</u> exhibited seasonal occurrence during June-October, which may have been related to environmental temperatures. There was a peak of occurrence in perch aged O++.

The occurrence of <u>Ancyrocephalus percae</u> was low, and previous British records of <u>A. paradoxus</u> referred to <u>A. percae</u>. There was a low occurrence of <u>Diplostomum spathaceum</u>. <u>D. gasterostei</u> was a common parasite of perch, and the intensity increased with host age. <u>Tetracotyle</u> sp. was recovered from the eye and swimbladder, though the occurrence at both sites was low. There was a higher intensity of <u>Tetracotyle</u> sp. in male perch, and the reasons for this were discussed. The results suggested that perch acquired new infections of <u>D. gasterostei</u> and <u>Tetracotyle</u> sp. whilst in shallow water during the summer months. The taxonomy of these metacerial parasites (particularly <u>D. gasterostei</u>) was considered in detail.

The seasonal development and maturation of _Bunodera luciopercae_ in molluscan (intermediate) and perch (definitive) hosts was studied under natural and laboratory conditions. Temperature was an important influence on the life history and development. As a result of secondary infection, the intensity increased in larger, cannabilistic perch.

There were no seasonal changes in the occurrence of _Diphyllobothrium_ sp. The incidence reached a peak in fish aged 2-2++. _Triaenophorus nodulosus_ was prevalent in fish that had spent at least two summers in the lake. The effect of host age on feeding habits of perch, along with seasonal changes in feeding habits, was a major influence on the epizootiology of _T. nodulosus_. There was a significant change in the size and structure of the _T. nodulosus_ population since 1957/58. The occurrence of _Bothriocephalus_ sp./_Eubothrium_ sp. was low, though the incidence tended to increase in older perch. _Proteocephalus_ sp. was only recorded from perch aged 0++.

There were no marked seasonal changes in the occurrence of _Camallanus lacustris_, though seasonal changes in the dynamics of the infection were discussed. There was a decline in the occurrence of larvigerous female nematodes during the winter months. The occurrence of _C. lacustris_ increased with host age, as older perch acquired the parasite as a result of their cannabilistic habits. _Cucullanus truttae_ was recorded from one perch. The incidence and intensity of _Raphidascaris cristata_ was low.

There were spring-summer and autumn-winter peaks in the occurrence and maturation of _Acanthocephalus clavula_, that were related to host feeding habits. Perch acquired the infection during their second year in the lake, and thereafter there was no marked change in occurrence with host age.

Overdispersion was common in the parasite fauna of perch, and the factors responsible for this were discussed. The influence of

D. gasterostei and T. nodulosus on perch was considered, and inter-
and intra-specific relationships within the parasite fauna investigated.

FOR MY PARENTS....IN MEMORY OF THINGS IN CLOTH BAGS

CHAPTER XI.

CHAPTER I

INTRODUCTION

Pearse (1926) stated that "the ecology of parasites offers an attractive field. It is hoped that it will be increasingly cultivated by scientific men. It should yield rich harvests, not only to scientists and scholars, but also to those who are interested in the advancement of the human race". However, it was not until the publication (in English) of the extensive reviews of Russian work (e.g. Dogiel et al., 1958; Bauer, 1959; Dogiel, 1962), that there was a significant development in the interest of the ecology of the parasites of freshwater fish in the British Isles and North America. An appreciation of the literature that is now available may be obtained from Hoffman (1967), Taylor (1970), Kennedy (1974), Chubb (1977) and Chubb (in prep.).

Many of the studies on ecological aspects of fish parasitology in the British Isles have been concerned with a single species (or related group of species) of parasites (e.g. Awachie, 1963; Hine & Kennedy, 1974a, b; Rojanapaibul, 1977), or with the study of the parasite fauna of the fish of a freshwater environment in general terms (Chubb, 1961, 1963; Rizvi, 1964; Mishra, 1966; Mishra & Chubb, 1969; Wootten, 1972, 1973). As a result of this, the details on the TOTAL parasite fauna of individual fish species (along with host-parasite relations) are often lacking.

Parasitologists have recognised for some time that the parasitic flora and fauna of an animal or plant, together with the host and its environment, form an interacting, ecological complex (Hair & Holmes, 1975). Pavlovski (cited by Dogiel, 1958) termed this complex a "parasitocoenosis", although the term "parasite-mix" (Noble, 1960) is now more frequently used. Since most fish harbour

several species of parasites simultaneously, the entire parasite-mix of the host must be considered to properly interprete host-parasite relationships (Cloutman, 1975). The community approach to the study of fish parasitology has been emphasised by Dogiel et al. (1958), Noble (1960) and Noble et al. (1963).

The parasite fauna of perch (Perca fluviatilis L.) at Llyn Tegid was chosen as the subject of a detailed investigation for several reasons.

There waa a considerable amount of comparative information on the parasite fauna of perch in the British Isles, though these studies were performed at shallow, eutrophic lacustine (or canal) environments (see Chapter IV). Llyn Tegid is a deep glacial lake, that is considered to be late oligotrophic-early mesotrophic in character. A substantial amount of data already existed on the lake, its fish and their parasite fauna (see Chapter II), and the University of Liverpool maintains a freshwater biology laboratory at the lakeside, where boats, nets and other equipment were conveniently available. Previous studies at Llyn Tegid (e.g. Chubb, 1961; Ail, 1973) indicated that perch could be caught in reasonable numbers for most of the year, and Sterba (1972) considered that perch was well suited to aquarium life. Whilst there were problems associated with the transfer of live, healthy fish from Llyn Tegid to Liverpool (see Chapter VII), several local Merseyside lakes contained large populations of perch that were easily seine netted for use in laboratory studies.

In the following chapters the parasite fauna of perch from Llyn Tegid (North Wales) is described in detail.

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CHAPTER II

DESCRIPTION OF THE ENVIRONMENT; ROUTINE FIELD AND LABORATORY TECHNIQUES

II.1 Description of the environment

Detailed descriptions of the geological physio-chemical and biological features of Llyn Tegid have been given by Chubb (1963), Hunt and Jones (1972a, b) and Woolland (1972). A brief description of the lake is included here.

Llyn Tegid lies in a glaciated valley 160m above sea level. It is the largest natural freshwater lake in Wales, and is situated in an area of considerable scenic beauty (the Snowdonia National Park). The town of Bala is found at the northern end of the lake. Llyn Tegid is approximately 6 Km long, by up to 1 Km wide, with a surface area of 4.5 square Km (1100 acres). The lake is rectangular in outline, with steep sides and gently sloping ends, and a flat bottom. Since the long axis lies in a northeast to southwest direction, the lake is exposed to the full force of the southwesterly gales.

The lake is fed by five rivers, and a number of small streams. The rivers are Afon Gly, Afon Twrch, Afon Dyfrdwy (Little Dee), Afon Lliw and Afon Llafar. The underlying rocks are predominantly acid sandstones and shales, and the catchment area is mainly used for upland grazing. There is a little limestone at the head of the Afon Glyn, which adds small quantities of calcium to the lake. However, the waters of Llyn Tegid are essentially soft, slightly acid or neutral, and poor in electrolytes (Ball and Jones, 1960). There is a pH of between 6.1-7.7 (Hunt and Jones, 1971a). The lake is drained at its' northern end by the river Dee.

Stratification usually occurs during the late spring and summer, although it may be upset by high winds. A thermocline normally forms at about 15m, and the lake becomes homothermal in late September-October.

Dŭnn (1952) found that the water in the hypolimnion became   little

depleted in oxygen. Whilst the later study of Hunt and Jones (1972a)

revealed a drop in oxygen saturation, it was found to be in excess of

50% saturated (even in midsummer). The lake temperatures recorded

during this study are shown in Figs. 2 and 3.

The maximum depth of the lake is 40m, and a bathymetric survey

was produced by Dr. J.W. Jones O.B.E. (University of Liverpool) in

1951 (Fig. 1). However, owing to the development of the Bala Catchment

(flood prevention) Scheme, there has now been a reduction of the area

within the 0-5m contour. Before the onset of the scheme in 1955, the

lake level was approximately 163.5m above sea level (Smith, pers. comm.).

There was a small fluctuation in level of about 2m (Hynes, 1961). The

completion of the scheme in 1956 has resulted in a drop in mean lake level.

Under present conditions the lake is maintained at about 160-161m in winter

and 162m in summer (Smith, pers. comm.). Llyn Celyn was formed by the

damming of the Afon Teweryn, in the headwaters of the River Dee System.

This was completed in 1964, and is important in preventing the irregular

and rapid changes in water level seen at Llyn Tegid between 1955-65 (Hunt

and Jones, 1972b).

The littoral fauna has been studied by Dunn (1952; 1961), Hynes (1961)

and Hunt and Jones (1972b). Before 1955, Llyn Tegid was composed of a

compact, gently shelving, rocky littoral zone. This abruptly gave way to

a steep sided, muddy sub-littoral at about 3-5m in depth. The lowering

of the mean lake level has resulted in the loss of much of the original,

rocky littoral zone. Hence the lake is now steep sided, and the bottom

muddy almost to the lake surface (Hunt and Jones, 1972a). Despite initial

drastic reductions in the littoral fauna, evidence exists that recolonisation

is occurring (Hynes, 1961; Hunt and Jones, 1972b). The long term effects

of the regulation of lake level have produced an enormous increase in the

total number of animals in the littoral zone. Hunt and Jones (1972b)

Fig. 1.   Bathynetric survey of Llyn Tegid.
          Contours in feet.

Fig 1

report that this is primarily because of huge increases in the populations of Chironomidae and Oligochaeta. They further consider that the gradual removal of silt by wave action, and the re-establishment of macro-vegetation will result in the littoral zone returning to its original physical status (assuming that the fluctuations in water level are not increased). The adaptation of the fauna and its reversion to the original composition is postulated (Hunt and Jones, 1972b).

The profundal fauna has been studied by Dunn (1952; 1961) and Hunt and Jones (1972a). Hunt and Jones also report a significant increase in the productivity of the profundal since the 1951/52 survey, again principally because of large increases in the Chironomidae and Oligochaeta. Since oxygen conditions in the profundal zone never fall below 50% saturation, it was concluded that the availability of food determined the abundance of the benthic fauna. The factors which may have contributed to this increased productivity are discussed by Hunt and Jones (1972a).

The zooplankton has been investigated by Thomas (1959) and Mills (in prep.).

Fourteen species of fish have been recorded from Llyn Tegid (Table I). The first record of rudd (S. erythropthalmus) was described by Andrews (in press). The biology of the fish has been investigated in detail by the staff and students of the Department of Zoology, University of Liverpool. These studies include: Jones (1953, 1956); Dunn (1954); Ball and Jones (1960, 1962); Ball (1961); Graham and Jones (1962); Siddiqui (1967, 1969); Haram (1965, 1968, 1971); Hancock (1972); Woolland (1972); Ali (1973); Rimando (1973); Chubb et al (1975); Woolland and Jones (1975) and Coles (in prep.).

The protozoan and metazoan fish parasites have been studied by Chubb (1961, 1963a, b, 1964a, b, c, 1970). Other studies include Ball (1957), Nicholas and Jones (1959), Aderounmu (1965, 1966, 1967); Abolarin (1966);

Table I. Fish species recorded from Llyn Tegid

1	<u>Salmo salar</u> L.	Salmon
2	<u>Salmo trutta</u> L.	Brown trout
3	<u>Thymallus thymallus</u> (L.)	Grayling
4	<u>Coregonus lavaratus</u> (L.)	Gwyniad
5	<u>Esox lucius</u> L.	Pike
6	<u>Cottus gobio</u> L.	Bullhead
7	<u>Perca fluviatilis</u> L.	Perch
8	<u>Phoxinus phoxinus</u> (L.)	Minnow
9	<u>Gobio gobio</u> (L.)	Gudgeon
10	<u>Noemacheilus barbatula</u> (L.)	Loach
11	<u>Rutilus rutilus</u> (L.)	Roach
12	<u>Scardinius erythrophthalmus</u> (L.)	Rudd
13	<u>Anguilla anguilla</u> (L.)	Eel
14	<u>Lampetra planeri</u> (Bloch)	Planer's Lamprey

Total 14 species

Haram (1968); Chattrabhuti (1974); Andrews and Rojanapaibul (1976);
Farenden (1976); Parr (1976); Rojanapaibul (1976, 1977); Abrahams (1977);
Cheyne (1977); Roscoe (1977) and Grainger (in progress). The symbionts
of the river limpet (<u>Ancylastrum fluviatile</u>) at Llyn Tegid have been
investigated by Eagen (1977). Chubb (1976) has reviewed the occurrence
of the parasites of the fish of the River Dee System, including Llyn
Tegid.

Llyn Tegid has a rather sparse avian fauna though gulls (Laridae),
cormorants (Phalacrocoracidae) and various species of duck are seasonally
abundant during the winter and early spring (Gittens, pers. comm.).
Descriptions of the vegetation have been given by several authors (e.g.
Chubb, 1963; Ali, 1973). Eaton (unpublished observations) has made a
recent, though brief, survey of the plant life at the south-west end of
the lake. <u>Callitriche</u> sp., <u>Myriophyllum alterniflorum</u> and <u>Nuphar lutea</u>
are all locally abundant in some bays. <u>Isoetes lacustris</u> and <u>Littorella</u>
sp. have declined in recent years, but are still present. <u>Juncus</u> sp. and
<u>Glyceria</u> sp. are found, though the shoreline environment produced by the
lowering of mean lake level is unsuitable for them at present. <u>Fontinalis</u>
sp. is found attached to rocks, and green filamentous algae and diatoms
are also present. Eaton considers that the erosion of the shore produced
by the low, winter lake level may have an important influence on the
establishment of rooted vegetation. The poor light penetration in the
water at Llyn Tegid (1% surface intensity at 10m depth) is a major factor
in determining the depth at which rooted vegetation can occur (Eaton,
unpublished observations).

The ecological classification of Llyn Tegid is late oligotrophic to
early mesotrophic, though tending towards the latter. In recent years
there has been an increased use of the lake by tourists (Hunt and Jones,
1972a; Gittens, pers. comm.). However, the Dee and Clwyd River Authority

Fig. 2. Monthly thermistor readings at Llyn Tegid (surface, 6m,

10m, 30m). January 1975 - April 1976.

Temperature (degrees Centigrade)

20

surface

6m

10m

10

30m

surface, 6m , 10m

30m

6

2

J F M A M J J A S O N D J F M A
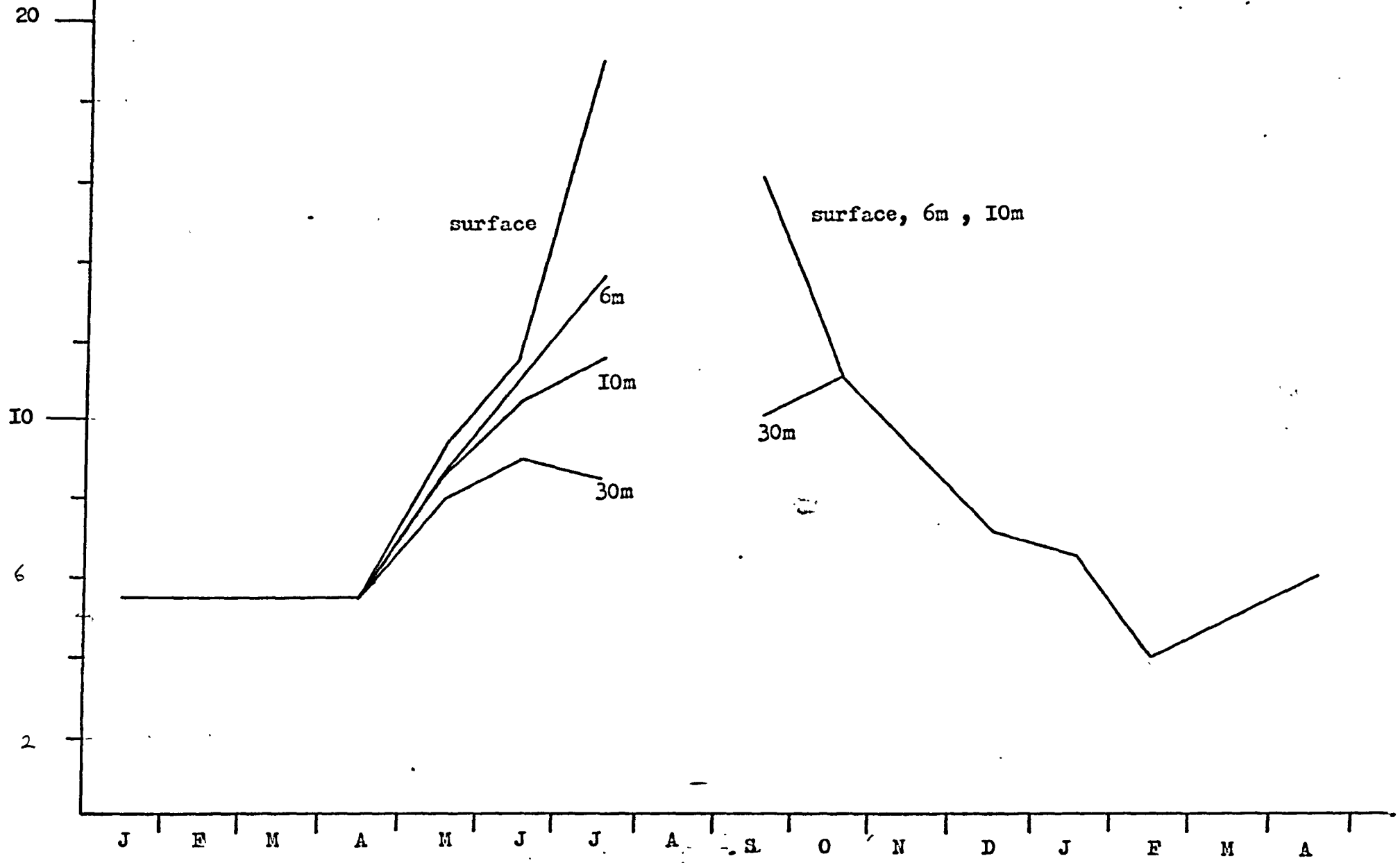
1975-76

Fig. 3.   Monthly mean maximum and minimum surface water temperature

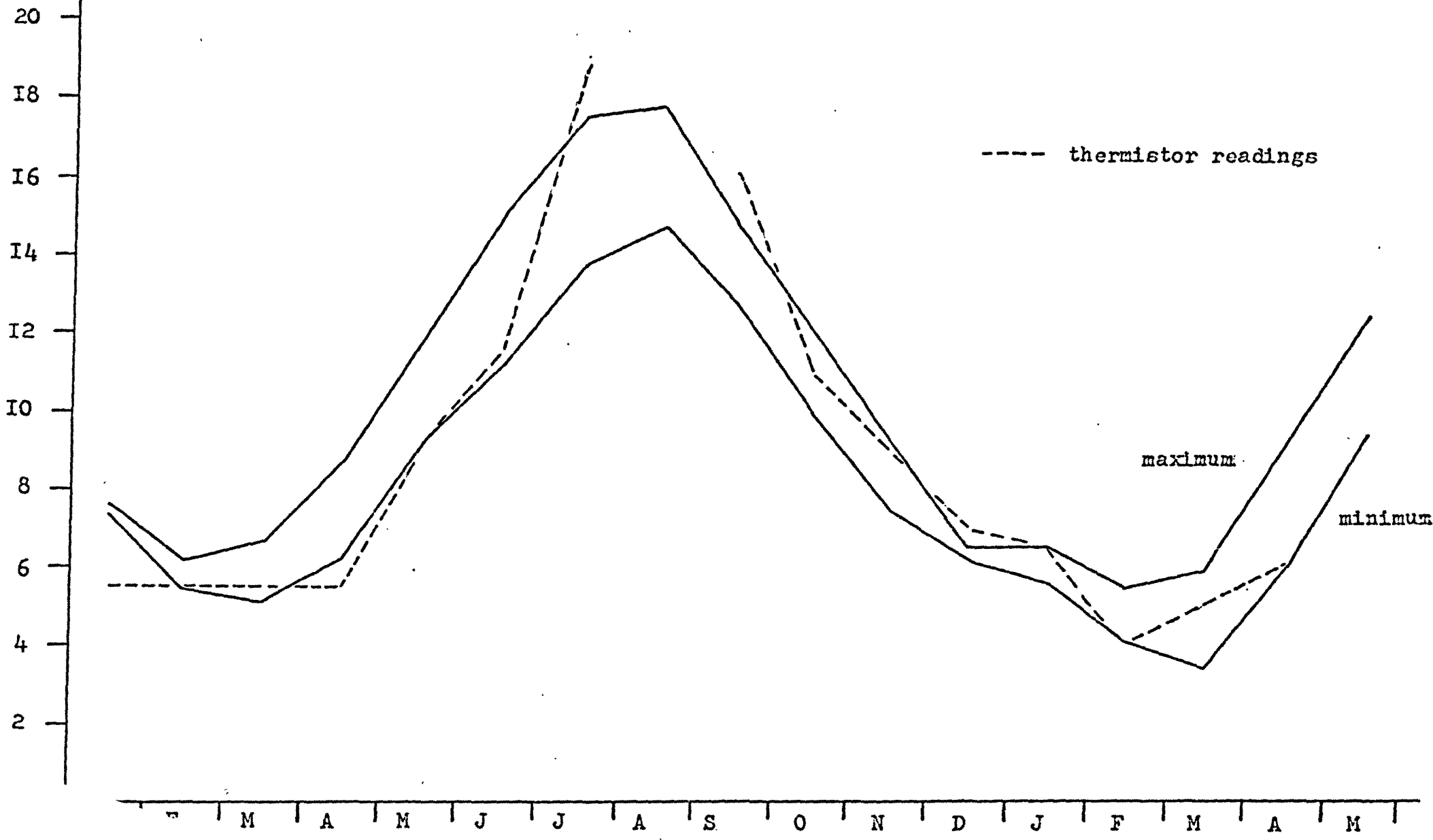at Llyn Tegid (outflow point) (courtesy of Dee and Clwyd

River Division, Vicars Lane, Chester); plus monthly thermistor

reading of surface water temperature. January 1975 - April

1976.

Temperature (degrees Centigrade)

-16-

thermistor readings

maximum

minimum

F M A M J J A S O N D J F M A M

1975-76

suggested that sewage deposition had not significantly increased
between 1951-52 and 1968-69 (Hunt and Jones, 1972a). Hynes (1961)
considered the lake to be mesotrophic and the mixed populations of
coarse and salmonoid fish indicate that the lake is of an intermediate
phase (Woolland, 1972). Eaton (unpublished observations) has found
the phytobenthos of Llyn Tegid to be typically mesotrophic.

II.2 Routine field and laboratory techniques

The routine field and laboratory techniques of this study are
described below. Methods used in the study of individual parasite
species will be described where relevant.

II.2.1 Field techniques

Perch may be caught using a variety of techniques, including traps,
seines, gill nets and trawls. Perch traps and beach seines have been
used extensively in the capture of perch from Llyn Tegid (e.g. Ali,
1973). Neither were used as a regular sampling technique in this study.

Traps are only seasonally effective, size selective and catch a
greater proportion of male fish. To avoid unnatural conditions of
crowding and possible lack of food (which might effect the parasite
fauna of the fish), frequent visits to retrieve, empty and reset the
traps would be necessary. This was considered impractical.

Beach seines are an excellent method for obtaining samples of live
fish. However, at Llyn Tegid, perch are present in the shallows principally
during   June-September. Therefore, whilst showing little size or sex
selectivity, beach seines were not capable of producing regular samples
of perch in all months of the year. Consequently, they were not routinely
used in this study at Llyn Tegid.

The perch from Llyn Tegid that were examined for parasites in this
survey were caught using:

    a. gill nets;

    b. midwater trawl;

    c. purse seine.

a.   Gill nets

To collect monthly data on the fish and their parasite fauna, gill nets were used. Gill nets require a minimum of maintenance and cleaning, and can be used under all but the most adverse weather conditions. Whilst markedly size selective, selectivity can be reduced by setting a range of mesh sizes (Banks, 1968).

Samples of perch were collected between January 1975 and February 1976 inclusive, using bottom set gill nets. A gang of four nets was set at each predetermined site. The mesh (knot to knot) measurements in each gang were 19mm, 26mm, 29mm and 32mm. The use of 9mm, 50mm and 60mm gill nets produced very few fish, and was abandoned.

On each visit the gill nets were set between 10.30-11.30h and lifted at 14.00-15.00h. In order to assess the seasonal movements of the fish, three gangs of gill nets were set at three different depths, at the south-west end of the lake (Fig. 4). Sites A (6m), B (12m) and C (18m) are shown. Occasionally a fourth gang was set at site D (12m). Sites C and D are particularly exposed, and poor weather conditions infrequently made the setting of the nets difficult or impossible.

The fish were carefully removed from the gill nets at the lakeside, killed and placed in polythene bags. Whilst fish from different mesh sizes were not segregated, fish caught at different sites were never mixed. The fish were then brought back to the department in ice cooled, insulated boxes. The following morning they were placed in a domestic refrigerator at 4-5°C.

b.   Mid-water trawl

Small perch (less than 11.0 cms, standard length) were only rarely caught using gill nets. Therefore, to obtain a sample of small perch a

Fig. 4.   The location of the sites used for gill netting at Llyn Tegid.

N

boathouse

A

D

B

C

approx. 500m

Bala
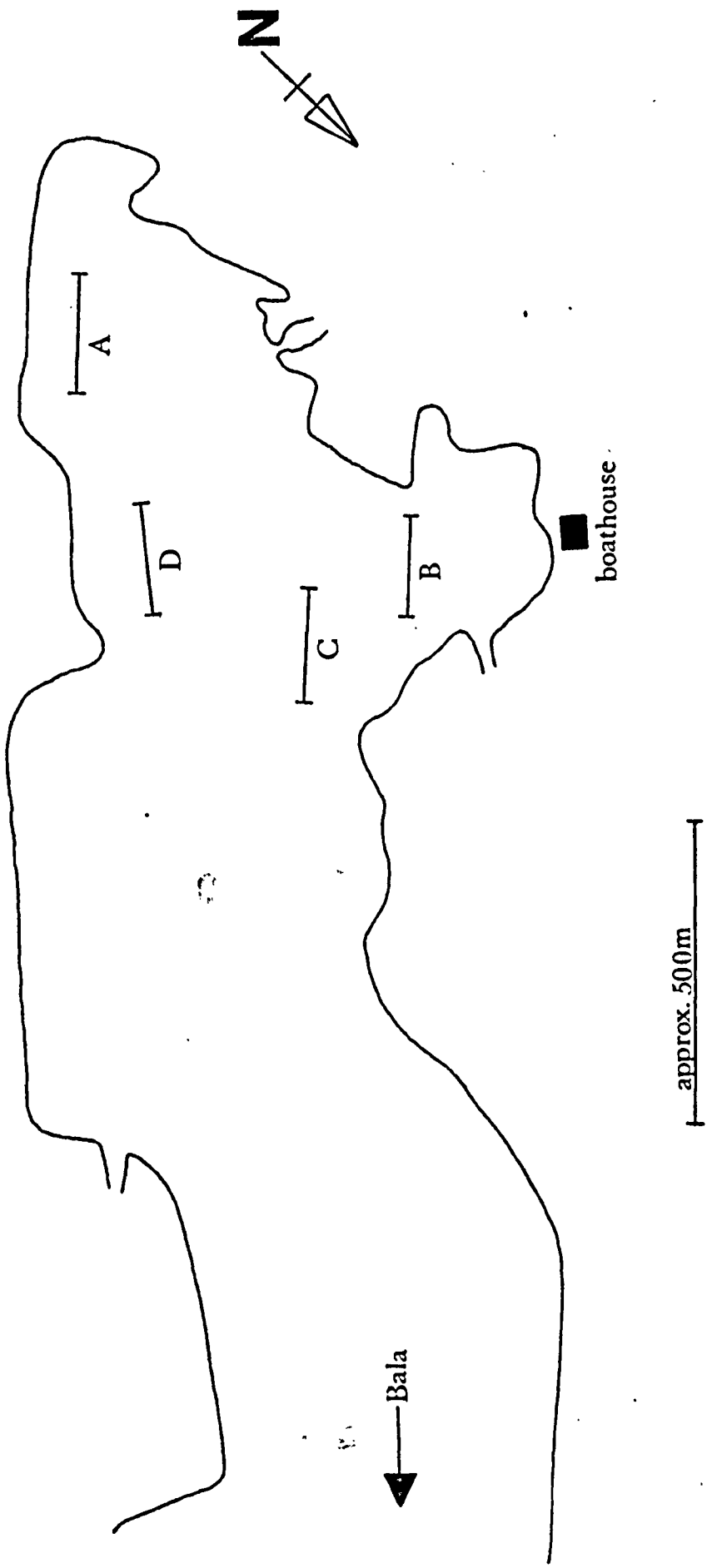
mid-water trawl was used. This was based on the design of Rupp and de Roche (1960), as described by Coles and Butterworth (1976). The fish were trawled from the south-west end of the lake in early March 1976. The samples were sorted and deep frozen at the lakeside laboratory. They were subsequently transferred to Liverpool for examination.

c. Purse seine

A small sample of perch fry (young of the year) were caught using a purse seine, in late July, 1976. This net was also described by Coles and Butterworth (1976). Following careful removal from the net, the fry were killed, placed in a polythene bag and transported to Liverpool. The same day the fry were placed in a refrigerator at $4-5^{\circ}C$. Thirty fry were randomly subsampled for detailed examination the following day.

Echo-location studies

It was attempted to correlate the traces produced by a Simrad commercial (continuous recording) echosounder, with gill net catches. At approximately bimonthly intervals during 1975, runs on a standard grid at the south-west end of the lake were performed. The echosounder was set to a constant sensitivity and scale, and the runs performed at a constant speed of 7 Km/hour. The results obtained proved difficult to interpret, and this is briefly discussed in Chapter III.

II.2.2 Laboratory examination of perch

As stated (in Chapter I), the fish were examined in an attempt to determine the TOTAL parasite fauna, associated pathological conditions, and relevant aspects of host biology. External protozoans, and external and internal metazoans, were of prime interest. The techniques of investigation were not designed to reveal the presence of any endoparasitic protozoans.

a. Gill net samples

On the day following capture, the total number of fish of each species,

from each site, was recorded. When very large samples of perch were
obtained, random subsamples were taken. It was intended to examine at
least 30 perch per month.

Within 36 hours of capture, the perch were externally examined.
During this time they were stored in a refrigerator, in polythene bags
to prevent dehydration. Each fish was given an accession number, and
examined as follows. The information was recorded on data sheets, one
sheet per fish.

Initially the accession number, site and date of collection were
noted. The standard length (to the nearest millimetre) and the total
weight (to the nearest 5 grams) were recorded. The body surfaces, fins, nostrils,
and buccal cavity were all examined macroscopically. Smears were taken from
these areas, and examined on a microscope slide. For dissection, isolation and
identification of stomach contents and parasites, and opercular reading, a
Wild M4 microscope was usually adequate. The four gill arches from each
branchial chamber were examined in a petri dish, containing a little tap
water.

All external parasites were identified, counted and the data recorded.
Ectoparasites were invariably examined in the fresh, living state. However,
the identity of mxyosporidian cysts were confirmed by examination of the
spores in polyvinyl lactophenol under oil emersion, after fixation in 5-10%
formalin. Monogeneans were examined fresh, and then relaxed in cold water,
fixed in formalin or A.F.A. (acetic-formol-alcohol) and lightly stained with
acetic haematoxylin (Chubb, 1962).

Finally the opercular bones were removed, dipped in boiling water, and
cleaned. Subsequently, they were examined for age determination, using
incident light on a dark background (Le Cren, 1947; Ali, 1973).

Each fish was labelled with its accession number and deep frozen.

At a later date the fish were gently thawed in cold water. A ventral
incision was made from the pericardial cavity to the anus, taking care to

avoid damaging the viscera. This incision was extended dorsally and anteriorly (after Amlacher, 1970). The lateral body wall was removed. The fish was sexed and the condition of the gonads assessed on the Nikolsky (1963) scale (Appendix I). The internal organs were then individually examined in a petri dish containing a little tap water.

The organs examined were:

1. Stomach. Fullness was established on a 0 (empty) to 5 (full and stretched) scale. The stomach was then slit open and the contents identified.

2. Pyloric caeca.

3. Intestine. This was divided into five equal lengths. Each portion was examined individually, and the data thus recorded.

4. Liver and gall bladder. The gall bladder was squashed and the contents examined. The liver was teased apart using mounted needles.

5. Wall of the swimbladder.

6. Gonads.

7. Urinary bladder and a portion of the posterior kidney.

8. Eyes. These were carefully removed from their orbit and examined individually.

9. Heart and pericardial cavity.

10. Lateral body musculature.

11. On infrequent occasions, the brain was examined.

The parasites were collected, and identified and counted. Where possible, an assessment of the state of development/maturation of the individual parasites was made. The process of deep freezing killed the endoparasitic Metazoa in a relaxed condition. They were then fixed and stored as follows, in tubes labelled with the fish accession number, the parasite species and the site of infestation. A more detailed consideration of the relaxation and fixation of parasites can be found in Chubb (1961); Chubb & Powell (1965) and Andrews (in press).

Digenetic trematodes

1. Larval digeneans (metacercariae) were routinely fixed in A.F.A. When encysted, some were excysted by light pressure beneath a coverslip, prior to fixation. Further details on the techniques used in the study of the taxonomy of these parasites are provided in Chapter VII.

2. Adult digeneans were fixed in A.F.A. and later stained in Borax Carmine.

Living digenetic trematodes can be killed and relaxed in hot water (Slusarski, 1958).

Cestoda

1. The plerocercoid stages of Pseudophyllidea were fixed in 5% formalin. Encapsulated forms were first removed from their capsules. The staining of such specimens was usually unnecessary, but can be achieved using Horen's Trichrome or Methylene Blue (Chubb, 1962; Schnur, 1969).

2. Mature adult tapeworms were not encountered. Plerocerciform juveniles were treated as above.

Living tapeworms should be relaxed in cold water before fixation, and alcoholic fixatives avoided (Schnur, 1969).

Nematoda

Nematodes were fixed in 70% alcohol and later cleared in lactophenol. Encysted juvenile forms were removed from their cysts, prior to fixation.

Living nematodes can be killed in an extended position in hot alcohol.

Acanthocephala

Acanthocephalans were fixed in A.F.A. and later stained in Borax Carmine. Live specimens should be relaxed in cold water.

b. Mid-water trawl sample

On arrival in Liverpool, the perch from this sample were partially thawed and their standard length recorded. Those less than 12.0 cm were retained for further examination. These fish were externally examined within

24 hours. The weight was recorded to the nearest 0.1 gm, after removing excess moisture with filter paper. The perch were then re-frozen, and examined internally at a later date. The information from these fish was recorded on "Paramount" punched data cards, one card per fish.

c. Purse seine sample

These perch fry were examined externally and internally whilst fresh, within 48 hours of capture. Weight was recorded to the nearest 0.1 gm, after removing excess moisture. Standard length was recorded to the nearest millimetre. The data collected from this sample were stored on a single data sheet

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CHAPTER III

BIOLOGY OF PERCH (Perca fluviatilis L.) FROM LLYN TEGID

III.1   INTRODUCTION

Perch (Perca fluviatilis) is a widely distributed and often studied fish. Within the Palaearctic region a second species (Perca schrenki Kessl.) occurs, while in North America the closely related yellow perch (Perca flavescens Mitchill) is found. Weatherley (1963) described the zoogeography of P. fluviatilis and P. flavescens, with special reference to the effects of high temperature. Nikolsky (1954), Wheeler (1969) and Sterba (1972) summarised some of our knowledge on the biology of P. fluviatilis, and Ali (1973) compiled a literature review on this subject. Recent publications include McCormack and Le Cren (1971), Lind et al. (1972, 1973), Ellonen and Lind (1973), Tenhenum et al. (1973) and Thorpe (1974) and Kennedy et al. (1975).

Aspects of the biology of perch have been studied at Llyn Tegid by Jones (1953), Dunn (1954), Chubb (1964), Siddiqui (1967) and Ali (1973). Coles (in prep.) is engaged in a study on the fish fry of Llyn Tegid, and has paid particular attention to those of perch.

In any comprehensive ecological study on the parasite fauna of fish, attention must be paid to certain aspects of host biology. Therefore, as part of this study on the parasite fauna of perch at Llyn Tegid, data were collected on relevant items of host biology (including feeding habits, seasonal activity and migration, growth rate, and gonad maturation and spawning).

III.2.   DESCRIPTION OF SAMPLES

Between January 1975-July 1976 a total of 559 perch were examined (Table I).

Gill net samples

Four hundred and sixty-five perch were examined from gill net samples taken between January 1975-February 1976 (Table I). The length frequencies of these fish are shown in Fig. 1 and 2.

The majority of the male fish that were examined were between 11.0-13.9 cm. Very few male perch below 11.0 cm and above 13.9 cm were caught using gill nets (Fig. 1). The majority of female perch that were examined were between 12.0-15.9 cm. A proportion (16.7%) were larger than this. Few female perch less than 12.0 cm were caught using gill nets (Fig. 2). The monthly mean length of male and female fish is shown in Table II.

The age frequencies of the male and female fish from the gill net samples are shown in Fig. 3 and 4. The age classes 3, 4 and 5 were dominant, with few fish younger than 3 or older than 7.

The gill nets caught a greater number of female perch. A x^2 analysis on the monthly sex ratio indicated that in all months (except October and November 1975) there was no significant different (P > 0.05) from a 2:1 sex ratio in favour of females (Table II).

The factors affecting gill net selection have been discussed by Banks (1968) and Haram (1968). In this present study the gill nets caught few perch less than 11.0 cm, and selected heavily for female fish. Within the population of perch above 11.0 cm there may be a greater number of female fish. Therefore, the gill nets effectively sample a greater proportion of the female population. Ali (1973) reported that once mature, female perch grew more rapidly than males. However, using 19 mm, 26 mm, 32 mm and 42 mm (knot-knot) gill nets during the autumn and winter, he caught 955 perch of which 44% were male and 56% were female. Over a period of 14 months, 183 male and 282 female perch were examined from the gill nets in this present

Table I.   Total perch examined between January 1975-July 1976.

	Number males	Number females	Number unsexed*	Total
Gill net samples (January 1975-February 1976)				
J	3	3		6
F	11	19		30
M	9	21		30
A	10	20		30
M	12	18		30
J	13	26		39
J	14	26		40
A	10	20		30
S	14	16		30
O	28	32		60
N	25	29		54
D	17	18		35
J	13	17		30
F	17	4		21
TOTAL	183	282		465
Trawl sample (March 1976)				
	18	11	35	64
Purse seine sample (July 1976)				
			30	30
GRAND TOTAL	201	293	65	559

N.B.   *Sex not distinguishable to the naked eye.

Table II.   Mean length of male and female fish, and sex ratio.   Gill net samples.   January 1975-February 1976.

	Total no. fish	Number male fish	Mean length	Variance	Number female fish	Mean length	Variance	x^2 2:1 sex ratio	Value of P
J	6	3	13.17	-	3	16.47	-	-	-
F	30	11	13.50	1.34	19	14.61	12.11	0.15	>0.05
M	30	9	12.70	0.58	21	13.63	4.20	0.15	>0.05
A	30	10	12.44	0.12	20	13.56	2.04	-	-
M	30	12	12.63	0.71	18	14.07	6.60	0.60	>0.05
J	39	13	13.23	0.24	26	13.52	2.62	-	-
J	40	14	12.24	0.18	26	14.25	5.38	0.05	>0.05
A	30	10	12.16	3.31	20	14.75	5.61	-	-
S	30	14	13.16	0.38	16	14.01	3.69	2.40	>0.05
O	60	28	12.68	0.17	32	14.99	11.42	4.80	<0.05
N	54	25	13.04	0.52	29	14.30	6.86	4.08	<0.05
D	35	17	12.88	0.21	18	15.04	17.55	3.65	>0.05
J	30	13	13.02	0.36	17	13.51	3.35	1.35	>0.05
F	21	4	12.43	-	17	13.27	1.59	1.96	>0.05
TOTAL	465	183	12.82	1.93	282	14.18	7.24	-	-

Fig. I. Length frquency male perch. Gill net samples. January
1975 – February 1976.

Male perch
total 183
mean length 12.8 cm
variance 0.70

FREQUENCY

50

3   40   66   48   10   9   3   I   2   I

9   10   11   12   13   14   15   16   17   18   19   20

LENGTH CM

Fig. 2. Length frequency female perch. Gill net samples. January 1975 – February 1976

FREQUENCY

Female perch
total 282
mean length 14.2 cm
variance 6.3

100

50

| I | 12 | 105 | 55 | 39 | 25 | 14 | 7 | 9 | 3 | 4 | 2 | 2 | 3 | 2 | | I |

9 10   11   12 13   14 15   16   17 18   19   20 21 22   23 24   25   31
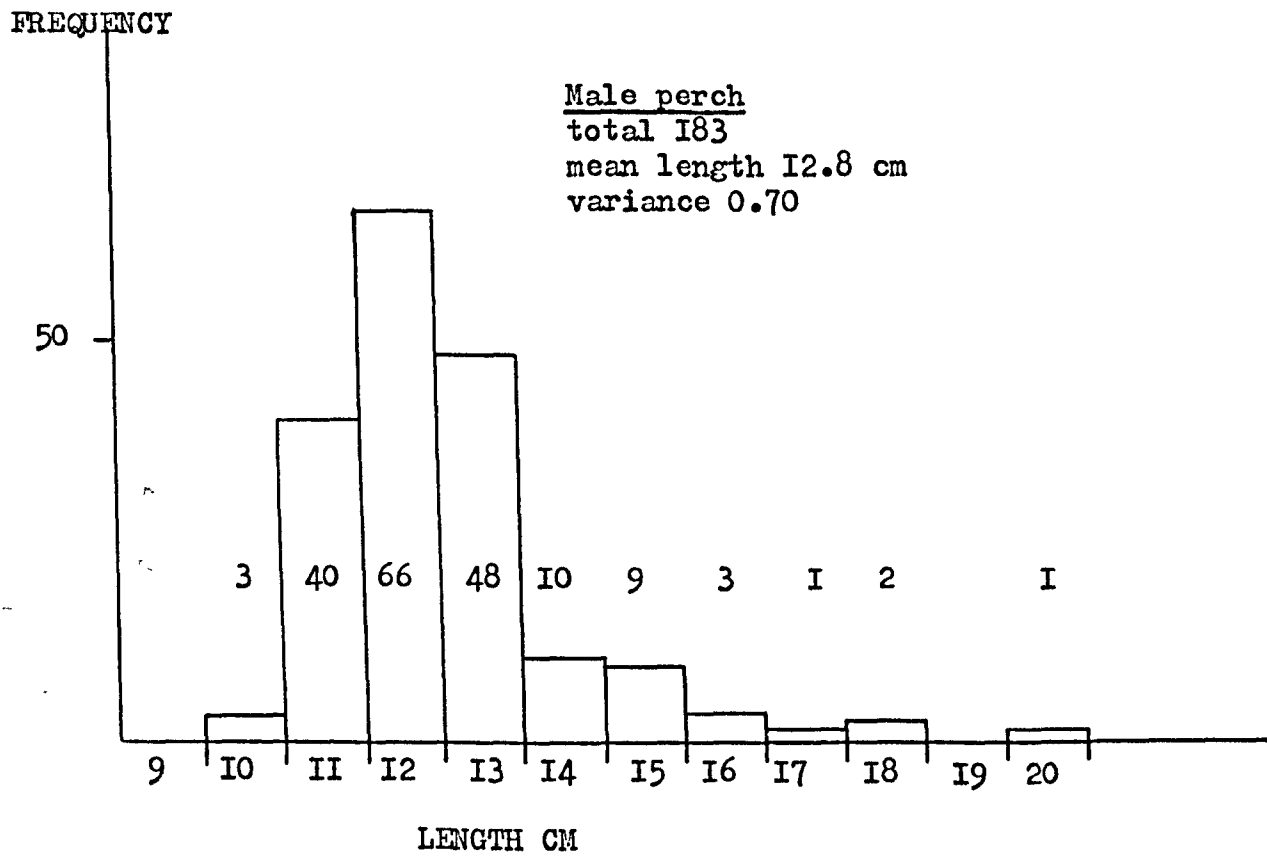
LENGTH CM
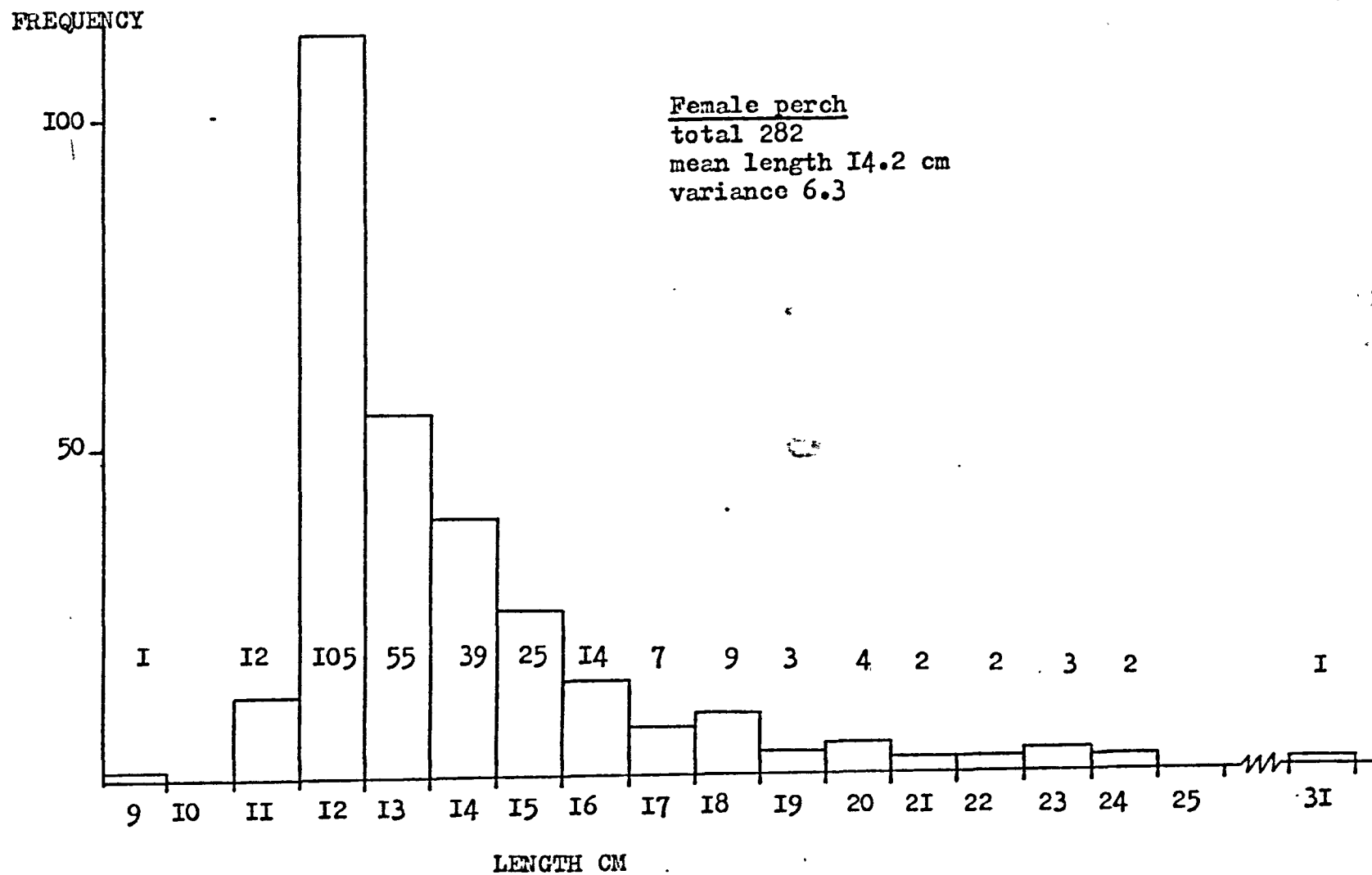
Fig. 3. Age frequency female perch

Fig. 4. Age frequency   male perch

Gill net samples. January 1975 – February 1976

FREQUENCY

Fig. 3

Total 282 female perch
mean age 4.4 yrs

2 87 98 38 27 20 7 2 I

Fig. 4

Total 183 male perch
mean age 4.3 yrs

2 51 66 40 16 6 I I

I 2 3 4 5 6 7 8 9 10 11 12

AGE YRS
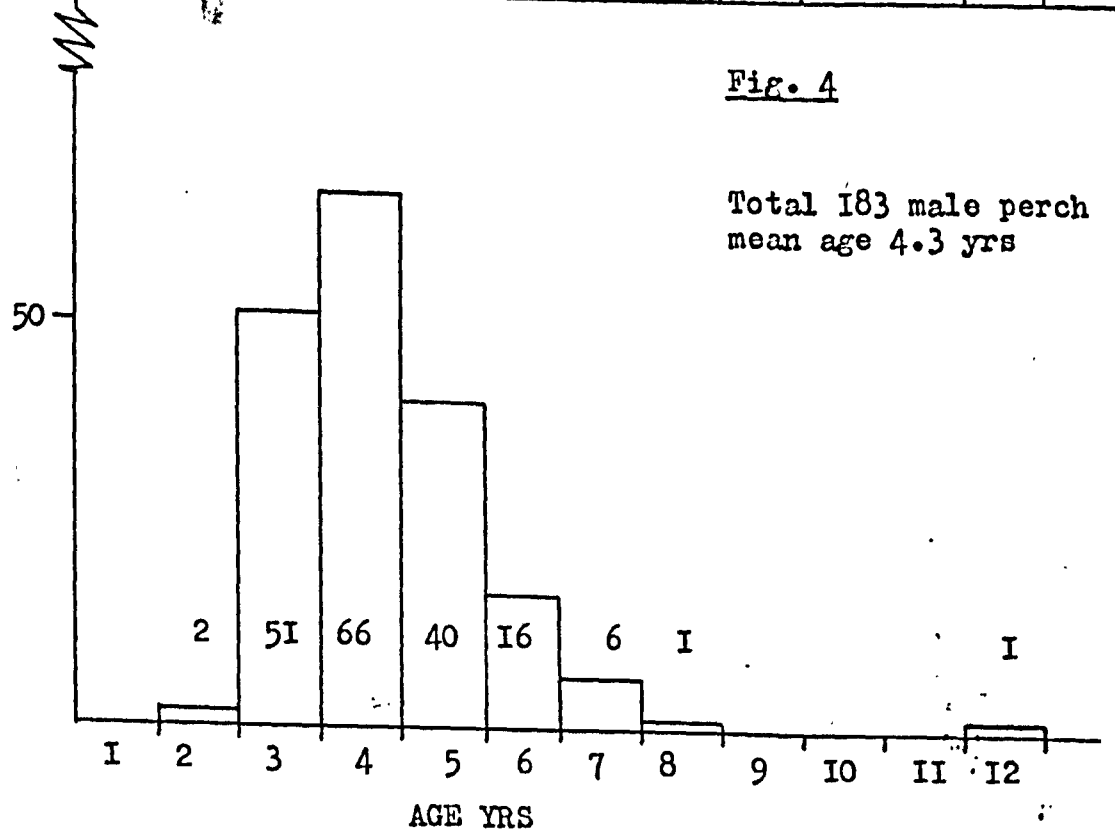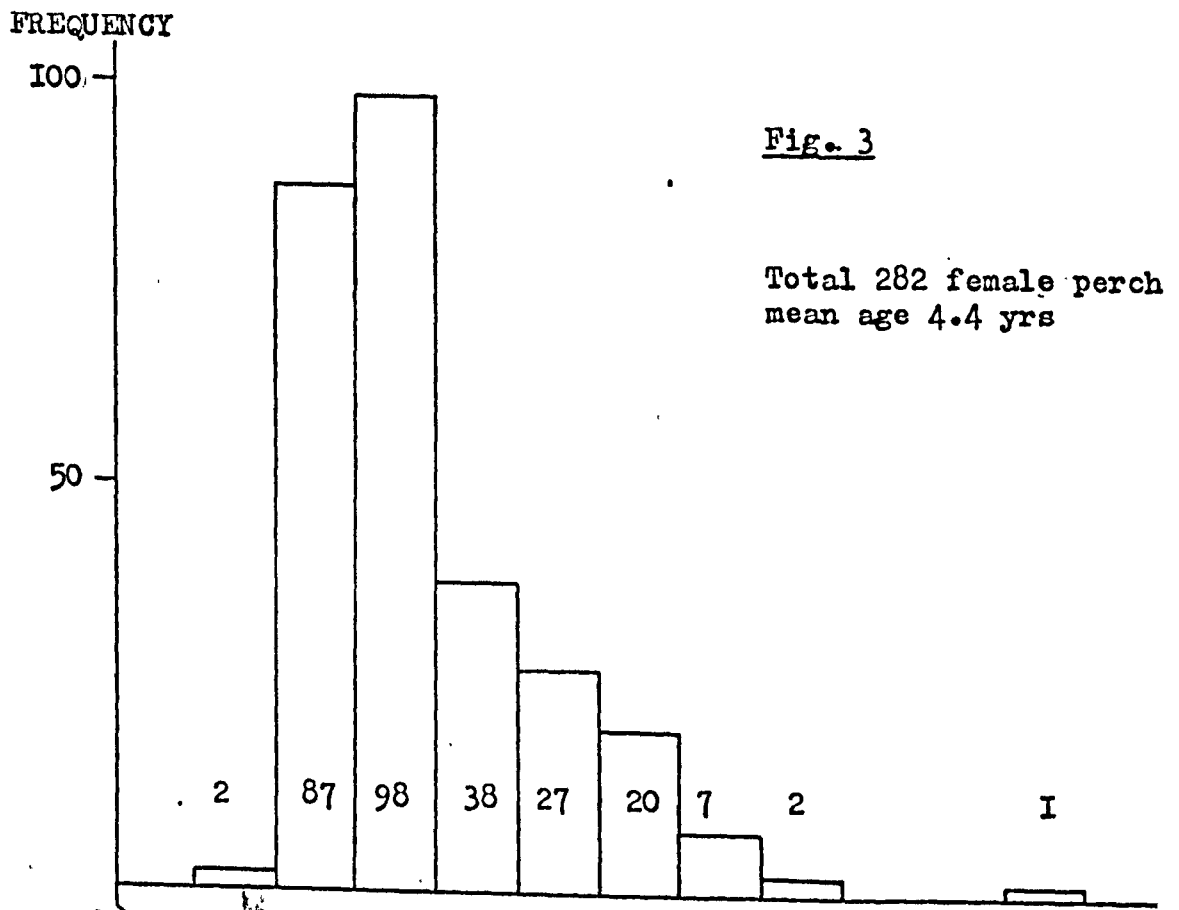
study. Nonetheless, during the autumn-winter months of September-January 1975/76, a sex ratio approaching 1:1 was found (Table I). Clearly there were seasonal factors involved in the selection of female perch by gill nets at Llyn Tegid.

Trawl sample

To obtain a sample of smaller, younger perch a mid-water trawl was used (see Chapter II).

Eighty-seven perch were caught in March 1976. Sixty-four of these were less than 12.0 cm (standard length) and retained. The remainder were not examined (Fig. 5 and 6).

Thirty-six 0++ perch were caught, all of which were less than 12.0 cm and retained. Twenty-six male and 26 female perch were caught, of which 18 males and 11 females were less than 12.0 cm. The age and length frequencies of the fish caught using the trawl are shown in Fig. 5-8. The mean length of the male, female and 0++ perch examined are shown in Table III.

Purse seine sample

To provide information on the feeding habits and parasite fauna of young perch fry, a purse seine was used. Thirty fry were examined, from a sample netted in late July 1976. At this time the fry were between 4-6 weeks old. The mean length of these fish was 2.3 (range 2.0-2.7)cm.

Table III. Mean length of perch examined. Trawl sample. March 1976.

	Male	Female	Unsexed*	TOTAL
Number fish examined	18	11	35	64
Mean length	10.8	10.5	5.4	7.8
Variance	-0.25	3.40	0.50	7.8

N.B. *Sex not distinguishable to the naked eye.

Fig. 5. Length frequency unsexed*and male perch

Fig. 6. Length frequency female perch

Trawl sample. March 1976.

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

FREQUENCY

'Fig. 5

unsexed
total number 35
mean length 5.4 cm
variance   0.49

male perch
total number 26
mean length 11.4 cm
variance   0.22

30

20

10

9   19   7

12   6   5   2   I

Fig. 6

20

female perch
total number 26
mean length 11.7 cm
variance 1.12

10

I

4   6   10   5

3   4   5   6   7   8   9   10   11   12   13   14   15

LENGTH CM
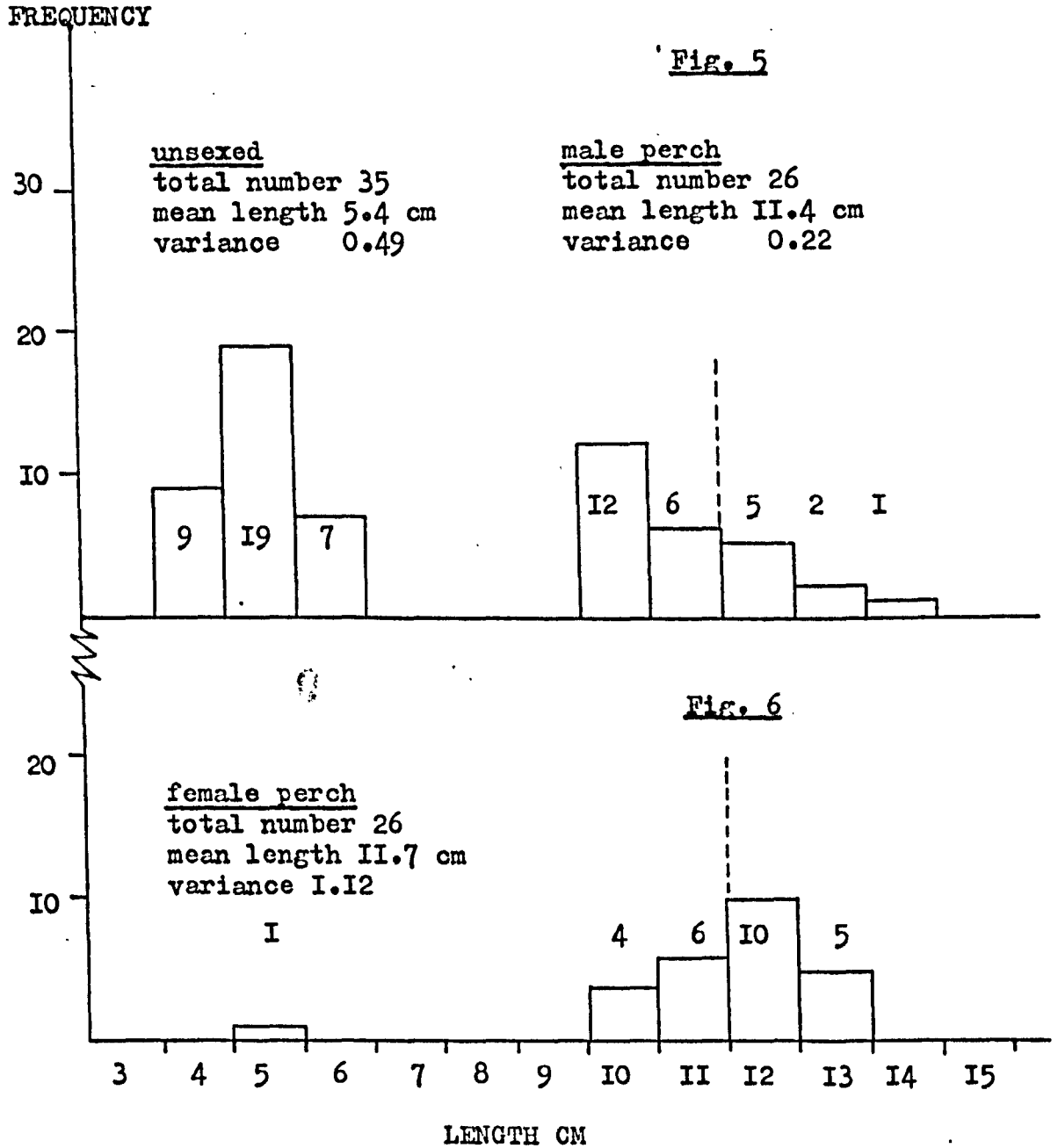
(N.B. Only perch less than 12.0 cm examined in this study)

Fig. 7. Age frequency unsexed[*] and male perch
Fig. 8. Age frequency female perch
   Trawl sample. March 1976.

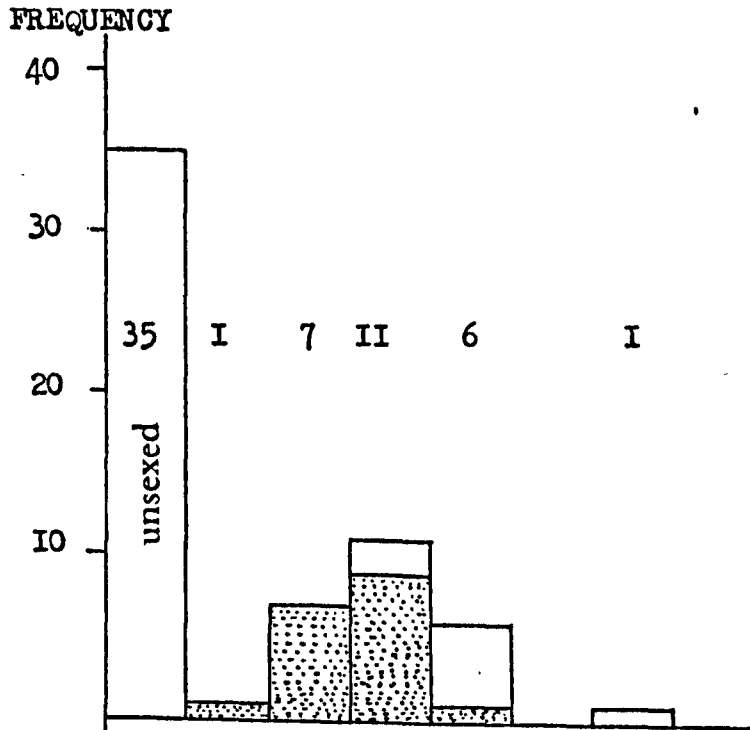(*...sex not distinguishable to the naked eye)

FREQUENCY

Fig. 7

35   I   7   II   6   I

Total number male perch
caught 26
examined 18

unsexed

Fig. 8

I   I   3   12   9
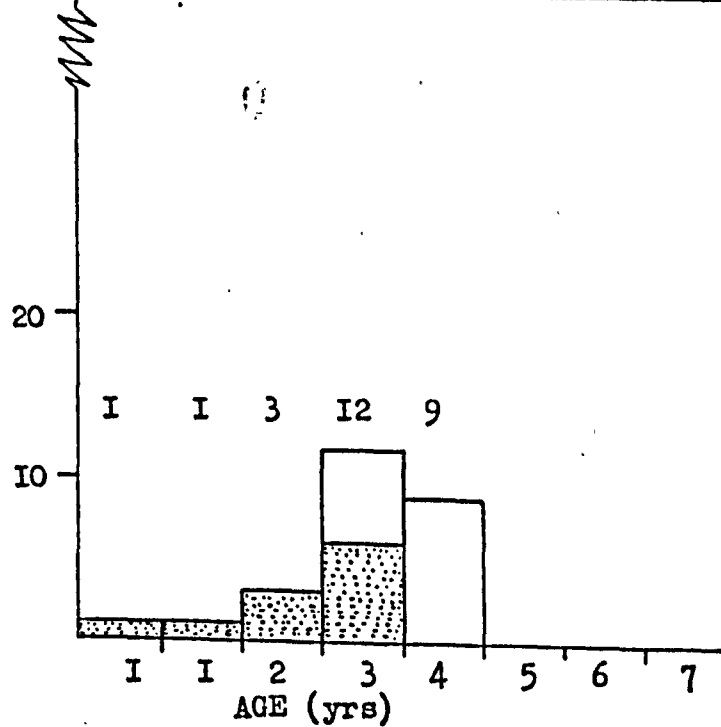
Total number female perch
caught 26
examined 11

AGE (yrs)

...examined in detail

III.3.   SEASONAL MOVEMENTS

Total gill net catches were used to determine the seasonal
migration and activity of perch. In addition, by the setting of
similar gangs of gill nets at standard sites it was hoped to
compare local variations in the parasite fauna. Unfortunately,
because of the small sample sizes from some sites during certain
months, this was only possible in a limited number of instances
(see later). Tables V-VIII show the total monthly gill net catches
at each site, as calculated for 10 hours fishing. Table IV shows
the number of perch examined from each site during each month.

Perch may be caught at sites B and D during most months of
the year (Table VI and VIII). However midwinter catches, especially
between December-February, were poor in comparison to most other
months. This may be a result of the reduced winter activity of the
fish during these, the coldest months of the year. In comparison,
gill net catches were usually high during the warmer, summer months
(Table VI and VIII).

Few perch were caught at site C (18m), and these fish may not
favour waters below 12-15m at Llyn Tegid. However, gill nets were
only set at the south-west end of the lake, and the distribution of
perch in deeper waters elsewhere in Llyn Tegid remains to be elucidated.

Perch may only be gill netted in large numbers at site A (6m)
during the summer months (June-September) (Table V). The use of purse
and beach seines in shallow water (< 6m) during these months often
yields large numbers of perch (Ali, 1973; Boyle, pers. comm.; Coles,
pers. comm.).

In common with other lacustrine populations, perch at Llyn Tegid
underwent a marked seasonal migration into shallow water. However,
they were present in water up to 12-15 m deep during all months of
the year. The shoreward migration at Llyn Tegid occurred after the

initial spring rise in water temperature (Chapter II, Fig. 3), at a time when the perch gonads are rapidly passing through the later stages of maturation and into the reproductive condition (section III.5). Allen (1935) postulated that the spring migration of perch into shallow water at Lake Windermere was controlled by the sexual development of the fish, and/or food abundance. The seasonal variations in the feeding habits of perch at Llyn Tegid are discussed in section III.6.

The autumn migration into deeper water appeared to coincide with the disappearance of the thermocline, as the lake became homothermal (see Chapter II, Fig. 3). The absence of perch from waters deeper than 12-15 m is in contrast with the observations of Allen (1935) and Worthington (1940) on Perca fluviatilis at Lake Windermere, and the observations of Ferguson (1958), Wells (1968) and Brazo et al. (1975) on P. flavescens from North America.

A Simrad echo sounder was used in an effort to establish the relationships that may exist between echo traces and gill net catches. The results proved difficult to interpret. Large gill net catches were often obtained when the echo trace indicated only small numbers of fish. The reason for this discrepancy may be explained by the following. Haram (1965) described the use of echo sounders in fishery research. He pointed out that echo sounders may fail to distinguish between large fish and small shoals, and vice versa. Dietritus and planktonic crustaceans may also give false readings. In addition, fish close to the lake bottom may not register at all. Since the gill nets used in this present study were bottom-set (and fished at 0-2m from the lake bottom), this latter point may be significant. However, echo runs were of limited duration which may also hinder the interpretation of the traces. It is interesting nonetheless to note that when the echo traces

Table IV.　Sites of capture of the perch examined.　Gill net samples.　January 1975–February 1976.

Month	Site A (6m) Total (M:F)	Site B (12m) Total (M:F)	Site C (18m) Total (M:F)	Site D (12m) Total (M:F)
J	–	–	–	6 (3:3)
F	6 (2:4)	15 (7:8)	–	9 (2:7)
M	–	21 (7:14)	–	9 (2:7)
A	–	23 (7:16)	–	7 (3:4)
M	–	30 (12:18)	–	–
J	30 (12:18)	9 (1:8)	–	–
J	30 (4:26)	10 (10:0)	–	–
A	30 (10:20)	–	–	–
S	–	30 (14:16)	–	–
O	7 (4:3)	30 (13:17)	13 (7:6)	10 (4:6)
N	6 (0:6)	24 (15:9)	8 (6:2)	16 (4:12)
D	–	29 (14:15)	–	6 (3:3)
J	6 (1:5)	24 (12:12)	–	–
F	–	15 (4:11)	–	6 (0:6)
TOTAL	115 (33:82)	260(116:144)	21 (13:8)	69(21:48)

TOTAL　465 (183:282)

N.B.　M　=　Male
　　　　F　=　Female

Table V. Fish catches at site A (6m). Gill net samples.

January 1975-February 1976.

Month	Estimated number fish per 10 hours fishing					Actual fishing time (hrs.)
	Perch	Roach	Pike	Gwyniad	Trout*	
J	-	-	1.8	-	-	3.5
F	7.5	15.0	3.8	6.3		8.0
M	-	-	-	-	-	3.5
A	4.6	-	1.5	1.5	-	6.5
M	2.9	-	-	-	-	3.5
J	250.0	108.0	1.7	-	-	6.0
J	68.0	5.0	-	-	-	6.5
A	40.0	26.0	2.0	-	2.0	5.0
S	245.0	-	-	-	-	4.0
O	11.0	-	-	-	-	6.5
N	17.0	9.0	-	-	-	3.5
D	NOT FISHED					0
J	24.0	12.0	-	-	-	2.5
F	NOT FISHED					

N.B. *Salmo trutta

Table VI. Fish catches at site B (12m). Gill net samples.

January 1975-February 1976.

| Month | Estimated number fish per 10 hours fishing | | | | | Actual fishing |
	Perch	Roach	Pike	Gwyniad	Trout*	time (hrs.)
J	NOT FISHED					-
F	18.8	16.3	-	15.0	-	8.0
M	50.9	56.4	1.8	20.0	-	5.5
A	61.5	9.2	-	7.7		6.5
M	114.3	40.0	-	25.7	-	3.5
J	102.5	-	-	35.0	-	4.0
J	31.0	-	-	25.0	-	6.5
A	-	2.0	-	32.0	-	5.0
S	125.0	67.5	5.0	7.5	-	4.0
O	123.0	42.0	5.0	11.0	-	6.5
N	70.0	3.0	-	107.0	-	3.5
D	53.0	10.0	-	-	-	5.5
J	66.0	4.0	-	30.0	-	5.0
F	23.0	19.0	-	-	-	6.5

N.B. *Salmo trutta

Table VII.   Fish catches at site C (18m). Gill net samples.

January 1975-February 1976.

Month	Estimated number fish for 10 hours fishing					Actual fishing
	Perch	Roach	Pike	Gwyniad	Trout*	time
J	-	-	-	20.0	-	3.5
F	-	-	-	13.8	-	8.0
M	-	-	-	48.6	-	3.5
A	4.6	-	-	44.6	-	6.5
M	-	2.7	-	28.0	-	7.5
J	-	5.0	-	70.0	-	6.0
J	-	-	-	376.0	-	2.5
A	-	-	-	70.0	-	5.0
S	-	-	-	78.0	-	4.0
O	18.0	2.0	-	73.0	-	12.5
N	23.0	-	-	84.0	-	3.5
D	-	-	-	4.0	-	2.5
J	-	-	-	90.0	-	5.0
F	13.0	-	-	165.0	-	3.0

N.B.   *Salmo trutta

Table VIII.   Fish catches at site D (12m). Gill net samples.

January 1975-February 1976.

Month	Estimated number fish for 10 hours fishing					Actual fishing time
	Perch	Roach	Pike	Gwyniad	Trout*	
J	5.2	1.0	-	91.3	-	11.5
F	18.8	18.8	-	53.8	-	8.0
M	54.5	30.8	-	79.6	-	5.5
A	47.7	12.3	1.5	9.2	-	6.5
M	12.5	-	-	-	-	4.0
J	NOT FISHED					-
J	NOT FISHED					-
A	NOT FISHED					-
S	NOT FISHED					-
O	81.0	32.0	-	20.0	-	3.5
N	90.0	15.0	-	32.0	-	3.5
D	36.0	7.0	-	-	-	3.0
J	NOT FISHED					-
F	NOT FISHED					-

N.B. *Salmo trutta

indicated an abundant fish population in the region of the gill nets, catches were invariably good. Hancock (1972) has used echo location techniques in conjunction with extensive mid-water gill netting, in a study on the diurnal movements of gwyniad (Coregonus lavaratus) at Llyn Tegid. Coles (in prep.) has combined the use of a mid-water trawl with an echosounder in his studies at Llyn Tegid.

III.4.   GROWTH RATE, GROWING SEASON, CONDITION FACTOR

Jones (1953) and Ali (1973) have examined the growth of Llyn Tegid perch.

The length of the growing season at Llyn Tegid is shown in Fig. 9. The percentage of "closed" opercula (i.e. opercula with outer, transparent winter band) dropped markedly from March-April. The opercula tended to remain "open" (indicating growth) until November-December. Ali (1973) found that there was a tendency for growth to chiefly occur during the summer months, with little growth during the winter and early spring. Le Cren (1958) has found a significant correlation between the annual growth of Lake Windermere perch, and the surface temperature of the lake in terms of degree days over $14^{o}C$. At Windermere perch appear to grow most between June-September.

The mean length for age of the gill net samples of adult fish taken between January-March 1975 and October-February 1975/76 are shown in Table IX. The mean length for age of the 36 O++ perch caught by trawl in March 1976 was 5.42 ($\pm 95\%$ confidence limits 0.23) cm. Since only perch of standard length < 12.0 cm were examined from the trawl, no calculations were made on the growth of older (1++ - 4++) perch from this sample. Ali (1973) found that the growth rate of perch at Llyn Tegid was poorer than that found in many other British and European studies. The reasons for this were discussed (Ali, 1973). As shown by Ali, the

Fig. 9. Incidence "closed" opercula of perch at Llyn Tegid. Gill net
samples. January 1975 - February 1976.

% INCIDENCE
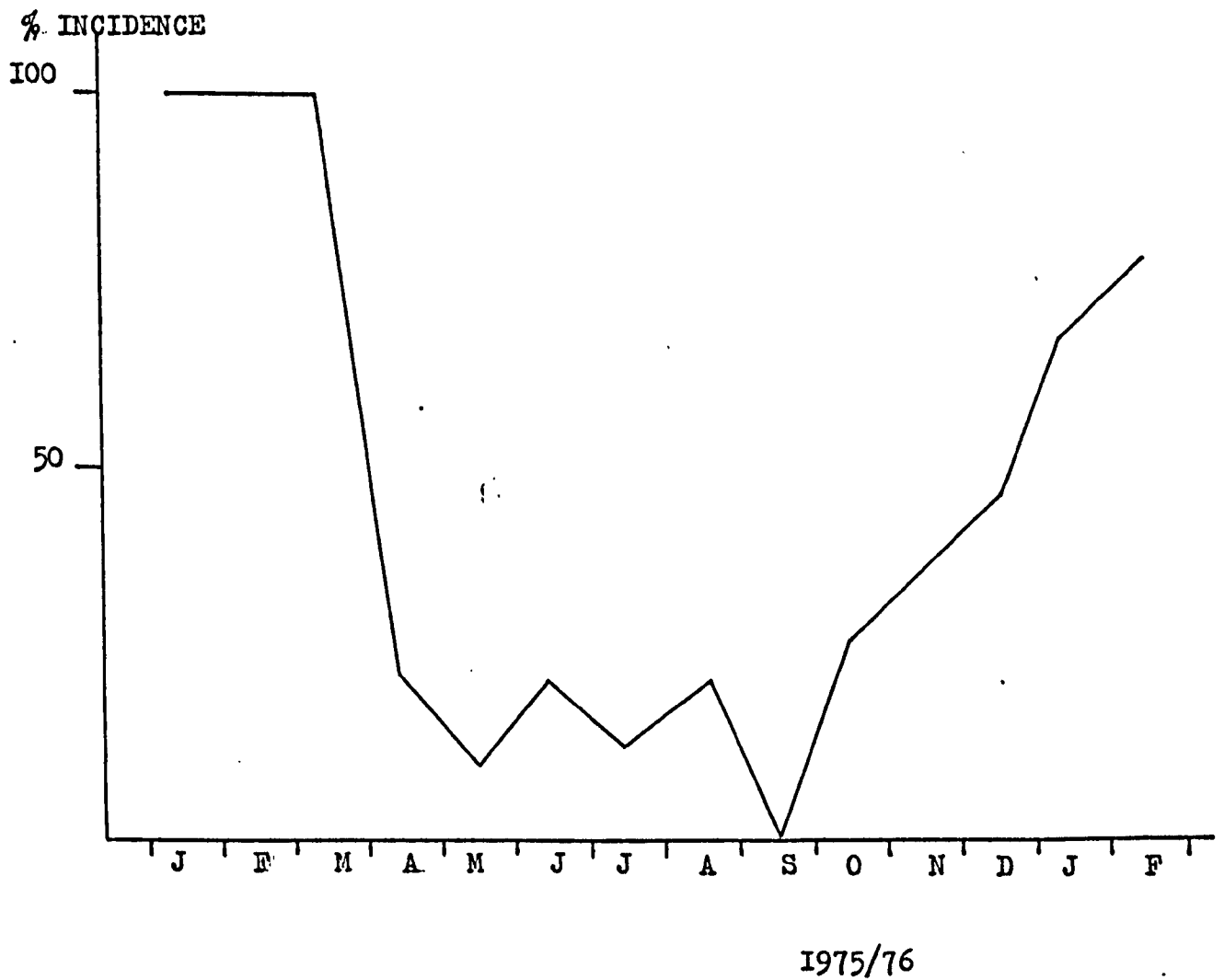
1975/76

Table IX.   Growth rate of perch from gill net samples.

January-March 1975 grouped with October-

February 1975/76.   All available data.

Age at next birthday (yrs.)	Male fish Mean length $\pm$ 95% C.L. (cm)		Female fish Mean length $\pm$ 95% C.L. (cm)	
3	11.6	(1)	-	(0)
4	12.30 $\pm$ 0.33	(28)	12.59 $\pm$ 0.22	(47)
5	12.52 $\pm$ 0.19	(46)	13.74 $\pm$ 0.50	(62)
6	13.61 $\pm$ 0.61	(23)	15.35 $\pm$ 0.91	(25)
7	14.14 $\pm$ 1.49	(8)	16.58 $\pm$ 1.75	(12)
8	15.86 $\pm$ 0.88	(5)	16.86 $\pm$ 1.91	(9)
9	-	(0)	20.96 $\pm$ 4.15	(5)
10	-	(0)	15.60	(2)
$\lessgtr$				
13	-	(0)	36.5	(1)

(Figures in parentheses are number of perch)

growth rate of female perch over 3 years of age may be greater than that of male perch of the same age (Table IX).

The weight in fish may be considered to be a function of their length (Hile, 1936). The cube law states that weight is proportional to the cube of the length of an _ideal_ fish. This presents us with a method of comparing the condition (or well being) of fish.

$$\text{Condition factor, } K = \frac{\text{weight} \times 10^4}{\text{length}^{n=3}}$$

Weight and length are measured in grammes and centimetres respectively. However, n is only equal to 3 in an ideal fish, that does not change shape with growth (Le Cren, 1951). It may be calculated with greater accuracy from the slope or regression line of a log length against log weight graph (Kesteven, 1947). K values were not calculated for the adult gill netted perch, because of the poor accuracy of the method of weighing these fish. However, K (using n=3) was calculated for each of the 0++ fish from the trawl sample of fish taken in March 1976. The effect of _Diplostomum gasterostei_ (Digenea) and _Triaenophorus nodulosus_ (Cestoda) on the K value of these fish is discussed in Chapter VII and VIII.

Ali (1973) found that n may be near the ideal value of 3 in male perch at Llyn Tegid, though may differ significantly from this ideal in female perch. In addition to sex of the fish, Ali found that the age of the fish, and the time of the year, influenced the length-weight relationship of perch at Llyn Tegid.

III.5.   GONAD MATURATION AND SPAWNING

The seasonal maturation of the male and female gonads is shown in Table X and XI. Perch at Llyn Tegid matured at 2-4 years of age, though males a little earlier than females. The following stages of gonad maturation refer to the Nikolsky (1963) scale (Appendix I).

Spawning occurred primarily between June-July. The female gonad then spent a short time at stage II (resting) before passing into stage III (developing), from September onwards (Table X). There was then a gradual increase in the size of the ovary, though maximum size was not attained until the following spring. The ovary appeared to pass rapidly through stages IV (maturity) and V (reproduction), primarily between February-May. One hundred percent of the female gonads examined in July were stage VI (spent) (Table X).

Spent male gonads only occurred in June-July (Table XI). The testes then rapidly passed through stage II, and into stage III. Testes which appeared to have reached their maximum size (stage IV) were found as early as October (Table XI). The testes developed into stage V from April onwards, though male gonads in this condition were found until July. Similar results have been reported by Le Cren (1951) and Nikolsky (1963). Spermatogenesis in percoid fish is usually completed in the autumn, with spermatids (and even spermatozoa) present within the testes through the winter. The female gametes lag behind and show their maximum increase in weight in the early spring (Nikolsky, 1963).

There is little detailed information on the environmental control of reproduction in teleost fish. Vlaming (1972) stated that only two perciform fish have been investigated, and in both photoperiod and temperature appeared important in regulating their sexual cycles. Swift and Pickford (1965) studied the seasonal variation in the hormone content of the pituitary of perch. The pituitary contained the maximum amount of growth hormone, gonadotrophins, thyrotrophin and corticotrophins during the spring and early summer. This was depleted in July, exhausted in August and then returned to a resting winter level. Over the winter there was a gradual increase in the gonadotrophic content of the pituitary which coincided with the maturation of the gonads the following spring.

Table X.   Seasonal changes in the development of female gonads.
Gill net samples.   January 1975-February 1976.

| Month | PER CENT AT STAGE | | | | | |
	I	II	III	IV	V	VI
J	-	-	100.0	-	-	-
F	5.3	-	94.7	-	-	-
M	4.8	-	85.7	9.5	-	-
A	5.0	-	80.0	10.0	-	5.0
M	-	-	77.8	22.2	-	-
J	-	-	11.5	3.8	26.9	57.7
J	-	-	-	-	-	100.0
A	-	70.0	-	-	-	30.0
S	6.3	12.5	81.2	-	-	-
O	6.3	15.6	78.1	-	-	-
N	6.9	13.8	79.3	-	-	-
D	16.7	11.1	66.7	5.6	-	-
J	11.8	11.8	70.6	5.9	-	-
F	-	-	82.4	17.6	-	-

Table XI. Seasonal development of male gonads. Gill net samples.
January 1975-February 1976.

Month	PER CENT AT STAGE					
	I	II	III	IV	V	VI
J	-	-	-	100.0	-	-
F	-	-	-	100.0	-	-
M	-	-	-	100.0	-	-
A	-	-	-	80.0	20.0	-
M	-	-	-	83.3	16.7	-
J	-	-	-	-	7.7	92.3
J	-	-	-	-	14.3	85.7
A	10.0	90.0	-	-	-	-
S	-	7.1	92.9	-	-	-
O	3.6	-	60.7	35.7	-	-
N	-	-	20.0	80.0	-	-
D	-	-	35.3	64.7	-	-
J	-	-	-	100.0	-	-
F	-	-	-	100.0	-	-

III.6.   FEEDING HABITS

The literature on the feeding habits of perch is extensive.

Previous studies at Llyn Tegid include Dunn (1954), Chubb (1964),

Siddiqui (1967) and Ali (1973).

The stomachs of 465 gill, perch were examined and the results

are shown in Table XII. In addition, the results obtained from the

analyses of the stomach contents of 64 trawled perch and 30 purse

seined fry are shown in Table XIII. The vomitting of stomach contents

in gill netted fish(McCormack, 1970),occasionally occurred particularly

at the deeper water sites (12m and 18m). The analyses of stomach

contents have been corrected to allow for this.

From Tables XII and XIII it is evident that perch at Llyn Tegid

feed on a wide variety of organisms. Dipteran larvae and pupae,

(principally Chironomidae), Asellus meridianus, Cladocera and Copepoda

are important dietary components. Fish and fish ova were less frequently

recorded. Cannabilism was the commonest form of feeding on fish, though

small undetermined cyprinids were also found in the stomachs of some

perch. The large variety of food organisms recorded may indicate that

perch was generally a non-selective feeder, and Ali (1973) considered

that availability was important in determining the ingestion of most

food items by perch at Llyn Tegid.

The relative importance of the various food items is similar to

the results of Chubb (1964), Siddiqui (1967) and Ali (1973), though

there may have been a fall in the ingestion of nymphal Ephemeroptera

and Plecoptera. The reduction in the importance of Gammarus pulex

and Ostracoda in the diet of perch since the Dunn (1954) study, is

still evident.

Seasonal variation in feeding habits

In order to assess the seasonal variation of the feeding habits

of perch, the results from the gill net samples of adult perch were used. The effect of fish age, length and sex on the feeding habits is discussed later.

Stomach fullness

The maximum number of empty stomachs were found between October-March (Fig. 10). However, food items were recorded from some stomachs in all months. Feeding activity was highest during April-September, and the maximum percentage of full stomachs was found in July.

The ingestion of certain food items exhibited distinct seasonal trends (Table XII). As a possible source of parasitic infection the following food organisms were of particular importance.

Gammarus pulex; Ostracoda

The organisms were only infrequently recorded from the stomach of perch in this study (Table XII and XIII).

Asellus meridianus

These isopods were eaten in all months, though there was a prominent spring peak. The results also indicated that there was also a smaller, autumn peak of A. meridianus ingestion by perch at Llyn Tegid (Fig. 11).

Cladocera

These plankton were most common in perch stomachs during June-September. They were ohly infrequently eaten by adult perch in other months (Fig. 12).

Copepoda

Copepod crustaceans were recorded from the stomachs of adult perch less frequently than Cladocera (Table XII). Cyclopoida were found in perch stomachs during most months (Fig. 12). However, the results suggest that these copepods were most often eaten from July onwards, with a peak in September (Fig. 12). Calanoid copepods were found in the stomachs of

Fig. IO. Incidence of empty stomachs.

Fig. II. Incidence of <u>Asellus meridianus</u> in perch stomachs.
Gill net samples. January I975 – February I976.

% INCIDENCE

Fig. IO.

50

Fig. II.

50

J F M A M J J A S O N D J F
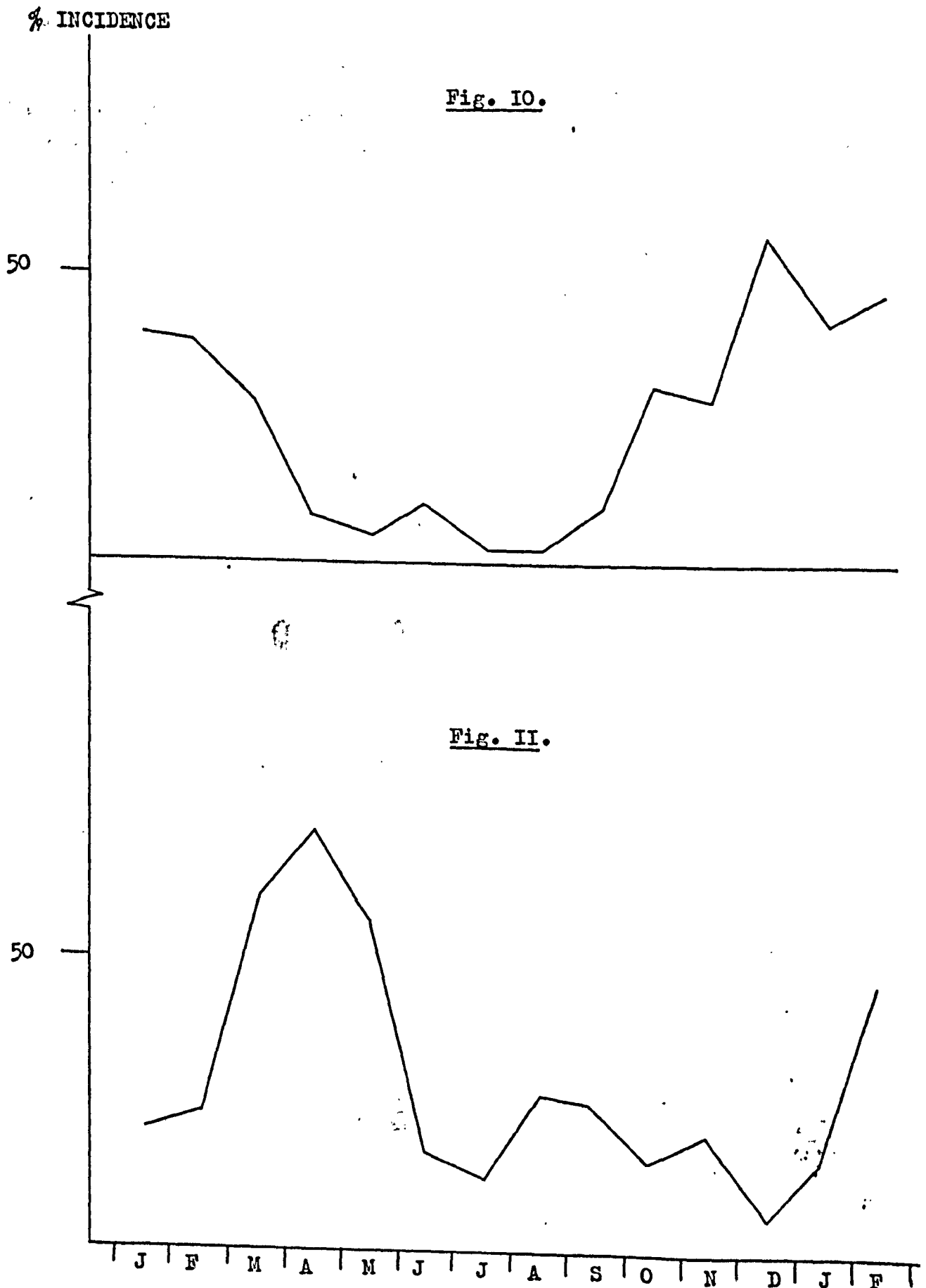
I975/76

Fig. I2. Incidence of zooplankton in perch stomachs. Gill net samples.
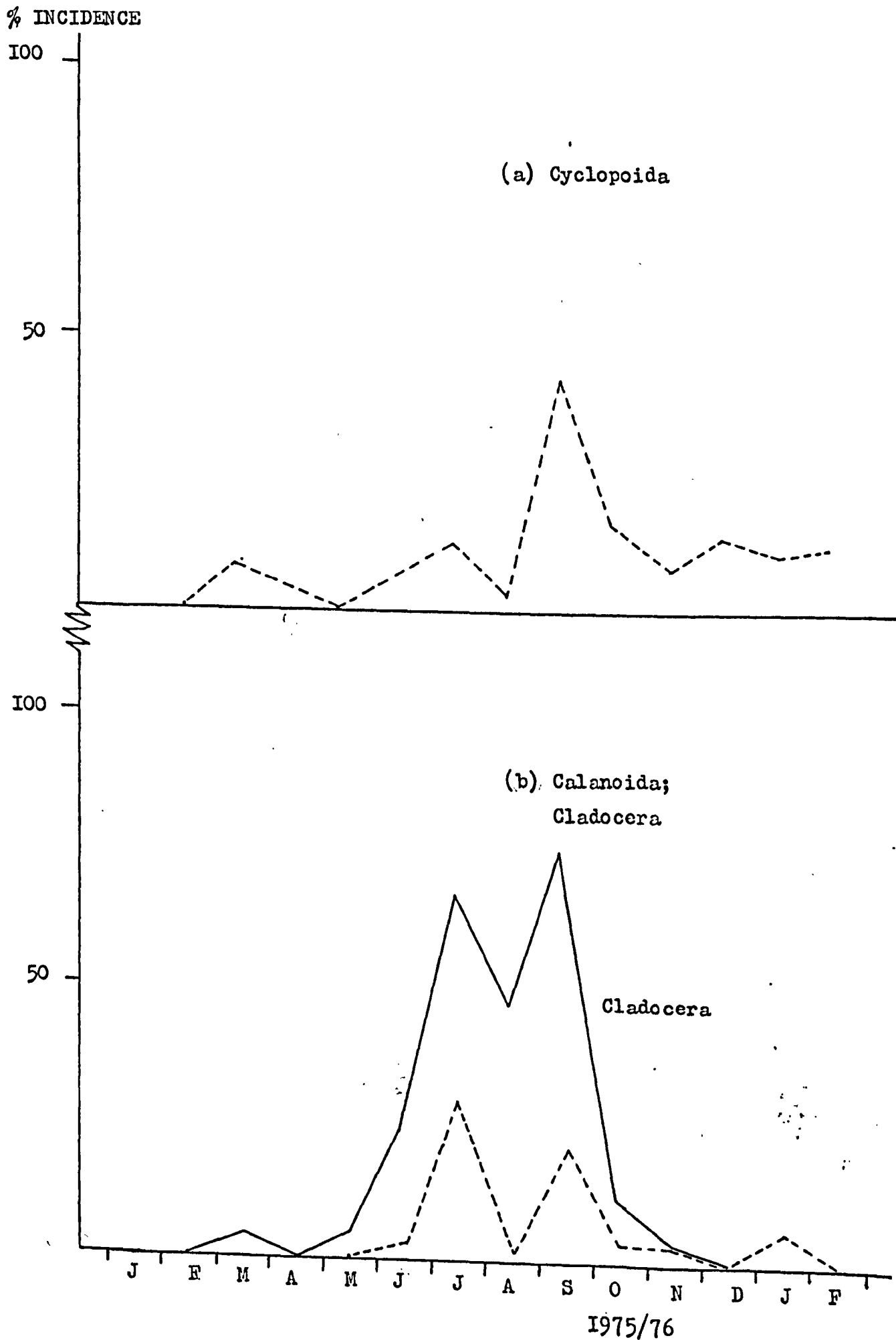January 1975 - February 1976.

Table XII.   The feeding habits of perch.   Gill net samples.   January 1975-February 1976.

FOOD ITEM	MONTHLY % OCCURRENCE 1975/1976														TOTAL
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	
Annelida	-	-	-	-	5.6	2.6	-	3.3	10.0	3.9	4.0	-	-	-	2.2
Bivalve Mollusca	-	3.9	-	-	-	-	-	-	5.0	-	-	-	-	-	0.6
Plecoptera (nymphs)	-	-	8.0	-	61.1	2.6	-	23.3	-	-	4.0	-	5.9	6.7	3.1
Ephemeroptera (nymphs)	-	-	-	4.5	-	-	-	13.3	-	-	-	7.1	-	-	1.9
Megaloptera (larvae)	-	3.9	-	-	-	2.6	-	-	-	-	-	-	11.8	-	1.3
Trichoptera (larvae)	-	-	12.0	-	-	-	2.6	6.7	-	3.9	4.0	-	5.9	6.7	3.1
Coleoptera (larvae)	-	-	-	-	5.6	-	-	-	-	-	-	-	-	-	0.3
Diptera (larvae)	-	7.7	36.0	59.1	100.0	52.6	61.5	73.3	55.0	30.8	20.0	21.4	35.3	20.0	45.0
Diptera (pupae)	-	-	4.0	4.5	55.6	76.3	84.6	60.0	60.0	3.9	-	-	-	6.7	33.1
Gammarus pulex	-	7.7	8.0	4.5	5.6	-	-	3.3	-	-	4.0	-	5.9	-	2.8
Asellus meridianus	20.0	23.1	60.0	72.7	55.6	15.8	12.8	26.7	25.0	15.9	20.0	7.1	17.6	44.7	28.8
Cladocera	-	-	4.0	-	5.6	23.7	66.7	46.7	70.0	11.5	4.0	-	-	-	21.9
Cyclopoida	-	-	8.0	4.5	-	7.9	12.8	3.3	42.0	15.4	8.0	14.3	11.8	13.3	10.0
Calanoida	-	-	-	-	-	2.6	28.2	3.3	20.0	3.9	4.0	-	5.9	-	6.9
Ostracoda	-	-	-	-	-	2.6	-	-	-	3.9	-	-	-	6.7	0.9
Hydracarina	-	-	-	-	-	-	12.8	10.0	20.0	-	-	-	-	-	3.8
Undet. Arthropoda	20.0	-	-	-	5.6	13.2	2.6	6.7	10.0	7.7	4.0	21.4	17.6	-	6.6
Fish	20.0	15.4	-	-	-	-	7.7	6.6	15.5	-	-	7.1	5.9	-	4.7
Fish ova	-	3.9	-	4.5	5.6	2.6	-	-	-	-	-	-	-	6.7	1.6
Plant remains	-	7.7	20.0	31.8	55.6	2.6	-	16.7	5.0	-	-	21.4	17.6	20.0	12.5
Dietritus	20.0	7.7	16.0	27.3	77.8	10.5	7.7	20.0	40.0	7.7	28.0	14.3	23.5	-	19.7
Number stomachs examined	6	30	30	30	30	39	40	30	30	60	54	35	30	21	465

Table XIII. Feeding habits of perch. Trawl and purse seine samples. March 1976 and July 1976.

FOOD ITEM	% OCCURRENCE	
	TRAWL SAMPLE MARCH 1976	PURSE SEINE SAMPLE JULY 1976
PLECOPTERA (nymphs)	4.7	-
DIPTERA (larvae)	12.5	-
DIPTERA (pupae)	-	3.3
Gammarus pulex	9.4	-
Asellus meridianus	43.8	-
CLADOCERA	10.9	100.0
CYCLOPOIDA	9.4	-
CALANOIDA	20.3	3.3
OSTRACODA	1.6	-
Undet. ARTHROPODA	6.2	-
FISH OVA	3.1	-
PLANT REMAINS	4.7	-
Empty stomachs	21.9	-
Number fish examined	64	30

adult perch less frequently than either of the above zooplankton

(Table XII). The occurrence of Calanoida in the stomachs of these

fish appeared to exhibit two peaks: June and September (Fig. 12).

From Table XII and Fig. 12 it is evident that there was a marked

fall in the occurrence of zooplankton in the stomachs of adult perch

in October. Small numbers of these crustaceans (particularly cyclopoid

Copepoda) were ingested during the autumn-winter (October-February)

(Fig. 12).

Fish

The remains of fish were found relatively infrequently within the

stomachs of perch (Table XII). The results suggest that the occurrence

of fish in the stomachs of perch at Llyn Tegid exhibited small summer

(July-September) and mid-winter (December-February) peaks (Table XII).

The above seasonal variations in the feeding habits of perch at

Llyn Tegid are similar to those reported by Chubb (1964), Siddiqui

(1967) and Ali (1973).

Effect of host age, length and sex on feeding habits.

Asellus meridianus

A. meridianus was not recorded from the stomachs of the perch fry

examined in July 1976 (Table XIII). The results obtained from the trawl

sample of fish are shown in Tables XIV and XV. In order to reduce the

effects of seasonal and non-seasonal ingestion of A. meridianus on this

aspect of the study, only the gill net data from March-May 1975 were used

(Tables XIV and XV). During these months a larger proportion of the adult

perch population appeared to be feeding on A. meridianus.

Perch of both sexes and a range of ages and sizes were found to have

ingested A. meridianus. This isopod had a low incidence in the stomachs of

perch at the end of their first year in the lake (aged 0++, length 3.0-8.9cm,

Table XIV and XV). Whilst few large, old perch were examined, the results

Table XIV. Effect of host length and sex on incidence of <u>Asellus</u>

meridianus in perch stomachs. Trawl and gill net

samples.

LENGTH (cm)	UNSEXED*		MALE		FEMALE	
	1	2	1	2	1	2
Trawl sample March 1976						
3.0	0	-	0	-	0	-
3.0-5.9	28	7.1	0	-	1	-
6.0-8.9	7	-	0	-	0	-
9.0-11.9	0	-	18	94.4	10	90.0
TOTAL	35	5.7	18	94.4	11	81.8
Gill net samples March-May 1975						
9.0-11.9	0	-	7	33.3	1	(100.0)
12.0-14.9	0	-	21	73.3	45	60.0
15.0-17.9	0	-	2	100.0	9	66.7
≥18.0	0	-	0	-	4	75.0
TOTAL	0	-	31	62.5	59	63.4

N.B.   *sex not distinguishable to naked eye

1 number fish examined

2 % incidence of food organism

Table XV.   Effect of host age and sex on incidence of Asellus

meridianus in perch stomachs.   Trawl and gill net

samples.

AGE (yrs.)	UNSEXED*		'MALE		FEMALE	
	1	2	1	2	1	2
Trawl sample March 1976						
0++	35	5.7	0	-	1	-
1++	0	-	1	(100.0)	1	-
2++	0	-	7	85.7	3	100.0
3++	0	-	9	100.0	6	100.0
4++	0	-	1	(100.0)	0	-
TOTAL	35	5.7	18	94.4	11	81.8
Gill net samples March-May 1975						
2-2++	0	-	1	(100.0)	0	-
3-3++	0	-	12	44.4	32	60.9
4-4++	0	-	6	50.0	10	75.0
5-5++	0	-	11	85.7	9	66.7
⩾ 6	0	-	1	(100.0)	8	57.1
TOTAL	0	-	31	62.5	59	63.4

N.B.   *, 1, 2 ...... see Table XIV

in Table XVI and XV suggest that the ingestion of <u>A. meridianus</u> was prevalent at certain times of the year in perch aged 2 years and above, and of length 9.0cm and over.

Ali (1973) found that ingestion of <u>A. meridianus</u> by perch at Llyn Tegid was predominant in fish 12.0-32.0cm (total length).

Cladocera

All of the 30 perch fry purse seined in July 1976 were found to have eaten Cladocera (Table XIII), and these crustaceans were found within the stomachs of 20.0% of 35 juvenile (0++) fish trawled in March 1976 (Table XVI and XVII). To reduce the effects of seasonal changes in feeding habits, only gill samples of perch taken between July-September were used (Table XVI and XVII). Whilst few young and few old, large perch were examined, the results suggest that during July-September the incidence of Cladocera in perch stomachs was high in fish 9.0-14.9cm, and aged 2-6+ (Table XVI and XVII). Of 32 female and 38 male perch gill netted between July-September, 63.5% and 44.8% respectively were found with cladocerans in their stomachs (Table XVI and XVII).

Cyclopoid Copepoda

Cyclopoid copepods were not recorded from the stomachs of the fry purse seined in July 1976 (Table XIII). Of the 35 juvenile perch (aged 0++) that were trawled in March 1976, 17.1% were found to have ingested these zooplankton (Table XVIII and XIX). In an effort to reduce the influence of seasonal variations in feeding habits, only the gill netted perch taken between September-October 1975 were used (Table XVIII and XIX). Adult perch between 9.0-17.9cm and aged 3-5++ were found to have ingested these organisms, though few young or old, large perch were examined (Table XVIII and XIX). Of 48 female and 42 male perch caught

by gill nets during July-October 1976, 27.2% and 18.8% respectively

had been feeding on cyclopoid Copepoda (Table XVIII and XIX).

Calanoid Copepoda

No calanoid copepods were recorded from the stomachs of the perch

fry purse seined in July 1976, while 54.3% of 35 juvenile fish trawled

in March 1976 had been feeding on these crustaceans (Table XIII, XX and

XXI). To minimise the effects of seasonal variations in the feeding

habits of perch on this aspect of the study only the gill netted perch

taken between July-September 1975 were used (Table XX and XXI). Only

one of 38 male perch (2.6%) had been feeding on calanoid copepods, while

17 of 62 female perch (28.3%) were found to have done likewise. The

reason for this difference is not known. Feeding on calanoid Copepoda

was most common in female perch 9.0-14.9cm, and aged 2-4+ (Table XX and

XXI).

Zooplankton (principally Cladocera) were important dietary components

of the perch fry examined in July (aged 4-6 weeks). From the trawl sample

of fish taken in March, it would appear that zooplankton (principally

calanoid Copepoda) were still important food organisms to perch aged

8-9 months. Therefore, perch aged less than 1-2 years may rely on these

organisms as food, at times of the year when older perch are feeding to

a large extent on other food items (e.g. Asellus meridianus). The relative

importance of each group of zooplankton (i.e. Cladocera, calanoid and

cyclopoid Copepoda), and perhaps the species within each group, may change

with increasing size and age of the fish. Smyly (1952) studied the feeding

habits of perch fry at Lake Windermere (Cumbria) between May-September.

The diet was principally zooplankton, supplemented by invertebrate bottom

fauna and other perch fry. Ali (1973) examined the stomachs of 8 fry

caught at Llyn Tegid in August. Zooplankton (mainly Cladocera) were the

most important dietary components. Ali also found that while perch up

Table XVI.   Effect of host length and sex on incidence of

Cladocera in perch stomachs.   Trawl and gill net

samples.

LENGTH (cm)	UNSEXED*		MALE		FEMALE	
	1	2	1	2	1	2
Trawl sample March 1976						
3.0	0	-	0	-	0	-
3.0-5.9	28	17.9	0	-	1	-
6.0-8.9	7	28.6	0	-	0	-
9.0-11.9	0	-	18	-	10	-
TOTAL	35	20.0	18	-	11	-
Gill net samples July-September 1975						
9.0-11.9	0	-	15	46.7	2	50.0
12.0-14.9	0	-	21	41.7	42	80.0
15.0-17.9	0	-	1	(100.0)	10	40.0
$\geqslant$18.0	0	-	1	-	8	13.8
TOTAL	0	-	38	44.8	62	63.5

N.B.   *, 1, 2 ...... Table XIV

Table XVII.   Effect of host age and sex on the incidence of

Cladocera in perch stomachs.   Trawl and gill net

samples.

AGE (yrs.)	UNSEXED*		MALE		FEMALE	
	1	2	1	2	1	2
Trawl sample March 1976						
0++	35	20.0	0	-	1	-
1++	0	-	1	-	1	-
2++	0	-	7	-	3	-
3++	0	-	9	-	6	-
4++	0	-	1	-	0	-
TOTAL	35	20.0	18	-	11	-
Gill net samples July-September 1975						
2-2+	0	-	0	-	2	100.0
3-3+	0	-	9	66.7	9	66.7
4-4+	0	-	13	40.0	29	77.8
5-5+	0	-	10	14.3	5	60.0
6-6+	0	-	4	66.7	8	50.0
$\geqslant 7$	0	-	1	-	9	22.2
TOTAL	0	-	38	44.8	62	63.5

N.B.   *, 1, 2 ...... see Table XIV

Table XVIII.   Effect of host length and sex on the incidence of

cyclopoid Copepoda in perch stomachs.   Trawl and

gill net samples.

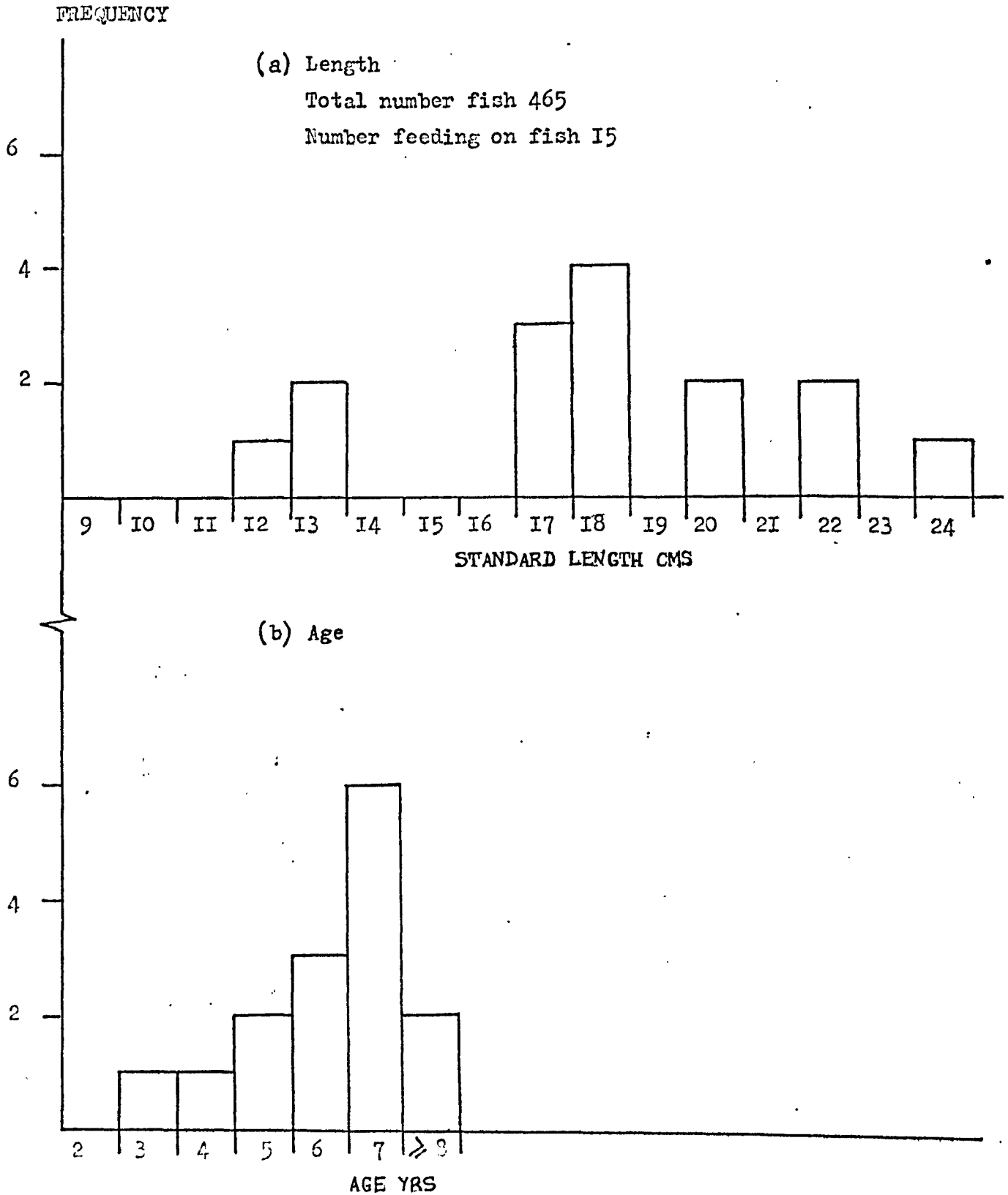| LENGTH (cm)	UNSEXED*		MALE		FEMALE	
	1	2	1	2	1	2
Trawl sample March 1976						
3.0	0	-	0	-	0	-
3.0-5.9	28	21.4	0	-	1	-
6.0-8.9	7	-	0	-	0	-
9.0-11.9	0	-	18	-	10	-
TOTAL	35	17.1	18	-	11	-
Gill net samples September-October 1975						
9.0-11.9	0	-	12	25.0	2	-
12.0-14.9	0	-	27	14.3	29	38.9
15.0-17.9	0	-	3	-	10	22.2
⩾18.0	0	-	0	-	7	-
TOTAL	0	-	26	18.8	48	27.8

N.B.   *, 1, 2 ...... see Table XIV

Table XIX. Effect of host age and sex on incidence of cyclopoid

Copepoda in perch stomachs. Trawl and gill net samples.

AGE (yrs.)	UNSEXED*		MALE		FEMALE	
	1	2	1	2	1	2
Trawl sample March 1976						
0++	35	17.1	0	-	1	-
1++	0	-	1	-	1	-
2++	0	-	7	-	3	-
3++	0	-	9	-	6	-
4++	0	-	1	-	0	-
TOTAL	35	17.1	18	-	11	-
Gill net samples September-October 1975						
2-2++	0	-	0	-	1	-
3-3++	0	-	10	16.7	10	60.0
4-4++	0	-	17	14.3	20	41.2
5-5++	0	-	10	50.0	6	-
≯6	0	-	5	-	11	-
TOTAL	0	-	42	18.8	48	27.8

N.B.   *, 1, 2 ...... see Table XIV

Table XX. Effect of host length and sex on the incidence of
calanoid Copepoda in perch stomachs. Trawl and gill
net samples.

LENGTH (cm)	UNSEXED*		MALE		FEMALE	
	1	2	1	2	1	2
Trawl sample March 1976						
3.0	0	-	0	-	0	-
3.0-5.9	28	57.1	0	-	1	-
6.0-8.9	7	42.9	0	-	0	-
9.0-11.9	0	-	18	-	10	-
TOTAL	35	54.3	18	-	11	-
Gill net samples July-September 1975						
9.0-11.9	0	-	15	6.7	2	50.0
12.0-14.9	0	-	21	-	42	35.0
15.0-17.9	0	-	1	-	10	10.0
$\geqslant$18.0	0	-	1	-	8	12.5
TOTAL	0	-	38	2.6	62	28.3

N.B. *, 1, 2 ...... see Table XIV

Table XXI.   Effect of host age and sex on incidence of calanoid

Copepoda in perch stomachs.   Trawl and gill net samples.

AGE (yrs.)	UNSEXED*		MALE		FEMALE	
	1	2	1	2	1	2
Trawl sample March 1976						
0++	35	54.3	0	-	0	-
1++	0	-	0	-	0	-
2++	0	-	0	-	0	-
3++	0	-	0	-	0	-
4++	0	-	0	-	0	-
TOTAL	35	54.3	18	-	11	-
Gill net samples July-September 1975						
2-2+	0	-	0	11.1	2	50.0
3-3+	0	-	9	-	9	33.3
4-4+	0	-	13	-	29	37.1
5-5+	0	-	10	-	5	4.0
≥6	0	-	5	-	17	5.9
TOTAL	0	-	38	2.6	62	28.3

N.B.   *, 1, 2 ...... see Table XIV

Fig. 13. Effect of host age and length on the occurrence of fish
ingestion by perch. Gill net samples. January 1975 -
February 1976.

FREQUENCY

(a) Length
Total number fish 465
Number feeding on fish 15

STANDARD LENGTH CMS

(b) Age

AGE YRS

to 24.0cm (total) length fed on larger planktonic crustaceans during the summer-autumn, zooplankton were only a major dietary component in perch less than 18.0 cm (total) length.

Fish

The remains of other fish were not found in the stomachs of perch from the July 1976 purse seine, or March 1976 trawl, samples (Table XIII). From the gill net samples of adult perch collected between January 1975- February 1976, 13 of 282 (4.6%) female perch and 2 of 183 (1.1%) male perch had been feeding on other fish (mainly perch). From Fig. 13 it would appear that feeding on other fish was most prevalent in perch above 16.9cm, and older than 4-5 years.

Ali (1973) found that fish (primarily perch and minnows, _Phoxinus_ _phoxinus_) were a main component of the diet of perch greater than 18.0cm (total) length.

In agreement with Ali (1973) there was found to be a detectable change in feeding habits with perch size. Nonetheless, seasonal availability had a pronounced effect on the ingestion of many organisms.

III.7.   SUMMARY

Relevant aspects of host biology were examined, and discussed in the light of previous research at Llyn Tegid. These results will be referred to in subsequent chapters.

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CHAPTER IV

THE PARASITE FAUNA OF PERCH, Perca fluviatilis L.

IV.1 INTRODUCTION

Kennedy (1974) has presented a compilation of the records of the parasites of the freshwater fish of the British Isles. The parasite fauna of perch has previously been studied in detail at six localities: Rostherne Mere, Cheshire (Rizvi, 1964); Shropshire Union Canal, Cheshire (Abolarin, 1966; Mishra & Chubb, 1969); Hanningfield Reservoir, Essex (Needham, 1969; Wootten, 1973a + b; 1974a + b); Ockendon Moat, Essex (Shillcock, 1972); Slapton Ley, Devon (Canning et al., 1973; Kennedy, 1975); and Loch Leven, Scotland (Campbell, 1974). Excluding the studies on the Shropshire Union Canal, all of these investigations have been at lacustrine, eutrophic environments.

The parasite fauna of perch from Llyn Tegid has been examined by Chubb (1963, 1964a, b, 1970), Abolarin (1966), Chattrabhuti (1974) and Roscoe, (1977). However, these studies were of a rather restricted nature. This is the first detailed investigation of the parasite fauna of perch from a mesotrophic environment in the British Isles.

The parasite fauna of perch has been studied at several continental European waters. These include: Lake Ladoga (Barysheva and Bauer, 1957); Lake Druzno (Kozicka, 1958, 1959; Wisniewski, 1958); Lake Dusia (Rauckis, 1970a, b); Lake Dargin (Wierzbicki, 1970, 1971); River Glomma (Halvorsen, 1971, 1972); Lake Võrtsjarv (Tell, 1971) and Lake Leginskie (Wierzbicka and Wierzbicki, 1971).

The yellow perch (Perca flavescens Mitchill) is a close relative of P. fluviatilis, and is a common North American fish. Studies on the parasite fauna of the yellow perch include: Mueller and Van Cleave (1932); Van Cleave and Mueller (1932, 1934); Bangham (1944, 1955); Bangham and Hunter (1939); Bangham and Venard (1946); Fischatel (1947, 1952, 1953);

Bangham and Adams (1954); Tedla and Fernando (1969, 1970a, b); Noble (1970); Cannon (1972, 1973); and Molnar et al (1974). Hoffman (1967) lists over 100 species of parasites from yellow perch. Shulman (1958) stated that with our present knowledge, a comparison between the fish parasites of European and Asian fish, and those of American fish, is impossible. Comparative data on the respective parasites, the determination of synonomy, the study of similarities and differences, etc. are all required. Therefore, the parasite fauna of yellow perch has not been discussed in detail here.

II.2 RESULTS

IV.2.1 Check list of the parasites of perch from the British Isles.

The check list of the parasites of perch from the British Isles (from Kennedy, 1974) is revised and brought up to date (Table I). Ignoring the records where confusion of identification may exist, at least 45 species of protozoan and metazoan parasites are listed.

IV.2.2 Present study

The parasites recorded from the perch in this study are shown in Tables II, III and IV. These represent the fish caught by gill net, trawl and purse seine respectively. "Incidence" is taken to indicate the percentage of the fish infected. Both the mean number of parasites per fish (infected and uninfected fish), and the mean number of parasite per infected fish (infected fish only) are provided.

From 559 perch a total of 16 protozoan and metazoan parasite species were recorded.

Fifteen species of parasites were recovered from 465 gill netted perch, 10 species from 64 trawled perch, and 3 species from 30 purse seined fry. The effects of season and host parameters of length, age

Table I. Parasite species checklist for perch in the British Isles

See Notes	Species	Locality	Reference
	PROTOZOA		
(?)	Apiosoma sp. (=Glossatella sp.) Loch Leven		Campbell (1974)
(1)	Epizooic vorticellids	Llyn Tegid	Abolarin (1966)
	Henneguya psorospermica Thélohan, 1895	Llyn Tegid	Chubb (1963) Present study
	Henneguya sp.	Rostherne Mere Rivers Blackwater, Chelmer, Roding	Rizvi (1964) Kennedy (1974)
	Ichthyophthirius multifiliis Fouquet, 1876	Princes Park (Merseyside)	Personal observations
	Myxobolus muelleri Bütshli, 1882	Serpentine (London), Llyn Tegid	Kennedy (1974) Present Study
(2)	Trichodinella epizootica (Raabe, 1950)	Shropshire Union Canal	Abolarin (1966)
(2)	Trichodina sp.	Slapton Ley	Canning et al. (1973)
	Trypanosoma percae Brumpt, 1906	Shropshire Union Canal Hanningfield Reservoir Slapton Ley	Abolarin (1966) Needham (1969) Canning et al. (1973)
		Gravel pits (Berks)	Kennedy (1974)
	MONOGENEA		
(3)	Ancyrocephalus paradoxus Creplin, 1839 Ancyrocephalus percae Ergens, 1966	Southern England Llyn Tegid Llyn Tegid	Dawes (1947) Chubb (1963) Present study
	Gyrodactylus sp.	Loch Leven	Campbell (1974)
	DIGENEA		
	I. Adults		
	Azygia lucii (Müller, 1776)	Dagenham (Essex)	Anderson (1971)
	Bucephalus polymorphus Baer, 1827	Boston (Lincs)	Kennedy (1974)
	Bunodera luciopercae (Müller, 1776)	Herts. Loch Lomond Llyn Tegid	Baylis (1939) Copland (1957) Chubb (1963) Roscoe (1977) Present study
		Rostherne Mere Shropshire Union Canal	Rizvi (1964) Mishra & Chubb (1969)
		Hanningfield Reservoir Loch Leven Boston (Lincs), Lake District, Shropshire, West Bromwich	Wootten (1973a,b) Campbell (1974) Kennedy (1974)
		Hale (Merseyside)	Personal observations

Table I (contd.)

See Notes	Species	Locality	Reference
	Crepidostomum farionis (Müller, 1784)	Loch Lomond	Copland (1957)
	Rhiphidocotyle illense (Ziegler, 1883)	River Roding Serpentine (London)	Shillcock (1972) Kennedy (1974)
	II. Metacercariae		
	Apatemon annuligerum (Nordmann) Odening, 1970		Blair, 1974
	Diplostomum gasterostei Williams, 1966	River Nidd (Yorks) Llyn Tegid	Sweeting, (1971a) Chattrabhuti (1974) Present study
(4)	Diplostomum spathaceum (Rud., 1819)	Slapton Ley Widespread, in many fish species; Recorded from perch N.B.Rostherne Mere Shropshire Union Canal Ockenden Moat Hanningfield Reservoir Llyn Tegid Princes Park,	Kennedy (1975) Kennedy (1974) Sweeting (1974) Rizvi (1964) Mishra & Chubb (1969) Shillcock (1972) Wootten (1973a, 1974a) Chattrabhuti (1974) Present study Personal observations
(4)	Diplostomum sp.	Hale (Merseyside) Widespread, in many fish species. Recorded from perch N.B.Llyn Tegid Loch Leven	Chubb (1970) Campbell (1974)
(?)	Ichthyocotylurus cucullus (Thoss, 1897)	Loch Leven	Campbell (1974)
(9)	Ichthyocotylurus sp. Tetracotyle percafluviatilis Linstow, 1856	Hanningfield Reservoir Grand Canal (Ireland) River Roding, Ockendon Moat	Wootten (1973a) Kane (1966) Shillcock (1972)
(9)	Tetracotyle variagatus (Creplin, 1825)	Lough Neagh (Ireland)	Vickers (1951)
	Tetracotyle sp.	Rostherne Mere Ireland Llyn Tegid	Rizvi (1964) Kane (1966) Present study
(5)	Tylodelphys clavata (Nordmann, 1832)	Rostherne Mere Hanningfield Reservoir Slapton Ley	Rizvi (1964) Wootten (1973a, 1974a) Kennedy (1974)
	Tylodelphys podicipina Kozicka & Niewiadomska, 1960	Hanningfield Reservoir Gravel pits (Thames Valley)	Wootten (1973a, 1974a) Kennedy (1974) Sweeting (1971a)
(?)	Tylodelphys sp. Undetermined metacercariae	Windermere	Sweeting (1971a) Rawson (1952)
	CESTODA		
	I. Adults (including juveniles)		
	Bothriocephalus sp.	Shropshire Union Canal	Mishra & Chubb (1969)

Table I (contd.)

See Notes	Species	Locality	Reference
		Ockenden Moat	Shillcock (1972)
		Llyn Tegid	Present study
	Cyathocephalus truncatus (Pallas, 1781)	Llyn Tegid	Chubb (1970)
	Eubothrium crassum (Bloch, 1779)	Ireland	Kane (1966)
		Loch Leven	Campbell (1974)
	Eubothrium sp.	Windermere	Rawson (1952)
		Llyn Tegid	Present study
	Proteocephalus filicollis (Rud., 1810)	Dagenham (Essex)	Kennedy (1974)
	Proteocephalus percae (Müller, 1780)	Swithland Reservoir	Rawson (1952)
		Shropshire Union Canal	Mishra & Chubb (1969)
		Rostherne Mere	Rizvi (1964)
		Hanningfield Reservoir	Wootten (1973a, 1974b)
		Serpentine (London)	Kennedy (1974)
(6)	Proteocephalus sp.	Boston (Lincs.), River Blackwater	Kennedy (1974)
		Llyn Tegid	Present study

II. Larvae (plerocercoids)

See Notes	Species	Locality	Reference
	Diphyllobothrium latum (l., 1758)	Garradice Lough (Ireland)	Hickey & Harris (1945)
(7)	Diphyllobothrium sp.	Windermere	Rawson (1952)
		Ireland	Kane (1966)
		Llyn Tegid	Present study
	Triaenophorus nodulosus (Pallas, 1781)	Llyn Tegid	Chubb (1963, 1964a) Present study
		Rostherne Mere	Rizvi (1964)
		Shropshire Union Canal	Mishra & Chubb (1969)
		River Avon (Hants.)	Hine (1970)
		Dagenham (Essex)	Anderson (1971)
		Preston-Lancaster Canal Serpentine (London)	Kennedy (1974)

NEMATODA

See Notes	Species	Locality	Reference
	Camallanus lacustris (Zoega, 1776)	Wiltshire	Baylis (1939)
		Swithland Reservoir Windermere	Rawson (1952)
		Llyn Tegid	Chubb (1963) Roscoe (1977) Present study
		Ireland	Kane (1966)
		Shropshire Union Canal	Mishra & Chubb (1969)
		Dagenham (Essex)	Anderson (1971)
		Hanningfield Reservoir	Wootten (1973a)
		Leeds-Liverpool Canal, Preston-Lancaster Canal, Serpentine (London), Boston (Lincs.)	Kennedy (1974)
		Princes Park, Meols, Hale (Merseyside)	Personal observations

Table I (contd.)

See Notes	Species	Locality	Reference
	Capillaris salvelini Polyanskii, 1952	Loch Leven	Campbell (1974)
	Cucullanus truttae (Fabricius, 1794)	Rivers Avon, Itchen, Test	Stranack (1966)
		Llyn Tegid	Present study
	Eustrongylides sp.	Serpentine (London)	Kennedy (1974)
(8)	Raphidascaris acus (Bloch, 1779)	Loch Leven	Campbell (1974)
(8)	Raphidascaris cristata (Linstow, 1872)	Llyn Tegid	Chubb (1963) Present study

ACANTHOCEPHALA

	Acanthocephalus anguillae (Müller, 1780)	Loch Lomond	Copland (1957)
		River Ouse	Kennedy (1974)
	Acanthocephalus clavula Duj., 1845)	Llyn Tegid	Chubb (1963, 1964c, 1968b) Parr (1976) Rojanapaibul (1976, 1977) Andrews & Rojanapaibul (1976) Roscoe (1977) Present study
		Ireland	Kane (1966)
		Slapton Ley	Canning et al (1973) Kennedy (1975)
	Acanthocephalus lucii (Müller, 1776)	Widespread, in many fish species. Recorded from perch.	Kennedy (1974)
		N.B. Rostherne Mere	Rizvi (1964)
		Shropshire Union Canal	Mishra & Chubb (1969)
		Princes Park (Merseyside)	Personal observations
	Echinorhynchus truttae (Schrank, 1788)	Loch Leven	Campbell (1974)
	Echinorhynchus sp.	Rivers Avon, Itchen, Test	Stranack (1966)
	Neoechinorhynchus rutili (Müller, 1780)	Loch Leven	Campbell (1974)
	Pomphorhynchus laevis (Müller, 1776)	Widespread, in many fish species. Recorded in perch.	Kennedy (1974)

ANNELIDA (Hirudinea)

	Hemiclepsis marginata (Müller, 1774)	Widespread, on many fish species. Recorded on perch.	Kennedy (1974)
		N.B. Rostherne Mere	Rizvi (1964)
	Piscicola geometra (L., 1761)	Widespread, on many fish species, not yet reported from Scotland Reported on perch	Kennedy (1974)
		N.B. Shropshire Union Canal	Mishra & Chubb (1969)

Table I (contd.)

See Notes	Species	Locality	Reference
	MOLLUSCA		
	Glochidia larvae	Fairly widespread, on a variety of fish species. Recorded on perch.	Kennedy (1974)
		N.B.Shropshire Union Canal	Mishra & Chubb (1969)
		Hanningfield Reservoir	Wootten (1973)
		Loch Leven	Campbell (1974)
	ARTHROPODA (Crustacea)		
	Achtheres percarum Nordmann, 1832	Several localities N.B.Rostherne Mere Hanningfield Reservoir	Kennedy (1974) Rizvi (1964) Wootten (1973)
	Argulus foliaceus L., 1758	Widespread on many fish species including perch.	Kennedy (1974)
		N.B.Rostherne Mere Shropshire Union Canal	Rizvi (1964) Mishra & Chubb (1969)
		Hanningfield Reservoir Slapton Ley	Wootten (1973) Canning et al. (1973) Kennedy (1975)

Notes

(?) Doubt as to the author's identification

(1) According to Chubb (1976) it is highly likely that these

protozoans belong to the genus Apiosoma.

(2) According to Lom & Stein (1966) Trichodina domerguei f percarum

Dogiel, 1940 is in fact Trichodinella epizootica. However,

confirmation of the Abolarin (1966) material is required (Chubb, 1976).

(3) Ergens (1966a) and Bykhovski & Nagibina (1970) have revised

the genus Ancyrocephalus Creplin, 1839. Studying the parasites of

the fish in Czechoslovakia and the U.S.S.R. respectively they

amended the genus: A. paradoxus Creplin, 1839 occurs on

Luciopercae lucioperca, and A. percae Ergens, 1966 on Perca

fluviatilis. The Chubb (1963) and Dawes (1947) material was

re-identified as A. percae, and the identity of the material

from the present study was established as A. percae (see Chapter VI).

(4) Diplostomum gasterostei was first described in 1966. Records of

D. spathaceum before that date may contain records of D. gasterostei.

D. gasterostei characteristically inhabits the humour and retina

of the fish eye, whilst D. spathaceum is normally associated with

the lens. Campbell (1974) records two types of diplostomulae;

one from the lens, the other from the vitreous body. Wootten

(1974) has found metacercarial D. spathaceum from the humour

that was morphologically identical to those from the lens. Further

aspects of their taxonomy are considered in Chapter VII.

(5) Synonym for Diplostomum clavatum.

(6) The Proteocephalus sp. recorded from perch at Llyn Tegid is likely

to be the species that matures in Coregonus lavaratus. This species

resembles P. pollanica (Gresson, 1952), but differs from it in a

number of factors (Chubb, 1970).

(7) Rawson (1952) reported the plerocercoid of this tapeworm from

the intestinal lumen of perch.

(8) Initial records of Raphidascaris in Britain were identified as R. cristata. There is now reasonable evidence to suggest that R. cristata is a synonym of R. acus (Davies, 1967).

(9) Odening & Bockhardt (1971) considered that T. percafluviatilis was synomynous with Cotylurus (Tetracotyle) varigatus.

Table II. Parasites of perch. Gill net samples. January 1975-February 1976

Total number fish 465

	Number infected	% incidence	Number parasites	Mean intensity/fish;infected fish		Max
PROTOZOA						
Henneguya psorospermica	14	3.0	222	0.5	15.9	153
Myxobolus muelleri	1	1.0	1	1	(1.0)	1
MONOGENEA						
Ancyrocephalus percae	5	1.1	9	1	1.8	5
DIGENEA						
Bunodera luciopercae	391	84.1	9171	19.7	23.4	686
Diplostomum gasterostei**	463	99.6	12610	27.3	27.1	159
D. spathaceum **	8	1.7	11	1	1.4	2
Tetracotyle sp. I **	93	20.0	170	1	1.8	10
Tetracotyle sp. II **	23	4.9	33	1	1.4	3
CESTODA						
Bothriocephalus sp./	14	3.0	21	1	1.5	5
Euhothrium sp. *						
Diphyllobothrium sp. ***	42	9.0	55	1	1.3	5
Triaenophorus nodulosus ***	420	90.3	1418	3.0	3.4	20
NEMATODA						
Camallanus lacustris	259	55.7	1085	2.3	4.2	41
Cucullanus truttae	1	1.0	1	1	(4.0)	(4)
Raphidascaris cristata*	21	4.5	31	1	1.5	4
ACANTHOCEPHALA						
Acanthocephalus clavula	141	30.3	515	1.1	3.7	35

TOTAL 15 species

N.B.

* juveniles
** metacercariae
*** plerocercoids

Table III. Parasites of perch. Trawl sample. March 1976.

Total number fish 64

	Number infected	% incidence	Number parasites	Mean intensity/ fish ; infected fish		Max
PROTOZOA						
Henneguya psorospermica	13	20.3	110	1.7	8.5	40
MONOGENEA						
Ancyrocephalus percae	3	4.6	3	1	1.0	1
DIGENEA						
Bunodera luciopercae	55	85.9	450	7.0	8.2	24
Diplostomum gasterostei**	55	85.9	514	8.0	9.4	40
Tetracotyle sp. I **	2	3.1	2	1	1.0	1
CESTODA						
Proteocephalus sp. *	6	9.4	12	1	2.0	3
Diphyllobothrium sp. ***	3	4.7	3	1	1.0	1
Triaenophorus nodulosus ***	35	54.7	152	2.4	4.3	28
NEMATODA						
Camellanus lacustris	12	18.8	44	1	3.8	16
ACANTHOCEPHALA						
Acanthocephalus clavula	17	26.6	37	1	2.2	7

TOTAL 10 species

N.B.

*   juveniles

** metacercariae

*** plerocercoids

Table IV.   Parasites of perch from Llyn Tegid. Pure seine

sample.   July 1976.

Total number fish   30

Parasite	No. fish infected	% incidence	Total no. parasites	Mean intensity per fish	per infected fish	Max.
DIGENEA						
Bunodera luciopercae						
	7	23.3	16	1	2.3	5
CESTODA						
Bothriocephalus sp./Eubothrium sp.*						
	8	26.7	13	1	1.6	5

N.B.   * juveniles

Table V. Parasites of perch from Llyn Tegid. Data from Table I.

Protozoa

Epizooic vorticellids (= _Apiosoma_ sp.?)	Body surfaces
Henneguya psorospermica	Gill filaments
Myxobolus muelleri	Buccal cavity

Monogenea

Ancyrocephalus percae	Gill filaments

Digenea

Bunodera luciopercae	Lumen of alimentary tract
Diplostomum fasterostei **	Humour/retina of eye
Diplostomum spathaceum **	Lens of eye
Tetracotyle sp. **	Encysted in swimbladder

Cestoda

Bothriocephalus sp./_Eubothrium_ sp. *	Lumen of alimentary tract
Cyathocephalus truncatus	Lumen of intestine
Proteocephalus sp. *	Lumen of intestine
Diphyllobothrium sp. ***	Viscera (encapsulated)
Triaenophorus nodulosus ***	Liver, and other viscera

Nematoda

Camallanus lacustris	Lumen of pyloric caeca and intestine
Cucullanus truttae	Lumen of intestine
Raphidascaris cristata *	Lumen of intestine, encysted onto wall of intestine

Acanthocephala

Acanthocephalus clavula	Lumen of pyloric caeca and intestine

N.B.

*   juveniles

**   metacercariae

*** plerocercoids

Table VI. Parasites of perch from British Isles.

Data from Table I.

PARASITE		ENVIRONMENT						
		1	2	3	4	5	6	7
PROTOZOA	?Apiosoma sp.		P					
	Epizooic vorticellids	P						
	Henneguya psorospermica	P			P			
	Mxgobolus muelleri	P						NOT
	Trichodinella epizoetica					P		EXAMIN
	Trichodina sp.						P	
	Trypanosoma percae				P		P	P
MONOGENEA	Ancyrocephalus percae	P						
	Gyrodactylus sp.		P					
DIGENEA (Adults)	Bunodera luciopercae	P	P	P	P	P		
DIGENEA (metacercaria)	Diplostomum gasterostei	P	*		*	*	P	
	D. spathaceum	P	*	P	P	P		P
	Diplostomum spp.		P					
	?Ichthyocotylurus cucullus		P					
	Ichthyocotylurus sp.			P				
	Tetracotyle perca/fluviatilis							P
	Tetracotyle sp.	P			P			
	Tylodelphys clavata				P	P	P	
	T. podicipina				P			
DIGENEA	TOTAL NUMBER SPECIES	4	3	5	4	2	2	2
	TOTAL NUMBER ADULTS	1	1	1	1	1	0	0
	TOTAL NUMBER METACERCARIAE	3	2	4	3	1	2	2
	% SPECIES METACERCARIAE	75	67	80	75	50	(100)	(100)
CESTODA (plerocercoids)	Diphyllobothrium sp.	P						
	Triaenophorus nodulosus	P			P	P		
(juveniles and adults)	Bothriocephalus sp.	P				P		P
	Cyathocephalus truncatus	P						
	Eubothrium crassum		P					
	Eubothrium sp.	P						

Table VI. (contd.)

PARASITE		ENVIRONMENT						
		1	2	3	4	5	6	7
	Proteocephalus percae			P	P	P		
	Proteocephalus sp.	P						
CESTODA	TOTAL NUMBER SPECIES	6	1	1	2	3	/	1
	TOTAL NUMBER WITH FISH DEFINITIVE HOST	5	1	1	2	3	/	1
	TOTAL NUMBER WITH WARM-BLOODED DEFINITIVE HOST							
	% "	17	(100)	(100)	100	100	/	(100)
NEMATODA	Camallanus lacustris	P	+	P		P		
	Capilliaria salvelini		P					
	Cucullanus truttae	P						
	Raphidascaris acus		P					
	R. cristata	P						
ACANTHOCEPHALA	Acanthocephalus clavula	P					P	
	A. lucii				P	P		
	Echinorhynchus truttae		P					
	Neoechinorhynchus rutili		P					
ANNELIDA	Hemiclepsis marginata				P			
	Piscicola geometra						P	
MOLLUSCA	Glochidia larvae		P	P		P		
ARTHROPODA	Achtheres percarum				P	P		
	Argulus foliaceus				P	P	P	P
TOTAL NUMBER SPECIES		18	11	11	11	12	6	3

N.B. 1 Llyn Tegid   5 Shropshire Union Canal
      2 Loch Leven   6 Slapton Ley
      3 Hanningfield Reservoir   7 Ockendon Moat
      4 Rostherne Mere

      ? Doubts as to identity
      P Present
      * D. gasterostei and D. spathaceum may be present
      + Camallanus sp. tentatively identified from stickleback
         (Campbell, 1974).

and sex are considered elsewhere.

IV.2.3   Check list of the parasites of perch from Llyn Tegid

Including the record from previous studies, 18 species of

parasites have been recorded from the perch at Llyn Tegid (Table V).

IV.3.   DISCUSSION

IV.3.1   Host specificity of the parasite fauna of perch from Llyn

Tegid.

The host specificity of many parasites is not absolute, and

may be influenced by morphological, physiological and ecological

factors (Pavlovskii, 1946a, b; Dogiel, 1958; Shulman, 1958; Williams, 1970; Baer,

1971).

The parasite fauna of a particular species of fish is built

up from parasites specific to that fish (or a higher phylogenetic

grouping of fish), parasites whose specificity is determined by an

intermediate phase in the life cycle, and parasites which appear to

exhibit little specificity (Chubb, 1970).

It is possible to divide the parasite fauna of Llyn Tegid perch

into five groups, according to their specificity to their fish host

(Table VII).

GROUP A.   Five species of parasites may be considered specific to

perch (and pike, Esox lucius). These include Bunodera luciopercae

and Cucullanus lacustris. Pike acquire many of their parasites

secondarily, by the ingestion of infected prey fish (Ergens, 1966b;

Mishra and Chubb, 1969). In addition, pike is the definitive host

of Triaenophorus nodulosus, whose plerocercoid is a common parasite

of perch.

GROUP B.   Five species of parasites are normally associated with

salmonoid fish. These include Cyathocephalus truncatus, Diphyllobothrium

sp. and Cucullańus truttae. The proteocephalid tapeworm recorded

from perch at Llyn Tegid is likely to be the species that matures

in gwyniad (Coregonus lavaratus) (see Table I, note (6)). Pseudo-

phyllidean plerocerciform juvenile cestodes were found in the

intestinal lumen of perch. They were of the Eubothrium/Bothriocephalus

type, though specific determination was not possible. It is probable

that the Eubothrium sp. is E. crassum (see Chapter VIII).

GROUP C. This group contains a single tapeworm, Bothriocephalus sp.

It is likely that this parasite is B. claviceps, a parasite of eels

(Anguilla anguilla) in Llyn Tegid.

GROUP D. This group of parasites appear to exhibit a reduced

specificity to their piscine hosts. These include Diplostomum

gasterostei, D. spathaceum and Acanthocephalus clavula.

GROUP E. The specificity of the epizooic vorticellids, Tetracotyle

sp. and Raphidiascaris cristata is undetermined. The epizootic

vorticellids were recorded from 2 of 11 perch, and 3 of 9 roach

(Rutilus rutilus) from Llyn Tegid (Abolarin, 1966). It is likely

that these protozoans are Apiosoma sp. (Chubb, 1976). Tetracotyle

sp. was recorded from the lens of the eye, and the swimbladder, of

perch (encysted at both sites). The taxonomy of this parasite is

considered in Chapter VII.

There is good evidence to suggest that Raphidiascaris cristata

is a synonym of R. acus (Davies, 1967). Moravec (1970) found that

the life history of R. acus may be complex. Certain fish may act

as the intermediate host, while predatory fish are the definitive

host. Some species of aquatic invertebrates can also act as reservoir

hosts. In Llyn Tegid, adult R. cristata have been found in eels and

brown trout (Salmo trutta), while juveniles have only been recorded

from perch (Chubb, 1963, 1976; present study).

Table VII. Host specificity of the parasite fauna of perch from British Isles.

Habitat and source of data	Group A. Parasites specific to perch	Group B. Parasites of salmonoid fish	Group C. Parasites of eels	Group D. Parasites with reduced specificity to their fish hosts	Group E. Parasites of undetermined specificity to their fish hosts
Llyn Tegid; Abolarin (1966) Chubb (1970) present study	Henneguya psorospermica Ancyrocephalus percae Triaenophorus nodulosus Bunodera luciopercae Camallanus lacustris	Cyathocephalus truncatus Diphyllobothrium sp. Eubothrium sp. Proteocephalus sp. Cucullanus truttae	Bothriocephalus sp.	Mxyobolus muelleri Diplostomum gasterostei Diplostomum spathaceum Acanthocephalus clavula	Epizootic vorticellids Tetracotyle sp. Raphidascaris cristata
Loch Leven; Campbell (1974)	B. luciopercae	Eubothrium crassum Capillaria salvelini Echinorhynchus truttae		Diplostomum spp. Neoechinorhynchus rutili Glochidia	?Apiosoma sp. Gyrodactylus sp. Raphidascaris acus
Rostherne Mere; Rizvi (1964)	H. psorospermica B. luciopercae Proteocephalus percae T. nodulosus Achtheres percarum			D. spathaceum Tylodelphys clavata Acanthocephalus lucii Hemiclepsis marginata Argulus foliaceus	Tetracotyle sp.

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(contd........)

Table VII. (contd.)

	Group A	Group B	Group C	Group D	Group E

Hanningfield Reservoir;
 	
Needham (1969)
 	
Wootten (1973a)
	Trypanosoma
	   percae
	B. luciopercae
	P. percae
	
	C. lacustris
	A. percarum
				D. spathaceum
				
				T. clavata
				Tylodelphys
				   podicipina
				Glochidia
				A. foliaceus
					Ichthyocotylurus sp.

Shropshire Union Canal;
 	
Abolarin (1966)
 	
Mishra and Chubb (1969)
	T. percae
	
	B. luciopercae
	P. percae
	
	T. nodulosus
	C. lacustris
			Bothriocephalus sp.	D. spathaceum
				
				A. lucii
				Piscicola
				   geometra
				Glochidia
				A. foliaceus
					Trichodinella
					   epizootica

Slapton Ley; Canning et al. (1973) Kennedy (1975)	T. percae			D. gasterostei T. clavata A. clavula A. foliaceus	Trichodina sp.
Ockendon Moat; Shillcock (1972)			Bothriocephalus sp.	D. spathaceum	Tetracotyle percafluviatilis

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IV.3.2   Comparative studies on the parasite fauna of perch from

the British Isles.

The parasite fauna of perch has now been studied in detail at

seven localities. The parasites recorded from these habitats are

listed in Table VI. These parasites are arranged according to their

specificity to their piscine host in Table VII.

Loch Leven is a large, shallow, eutrophic lake (Fraser, 1974;

Thorpe, 1974a). The lake supports a large population of aquatic

birds, whose parasites have been investigated by Fraser (1974).

The dominant fish species are brown trout (Salmo trutta), perch, pike,

minnow (Phoxinus phoxinus) and stickleback (Gasterosteus aculeatus).

The once abundant eel (Anguilla anguilla) population has now declined

(Thorpe, 1974b).

Eleven species of parasites have been recorded from the perch

(Campbell, 1974). It was noted that there were few parasites specific

to perch (Table VII, group A). A large proportion of the perch parasite

fauna had a reduced specificity to its' fish hosts (Table VII, group D).

As at Llyn Tegid, a number of principally salmonoid parasites were

recorded from perch.

Rostherne Mere is a eutrophic lake with a large population of

coarse fish (Rizvi, 1964; Chubb, 1970). Perch, pike and roach (Rutilus

rutilus) are all abundant. Eels are present, but have not been examined

parasitologically. There is a large population of aquatic birds at

Rostherne Mere.

Eleven species of parasites have been recorded from perch (Rizvi,

1964). The parasite fauna is made up of parasites specific to perch

(Table VII, group A), and parasites of reduced specificity to their

piscine hosts (Table VII, group D).

Hanningfield Reservoir is a large, recently constructed, eutrophic lake (Wootten, 1973a). There is a large aquatic avian fauna, and abundant populations of brown trout, rainbow trout (Salmo gairdneri), perch and ruffe (Gymnocephalus cernua). Roach and sticklebacks are common, though eels are only infrequently encountered. There is one unconfirmed report of pike in the lake (Wootten, 1972).

The steep sides to the lake have resulted in a reduced littoral zone and a limited littoral fauna. The scarcity of certain suitable intermediate hosts may explain the absence of some parasites from the lake (Wootten, 1973a). Tedla and Fernando (1970a) recorded a reduced parasite fauna in yellow perch (Perca flavescens) from a lake with a small littoral zone and scant littoral fauna. Rauckis (1975) has reported a reduced parasite fauna from bream (Abramis brama) from a lake with a poor bottom fauna.

Eleven species of parasites were recorded from perch at Hanningfield Reservoir (Needham, 1969; Wootten, 1973a). The perch parasite fauna is very similar to that recorded at Rostherne Mere (Table VII). At Hanningfield Reservoir, Bothriocephalus claviceps is recorded from eels, though not perch.

The Shropshire Union Canal is a slow moving, essentially eutrophic environment, corresponding to the bream-trout zone of a river (Chubb, 1970). Perch, pike, roach, bream and eels are all present (Mishra and Chubb, 1969).

Twelve species of parasites were recorded from perch (Abolarin, 1966; Mishra and Chubb, 1969). The parasite fauna of perch is similar to that at Rostherne Mere or Hanningfield Reservoir (Table VII). However, in the canal perch there were fewer larval digeneans that require a warm blooded definitive host (Table VIII). Bothriocephalus sp. has been recorded from perch.

Slapton Ley is a shallow, eutrophic lake, with perch, pike and roach as the dominant fish species (Mercer, 1966; Kennedy, 1975, 1976). Brown trout, rudd (Scardinius erythrophthalmus), sticklebacks and eels are also present.

Only six species of parasites have been recorded from perch, with no adult Digenea, Cestoda or Nematoda (Canning et al., 1973; Kennedy, 1975). The paucity of the parasite fauna of the fish at Slapton Ley is a result of the history and isolation of the lake. Kennedy (1975) concluded "that these factors have played a more important part in the formation of its' (Slapton Ley) parasite fauna, than the presence of a particular fish species, the specificity of the parasites, or the fact that the lake is eutrophic".

Ockendon Moat is a small, recently constructed, eutrophic lake (Shillcock, 1972). It has steep sides and a limited benthic invertebrate fauna. Perch, roach, rudd and crucian carp (Carassius carassius) are present. The fish of this lake have a very limited parasite fauna. Perch is recorded as host to three parasite species (Table VII). Two of these may have been introduced from piscivorous birds, and the other (Bothriocephalus sp.) may be a parasite of eels.

The highly individual nature of the perch parasite fauna at Slapton Ley and Ockendon Moat is interesting. Dogiel (1958) has previously described a depleted parasite fauna of perch from small and/or isolated habitats.

Apart from the last two environments, the dominant members of the parasite fauna of perch are species specific to perch (Table VII, group A), plus parasites of reduced specificity to their fish hosts (Table VII, group D). However, species such as Henneguya psorospermica and Ancyrocephalus percae often have a low incidence and intensity of infection. When present Bunodera luciopercae, certain strigeid metacercariae, Proteocephalus percae, Triaenophorus nodulosus, Camallanus

lacustris and Acanthocephalus sp., are often important members of the parasite fauna of perch. Nonetheless, the occurrence of these parasites (and their abundance) may vary from one environment to the next. In addition, the presence of salmonoid and/or eel parasites in perch from certain habitats has been noted. These results are in disagreement with Halvorsen (1971), who found that the same fish from a variety of habitats harboured a very similar parasite fauna. The parasite fauna of perch from the British Isles is seen to vary, and the factors that influence this variation are discussed later. The absence of species of parasites from apparently suitable environments may be taken as an indication of the individuality of freshwater habitats, or a reflection on our lack of knowledge concerning the factors controlling the distribution of fish parasites.

The number of parasites recorded from perch at Llyn Tegid is greater than that recorded from any other study in the British Isles (Table VI). The large number of parasites that are specific to perch, plus those of salmonoid fish (found parasitic in perch) are thought to account for this. Smaller numbers of species have been recorded from perch at other salmonoid containing waters. At Loch Leven, there are few parasites specific to perch, and at Hanningfield Reservoir no principally salmonoid parasites have been recorded from perch (Table VII).

Triaenophorus nodulosus is excluded from environments containing suitable first and second intermediate hosts, by the absence of the definitive host, pike. T. nodulosus is a parasite of perch at Llyn Tegid, Rostherne Mere and the Shropshire Union Canal (Table VI). Pike are thought to be absent from Hanningfield Reservoir. Loch Leven contains pike, yet T. nodulosus is absent from the lake (Campbell, 1974). Since conditions would appear suitable for the parasite, T. nodulosus may never have occurred in the lake (a further indication of the

individuality of the parasite fauna of perch from Loch Leven).

Alternatively, the suggested extinction of pike from Loch Leven

by 1934 (Johnstone, 1934) may have served to remove this parasite.

Cannon (1973), has suggested that heavy fishing may lead to the

extinction of some parasites, and a reduction in parasite diversity.

Additionally, there may be other (as yet undetermined) factors

controlling the distribution of T. nodulosus in the British Isles.

Robertson (1953) and Campbell (1974) have found few parasite species

in pike from a number of Scottish lochs.

Wisniewski (1958) concluded that the parasite fauna of birds

prevail in shallow, eutrophic lakes, and is characteristic of them.

Esch (1971) has shown that in eutrophic lakes in U.S.A. bass and

sunfish harboured a proportionally larger number of larval helminths

(most of which mature in piscivorous birds and mammals), than in a

similar oligotrophic lake. He suggested that this reflected the

greater importance of warm blooded animals as tertiary predators

in eutrophic lakes. A large number of species of metacercariae,

often with a high intensity of infection, were recorded from yellow

perch in Laurel Creek, Ontario. Molnar et al. (1974) ascribed this

to the abundant local avian fauna.

Table VIII shows the number and percentage of the Digenea and

Cestoda parasites of perch from the seven British localities, that

mature in warm blooded definitive hosts.

At Loch Leven, Hanningfield Reservoir and Rostherne Mere there

are abundant populations of piscivorous birds. In all these lakes

at least half of the digeneans and cestodes parasitic in perch,

mature in birds. Birds may markedly influence the parasite fauna

of perch from small and/or isolated habitats, such as Slapton Ley

and Ockendon Moat (Tables VI to VIII).

Table VIII.   Digenea and Cestoda parasites of perch that require

a warm blooded definitive host.

	ENVIRONMENT						
	1	2	3	4	5	6	7
Number Digenea and Cestoda parasitic in perch	10	4	6	6	5	2	3
Number of Digenea and Cestoda in perch that require warm blooded definitive host	4	2	4	3	1	2	2
% Digenea and Cestoda in perch that require a warm blooded definitive host	40	50	67	50	20	(100)	(67)

N.B.   1 = Llyn Tegid   5 = Shropshire Union Canal

2 = Loch Leven   6 = Slapton Ley

3 = Hanningfield Reservoir   7 = Ockendon Moat

4 = Rostherne Mere

(Data from Table I)

At Loch Leven, Hanningfield Reservoir and Rostherne Mere there are
abundant populations of piscivorous birds. In all these lakes at least
half of the digeneans and cestodes parasitic in perch, mature in birds.
Birds may markedly influence the parasite fauna of perch from small
and/or isolated habitats, such as Slapton Ley and Ockendon Moat
(Tables VI to VIII).

The Shropshire Union Canal has a relatively poor aquatic avian
fauna. Only 1 out of 5 of the Digenea and Cestoda parasites of perch
mature in birds.

Llyn Tegid has a seasonally abundant avian fauna. Whilst only
40% of the digeneans and cestodes of perch mature in birds, the
NUMBER of species is comparable with other habitats. The apparent
reduction in the importance of birds as the definitive host to certain

helminths of perch is caused by the large number of Cestoda present

that mature in fish (Tables VI and VIII). Out of 10 species of

Digenea and Cestoda, 6 mature in fish. Of these 6, 3 mature in

salmonoid fish and one is typically a parasite of eels. Dogiel

(1958) described the effect that fish abundance may have on the

parasite fauna of other fish in the same habitat. He stated that

a group of fish dominating a habitat may exert some degree of

influence on the parasite fauna of host species outside that group.

This process tends to favour the spread of parasites from their

original host to other, initially non-specific, host species. Shulman

(1958) pointed out that host specificity may change and develop during

the course of evolution. This spread of parasites may eventually lead

to the conquest of new host species (Dogiel, 1958). The salmonoid

parasites recorded from perch may have a low incidence and intensity

of infection in perch. From Table VII, it can be seen that perch

may acquire parasites that are normally associated with salmonoid

fish (and eels) occurring in the same environment. Perch are carnivorous

and feed on a wide variety of organisms. They may acquire these para-

sites in two ways. They may become infected by feeding on intermediate

hosts containing infective parasite stages, or by secondary infection

by the ingestion of infected salmonoids (and eels). In the environments

studied, perch do not appear to harbour any parasites, that are primarily

associated with salmonoid fish in the same environment, that have direct

life cycles (e.g. Protozoa, Monogenea), or that rely on active penetration

of the piscine host (e.g. strige$\overset{o}{\underset{\wedge}{i}}$d metacercariae). Whilst the techniques

of the investigations in question may have failed to reveal these parasites,

morphological, ecological or physiological aspects of host specificity

may have prevented the infection.

In environments containing eels, it is not uncommon to find perch

infected by <u>Bothriocephalus</u> sp. This may be assumed to be <u>B. claviceps</u>, though in most instances, specific determination has not been possible from the perch material. Van Cleave and Mueller (1934) found juvenile <u>B. claviceps</u> in Oneida Lake (U.S.A.) in hosts unsuited to bring the worms to sexual maturity. They attributed this to the fact that the infective stage is transmitted by copepods, and any fish eating these is exposed to infection with juvenile <u>Bothriocephalus</u>. Jarecka (1959) showed that from the copepod host the procercoid passed to small fish and did not penetrate the gut wall but remained in the intestine. Salmonoid fish are dominant members of the ichthyofauna at Llyn Tegid, Loch Leven and Hanningfield Reservoir. Within these environments there can be seen to be some spread of parasites from salmonoid fish to perch, and/or vice versa.

Several principally salmonoid parasites have been recorded from perch at Llyn Tegid. Chubb (1976) reviewed the previous studies on the parasites of brown trout at Llyn Tegid. The plerocercoid of <u>Triaenophorus nodulosus</u> has been recorded from trout, though very rarely.

At Loch Leven, the dietary components of brown trout and perch were the same (Thorpe, 1974b). <u>Asellus</u> sp. and perch fry were very important to both fish. The occurrence of salmonoid parasites in perch has been noted. There were few parasites specific to perch present in Loch Leven. Hence, some were recorded from trout. It is interesting to note that the seasonal occurrence of <u>Raphidascaris</u> <u>acus</u> in trout, coincides with the seasonal occurrence of this nematode in perch, and a peak of perch ingestion by trout. Trout (and large perch) may acquire <u>R. acus</u> from small perch. Campbell (1974) found that <u>R. acus</u> was most common in trout exceeding 29.5 cm in length.

Hanningfield Reservoir has large populations of coarse fish, and brown and rainbow trout. The trout are maintained on a "put and take"

basis and do not spawn in the lake. A number of parasites specific to perch have been recorded from both species of trout, though perch does not harbour any salmonoid parasites (Wootten, 1973a). This may be a reflection upon the relatively small number of salmonoid parasites recorded from the lake. Additionally, trout are not introduced into Hanningfield Reservoir until approximately 25.0 cm long (Wootten, 1972). This reduces the possibility of perch acquiring salmonoid parasites by the ingestion of young, infected trout. However, Eubothrium crassum was recorded from 5.5% of 165 ruffe at Hanningfield Reservoir (Wootten, 1973a). The absence of Crepidostomum spp. (especially C. meteocus), and the identification of Bunodera luciopercae from trout is interesting. C. meteocus is recorded from trout, and B. luciopercae from perch, at Llyn Tegid and Loch Leven. At each environment neither parasite has been recorded from its' corresponding atypical host. If immature C. meteocus were to occur in perch infected with B. luciopercae, confusion of identification is possible. The reverse applies to B. luciopercae in trout infected with C. meteocus. However, at Hanningfield Reservoir, only 5.3% of 65 brown trout were found to be infected with B. luciopercae, which suggested that this fish was not a major host to B. luciopercae (see Chapter VII).

IV. 3.3 Comparative studies on the parasite fauna of perch from continental Europe.

A number of the salient comparative studies on the parasite fauna of perch from continental European waters are considered here.

The parasite fauna of perch has been studied at a number of lacustrine environments. These include: Lake Druzno (Kozicka, 1958, 1959; Wisniewski, 1958); Lake Dusia (Rauckis, 1970a, b); Lake Dargin (Wierzbicki, 1970, 1971); Lake Vörtsjarv (Tell, 1971) and Lake Leginskie (Wierzbicka and Wierzbicki, 1971). In addition, the parasite fauna

perch has been examined in less detail at Lake Ladoga (Barysheva and Bauer, 1957) and the River Glomma (Halvorsen, 1971, 1972). At Lake Ladoga only 30 perch were examined, primarily between June-August (1948). Nonetheless, 24 species of protozoan and metazoan parasites were recorded, and these are listed by Barysheva and Bauer (1957).

Detailed interpretations on the parasite fauna of perch from the River Glomma are difficult. Only a small number of fish (64) were examined, and only over a limited number of months. The perch examined were all greater than 17.9 cm long. Halvorsen (1971) pointed out that the survey was "restricted to helminths and parasitic Crustacea, and to those parasites to which the fish examined were the only or final hosts". Nematodes were completely omitted. Five species of parasites were recorded from perch: Bunodera luciopercae, Azygia lucii, Proteocephalus percae, Acanthocephalus lucii and Neoechinorhynchus rutili. From these results, Halvorsen (1971) concluded that the composition of the parasite fauna of the fish of the River Glomma was more complex than might be expected for fish at the limit of their geographical distribution. Dogiel (1958) considered the factors influencing the composition of the parasite fauna of fish at the limit of their distribution. He pointed out that parasites cannot exist in areas where suitable intermediate and definitive hosts do not occur together. In addition, animals at the limit of their distribution may become less common, and this may effect the survival of some parasite species to which they are host. Bykhovskaya and Bikhovski (1940) have studied the parasites of perch near the southern limits of its' distribution (Akhtainskye Limany). Despite the rich fauna of the area, perch had a reduced parasite fauna of 5 species (Clinostomum sp., Proteocephalus percae, Acanthocephalus lucii, Ergasilus sieholdi and Piscicola geometra).

Reasonably comprehensive data are available on the perch

parasite fauna from four of the above continental lakes. In the

fifth (Lake Leginskie), perch has a parasite fauna similar to that

at Lake Dargin (see below), though differences in the degree of

infestation exist (Wierzbicka and Wierzbicki, 1971).

The parasite fauna of perch from Lake Druzno, Lake Dusia, Lake

Dargin and Lake Vôrtsjarv are presented in Table IX. The parasite

fauna of perch is seen to be similar to that recorded at Rostherne

Mere and Hanningfield Reservoir, in the British Isles. Many of the

parasites recorded from perch in continental waters are present in

the British Isles, and may occur associated with perch (see Table IX;

data from Kennedy, 1974). Nonetheless, fewer parasite species have

been recorded from perch at each of the seven British localities,

than in most European studies. There may be several reasons for this.

Continental studies often place a greater emphasis on assessing the

TOTAL (protozoan and metazoan) parasite fauna of fish. In addition,

the ichthyofauna of many continental lakes is considerably more varied

than at similar lakes in the British Isles. Within such environments

there is often a greater diversity of parasite species, which may

facilitate their spread into hosts that are normally considered

atypical. The lack of uniformity in the parasite fauna of perch

from the British Isles may reflect the variety of environments, that

have been investigated, when compared to the examples taken from the

available continental literature. Finally, there may be differences

in the distribution pattern of fish parasites in the British Isles

when compared to continental Europe, and a degree of confusion may

exist as to the precise identity of certain parasites (especially

larval Digenea).

At Lake Druzno, Lake Dusia, Lake Dargin and Lake Vôrtsjarv, over

half of the digenean parasites of perch mature in a warm blooded

Table IX. Parasites of perch from four European lakes

PARASITE	Environment				See Note 5
	1	2	3	4	5
PROTOZOA					
Apiosoma sp.		P			P
Chilodinella cyprini (Moroff, 1902)			P		P
Dermocystidium percae (Riechenback-Klinke, 1950)		P			?
Henneguya creplini (Gurley, 1895)			P		?
Henneguya psorospermica Thélohan, 1895	P	P		P	P
Mxyobolus sp.	P				P
Trichodina domerguei f acuta Lom, 1961		P			?
Trichodina urinaria Dogiel, 1940		P	P		?
Trichodina sp.			P	P	P
Trichophyra intermedia Prost, 1952		P			?
MONOGENEA					
* Ancyrocephalus paradoxus Creplin, 1839	P		P	P	P
* Ancyrocephalus percae Ergens, 1966		P			?
Gyrodactylus sp.		P			P
DIGENEA (adults)					
Azygia lucii (Müller, 1776)	P		P	P	P
Bucephalus polymorphus (Baer, 1827)				P	P
Bunodera luciopercae (Müller, 1776)	P	P	P	P	P
Phyllodistomum folium (Olfers, 1816)				P	P
Rhipidocotyle illense (Ziegler, 1883)	P		P		P
Sphaerostoma bramae (Müller, 1776)		P			P
DIGENEA (metacercaria)					
Cotylurus pileatus (Rud., 1802)		P			?
** Cotylurus platycephalus (Creplin, 1825) Szidat, 1928		P			?
Diplostomum spathaceum (Rud., 1819)	P	P	P	P	P
*** Posthodiplostomum brevicaudatum (Nordman, 1832) Kozicka, 1958	P	P	P	P	
Paracoenogonimus ovatus Katsurada, 1914		P			
Rhipidocotyle illense (Ziegler, 1883)	P	P			P
Tetracotyle echinata (Diesing, 1858)				P	?
** Tetracotyle percafluviatilis Linstow, 1856				P	P
Tetracotyle sp.	P				P
Tylodelphys clavata Nordman, 1832 (= Diplostomum clavatum)	P	P	P	P	P
Tylodelphys podicipina Kozicka & Niewiadomska, 1960				P	P
CESTODA (adults)					
Proteocephalus percae (Müller, 1780)	P	P	P	P	P

Table IX (contd.)

PARASITE	Environment				See Note
	1	2	3	4	5
CESTODA (plerocercoids)					
Diphyllobothrium latum (L., 1758)	P			P	P
Ligula intestinalis (L., 1758)			P		P
Triaenophorus nodulosus (Pallas, 1781)	P	P	P	P	P
NEMATODA					
Camallanus lacustris (Zoega, 1776)	P	P	P	P	P
C. truncatus (Rud., 1814)				P	
Desmidocercella numidica (Secrat, 1920) Yorke & Maplestone, 1926 (larvae)	P⊕		P		
Desmidocercella sp. (larvae)		P			
Eustrongylides sp.				P	P
Raphidascaris acus (Bloch, 1779) (larvae & adults)		P		P	P
Rhabdochona sp. (larvae)				P	P
Spiruridae (larvae)				P	?
ACANTHOCEPHALA					
Acanthocephalus clavula (Duj., 1845)	P				P
A. lucii (Müller, 1776)	P	P	P	P	P
ANNELIDA (HIRUDINEA)					
Piscicola geometra (L., 1761)		P	P	P	P
MOLLUSCA					
Glochidia larvae	P	P	P		P
ARTHROPODA (CRUSTACEA)					
Achtheres percarum Nordman, 1832	P		P	P	P
Argulus foliaceus L., 1758	P	P	P	P	P
Ergasilos sieboldi Nordman, 1832	P		P	P	P
total number species	22	26	23	26	-
total number Digenea & Cestoda species	10	11	10	12	-
total number Digenea & Cestoda with warm blooded definitive host	5	6	5	6	-
% _____ " _____	50.0	54.5	50.0	50.0	-

N.B.

1. Lake Druzno.
2. Lake Dusia×

Data from: Kozicka (1958, 1959)
Rauckis (1970a)

Table IX (contd.)

3.	Lake Dargin.	Data from: Wierzbicki (1970)
4.	Lake Vôrtsjarv	Tell (1971)
5.	Present in fish from British Isles	Kennedy (1974)

P   Present

?   May be present

-⊕-   Doubt as to identity

×   Small number of perch examined

*   See Table I, note (3)

**   Rauckis (1968) considered that T. percafluviatilis was synonymous with Cotylurus platycephalus. Odening & Bôckhardt (1972) disputed this, but considered that T. percafluviatilis was synonymous with C. variagatus.

***   Synonymous with Neascus brevicaudatum (Nordman, 1832). See Kozicka (1958).

definitive host (Table IX). The influence of the local warm

blooded animal populations (especially birds) upon the parasite

fauna of fish was described by Wisniewski (1958) and Esch (1971),

and has been discussed in section IV.3.2.

A salmonoid fish (Coregonus albula), is a dominant member of

the ichthyofauna at Lake Dusia and Lake Dargin (Rauckis, 1970b;

Wierzbicki, 1970). In both habitats, the parasite fauna of perch

is influenced little by the presence of this fish in the same

environment. This is in contract to the situation that has been

observed at Llyn Tegid and Loch Leven (in the British Isles). In

both these environments, the resident salmonoid fish parasite fauna

influenced, to some extent, the parasite fauna of perch in the same

environment (section IV.3.2.). However, perhaps the situation at

these two continental lakes resembled that at Hanningfield Reservoir.

At Hanningfield Reservoir, the parasite fauna of trout is depleted,

and no salmonoid parasites were recorded from perch. Rauckis (1970b)

recorded very few parasites typical of salmonoid fish, from C. albula

at Lake Dusia. There is a large salmonoid element, with a varied

parasite fauna, within the ichthyofauna of Lake Ladoga. Barysheva

and Bauer (1957) have recorded a number of principally salmonoid

fish parasites from perch, including Henneguya zschokkei, Cyathocephalus

truncatus and Echinorhynchus salmonis. Within the fauna of Lake Ladoga

a number of relict marine and estuarine forms are found. This has

enabled several relict parasite species to survive and persist, of
                                        fected
which Corynosoma semerme and C. strumosum in fat perch.

The above studies indicate that the parasite fauna of perch from

many continental lakes resembles that found in studies on similar lakes

in the British Isles. However, many continental populations of perch

harbour a more varied parasite fauna than has been reported from British

studies. The reasons for this were discussed.

IV.3.4. Characterisation of the parasite fauna of fish

The ichthyofauna of a natural habitat is largely dependent upon the characters of that habitat. Deep, oligotrophic lakes have a dominant salmonoid fish fauna, whereas shallower, eutrophic environments are primarily cyprinid waters (with carp, bream, tench as the characteristic fish). Intermediate lakes contain mixed populations, with perch and pike often present in large numbers (Varley, 1967).

Closely related to the host specificity of fish parasites, is the concept of characterisation of parasite fauna.

Wisnewski (1958) pointed out that the fauna of any body of water is related to the type of water (i.e. oligotrophic, mesotrophic, eutrophic, etc.). If the freeliving fauna is thus dependent, then the parasite fauna superimposed upon the freeliving community, might also be related to the type of water. The ability to anticipate the occurrence of certain parasite species, given a knowledge of the type of habitat, would be of great value in fisheries diagnostics.

Chubb (1962, 1963, 1964b, 1970) and Mishra and Chubb (1969) considered this concept further. Owing to the development of a high degree of host specificity by many parasites, if a species of host is regarded as typical for an environment, then it's associated specific parasites are also typical for the same environment (Chubb, 1963). However, the importance of host specificity at ALL stages in the life history was indicated, and the individuality of freshwater habitats stressed. Within the parasite fauna of the fish of Llyn Tegid, distinct elements were recognised. The parasite fauna of salmonoid fish was said to be characteristic of oligotrophic waters, whilst the coarse fish parasites were considered characteristic of eutrophic waters. Species of low specificity to their fish host,

and an element usually associated with eels, may occur in a range of habitats. This was largely supported by observations on the oligotrophic Llyn Padarn (Chubb, 1964b; Powell, 1966), and the eutrophic Rostherne Mere (Rizvi, 1964). This concept was rejected by Halvorsen (1971). He found that the fish parasite fauna from the River Glomma (Norway) was more complex than might be expected for fish at the limit of their geographical distribution. The same species of fish from a range of habitats harboured a very similar parasite fauna. It was concluded that the parasite fauna of a habitat may contribute little to the further characterisation of freshwater habitats, and that the fish parasite fauna will largely depend upon the fish species present.

Esch (1971) proposed that the predator-prey relationships within an aquatic ecosystem provide the best potential biological index for predicting the composition of a parasite fauna. In an oligotrophic ecosystem, the majority of parasites complete their life cycles within interacting members of the aquatic fauna, especially fish. The oligotrophic community is relatively closed, with negligible aquatic-terrestrial interaction. Conversely, the parasite fauna of the eutrophic ecosystem reflects extensive aquatic-terrestrial inter-action. Thus, the ecosystem is more open. As the biota changes during succession, the nature of the predator prey interaction also changes, and this will result in quantitative and qualitative alteration in the parasite fauna (Esch et al., 1975). Wisniewski (1958) concluded that the parasite fauna of birds prevail in eutrophic lakes. Wootten (1973a) found that the introduction of trout into Hanningfield Reservoir resulted in an oligotrophic element being introduced into the fish parasite fauna of the lake. The parasite fauna of the fish was con-sidered not characteristic of the eutrophic nature of the environment, and this was taken to support the view of Halvorsen (1971), that the

parasite fauna of fish may contribute little to characterisation

of freshwater habitats (Wootten, 1973a). The composition of the fish

parasite fauna was influenced more decisively by the fish species

composition than by other limnological factors. However, the influence

of the limited benthic invertebrate fauna, and the abundant local

piscivorous bird fauna, was noted.

Slapton Ley is a small, isolated, essentially eutrophic lake

in southern Devon. Kennedy (1975) was able to recognise an oligo-

trophic element (the parasite fauna of trout), an eel element, and

a remaining eutrophic, or cyprinid, element. Kennedy concluded (in

agreement with Halvorsen, 1971 and Wootten, 1973a) that the degree

of similarity between the parasite fauna of any two lakes will depend

to a large extent upon the species of fish that are present, and not

necessarily on the similar trophic state of the environments. The

highly individual nature of the fish parasite fauna at Slapton Ley was

attributed to geographical and historical factors, and the predator-

prey relationships were seen to be of crucial importance in determining

the composition of the parasite fauna of a body of water (Kennedy,

1975).

The parasite fauna of perch from seven localities in the British

Isles is summarised in Table IV. Let us consider how these results

may be interpreted in terms of the existing views concerning the

characterisation of the parasite fauna of fish, as applied to a single

species, perch.

In agreement with Wisniewski (1958) and Esch (1971), the parasite

fauna of perch from eutrophic environments is markedly influenced by

the presence of abundant piscivorous bird populations. This has been

discussed in section IV.3.2.

The parasite fauna of perch was not the same in each of the seven

localities, and may vary from one environment to the next. This denies

the view of Halvorsen (1971), that the same fish species in a range

of habitats, harbours a similar parasite fauna.

Halvorsen (1971), Wootten (1973a) and Kennedy (1975) all consider

that the composition of the parasite fauna of an environment will

depend to a large extent upon the resident ichthyofauna. Concerning

the parasite fauna of perch, the results shown in Table VII largely

confirm this. In environments containing only coarse fish (e.g.

Rostherne Mere, Shropshire Union Canal), the composition of the perch

parasite fauna consists of parasites specific to perch, plus parasites

with reduced specificity to their piscine hosts (Table VII, group A

and D).

The presence of eels in the same environment may lead to the

infection of perch with juvenile B. claviceps (Table VII, group C).

Certain species of parasites have an undetermined host specificity

(Table VII, group E). In environments containing salmonoid fish, a

number of species of parasites normally associated with salmonoid fish

may be found infecting perch. According to Chubb (1963) parasites

specific to salmonoid fish are characteristic of oligotrophic waters.

Therefore, the presence of such parasites within the parasite fauna

of perch from mesotrophic salmonoid/coarse fish waters is to be expected.

However, similar parasites have been recorded from perch at Loch Leven,

an eutrophic environment that contains trout (Salmo trutta) and coarse

fish. The parasite fauna of trout from four lakes in the British Isles

is shown in Table X. The trout at Loch Leven have as diverse and

abundant a parasite fauna, as those from Llyn Padarn or Llyn Tegid.

The number of species of metazoan parasites specific to trout are also

similar in all three lakes. (The parasite fauna of trout from Hanningfield

Reservoir is considered below). Therefore, the presence of trout, along

with its typical parasite fauna, in the eutrophic Loch Leven may be taken

to contradict the concept of characterisation, and support the views of

Table X. Parasite fauna of trout (Salmo trutta) from four

British Lakes.

	Llyn Padarn; Oligotrophic	Llyn Tegid; Mesotrophic	Loch Leven; Eutrophic	Hanningfield Reservoir; Eutrophic
Number parasite species from trout	16	17	23	13
Number metazoan species from trout	16	16	17***	13
Number parasites of salmonoid fish from trout	12	11	13*	5**
Data from	Chubb, 1970	Chubb, 1976	Campbell, 1974	Wootten, 1973a

N.B.

* Includes Sterliadchona tennuissima and Eustrongylides sp.

** Excludes Anisakis sp.

*** Includes two species of Diplostomum.

Halvorsen (1971), Wootten (1973a) and Kennedy (1975). However, Wisniewski (1958) indicated the need for a large series of observations to be made, on a range of habitats. Therefore, the significance of the fish parasite fauna at Loch Leven requires comparison with results from other natural eutrophic trout/perch environments. The presence of trout (along with their associated parasites) in an eutrophic lake, has previously been taken by Wootten (1973a) to invalidate the concept of characterisation. However, these results (from Hanningfield Reservoir) require careful consideration. Trout, and many of their parasites, are maintained in the lake by a stocking programme. It seems likely that if this programme were to cease, the trout population would decline, and

many of their parasites become rare, or disappear. The parasite fauna at Hanningfield Reservoir would then take on a character typical for an eutrophic lake. The absence of certain benthic intermediate hosts has been noted. In addition, the parasite fauna of trout at Hanningfield Reservoir is relatively poor, in terms of species typical of salmonoid fish (Table VII). This may explain the absence of such parasites from perch at this locality.

Perch are found in a variety of habitats, though are often abundant in lakes of mesotrophic-eutrophic status. Assuming the concept of characterisation, as applied to the parasite fauna of perch, the parasites specific to perch are a characteristic element of the parasite fauna of such waters. From the existing results on the parasite fauna of perch, this view is largely supported, allowing for the individuality of freshwater habitats (especially Loch Leven, Slapton Ley and Ockendon Moat). The absence of species of parasites from Llyn Tegid, that are commonly associated with perch from more eutrophic waters (e.g. Proteocephalus percae, Achtheres percarum, etc.) requires further investigation in additional mesotrophic habitats. It may be postulated that the parasite fauna of perch from environments closer to oligotrophy might be depleted, and the species of parasites characteristic of eutrophic waters, rare or missing. However, perch are not often found in such environments, and we have no satisfactory comparative data. Barysheva and Bauer (1957) have studied the parasite fauna of the fish of Lake Ladoga, an environment considered by Zhadin and Gerd (1963) to be ultra-oligotrophic. However, the biological conditions within the lake vary extremely. There are warm, littoral regions where the flora and fauna are abundant, but also deep water regions where life is scant (Barysheva and Bauer, 1957). However, compared to other inner-water regions of the U.S.S.R., Lake Ladoga has a relatively low output of fish, but is distinguished by producing

salmonoid fish of a high body weight. Within this environment, perch harboured a large and varied parasite fauna that is comparable to that seen in more distinctly eutrophic lakes. Whilst only 30 perch were examined (principally between June-August 1948), 24 species of parasites were recorded. These included the typical perch parasites Bunodera luciopercae, Proteocephalus percae and Triaenophorus nodulosus as well as three species of salmonoid fish (Henneguya zychokkei, Cyathocephalus truncatus, and Echinorhynchus salmonis). Therefore, the shallow, littoral regions of higher productivity in Lake Ladoga may favourably influence the parasite fauna of perch, perhaps permitting the existence of a typical perch parasite fauna in a possibly otherwise unfavourable environment. Clearly, the distribution of perch and its parasite fauna in Lake Ladoga requires further investigation, and the results should be compared to studies on further, oligotrophic habitats. Observations on the parasite fauna of yellow perch (Perca flavescens) from a range of environments in North America were inconclusive, with respect to the concept of characterisation (Tedla and Fernando, 1970a).

In summary, the concept of characterisation (Wisniewski, 1958; Chubb, 1962, 1963, 1964b, 1970; Mishra and Chubb, 1969) has been challenged by Halvorsen (1971), Wootten (1973a) and Kennedy (1975). They consider that the parasite fauna of an environment will depend to a large extent upon the fish species present, rather than upon other limnological factors. The results from the studies on the parasite fauna of perch largely confirm this. Nonetheless, further observations, on a greater range of environments, are required, in order to elucidate fully the inter-relationships that exist between parasite, host and environmental specificity.

IV.4.   Conclusions: factors effecting the composition of the parasite fauna of perch.

Within the range of environments studied, the composition of the

parasite fauna of perch may be influenced by a number of factors.
These include:

a.   diversity and abundance of the aquatic invertebrate fauna;

b.   diversity and abundance of the ichthyofauna:

       (1)   presence or absence of salmonoid

            fish, pike and eels,

       (2)   their relative abundance;

c.   abundance of the local piscivorous avian fauna;

d.   history and geographical isolation of the environment.

In order to understand the factors influencing the composition
of the parasite fauna of fish, a large series of observations need to
be made on a variety of habitats (Wisniewski, 1958). This clearly
applies to the parasite fauna of perch. Geographically isolated
lakes (Slapton Ley) and small, recently constructed lakes (Ockendon
Moat) may have highly individual fish parasite fauna. The presence
of parasite species considered characteristic of perch is not entirely
predictable (Loch Leven) and the influence of the parasite fauna of
other members of the ichthyofauna may vary from one environment to the
next (Llyn Tegid, Loch Leven, Hanningfield Reservoir). Thus, the
individuality of freshwater habitats is emphasised, and the need for
a greater number of observations, on a variety of habitats, will
elucidate further the factors controlling the composition of the
parasite fauna of perch in particular (and of fish in general).

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CHAPTER V

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

INTRODUCTION

Two species of Protozoa were recorded from perch during

this study at Llyn Tegid. Both species were Myxosporidia:

Myxobolus muelleri and Henneguya psorospermica.

V. ORDER Myxosporidia Bütschli, 1881

V.1   FAMILY Myxobolidae Thélohan, 1892

GENUS Myxobolus Bütschli, 1882

Myxobolus muelleri Bütschli, 1882

V.11   INTRODUCTION

Myxosporidia are common protozoan parasites of freshwater

and marine fish. The spores are the most conspicuous stage in

the life cycle and consist of shell valves, polar capsules

(each containing a polar filament) and a sporoplasm which may

contain an iodinophilous vacuole. Six nuclei are usually

present; 2 valve nuclei, 2 polar nuclei and 2 sporoplam nuclei.

The spores have a rigid definite structure and provide the basic

taxonomic characters for the group. Spores are the dispersal

phase in the life cycle and are produced by trophozoites.

The trophozoites may be amoeboid (as inside hollow organs, e.g.

gall bladder) or in the form of diffuse infiltrations or capsules

(Davies, 1968).

In agreement with Walliker (1968), Rogers & Gaines (1975)

considered that the genus Myxosoma Thélohan, 1892 was synonomous

with Myxobolus. All members of the genus Myxobolus are histozoic,

and the vast majority possess spores with two polar capsules.

Myxobolus muelleri has previously been recorded in the

British Isles by Davies (1968) in chub (Leuciscus cephalus),

dace (Leuciscus leuciscus) and roach (Rutilus rutilus) from the

River Lugg (Hereford), by Walliker (1967) in dace from the

Lee Navigation Canal (Herts.), by Anderson (1971) in bream

(Abramis brama) from Dagenham (Essex), by Lees (in Kennedy,

1974) in perch (Perca fluviatilis) from the Serpentine (London),

and by Davies (1976) in dace from the Emral and Wych Brooks

in the River Dee System. In addition, Myxobolus sp. has been

recorded from roach, rudd (Scardinius erythrophthalmus) and

minnow (Phoxinus phoxinus) (Williams, 1964; Kane, 1964;

Canning et al.,1973; Campbell, 1974; Kennedy, 1974).

V.12   OBSERVATIONS

Two white, roughly spherical capsules approximately 0.5 cm

in diameter, were found in the lower left hand region of the

buccal cavity (adjacent to the gills) of a female perch

(aged 3++ years, standard length 12.5 cm) caught at Llyn Tegid

by gill net in April 1975. Concurrent with this infection was

the heavy infection of the gills of the same fish with a

total of 153 capsules of Henneguya psorospermica.

The capsules from the buccal cavity were fixed in 5% formalin

and a sample of the enclosed spores examined in polyvinyl lactophenol

(Davies, 1968). The spores were identified as Myxobolus muelleri

according to Bykhovskaya-Pavlovskaya et al. (1962). The spores

consisted of a flattened spherical shape with a prominent

intercapsular process. The spores measured 10.5 - 12.0 u long

by 8.5 - 10.0 u wide by 5.5 - 7.5 u thick.

V.13   DISCUSSION

Davies (1968) showed that the size of the spores of

M. muelleri varied depending on the host species and the type of

tissue infected. The variation in spore size and form has lead

to confusion in the taxonomy of the genus Myxobolus, and many

new species have been described without sufficient evidence

(Davies, 1968).

Two capsules were found on a single perch from Llyn Tegid,

out of 559 fish examined (including 30 perch fry) over the

period January 1975 - July 1976. This is a new parasite record

for Llyn Tegid, though M. muelleri has been recorded elsewhere

in the River Dee system (Davies, 1976). It is interesting to

note the concurrent heavy infection with H. psorospermica,

though its significance is not known (see section V.23).

V.14   SUMMARY

The occurrence of M. muelleri in Llyn Tegid is a new

species record for the lake.

V.   ORDER Myxosporidia Bütschlii, 1881

V.2   FAMILY Myxobolidae Thélohan, 1892

          GENUS Henneguya Thélohan, 1892

          Henneguya psorospermica Thélohan, 1895

V.21   INTRODUCTION

The genus Henneguya are histozoic parasites with a vegetative

stage in the form of a polysporous cyst (Bykhovskaya-Pavlovskaya

et al.,1962). The spores grossly resemble spermatozoa, possess

two anterior polar capsules and usually have an elongate posterior

process which may be separated along the sutural plane (McCraren et al.,

1975).

Henneguya psorospermica has been recorded from perch (Perca

fluviatilis) and pike (Esox lucius) at Llyn Tegid (Chubb, 1963, 1976),

from perch and pike from Rostherne Mere (Cheshire) (Rizvi, 1964), and

from pike in the River Lugg (Hereford) (Davies, 1967, 1968).

In addition, Henneguya sp. has been recorded from a number of

fish species, including perch, from the Rivers Blackwater,

Chelmer and Rǿding (Essex) (Kennedy, 1974). Henneguya sp.

has also been recorded from the fish (not perch) of Loch

Leven (Scotland) (Campbell, 1974) and the Fen drains (Lincs)

(Kennedy, 1974).

The spores of Henneguya oviperda closely resemble those of

H. psorospermica (Bykhovskaya-Pavlovskaya et al.,1962). H. oviperda

has been recorded from pike in the British Isles (Davies, 1968;

Mishra & Chubb, 1969).

V.22   RESULTS

The myxosporidian parasite infesting the gills of perch

at Llyn Tegid was identified as H. psorospermica according to

Bykhovskaya-Pavlovskaya et al. (1962). The cysts were usually

situated at the distal end of the gill filaments. Each cyst

was white, ovoid in shape, and measured 1 - 3mm in diameter.

The gill arches in each branchial chamber were numbered I - IV;

I being the most external of the arches, and IV the most

internal of the arches. The number of cysts found on each gill

arch is shown in Table I. The cysts were most common on gill

arches I - III, and found less often on gill arch IV. The

cysts of H. psorospermica were not found at any other site in

perch. A monogenean, Ancyrocephalus percae also infrequently

infected the gills, and another myxosporidian, Myxobolus muelleri

was recorded from the buccal cavity of a single fish in April (1975)

(see section V.13 and Chapter VI). Because of the low incidence

of these three parasites the relationships that might exist between

them could not be investigated. Nonetheless, A. percae was never recorded from the gills of perch infected with H. psorospermica, and the single occurrence of M. muelleri was on a perch harbouring the maximum number (153) of cysts of H. psorospermica recorded in this study.

The cysts of H. psorospermica were fixed in 5 - 10% formalin and the contents examined in polyvinyl lactophenol (Davies, 1968). Tailed spores were present in all months that cysts were recorded. No tail-less spores were seen. From samples taken at various times of the year, the measurements of the spore were: length of spore body 10.0 - 15.5 um; width of spore body 7.5 - 9.5 um; thickness of spore body 5.5 - 7.5 um; length of caudal processes 19.0 - 32.0 um; polar capsules 5.0 - 7.5 um long by 2.0 - 2.5 um in diameter.

Gill net samples (January 1975 - February 1976)

From 465 adult perch, a total of 222 cysts were recovered from 14 fish. The incidence of infection was 3.0% and the mean intensity/ infected fish was 15.9 (maximum 153).

The cysts were present between January - May 1975 and November - February 1975/76 (Table II). During these months the number of cysts/infected fish fluctuated irregularly. Heavily infected fish were occasionally found (Table II). The monthly changes in occurrence are shown in relation to lake temperature in Fig. 1. It would appear that when the water temperature exceeds $10^{o}C$ at the surface, 6m and 10m, H. psorospermica cysts are not found on adult perch.

Fig. 1.   Seasonal changes in incidence of <u>Henneguya psorospermica</u>.

Number fish examined
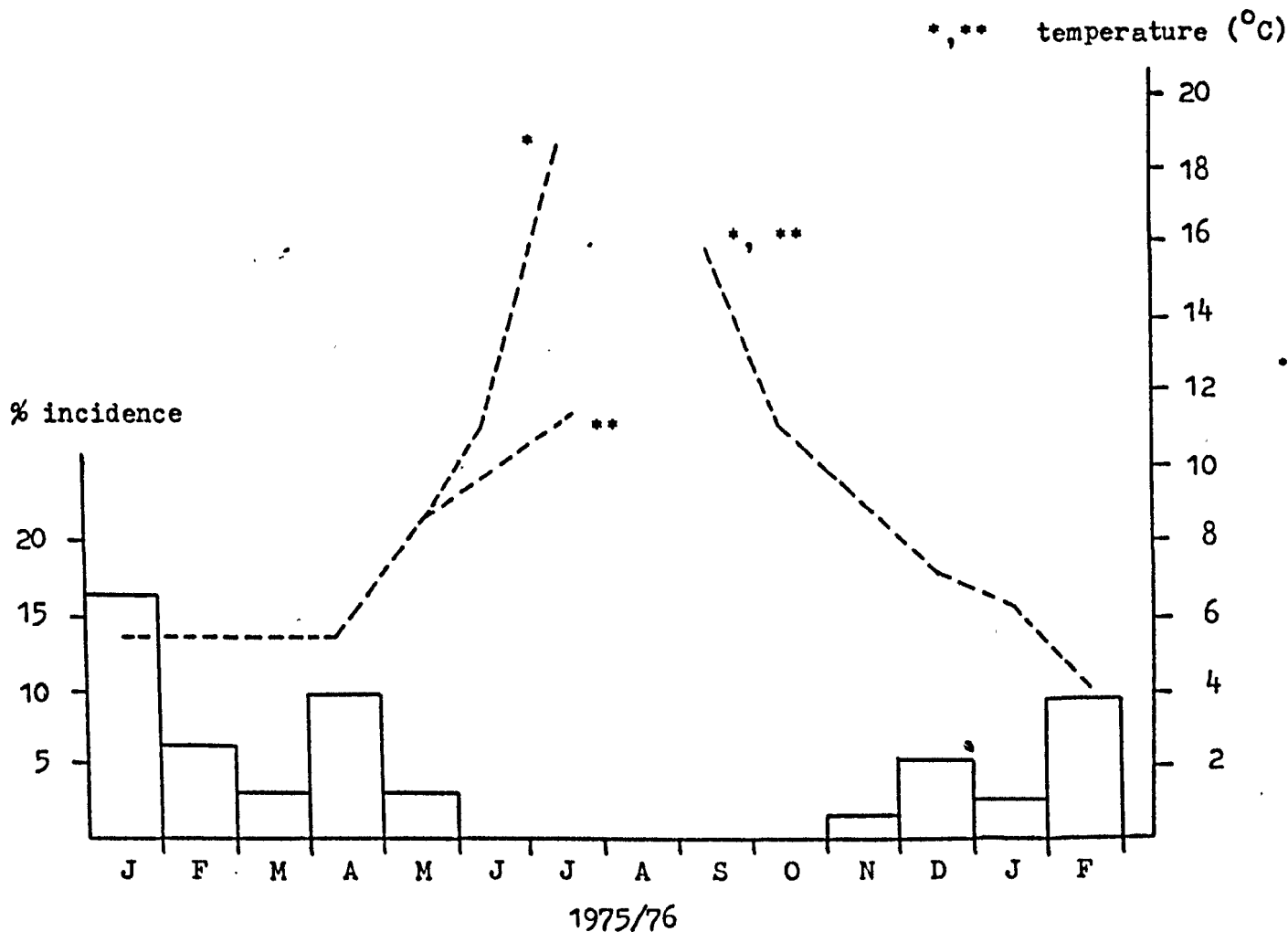
	J	F	M	A	M	J	J	A	S	O	N	D	J	F
Number fish examined	6	30	30	30	30	39	40	30	30	60	54	35	30	21
Surface*	5.5	5.5	5.5	5.5	9.0	11.5	19.0	(-)	16.0	11.0	9.0	7.0	6.5	4.0
6m	5.5	5.5	5.5	5.5	8.5	11.0	14.0	(-)	16.0	11.0	9.0	7.0	6.5	4.0
10m**	5.5	5.5	5.5	5.5	8.5	10.5	11.5	(-)	16.0	11.0	9.0	7.0	6.5	4.0

- TEMPERATURE -

Table I. Distribution of cysts of <u>Henneguya psorospermica</u> on the gills of adult perch. Gill net samples. January 1975 - February 1976.

| External | Gill arch [*] | | Internal |
I	II	III	IV
1		2	
2			
	2		
1	1	2	
85	31	29	8
	2	1	
	1		
	1		
	2		
2	2	3	
3	3	4	2
3		1	
5	15	2	6
Total 102	60	44	16

Total number cysts 222

N.B.

[*] Total infection on gill arches in right and left branchial chamber summed

Table II. Infection of perch with Henneguya psorospermica.

Gill net samples. January 1975 - February 1976.

Month	No. fish examined	Age (yrs)	Length (cm)	Sex	No. cysts	Monthly mean intensity/ infected fish
			Infected host data			
J	6	4++	13.0	M	3	(3.0)
F	30	8++	24.5	F	2	
		7++	17.5	M	1	1.5
M	30	3++	13.5	F	4	(4.0)
A	30	3++	12.5	F	153*	
		6	13.3	F	3	
		3+	12.4	F	1	(52.3)
M	30	3+	12.2	M	1	(1.0)
J	39		-negative-			
J	40		-negative-			
A	30		-negative-			
S	30		-negative-			
O	60		-negative-			
N	54	4++	17.9	F	2	(2.0)
D	35	4++	12.5	F	7	
		4++	14.3	F	12	9.5
J	30	4++	11.6	F	4	(4.0)
F	21	3++	14.0	F	28	
		3++	11.5	M	1	14.5
Total	465	14		4M/10F	222	15.6 (maximum 153)

N.B.

Sex of host: M = male

                    F = female

* concurrent infection with Myxobolus muelleri

Trawl sample (March 1976)

From 65 perch a total of 110 cysts were recovered from 13 fish. The incidence of infection was 20.3% and the mean intensity/infected fish was 8.5 (maximum 40).

Purse seine sample (July 1976)

None of 30 perch fry were infected.

Effects of host age and length

The effects of host age and length on the infection of H. psorospermica are shown in Tables III and IV.

None of 30 perch fry aged 4 - 6 weeks (0+, 2.0 - 2.7 cm long) were infected. The incidence of infection appears to reach a peak in perch aged 8 - 9 months (0++, 3.0 - 8.9 cm long). Of 36 perch examined after spending their first winter in the lake, 33.3% were infected (Tables III and IV). The incidence of infection in the 28 adult perch (aged 1++ - 4++ years, 9.0 - 11.9 cm long) from this sample was 3.6%. In the adult fish caught by gill net (aged 2++ - ≥ 6, 9.0 - ≥ 18.0 cm long) the incidence of infection was low and fluctuated very little (Tables III and IV).

The 0++ perch may harbour, on average, a larger number of cysts/infected fish than the older adult perch (Table V). In the adult perch a greater proportion of the fish harboured 1 - 4 cysts, while in the 0++ perch a greater proportion harboured 5 cysts or over. The most heavily infected fish was an adult, gill netted perch, though this may be a reflection of the much larger sample size of these fish.

Table III. Effects of host age on the incidence of <u>Henneguya</u> <u>psorospermica</u> cysts. Gill net, trawl and purse seine samples. January 1975 - July 1976.

Age (yrs)	Number fish examined	Number fish infected	% incidence
Purse seine sample (July 1976)			
0+	30	-	-
Trawl sample (March 1976)			
0++	36	12	33.3
1++ - 4++	28	1	3.6
Gill net samples (January 1975 - February 1976)			
2 - 3++	142	6	4.2
4 - 5++	242	5	2.1
≯6	81	3	3.7
Total	559	27	4.8

Table IV. Effect of host length on the incidence of <u>Henneguya</u>
<u>psorospermica</u> cysts. Gill net, trawl and purse seine samples.
January 1975 - July 1976.

Length (cm)	Number fish examined	Number fish infected	% incidence
Purse seine sample (July 1976)			
2.0-2.7	30	-	
Trawl samples (March 1976)			
3.0-8.9	36	12	33.3
9.0-11.9	28	1	3.6
Gill net samples (January 1975 - February 1976)			
9.0-11.9	56	2	3.6
12.0-14.9	321	9	2.8
15.0-17.9	59	2	3.4
$\geqslant$18.0	29	1	3.5
Total	559	27	4.8

Table V. Effect of host age on intensity of infection with

Henneguya psorospermica. Gill net and trawl samples.

January 1975 - March 1976.

	Number fish examined	Number fish infected	% incidence	% infected fish harbouring: 1-4 cysts	$\geqslant$5 cysts
0++ perch: trawl sample					
	36	12	33.3	41.7	58.3
1++-12++: gill net and trawl samples					
	493	15	3.0	73.3	26.7
Total	529*	27	-	-	-

N.B.

* Purse seine sample of perch fry not included

Effect of host sex

The greater number of adult female fish that were infected (see Table II) is thought to be a reflection upon the greater proportion of female fish in the gill net samples (see Chapter III).

V.23   DISCUSSION

The spores of H. psorospermica are very similar to those of H. oviperda, a parasite of the ovaries of pike (Bykhovskaya-Pavlovskaya et al., 1962). Mishra (1966) and Mishra & Chubb (1969) only found H. oviperda from pike at the Shropshire Union Canal (Cheshire), whilst Davies (1968) recorded both species from pike at the River Lugg (Hereford). Rizvi (1964) found H. psorospermica in perch and pike from Rostherne Mere (Cheshire) and only this species has been recorded from perch and pike at Llyn Tegid (Chubb, 1963, 1976). In continental Europe, Barysheva & Bauer (1957) found pike infected with H. oviperda and H. psorospermica while perch only harboured the latter species, at Lake Ladoga (U.S.S.R.). Rauckis (1970a & b), working at Lake Dusia (U.S.S.R.) produced similar results. At Lake Druzuo (Poland) only pike were found to be infected with H. psorospermica (Kozicka, 1959), while Tell (1971) found that perch and pike at Lake Võrtsjarv (U.S.S.R.) were infected. Davies (1968) considered that the marked difference in the size of the cyst produced by H. oviperda and H. psorospermica, along with the different sites of infection and the fact that one species may occur without the other indicated that both of these parasites should be treated as separate species.

Because of the low level of incidence of infection with
H. psorospermica, A. percae and M. muelleri determination of the
relationships that may exist between them was difficult. Tedla &
Fernando (1969, 1970) reported similar low incidence concerning
the gill parasites of yellow perch (Perca flavescens). An
An antagonistic relationship has been noted on the gills of
Gadus merlangus between the monogenean Diclidophera merlangi and
the copepod Clavella devastatrix (Dogiel, 1958, 1962) and
C. adunca (Kahata, 1960). In both instances the infestation
with one of the two parasites was high (Kahata, 1960).

Noble et al. (1963) found a highly significant association
between Trichodina sp. and Gyrodactylus elegans, with the former
feeding on bacteria from the secondary infection of the gills
caused by the hooks of the latter. Mackenzie (1969) found a
highly significant association between two ciliates (Trichodina
borealis and Scyphidia aduncouveleata) infecting the gills of
plaice (Pleuronectes platessa). There was no significant association
or antagonism between Gyrodactylus unicopula and either of the
ciliates, and the association between the two ciliates was
unaffected by the presence of the monogenean (Mackenzie, 1970).

The cysts of H. psorospermica were not randomly distributed
over the gills of perch. A greater proportion of the cysts were
found on gill arches I - III, and they were situated at the distal
ends of the gill filaments. The non-random distribution of
monogenetic trematode parasites on the gills of fish has been
reported by several workers, including Llewellyn (1956), Owen
(1963), Wiles (1968), Paling (1969), Smith (1969), Arme &
Halton (1972) and Wootten (1974). Some species, such as

Discocotyle sagittata on brown trout (Salmo trutta) may actively

avoid the greater volumes of water passing over gill arches II

and III of this fish, and are to be found in greater numbers

on gill arch I. However, Wootten (1974) found that Dactylogyrus

amphibothrium infecting ruffe (Gymnocephalus cernua) occurs on the

gill arches where the water flow is greatest, though the

parasite may select a site of attachment where it is not

subjected to the full force of the respiratory current.

It was suggested that the distribution of D. amphibothrium on

the middle two gill arches of ruffe may reflect the larger

surface area available for the parasite to attach (Wootten, 1974).

Llewellyn (1956) and Suydam (1971) considered that the gill site

specificity of diclidophoran monogeneans is a result of the

strength and direction of the respiratory current passing over

the gills, rather than active selection by the parasite. The

differential distribution of the leech, Cystobranchus mammillatus

on the gill and gill surfaces of burbot (Lota lota) was considered

by Halvorsen (1971) to be a result of active selection by the

parasite.

Wootten (1974) found that in ruffe, using glochidia

larvae as "marker parasites", the water flow was greatest

over gill arches II and III, and that more water passes over

the distal ends of the filaments than the proximal ends. Spores

are thought to be the dispersal phase in the life history of

myxosporidians (Davies, 1968), though the exact mode of transmission

of Henneguya spp. has not been demonstrated (McCraren et al., 1975)

Infections with some Myxosporidia are initiated when, after the

ingestion of spores, the valves open and the sporoplasm emerges

and penetrates the intestinal epithelium, and is carried to its site of infection in the blood stream (Canning et al., 1973). However, studies on Ceratomyxa shesta (a parasite of certain salmonid fish) have indicated that the spores produced as the terminal product of the infection may not be the infective agent of this parasite (Schafer, 1968). From the distribution of cysts of H. psorospermica on perch, where the surface area and water flow are probably greatest (over the distal ends of gill arches I - III), it would appear that the infective agent of this parasite may be passively inhaled with the respiratory current. Nonetheless, the possibility of a blood borne infective agent should not be ignored, and is likely to exist in the closely related H. oviperda.

There have been few detailed studies on the seasonal occurrence of myxosporidian parasites of fish in general, and of H. psorospermica in particular. Rizvi (1964) examined pike at Rostherne Mere between September - March. The parasite was present in all months, though the incidence was highest in September - October (62.5 - 85.7%) and March (66.6%), and lowest in December (13.3%) and January - February (50.0%). No data were available for the spring - summer months. Davies (1968) examined small numbers of pike infected with H. psorospermica, and found that the parasite was most abundant during May - August (40.0 - 87.5% incidence). The parasite was absent for the other months of the year, though too few pike were examined to assess its seasonal occurence (Davies, 1968). Rackis (1970a & b) examined small numbers of pike and perch during all seasons of a single year. H. psorospermica infected

both fish. In perch the incidence was highest in April-May (30.7%) and low in January-March (13.3%) and June-July (6.6%). The parasite was not recorded from perch in October-November (Rauckis, 1970a). In pike the incidence was highest in October-November (33.3%) and lowest in April-May (6.2%). During January-March and June-July the incidence was 9.0% and 13.3% respectively (Rauckis, 1970b). Chubb (1963) recorded H. psorospermica from the gills of 5 of 104 (4.8%) pike examined from Llyn Tegid, though it was not possible to determine any seasonality of occurrence. The present study revealed that the incidence of H. psorospermica cysts on perch is low. Out of 465 adult fish gill netted over 14 months, 3.0% were infected. The parasite cysts were absent from perch during June-October, despite the large numbers of fish that were examined. Analysis of this result using a 2 by 2 contingency table (Table VI), indicated that there was a highly significant difference (P < 0.01 > 0.001) in the incidence of infection during January-May 1975 and November-February 1975/76, when compared to June-October 1975. Cysts were absent from perch during June-October, when the lake temperature at surface, 6m and 10m exceeded 10°C. Temperature might effect the occurrence of the parasite directly, or via host reactions to the infection. Lom (1969) stated that the trophozoites of H. psorospermica developed in the gill platelets of perch during the winter months. In the spring the cysts ripen, burst and discharge spores. Lom found that when perch infected with developing plasmodia of H. psorospermica were transferred from cold water to water at 20°C, host cells penetrated the cyst, the parasite degenerated and the infection disappeared. The effect of temperature on the immune responses of fish is well established (e.g. Corbel, 1975), and Lom (1969) suggested that fish antibodies might become active at higher temperatures, adversely effect the parasite cyst ultimately aid in its destruction. It is interesting to note that cysts of H. psorospermica were present on

Table VI.　Analysis of seasonal occurrence of <u>Henneguya</u>
<u>psorospermica</u> (2 by 2 contingency table).

!	Number fish		Total
	infected	uninfected	
January-May 1975,			
November-February 1975/76	14	252	266
June-October 1975	0	199	199
Total	14	451	465

$$X^2 = 9.072, \text{ 1 degree of freedom}$$

$$P < 0.01 > 0.001$$

pike at the River Lugg during May-August, when the water temperature
was 12-19°C (Davies, 1967, 1968). Similarly, Rauckis (1970a, b)
recorded H. psorospermica from perch and pike at Lake Dusia during
June-July, though the incidence of infection was lower than in most
other samples.

Some related species of myxosporidians have been reported as
exhibiting somewhat similar cycles of seasonal occurrence to that
reported for H. psorospermica on perch at Llyn Tegid. Ergens (1966)
found that pike at the Lipno Reservoir (Czechoslovakia) were infected
with H. lobosa, with a peak of incidence and intensity each autumn,
followed by a sharp decline each spring. Izyumova (1960) reported
similar results concerning the H. lobosa infection of pike at the
Rybinsk Reservoir (U.S.S.R.). Meyer (1970) found that the incidence
of Henneguya sp. on catfish (Ictalurus punctatus) in North America
was highest in March-April, and suggested that spore formation was
greatest during the period just prior to host spawning. However,
Vik (1960) reviewed the occurrence of H. zschokkei in Norwegian
coregonine fish and suggested that the seasonal occurrence reported
by some workers may have been the result of sampling errors and
deficiencies, rather than the actual absence of the parasite.

Perch biology at Llyn Tegid (particularly feeding habits and
distribution of fish in the lake) exhibited marked seasonal changes,
and it is suggested that these factors might produce seasonal changes
in the transmission of the infective agent of H. psorospermica. The
exact mode of transmission of Henneguya spp. is not known (McCaren
et al., 1975). However, it is generally assumed that spores are the
infective agent of Myxosoma cerebralis and infections have been produced
by exposing rainbow trout (Salmo gairdneri) to mud from ponds which
previously contained infected fish (Halliday, 1976). Benthic invertebrates
were eaten by perch at Llyn Tegid during all months of the year (see

Chapter III). Nonetheless, there was (for example) a spring (March-May) peak of incidence of _Asellus meridianus_,,and a spring-late summer (March-September) peak of incidence of larval Diptera, in the stomachs of this fish. In addition, perch were only found in shallow water (6m or less) in large numbers during June-September (see Chapter III). Because of the low incidence of infection it was not possible to detect any differences in the occurrence of _H. psorospermica_ at different sites in the lake, though cysts were absent from fish at 6m _and_ 12m during June-October.

The absence of cysts of _H. psorospermica_ from the perch fry examined in July (aged 4-6 weeks) may have been a reflection on the small sample size, or the fact that developing plasmodia of this parasite are adversely effected by warm temperatures (Lom, 1969). The occurrence of the early developmental stages of _H. psorospermica_ in perch at Llyn Tegid was not investigated. The peak of incidence and intensity of infection in juvenile perch (aged 8-9 months) may have been the result of an increased resistance of older fish to infection. In comparison, many authors (e.g. Sindermann and Rosenfield, 1954; Sindermann, 1966) have noted that _Kudoa clupeidae_ (a myxosporidian that parasitises certain clupeoid fish of the North Atlantic) only occurred in smaller, younger host individuals (Lom, 1970). Sindermann (1966) stated that up to 75.0% of one year old herring (_Clupea harengus_) were infected, while adult fish were not parasitised. Such increasing age immunity to parasitic infestation is often non-specific, and may result from morphological, physiological and/or ecological changes of the host with increasing host age (Bauer, 1958, 1959). The transmission of _Myxosoma cerebralis_ by spores in mud has been noted. If this mode of transmission also applies to _H. psorospermica_, and change in feeding habits that resulted in the ingestion of fewer benthic invertebrates might also influence the transmission of this parasite. However, the fall in the occurrence of _H. psorospermica_ in adult perch cannot be attributed to a

change in feeding habits, since benthic invertebrates (e.g. Asellus
meridianus, see Chapter III) were eaten by perch of a range of ages and
sizes. It is of interest to note that at Llyn Tegid, young of the
year and adult perch harboured cysts of H. psorospermica at a time
of the year when, young of the year fish inhabited for the first time,
the deeper regions of the lake, along with the adult fish. Llewellyn
(1962) found that the pelagic larvae of shad (Trachurus trachurus)
were free of monogenean gill parasites. In late September-October
when the young fish descended to the sea bottom, they acquired onco-
miracidia. The parasites developed slowly, and reached maturity the
following summer. Eggs were deposited and sank into deeper water,
where they developed to produce a high density of oncomiracidia by
September-October. After feeding in the surface waters for several
months the fish returned to deep water, and were again exposed to
infection.

SUMMARY

Cysts of H. psorospermica were recorded from the gill filaments
of perch.

There was a peak of incidence and intensity of infection in
juvenile perch (aged 8-9 months), while the incidence and intensity
in adult perch (aged $>$ 1) was low.

In adult perch there was a seasonal pattern of occurrence of
cysts of H. psorospermica.

The influence of temperature and variations in host biology on
the occurrence of H. psorospermica were discussed.

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CHAPTER VI

THE MONOGENEAN PARASITE OF PERCH (_Perca fluviatilis_ L.) FROM LLYN TEGID

INTRODUCTION

A single species of monogenean was recorded from perch: _Ancyrocephalus percae_.

VI.   FAMILY   Dactylogyridae   Bykhovskii, 1933

       GENUS   Ancyrocephalus   Creplin, 1839

          Ancyrocephalus percae Ergens, 1966

VI.1.   INTRODUCTION

The genus Ancyrocephalus are oviparous monogeneans of the family Dactylogyridae. Members of this genus are principally parasitic on freshwater and marine fish, especially percids (Bykhovskaya-Pavlovskaya et al., 1962). Bykhovskii and Nagibina (1970) revised and amended the genus to include only two species: Ancyrocephalus paradoxus Creplin, 1839 from pike-perch (Lucioperca lucioperca) and Ancyrocephalus percae Ergens, 1966 from perch (Perca fluviatilis). Dontsov (1972) described Ancyrocephalus gussevi n. sp. from the pike-perch Lucioperca volgensis in the U.S.S.R.

A species of monogenean identified as A. paradoxus was first recorded from the British Isles by Dawes (1947). Chubb (1961, 1963) reported the only other record of this species from the British Isles, when he found a single specimen on one of 8 perch examined from Llyn Tegid in 1957/58.

VI.1.2   OBSERVATIONS

The monogenean that infected perch at Llyn Tegid was identified as A. percae according to Ergens (1966). The measurements of this material, along with the measurements of A. percae and A. paradoxus from Ergens (1966) are given in Table I. The form of the second pair of haptor anchors is shown in Fig. I, though no detailed observations were made on form of the chitinoid parts of the vagina.

Twelve specimens of A. percae were recorded from 5 of 465 perch (1.1%) that were caught by gill nets between January 1975-February 1976.

The mean intensity/infected fish was 1.1 (maximum 4). In addition, three specimens of A. percae were removed from three of 64 perch (4.6%) caught by trawl in March 1976. The mean intensity/infected fish was 1.0 (maximum 1). None of 30 perch fry (aged 4-6 weeks) examined in July 1976 were infected.

Data on the infected fish are presented in Table II. The parasites were found at the proximal end of the gill filaments, close to the gill arch. There appeared to be no preference for a particular gill arch, or for a particular region of individual gill arches.

Table I. Measurements of Ancyrocephalus spp.

| | A. percae | | A. paradoxus |
	Llyn Tegid*	Ergens (1966)**	Ergens (1966)
Body length	1080	1010-1790	2340-4680
width	270	240-390	390-780
Length copulatory complex	55	67-84	135-156
Length marginal hooks	15	16-19	17-20
Length anchors: 1st pair	50	51-61	56-63
2nd pair	57	49-57	50-60

N.B. All measurements in um, taken according to Ergens (1966).

* Measurements of a single specimen. Relaxed in cold water, formalin fixed, and stained in Acetic Haematoxylin (see Chapter II).

** Fixed paratype specimens.

Fig. I. Camera lucida drawing to show the form of the second pair of
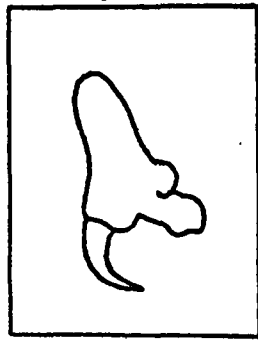haptor anchors. of <u>Ancyrocephalus percae</u> from perch at Llyn
Tegid.

50 um
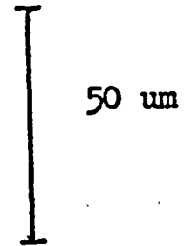
Table II. Occurrence of <u>Ancyrocephalus percae</u>. Gill net and
trawl samples. January 1975-March 1976.

Date	HOST DATA Age (yrs.)	Length (cm)	Sex	Number parasites
GILL NET SAMPLES				
February 1975	3++	12.5	F	4
April 1975	5+	16.4	F	2
October 1975	8+	23.2	F	1
November 1975	8++	23.9	F	1
December 1975	5++	13.2	M	1
TRAWL SAMPLE				
March 1976	0++	5.6	?	1
	0++	6.1	?	1
	0++	4.8	?	1
			TOTAL	12

N.B. M = Male

F = Female

? = Sex not distinguishable to naked eye

VI.1.3   DISCUSSION

A. percae was first described by Ergens (1966) from perch in the
River Tepĺa (Czechoslovakia). Consequently, records of A. paradoxus
prior to that date may contain records of A. percae. A. percae resembles
A. paradoxus both morphologically and metrically (Ergens, 1966). However,
the main differences were: form of the connecting bars of both pairs of
anchors; form of the marginal hooks; and mainly the measurements of the
copulatory complex. The material obtained in the present study was

identified as <u>A. percae</u>. The size of the copulatory complex and

the form of the second pair of haptor anchors were considered to be

particularly diagnostic of this species (Table I, Fig. I).

Comparison of the Dawes (1947) description of <u>A. paradoxus</u> with

the Ergens (1966) descriptions, along with the examination of the

Chubb (1961, 1963) material, indicated that previous records of <u>A.</u>

<u>paradoxus</u> from the British Isles referred to <u>A. percae</u>. Ergens (1966)

considered that these parasites were highly host specific and stated that

their occurrence on other fish species than their specific host should

be regarded as accidental infections.

The incidence and intensity of infection of <u>A. percae</u> and <u>A. paradoxus</u>

is usually low. At Llyn Tegid, <u>A. percae</u> was recorded from 8 of 559 perch

(1.4%) (including 30 fry) that were examined between January 1975-July 1976.

Rauckis (1970) found this species on 6.6% of the adult perch he examined

during January-March, from Lake Dusia (U.S.S.R.). The infection was absent

from the fish for the rest of the year. Bykhovskaya-Pavlovskaya (1940)

recorded three specimens of <u>A. paradoxus</u> from the gills of one of 226

perch examined from lakes in the Karelia region of U.S.S.R. Wierzbicki

(1970) found that 1.2% of 504 perch from Lake Dargin (Poland) were infected,

and noted that Milicer (1938) and Bykhovskii (1957) had found similar

results. Tell (1971) reported <u>A. paradoxus</u> from 3.2% of 250 perch (and from

12.5% of 40 pike-perch, <u>Lucioperca lucioperca</u>) examined from Lake Vórtsjarv

(U.S.S.R.).

At Llyn Tegid, <u>A. percae</u> was recorded from adult perch during the

spring (February and April) and during the autumn/winter (October-December),

and may be absent from the fish during the summer months. However,

seasonal variations in occurrence may be difficult to detect in parasites

that have a low incidence and intensity of infection. Rawson and Rogers

(1972a and b) studied the seasonal abundance of the ancyrocephalinaen

monogeneans on largemouth bass (<u>Micropterus salmoides</u>) and bluegill (<u>Lepomis</u>

macrochirus). Clavunculus bifurcatus on L. macrochirus was most abundant during the autumn and least abundant during the mid-summer months. Rawson and Rogers found that peaks in abundance of a variety of related monogeneans was a temperature associated phenomenon. Chubb (1977) considered that temperature is an important factor influencing the seasonal abundance of the monogenean parasites of freshwater fish. Izyumova (1958) found that perch at the Rybinsk Reservoir (U.S.S.R.) were parasitised all the year round by A. paradoxus, but with a lowered rate and intensity of infection in the winter. Wierzbicki (1970) found this parasite was present on perch only in the autumn and January, at Lake Dargin (Poland). Chubb (1977) summarised our knowledge on the seasonal occurrence of this parasite, and reported that the findings of Wegener (1909) and Malakhova (1961) were in accordance with those of Wierzbicki (1970). Chubb considers that in the light of errors in the descriptions of some species noted by Bykhovskii (1957), the revision of the Czechoslovak material by Ergens (1966), with the description of A. percae in the latter paper, and the revision of the genus by Bykhovskii and Nagihina (1970) it is likely that the conflicting patterns of occurrence can be explained by a confusion of specific identity. It should be noted that Komarova (1964) found pike-perch in the Dneper Delta (U.S.S.R.) infected with A. paradoxus during all months that the fish were examined (April- August, October). There was little fluctuation in the incidence and intensity of infection. Rauckis (1970) found perch infected with A. percae in Lake Dusia during January-March.

Perch of all ages and sizes may be infected with A. percae. The absence of the parasite from perch fry examined in July (1976) may be a reflection upon the small number of fish (30) that were examined. Alternatively, the parasite appeared to be absent from adult fish during the summer months, and its absence from perch fry may be a seasonal phenomenon, or reflect the unsuitability of young perch as hosts. However,

perch aged 8-9 months (0++) examined in March (1976) were found to harbour the parasite.

Four out of five of the infected adult fish (gill net samples) were female. It is not known whether this parasite shows a differential preference for female perch. Paling (1965) found that male trout (Salmo trutta) between the ages 5-7 years carried significantly more Discocotyle sagitta than female trout of the same age. However, in this study at Llyn Tegid a far greater number of female perch (282) were examined from the gill nets than male perch (183) (see Chapter III).

VI.1.4   SUMMARY

The presence of A. percae from perch at Llyn Tegid is recorded. It is considered that previous records of A. paradoxus from the British Isles referred to A. percae.

Aspects of seasonal occurrence and the influence of host age, length and sex were discussed.

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CHAPTER VII

THE DIGENEAN PARASITES OF PERCH (Perca fluviatilis L.) FROM

LLYN TEGID

INTRODUCTION

Four species of digeneans were found parasitic in perch at

Llyn Tegid. There was a single species of adult digenean (Bunodera

luciopercae), along with three species of metacercariae (Diplostomum

gasterostei, D. spathaceum and Tetracotyle sp.).

VII.1. Family Diplostomatidae Poirier, 1886

Diplostomum gasterostei Williams, 1966

Diplostomum spathaceum (Rud., 1819)

VII.1.1   INTRODUCTION

Diplostomulum metacercariae of the family Diplostomatidae

reach maturity in the intestines of birds, chiefly members of the

Laridae (gulls) (Sweeting, 1971b). A lymnaeid snail is the host

to the polyembryonic stages, and the second intermediate host is

normally a freshwater fish, less often an amphibian.

Kennedy (1974) has reviewed the occurrence of Diplostomulum

metacercariae in the freshwater fish of the British Isles. Diplostomum

gasterostei, D. petromyzi-fluviatilis, D. phoxini, D. spathaceum, D.

truttae, and Diplostomum sp. have all been recorded, along with

Tylodelphys clavata and T. podicipina. In addition, Sweeting (1971a)

suggested the presence of a new species of Tylodelphys from the British

Isles, noting that a similar form occurred in Lake Ladoga (U.S.S.R.).

D. gasterostei was first described from the retina of the eye

of stickleback (Gasterosteus aculeatus) by Williams (1966a), and

this parasite is discussed at greater length in later sections.

D. petromyzi-fluviatilis was originally described from Europe

by Diesing (1850), and from the British Isles by Brown (1899). Sweeting

(1976) has experimentally demonstrated the life cycle. Metacercariae

were recovered from the central nervous system of lamprey (Lampetra

fluviatilis) from the River Ure (Yorkshire). Adult parasites were

obtained by the feeding of metacercariae to immunosuppressed ducks

(Anas platyrhynchus). Miracidia from the eggs in the faeces of

infected ducks were used successfully in the infection of a molluscan

intermediate host, Bithynia tentaculata (Sweeting, 1976).

Rees (1955) examined the adult and diplostomulum stage of D.

phoxini, and experimentally demonstrated part of the life cycle.

D. phoxini metacercariae in the brain of infected minnows (Phoxinus

phoxinus) were fed to domestic ducks, and adult parasites recovered.

Rees (1957) described the furcocercaria of D. phoxini from Lymnaea

pereger, and experimentally infected minnows. Fully developed D.

phoxini metacercariae were obtained 28 days after entering the fish

(Rees, 1957).

The life cycle of D. spathaceum is well known (Ginetsinskaya,

1958). Birds become infected by feeding on fish harbouring the

metacercaria. Eggs leave the avian definitive host, hatch in water,

and the miracidia may infect a range of freshwater snails, including

Lymnaea stagnalis, L. palustris, L. ovata, L. auricularia and L.

pereger (Styczynska-Jurewicz, 1959). Within the mollusc, sporocysts

give rise to furcocercariae termed Cercaria C (Szidat, 1924; Canning

et al., 1973). These cercariae possess two pairs of penetration glands

posterior to the ventral sucker, where ducts run anteriorly and dis-

charge their contents through apertures in the oral sucker. It would

appear that the products of these glands are lubricants or adhesive

secretions rather than lytic in their action (Erasmus, 1958,1972;

Canning et al., 1973). Haas (1969, 1974a, b, 1975) has studied the

behaviour of Cercaria C, and investigated the attachment, penetration

and chemical invasion stimuli. Erasmus (1958, 1959) studied the

morphology, biology and development of the closely related Cercaria

X, with particular reference to its penetration and migration with

the piscine intermediate host.

Once inside the fish strigeoid cercariae actively migrate to

their preferred site of development. However, there is some degree

of controversy over the route of migration. Davis (1936), Ferguson

(1943) and Johnston (1971) have found that the bloodstream is the most

important route, while Erasmus (1959) and Ratanarat-Brockelman

(1974) have found that the connective tissue and muscles are the

most important route. The factors to which the larvae orientate

within the fish body are not known, though Ferguson (1943) suggested

that in the case of eye-flukes they may be associated with eye tissues.

Several arguments have been put forward in favour of the bloodstream

route of migration (Betterton, 1974). There is an agreed non-random

migration of the cercariae (Ferguson, 1943; Erasmus, 1959; Johnson,

1971), and it is difficult to conceive an anterior-posterior gradient

to which the cercariae could orientate within the connective tissues

(Betterton, 1974). The involvement of the circulatory system would

provide passage to the head region, where the heart and large blood

vessels are situated. Betterton (1974) observed that the penetrating

cercariae of D. spathaceum followed the path of least mechanical

resistance, and the bloodstream is the known route of other tissue

penetrating helminths (e.g. hookworms, schistosomes) (Chandler and

Read, 1961). Betterton considered that these arguments, along with the

observations of considerable numbers of cercariae in the hearts of

infected fish, strongly indicated that the blood stream is an important

route of migration of these parasites.

The host specificity of D. spathaceum to its piscine intermediate

hosts is discussed later. The life cycle of D. spathaceum has been

followed in the brackish waters of the Baltic Sea by Cichowlas (1961).

The first intermediate host was Radix ovata var. baltica, and meta-

cercariae were found in a variety of fish. The definitive host was

the gull (Larus ridibundus). Dartnall et al. (1972) have recorded

D. spathaceum from stickleback at brackish water sites in the Norfolk

Broads. In addition, Dartnall (1972, 1973) has studied the parasites

of the stickleback and the nine-spined stickleback (Pungitius pungitius)

from several localities in the British ᴵsles, and found that D. spathaceum may occur in both fresh and brackish water environments.

Lal (1953) described D. truttae sp. from the vitreous humour of brown trout (Salmo trutta) in Scotland and undetermined species of Diplostomum have been recorded from the fish of the British Isles on a number of occasions, (Kennedy, 1974).

The in vitro cultivation of D. spathaceum metacercariae to egg production was achieved for the first time by Kannangra & Smyth (1974), who also achieved an improved vitelline and growth response in D. phoxini. The structure and function of the adhesive organs in D. phoxini and D. spathaceum has been studied by Lee (1962) and Ohman (1965) respectively, and Erasmus (1972) summarised the available information on this subject.

The pathogenic nature of the Diplostomum infection of fish has been noted by many authors, including Davis (1936), Rushton (1937, 1938), Baylis (1939), Ferguson (1943), Dawes (1952), Bauer (1958, 1959), Ginetskaya (1958), Kozicka (1958), Erasmus (1959), Styczynska-Jurewicz (1959), Bauer et al. (1964, 1969), Larson (1964, 1965), Haen & Ryan (1967), Williams (1967), Ashton et al. (1969), Sweeting (1971a, b), Hoffman (1973), Oun & Sirak (1973) and Molnar (1974).

Cort et al. (1960a, b) and Shigina (1971, 1972) have recorded the infection of strigeoid trematode larval stages with microsporidian (Protozoa) hyper-parasites. Shigina (1971, 1972) noted the marked pathogenic effects of Nosema sp. on the metacercariae of D. spathaceum. Dissanaike (1957) reviewed the occurrence of protozoan hyper-parasites of helminths (i.e. Trematoda, Cestoda, Nematoda, Acanthocephala). In comparison Dubinina (1956) and Chiriac et al. (1975) have recorded Tetracotyle sp. metacercariae hyper-parasitic within ligulid (Cestoda) plerocercoids.

The biology and taxonomy of Tylodelphys clavata and T. podicipina has received the detailed attention of Kozicka and Niewiadomska (1960a, b) and Niewiadomska (1960, 1963a, b). Other studies from continental Europe

include Maksimova (1958), Kozicka (1958), Rauckis (1970a, b), Wierzbicki
(1970), Tell (1971) and Lucky (1973). T. clavata and T. podicipina
have been studied in the British Isles by Sweeting (1971a, b), Wootten
(1974), Kennedy (1975) and Sweeting & Powell (1977).

Relevant studies on the larval trematode infestations of British
freshwater molluscs have included Harper (1929), Rees (1932), Isles
(1960), Nasir and Erasmus (1964), Probert and Erasmus (1965), Probert
(1966) and Williams (1966b).

VII.1.2   ADDITIONAL MATERIALS AND METHODS

Routine field samples

The routine examination of perch for parasites was described
in Chapter II. Prior to examination the eyes were deep frozen.
After thawing they were carefully removed and dissected in tapwater.
Parasites in the lens and the humour/retina were collected and then
fixed in A.F.A. Samples of these were stained in Borax Carmine or
Delafields Haematoxylin.

Preparation and examination of material for taxonomic study

Samples of perch were collected from Llyn Tegid, killed at the
lakeside and taken to Liverpool in chilled, insulated boxes. They
were stored overnight in a refrigerator at 4-5°C. The following day
the fish were examined for metacercarial infestations of the eye.
Live parasites were collected in 0.85% sodium chloride solution (saline),
and examined in a compressorium at low and high power. Particular
attention was paid to the protonephidial and paranephidial parts of
the excretory system. The flame cells of the protonephridial system
were often more clearly visible after storing the parasites for 1-2
days in saline at 4-5°C.

Samples of living metacercariae were also killed and relaxed in

hot water at 60-70°C (Slusarski, 1958; Hoffman, 1960) and fixed in

10% buffered formalin (Tinsley and Sweeting, 1974). This was not

carried out on the D. spathaceum found parasitic in perch because

of the low incidence and intensity of infection. For comparative

purposes D. gasterostei from perch at Slapton Ley (Devon) and D.

spathaceum from roach (Rutilus rutilus) at Llyn Tegid were prepared

in a similar fashion. In addition, D. gasterostei from perch at

Llyn Tegid were relaxed in 0.85% saline at 4-5°C and fixed in ice

cold buffered formalin (Tinsley and Sweeting, 1974).

These diplostomulae were later stained in Borax Carmine or

Delafields Haematoxylin, and various measurements taken as indicated

in Fig. I and Table I.

Histological determination of the site of infestation in the eye

Perch were gill netted from Llyn Tegid during 1975. The fish

were killed at the lakeside and dissected immediately. The eyes were

carefully removed intact and fixed in a good excess of formal- saline.

After 48 hours the fixative was decanted and replaced with fresh. The

eyes were then stored, and subsequently processed within 6-9 months of initial

fixation (as indicated in Appendix II). Sections were cut on a rotary

microtome at 6-10um and stained with a Modified Masson-Heidenhain stain

(Casⱡon, 1950). Photographs were taken using a Leitz photo-microscope.

VII.1.3   RESULTS

Description of Diplostomum gasterostei from perch at Llyn Tegid

The body of the metacercariae was flat, leaf-like with a concave

ventral surface. The division into large forebody and smaller hindbody

was only clearly visible in living material. There was a large adhesive

organ, and the oral and ventral suckers and lateral pseudosuckers were

all easily observed in living or preserved specimens. The gut bifurcated

Figure 1. <u>Diplostomum gasterostei</u> killed in hot water; fixed in 10% buffered formalin. Stained in Delafields Haematoxylin (x500).

L   =   total body length

W   =   width of body at widest point

A   =   distance between pharynx and ventral sucker

B   =   distance of ventral sucker from anterior end
        of body

AO =   adhesive organ

Ex =   excretory bladder

Exp =   excretory pore

G   =   branches of gut

OS =   oral sucker

Ph =   pharynx

Ps =   lateral pseudosuckers

Vs =   ventral sucker

Fig 1
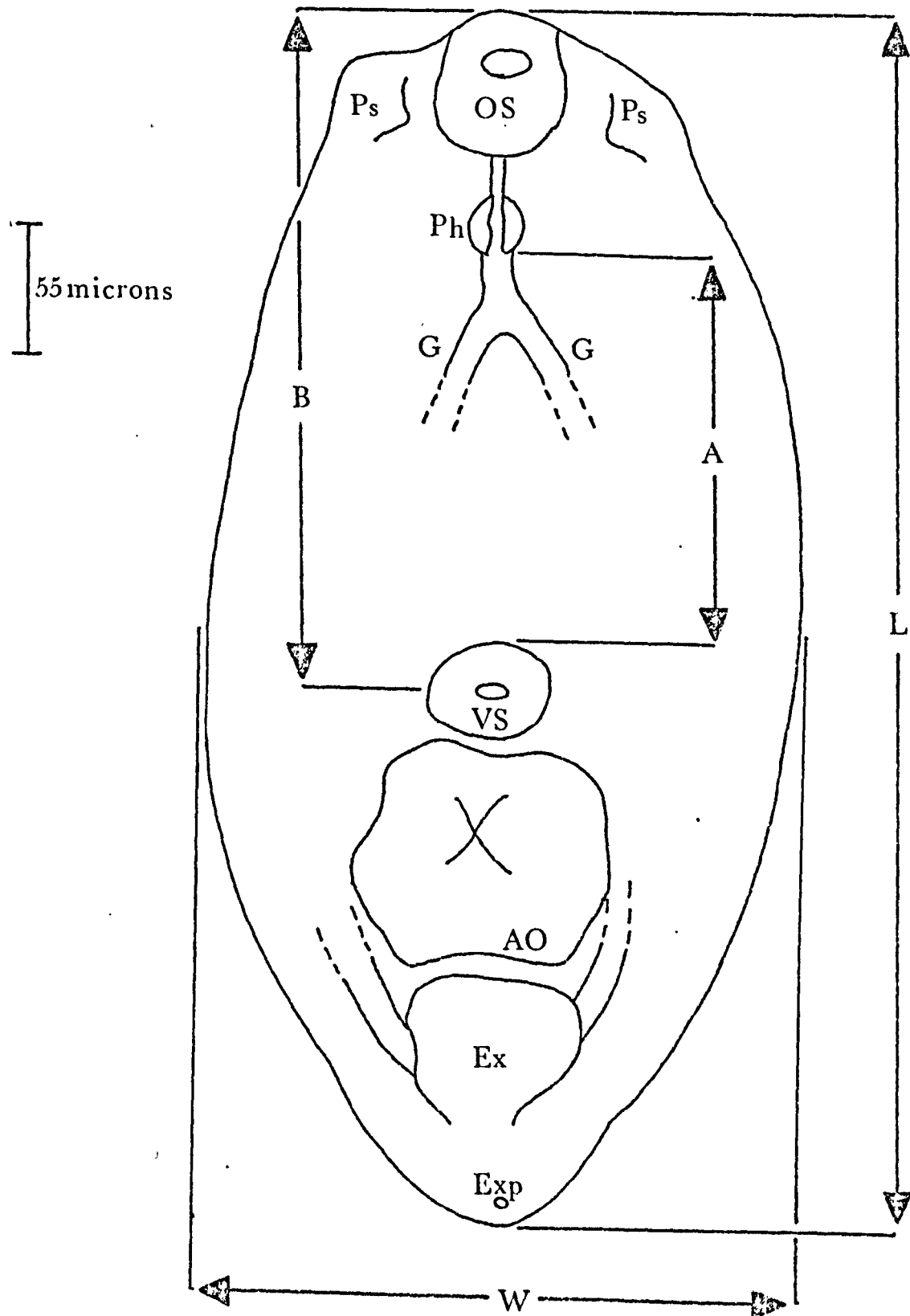
Table I. Measurements of _Diplostomum_ spp.

Diplostomum gasterostei (humour/retina of eye)

1. _Perca fluviatilis_, Llyn Tegid, June 1976. Relaxed in cold saline (4-5°C).

2. _Perca fluviatilis_, Llyn Tegid, June 1976. Killed in hot water (60-70°C).

3. _Perca fluviatilis_, Slapton Ley (Devon), August 1976. Killed in hot water (60-70°C).

Diplostomum spathaceum (lens of eye)

4. _Rutilus rutilus_, Llyn Tegid, June 1976. Killed in hot water (60-70°C).

N.B. All diplostomulae were then fixed in 10% buffered formalin and stained in Borax Carmine (or Delafields Haematoxylin).

See Fig. I for details of measurements taken.

Table I. Measurements of _Diplostomum_

Measurements (all in um)			_Diplostomum gasterostei_			_D. spathaceum_
			1	2	3	
BODY:	length (L),	maximum	480um	460um	600um	480um
		minimum	380	340	440	360
		mean of 10	424	423	495	415
	width (W),	maximum	240	270	280	220
		minimum	180	190	220	180
		mean of 10	217	222	240	193
ORAL SUCKER:	length,	maximum	-	60	55	50
		minimum	-	45	45	45
		mean of 10	-	52	50	46
	width,	maximum	-	55	45	55
		minimum	-	40	40	40
		mean of 10	-	45	43	45
VENTRAL SUCKER:	length,	maximum	40	40	50	45
		minimum	25	35	35	20
		mean of 10	39	37	41	37
	width,	maximum	45	55	55	45
		minimum	30	35	35	25
		mean of 10	40	44	46	40
PHARYNX:	length,	maximum	-	55	50	35
		minimum	-	35	35	30
		mean of 10	-	43	41	33
	width,	maximum	-	30	25	20
		minimum	-	15	20	15
		mean of 10	-	20	21	19
ADHESIVE ORGAN:	length,	maximum	100	100	115	80
		minimum	60	40	75	60
		mean of 10	77	76	94	68
	width,	maximum	85	95	120	95
		minimum	65	70	80	45
		mean of 10	79	89	94	65
Pharynx to ventral sucker (A)		maximum	160	135	175	200
		minimum	110	85	90	125
		mean of 10	130	115	135	162
Anterior end to ventral sucker (B)		maximum	260	260	300	300
		minimum	195	190	230	215
		mean of 10	222	225	248	264
Ratio $(B/L) \times 100$,		maximum (%)	55.0	59.1	57.7	68.3
		minimum (%)	47.7	47.8	41.7	59.7
		mean of 10(%)	52.4	53.4	52.3	63.8

just posterior to the pharynx and each caecum extended to beyond the anterior edge of the excretory bladder. The gut often contained dark granules, which may have been ingested retinal tissue. There was a large excretory bladder posterior to the adhesive organ, and the excretory pore was situated at the distal end of the hindbody.

The paranephridial excretory system was clearly visible in living metacercaria. There were large numbers of spherical or smoothly irregular calcareous corpuscles. They measured less than 15um in diameter. The average number of calcareous corpuscles in 10 specimens was 498 (maximum 702, minimum 332). Their distribution varied, but they were usually most abundant over the forebody region between the pharynx and the ventral sucker. Within this region they formed a broad band across the body, which extended posteriorly in the lateral areas of the parasite (see Plate 1). The flame cells of the protonephridial excretory system were only visible in living material, and often could not be studied for long periods in the same specimen. There appeared to be between 30-50 pairs of flame cells, which were particularly abundant in the posterior half of the forebody, in the region of the adhesive organ.

When D. gasterostei metacercariae from perch at Llyn Tegid were either relaxed in cold saline or killed in hot water (prior to fixation), there resulted no major differences in the body measurements (Table I). In both instances the ventral sucker was situated equatorically, approximately half way along the ventral surface of the parasite (Table I, (B/L) x 100).

Site of infection in perch at Llyn Tegid.

Routine dissection suggested that the metacercariae of D. gasterostei may be present in the vitreous humour and retina of the perch eye. However, the histological examination of a small number of perch eyes demonstrated the presence of these parasites only in the pigment layer of the retina

(Plate 3 2). The metacercariae were not encysted or enclosed within a host reaction of any kind. Until further histological studies are made, it is assumed that the parasite may occur in the humour and retina of perch at Llyn Tegid.

Comparative morphology of D. gasterostei from perch at Llyn Tegid and Slapton Ley, and D. spathaceum from roach at Llyn Tegid.

The similarity of the morphology of D. gasterostei from perch at Llyn Tegid prepared by two methods has been noted. When D. gasterostei from perch at Llyn Tegid was compared to D. spathaceum infecting roach, it can be seen that the two metacercariae were very similar (Table I). However, the adhesive organ and pharynx of D. gasterostei was found to be larger than that of D. spathaceum. In addition, the ventral sucker of the latter species was consistently situated at a position posterior to that observed in D. gasterostei. This is illustrated in Table I, when the position of the ventral sucker is expressed as a percentage of the total body length ((^{B}/L) x 100).

The number and distribution of the calcareous corpuscles was distinctly different in D. gasterostei from perch at Llyn Tegid, when compared to that of D. spathaceum from roach. There were invariably more calcareous corpuscles in D. gasterostei, and they were more widely distributed in the body (Plates 1 and 2).

The material of D. gasterostei from perch at Slapton Ley was larger than that from perch at Llyn Tegid (Table I). Whilst the adhesive organ was larger in the specimens from Slapton Ley, the oral and ventral suckers and pharynx measurements were similar. The ventral sucker was situated in a position similar to the specimens of D. gasterostei examined from Llyn Tegid (Table I).

PLATES

<u>Diplostomum gasterostei</u> and <u>Diplostomum spathaceum</u>

<u>Plate I</u>
<u>Diplostomum gasterostei</u>
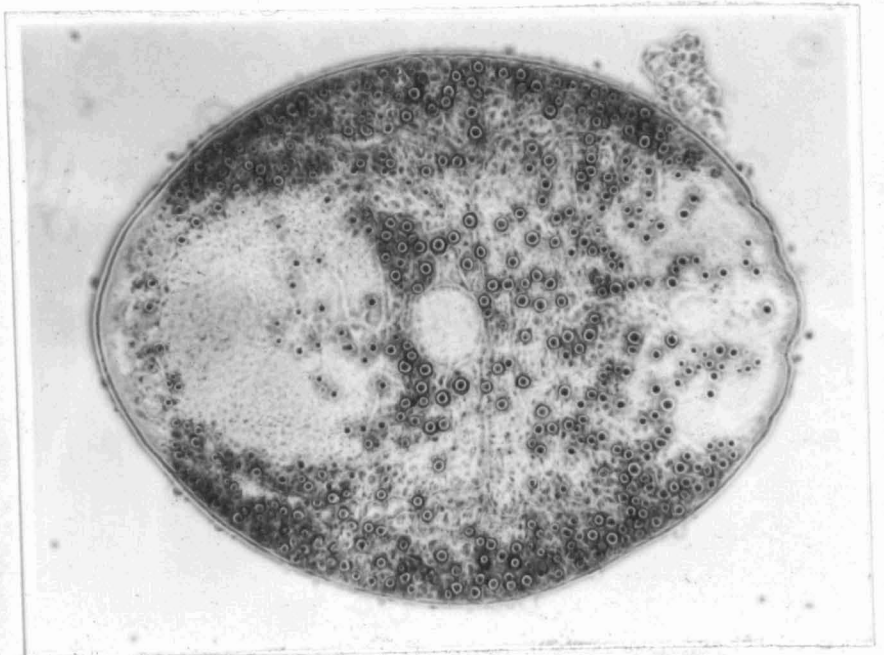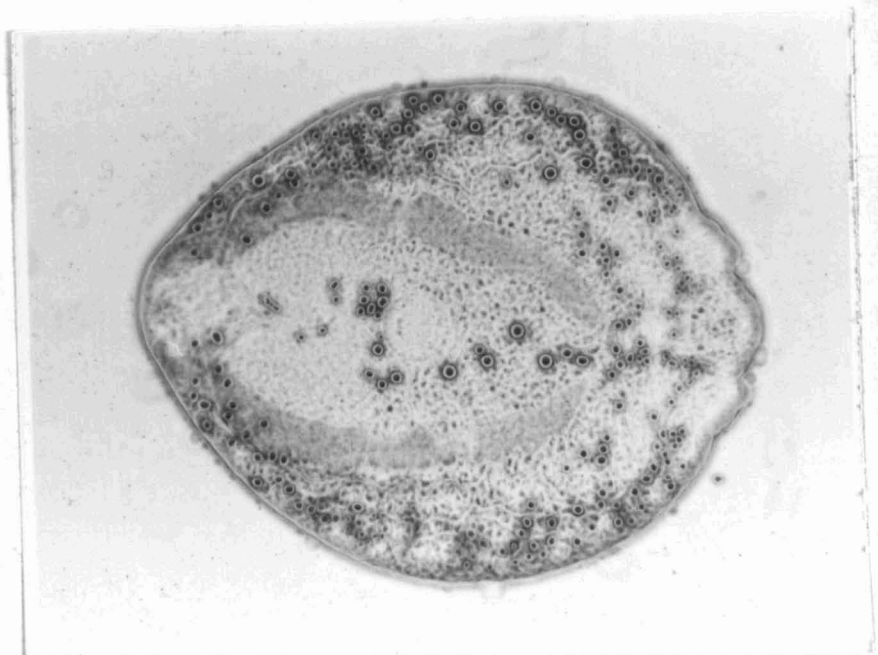Perch humour/retina
Llyn Tegid

<u>Plate 2</u>
<u>Diplostomum spathaceum</u>
Perch eye lens
Princes Park, Merseyside

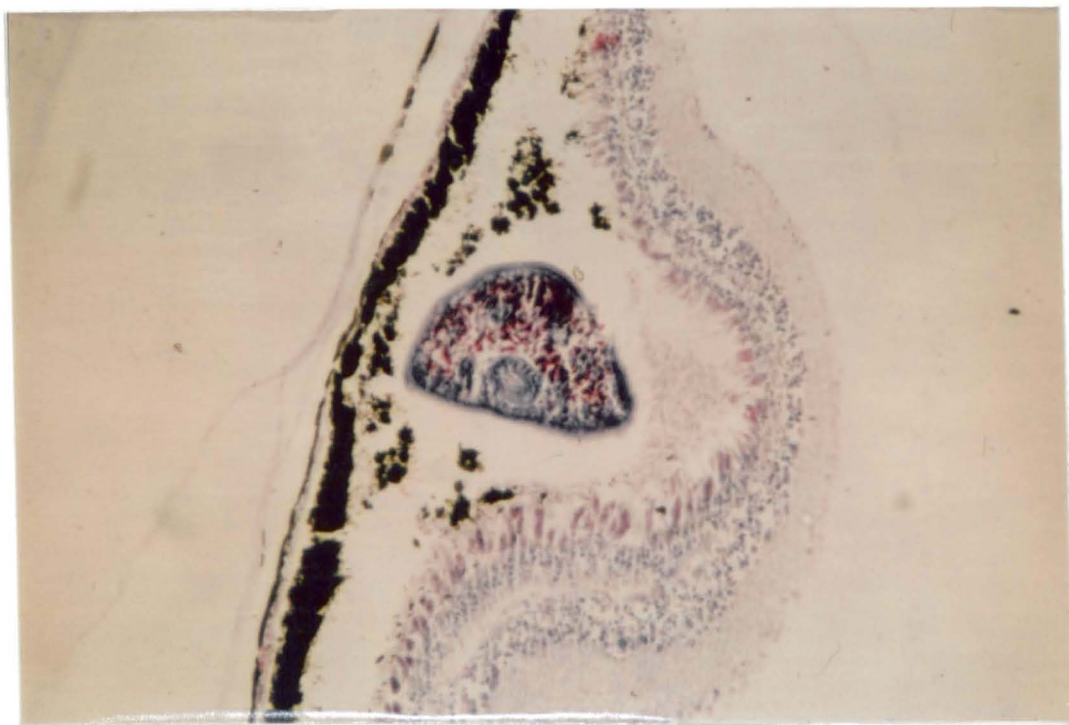Photographed live in 0.85% saline, under a compressorium
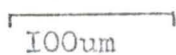
Scale ├────┤
100um

PLATES (cont.)

Plate 3

Site of infestation of Diplostomum gasterostei

Perch, Llyn Tegid

Fixed in Formal-saline, stained with Modified Masson-Heidenhain (Casson,
1950)

Scale   ┌─────────┐
              100um

Identification of D. spathaceum from perch at Llyn Tegid.

The incidence and intensity of infection of perch at Llyn Tegid with D. spathaceum was very low. Consequently it was very difficult to obtain reasonable amounts of material. However, the metacercariae from the lens of perch were identified on the following points.

1. Site of infestation - lens.

2. Position of ventral sucker in frozen, fixed and stained material, and in living material. The ventral sucker was invariably situated in a position posterior to that seen in D. gasterostei from the humour/retina of perch prepared in a similar manner.

3. Distribution and abundance of calcareous corpuscles. In the metacercariae that infested the lens of the eye of perch at Llyn Tegid, the distribution and abundance of the calcareous corpuscles was similar to that seen in D. spathaceum from the lens of roach, yet different to that seen in D. gasterostei from the humour/retina of perch (Plates 1 and 2).

Field studies on the Diplostomum spathaceum infection of perch at Llyn Tegid.

A total of 11 metacercariae were removed from the eye lens of 8 of 465 (1.7%)adult perch that were gill netted from Llyn Tegid between January 1975-February 1976. The mean intensity/infected fish was 1.4 (maximum 2). The results are summarised in Table II.

No metacercariae were found in the lens of the perch that were trawled in March 1976, or purse seined in July 1976.

Seasonal aspects of the Diplostomum spathaceum infection

From Table II it is apparent that D. spathaceum may occur in adult perch at all times of the year.

Table II. Infection with <u>Diplostomum spathaceum</u>. Gill net samples. January 1975 - February 1976.

MONTH		HOST DATA:			NUMBER:	
	SEX	AGE(yrs.)	LENGTH(cm)	<u>D. spathaceum</u>	<u>D. gasterostei</u>
FEB. 1975	F	3++	12.0	2	40
	F	3++	13.0	1	50
JUNE 1975	M	6+	13.5	1	15
	M	3+	13.0	1	67
AUG. 1975	M	4+	13.0	2	28
SEPT. 1975	M	5+	13.2	2	67
OCT. 1975	M	4+	12.1	1	14
JAN. 1976	M	3++	13.0	1	26
TOTAL	6M:2F	-	-	11	-

TOTAL NUMBER FISH 465

NB.   M = Male

       F = Female

Table III.   Seasonal aspects of the _Diplostomum gasterostei_ infection.
Gill net samples.   January 1975 - February 1976.

Month	No. fish examined	No. fish infected	% incidence	No. parasites	mean no./ fish	Maximum
J	6	6	100.0	155	25.8	51
F	30	30	100.0	1016	33.9	81
M	30	30	100.0	899	29.9	159
A	30	30	100.0	743	24.8	60
M	30	30	100.0	548	18.3	59
J	39	39	100.0	1371	35.2	90
J	40	40	100.0	1148	28.2	83
A	30	29	96.7	1055	35.2	135
S	30	30	100.0	852	28.4	74
O	60	60	100.0	1445	24.1	104
N	54	54	100.0	1385	25.6	99
D	35	35	100.0	898	25.7	119
J	30	30	100.0	666	22.2	74
F	21	20	95.2	429	20.4	84
TOTAL	465	463	99.6	12610	27.3	159

Table IV. Effect of host age and length on the _Diplostomum gasterostei_ infection. Trawl sample. March 1976.

Age (yrs.)	Length (cm)	No. fish examined	% incidence	Total no. parasites	Mean/fish	Maximum	Variance
0++	3.0 - 8.9	36	75.0	88	2.4(3.3)	12	6.65
1++ 4++	9.0 - 11.9	28	100.0	426	15.2(15.2)	40	82.17
TOTAL		64	85.9	514	8.0(9.3)	40	-

N.B. Figures in parentheses are mean intensity/infected fish

Table V. Effect of host age on the _Diplostomum gasterostei_ infection Male perch. Gill net samples. January 1975-February 1976.

Age (yrs.)	No. fish examined	% incidence	Total no. parasites	Mean/fish	Maximum	Variance
2-2++	2	100.0	51	25.5	32	-
3-3++	51	98.0	1133	22.1	67	255.21
4-4++	66	100.0	1691	25.6	119	417.34
5-5++	40	100.0	1206	30.2	77	373.77
≥ 6	24	100.0	1121	46.7	159	1841.26
TOTAL	183	99.5	5202	28.4	159	-

Table VI. Effect of host age on the <u>Diplostomum gasterostei</u> infection.

Female perch. Gill net samples. January 1975-February 1976.

Age (yrs.)	No. fish examined	% incidence	Total no. parasites	Mean/fish	Maximum	Variance
2-2++	2	100.0	35	17.5	75	-
3-3++	87	100.0	2028	23.3	74	246.45
4-4++	98	100.0	2552	26.0	104	376.72
5-5++	38	100.0	1068	28.1	99	568.04
≥6	57	98.2	1725	30.3	100	531.16
TOTAL	282	99.6	7408	26.3	104	-

Table VII. Effect of host length on the <u>Diplostomum gasterostei</u> infection

Male perch. Gill net samples. January 1975-February 1976.

Length (cm)	No. fish examined	% incidence	Total no. parasites	Mean/fish	Maximum	Variance
9.0-11.9	43	97.7	1004	23.3	118	399.83
12.0-14.9	124	100.0	3462	27.9	119	464.47
15.0-17.9	13	100.0	570	43.8	159	1535.39
≥18.0	3	100.0	166	53.3	135	-
TOTAL	183	99.5	5202	28.4	159	-

Table VIII. Effect of host length on the Diplostomum gasterostei

infection. Female perch. Gill net samples. January

1975—February 1976.

Length (cm)	No. fish examined	% incidence	Total no. parasites	Mean/fish	Maximum	Variance
9.0– 11.9	13	100.0	250	19.2	41	146.30
12.0– 14.9	197	100.0	4737	24.0	83	250.05
15.0– 17.9	46	100.0	1510	32.8	99	764.44
≥18.0	26	96.2	911	36.4	104	737.50
TOTAL	282	99.6	7408	26.3	104	–

Table IX. Effect of Diplostomum gasterostei on the growth of O++

perch. Trawl sample. March 1976.

	Mean length (cm)
Uninfected fish	5.41 ± 0.31 (9)
Infected fish	5.42 ± 0.29 (27)
Total number of fish 36	

N.B. Mean length ± 95% confience limits. Figures in parentheses are

number of fish examined.

Effect of host age, length and sex on the <u>Diplostomum spathaceum</u> infection.

The absence of <u>D. spathaceum</u> from purse seined fry (aged 4-6 weeks, mean length 2.3 cm, maximum 2.7 cm), and trawled fish aged 8-9 months (length 3.0-8.9 cm) may be a reflection on the low incidence of this parasite and the small sample sizes examined. In the adult fish that were gill netted it appeared that perch of all ages may be infected (Table II). However, there were no infected perch larger than 13.5 cm, though this may again be a result of the low incidence of the parasite in relation to sample size. No heavily infected fish were found.

Six male and two female perch from the gill nets were infected. Whilst a greater number of female fish were caught by this method, the greater number of infected male fish is not thought to be significant.

Field studies on the <u>Diplostomum gasterostei</u> infection of perch at Llyn Tegid.

Of 465 adult perch caught by gill nets between January 1975-February 1976, 463 (99.6%) were infected with a total of 12610 <u>D. gasterostei</u>. The mean intensity/fish was 27.3 (maximum 159) (Table III).

Of 64 fish examined from the trawl sample in March 1976, 55 (85.9%) were infected with a total of 514 <u>D. gasterostei</u>. The mean intensity/ fish was 8.0 (maximum 40). The mean intensity/infected fish was 9.3 (Table IV).

None of the 30 perch fry examined from the purse seine in July 1976 were infected.

Effect of host age, length and sex on the <u>Diplostomum gasterostei</u> infection.

None of 30 fry (aged 4-6 weeks; mean length 2.3, maximum 2.7 cm) were infected. However, 27 of 36 (75.0%) perch aged 0++ (8-9 months; length 3.0-8.9 cm) were infected in March (1976). The majority of the infected fish (25) harboured between 1-5 metacercariae (Fig. 2). Twenty-

eight adult perch (aged 1++-4++ years; length 9.0-11.9 cm) were also examined from the same trawl sample. The incidence of D. gasterostei in these fish was 100.0%, and the intensity was also higher (Table IV, Fig. 2). More than half of these fish (19) harboured over 10 metacercariae.

The adult male and female fish from the gill net samples were treated separately. In male and female fish of all ages and sizes, the incidence of D. gasterostei was high and only rarely fell below 100.0% (Table V-VIII). Within increasing age and length the mean intensity/fish increased, reaching a peak in the oldest, largest perch (Table V-VIII).

Of 183 male fish, 182 (99.5%) were infected with a mean intensity/ fish of 28.4 (maximum 159). Of 282 female fish, 281 (99.6%) were infected with a mean intensity/fish of 26.3 (maximum 104). Therefore, the incidence and mean intensity/fish in adult male and female perch was similar (Table V and VII).

In all length and age groups of both male and female perch, the variance of the parasite counts was very much greater than the mean (Table V-VIII). The overdispersed nature of the parasite population is shown in Fig. 3-6. With increasing age and length there appeared to be a tendency for an increase in the occurrence of heavily infected male and female perch (Fig. 3-6).

Seasonal aspects of the Diplostomum gasterostei infection; effect of site of capture of perch.

From Table III there appears to be no marked seasonal fluctuations in the incidence or mean intensity/ fish, and heavily infected fish were caught in most months. The results in Table III represent the monthly totals of fish caught from between one to four sites in Llyn Tegid. Sufficient numbers of perch were not examined to treat the infection at each site separately (see Chapter III).
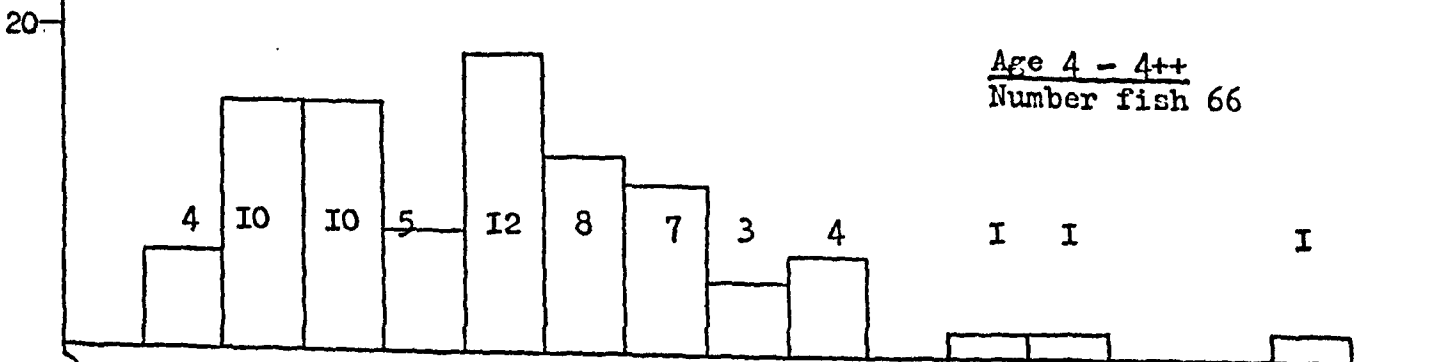
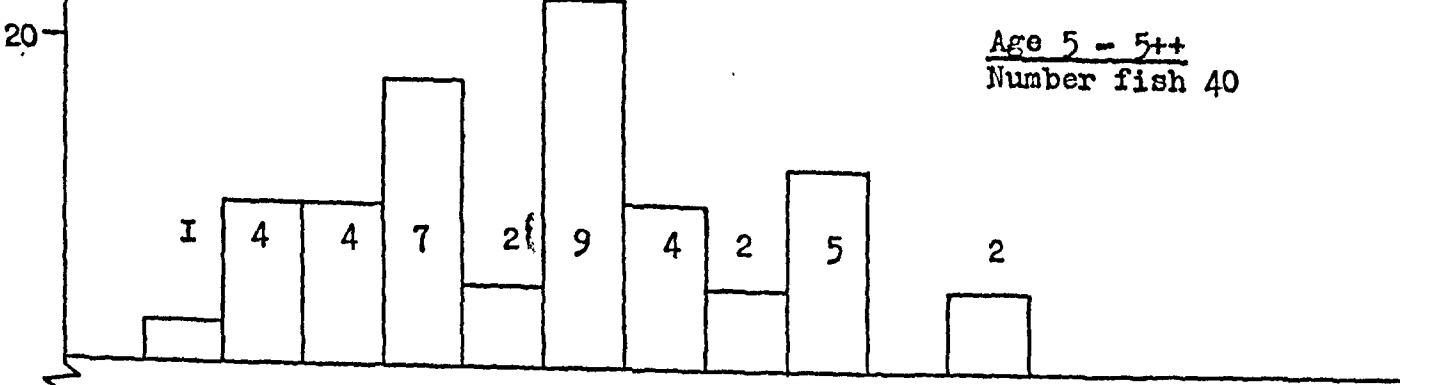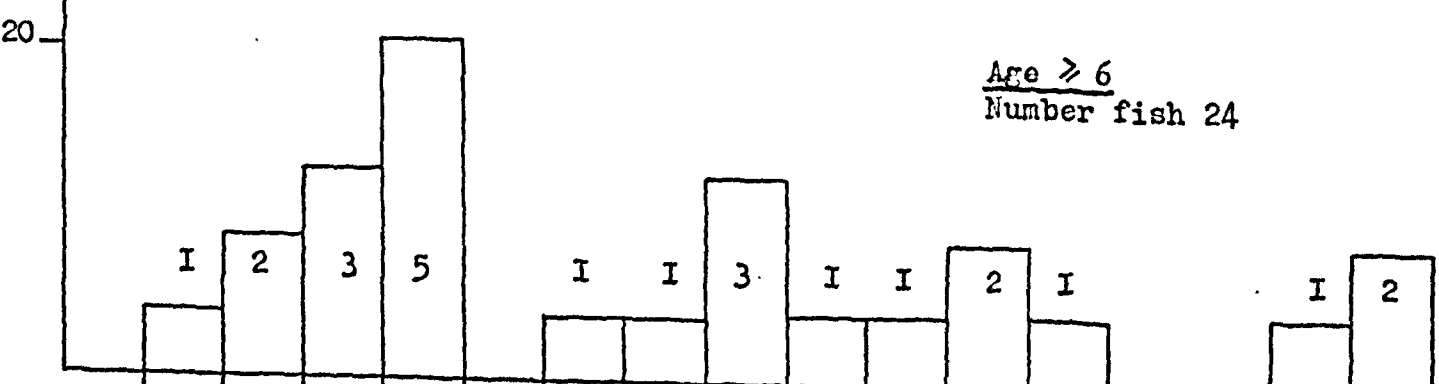Fig. 2. Frequency distribution _Diplostomum gasterostei._
Trawl sample. March 1976
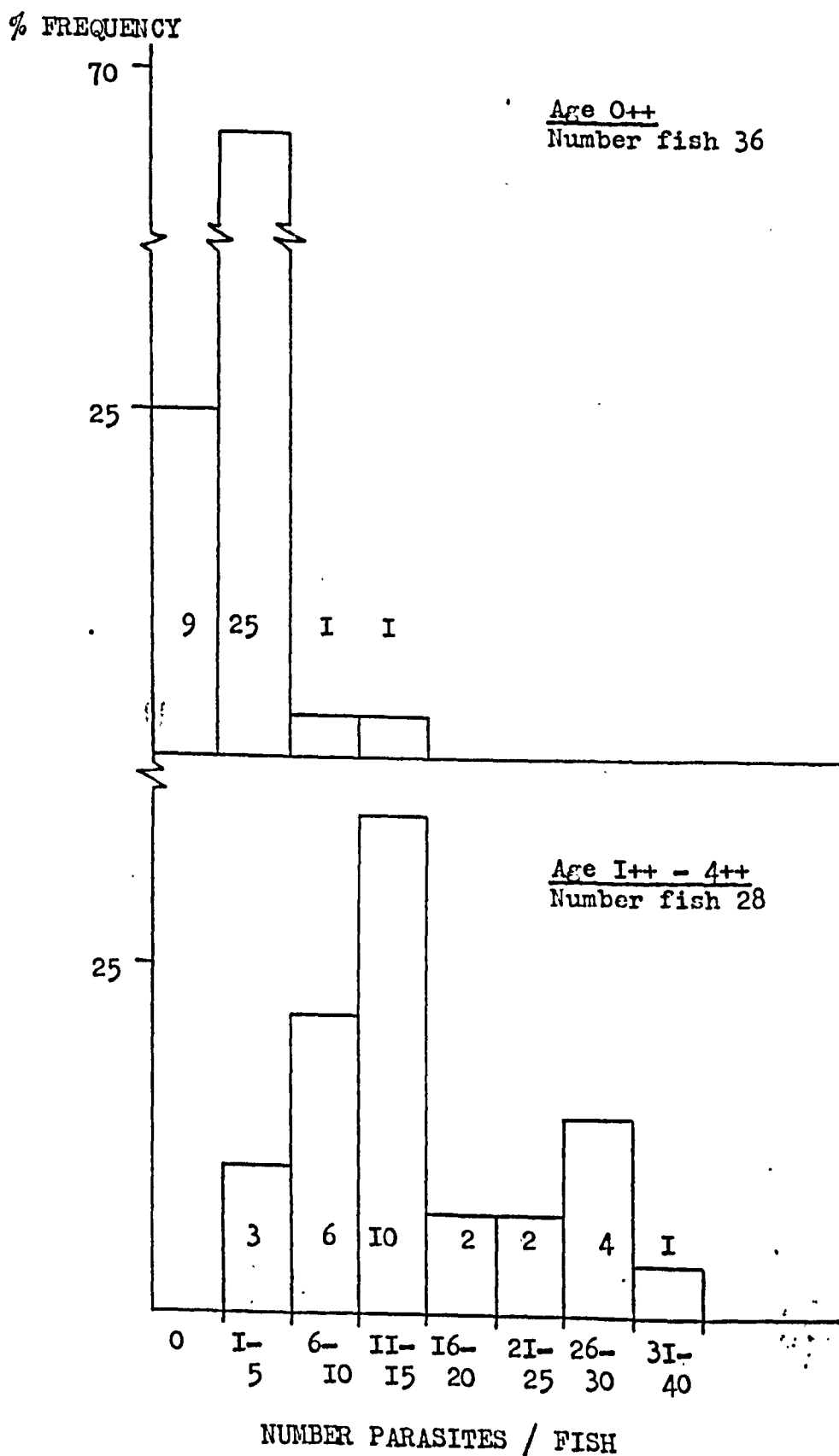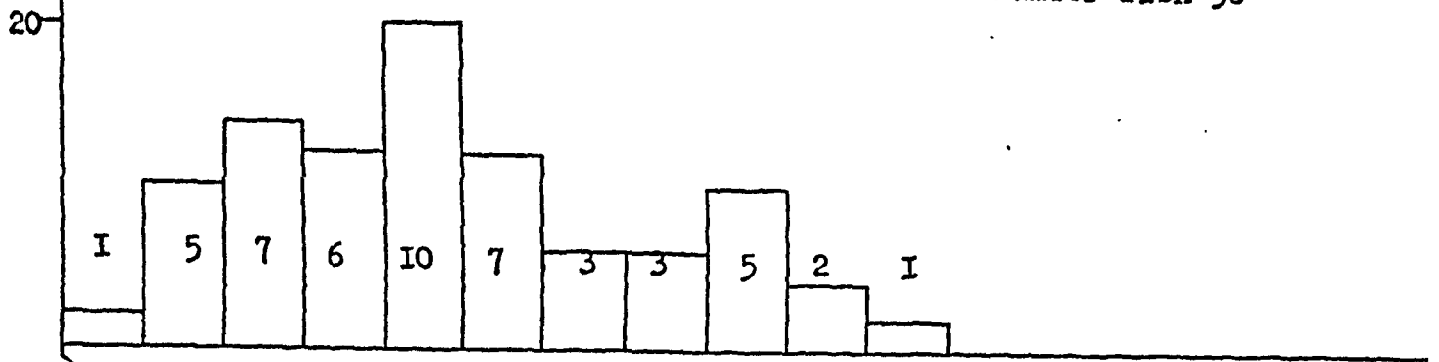
% FREQUENCY

Age 0++
Number fish 36

Age I++ - 4++
Number fish 28

NUMBER PARASITES / FISH

Fig. 3. Effect of host age on frequency distribution of _Diplostomum_ _gasterostei_. Male perch. Gill net samples. January 1975 - February 1976
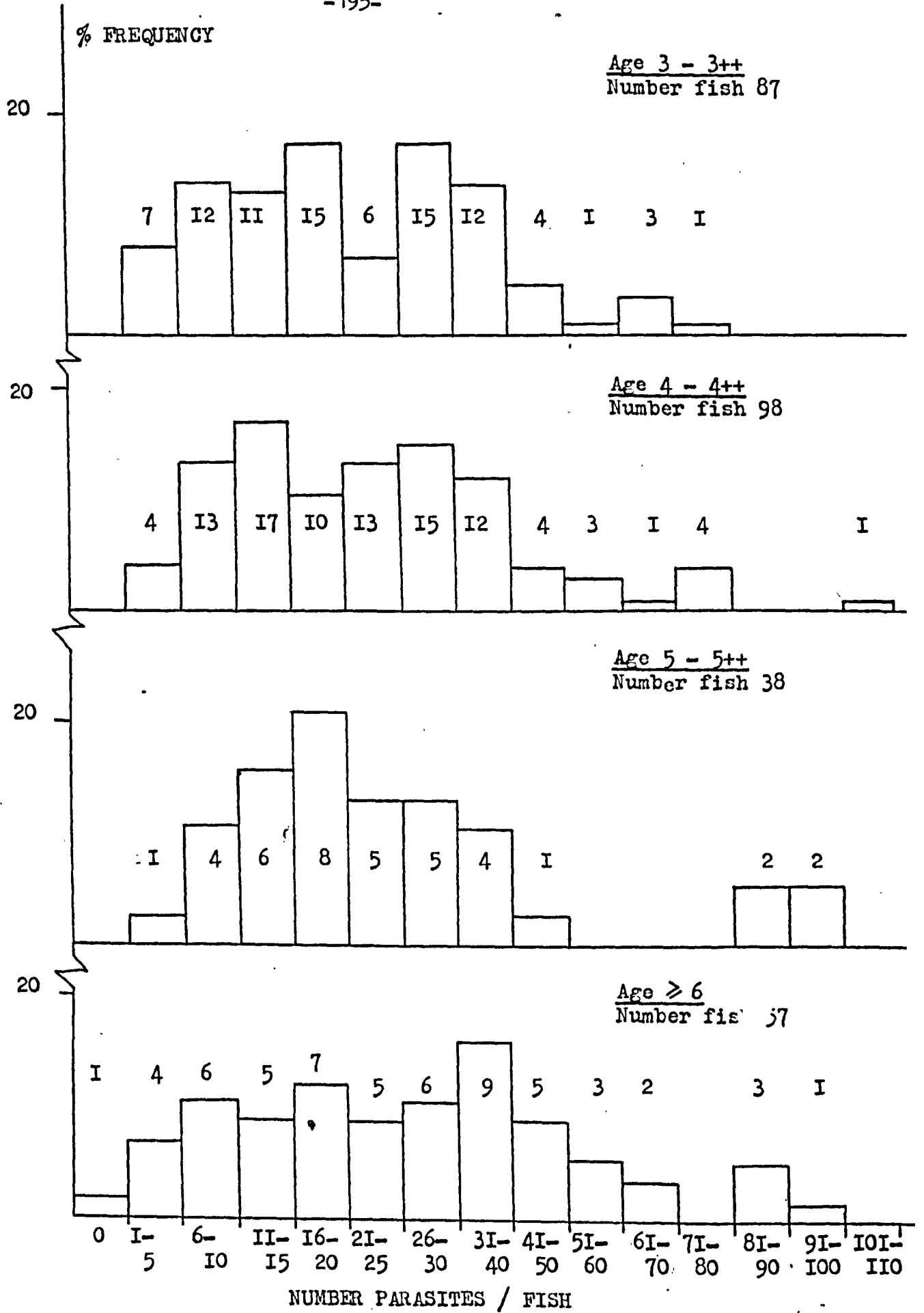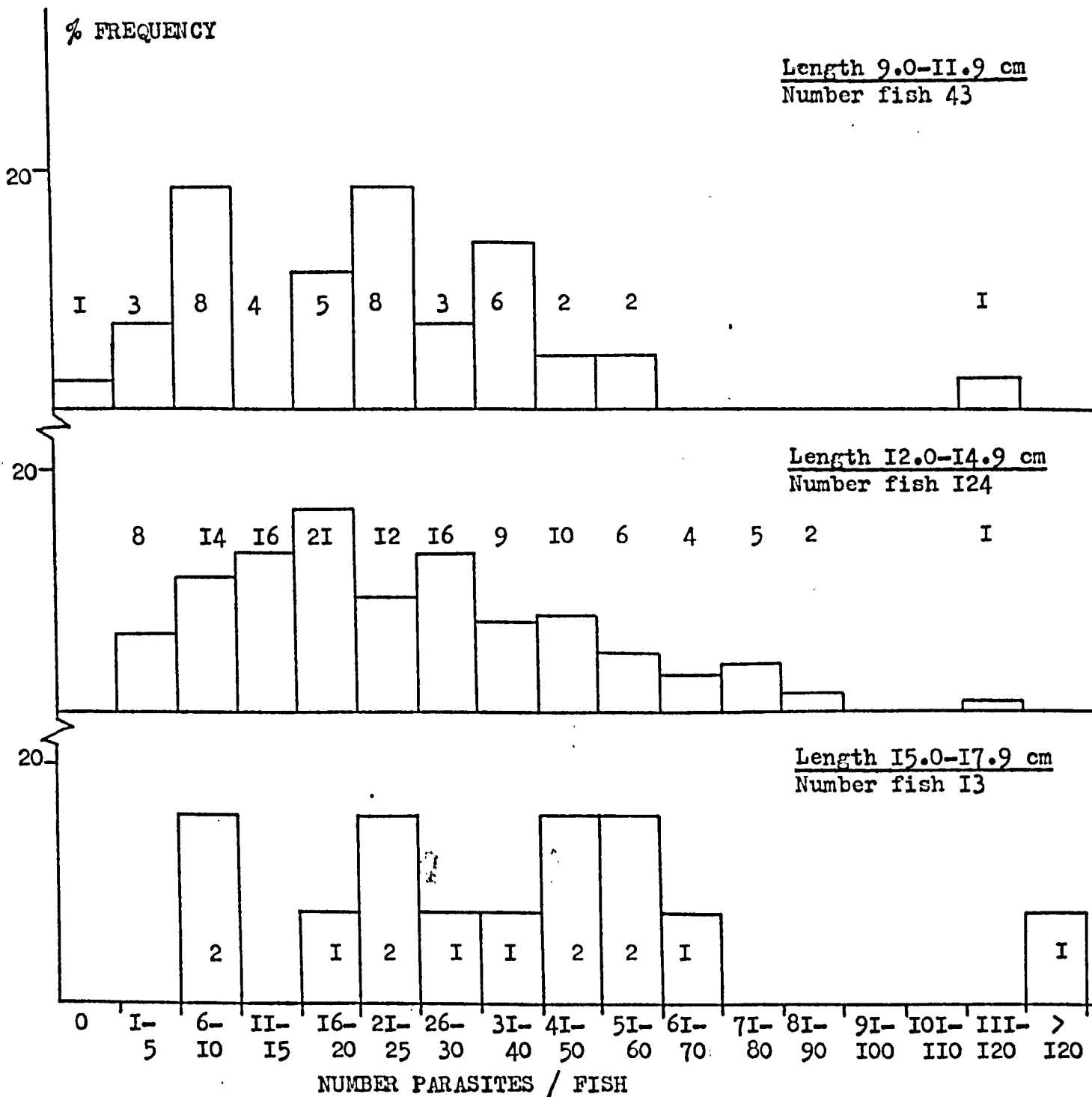
% FREQUENCY

Age 3 - 3++
Number fish 87

7 I2 II I5 6 I5 I2 4 I 3 I

20

Age 4 - 4++
Number fish 98

20

4 I3 I7 I0 I3 I5 I2 4 3 I 4 I

Age 5 - 5++
Number fish 38

20

·I 4 6 8 5 5 4 I 2 2

Age ⩾ 6
Number fis⸱ ⸴7

20

I 4 6 5 7 5 6 9 5 3 2 3 I

| 0 | I-5 | 6-10 | II-15 | I6-20 | 2I-25 | 26-30 | 3I-40 | 4I-50 | 5I-60 | 6I-70 | 7I-80 | 8I-90 | 9I-100 | I0I-110 |

NUMBER PARASITES / FISH

Fig. 4. Effect of host age on the frequency distribution of Diplostomum
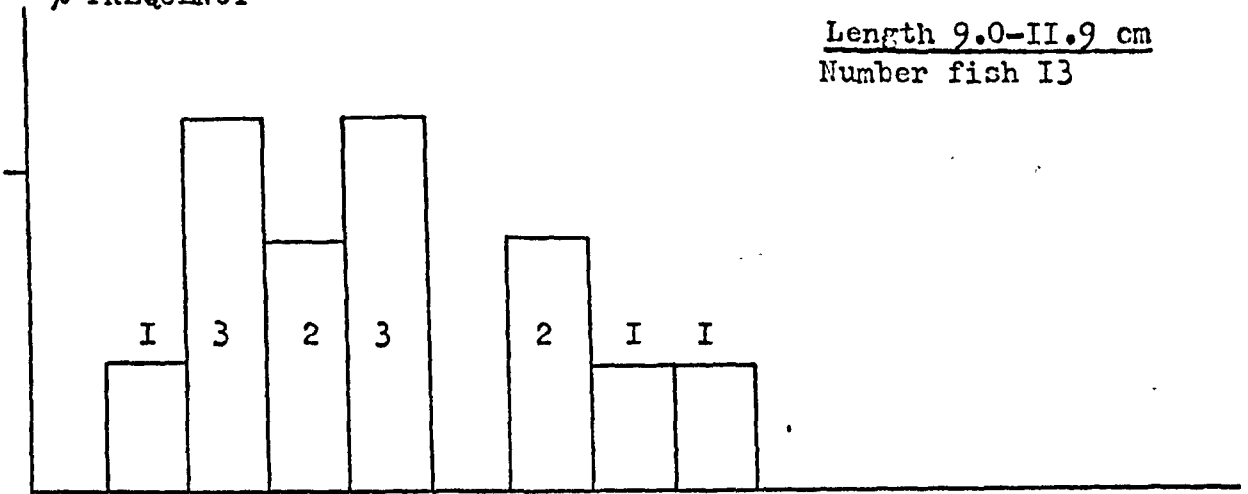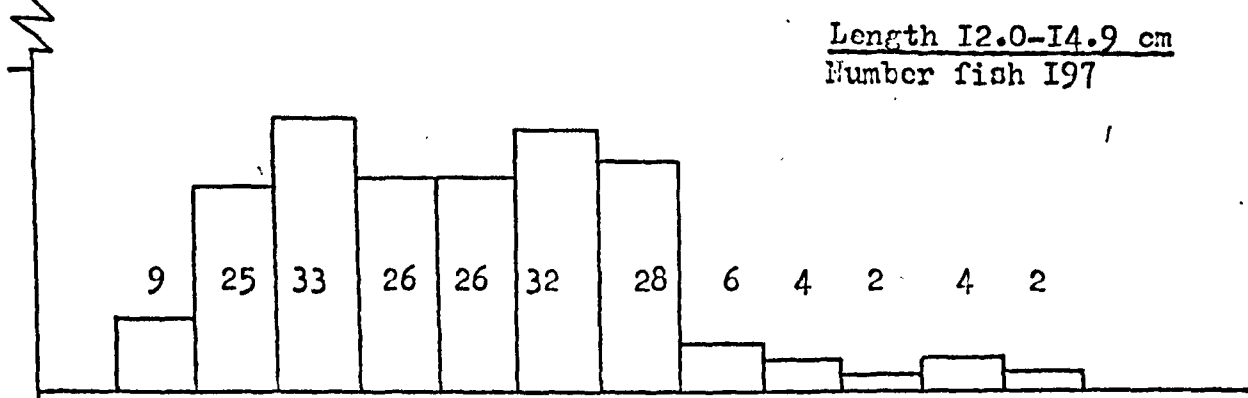gasterostei. Male perch. Gill net samples. January 1975 -
February 1976.

Fig. 5. Effect of host length on the frequency distribution of Diplostomum gasterostei. Male perch. Gill net samples. January 1975 - February 1976.
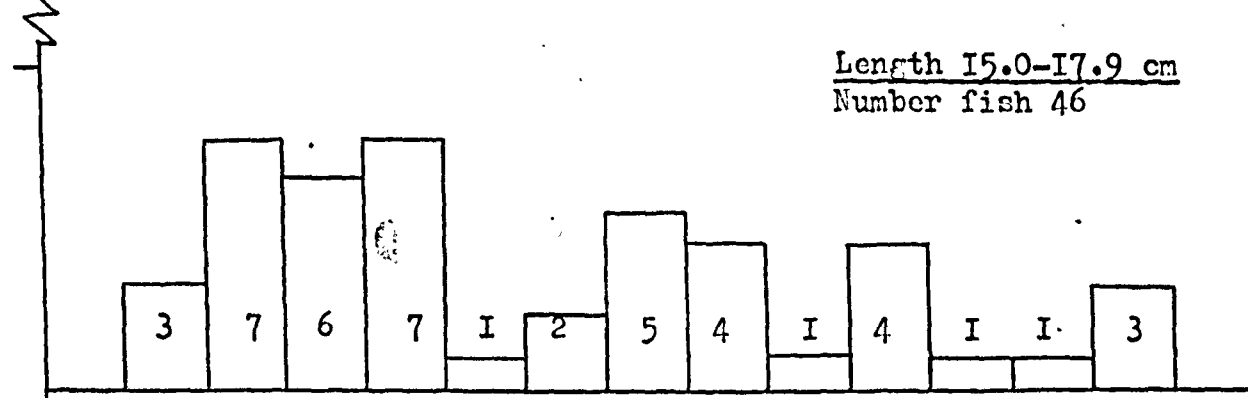
% FREQUENCY

Length 9.0-11.9 cm
Number fish 13

I 3 2 3   2   I I

Length 12.0-14.9 cm
Number fish 197

9 25 33 26 26 32 28 6 4 2 4 2

Length 15.0-17.9 cm
Number fish 46

3 7 6 7 I 2 5 4 I 4 I I· 3

Length ≥ 18.0 cm
Number fish 26

I 3 I   3 2 5 3 3 I   3   I

0 I-   6-   II-   I6- 2I- 26- 3I- 4I- 5I- 6I- 7I- 8I- 9I-   IOI-
   5   IO   I5   20   25   30   40   50   60   70   80   90   IOO   IIO
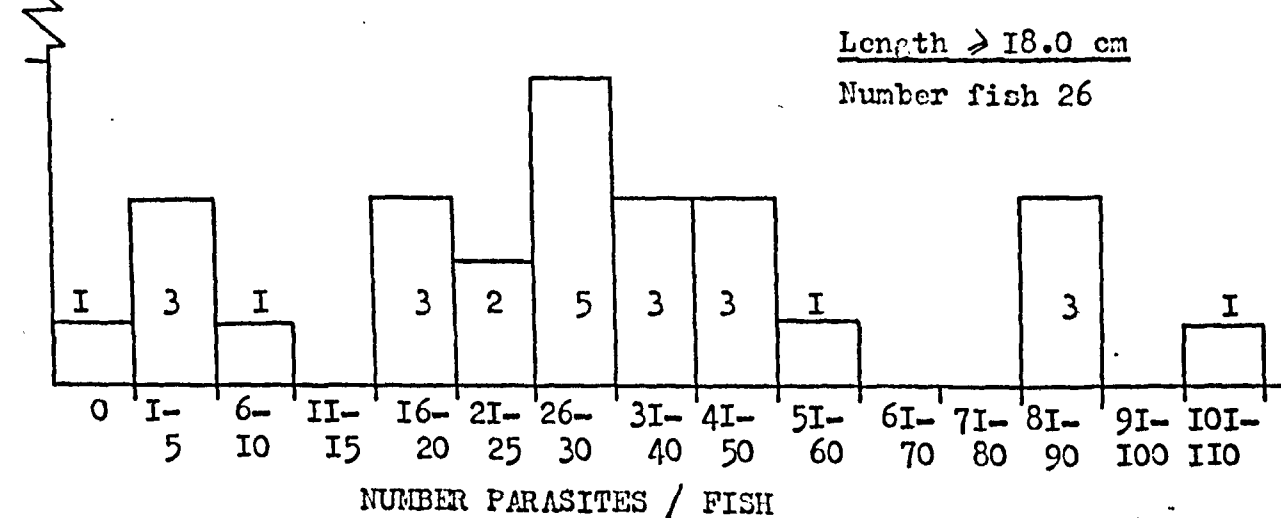
NUMBER PARASITES / FISH

Fig. 6. Effect of host length on the frequency distribution of
Diplostomum gasterostei. Female perch. Gill net samples.
January 1975 - February 1976.

Perch are present in deeper water (12m) during the whole year at Llyn Tegid. However, they are only abundant in shallow water (6m, or less) between early June - late September (see Chapter III). The infection of perch with D. gasterostei at site A (6m) and site B (12m) was compared during the months of June-August (site A) and May-July (site B). The results are shown in Fig. 7. The infection at the shallower site (A) was heavier than at the deeper site (B). There were more heavily infected fish found at site A (Fig. 7). When the length frequencies of the fish at the two sites were compared, it was apparent that slightly more larger perch were caught at site A (Fig. 8). At site A 62% of the fish (56)were over 12.9 cm long whilst at site B only 41% of the fish (19) were of the same size (Fig. 8).

Influence of Diplostomum gasterostei on the growth rate and condition factor of perch.
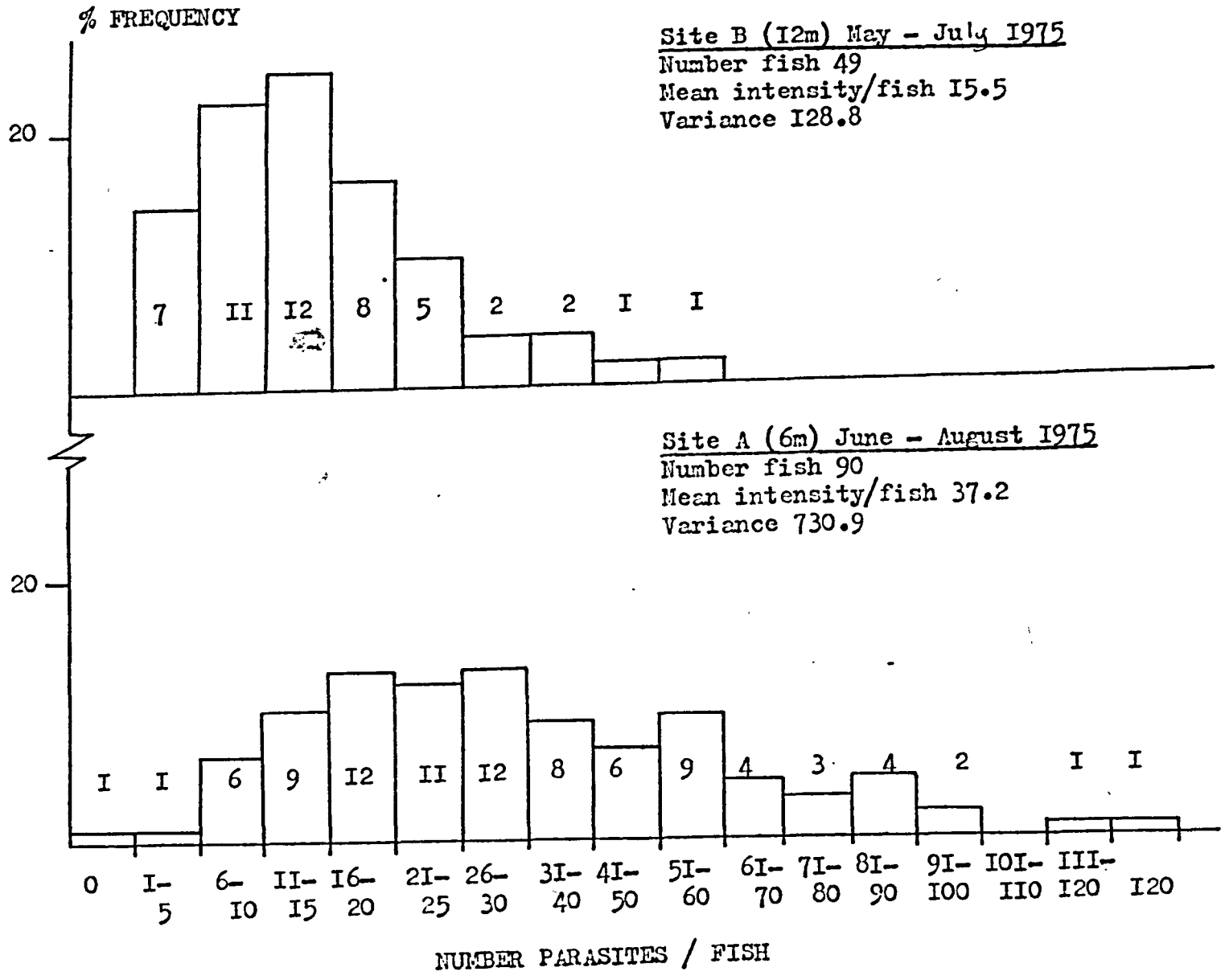
The high incidence and intensity of the D. gasterostei infection of perch at Llyn Tegid has been indicated. During the examination of a total of 559 perch of a range of ages and sizes no signs of gross pathology were observed.

(i) Growth rate

The effect of D. gasterostei on the growth rate of the perch aged 0++ caught by the trawl was examined. The results are shown in Table IX. From this small sample there appeared to be no reduction in the growth rate of 0++ perch infected with a mean intensity/infected fish of 3.3.

The infection is prevalent in adult fish of all ages. Substantial numbers of male and female fish aged 4-4++ years were caught, and therefore the effect of D. gasterostei on the growth of these fish examined. The mean length of male and female perch, aged 4++ years caught between January-March 1975 and October-February 1975/76, (gill

Fig. 7. Frequency distribution of Diplostomum gasterostei. Gill net samples. Site B May – July 1975, site A June – August 1975.

% FREQUENCY

Site B (12m) May – July 1975
Number fish 49
Mean length 13.2 cm
Variance 3.9

Site A (6m) June – August 1975
Number fish 90
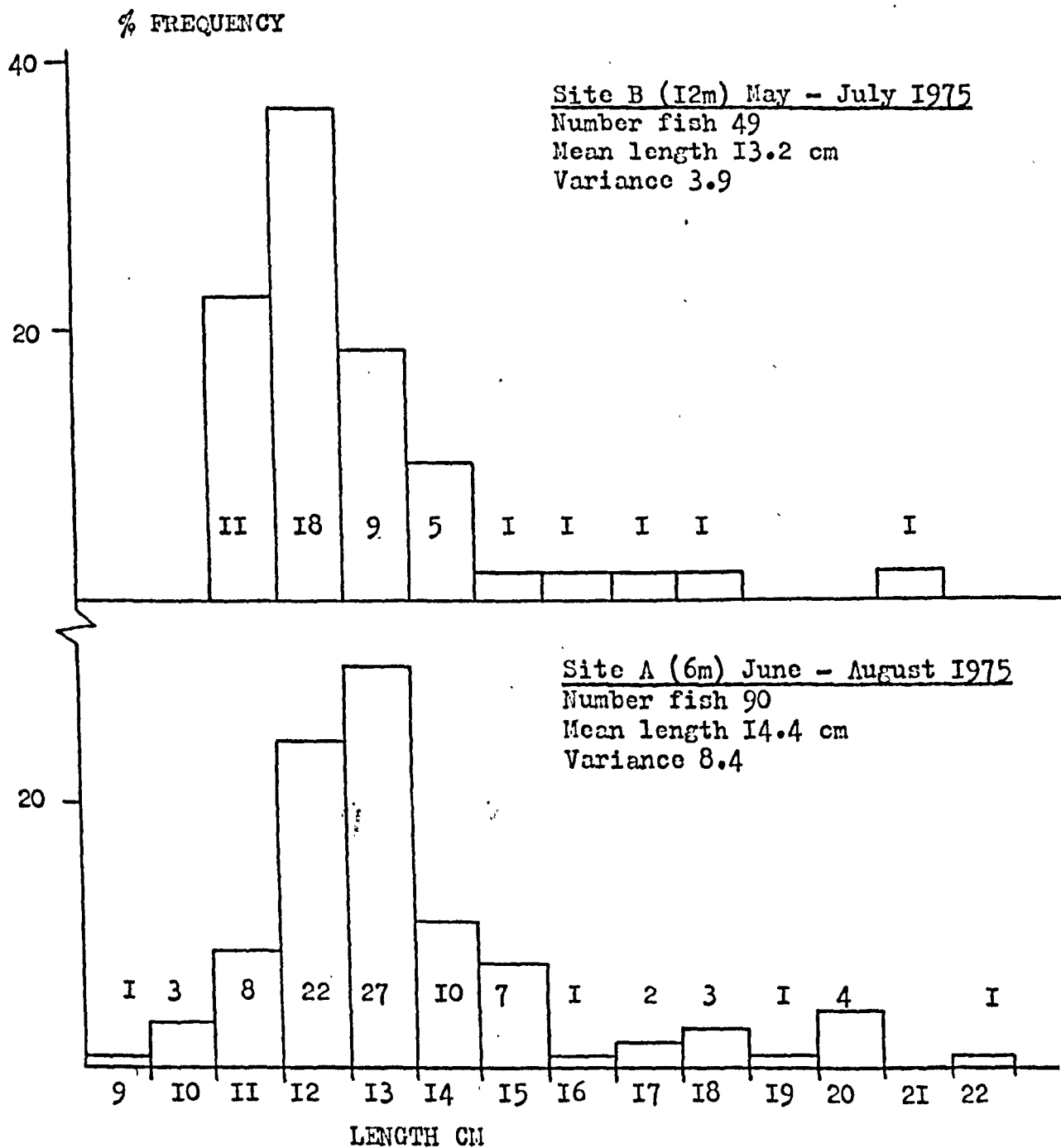Mean length 14.4 cm
Variance 8.4

LENGTH CM

Fig. 8. Length frequency of perch. Gill net samples. Site B May – July 1975, site A June – August 1975.

Table X. Effect of Diplostomum gasterostei on the growth of perch aged 4-4++ years. Gill net samples. January-March 1975, October 1975-February 1976.

Number parasites/fish	MEAN LENGTH ± 95% C.L.	
	Male fish	Female fish
0	-	-
1 - 15	12.61 ± 0.28 (20)	13.25 ± 0.65 (26)
16 - 30	12.61 ± 0.36 (16)	13.46 ± 0.89 (18)
>30	12.48 ± 0.42 (10)	14.34 ± 1.08 (16)
Total (overall)	12.52 ± 0.19 (46)	13.74 ± 0.50 (60)

N.B. Figures in parentheses are number of fish examined.

net samples) was calculated for fish harbouring no metacercariae,
1-15, 16-30 and > 30. The results are shown in Table X. Because
of the high incidence of infection no uninfected perch were available.
Thus it is impossible to compare the effect of this parasite on the
growth of infected and uninfected fish. However, at the three
remaining levels of infection there appeared to be no marked change
in the mean length of male and female perch aged 4++ years harbouring
increasing numbers of metacercariae (Table X).

To avoid unnecessary errors only perch caught during the essentially
non-growing months of October-March were used (see Chapter III). None-
theless, because of the relatively small number of fish that were
examined aged 4++, perch from two growing seasons were treated 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 D. gasterostei on the condition factor of the O++
trawl caught fish was examined. The condition factor was calculated
as described in Chapter III, after Graham and Jones (1962). The mean
K value of 27 infected fish was 145.8 ($\pm$ 95% confidence limits 5.9),
while the mean K value of 9 uninfected fish was 157.9 ($\pm$ 18.1). Bearing
in mind the small number of fish examined and the widely varying values
of K obtained, there appears to be no marked effect of D. gasterostei on
the condition factor of O++ perch infected with a mean intensity/infected
fish of 3.3.

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

Association between Diplostomum spathaceum and Diplostomum gasterostei

From Table II it can be seen that perch infected with D. spathaceum

harboured varying numbers of D. gasterostei. There was no apparent relationship between the occurrence of D. spathaceum and the intensity of infection with D. gasterostei.

VII. 1.4   DISCUSSION

Four groups of metacercariae were recognised by Hoffman (1960) in his synopsis of the strigeoid digenetic trematodes (superfamily Strigeoidea Railliet, 1919) infecting fish. The characters of these four groups are summarised in Table XI.

Within the Diplostomulum group (Table XI) two forms may be recognised: Tylodelphylus and Diplostomulum, and are separated from one another by the following features (Skryabin, 1960; Sweeting, 1971a; Tinsley & Sweeting, 1974).

(i) Forebody and hindbody are separated by a definite "waist" in Diplostomulum, but continuous in Tylodelphylus.

(ii) Calcareous corpuscles are spherical in Diplostomulum, but oval in Tylodelphylus.

(iii) Lappets (lateral pseudo suckers) are more pronounced in Diplostomulum, producing a distinctly trilobed anterior end.

(iv) Adhesive organ and ventral sucker are relatively smaller, and the adhesive organ is situated more posterior, in Tylodelphylus.

Following the observations of Berrie (1960), Williams (1966a) erected a new species of Diplostomum (≡ D. gasterostei) from material that was formerly included with D. spathaceum. The features that may be used to separate the two species include: site of infestation in the fish eye (D. spathaceum - lens, D. gasterostei - humour/retina); the more posterior position of the ventral sucker in D. spathaceum; the larger number of calcareous corpuscles in D. gasterostei (Williams, 1966a; Sweeting, 1971a). According to these features the metacercariae

Table XI. Classification of strigeoid metacercarial forms (after

Hoffman, 1960; Sweeting, 1971b).

Tetracotyle	Diplostomulum*	Neascus	Prohemistomulum
HINDBODY			
small	small	large	absent
CYST			
present	absent	present	present
LATERAL PSEUDOSUCKERS			
present	present	absent	absent
PARANEPHRIDIAL EXCRETORY SYSTEM			
large, extends anteriorly, vacuolated with calcareous concretions	small, tubular, with calcareous corpuscles	large, anestomosing, with calcareous corpuscles	large, two main vessels with calcareous corpuscles

N.B. *Diplostomulum is partly synonymous with Diplostomum.

Displostomum is the generic name applied to metacercariae

whose adult form is known to comply with the characters

of the genus. Diplostomulum refers to the metacercarial

form of Diplostomum, and may be used when the adult form

is unknown (Sweeting, 1971a).

inhabiting the lens of perch at Llyn Tegid was identified as D. spathaceum, and the metacercariae inhabiting the humour/retina was identified as D. gasterostei.

LaRue (cited by Sweeting, 1971a) suggested that the adhesive structures of the Strigeidae were developed relatively recently and were adaptive in origin. He considered that taxonomic systems involving adhesive structures were superficial and not indicative of generic relationships. Therefore, the use of the position of the ventral sucker should be regarded as an aid to the identification of the species, rather than an absolute taxonomic character (Sweeting, 1971a). In addition, Sweeting (1974) has found that in the pre-metacercarial stages of D. spathaceum from the lens of sticklebacks the ventral sucker may be situated pre-equatorially, rather than post-equatorially as in the metacercaria. The number of calcareous corpuscles is not an absolute feature of each species and may vary with the age of the metacercaria and the fish host species, (Sweeting, 1971a). The site of infestation in the fish eye is usually regarded as an important criterion for distinguishing between D. spathaceum and D. gasterostei. However, Wootten (1974) found D. spathaceum in the vitreous humour of perch that were morphologically identical with those from the lens. D. gasterostei was originally described from the retina of stickleback by Williams (1966a). This species has also been recorded from the retina of stickleback by Hopkins (1959), Berrie (1960), Chappell (1969a) and Pennycuick, (1971a); from the retina of perch, roach, brown trout and gwyniad (Coregonus lavaratus) by Chattrabhuti (1974); from the retina and humour of perch, roach, bream (Abramis brama), Chub (Leuciscus cephalus), stickleback and grayling (Thymallus thymallus) by Sweeting (1971a); from the retina and humour of perch in the present study; and from the humour of perch by Kennedy (1975), and from the humour of ruffe (Gymnocephalus cernɣa) and roach by Kennedy et al. (1975). Metacercariae

of the _Diplosomulum_ group often exhibit a high degree of site specificity within their piscine hosts. The reports of _D. gasterostei_ from the retina and/or humour of fish eyes may reflect the techniques of dissection of the individual workers, since the exact location is difficult to determine without the use of histological methods. Alternatively, _D. gasterostei_ may be capable of infecting both sites within the eye, though the records do not suggest that the site of infestation is influenced by the species of fish. Finally, the presence of _D. gasterostei_ in two sites in the eyes of fish may indicate the existence of at least two separate species: one from the retina, and one from the humour (Sweeting, pers. comm.)

A summary of the morphological measurements of _D. gasterostei_ from a number of studies in the British Isles is given in Table XII. A considerable degree of variation exists in the dimensions that have been recorded, which may be a result of the methods of examination used by the individual workers, the species of fish investigated, the age of the metacercariae that were examined, and perhaps the exact specific identity of the parasites. Despite the variations in the site of occurrence in the fish eye, the ventral sucker of _D. gasterostei_ was (in all instances) situated at a position anterior to that observed in _D. spathaceum_ in the same study (Williams, 1966a; Sweeting, 1971a; Chattrabhuti, 1974; present study, Table I).

Shigin (in Skryabin, 1971) considered that _D. gasterostei_ was synonymous with _D. pungiti_. The measurements of _D. gasterostei_ from five sources in the British Isles, along with the measurements of _D. pungiti_ from Shigin (1976), are provided in Table XII . Whilst the variations in the measurements of _D. gasterostei_ have been indicated, the measurements of _D. pungiti_ differ from those of _D. gasterostei_ on a number of points. In particular, the size of the oral and ventral suckers and the size of the adhesive organ are, in some instances,

Table XII.   Measurements of <u>Diplostomum gasterostei</u> and <u>Diplostomum pungiti</u>.

-207-

Measurements um			Williams,* 1966a	Sweeting,** 1971a	Chattrabhuti,*** 1974	Present study****		D. pungiti Shigin, 1976
						Llyn Tegid	Slapton Ley	
BODY:	length,	-mean/10	280um	390um	um	423um	495um	um
		range	220-330	342-420	316-402	340-460	440-600	410-655
	width,	mean/10	210	289	-	222	240	-
		range	210-220	228-325	180-290	190-270	220-280	240-330
ORAL SUCKER:	length,	mean/10	40	60	-	52	50	-
		range	30-50	56-66	30-32	45-60	45-55	60-90
	width,	mean/10	30	47	-	45	43	-
		range	20-40	42-52	30-32	40-55	40-45	47-67
VENTRAL SUCKER:	length,	mean/10	30	45	-	37	41	-
		range	30-40	38-64	32-33	35-40	35-50	57-77
	width,	mean	30	55	-	44	46	-
		range	30-40	47-67	32-32	35-55	35-55	65-83
ADHESIVE ORGAN:	length,	mean/10	50	98	-	76	94	-
		range	20-60	77-117	40-41	40-100	75-115	85-140
	width,	mean/10	70	122	-	89	94	-
		range	60-80	97-141	43-45	70-90	80-120	105-140
PHARYNX:	length,	mean/10	30	41	-	43	41	-
		range	20-30	37-47	21-26	35-55	35-50	-
	width,	mean/10	10	24	-	20	21	-
		range	10-10	19-27	11-14	15-30	20-25	-

N.B.   *Flattened between two slides, fixed in warm 5% formalin.   **Fixed unflattened in 10% buffered formalin.

   ***Living material: range of mean values of expanded and contracted metacercariae.

   ****Killed in hot water, fixed in 10% buffered formalin.

distinctly different. However, the metacercariae were prepared in a variety of ways and the importance of standardisation of techniques was stressed by Shigin (1976). In addition to these differences, the number of calcareous corpuscles recorded from D. gasterostei (394-586: Sweeting, 1971a; 332-702: present study) are much less than the range for D. pungiti (2158-2873: Shigin, 1976). Bearing in mind the remarks of LaRue concerning the use of adhesive structures as taxonomic characters, along with the fact that the number of calcareous corpuscles may vary with the age of the metacercaria and the host species (Sweeting, 1971a), it would appear that D. gasterostei should be regarded as distinct from D. pungiti. However, the taxonomic relationships between D. gasterostei and D. pungiti, and between the former species and other Diplostomum metacercariae (e.g. D. baeri), require further investigation before a definitive statement can be made on the validity of D. gasterostei.

As already indicated metacercariae identified as D. gasterostei have been recorded from 10 species of British freshwater fish: perch, ruffe, roach, bream, chub, stickleback, brown trout, grayling and gwyniad (Sweeting, 1971a; Chattrabhuti, 1974; Kennedy, 1974, 1975; Kennedy et al. 1975). Perch has been recorded as host from Llyn Tegid (Chattrabhuti, 1974; present study), River Nidd (Sweeting, 1971a) and Slapton Ley (Kennedy, 1975). In addition, Campbell (1974) recorded two types of Diplostomulum from the eyes of perch at Loch Leven, where D. gasterostei was tentatively identified from the eyes of stickleback. With the description of D. gasterostei by Williams (1966a), it is likely that many reports of D. spathaceum pre-1966 contained records of D. gasterostei (Sweeting, 1971a). Nonetheless, metacercariae identified as D. spathaceum have been recorded from a large number of species of fish from the British Isles (Kennedy, 1974; Sweeting, 1974; Chubb, 1976), and these records from perch are summarised in Chapter IV, Table I.

Chattrabhuti (1974) recorded D. spathaceum from the lens of 5.0% of 20 perch and 100.0% of 28 roach at Llyn Tegid. None of 20 gwyniad were infected, and a single brown trout did not harbour the parasite. The results from the present study show that in occurrence of this parasite in perch is low, and it is unlikely that this fish is an important host in the life cycle at Llyn Tegid.

Bearing in mind the confusion of identification that existed before the Williams (1966a) description of D. gasterostei, only records of D. spathaceum from perch post-1966 will be considered here.

Shillcock (1972) recorded D. spathaceum from 3.9% of 127 perch from Ockendon Moat (Essex). The mean intensity/infected fish was 1.2. Chattrabhuti (1974) found 5.0% of 20 perch from Llyn Tegid infected, whilst the present study has found an incidence of 1.7% in 465 adult perch. The mean intensity/infected fish recorded in the latter study was 1.4. Sweeting (1974) found that 18 perch from the Lancaster Canal (Yorkshire) harboured a mean intensity/fish of 1.5. Wootten (1974) recorded D. spathaceum from 79.0% of 181 perch from Hanningfield Reservoir (Essex), and the mean intensity/infected fish was 5.7. It is pertinent to note that Wootten (1974) recorded D. spathaceum from the lens and the humour of perch at Hanningfield Reservoir. Andrews (unpublished observations) has investigated the D. spathaceum infection of perch at two localities on Merseyside (Princes Park Lake, and a small pond in Hale, Speke). In both instances the parasite was identified on the basis of their site of infestation, position of the ventral sucker, and the number and distribution of calcareous corpuscles, in living material (as indicated above). At both localities the incidence in two small samples of perch was high (approaching 100.0%), though the number of parasites per fish was between 7-15. Heavily infected fish were not found.

From these recent studies in the British Isles it appears that the incidence of D. spathaceum in perch may vary from one locality to the next, though the intensity is usually low.

Recent continental European studies on the D. spathaceum infection of perch included those of Rauckis (1970a), Tell (1971), Wierzbicki (1970) and Wierzbická and Wierzbicki (1971). Rauckis (1970a) found that the incidence of infection in 58 perch from Lake Dusia (U.S.S.R.) varied from 80.0% in January-March to 100.0% in June-July and October-November. The range of intensity was 1-79. Tell (1971) studied the parasites of perch from Lake Vôrtsjarv (U.S.S.R.). Of 250 perch that were examined, 80.0% were infected with a range of intensity of 2-200. At Lake Dargin (Poland), Wierzbicki (1970) found that 30.9% of 504 perch were infected, and the maximum number of parasites from a single fish was 17. Wierzbicka & Wierzbicki (1971) considered that D. spathaceum was a "relatively scarce" parasite of perch at Lake Leginskie (Poland).

Clearly there were conflicting patterns of occurrence of D. spathaceum in continental studies. As has been shown for the D. spathaceum infection of perch in the British Isles, the incidence of infection may vary from one locality to the next. However, in continental Europe it would appear that perch may harbour very high individual intensities of D. spathaceum.

While under natural conditions ecological and/or behavioural mechanisms may be important in affecting the level of eye-fluke infestation in some fish species, Sweeting (1974) has shown under experimental conditions that perch is less susceptible to infection with D. spathaceum than (for example) minnows (Phoxinus phoxinus). The greater resistance of perch to infection with D. spathaceum is likely to be related to the prevention of cercarial penetration of the fish (lack of penetration stimulus, physical impenetrability of perch integument), or post-penetration phenomena (from Blair, 1976). Blair (1976) considered that existing evidence indicated that the characteristic host range of strigeoid metacercariae was

primarily related to post-penetration phenomena. Fleisherova (1972) found that _Cercaria_ C penetrated the tadpoles of the anurans _Bombina bombina_, _Pelobates fuscus_ and _Rana esculenta_, but the cercariae did not become concentrated in the eye, but were disorientated and distributed throughout the body. Caudate amphibians, _Triturus vulgaris_ and _Salamandra salamandra_, were refractory to infection with the cercariae. In addition, Betterton (1974) found that _Cercaria_ C penetrated brown and rainbow trout in equal numbers, but fewer became localised in the eyes of the former species. However, the mechanisms of such phenomena are poorly understood, but may involve one or more of the following (Betterton, 1974; Sweeting, 1974): the disorientation of migrating cercariae; the greater destruction of cercariae by host reaction; the greater impenetrability of the tissues of some fish. Nonetheless, the possibility of the lack of penetration stimuli, or the greater impenetrability of the perch integument should not be overlooked.

Bearing in mind the fact that perch is less susceptible to infection with _D. spathaceum_ than many cyprinids (Sweeting, 1974), the high individual intensities of infection in some continental European studies may be explained by one (or both) of the following. There are 14 species of _Diplostomum_ recorded from the fish and cyclostomes of the U.S.S.R. (Shigin, 1976), and their taxonomy is complex. Therefore the possibility of mis-identification was great. Alternatively, there may exist ecological and/or behavioural mechanisms which may (under certain circumstances) overcome the higher resistance of perch to infection.

At Llyn Tegid, perch and gwyniad are commonly infected with _D. gasterostei_. Chattrabhuti (1974) recorded this parasite from 17 of 20 perch (85.0%) and 16 of 20 gwyniad (80.0%), while only one of 28 roach (3.6%) was infected. In the same study a single specimen of brown trout was examined and found to be infected (Chattrabhuti, 1974). The results obtained in the present study show that _D. gasterostei_ is a

very common parasite of perch at Llyn Tegid (Tables III & IV).

Diplostomulum metacercariae of the family Diplostomatidae reach

maturity in the intestines of birds, chiefly members of the Laridae

(gulls) (Sweeting, 1971b). Ducks and pigeon have been demonstrated

as suitable experimental hosts to D. gasterostei (Berrie, 1960;

Williams, 1966a), though the definitive host has not been established

under natural conditions. Various species of ducks and gulls, and the

cormorant (Phalacrocorax carbo) are seasonally abundant at Llyn Tegid

(see Chapter II). Wootten (1974) considered that small coarse fish

(perch, ruffe Gymnocephalus cernʉa, and roach) were important hosts in

the transmission of D. spathaceum and Tylodelphys clavata at Hanningfield

Reservoir (Essex), since these fish are easily preyed upon by piscivorous

birds. Whilst perch is not an important host to D. spathaceum at Llyn

Tegid (see above), it seems likely that this fish is an important

functional host in the life cycle of D. gasterostei. Nonetheless, the

infection is also prevalent in gwyniad, and brown trout has been found

infected, at Llyn Tegid (Chattrabhuti, 1974). Whilst larger salmonᵒid

fish may be less easily preyed upon than coarse fish by some species of

gulls (Halvorsen, 1970), the possibility of cormorants acting as definitive

host to D. gasterostei should be noted. These birds can dive to considerable

depths and may prey upon a variety of fish species.

Berrie (1960), Williams (1966a, b) and Pennycuick (1971a) reported

that the first intermediate host to D. gasterostei was Lymnaea pereger.

This species of snail may also host several other digeneans, including

D. spathaceum and Tylodelphys clavata (Bauer, 1959; Niewiadomska, 1960;

Williams, 1966b; Erasmus, 1972). Hunt & Jones (1972a) found L. pereger

in the littoral fauna of Llyn Tegid, and reported one instance of this

species in the profundal zone. L. pereger was considered "regular, though

not abundant" in some sheltered littoral areas, whilst in more exposed

areas it was "rare, or present in small numbers" (Hunt & Jones, 1972a).

Reports have suggested that the incidence of infection in <u>L. pereger</u>

is usually low. Williams (1966a) found one of 550 snails infected

with cercariae of <u>D. gasterostei</u>, whilst Pennycuick (1971a) recorded

the infection from one of 50 snails. Pike (1968) examined <u>L. pereger</u>

from a habitat where sticklebacks and ten-spined sticklebacks (<u>Pungitius</u>

<u>pungitius</u>) harboured <u>Diplostomum</u> spp. and found none of 1467 snails

infected with the cercariae of the <u>Diplostomum</u> type.

In the above studies of the incidence of infection in the molluscan

host, fish from the same habitat invariably harboured a high incidence

of infection. It would appear that only a small proportion of the local

snail population need to be infected to maintain a high level of infection

in the fish population. Bauer (1971) stated that the complex embryology

of digeneans in their molluscan intermediate host contributes greatly to

the efficiency of the life cycle, by augmenting to some considerable

extent the number of infective larvae that are produced. It is of interest

to note one of the most impressive observations on this subject. Meyerhof

and Rothschild (1940) infected a single <u>Littorina littorea</u> with a miracidium

of <u>Cryptocotyle lingua</u>. Over a period of 5 years an average of 830 cercariae/

day were produced by the mollusc. However, some digeneans (e.g. <u>Paragonimus</u>)

may only produce a few hundred cercariae from a single miracidium (Chandler

and Read, 1961). In comparison, Raishite (1970) has studied the reproductive

productivity of the strigeoid <u>Apatemon gracilis</u> in <u>Physa fontinalis</u> and

<u>Planorbis planorbis</u>. Whilst the number of cercariae produced was related

in a linear fashion to the weight of the mollusc, <u>P. fontinalis</u> produced

more cercariae/day than <u>P. planorbis</u>. From naturally infected molluscs

maintained at 17-23°C over a period of 14 days, 1283 cercariae/day was

produced by one <u>P. fontinalis</u>, while 870 cercariae/day were shed by one

<u>P. planorbis</u> (Raishite, 1970).

Parasites often have an overdispersed or clumped distribution in their

host population (e.g. Kennedy, 1968, 1970, 1972; Kennedy & Hine, 1969;

Crofton, 1971a; Pennycuick, 1971b; Anderson, 1974; Boxshall, 1974a, b;

Hine & Kennedy, 1974; Kennedy & Rumpus, 1977; etc.). The overdispersed

nature of the D. gasterostei infection of perch at Llyn Tegid has been

noted. Under present conditions, perch that have spent less than a year

in the lake (aged O++) will have been exposed to a limited number of

cercariae. This may be influenced by the timing of perch spawning and

the consequent appearance of fry in relation to cercarial abundance,

along with the relatively small surface area of the young fish. Therefore

the intensity of infection in young of the year perch was low, and marked

overdispersion of the parasite population unlikely. Similar results were

obtained in the study of Triaenophorus nodulosus (Cestoda) in perch at

Llyn Tegid (see Chapter VIII). Further details of the infection in one

and two year old perch are required since few fish of this age were

examined. It would appear that the incidence reaches a maximum of 100.0%

in fish during their second and third years in the lake. With the exposure

of fish to infection in successive years, along with the probable extended

life span of the parasite (see later), the intensity of infection rises

and develops into a marked overdispersed form. Crofton (1971a) and Elliot

(1971) have discussed some of the factors which favour overdispersion in

parasite and animal populations respectively. Kennedy (1970) summarised

some of the knowledge concerning overdispersion in populations of fish

parasites. The clumped distribution of D. gasterostei in perch at Llyn

Tegid may be influenced by a number of factors, including physiological

variations in the susceptability of individual fish to infection, or

individual variations of behaviour which may bring some fish into the

vicinity of cercariae more often than others. In addition, the emergence

of cercariae from molluscs is not continuous, but occurs in bursts that

are separated by irregular intervals of time, and the number of cercariae

produced may vary from day to day (Erasmus, 1972). Mackenzie and Liversidge,

(1975) obtained a close fit of the negative binomial to the observed

distribution of metacercariae of <u>Stephanostomum baccatum</u> in plaice

(<u>Pleuronectes plattessa</u>). Wolfgang (1955) suggested that infection

of the molluscan host with <u>S. baccatum</u> probably built up over a period

of time and culminated in the simultaneous release of large numbers

of cercariae. This would then lead to the observed overdispersed

nature of the infection in place (Mackenzie and Liversedge, 1975).

Pennycuick (1971a, b) pointed out that since <u>D. gasterostei</u> infected

the fish by penetration, and since the infected snail released a large

number of cercariae over a short period of time, there was the chance

that a few fish would become very heavily infected. Therefore, at Llyn

Tegid, it seems likely that this may also have been a contributing

factor in influencing the overdispersed nature of the <u>D. gasterostei</u>

infection of perch.

Kennedy (1970) suggested that in fish-(larval) parasite systems

where the parasite is long lived and does not adversely effect the host,

the infection may build up with increasing host age. The life span of

<u>D. spathaceum</u> has been reported as at least $3\frac{1}{2}$ years in roach (Shigin,

1964) and as at least 6 years in goldfish (<u>Carassius auratus</u>) (Sweeting,

1971a). However, Timmermann (1936) (cited by Bauer <u>et al.</u>, 1969) stated

that <u>Diplostomum</u> metacercariae may only live for one month at $16^{\circ}C$, and

Bauer <u>et al.</u>, (1969) considered that their life span may vary with the

specific identity of the parasite and host. The increase of infection

with <u>D. spathaceum</u> with host age has been noted by several workers,

including Mishra (1966), Sweeting (1974) and Wootten (1974). In the

adult perch at Llyn Tegid there was an increase in the mean intensity

of <u>D. gasterostei</u> increasing host age and length. Similar results have

been reported by Williams (1966a), Chappell (1969b); Pennycuick (1971c);

Kennedy (1975) concerning <u>D. gasterostei</u>, by Bibby (1972) concerning

<u>D. phoxini</u>, and by Kennedy (1975) and Sweeting and Powell (1977) concerning

Tylodelphys clavata. Such increases may be most easily explained by the accumulation of long-lived (> one year) parasites with host age (Kennedy, 1970). However, other factors to consider are the increased surface area of older fish facilitating the penetration of larger numbers of cercariae (Bibby, 1972; Betterton, 1974), and the possibility of ecological and/or physiological mechanisms increasing the susceptability of older, larger fish to infection.

Nonetheless, in intermediate host-parasite systems such as these, if the parasite decreases the hosts chances of survival, the infection may level off (or decrease) as older, more heavily infected fish die (Kennedy, 1970). This effect has been postulated on a number of occasions concerning the parasites of fish, and is discussed in relation to Triaenophorus nodulosus (Cestoda) in Chapter VIII. Examples where this may have occurred in metacercarial infestations were D. gasterostei in stickleback (Pennycuick, 1971c), D. spathaceum and T. clavata in rainbow trout (Salmo gairdneri) and T. clavata in perch (Wootten, 1974), D. spathaceum and T. clavata in roach (Kennedy, 1975) and T. podicipina in perch (Sweeting and Powell, 1977). Other factors which may reduce the infection in older fish include the increased destruction of penetrating cercariae by the host reactions, and the possible spatial separation of fish from the cercariae (Wootten, 1974). However, Timmermann (in Bauer et al., 1969) found that diplostomiasis does not create immunity and that infection may take place regardless of the intensity of the previous infection, though Betterton (1974) suggested that there may be an increase in the impenetrability of brown trout tissues with age which might influence the migration of cercariae of D. spathaceum. Older fish that spend more time in the deeper water regions (away from the molluscan intermediate hosts in the littoral zone) may not come into contact with the cercariae to the same extent as younger, more littoral dwelling fish (Wootten, 1974). Stycznska-Jurewicz

(1959) found that the intensity of infection of D. spathaceum in the fish Leucaspius delineatus that were maintained in experimental cages, was inversely related to the distance from the shore.

Crofton (1971a) proposed the lethal level concept that stated that the majority of parasites 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, and result in the regulation of host and parasite population size. This is discussed further in Chapter VIII. From the results of this study at Llyn Tegid it appears that perch heavily infected with D. gasterostei do not experience reduced longevity. The intensity of infection increased with host age (and length) and there was no evidence of the death of older, heavily infected perch.

Tinsley and Sweeting (1974) reported the marked overdispersed nature of the infection of Diplostomulum (Tylodelphylus) xenopodis in the clawed toad (Xenopus laevis), but noted that there were no apparent injurious effects as a result of very heavy infestations. However, it was suggested that the penetration of large numbers of cercariae over a short period of time might be damaging. Freeman (1964), Williams (1967) and Hoffman (1973) have all noted the potentially pathogenic nature of the cercarial invasion of fish. Erasmus (1972) stated that the pathogeneity of such invasions may be so severe that small fish exposed to very large numbers of cercariae may die within minutes. However, such extreme conditions do not often occur in nature, and are usually associated with conditions of crowding in small bodies of water. Invasions of large numbers of cercariae of D. spathaceum are known to the pathogenic to fish, especially fry (e.g. Ginetskaya, 1958; Bauer, 1959; Styczynska-Jurewicz, 1959; Molnar, 1974), and this probably applies to D. gasterostei (Pennycuick, 1971d).

The results of this study indicated that, under present conditions, the infection of young of the year perch was light and heavy losses as a result of cercarial diplostomiasis were unlikely. However, the intensity of infection appeared to rapidly build up as fish spend successive years within the lake. This might, in some instances, prove pathogenic if the numbers of penetrating cercariae were large.

Spall and Summerfelt (1970) have studied the effects of Posthodiplosomum minimum on its piscine intermediate hosts. Mortality oberved within two days of exposure to cercariae was thought to be the result of embolism or haemorrhage as the parasite penetrated the target organ. Mortality between 5-20 days post cercarial penetration may have resulted from mechanical damage, haemal congestion, haemorrhage or toxaemia from the activity of the invading cercariae, or from growth and development of the metacercariae. Host mortality was primarily related to the activity of the unencysted parasite, and mortality after encystment (approximately 19 days post invasion) was infrequent (Spall and Summerfelt, 1970). However, Hoffman and Hutcheson (1970) have reported the pathogenecity of P. minimum centrachi metacercariae from an unusual host, white perch (Roccus saxatilis). Within the fish the metacercariae were found atypically in the musculature and eye orbit, rather than their more usual visceral sites. It was suggested that the metacercariae of P. minimum centrachi reduced the fish population from 25,000 to 150 over a period of 3-4 months. Nonetheless, it is likely that penetrating cercariae may have played an important part in this epizootic.

The effect of metacercariae on the growth of their piscine hosts has been reported by Hunter and Hunter (1938) concerning Uvulifer ambloplitis, Huggins (1959) and Smitherman (1964) concerning P. minimum, Szidat and Nani (1951, 1952) concerning Diplostomum mordax and Tylodelphys destructor, and by Bauer et al. (1969) concerning Diplostomum spp. From the examination of a small sample of perch aged 0++ infected with a mean intensity/infected fish of 3.3, there was no reduction in growth rate when compared to

uninfected fish. Similarly, there was no reduction in the growth of 4 year old male and female fish infected with increasing number of D. gasterostei, up to a level of at least 30 parasites/fish. Eschmeyer and Cheatum (1938) found that the metacercariae of Neascus bulboglossa did not reduce the growth rate of yellow perch, Perca flavescens.

The condition factor of fish parasitised with metacercariae has on a number of occasions been compared with that of uninfected fish (Elliot and Russot, 1949; Rabideau and Self, 1953; Fox, 1962; Lewis and Nickum, 1964). In all instances there was found to be no appreciable relationship between the condition factor of the fish and the occurrence of the metacercariae. In this study the condition factor of a small sample of perch aged 0++ was not reduced by an intensity of 3.3 parasites/ infected fish. Spall and Summerfelt (1970) considered that the condition factor of the host is not a sensitive index of the sublethal effects of these parasites. Coble (1970) was unable to demonstrate that parasitism by yellow grub (Clinostomum marginatum) increased the susceptability of minnow (Pimephales promelas) to predation by large mouth bass (Micropterus salmoides). Vaughan & Coble (1975) found that the Neascus infection of yellow perch did not increase their vulnerability to predation, their tolerance of high temperature or influence their length-weight relationship. In contrast, Pennycuick (1971d) found that D. gasterostei reduced the condition factor of sticklebacks, though the effect was not as marked as that of Schistocephalus solidus (Cestoda).

Hoffman (1973) considered that the pathogeneicity of a parasite will depend on its invasive powers, its ability to reproduce rapidly or accumulate within the environment, the various reactions of the host, and the general state of health of the host. Superimposed upon this is the availability of food to the host, sub-optimum environmental conditions, circadian and seasonal changes in temperature, and perhaps

other variables (Hoffman, 1973). Meyer (1970) has shown that parasitic diseases on fish farms in southern U.S.A. were most prevalent in April, when fish were spawning and the temperature optimal for many parasites. Because some parasites are present on or in fish that appear otherwise healthy, it is probable that the small amount of host tissue consumed (or space occupied) does little detectable damage (Hoffman, 1973). In these instances the complex conditions of the external environment may have produced as much influence on the parasite population as the defence mechanisms of the host. However, if environmental conditions change, and these changes enhance the development of a large population of the same parasites, the host may be overwhelmed. Hoffman concluded that parasites are a constant potential threat to the life and health of the fish host.

The combined effect of D. gasterostei and Triaenophorus nodulosus (Cestoda), in relation to their overdispersed distribution, on perch at Llyn Tegid is briefly discussed in Chapter XI.

In fisheries where diplostomiasis is a problem, Bauer et al. (1969) recommended control by the elimination of the molluscan intermediate host or the avian definitive host. Snails may be controlled by the annual draining and drying of ponds or by the use of copper sulphate (Hoffman and Meyer, 1974). Bayluscide (aminoethanol dichloronitrito-salicylanilide) will also control all stages of snails but is toxic to fish. However, the life span of this chemical in the water is limited, and fish may be restocked after 3 weeks (Hoffman and Meyer, 1974). In addition, Frescon (n-tritylmorpholine) has been used to control snails in Great Britain and Africa, and may cause minimal harm to other aquatic invertebrates, fish and other wildlife (Crossland et al., 1971; Hoffman and Meyer, 1974).

Rees (1932) studied the seasonal incidence of several species of cercariae in Lymnaea pereger from southern Wales. She reported peaks of cercarial incidence in May and September. Pennycuick (1971a) studied the D. gasterostei infection of sticklebacks from Priddy (southern England),

and suggested that there was a single peak in cercarial incidence in

L. pereger during May-June. Erasmus (1972) stated that the incidence

of cercariae in freshwater and marine molluscs generally shows two

peaks: late spring (May), and late summer (September-October). This

may be a result of a number of influences, but in European countries

the peaks often coincide with changes within the molluscan fauna.

L. pereger is short lived, spawns in late spring and then dies (Probert,

1966). Therefore the initial peak of cercarial production coincides with

the infection the previous summer. As the young snails grow, more become

infected with larval trematodes and the second peak of cercarial production

occurs during late summer. Erasmus (1972) considered that in a species of

mollusc that lives for one year, the second peak in the late summer may

be small, with the majority of the young molluscs uninfected or harbouring

sporocyst and/or redial stages.

Timmermann (in Bauer, 1959) reported that the cercariae of D. spathaceum

emerged from their molluscan host in large numbers at temperatures of 10°C

or above. As the temperature rises the emergence increased and attained

a maximum at 18°C. At temperatures below $9-10^{o}$C the cercariae ceased activity.

Infection of the piscine host may occur at $13-18^{o}$C, or above (Timmermann,

in Bauer, 1959).

Whilst the life span of the cercariae of digenetic trematodes is

variable, for a particular cercaria there is an optimum free swimming

period beyond which the ability of the cercaria to penetrate, migrate

and/or encyst is greatly reduced (Erasmus, 1972). The life span of the

cercariae of D. spathaceum has been reported as 48 hours (Schäperclaus,

1954, cited by Styczynska-Jurewicz, 1959; Styczynska-Jurewicz, 1959).

It seems likely that the release of cercariae of D. gasterostei

and D. spathaceum from the molluscan hosts at Llyn Tegid occurred

primarily during the warmer summer months. The lake temperature exceeded

10°C at the surface, 6m and 10m between June-October (1975), at a time of

the year when perch were present in large numbers in shallow (6m, or less) water. Wootten (1974) has suggested that fish which do not inhabit the shallow, littoral regions at Hanningfield Reservoir (Essex) may have a reduced infection with D. spathaceum and T. clavata. Styczynska-Jurewicz (1959) found that the intensity of infection by D. spathaceum of the fish Leucaspius delineatus held in cages, varied inversely with the distance from the shore. However, the cercariae were found to expand beyond the limit of the habitat of the molluscan inter- mediate hosts. Nonetheless, it would appear that perch acquire the majority of their D. gasterostei whilst in the shallower regions of Llyn Tegid, during the summer months. When the intensity of infection at the shallow (6m) and deeper (12m) sites was compared, it was found to be markedly higher at the former site (Fig. 7). This may be explained in part by the greater number of larger (and perhaps more heavily infected) fish caught at the 6m site (Fig. 8). Chappell (1969a) found that observed seasonal changes in the parasite fauna of sticklebacks could be related to seasonal fluctuations in the fish population. However, it is likely that the higher intensity of infection at the shallower site is also related to the seasonal infection process of perch with cercariae of D. gasterostei. At the end of the summer-autumn (September—October) the more heavily infected fish from the shallower regions of the lake will return to deeper water. At this time these heavily infected fish will mix with the more lightly infected (from deeper water) perch and this may obscure any seasonal aspects of the infection process. Unfortunately, insufficient numbers of perch were caught at site A (6m) during the rest of the year to permit further comparisons. This explanation presupposes that the perch population in shallow water during the summer months is discrete and separate from the population in deeper water. This is discussed in relation to other parasitic infestations at Llyn Tegid in Chapter XI.

Wierzbicki (1970) found that there were two peaks in the seasonal incidence and intensity of D. spathaceum in perch at Lake Dargin (Poland). The initial spring peak that was observed was slightly larger than the later autumn peak (Wierzbicki, 1970). Pennycuick (1971a) also reported the seasonal occurrence of the D. gasterostei infection of sticklebacks at Priddy (southern England). She found a single peak in the occurrence during the summer autumn (June onwards) followed by a gradual decrease to the following spring (March-April). The changes in the intensity of infection were more marked than the changes in incidence. Kennedy (1975) found distinct seasonal changes in the infection of perch with D. gasterostei at Slapton Ley (Devon). The incidence and intensity of infection was highest in the summer (June-September) and declined to a minimum in the late winter (January-March). There then followed a rise during the spring-summer (April-June), probably as a result of new infections. Pennycuick (1971a) and Kennedy (1975) both suggested that the decline in the infection seen during the winter months may be a result of the disappearance of the more heavily infected fish from the population. Similar effects have been postulated concerning the metacercarial infections of warmouth (Chaenobryttus gulosus) (Hall, 1932) (cited by Spall and Summerfelt, 1970), and white crappie (Pomoxis annularis) (Spall and Summerfelt, 1969).

In contrast, Chappell (1969a) found no seasonal fluctuations in the infection of sticklebacks with D. gasterostei from a pond in Yorkshire (northern England). Wootten (1974) found no seasonal patterns in perch, ruffe, brown trout and rainbow trout infected with D. spathaceum, T. clavata and T. posicipina at Hanningfield Reservoir (Essex). The incidence of D. huroneuse in yellow perch from Ontario (Canada) did not exhibit any seasonal changes (Tedla and Fernando, 1969). It would appear that in environments such as Llyn Tegid, where the incidence and

intensity of infection is high, it may be difficult to demonstrate any seasonal fluctuations in the occurrence of strigeoid metacercariae. However, if the incidence or intensity of infection in lower, and/or there is a seasonal parasite induced host mortality, the effects of the seasonal recruitment of the cercariae into the piscine hosts may be more marked. Sweeting (1974) studied the D. spathaceum infection of sticklebacks from the Leeds-Liverpool Canal in Yorkshire. Over a period of 12 months 93.0% of 301 fish were infected. By dividing up the parasites from the lens of the fish into an intermediate stage between cercariae and metacercariae, and metacercariae, he demonstrated the seasonal occurrence of the intermediate forms. The frequency of the pre-metacercarial stages rose from 25.0% in April-May to 91.5% in August-September, indicating that recruitment had occurred between June-September (Sweeting, 1974).

Chattrabhuti (1974) recorded 80.0% of 20 gwyniad infected with D. gasterostei at Llyn Tegid. These fish were never caught in large numbers in shallow water (6m) using gill nets (Chapter III). However, Haram (1968) has found that these fish show complex diurnal and seasonal migrations, and Coles (pers. comm.) has caught large numbers of gwyniad in water less than 6m deep during the summer months (June-July) at Llyn Tegid. Therefore the infection of gwyniad may be a result of their migration from deep to shallower water during the months when cercariae are available, or because of the dispersal of the cercariae beyond the limits of the molluscan intermediate host (as seen by Styczynska—Jurewicz, 1959, concerning D. spathaceum).

Becker and Brunson (1966) suggested that rainbow trout may become infected with D. flexicaudum by the ingestion of molluscs containing "precocious metacercariae". This method would allow the infection of fish at temperatures too low to permit the release of cercariae. At Llyn Tegid molluscs were of very limited importance in the diet of perch,

and L. pereger never recorded from their stomach contents (Chapter III).

Whilst molluscs were a significant part of the diet of gwyniad at Llyn

Tegid, these were mainly Pisidium sp. (bivalves) (Haram and Jones, 1971).

Therefore, in accordance with the observations of Wootten (1974) concerning

the D. spathaceum infection at Hanningfield Reservoir (Essex), the

ingestion of infected molluscan intermediate hosts by perch and gwyniad

at Llyn Tegid can only be of minor (if any) importance in the transmission

of D. gasterostei and D. spathaceum.

VII.1.5   SUMMARY

Diplostomum spathaceum

D. spathaceum was identified from the lens of perch from Llyn Tegid,

and Princes Park Lake and Hale (Merseyside) on the basis of the site of

occurrence, the position of the ventral sucker and the number and distribution

of the calcareous corpuscles.

There was a very low incidence and intensity of infection at Llyn

Tegid, with no evidence of seasonal occurrence. Perch of both sexes,

and a range of lengths and ages, were infected.

The host specificity of D. spathaceum was discussed, and it was

suggested that the low intensity of infection of perch may be a result

of undetermined post-penetration phenomena. The high individual intensities

of infection in some continental European studies require further examination

in the light of the complicated taxonomy of this group.

Diplostomum gasterostei

Histological examination of a small number of perch eyes demonstrated

the presence of D. gasterostei in the retina of the eye. Routine dissection

techniques suggested that this parasite also occurred in the humour.

The morphology of D. gasterostei from perch at Llyn Tegid was compared

with that of D. gasterostei from perch at Slapton Ley (Devon), and with

results from previous studies, and with D. spathaceum from roach at Llyn

Llyn Tegid. The two species were separated on the basis of their site of infectation in the eye, the position of the ventral sucker, and the number and distribution of calcareous corpuscles. Until further comparisons can be made, D. gasterostei should be regarded as a separate species to D. pungiti.

D. gasterostei was a common parasite of perch at Llyn Tegid, and it is likely that this fish is an important functional host in the life cycle. There were no signs of any harmful effects as a result of infeʃtation with this parasite.

The parasite population was markedly overdispersed in the adult perch. Factors affecting this overdispersion were discussed. The incidence of infection was high in perch aged one year or above. The mean intensity of infection increased with host age and length as a result of the accumulation of the parasites with time. Other factors which might influence the infection in older fish were mentioned. There was no difference in the incidence, intensity or frequency distribution of the parasite in adult male and female perch.

Perch became infected during the summer months when they were present in shallow water. The high incidence and intensity of infection obscured the seasonal aspects of the infection process. The dispersal of cercariae beyond the littoral habitat of the molluscan first inter-mediate host was discussed.

VII.2.   Family Strigeidae Raillet, 1919

Tetracotyle sp.

VII.2.1   INTRODUCTION

Tetracotylid metacercariae are characterised by an oval or ovate-oblong forebody, a short rounded hindbody which may be inconspicuous, a reserve bladder consisting of a large continuous space occupying the

dorsal and lateral regions of the forebody (with an extension into the ventral lip of the anterior suctorial pocket) and small calcareous consecretions in the reserve excretory vessels, a pair of lateral pseudosuckers, and a true cyst of parasite origin (Hoffman, 1960). Hughes (1928), Hoffman (1960) and Dubois (1968) have produced synopses concerning the Tetracotyle group.

Odening (1970) and Odening and Beckhardt (1971) have studied the life cycle of Cotylurus variagatus (= C. cumulitestis, Tetracotyle percafluviatilis). At a mean water temperature of $20^{\circ}C$, miracidia hatched from the eggs after 18-23 days. The first intermediate host was the snail Valvata piscinalis. Furcocercariae developed within sporocysts, and first appeared after 54-61 days post infection (mean water temperature $20^{\circ}C$). Perch (Perca fluviatilis), pike-perch (Lucioperca lucioperca) and ruffe (Gymnocephalus cernÿa) were the second intermediate hosts. The definitive host was the gull (Larus ridibundus), within which the adult parasite was found in the small intestine and rectum. The longevity of the parasite in the definitive host was 10-30 days.

The life cycle of Cotylurus erraticus has been studied by Olson (1970). Eggs were obtained from laboratory infected gulls (Larus californius). At $24^{\circ}C$ most eggs hatched after 15-16 days. Mother and daughter sporocysts developed in Valvata lewisi, and furcocercariae emerged 35 days post infection. The metacercaria parasitises in the pericardial cavity of various salmonoid fish. The metacercariae developed to adult after 4 days in the intestines of gulls (Olson, 1970).

Niewiadomska and Kozicka (1970) and Wootten (1973c) have provided further details on the biology of this parasite under natural conditions. Johnson (1971) considered that the blood stream was the most important route of migration of the cercariae through the body of rainbow trout (Salmo gairdneri).

Blair (1976) recently studied the life cycle of Apatemon gracilis.
Cercariae were obtained from naturally infected snails, Lymnaea pereger.
Metacercariae were found in naturally infected rainbow trout, sticklebacks
(Gasterosteus aculeatus) and stone loach (Noemachielus barbatulus). The
infection of rainbow trout, brown trout and sticklebacks was obtained
under experimental conditions. Blair (1976) confirmed the identity of
the metacercariae in experimentally infected ducklings. Adult worms
have been previously raised in ducklings and chicks (Yamaguti, 1933;
Crocombe, 1959; Hoffman, 1959; Vojteck, 1964; Lester, 1974; all cited
by Blair, 1976). Canning et al. (1973) have found leeches (Erpobdella
octoculata, Helobdella stagnalis, Hemiclepsis marginata, Glossiphonia
complanata and Theromyzon tessulatum) infected with the metacercariae of
Apatemon gracilis (and Cotylurus cornutus).

The pathogenic nature of tetracotylid metacercarial infestations of
fish have been noted by several authors, including Bauer (1958), Kozicka
(1958) and Bauer et al. (1969). Bauer (1958) considered that such in-
festations of the host were more pathogenic than those of the peritoneum.

VII.2.2   RESULTS

Description of the material

Similar metacercariae were found at two sites within the perch from
Llyn Tegid: encysted onto the outside of the lens in the posterior
(vitreous) chamber of the eye; encysted in the swimbladder. In both
instances the cysts were easily visible, spherical to oval in shape
and opaque-white in colour. The cyst enclosed a parasite, the dimensions
of which were smaller than the internal measurements of thecyst (Fig. 9).
The measurements of the cyst and parasite from the eye and swimbladder
are shown in Table XIII. The measurements are based on frozen, A.F.A.
fixed, and then stained material. A small number were examined live in
0.85% sodium chloride solution (saline).

The body of the metacercariae was indefinitely divided into fore- and hindbody. There was a large adhesive organ which was clearly visible, along with the oval and ventral suckers. The oral sucker was smaller than ventral sucker (Table XIII). At the level of, or just posterior to, the oral sucker there were a pair of lateral pseudosuckers which were not clearly visible. The pharynx was oval and measured approximately 35-40 um long by 15-30 um wide. In the material examined, the ventral sucker was situated post-equatorially, just anterior to the adhesive organ (Fig. 9).

The measurements of the metacercariae at the two sites were similar, though there were a number of discrepancies. The length of the parasite was similar in both instances, though the width of those from the eye was less than those from the swimbladder. In addition, the oral sucker, ventral sucker and adhesive organ were all larger in the metacercariae from the eye (Table XIII).

The metacercariae were designated as Tetracotyle sp. I (from the swimbladder) and Tetracotyle sp. II (from the eye).

Occurrence of Tetracotyle sp.

None of the 30 perch fry that were purse seined in July (1976) were infected.

Of 36 0++ (3.0-8.9cm) perch trawled in March (1976), two were infected (5.6%), each with one metacercaria of Tetracotyle sp. I. The 28 perch aged 1++-4++ (9.0-11.9cm) from the same sample were uninfected.

Tetracotyle sp. I was found in the swimbladder of 93 of 465 (20.0%) of the adult perch gill netted between January 1975-February 1976. The mean intensity/infected fish was 1.8 (maximum 10) (Table XIV). Tetracotyle sp. II occurred on the eye lens of 23 of 465 of the gill netted perch (4.9%). The mean intensity/infected fish was 1.4 (maximum 3) (Table XV).

Fig. 9. _Tetracotyle_ sp. I from swimbladder of perch.
Gill netted August 1975. Frozen, formalin fixed,
and stained with Borax Carmine. Camera lucida
drawings at x125 and x500.

AO   Adhesive organ
C   Cyst wall
OS   Oral sucker
Ps   Lateral pseudosucker
VS   Ventral sucker

Fig. 9. <u>Tetracotyle</u> sp. I.

(a) Encysted x125

500um
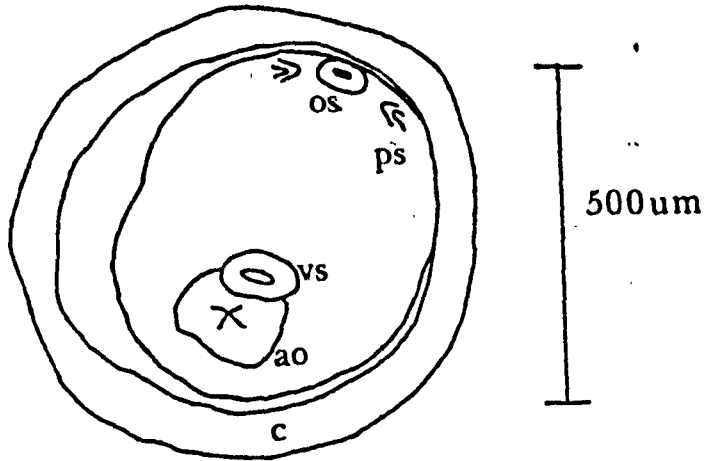
(b) Posterior region x500

50um
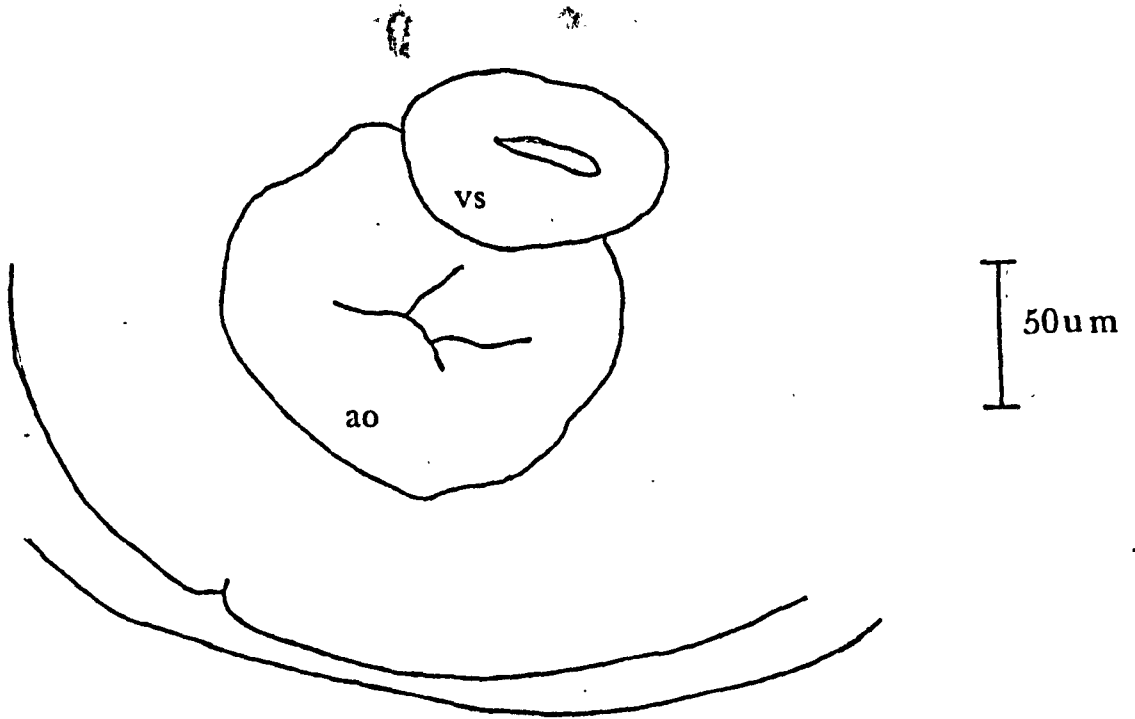
Table XIII.   Measurements of <u>Tetracotyle</u> sp. from swimbladder and
eye lens of perch.   Gill net samples at various times
of year (January 1975-February 1976).

um*		SWIMBLADDER (I)		EYE LENS (II)	
		Mean 10 specimens	Range	Mean 10 specimens	Range
CYST:	length	595	520-660	618	510-900
	width	457	420-580	407	340-510
PARASITE:	length	457	380-560	470	410-500
	width	393	320-480	195	160-230
ORAL SUCKER:	length	50	45-55	61	55-65
	width	54	40-65	78	60-90
VENTRAL SUCKER:	length	59	40-80	88	85-95
	width	88	85-95	120	110-130
ADHESIVE ORGAN:	length	114	95-120	178	145-225
	width	129	105-150	197	180-230

N.B.   *All material frozen, formalin fixed, stained in Borax Carmine.

Seasonal aspects of the infection

(i) Tetracotyle sp. I.

The monthly incidence and mean intensity/infected fish from the adult gill netted perch are shown in Table XIV. The parasite was present in all months, and the intensity fluctuated between 1.0-3.0. However, the results suggest that there may be a peak of incidence in June, July and August (Table XIV).

The seasonal occurrence of Tetracotyle sp. I was investigated further (Fig. 10 & 11). During April-May the incidence of infection at site B (12m) was low and the majority of the fish were uninfected or harboured a single metacercariae (Fig. 10). In June-July the incidence of infection at site A (6m) was higher and there was a rise in the intensity of infection (Fig. 10). From a small sample of 19 perch, the infection at site B during June-July was low and similar to that observed in April-May (Fig. 11). During October-November, the infection at site B was also similar to that recorded during April-May and June-July (Fig. 11). Insufficient numbers of fish were captured during the remaining months of the year to permit further comparisons (see Chapter III).

(ii) Tetracotyle sp. II.

The monthly incidence and mean intensity/infected fish from the gill net samples are shown in Table XV. This parasite was absent from the samples taken in February (1975) and January (1976). The intensity fluctuated from month to month, but was usually between 1.0-2.0 (Table XV). The incidence of infection was very low, without any distinct seasonal trends. However, the highest value of the incidence was recorded in August (10.0% of 30 fish) (Table XV).

Effects of host sex

(i) Tetracotyle sp. I.

Fig. 10. Frequency distribution of <u>Tetracotyle</u> sp. I in perch
from two sites in Llyn Tegid. Gill net samples.

% FREQUENCY

Site B (I2m) April/May 1975
Number fish 53

Site A (6m) June/July 1975
Number fish 60

NUMBER PARASITES / FISH
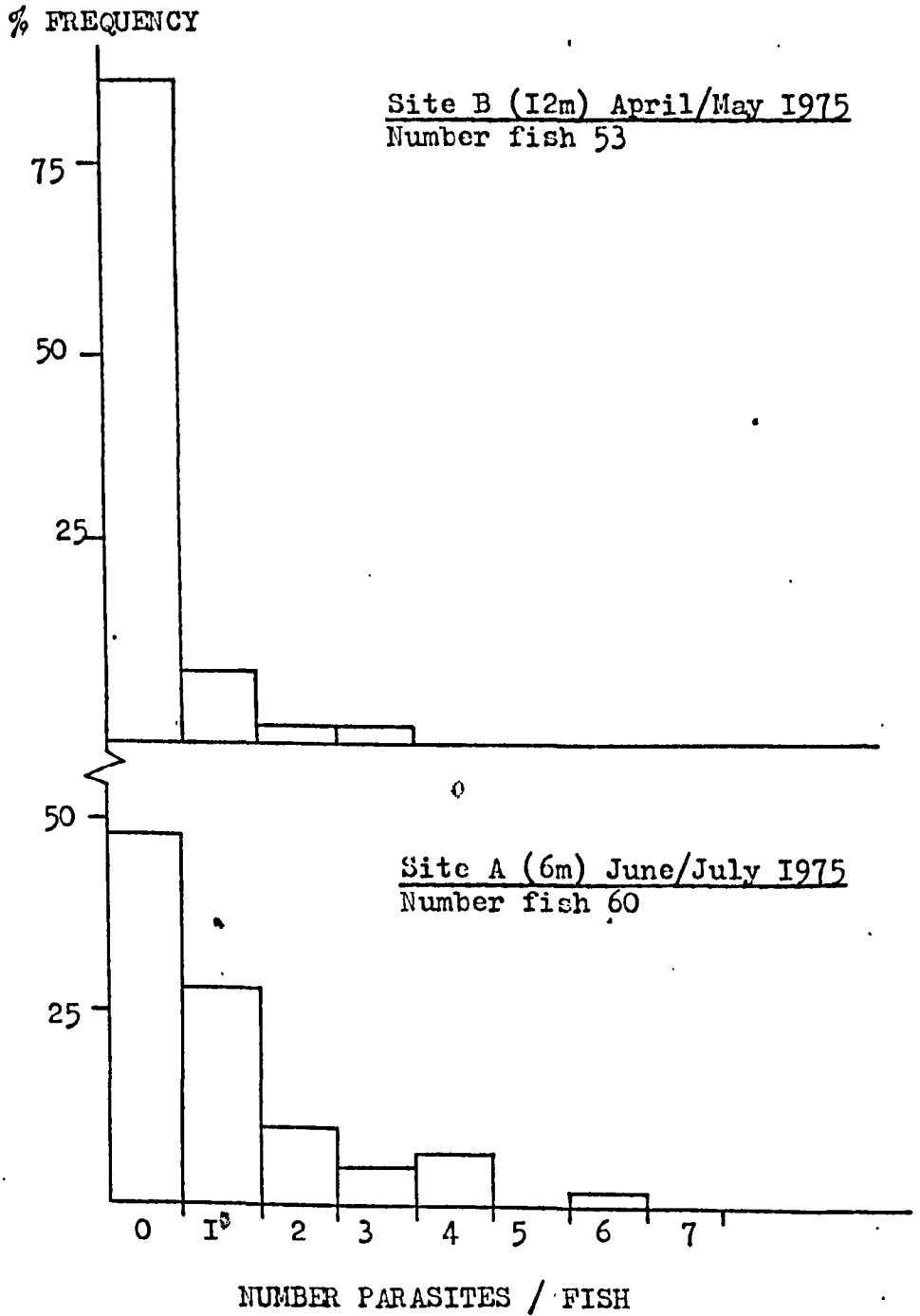
Fig. II. Frequency distribution of <u>Tetracotyle</u> sp. I in perch
from site B (12m). Gill net samples. June/July 1975,
and October/November 1975.

% FREQUENCY

Site B (12m) June/July
Number fish 19

Site B (12m) October/
November
Number fish 54

NUMBER PARASITES / FISH
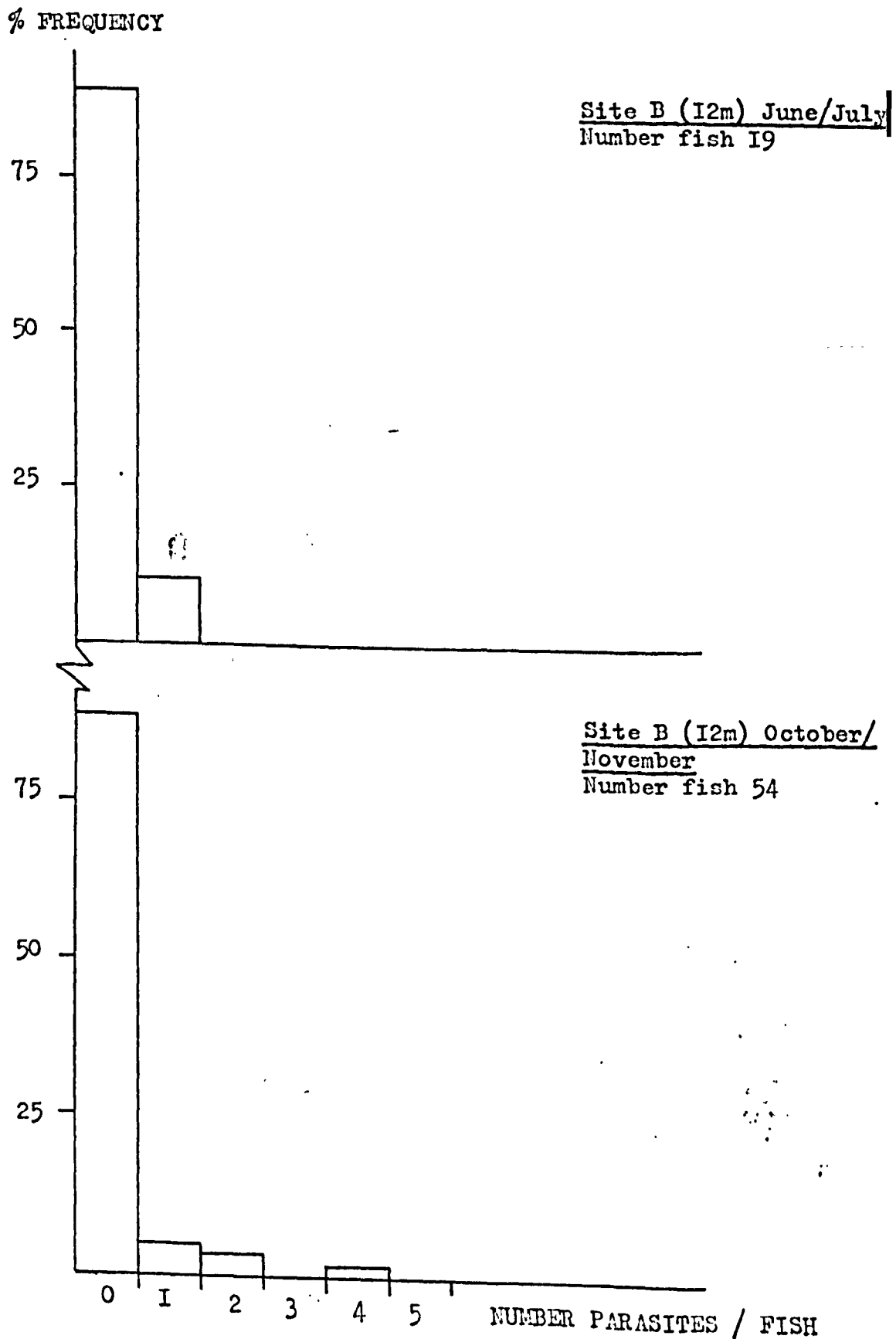
Table XIV. Seasonal aspects of the <u>Tetracotyle</u> sp. infection from the swimbladder of perch. Gill net samples. January 1975-February 1976.

Month	Number fish examined	% incidence	Total number parasites	Mean/infected fish	Maximum
J	6	16.7	2	(2)	2
F	30	10.0	4	1.3	2
M	30	13.3	10	2.5	5
A	30	10.0	6	2.0	3
M	30	13.3	4	1.0	1
J	39	48.7	37	1.9	6
J	40	35.0	25	1.8	4
A	30	30.0	27	3.0	10
S	30	6.7	3	1.5	2
O	60	16.7	15	1.5	4
N	54	14.8	11	1.4	2
D	35	22.9	17	2.1	8
J	30	16.7	5	1.0	1
F	21	14.3	4	1.3	2
TOTAL	465	20.0	170	1.8	10

Total number infected fish 93

Table XV. Seasonal aspects of the _Tetracotyle_ sp. II infection from
the eyes of perch. Gill net samples. January 1975-February
1976.

Month	Number fish examined	% incidence	Total number parasites	Mean/infected fish	Maximum
J	6	16.6	3	(2)	3
F	30	-	-	-	-
M	30	6.7	4	2.0	3
A	30	3.3	1	(1)	1
M	30	6.7	4	2.0	3
J	39	2.6	1	(1)	1
J	40	7.5	3	1.0	1
A	30	10.0	4	1.3	2
S	30	3.3	1	(1)	1
O	60	5.0	4	1.3	2
N	54	7.4	5	1.3	3
D	35	2.9	1	(1)	1
J	30	-	-	-	-
F	21	4.8	2	(2)	1
TOTAL	465	4.9	33	1.4	3

Total number infected fish 23

Fifty-five of 282 female gill netted perch (19.5%) were infected, with a mean intensity/infected fish of 1.5 (maximum 4). Thirty-seven of 183 male gill netted perch (20.2%) were infected with a mean intensity/ infected fish of 2.3 (maximum 10). These results suggest that while the incidence of infection was similar in male and female fish, the former may be more heavily infected.

The infection in male and female perch is illustrated in Fig. 12. In both sexes the distribution pattern of the parasite was overdispersed. A X^2 test (variance to mean ratio) (Elliot, 1971) gave the following results:

FEMALES, X^2 503.90, d + 14.98, P < 0.001;

MALES, X^2 605.40, d + 17.93, P < 0.01.

No female perch harboured more than 4 metacercariae, while 5 of 37 infected male fish (13.5%) contained between 5-10 parasites (Fig. 12).

(ii) Tetracotyle sp. II.

Sixteen of the 23 infected gill netted fish (69.6%) were female (Table XVIII). However, this may be a reflection upon the greater number of female fish that were examined (see Chapter III). The occurrence of Tetracotyle sp. II was not sufficiently high to consider the effects of host sex further.

Effect of host age and length

(i) Tetracotyle sp. I.

The results from the sample of perch that were trawled in March (1976) indicated that perch may acquire the infection during their first year in Llyn Tegid. However, the incidence and intensity of infection in young of the year fish was very low. The absence of the infection from the purse seined fry and the adult trawled perch may be a reflection on the small sample sizes.

The effect of host age and length in the adult male and female gill

Fig. I2. Frequency distribution of <u>Tetracotyle</u> sp. I.
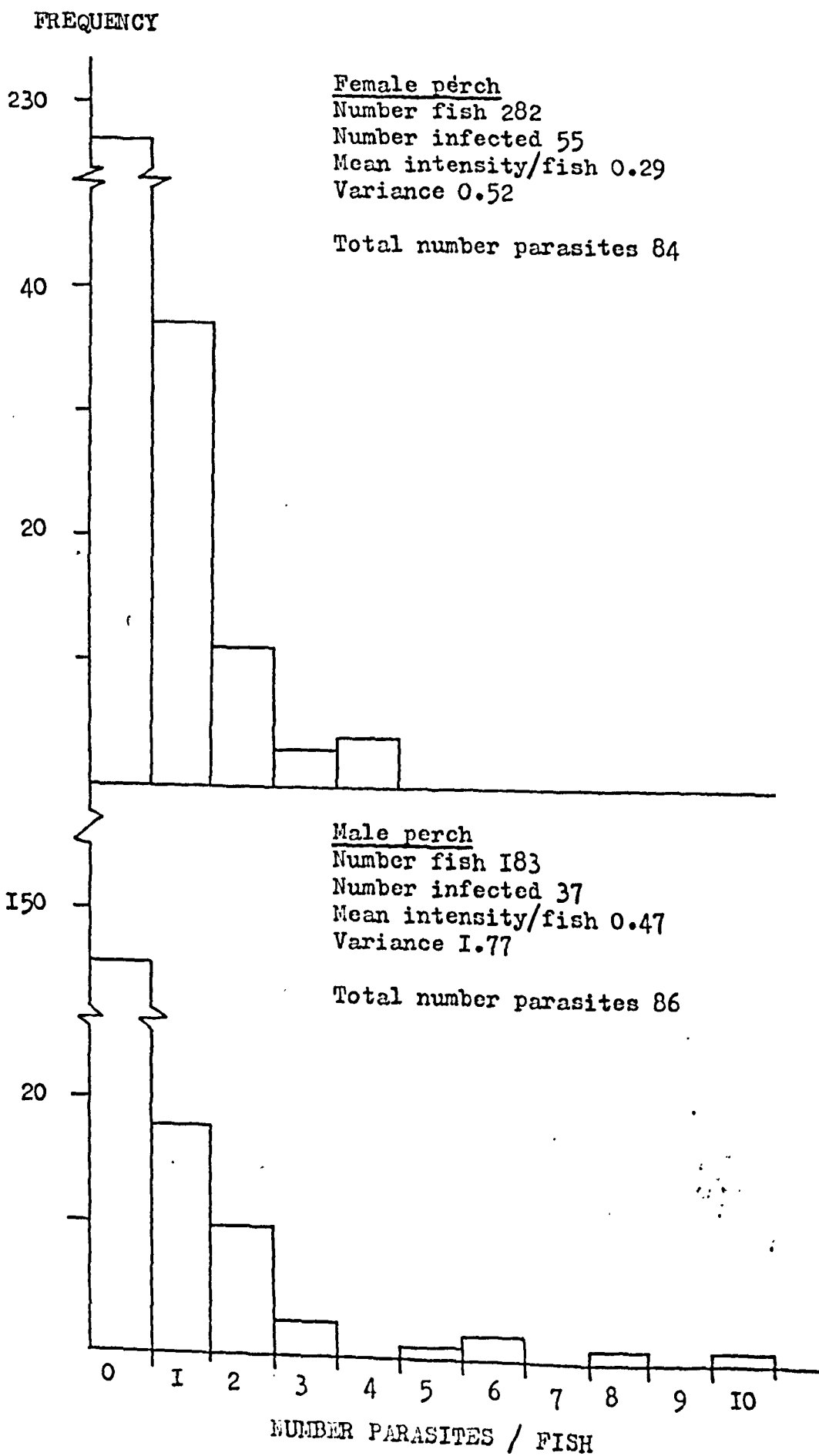Gill net samples. January I975 – February I976.

FREQUENCY

230 –

Female perch
Number fish 282
Number infected 55
Mean intensity/fish 0.29
Variance 0.52

Total number parasites 84

40 –

20 –

Male perch
Number fish I83
Number infected 37
Mean intensity/fish 0.47
Variance I.77

Total number parasites 86

I50 –

20 –

0   I   2   3   4   5   6   7   8   9   I0

NUMBER PARASITES / FISH

Table XVI.   Effect of host age on <u>Tetracotyle</u> sp. I infection of

swimbladder of perch.   Gill net samples.   January 1975–

February 1976.

Age (yrs.)	Number fish examined	Number fish infected	% incidence	Mean/infected fish	Maximum
MALE FISH					
2-2++	2	-	-	-	-
3-3++	51	6	11.8	1.7	3
4-4++	66	14	21.2	1.4	3
5-5++	40	8	20.0	2.8	8
6-6++	16	6	37.5	3.7	10
⩾7	8	3	37.5	4.0	6
FEMALE FISH					
2-2++	2	-	-	-	-
3-3++	87	12	13.8	1.5	3
4-4++	98	15	25.5	1.4	4
5-5++	38	5	13.2	1.2	2
6-6++	27	7	25.9	2.1	4
⩾7	30	6	20.0	1.7	4

Table XVII.   Effect of host length on <u>Tetracotyle</u> sp. I infection of
swimbladder of perch.   Gill net samples.   January 1975-
February 1976.

Length (cm)	Number fish examined	Number fish infected	% incidence	Mean intensity/ infected fish	Maximum
MALE FISH					
9.0-11.9	43	9	20.9	2.9	10
12.0-14.9	124	25	20.2	2.0	8
15.0-17.9	13	2	15.4	1.5	2
$\geqslant$ 18.0	3	1	33.3	(6)	.6
FEMALE FISH					
9.0-11.9	13	3	23.1	1.0	1
12.0-14.9	197	40	20.3	1.6	·4
15.0-17.9	46	6	13.0	1.3	2
$\geqslant$ 18.0	26	6	23.1	1.5	3

Table XVIII. Infection of the lens of perch with _Tetracotyle_ sp. II.

Gill net samples. January 1975—February 1976.

MONTH	SEX	LENGTH (cm)	AGE (yrs.)	NUMBER LENS (II)	Tetracotyle sp. SWIMBLADDER (I)
1/75	F	24.4	6++	3	0
3/75	F	12.5	3++	1	0
	M	15.0	6++	3	0
4/75	F	14.7	5+	1	0
5/75	F	13.9	3+	1	1
	F	17.4	6+	3	0
6/75	F	14.0	3+	1	0
7/75	F	18.5	6+	1	3
	F	13.0	4+	1	1
	F	12.0	3+	1	0
8/75	F	17.4	7+	1	0
	F	12.7	4+	1	0
	M	13.0	4+	2	1
9/75	M	15.4	6+	1	1
10/75	F	19.9	8+	2	0
	F	15.3	4+	1	0
	F	14.0	4++	1	1
11/75	M	18.2	6++	1	0
	F	12.5	5+	1	0
	M	12.4	4++	1	0
	M	11.8	3++	2	0
12/75	M	12.3	4++	1	1
2/76	F	14.2	5++	2	0

netted perch is shown in Table XVI and XVII. The infection was present in fish of all ages and lengths, though the incidence of infection may be lower in fish aged 2-3++. A one way analysis of variance was applied to the log (x+1) transformed parasite counts in male fish aged 3, 4, 5 and 6 years, and in female fish aged 3, 4, 5, 6 and $\geq$ 7 years. In both instances there was no significant difference in the mean intensity/infected fish in fish of different age classes (MALE PERCH: F + 1.92, $v_1 = 3$, $v_2 = 30$, P $>$ 0.05; FEMALE PERCH: F = 1.17, $v_1 = 4$, $v_2 = 50$, P$>$ 0.05). The adequacy of the transformation was checked by graphical means (Elliot, 1971).

(ii) Tetracotyle sp. II.

From Table XVIII it can be seen that adult gill netted perch of all ages and lengths were infected. The absence of the infection from the purse seined and trawled samples may be a reflection on the very low incidence of this parasite in relationship to the sample sizes of fish examined.

Relationship between the infection with Tetracotyle sp. I and Tetracotyle sp. II.

The results are summarised in Table XVIII. Perch infected with Tetracotyle sp. II may be uninfected, or harbour 1-3 metacercariae, of Tetracotyle sp. I. There was no apparent relationship between the incidence and intensity of the two infections (Table XVIII).

VII.2.3   DISCUSSION

The division of the strigeoid metacercariae that parasitise fish into four groups has been noted in section VII.1.4 (after Hoffman, 1960; Sweeting, 1971b).

The Tetracotyle sp. infecting the eyes of perch was similar to that found infecting the swimbladder, though they differed on a number of

points (Table XIII). Whilst the infection of the eye and of the swimbladder may have represented two species of metacercariae, it is possible that the observed morphological differences may have been a result of the different sites of infection influencing the dimensions of a single species of parasite.

Sweeting (1971a, b) and Tinsley and Sweeting (1974) considered the effect of site of infection on the host reaction to strigeoid metacercariae. It was considered that certain areas of the host body (e.g. lens of eye, vitreous humour, etc.) are immunologically inert or attenuated. In sites such as these there is no encapsulation of the parasite by the host, and the parasite produces no endogenous cyst. The host reaction (or lack of it) and the typically unencysted state of many strigeoid metacercariae were thought to be closely correlated (Tinsley and Sweeting, 1974). In contrast, strigeoids inhabiting musculature (Cotylurus sp.), skin (Posthodiplosomum sp.) and to a variable extent the body cavity (Neascus sp.) are encysted. No observations were made on the nature of the cyst surrounding Tetracotyle sp. in perch at Llyn Tegid. However, the presence of the encysted parasite in an immunologically inert site such as the lens/vitreous humour of the eye, may have been a result of the parasite producing an endogenous cyst that is normally associated with its more usual occurrence in the swimbladder of the host.

The occurrence of metacercariae in perch from the British Isles was summarised in Chapter IV, Table I. The infection of perch with Apatemon annuligerum, Ichthyocotylurus cucullus, Ichthyocotylurus sp., Tetracotyle percafluviatilis, T. variagatus and Tetracotyle sp. is of relevance here. In addition, Rawson (1952) recorded undetermined metacercariae from perch (at Lake Windermere) (see Chapter IV, Table I).

Rizvi (1964) found that the perch at Rostherne Mere (Cheshire) were infected with Tetracotyle sp. The infection was situated in the peritoneum

and pericardial cavity, and was present throughout the year. The
intensity of infection ranged between 20-310. Shillcock (1972) found
9.0% of 127 perch from Ockendon Moat (Essex) were infected with T.
percafluviatilis. The mean intensity/infected fish was 5.3. There
was a high incidence of infection of perch at Loch Leven (Scotland)
with metacercariae tentatively identified as Cotylurus cucullus/Tetracotyle
communis. The encysted metacercariae were commonly found in the swimbladder,
and less often on the heart and pericardial wall (Campbell, 1974). Wootten
(1973a) recorded Ichthyocotylurus sp. from the abdominal cavity of 45.9%
of 181 perch from Hanningfield Reservoir (Essex). Continental European
studies on tetracotylid infestations of perch include Bykhovskaya-Pavlovskaya
(1940), Barysheva and Bauer (1957), Kozicka (1958; 1961), Rauckis (1968,
1970a), Odening and Böckhardt (1971) and Tell (1971). In the majority
of these studies the infection was located at various visceral sites in
the fish, particularly the heart and swimbladder. However, Kozicka (1958)
found large metacercariae free and encysted in the brain and vitreous
humour of the eye of perch from Lake Druzno (Poland). The metacercariae
from the brain were designated Tetracotyle sp. 1 and those from the eye
Tetracotyle sp. 2. Kozicka (1961) later identified Tetracotyle sp. 1 as
T. annuligerum.

The incidence and intensity of the infestation of perch at Llyn
Tegid with Tetracotyle sp. (I and II) was low. The results suggested
that perch acquired the infection during their first year in the lake.
From 36 fish examined at the end of their first year in Llyn Tegid 5.6%
were infected with Tetracotyle sp. I. Few fish aged 1-2++ years were
captured, and hence the level of infection in these fish remains questionable.
However, it would appear that during the second and third years that the
perch spend in the lake, the incidence of infection rises, reaching a
peak in fish aged 4-4++. Thereafter, the incidence may have remained
constant, with the infection present in even the oldest, largest perch.

There is no significant increase in the mean intensity/infected adult

male and female fish with increasing host age. Since strigeoid meta-

cercariae are often long lived, it might be expected that the intensity

of infection would rise with increasing host age and length (as with

Diplostomum gasterostei, section VII.1). However, with the observed

low incidence of infection with Tetracotyle sp. in perch at Llyn Tegid,

superimposed infections may have been relatively uncommon. In addition,

behavioural and/or physiological factors may influence the occurrence

of superimposed infections. Wootten (1974) found an increase of the

infection of Diplostomum spathaceum and Tylodelphys clavata in rainbow

trout and of T. clavata in perch up to a certain point, with a decrease

in older, larger fish. Wootten attributed this to an increasing number

of cercariae being destroyed after penetration by host reaction, or the

spatial separation of fish from the cercariae.

Fish parasitic digeneans of the Order Strigeidida are characterised

by utilising a gastropod molluscan first intermediate host (Bykhovskaya-

Pavlovskaya et al., 1962). The seasonal release of cercariae by molluscan

intermediate hosts of digenetic trematodes has been noted by several

authors (e.g. Rees, 1932; Sindermann and Farin, 1962; Olson, 1970;

Pennycuick, 1971a; Erasmus, 1972; etc.) and was discussed in section

VII.2.3. In addition, Styczynska-Jurewicz (1959) has found that the

infection of Diplostomum spathaceum in the fish Leucaspius delineatus

held in cages at varying distances from the shore, varied inversely with

the distance from the shore. The abundance of cercariae was greatest

near the littoral zone where the molluscan intermediate hosts were most

abundant. At Llyn Tegid it appeared that perch primarily acquired

Tetracotyle sp. I while in shallow water during the summer months (June-

September). The incidence (and to a lesser extent the intensity) of

infection rose when perch migrated from deep to shallow water. This

was presumably a result of the acquisition of the infection in the

shallow, littoral zone. At the end of September the fish from the shallows returned to deeper water, and there was an apparent fall in the incidence (and intensity) of the infection. Since the intensity of infection was not sufficiently high to postulate parasite induced host mortalities, the observed fall in the occurrence of Tetracotyle sp. I may be a result of one or both of the following factors. The metacercariae may have a short life span, and the infection may disappear after 2-3 months. However, digenean cercariae are frequently shed during the warmest months of the year in temperate regions. This along with the occurrence of the metacercariae in all months of the year, suggested that the metacercariae probably live for an extended period of time. Therefore the fall in the incidence and intensity of Tetracotyle sp. I in the autumn may be a result of the mixing of more heavily infected fish from shallow water, with the more lightly infected fish from deeper water. This was suggested for Diplostomum gasterostei (see section VII.2.3), in relation to the lack of seasonality observed for that parasite, and is discussed further in Chapter XI.

The incidence of infection with Tetracotyle sp. I was similar in male and female perch. However, these appeared to be a higher mean intensity/ infected male fish. The frequency distributions of the parasite counts in male and female fish suggested that this may have resulted from the chance capture of a small number of heavily infected male perch, since the parasite population was shown to be overdispersed. However, there may have been ecological and/or physiological reasons for this discrepancy. Male perch may be physiologically more suitable for infection with Tetracotyle sp. I, though supporting evidence is lacking. Alternatively, male fish may spend a longer period in shallow water, during the spring-summer months when the cercariae are presumably released. Wheeler (1969) stated that male perch precede the females onto the spawning beds.

VII.2.4   SUMMARY

Tetracotyle sp. were found encysted onto the eye lens and in the swimbladder of perch at Llyn Tegid. This was a new parasite record for the lake. Further investigations are needed to elucidate the taxonomic relationships between the two forms, and their exact identity.

The two infections were considered separately. The incidence of infection with Tetracotyle sp. II (lens) was very low and did not permit extensive analysis. There was an apparent peak in incidence in August. More data were available for Tetracotyle sp. I (swimbladder). The incidence of infection was low, and it appeared that the fish acquired the infection during the summer months, primarily whilst in shallow water. The incidence and intensity of infection was higher in fish from the shallows during the summer months, and this may be a further indication of the discrete nature of the shallow and deep water perch populations during these months. In the autumn, the fish from the shallows returned to deeper water, where they mixed with the more lightly infected fish, which resulted in an apparent fall in the incidence and intensity of infection. The parasite was present in fish that had spent a 'single summer in the lake (aged 0++), and the incidence reached a peak in fish aged 4-4++. Thereafter the incidence may have remained constant. The intensity of infection did not increase with the age of adult perch. This may be related to the life span of the metacercariae being one year (or less), or the low incidence of infection reducing the likelihood of superimposed infections. Other factors which may have influenced the infection in older fish were considered. Male fish were more heavily infected than females, which may be a result of their greater physiological suitability to infection, or the fact that male perch are thought to precede the females onto the spawning beds in the spring-summer, and may hence spend a greater period of time in contact with the cercariae.

VII.3   Family Allocreadiidae Stossich, 1904

Genus Bunodera Raillet, 1896

Bunodera luciopercae (Müller, 1776)

VII.3.1   INTRODUCTION

Adult digeneans of the family Allocreadiidae are common

parasites of the digestive tract of freshwater and marine fish

(Bykhovskaya-Pavlovskaya et al. (1962). Kennedy (1974) reviewed

the occurrence of parasites in the freshwater fish of the

British Isles, and recorded the following species of allocreadiid

flukes: Allocreadium isoporum, A. transervale, Bunodera luciopercae,

Crepidostomum farionis, C. meteocus and Sphaerostoma bramae. Bunodera

luciopercae is a Holarctic species, and the genus is closely related

to both Allocreadium and Crepidostomum (Hopkins, 1934; Cannon, 1971).

B. luciopercae is a common parasite of perch (Perca fluviatilis)

in the British Isles and Europe, and of yellow perch (P. flavescens)

in North America (Bykhovskaya-Pavlovskaya et al., 1962; Hoffman,

1967; Kennedy, 1974). In the British Isles, B. luciopercae has

been recorded from perch at a number of localities (see Chapter IV,

Table I). This parasite has also been recorded from pike (Esox

lucius) from the Shropshire Union Canal (Cheshire) and Loch Leven

(Scotland) (Mishra & Chubb, 1969; Campbell, 1974), from ruffe

(Gymnocephalus cernɣa), ten-spined stickleback (Pungitius pungitius)

and brown trout (Salmo trutta) from Hanningfield Reservoir (Essex)

(Wootten, 1973a, b), and from brown trout in Scotland and Ireland

(Ritchie, 1915; Vickers, 1951).

The life cycle of B. luciopercae was described by Wisniewski

(1958), who found that bivalves (Sphaerium corneum and S. rivicola)

were the natural first intermediate hosts in Poland. Wisniewski

also found the metacercariae in naturally infected copepods

(Mesocyclops oithonoides and M. crassus), and experimentally

infected several species of cladocerans and an ostracod.

Moravec (1969) described the larval development of B. luciopercae

in Pisidium casertanum and P. personatum under experimental conditions,

but was unable to infect S. corneum. In North America, Cannon (1971)

found that P. variabile was a suitable first intermediate host, and

that species of cladocerans, amphipods and larval ephemeropterans

were suitable experimental second intermediate hosts.

VII.3.2   ADDITIONAL MATERIALS AND METHODS

Seasonal maturation of Bunodera luciopercae

The state of maturity of the flukes from the perch at Llyn

Tegid was assessed on a modified Wootten (1973c) scale (see

Appendix III).

In vitro hatching of eggs of Bunodera luciopercae

Perch were gill netted from Llyn Tegid during late April 1976.

The fish were killed at the lakeside and transported to Liverpool

in chilled, insulated boxes. They were stored overnight in a

refrigerator at 4-5°C. The following morning the alimentary tract

of the fish was removed, and dissected in 0.85% sodium chloride

solution (saline). Gravid B. luciopercae were collected, washed

several times in saline and then dissected in dechlorinated tap

water. The eggs of several B. luciopercae were mixed and then

subsampled for use in the following experiments.

(a) Temperature 20-24°C. Two dishes were maintained under natural environmental daylength conditions, while two dishes were maintained in total darkness.

(b) Temperature 13-21°C; and (c) temperature 17-22°C. Four dishes were maintained at each temperature under natural daylength conditions. Four dishes were kept at each temperature in total darkness.

(d) Temperature 1-8°C. Four dishes were maintained in total darkness.

(e) Temperature 1-8°C/22-24°C. Two dishes were kept at the lower temperature for 26 days, and then exposed to 22-24°C. The experiment was performed in total darkness.

Each day the dishes were examined using a binocular microscope, and any miracidia removed.

Intra-molluscan development of Bunodera luciopercae

(1) Natural infection at Llyn Tegid

Bivalves were sampled at approximately bimonthly intervals, between February 1976 - March 1977. The molluscs were collected from a depth of 1-2m, at a site directly in front of the University laboratory at Llyn Tegid, using a Petersen grab. In Liverpool, the bivalves were sorted and examined within 48 hours of collection. Only Pisidium sp. were encountered. These molluscs were squashed onto a microscope slide using a coverslip and examined at low and high power.

(2) Laboratory studies on the infection of Pisidium sp.

Pisidium sp. (whose specific identity* is under investigation by

* Identified as Pisidium casertanum and P. personatum (MacMillan, pers. comm., 1977).

Mrs. M¢cMillan of the Liverpool Museum) were obtained from a fish-free pond at Prescott (Merseyside). The absence of digenetic trematode stages resembling B. luciopercae was confirmed by the examination of 50 pisidia in February 1976. There was a low incidence of metacercariae of the echinostome type.

Samples of Pisidium sp. were subsequently collected in March-April 1976. Batches of 200 bivalves were maintained in polythene trays measuring 25 x 15 x 12 cm (deep), in 5-8 cm of dechlorinated tapwater. The water was gently aerated and fine sand was used as a substrate. The molluscs were fed on fragments of Elodea sp. from a culture in the Parasitology Aquarium, on boiled, dried, crushed lettuce leaves (after Mahoney, 1966) and on Aquarian Vegetable Diet flaked fish food.

The pisidia were infected with B. luciopercae as follows. The eggs were removed from gravid flukes as described as above. The eggs from 10 gravid B. luciopercae were used to infect each tray of 200 molluscs. Until hatching was seen to have begun the eggs were maintained in dechlorinated tapwater at $20^{\circ}C$. When hatching started (usually after 5-6 days), the eggs were added to each tray of molluscs, and left for a further 10 days at $20^{\circ}C$. By this time infection was assumed to have occurred, and the trays of molluscs were removed to the following experimental conditions. Day 0 of the experiment was taken as the first day at the experimental temperature. Two trays of 200 pisidia were maintained at each temperature and the daylength was 16h/8D in all instances.

(a) Temperature 4-8°C

(b) Temperature 16-21°C

(c) Ambient, unheated room temperature (see Fig. 13).

At regular intervals the molluscs were examined for infection with B. luciopercae as described above.

Maturation of Bunodera luciopercae in laboratory perch

Despite the large amount of literature concerning the seasonal maturation of the digenean parasites of fish (see Chubb, in prep. for a review), there have been very few attempts to study this phenomenon under controlled, laboratory conditions. This may be a result of several factors, particularly the problems often associated with the maintenance of large numbers of infected fish, and the complex nature of the life cycle of these parasite, inhibiting large scale experiments.

Initial observations at the University of Liverpool indicated that perch was an excellent laboratory fish, and fared well under a range of experimental conditions. Large numbers of infected perch could not be caught at Llyn Tegid and transported live to Liverpool. Gill netting, trapping (wire mesh Windermere perch traps) and trawling (see Chapter II) all provided fish of poor quality. In addition, whilst large numbers of live infected perch could be caught in August and September by the use of beach seines, their successful transport to Liverpool proved difficult. Bearing these problems in mind, along with the slow intra-molluscan development of B. luciopercae (Moravec, 1969; Cannon, 1971), and the need for the large scale maintenance of infected pisidia and crustacean intermediate hosts, it was decided to investigate the

Fig. I3. Temperature range of Pisidium sp. culture. Ambient, unheated room temperature. May I976 – February I977.
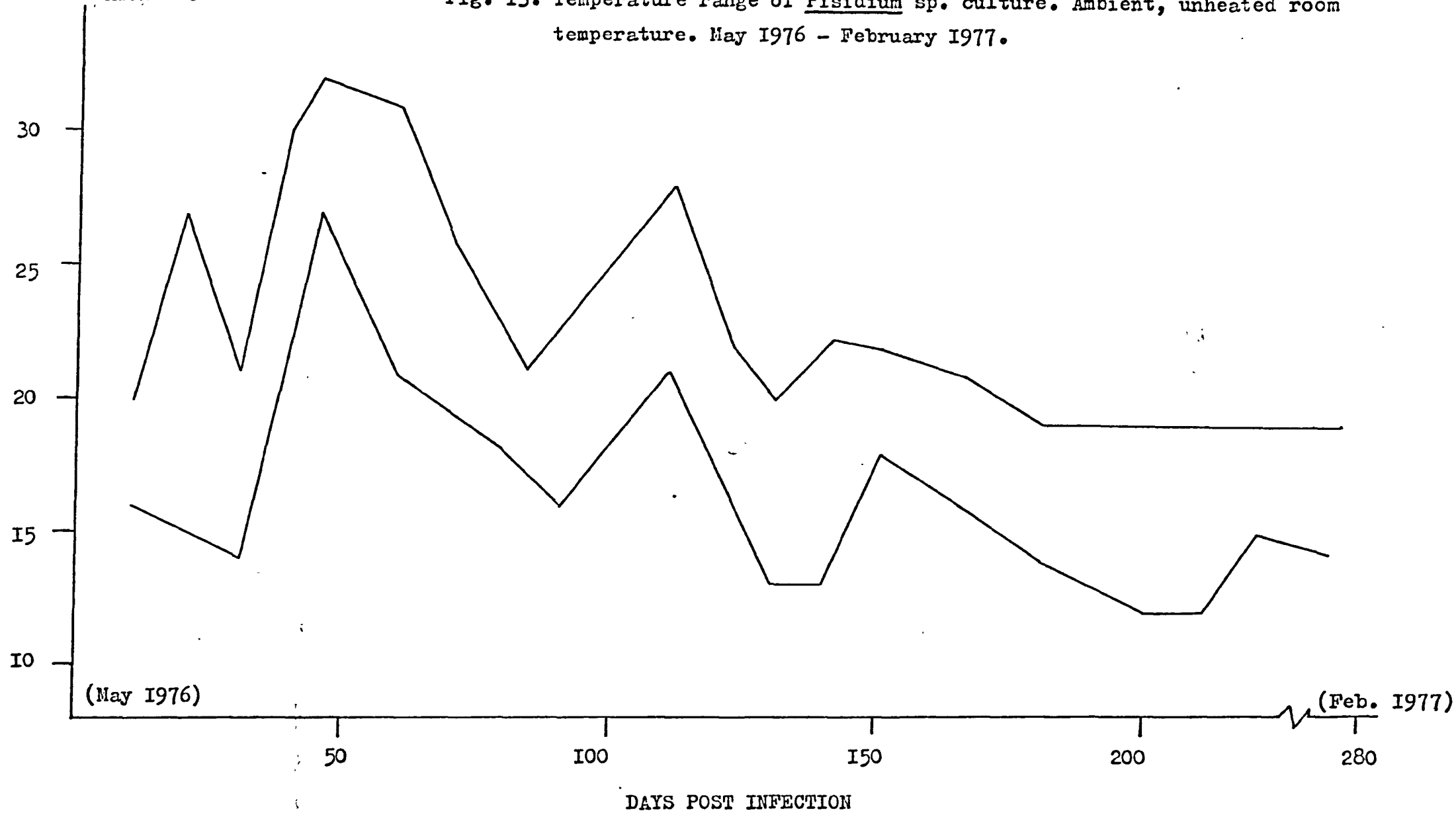
the possibility of the transfer of live B. luciopercae directly from dead infected to live uninfected perch. Similar techniques have been used by Goodchild (1954) in the study of gorgoderine digenetic trematodes from the urinary bladder of the frogs Rana pipiens and R. catesbieana by Goodchild (1958a, b) in the study of the digenean Schistosomatium douthittii and the cestode Hymenolepis diminuta in rats, by Bacha (1962) concerning the transfer of the digenean Zygocotyle lunata from one rat to another, by Read (1967) in the study of longevity in Hymenolepis diminuta in rats, by Willemse (1968) in the study of the host specificity of the cestodes Proteocephalus fillicollis and P. ambiguus in various species of fish, by Hnath (1969) in the experimental investigation of the secondary invasion of the trout Salvelinus fontinalis by the acanthocephalan Echinorhynchus salmonis, and by Hiscox & Brocksen (1973) in the study of the nematode Bulbodacnitis ampullastoma in the trout Salmo gairdneri.

In a trial experiment stage (1) B. luciopercae (see Appendix III) were dissected from perch gill netted and killed at Llyn Tegid several hours previous, and transferred per os (in 0.85% saline) into uninfected, laboratory perch. The experiment produced a high degree of success. Subsequently Ringer-Locke solution (Gatenby & Painter, 1937) and Young's teleost saline (Harris, 1971) were used as the transfer medium, though this did not result in any increase in the degree of success.

Therefore, in order to study the maturation of B. luciopercae in its definitive host under laboratory conditions, large numbers of small perch (10.0-12.0 cm) were beach seined from Princes Park Lake (Merseyside) where the infection was known to be absent. Their

initial treatment, quarantine and care was described by Andrews (1976).

After a period of at least six weeks in the laboratory, these fish were infected with B. luciopercae as follows. Perch were gill netted from Llyn Tegid during September and October 1976. They were killed at the lakeside and transported to Liverpool in chilled, insulated boxes. The alimentary tract of the fish was removed and dissected in 0.85% saline. Active, apparently healthy stage (1) - early stage (II) B. luciopercae (see Appendix III) were removed, washed several times in fresh saline, and then transferred per os into the stomachs of uninfected perch from Princes Park Lake. Approximately 10 flukes were administered to each fish in a small quantity of 0.85% saline, using a smooth ended Pasteur pipette with a vaselined tip. During this operation the recipient was starved for 12 hours prior to infection, and was offered food on several occasions directly following infection. Ginetskaya (1958) stated that host starvation speeded the passage of procercoids of Triaenophorus nodulosus (Cestoda) through the stomach and into the intestine of piscine second intermediate hosts. This consequently resulted in a greater level of infestation (Ginetskaya, 1958).

The time taken from the removal of fish from the gill nets (and their consequent death) at Llyn Tegid, to the transfer of B. luciopercae into uninfected perch at Liverpool, was between 6-8 hours.

The fish were then kept at 20°C for 12-36 hours, and subsequently maintained under the following experimental conditions.

(a) Temperature: constant cool. Fifteen infected perch were maintained in two polythene bins of 45 litres of aerated tapwater, in a cold-

room set to run at 6°C. The temperature of the water in which

these fish were maintained fluctuated between 4-8°C.

(b) Temperature: constant warm. Three 135 litre glass aquaria were

used to maintain 15 infected perch at a water temperature of 16-20°C.

The temperature in each aquarium was maintained within these

limits by the use of two 100 watt aquarium heaters plus thermostat.

The water was well aerated.

(c) Temperature: natural environmental. Three 135 litre glass

aquaria were used to maintain 15 infected perch at natural environmental

temperatures. The aquaria were maintained in a sheltered (yet open-

sided) aviary on the roof of the University of Liverpool. The

experiment ran from October 1976 - March 1977, and the range of air

temperatures recorded are shown in Fig. 14. Slight aeration was

supplied.

(d) Temperature: constant cool/constant warm. Fifteen infected

perch were kept in a polythene bin of 65 litres of aerated tapwater

in a cold-room set to run at 6°C for 43 days. During this period

the water temperature fluctuated between 4-8°C. On day 43 these fish

were removed from the cold-room and the temperature of the water in

which they were maintained was allowed to slowly rise to room

temperature (approximately 20°C). On day 44 these fish were

transferred to two 135 litre glass aquaria containing well aerated

tapwater. The temperature of these aquaria was kept at 16-20°C

as described above.

In all instances the daylength was kept constant at 16L/8D.

Natural daylight was excluded by the use of black polythene sheeting

and dark insulation tape. The long-day conditions were supplied by

the use of Grolux aquarium lighting equipment and electrical time

switches. The fish were fed ad libitum on live tubifex, maggots

Fig. I4. Range of air temperatures in perch — Bunodera luciopercae experiment. Natural environmental temperatures.
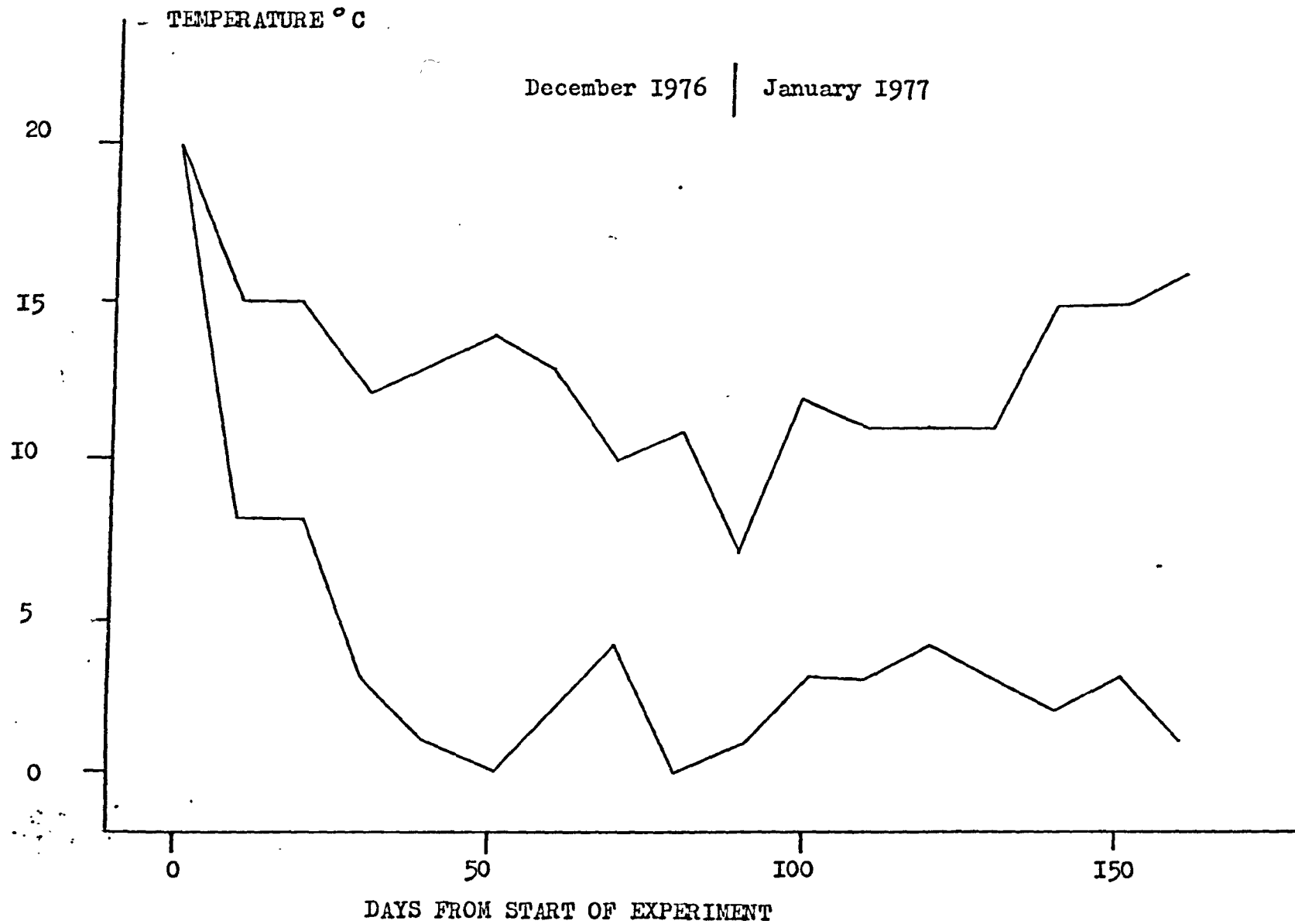
and mealworms (Tenebrio larvae). Dietritus was siphoned from each aquarium at weekly intervals and 20% of the water replaced with fresh tapwater (at the correct temperature).

At regular intervals perch were killed by a blow to the head and examined for B. luciopercae. The parasites were examined live in 0.85% saline, and their state of maturity assessed on a modified Wootten (1973c) scale (see Appendix III). The flukes were then killed in a relaxed condition by the use of hot (60-70°C) water (Slusarski, 1958), before fixation in 5-10% formalin. For future reference the parasites were stained in Borax Carmine, dehydrated, cleared and mounted in D.P.X.

Day 0 was the day at which the fish were placed at their experimental temperature (i.e. 12-36 hours post infection).

VII. 3.3   RESULTS

VII. 3.31 Field Studies

Bunodera luciopercae was found in 391 of 465 (84.1%) of the adult perch gill netted from Llyn Tegid between January 1975 - February 1976. The mean intensity/infected fish was 23.4 (maximum 686). The mean intensity/fish was 19.7. Seven of the 30 perch fry examined in July 1976 were infected (23.3%), with a mean intensity/infected fish of 2.3 (maximum 5). The mean intensity/ fish was < 1. Of 64 perch trawled in March 1976, 55 (85.9%) were infected with a mean intensity/infected fish of 8.2 (maximum 24). The mean intensity/fish was 7.0.

Seasonal occurrence

The seasonal changes in incidence and intensity of the infection

are shown in Table XIX. The incidence was high (100.0%) during

January - April 1975. In May 1975 the incidence began to fall,

and reached a minimum of 15.0% in July. During August 1975 the

incidence rose sharply to 90.0%, and remained high until the

end of the study period (February 1976) (Table XIX).

The intensity of infection followed similar seasonal trends.

During the autumn - spring months of January - March 1975 and

October - February 1975/76, the intensity usually fluctuated between

13.4 - 20.9 (Table XIX). The high intensity of infection in

February 1975 is a result of a single perch harbouring 686 flukes

(Table XIX). The intensity began to fall in April 1975 and reached

a maximum of 2.9 in June 1975. There was a slight increase of

the intensity during July 1975, followed by a marked peak during

August and September (Table XIX). In October 1975 the intensity

fell to a lower constant autumn - winter value (Table XIX).

Seasonal maturation

The maturation of B. luciopercae in perch at Llyn Tegid went

through a succession of stages which culminated in maximum egg

production during April - June 1975. The following stages of

maturity refer to the modified Wootten (1973) c scale shown in Appendix III.

Juvenile stage (I) flukes were present (which may be taken to

indicate recruitment) in all months except June 1975 (Table XX,

Fig. 21). However, maximum recruitment occurred during August

and September (and to a lesser extent October and November) 1975

as shown by the large numbers of stage (I) B. luciopercae present

in those months (Table XX).

Table XIX. Seasonal occurrence of Bunodera luciopercae. Gill net

samples. January 1975 - February 1976

Month	Number Fish Examined	% Incidence	Total Number Parasites	Mean Intensity/ Infected Fish	Maximum
J	6	100.0	107	17.8	52
F	30	100.0	1382	46.1	686
M	30	100.0	401	13.4	53
A	30	100.0	204	6.8	29
M	30	83.3	241	9.6	55
J	39	56.4	64	2.9	15
J	40	15.0	68	11.3	50
A	30	90.0	1645	60.9	594
S	30	96.7	1780	61.4	207
O	60	86.7	1090	20.9	219
N	54	88.9	863	17.9	85
D	35	100.0	520	14.8	65
J	30	100.0	434	14.7	63
F	21	100.0	371	17.7	51
Total	465	84.1	9171	23.4	686

Total Number Infected Fish 391

Table XX. Seasonal maturation of <u>Bunodera luciopercae</u>. Gill net
samples. January 1975 - February 1976

Month	Total Number Parasites	% at Stage				
		(I)	(II)	(III)	(IV)	(V)
J	107	53.3	36.4	10.3	-	-
F	1382	17.6	63.0	18.1	1.3	-
M	401	3.7	45.4	43.6	4.7	2.2
A	204	3.9	18.1	37.7	7.8	32.4
M	241	0.8	1.6	51.4	25.5	20.6
J	64	-	-	3.0	15.2	81.8
J	68	97.0	-	-	-	3.0
A	1645	100.0	-	-	-	-
S	1780	98.9	1.1	-	-	-
O	1090	61.7	38.0	0.3	-	-
N	863	61.9	32.9	5.2	-	-
D	520	35.2	64.8	-	-	-
J	434	43.8	54.4	1.8	-	-
F	371	10.8	60.9	26.7	1.6	-

Total Number Parasites 9171

Stage (II) flukes were present from January - May 1975

(Fig. 21). They then appeared again in September, and were common

between October - February 1975/76 (Table XX, Fig. 21).

Stage (III) parasites occurred in most months, though they

were absent during July - September (and December) 1975 (Fig. 21).

However, this stage was most common between March - Mat 1975 and

February 1976 (Table XX, Fig. 21).

B. luciopercae at stage (IV) (containing eggs) first appeared

in February (1975 and 1976), and were present until June 1975 (Fig. 21).

Their low occurrence may indicate that the parasite passes from

stage (III), rapidly through stage (IV), and into stage (V) (Fig. 21).

Gravid stage (V) flukes were present between March - July 1975

(Fig. 21).

The seasonal maturation of B. luciopercae is shown in relation

to lake temperature (at 6m) in Fig. 21.

Effect of host sex

The results on the infection in adult male and female perch

gill netted between January 1975 - February 1976 are shown in Fig. 15.

In both instances the very overdispersed nature of the infection is

clear, with the variance much greater than the mean. The incidence

of infection was similar in fish of both sexes (males: 83.6% of 183

fish; females: 84.4% of 282 fish). The mean intensity/infected fish

was 17.2 and 27.5 in male and female perch respectively. These values

were compared and no significant difference found ($F = 1.19$, v_1 182,

v_2 281, $P > 0.05$; $d = +1.92$, $P > 0.05$). However, the high value of d

may indicate that the difference between the mean intensity in male

and female fish was approaching significance ($P = 0.05$, $d = 1.96$).

Fig. I5. Frequency distribution of <u>Bunodera luciopercae</u> in male and female perch. Gill net samples. January I975 — February I976.

% FREQUENCY

<u>Total number MALE fish</u> I83
Total number parasites 2627
Mean intensity/fish I4.4
Variance 2849.3

<u>Total number FEMALE fish</u> 282
Total number parasites 6544
Mean intensity/fish 23.2
Variance 2474.8

NUMBER PARASITES / FISH⟶

-264-
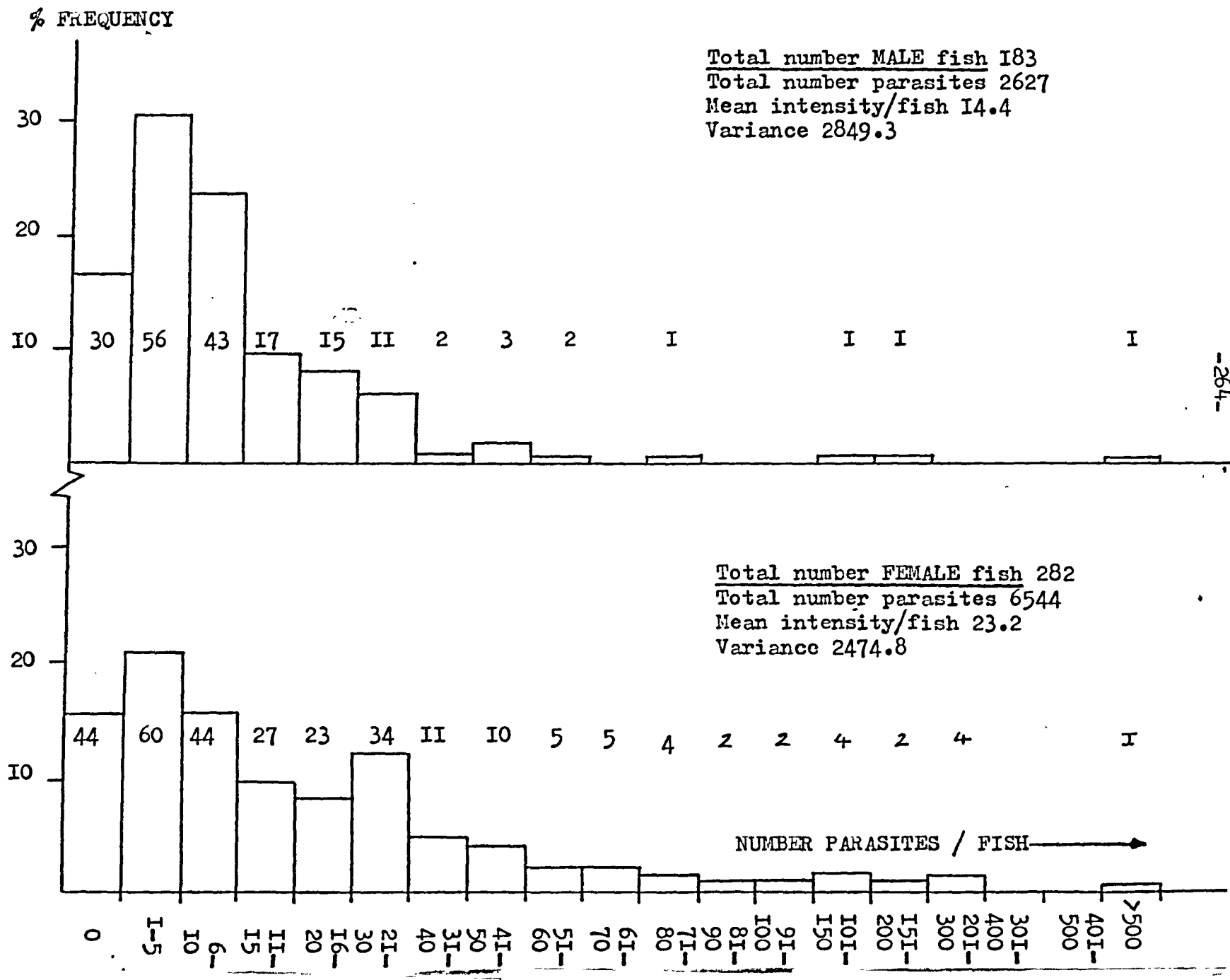
Effect of host age and length

Gravid <u>B. luciopercae</u> were found in juvenile perch (aged 8-9 months, length 3.0 - 8.9 cm) examined in March 1976, and in adult fish of all lengths and ages.

The effect of host age and length on the incidence and intensity of infection is shown in Table XXI and XXII. The incidence of infection was lowest in perch fry during their first summer in the lake. Of a sample of 30 fry examined in July 1976, 23.3% were infected with stage (I) flukes. The mean intensity/infected fish was 2.3 (Table XXI and XXII). The incidence of infection in the perch aged 0++ (8-9 months, length 3.0 - 8.9 cm) was 86.1%, while the mean intensity/infected fish was 6.5 (Table XXI and XXII). The incidence and intensity in the perch aged 1++ - 4++ (length 9.0 - 11.9 cm) from the trawl sample was similar to that found in the samples of adult gill netted perch aged 2 - 3++ (length 9.0 - 11.9 cm) (Table XXI and XXII).

The infection was prevalent in all length and age groups of adult gill netted perch (Table XXI and XXII). In perch less than 7 years old the intensity of infection reached a peak in the age group 4 - 6++ (Table XXI). The high value of intensity in the 2 - 2++ age group was a result of a single perch harbouring 89 parasites. In the oldest age group ($\geqslant$ 7) there was a sharp increase in the mean intensity/infected fish (Table XXI). The intensity of infection was similar in the perch of length groups 9.0 - 11.9 cm and 12.0 - 14.9 cm (Table XXII). In the perch larger than this there was a distinct increase in the mean intensity/infected fish (Table XXII).

To investigate the effect of host length further, the gill netted fish were divided into two length groups: 9.0 - 14.9 cm and $\geqslant$ 15.0 cm

Table XXI. Effect of host age on the occurrence of <u>Bunodera luciopercae</u>

Age (yrs)	Number Fish Examined	% Incidence	Mean Intensity/ Infected fish	Maximum
Purse seine sample (July 1976)				
0+	30	23.3	2.3	5
Trawl sample (March 1976)				
0++	36	86.1	6.5	21
1++ - 4++	28	85.7	10.3	24
Gill net samples (January 1975 - February 1976)				
2 - 2++	4	100.0	23.8	89
3 - 3++	138	84.8	12.3	99
4 - 4++	164	86.6	19.3	219
5 - 5++	78	89.7	19.2	162
6 - 6++	43	67.4	21.1	105
⩾7	38	76.3	101.6	686

Table XXII. Effect of host length on the occurrence of <u>Bunodera</u>
<u>luciopercae</u>

Length (cm)	Number Fish Examined	% Incidence	Mean Intensity/ Infected Fish	Maximum
Purse seine sample (July 1976)				
2.0 - 2.7	30	23.3	2.3	5
Trawl sample (March 1976)				
3.0 - 8.9	36	86.1	6.5	21
9.0 - 11.9	28	85.7	10.3	24
Gill net samples (January 1975 - February 1976)				
9.0 - 11.9	56	85.7	11.3	39
12.0 - 14.9	318	85.8	15.7	162
15.0 - 17.9	59	84.7	56.4	686
$\geqslant$ 18.0	29	70.0	70.1	594

(Fig. 16). In both instances the incidence of infection was similar

(9.0 - 14.9 cm 85.1% of 377 fish; $\geqslant$15.0 cm 79.5% of 88 fish).

However the mean intensity/infected fish was much higher in the

larger length group (Fig. 16). In the infected fish between 9.0 -

14.9 cm 55.5% harboured 1 - 10 B. luciopercae, while in the infected

fish $\geqslant$15.0 only 32.9% did so. In addition, in the larger length

group there was a greater occurrence of very heavily infected fish

(Fig. 16).

Effect of site of capture

Site A and site B

The results of a comparison of the infection at site A (6m)

and site B (12m) are shown in Table XXIII. The incidence was

similar at both sites. Since infection at these two sites was

compared during the summer months of June - July, the incidence

of infection was low (Table IXX). An F-test revealed a significant

difference in the variances of the mean intensity/infected fish at

site A and B (F = 5.14, v_1 20, v_2 7, P< 0.05). Consequently, the

parasite counts were transformed using a log(x+1) transformation.

The results indicate that there was no significant difference in

the mean intensity/infected fish at the two sites during June - July

1975 (F = 1.2, $v_1$20, v_2 7, P >0.05; t = 1.6, degrees of freedom 27,

P >0.05).

Site B and site D

The infection at these two (12m) sites was compared during

two periods: February - April 1975 and October - December 1975.

The results are summarised in Fig. 17 and 18. February - April:

100.0% of the fish from both site B and D were infected. In

addition, the frequency distribution of the parasite counts, and
the mean intensity/infected fish were similar (Fig. 17). October -
December: at site B 90.4% of the fish were infected, and at site
D 93.8% were infected. An F-test indicated a significant difference
between the variances of the mean intensity/infected fish at the
two sites (F = 5.18, v_1 29, v_2 74, P < 0.05). Consequently, a
t-test was applied to the log(x+1) transformed parasite counts.
There appeared to be a significant (though not highly significant)
difference in the mean intensity/infected fish (F = 1.31, v_1 29,
v_2 74, P > 0.05; t = 2.5, degrees of freedom 103, P < 0.05 > 0.01),
with the perch at site D more heavily infected. (The mean lengths
of the fish were: site B, 13.9 cm, variance 12.9; site D, 13.9 cm,
variance 3.8.)

Table XXIII. Occurrence of Bunodera luciopercae at site A and B.
Gill net samples. June - July 1975

Site	Number Examined	Fish Infected	% Incidence	Mean Intensity/ Infected Fish	Variance	Maximum
A (6m)	60	21	35.0	4.3	114.6	50
B (12m)	19	8	42.1	5.5	22.3	15

% FREQUENCY

Male & female perch, 9.0 - 14.9 cm
Number fish 377
Incidence 85.1%
Mean intensity/infected fish 15.1

30

20

10

56 98 80 41 32 38 10 6 5 5   I 2 2 I

Male & female perch, ≥ 15.0 cm
Number fish 88
Incidence 79.5%
Mean intensity/infected fish 60.3

20

10

18 17 6 7 4 6 4 7 2 I 4 I   3 2 4   2

0 1-5 6-10 11-15 16-20 21-30 31-40 41-50 51-60 61-70 71-80 81-90 91-100 101-150 151-200 201-300 301-400 401-500 >500

NUMBER PARASITES / FISH

Fig. 16. Effect of host length on Bunodera luciopercae infection.
Gill net samples. January 1975 - February 1976.
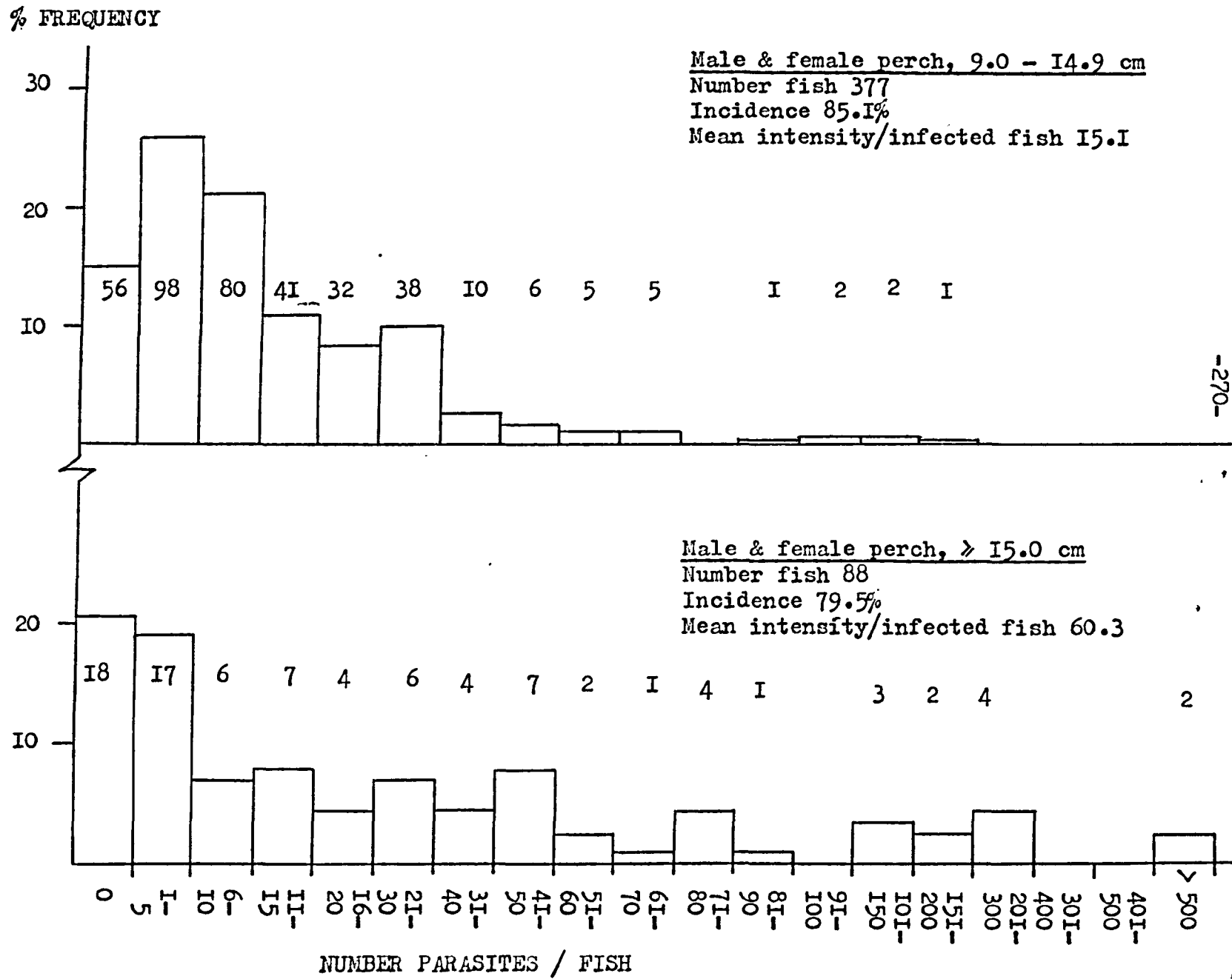
Fig. I7. Occurrence of <u>Bunodera luciopercae</u> at site B (I2m) and site
    D (I2m). Gill net samples. February - April I975.

% FREQUENCY

Site D

Number fish 25
Number infected 25
Mean intensity 9.9
Variance II2.5

Site B

Number fish 59
Number infected 59
Mean intensity II.I
Variance 77.4

NUMBER PARASITES / FISH
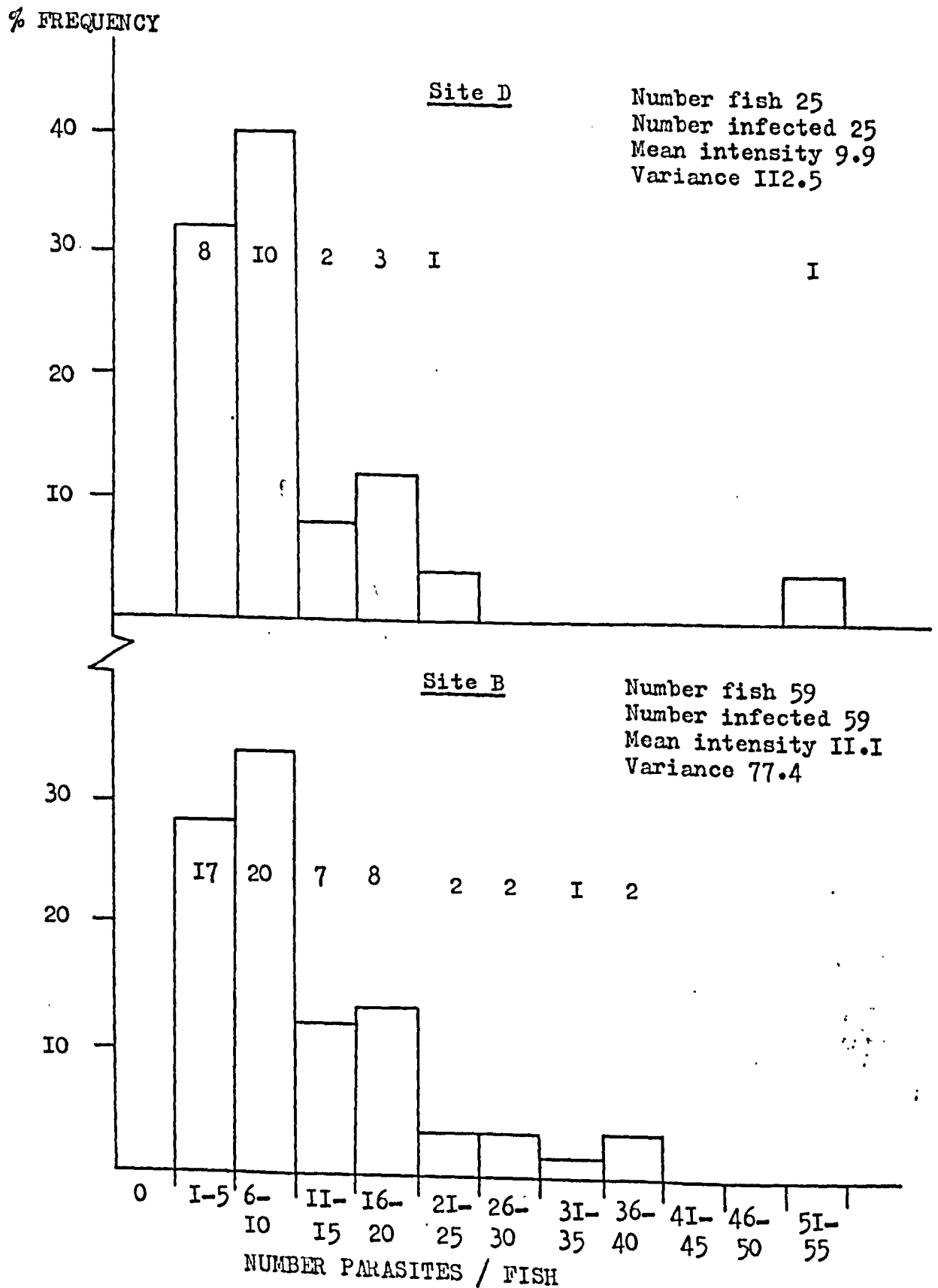
Fig. I8. Occurrence of <u>Bunodera luciopercae</u> at site B (I2m) and site
D (I2m). Gill net samples. October I975 - December I975.

% FREQUENCY

Site D

Number fish 32
Number infected 30
Incidence 93.8%
Mean intensity/infected
fish 23.0
Variance 902.4

30

20

2 5 6 3 4 4 2 2 I I I 2

IO

Site B

Number fish 83
Number infected 75
Incidence 90.4%
Mean intensity/infected
fish I3.I
Variance I74.2

30

20

IO

0, I-5 6- II- I6- 2I- 26- 3I- 4I- 5I- 6I- 7I- 8I- 9I- >
         IO   I5   20   25   30   40   50   60   70   80   90 IOO IOO

NUMBER PARASITES / FISH
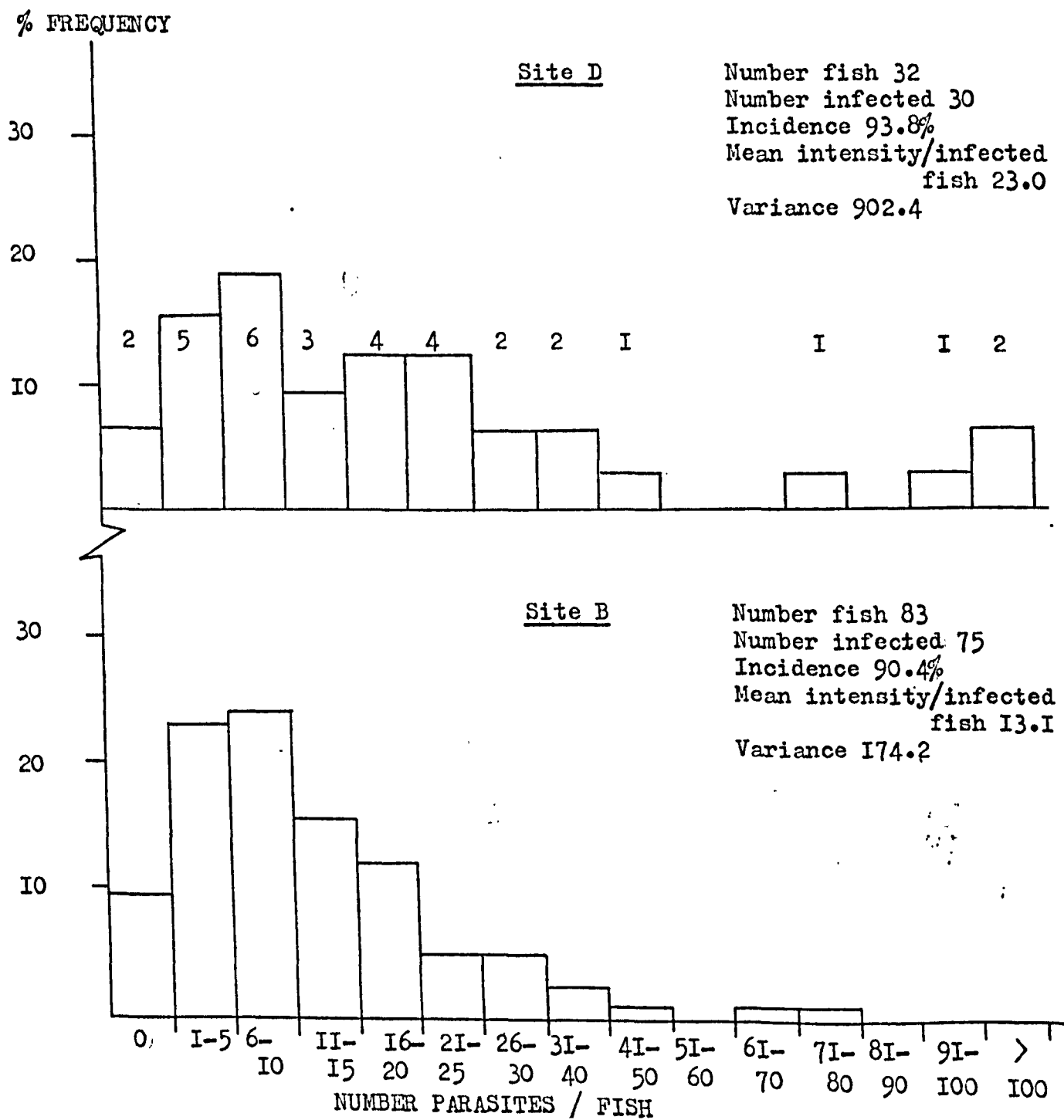
Site of occurrence of <u>Bunodera luciopercae</u> within the alimentary

tract of perch

There were no obvious seasonal changes of site preference

within the alimentary tract. Therefore the results from the gill

net samples taken during January 1975 - February 1976 were combined

(Fig. 19). Over this period the pyloric caeca harboured the

largest number of flukes. However, significant numbers were also

found at the intestinal sites I - V (Fig. 19). Few flukes were

found in the stomach, and the gall bladder was infected once

(Fig. 19).

The relationship between the intensity of infection and the

distribution of the parasites in the pyloric caeca and intestine

is shown in Fig. 20. Only the results from August and September

were used when the intensity was particularly high, and the

majority of the flukes at stage (I). Because of the small numbers

of parasites found in the stomach, this site was not included.

To reduce any effects of host size on the relationship, only

were $<$ 15.0 cm were used. The results in Fig. 20 suggest that

as the intensity of infection increased, a greater proportion of

the parasites were found at more posterior sites within the

alimentary tract (Fig. 20).

Natural infection of <u>Pisidium</u> sp. at Llyn Tegid

Over a period of 14 months (February 1976 - March 1977) 244

<u>Pisidium</u> sp. were examined from Llyn Tegid. Of these, 22 (9.1%) were

infected. The results are summarised below (all measurements are in

um, and refer to fresh, living material).

February 1976: Three of 39 (7.7%) molluscs were infected with redial

Fig. 19. Site of occurrence of <u>Bunodera luciopercae</u> in perch. Gill net samples. January 1975 - February 1976.

% OF TOTAL NUMBER PARASITES

Total number of parasites 9171
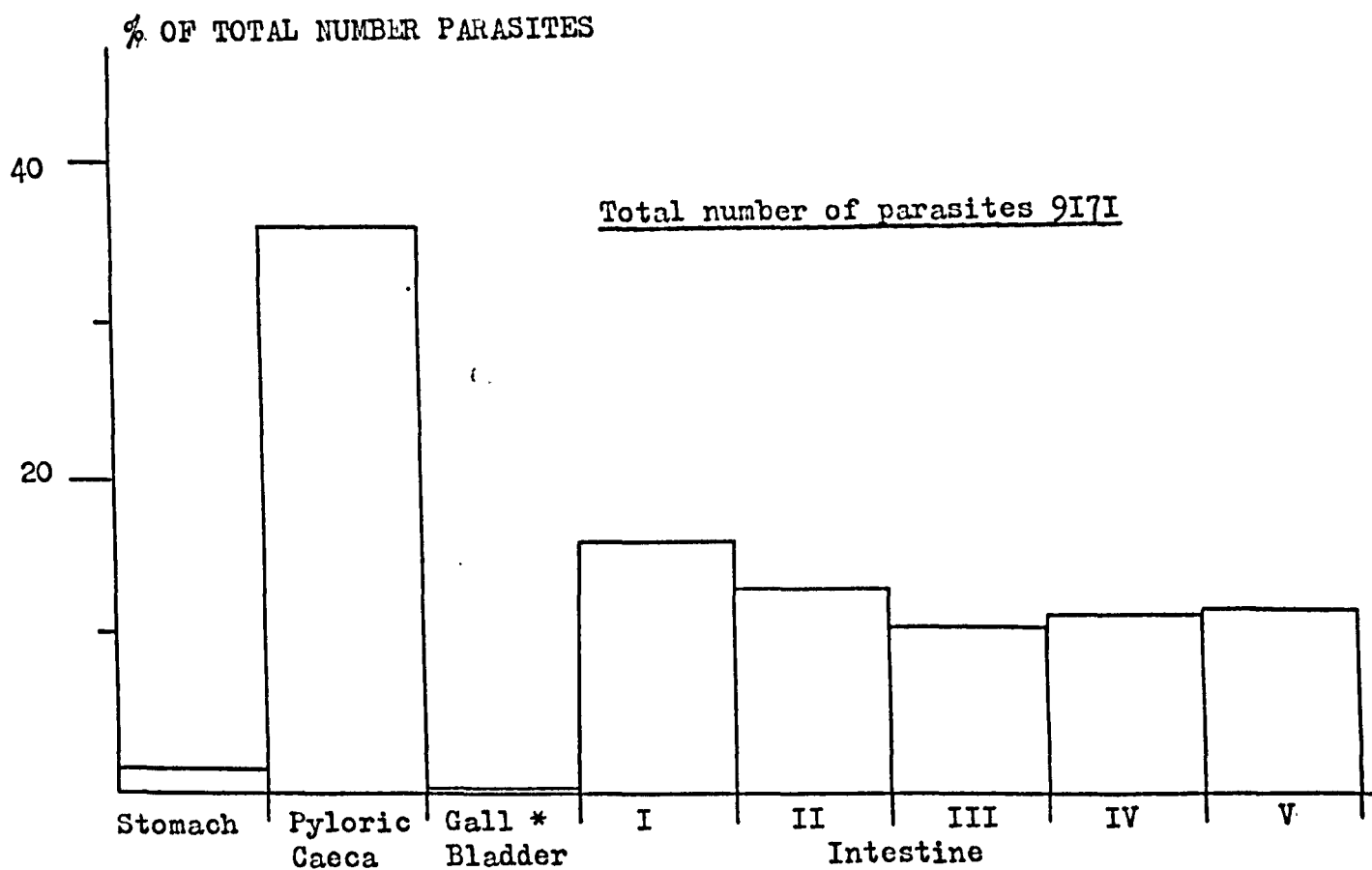
(NB. * Eight <u>Bunodera luciopercae</u> (0.09% of total) were found in the gall bladder of a single perch that harboured a total of 686 flukes.)

Fig. 20. Site of occurrence of <u>Bunodera luciopercae</u> at three
levels of intensity. Gill net samples. August —
September 1975. All fish less than 15.0 cm.

% OF TOTAL NUMBER OF PARASITES
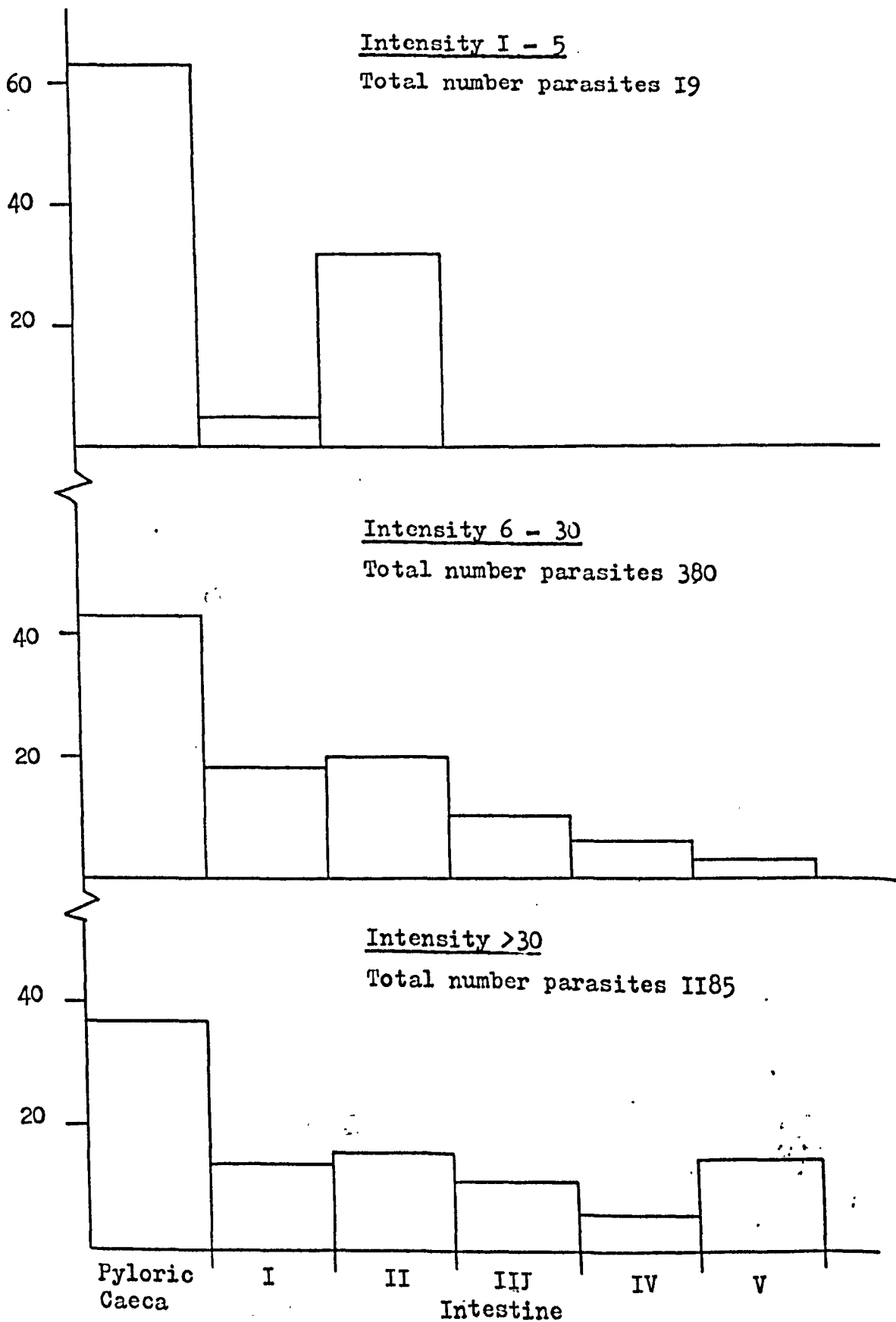
Intensity I - 5
Total number parasites 19

Intensity 6 - 30
Total number parasites 380

Intensity >30
Total number parasites 1185

Pyloric Caeca   I   II   III   IV   V
Intestine

Fig. 2I. Seasonal maturation of Bunodera luciopercae. Gill
net samples. January I975 - February I976.

% INCIDENCE

Stage (I)

Stage (II)

Stage (III)

Stage (IV)

Stage (V)

LAKE *
TEMP.

J F M A M J J A S O N D J F

I975/76
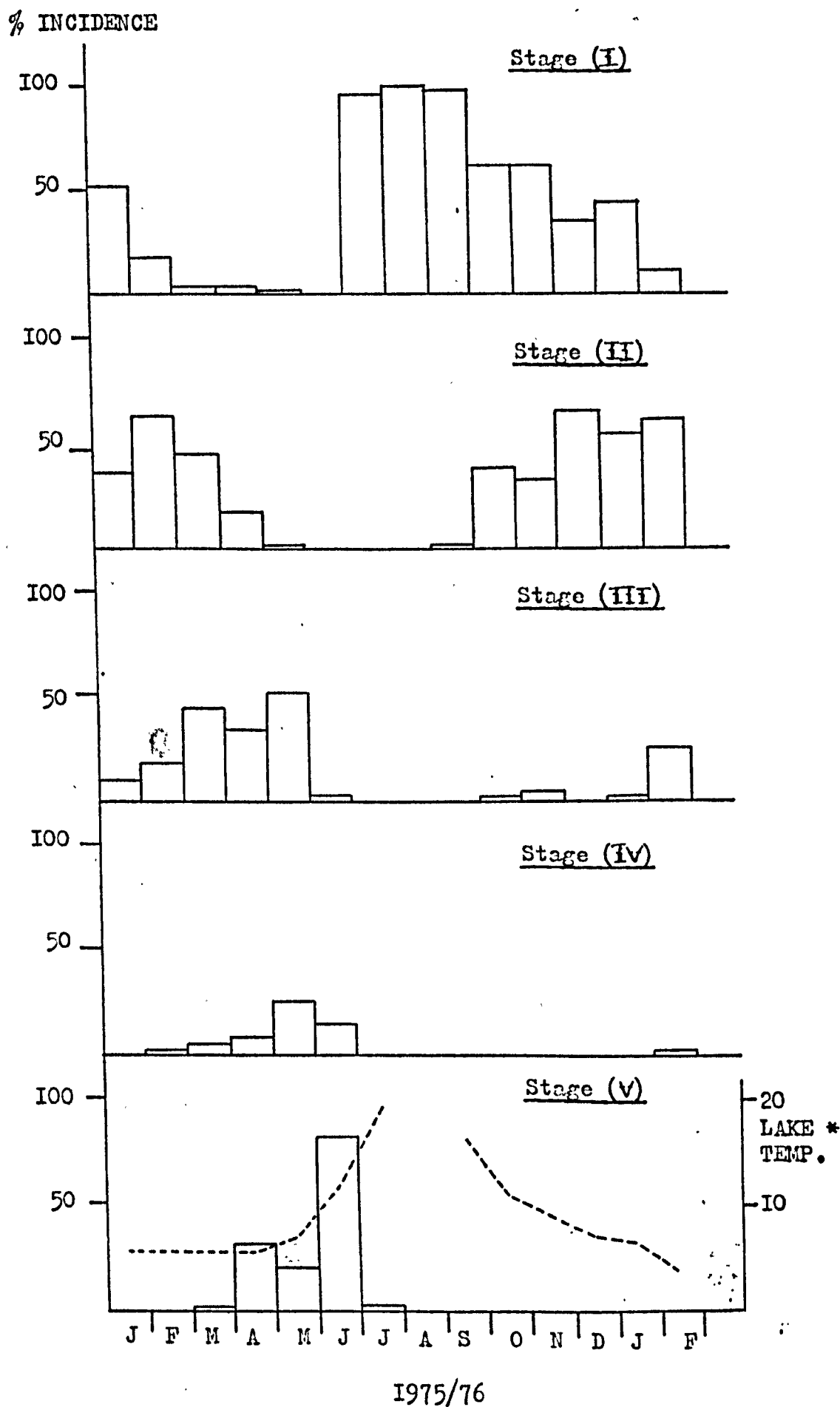
(*...in degrees Centigrade, at depth 6 m)

stages containing immature tailed cercariae with eye spots.

March 1976: Three of 43 (6.9%) bivalves were infected with rediae containing immature tailed cercariae with eye spots.

May 1976: Three of 50 (6.0%) molluscs were infected with empty redial stages or young sporocysts.

July 1976: Two of 26 (7.7%) pisidia were infected with redial or sporocyst stages. The rediae measured approximately 340 x 85 wide, pharynx 35 diameter.

September 1976: Two of 22 (9.9%) bivalves were infected with redial stages, or rediae containing embryos of daughter rediae. The measurements of the mother rediae were 300 - 500 long.

November 1976: Three of 22 (13.6%) molluscs were infected with rediae containing daughter rediae, or rediae containing immature tailed cercariae with eye spots. The latter rediae measured 980 - 1200 long pharynx 40-45 x 35 wide.

January 1977: Four of 25 (16.0%) pisidia were infected with rediae (800 - 1250 long) containing immature tailed cercariae (total length 200 - 225) with eye spots.

March 1977: Two of 17 (13.3%) bivalves were infected with rediae (840 - 1100 long) containing immature tailed cercariae (total length 280 - 340, body length 190 - 220) with eye spots.

The infection was present in all months through there was a distinct seasonal pattern of development of the parasite. The pisidia appeared to become infected by May, when young sporocyst stages were found. Rediae were first seen in July, and were present containing daughter rediae until November. Immature cercariae were seen within rediae by November, and were present until March (1976 and 1977). The disappearance of immature cercariae within rediae between March and May (1976), along with the presence of empty rediae in the latter

month, suggested that cercariae were released sometime between late March and early May 1976.

VII. 3.32 Laboratory studies

In vitro hatching of eggs of Bunodera luciopercae

The results are summarised in Table XXIV.

Over the temperature range 17-24°C, under natural conditions of daylength (during April) hatching was first observed after 5 days. Active miracidia were present until day 9-12 (Table XXIV). Over the temperature range 13-21°C, under similar natural conditions of daylength, hatching was first observed on day 6-7. However, the percentage hatch appeared to remain low until day 10 (Table XXIV). None of the eggs kept at 1-8°C (in total darkness) hatched by day 30. However, eggs previously maintained under these conditions for 26 days, hatched after 4 days at 22-24°C (though the percentage hatch was very low) (Table XXIV).

At temperatures of 13-21°, 17-22° and 20-24°C, the absence of light delayed the onset of hatching by several days (Table XXIV). This was particularly pronounced at the temperature range 13-21°C. The effect of light on the hatching of eggs kept at 1-8°C was not examined.

Laboratory infection of Pisidium sp.

The results from infected pisidia maintained at three temperatures under conditions of constant (16L/8D) daylength are summarised below. All measurements are in um, and refer to fresh, living material.

(a) Temperature 4-8°C. Molluscs were examined up to 300 days post infection (p.i.). The parasites did not develop beyond the sporocyst stage, and only 3.8% of the pisidia were found to be infected.

Table XXIV. <u>In vitro</u> hatching of eggs of <u>Bunodera luciopercae</u>

Temperature °C	Light/ Dark*	Number Trials	Hatching First Observed**	Comments
20-24	Light	2	5	No miracidia seen after day 12
	Dark	2	8	
13-21	Light	4	6-7	Low % hatch until day 10
	Dark	4	11-12	Low % hatch until day 15-17
17-22	Light	4	5	No miracidia seen after day 9
	Dark	4	8-9	
1-8	Dark	2	-	No hatch seen by day 30
1-8/22-24	Dark	2	30	Kept at 1-8°C for 26 days. Temperature increased on day 26; low % hatch began 4 days later.

*   Light = Natural daylength conditions

    Dark = Total darkness

** Number of days after start of trial

By day 37 p.i. the sporocysts measured approximately 50 in diameter, and had reached approximately 105 by day 190. Bivalves examined on day 223, 275 and 300 p.i. were all uninfected.

(b) Temperature 16-21°C. The infection was followed for 308 days p.i., during which time 26.8% of the molluscs were found infected. The changes in the development of the parasite are summarised in Table XXV. Large, active rediae were first seen on day 49 p.i., though degenerating sporocysts were seen as late as day 187 p.i. The division of the germ ball was observed by day 87 p.i., and mother rediae containing daughter rediae were seen from day 222 until day 308 p.i. Cercarial stages were not observed (Table XXV).

(c) Ambient room temperatures (Fig. 13). Pisidia were examined for 190 days p.i. Up to day 50 p.i. 26.1% of the molluscs that were examined were infected. Between day 50 p.i. and day 87 p.i. only 1.5% were found infected. After day 87 p.i. the infection had apparently disappeared. Only sporocyst stages (83 x 130 to 150 (diameter)) were encountered. The experiment was discontinued after day 190 p.i.

Between day 40-60 p.i. very high temperatures were attained in the pisidia culture maintained at ambient, room temperature (Fig. 13). This was a result of the warm summer temperatures in 1976. It is probable that temperatures in excess of 30°C may have had a detrimental effect on the bivalves and/or the B. luciopercae infection. Large numbers of dead pisidia

were found in the latter stages of this experiment.

Maturation of Bunodera luciopercae in laboratory maintained perch

Infected perch were maintained under conditions of constant daylength (16L/8D) at four thermal regimes.

(a) Temperature: constant cool. Perch were dissected on day 13, 28, 35, 92, 137 and 158. In the fish examined on day 13-92 (late December) only stage (I) and stage (II) B. luciopercae were found. On day 137 (late January - early February) flukes at stage (III) and stage (IV) were recovered. At the completion of the experiment on day 158 (early March), flukes at stage (IV) and stage (V) were present.

From a total of 15 fish that were initially infected, 13 (86.7%) were later found to harbour the parasite, at a mean intensity/infected fish of 3.8.

(b) Temperature: constant warm. Perch were examined on day 21, 30, 83, 130 and 165. Between day 21-83 (early-mid December) flukes at stage (I) to (III) were found. Stage (I) were recovered on day 21 and 30, while stages (II) and (III) occurred on day 83. The infection was absent from the perch on day 130 (late January) and day 165 (early-mid March).

Nine of the original 15 fish were found infected (60.0%), and the

Table XXV. Intra-molluscan development of <u>Bunodera luciopercae</u> at 16-21°C.

Days (p.i.*)	Stage(s) Present	Measurements** (um)
28	Sporocysts	85-100 (diameter)
35	Sporocysts	100-125 (diameter)
49	Sporocysts (degenerating) Rediae	60-75 (diameter) 350-400 (long), pharynx 40x35 (wide)
63	Sporocysts, and sporocysts containing redia Rediae	130-155 (diameter) 270-320 (long) by 60-65 (wide), pharynx 35 (diameter)
87	Rediae; germ ball dividing	330-420 (long by 55-90 (wide)
107	Sporocyst (degenerating); Rediae; germ ball dividing	75 (diameter) 205 (long) by 55 (wide), pharynx 35 (diameter)
187	Sporocyst (degenerating)	80 (diameter)
222	Rediae; containing daughter rediae	
274	Rediae; containing daughter rediae	
308	Rediae containing daughter rediae	Rediae: 190-900 (long) Daughter rediae: 135 (long)

N.B. * = post infection

  ** = Measurements refer to fresh, living material

mean intensity/infected fish was 3.6.

(c) Temperature: natural environmental. Perch were dissected on day 20, 42, 69, 100, 120 and 168. On day 20 and 42 (mid November) flukes at stage (II) and stage (III) were present. On day 69 (early December) only B. luciopercae at stage (III) were encountered, and by day 100 (early January) stage (III) and stage (IV) parasites were present. On day 168 (late January) only stage (IV) were found, and by day 168 (mid March) stage (V) flukes were present.

Of the 15 fish that were originally infected, 10 (66.7%) were later found to harbour the parasite at a mean intensity/infected fish of 3.0.

(d) Temperature: constant cool/constant warm. Perch were examined on day 20, 43, 72, 100, 135 and 170. The perch were moved from 4-8°C to 16-20°C on day 44. While at 4-8°C the parasites developed in a manner similar to that seen at (a) (constant cool temperature) above. Stage (I) and stage (II) flukes were present on day 43 (mid November). On day 72 (early-mid December) and day 100 (early January), B. luciopercae at stage (II) and stage (III) were found. The infection was absent on day 135 (late January) and day 170 (mid March).

Eight of the original 15 (53.3%) infected fish were found to harbour the parasite, at a mean intensity/infected fish of 4.1.

Feeding habits and gonad development of experimental fish

Perch maintained at 16-20°C fed voraciously throughout the experiment, while perch maintained at natural environmental temperatures fed steadily. The fish kept at 4-8°C ate small amounts of live food until

day 120. Thereafter these fish fed steadily. The fish kept at 4-8°C for 43 days fed on small amounts of live food. On their transfer to 16-20°C (on day 44) their appetite increased over a period of weeks, to assume the proportions of that of the fish maintained at this temperature throughout.

In all four experiments the gonads of adult male and female perch did not develop beyond early stage III (see Appendix I).

Therefore, gravid stage (V) B. luciopercae were present in perch maintained at 4-8°C and at natural environmental temperatures (Fig. 14), after 158 and 168 days respectively. However, the development of the flukes under these two regimes differed for the first 92-100 days. At the constant cool temperature, B. luciopercae did not appear to develop beyond stage (II) until after day 92. In contrast, at natural environmental temperatures stage (III) parasites were present from day 20, and stage (IV) flukes found on day 100. It is of interest to note that perch maintained at 4-8°C refused food between day 35-120, whilst the fish kept at natural environmental temperatures fed throughout the experiment.

In fish maintained at the constant warm temperature of 16-20°C, the development of B. luciopercae did not proceed beyond stage (III). The infection was absent from the fish after day 83. In fish that were kept at 4-8°C for 43 days and then warmed to 16-20°C, the development of B. luciopercae reached stage (III) by day 72 and day 100. In comparison to the fish maintained at the constant warm temperature, the infection disappeared by day 135.

VII. 3.4   Discussion

The life cycle of <u>Bunodera luciopercae</u> involves a bivalve

molluscan first intermediate host, an arthropod second intermediate

host and a piscine definitive host (Wisniewski, 1958; Moravec, 1969;

Cannon, 1971).

Field and laboratory observations have indicated that <u>B. luciopercae</u>

may develop within several species of bivalves of the genera <u>Pisidium</u>

and <u>Sphaerium</u> (Wisniewski, 1958; Moravec, 1969; Cannon, 1971). In

their study at Llyn Tegid, Hunt and Jones (1972b) recorded <u>Pisidium</u>

<u>lilljeborgii</u> as a "regular though not abundant"member of the littoral

and profundal fauna. In addition, <u>P. milium</u> was recorded on two

occasions, and <u>Sphaerium corneum</u> once (Hunt and Jones, 1972b).

Samples of <u>Pisidium</u> sp. were examined from Llyn Tegid at regular

intervals during 1976/77. Whilst critical determination of the species

was not attempted, it is likely that the majority of the 244 pisidia

were <u>P. lilljeborgii</u>. No <u>Sphaerium</u> sp. were encountered. Twenty-two

(9.1%) of the bivalves were infected with sporocyst, redial and redial

with immature cercariae, stages of a digenetic trematode. The stages

were very similar to those obtained in the laboratory infection

of pisidia with <u>B. luciopercae</u>. However, <u>Crepidostomum farionis</u>

is also know$_\wedge$ to occur in Llyn Tegid (Chubb, 196$\overset{a}{3\!\!\wedge}$), and may also

utilise <u>Pisidium</u> (and to a lesser extent <u>Sphaerium</u>) spp, as its

first intermediary (Brown, 1927; Awachie, 1968). Whilst, <u>C. farionis</u>

does not possess a sporocyst generation (Brown, 1927), the similarity

of the redial and immature cercarial stages may have caused a degree

of confusion of identification. Mature cercariae were not observed,

though their specific identity may be determined by their flame

cell formulae. Both species possess opthalmoxiphido-cercariae, though

the arrangement of the flame cells differ: <u>B. luciopercae</u>, 2 [(3+3+3)+

(3+3+3)] = 36 (Wisniewski, 1958; Cannon, 1971); <u>C. farionis</u>,

2[(2+2)+(4+3+3+3)] = 38 (Brown, 1927). However, the infection of

<u>C. farionis</u> at Llyn Tegid was not prevalent, when Chubb (1963a)

recorded the parasite from 3 of 76 (3.9%) grayling (<u>Thymallus</u>

<u>thymallus</u>). In addition, Awachie (1968) has shown that in the

nearby Afon Terrig, <u>C. farionis</u> sheds its eggs during the spring

(April onwards) at a time when grayling at Llyn Tegid may be spawning

in the feeder streams. Therefore, these factors would seem to

minimise the chances of infection of pisidia at Llyn Tegid with the

larval stages of <u>C. farionis</u>. <u>Crepidostomum meteocus</u> is another allocreadiid

fluke that occurred at Llyn Tegid, and the infection may be more

prevalent than <u>C. farionis</u> (Chubb, 1963a, 1976). However, the life

cycle of <u>C. meteocus</u> has not been studied in detail, and while Thomas

(1958) suggested that the molluscan intermediate host may be <u>Pisidium</u> spp.,

Awachie (1968) found that <u>Lymnaea pereger</u> was the molluscan intermediary

in his study on the Afon Terrig (North Wales).

Large numbers of Cladocera, Copepoda and Ostracoda were examined

from the Polish lakes of Druzno, Goldapiwo and Mamry for the metacercariae

of <u>B. luciopercae</u> (Wisniewski, 1958). At Lake Druzno <u>Mesocyclops</u>

<u>oithonoides</u> was infected, whilst at Lakes Goldapiwo and Mamry <u>M. crassus</u>

was infected. The incidence of infection was extremely low.

Wisniewski (1958) went on to experimentally demonstrate that the

cladocerans <u>Daphnia pulex</u>, <u>Simnocephalus expinosus</u> and <u>Eurycercus</u>

<u>lamellatus</u>, along with the ostracod <u>Notodromas monacha</u>, may also

serve as second intermediaries to <u>B. luciopercae</u>. In his studies in

North America, Cannon (1971) experimentally infected 1 of 47 <u>Daphnia</u>

<u>similis</u> (Cladocera), 4 of 10 <u>Hyallela azteca</u> and 6 of 11 <u>Crangonynx gracilis</u>

(Amphipoda), and 1 of 3 larval <u>Siphonolurus quebecensis</u> (Ephemeroptera).

Observations on the seasonal occurrence of <u>B. luciopercae</u> in relation to perch feeding habits, implicated cladoceran and/or copepod crustaceans as the second intermediate hosts at Llyn Tegid. This is discussed later. Several species of Cladocera and Copepoda have been recorded from the lake (Thomas, 1959; Mills, in prep), including <u>Daphnia hyalina</u>, <u>D. obtusa</u>, <u>Cyclops albidus</u>, <u>C. abyssorum</u> (? var. prealpinus), <u>C. agilis</u>, <u>C. viridis</u> and <u>Diaptomus gracilis</u>. However, none of these have been examined at Llyn Tegid as the potential hosts for the larval stages of parasitic helminths. Wootten (1973c) found a positive association between the presence of <u>B. luciopercae</u> and <u>Proteocephalus percae</u> (Cestoda) in perch at Hanningfield Reservoir (Essex). This result was attributed to the two helminths both utilising planktonic intermediate hosts (Wootten, 1973c). Nonetheless ostracods, amphipods and larval ephemeropterans have been experimentally infected with the metacercariae of <u>B. luciopercae</u> (Wisniewski, 1958; Cannon, 1971). In addition, several other species of allocreadiid flukes utilise non-planktonic second intermediate hosts. The life cycle of many <u>Crepidostomum</u> spp. involve amphipods, crayfish or insects as hosts to their metacercariae (e.g. ~~Thomas~~ Brown, 1927; Hopkins, 1934; Talbot & Hutton, 1935; Choquette, 1954; Awachie, 1968). Anderson <u>et al.</u> (1965) found that the caddis (<u>Rhyacophila grandis</u>) and various larval Chironomidae were second intermediate hosts to <u>Bunoderella</u> <u>mettrei</u>. Similarly, insects have been implicated in the life cycle of <u>Allocreadium</u> spp. (Peters, 1957; Wootten, 1957). Hoffman (1955) could not demonstrate the life cycle of <u>Bunodera eucaliae</u> (a parasite of the stickleback, <u>Eucalia inconstans</u>), but suggested that there may be no second intermediate host. Cannon (1971) considered that the

life cycle and taxonomic status of this species required further
investigation.

Perch are the only fish recorded as host to B. luciopercae in
Llyn Tegid, and from the whole of the River Dee system (Chubb, 1976).
Records from other fish in the British Isles probably represent spurious
infections that are of little biological significance to the parasite.
For example, Wootten (1973a, c) found that at Hanningfield Reservoir
(Essex), perch, ruffe, ten-spined sticklebacks and brown trout all
harboured the infection. However, whilst gravid flukes were recovered
from perch, ruffe and brown trout, Wootten (1973c) considered that
because of the low incidence and intensity of infection in ruffe,
stickleback and trout, perch was the undoubtedly most important piscine
host. Nonetheless, in continental Europe, other fish (particularly
pike-perch, Lucioperca lucioperca) may be important hosts to
B. luciopercae (Ginetskaya, 1958; Bauer, 1959; Bykhovskaya-Pavlovskaya
et al., 1962).

Pike is often recorded as host to B. luciopercae (e.g. Mishra &
Chubb, 1969; Rařckis, 1970b; Tell, 1971; Campbell, 1974) and it is
likely that this fish becomes secondarily infected by the ingestion
of infected prey fish (Mishra & Chubb, 1969). Ergens (1966) and Mishra
& Chubb (1969) considered that the parasite fauna of pike was influenced
by the parasite fauna of its prey fish, and Wootten (1973c) suggested
that brown trout at Hanningfield Reservoir (Essex) may acquire
B. luciopercae by feeding on infected, small perch. The secondary
infection of large perch with B. luciopercae is discussed later.

In agreement with the observations of many other workers on
the distribution of fish parasites in the host population, the
distribution of B. luciopercae in perch at Llyn Tegid was markedly
overdispersed. Studies on the intestinal parasites of fish that have

produced similar results include Thomas (1964), Kennedy (1968),

Kennedy & Hine (1969), Cannon (1972), Anderson (1974), Hine & Kennedy

(1974) and Stromberg & Crites (1975). Overdispersion of this nature

results in a relatively small proportion of the host population

harbouring a relatively large proportion of the parasite population,

and may (in some instances) have important consequences in the

regulation of host and parasite population size (Crofton, 1976). 71a

This is discussed in more detail in Chapter VIII, concerning

Triaenophorus nodulosus (Cestoda).

The infection patterns of helminths in fish populations are

influenced by a number of factors, including the availability of

infective larvae, host feeding habits, behaviour and susceptibility

to infection, parasite mortality, and abiotic factors such as

temperature (Kennedy, 1970). The interaction of these factors frequently

results in an extreme variability in the incidence and intensity

of infection, and the overdispersion of fish parasite populations

(Stromberg & Crites, 1975).

The incidence and intensity of infection, and more precisely

the frequency distribution of the parasite population, was similar

in adult male and female perch. Cannon (1972) found that the

incidence of B. luciopercae and B. sacculata was not significantly

different in male and female yellow perch, from Lake Opeongo

(Canada).

Perch fry acquired B. luciopercae during their first few weeks

of life in Llyn Tegid. Young of the year fish examined the following

spring (aged 8-9 months) harboured mature, gravid flukes. By this

time, the incidence (and to a lesser extent the intensity) had risen,

presumably as a result of the plankton-rich diet of these fish (see

Chapter III).

The incidence and intensity of infection was similar in perch

aged 1++ - 6++, and length 9.0 - 14.9 cm. However, within this

grouping there were signs of an increase of intensity in the older,

larger perch. However, in perch aged 7 years or above (and $\geqslant$ 15.0 cm)

there was a distinct increase in the intensity of infection (Table XXI

and XXII, Fig. 16). It appeared that this was a result of fewer

large perch having an intensity of 1-10 flukes, along with the

presence of a greater number of very heavily infected fish (Fig. 16).

Observations on the feeding habits of perch suggested that this

was because of the cannabilistic feeding habits of larger fish.

Cannabilism was most prevalent in perch aged over 5 years, and

longer than 16.9 cm (see Chapter III). In comparison, plankton

feeding was uncommon in these fish, and predominated in smaller

younger perch (Chapter III). Rizvi (1964) found a similar increase

in the intensity of infection in perch at Rostherne Mere (Cheshire).

Incidence reached a peak in perch aged 3+, and then remained

constant. The intensity of infection increased steadily with host

age, though very heavily infected fish (maximum 1872) were most

common in the age group 5+ - 10+ (Rizvi, 1964). Banks (1968)

noted a marked change in the feeding habits of perch at Rostherne

Mere with increasing size. Cannabilism occurred in all length

groups, but was most extensive in fish >17.9 cm. Wootten (1973c)

found that the highest mean intensity of infection of perch at

Hanningfield Reservoir (Essex) was in fish aged 1+ - 2+ (15.0 - 19.9 cm).

This was seen to be a reflection of the extensive plankton feeding

habits of these fish (Wootten, 1973c). However, small numbers of

larger perch were very heavily infected with B. luciopercae (maximum

394 parasites), and Wootten considered that this might be a result of

the secondary infection of predatory perch from infected prey fish.

From these studies it seems that small, plankton feeding perch may

harbour appreciable numbers of B. luciopercae and form a reservoir

of infection for larger, more predatory perch. This may greatly

enhance overdispersion, and result in a small number of large fish

harbouring a very large number of parasites (Llyn Tegid: maximum 686).

Van Cleave & Mueller (1934) concluded that Bunodera sacculata was

restricted to shallow water in Lake Oneida (North America). Similarly,

Wierzbicki (1971) reported that B. luciopercae most frequently occurred

in the shallow regions of Lake Dargin (Poland), where the intensity

of infection reached 100 parasites/fish. In littoral and deeper

regions of the lake, the intensity of infection was much lower

(Wierzbicki, 1971). Cannon (1972) found that during May at Lake

Opeongo (Canada), there was no difference in the incidence of

B. luciopercae and B. sacculata with depth of host (yellow perch)

habitat. The results from Llyn Tegid suggested that during June -

July, there was no difference in the incidence or intensity of

infection at a 6m and 12m site. Since perch at Llyn Tegid inhabit

the deeper water sites (down to 12m) during all months of the year,

and since gravid B. luciopercae were shed before the spring migration

into shallow water, it seems likely that pisidia at various depths

may harbour the infection. Hunt & Jones (1972b) found Pisidium

lilljeborgii from the littoral zone down to a depth of 40m, and

it would be of interest to compare the development of B. luciopercae

in pisidia from shallow and deeper water locations. The infection

of pisidia at littoral and deep water sites may have resulted in the

involvement of littoral and pelagic species of zooplankton in the life

cycle of B. luciopercae at Llyn Tegid. During the summer months the

perch in shallow water may acquire the infection from infected littoral

second intermediate hosts, and the zooplankton in deeper water may form

a reservoir of infection for these perch when they return to 12m in

the autumn.

The infection with B. luciopercae was compared at two 12m sites during a spring (February - April) period and an autumn - winter (October - December) period. The incidence and intensity of infection was similar during the spring period (Fig. 17). While the incidence of infection was similar at both sites during October - December there was a significant (though not highly significant) difference between the intensity at each site (Fig. 18). The mean length of the fish at the two sites was identical, although fish of a greater range of sizes were caught at the less heavily infected site (B). The frequency distribution of the infection at the two sites (Fig. 18) suggested that the difference in intensity may be a result of a small number of heavily infected fish present at site D, as a reflection of the overdispersed nature of the parasite distribution.

B. luciopercae occurred within the villi of the intestines of yellow perch, though because of its large size projected into the intestinal lumen (Cannon, 1972).

Crompton (1973) reviewed the sites occupied by some parasitic helminths within the alimentary tract of their vertebrate host. Most studies indicated that intestinal dwelling Digenea are restricted to the paramucosal lumen and mucosal or epithelial tissues. Such parasites often feed by browsing on the mucosa or epithelial tissues and probably ingest cells, blood, products of host digestion and their own histolytic secretions, and micro-organisms (Crompton, 1973). The cellular debris produced by the constant renewal of intestinal epithelium may be a major item in the diet of many such trematodes. In addition, trematodes possess the ability to absorb nutrients across their tegument (e.g. Isseroff & Read, 1969), though unequivocal evidence for this phenomenon is lacking (Crompton, 1973).

Smyth (1966) stated that the intestinal lesions produced by trematodes are relatively negligible, though some forms do produce localised foci of inflammation. This lack of reaction, and the large populations of grazing trematodes found in the alimentary tract of some vertebrates, may be related to the rapid turnover rate of intestinal epithelial cells (Smyth, 1966; Crompton, 1973).

There is very little information on the effect of intestinal trematodes on fish (Hoffman, 1973). Markevich (1951) (cited by Bykhovskaya-Pavlovskaya et al., 1962) stated that heavy infestations of B. luciopercae may cause inflammation of the intestinal walls. Wales (1958) found that heavy infestations of Crepidostomum sp. (? farionis) may produce similar effects in trout (Salvelinus fontinalis and Salmo gairdneri). In this latter study on two lakes in California (North America), up to 446 flukes were found in the intestine of a single fish.

Whilst no detailed observations were made on the histopathology of the alimentary tract of perch at Llyn Tegid, it would appear that B. luciopercae did not have any marked pathogenic effects, despite very high individual intensities of infection.

Cheng & James (1960) studied the histopathology of Crepidostomum sp. in the molluscan intermediate host Sphaerium striatum. Mother rediae were found on the gills whilst daughter rediae occurred in the hepato-pancreas. Sections of infected bivalves revealed that the liver mass was almost completely destroyed, and phase microscopy revealed the presence of liver cells in the gut of several daughter rediae. Cheng & James (1960) considered that heavy infestations may result in the death of the mollusc. Smyth (1966) and Erasmus (1972) considered further aspects of the host-parasite relationships between Digenea and their molluscan intermediaries.

Cannon (1972) studied the infection of yellow perch with
Bunodera sacculata, B. luciopercae and Crepidostomum cooperi, at
Lake Opeongo (Canada). Juvenile worms showed microhabitat differences
within the intestine of the fish. Juvenile B. luciopercae (which
matured much more slowly than the other two species) initially
inhabited the gall bladder, and migrated into the intestine as it
matured (Cannon, 1972). This was taken to be a result of the presence
in the intestine of the closely related, and potentially competitive,
B. sacculata and C. cooperi. From the present study at Llyn Tegid,
B. luciopercae did not commonly infect the gall bladder of perch.
A single perch was found with the parasite in its gall bladder, but
this was thought to be a result of the very high intensity of infection
in this individual (Fig. 19). The majority of other European studies
have failed to fully examine the gall bladder of perch, as a site of
infection for B. luciopercae. However, it would appear that in
localities such as Llyn Tegid, where the potentially competitive
species are absent, juvenile B. luciopercae may enter directly into
the pyloric caeca and intestine, without the obligatory gall
bladder phase seen by Cannon (1972) in North America.

Cannon (1972) also reported a microhabitat difference of the
adult B. sacculata, B. luciopercae and C. cooperi. B. sacculata was
found predominantly in the anterior intestine, while B. luciopercae
occurred in the hind intestine. C. cooperi was restricted to the
pyloric caeca and intercaecal region (Cannon, 1972). In contrast to
this, it is interesting to note the distribution of B. luciopercae in
perch from the British Isles where the above potential competitors
do not occur. Rizvi (1964), Mishra & Chubb (1969) and Wootten (1973a, c)
all recorded B. luciopercae from the pyloric caeca and intestine of
perch. A similar distribution of this parasite was found in the perch

at Llyn Tegid (Fig. 19). In addition, during August and September
when there was a high mean intensity of infection, the effect of
intensity of infection on the distribution of B. luciopercae was
examined. The results suggested that as the intensity of
infection increased, there was a tendency for the parasite to
spread into the more posterior regions of the intestine (Fig. 20).
This may have been a result of intra-specific competition at high
intensities causing the flukes to inhabit more posterior (and perhaps
less favourable) sites. However, since the B. luciopercae population
is thought to be under a dynamic condition, characterised by the
high input and output of parasites during August and September (see
later), this requires further investigation at other times of the
year. The results from this study did not permit such a further
investigation. In comparison, Chappell et al. (1970) and Hopkins
(1970) have noted that the details of the ontogenetic and circadian
migrations of the cestode Hymenolepis diminuta in rats, were affected
by intra-specific competition at increasing levels of infection.

Holmes (1973) has reviewed site selection in parasitic helminths,
with particular reference to inter-specific interactions (especially
competitive exclusion and site segregation). Holmes (1973) concluded
that host-parasite relationships are further complicated by the
presence of other species of parasites. Site selection (and short-
term movements) may be modified by the presence of related parasites,
and parasites respond to the regular occurrence of competitors
by niche specialisation in the same way as free living organisms.
This is considered in relation to the intestinal parasite fauna of
perch in Chapter XI.

Cannon (1972) contrasted the difference in the intensity of infection
of B. luciopercae in North American and European studies. Tedla &

Fernando (1969) found that the mean intensity of infection of yellow perch was low in their study at Lake Ontario (Canada). Cannon (1972) found that only 27.3% of the yellow perch from Lake Opeonge (Canada) harboured more than five worms. In contrast, European studies have often revealed very high mean and individual intensities (e.g. Rizvi, 1964; mean intensity/infected fish 105, maximum 1872; Wierzbicki, 1970: maximum 2400; Wootten, 1973c: mean intensity/infected fish 31.7, maximum 394; present study (gill net samples): mean intensity/infected fish 23.4, maximum 686). This may be related to the absence of closely related, potential competitors (e.g. B. sacculata, C. cooperi), though there are likely to be other epizootiological influences to be considered. At the Shropshire Union Canal (Cheshire) the mean intensity/infected fish was 4.3 (maximum 19) (Mishra & Chubb, 1969).

Hatching of the eggs of B. luciopercae was observed after 5 days at 17-24°C, and after 6-7 days at 13-21°C (both under natural conditions of daylength). However, in the latter instance the percentage hatch remained low until day 10. These observations agree with those of Moravec (1969), who found that B. luciopercae miracidia escaped after 5-7 days at 20-24°C. However, Chertkova (1971) found that the hatching of B. luciopercae eggs took 24 days at 20-21°C and 10-15 days at 24-26°C. The longer time taken for the eggs to hatch in this latter study may reflect the exact stage at which the eggs had reached at the start of the experiments. Moravec (1969) found that the eggs obtained from the uterus of adult B. luciopercae were at a variety of stages of development. Under culture he observed the non-random development of eggs, with some retarded and others which did not develop at all. Cannon (1971) found that under natural conditions, the eggs

within gravid B. luciopercae may contain fully developed miracidia and hatch immediately on passing out from the fish.

In the present study at a temperature of 1-8°C (in total darkness), hatching had not occurred after 30 days. Nonetheless, the warming of eggs kept at this temperature for 26 days to 22-24°C, resulted in their hatching after a further 4 days (experiment performed in total darkness). However, the viability of these eggs may have been effected, since very few were observed to hatch. Chertkova (1971) found that the eggs of B. luciopercae would remain viable for 210 days, but would not develop at -2 to -5°C. They also failed to survive a temperature of 34-35°C for one week (Chertkova, 1971).

At 13-21°C, 17-22°C and 20-24°C the absence of light (in the form of natural conditions of daylength) resulted in the delay of the onset of hatching for several days (Table XXIV). This was particularly pronounced at 13-21°C, when the percentage hatch remained low until day 10 and day 15-17 under light and dark conditions respectively. Unfortunately, the effect of light on the hatching of eggs kept at 1-8°C was not investigated. However, these observations contrast with those of Chertkova (1971) who found that the absence of light had no effect on the incubation period of eggs of B. luciopercae.

The eggs of B. luciopercae are operculate and contain mature miracidia (Moravec, 1969; Cannon, 1971). Hatching in trematode eggs of this kind is frequently controlled by a number of factors, particularly light, temperature and salinity (Smyth, 1962, 1966; Erasmus, 1972). Light may play an important role in the hatching of operculate eggs, and the hatching of such eggs that have been kept in the dark may be a result of exposure to light during the experimental processes (Smyth, 1962). In general terms, fully developed trematode eggs kept in the dark at 20-25°C either exhibit

a very low hatching rate or do not hatch at all (Erasmus, 1972).
Clearly the periodical exposure of B. luciopercae eggs to light during
the course of the experiment may have resulted in hatching, but after
a longer period than the eggs maintained under normal light conditions.
The hatching of Fasciola hepatica eggs has been studied in detail by
Rowan (1956, 1957) and Wilson (1968), though Cannon (1971) considered
that the hatching process of B. luciopercae may differ to that reported
for F. hepatica.

The daily examination of the in vitro hatching experiments revealed
that the miracidium of B. luciopercae may live for at least 24 hours.
However, since the miracidia of digenetic trematodes rely on their
endogenous food reserves for energy, it is unlikely that many survive
longer than 24 hours (Smyth, 1962).

Swimming miracidia of B. luciopercae frequently changed shape,
rotated anti-clockwise and showed an initial positive photo-taxis
(Cannon, 1971). No attraction to pisidia or pisidia tissues was
observed, but an increased rate of swimming and turning preceded
the secretion of droplets from the apical gland. This adhesive
substance firmly attached the miracidium to a substrate (Cannon,
1971). Cannon also noted that as the secretion from the lateral
gland was extruded, the miracidium appeared to burrow into it, and
that this was accompanied by the sloughing of the ciliated epidermal
plates. Within 20-30 minutes the miracidium (now a sporocyst) was
enclosed by this secretion (Cannon, 1971).

Moravec (1969) and Cannon (1971) have studied the intra-molluscan
development of B. luciopercae under experimental conditions, at 20-24°C
and 20°C respectively. Young sporocysts gradually increased in size,
and reached a maximum after 56-70 days. At this time the first generation

of rediae escaped from the sporocysts (Moravec, 1969; Cannon, 1971).
In the experiments of the present study (at 16-21°C) large active
rediae were found early on day 49, though sporocysts containing
rediae were present on day 63. Cannon (1971) found that sporocysts
degenerated after 100 days, and in this study (at 16-21°C) degenerate
sporocysts were seen as late as day 187. The development of several
allocreadiid flukes through a mother and daughter redial generation
has been established (e.g. Crepidostomum farionis, Brown, 1927;
Allocreadium alloneotenicum, Wootten, 1957). Moravec (1969) described
the development of two redial generations in B. luciopercae. After
the appearance of the first mother rediae on day 67, their growth
and development proceeded slowly. The single ball of germ cells
divided after 116 days, and by day 167 relatively large embryos
filled the body of the mother rediae. Daughter rediae were ready
to leave the mother redia after 241 days. In comparison, from the
experiments performed in the present study (16-21°C), the ball of
germ cells was seen to divide as early as day 87. Few molluscs were
examined between day 107-222. However, it would appear that (in
agreement with Moravec, 1969) the development of the mother rediae
then proceeded slowly, with daughter rediae within mother rediae
observed on day 308. Moravec (1969) found that daughter rediae
contained cercarial embryos by day 363.

The development of B. luciopercae in pisidia maintained a 4-8°C
did not proceed beyond the sporocyst stage. Sporocysts were present
until day 190, but the infection was apparently absent by day 223.
It is not known whether sporocysts of B. luciopercae can overwinter
and develop into rediae the following spring. The effect of an increase
in temperature on the pisidia infection maintained at 4-8°C was not
investigated. Erasmus (1972) stated that the autumn-winter decrease

in environmental temperatures prevents recently acquired infections of molluscs from reaching maturity. He suggested that infections acquired during the late summer may overwinter and continue their development in the spring. The low incidence of infection in the pisidia maintained at 4-8°C may be an indication that the sporocyst does not survive low temperatures very well, or may have been a result of the ease which small sporocysts can be overlooked.

Cannon (1971) found a distinct eye spot in the rediae of Bunodera sacculata and B. luciopercae in natural infestations of pisidia at Lake Opeongo (Canada). No such eye spots were observed in the field or experimental infections of this study.

The development of B. luciopercae in a naturally infected populations of Pisidium sp. was somewhat different to that observed under experimental conditions (16-21°C) in the present study, and to that reported from the experimental studies of Moravec (1969) and Cannon (1971). The possibility of confusion of the redial stages of B. luciopercae with those of Crepidostomum farionis has been noted. The presence of young sporocysts in pisidia at Llyn Tegid in May (lake surface temperature 9°C) indicated that infection had occurred at this time, when the loss of gravid flukes, from perch was under way. At Llyn Tegid, sporocysts had given rise to mother rediae by July. Assuming infection to have occurred in mid-May, this was approximately 60 days post infection (p.i.), and agreed with the existing laboratory observations (Moravec, 1969; present study, 16-21°C). Development proceeded and embryos of daughter rediae within mother rediae were seen in September (approximately 120 days p.i.), which may be a little earlier than observed under experimental conditions (Moravec, 1969; present study, 16-21°C). Similarly, well developed

daughter rediae were visible within mother rediae by November (approximately 180 days p.i.). However, these differences may not be significant, and perhaps represent the differential times of infection of individual pisidia under natural conditions, and the relative times of sampling during each bimonthly period. Samples of pisidia were usually obtained mid-month, but additional samples were occasionally required towards the end of the month. The appearance of immature cercariae within rediae during November, and more commonly January and March was more interesting. It seems unlikely, in view of the slow development of redial generations in B. luciopercae, that the cercariae observed in November were present within second generation rediae. Therefore two explanations may be offered for this occurrence. Firstly, that the rediae found containing immature cercariae in November were daughter rediae of Crepidostomum farionis. Such stages are known to occur in Pisidium amnicum between October-April (Brown, 1927). Alternatively, the life cycle of B. luciopercae may be capable, under natural conditions, of developing through a single redial generation rather than two. Moravec (1969) found that the time taken for daughter rediae to contain cercarial embryos was 363 days, and observations in the present study (at 16-21°C) indicated that they were not present by day 308. Bearing in mind the possibility of confusion of identification with C. farionis, immature cercariae of B. luciopercae may have been present in January (approximately 240 days p.i.) and March (approximately 300 days p.i.). This is a much shorter period of time than has been observed in the above experiments, and may have resulted from falling autumn-winter lake temperatures stimulating the production of immature cercariae. Mature cercariae were not observed, though the disappearance of rediae and immature cercariae between March-May, suggested that the spring-rise in lake

temperature may have stimulated cercarial maturation and release over a short period of time. Cannon (1971) found that the cercariae of B. luciopercae were released from pisidia at Lake Opeongo (Canada) during June, when the lake temperature reached 15°C. In comparison, Brown (1927) found that the cercariae of Crepidostomum farionis swarmed abundantly during June-July in certain rivers in Yorkshire. These cercariae were present, though in small numbers, until September (Brown, 1927).

Since the intra-molluscan cycle of B. luciopercae takes one year (Moravec, 1969; Cannon, 1971; present study) and the mollusc hosts may only live for one year (Heard, 1965), co-ordination of the life cycle is essential to ensure the infection of bivalves shortly after birth (Cannon, 1972). The factors influencing the maturation of B. luciopercae in perch and the subsequent release of gravid flukes are discussed later.

The cercariae of B. luciopercae showed initial photo-taxis, after which they sank and alternatively attached to, and swam along, the bottom (Cannon, 1971). They lived for 12 hours at 20°C (Cannon, 1971). Metacercariae of B. luciopercae become infective after 7-21 days (Wisniewski, 1958; Cannon, 1971).

The seasonal occurrence and maturation of B. luciopercae in its definitive host has been reported by many workers (e.g. Layman, 1940; Komarova, 1941; Dogiel, 1958; Bauer, 1959; Kozicka, 1959; Malakhova, 1963; Rizvi, 1964; Tedla & Fernando, 1969; Ravckis, 1970a; Wierzbicki, 1970; Cannon, 1972; Halvorsen, 1972; Wootten, 1973c; Campbell, 1974). B. luciopercae matured over the winter, with the production of gravid worms in the spring-summer. The incidence and intensity of infection usually reached a minimum during the summer. In some studies the parasite was then absent from the fish for 1-2 months (e.g. Layman, 1940;

Cannon, 1972; Wootten, 1973b), while in others there was an overlap

of successive generations (e.g. Rizvi, 1964; present study).

Egg production in B. luciopercae at Llyn Tegid had begun in

February at a time when lake temperatures were at a minimum. This

is in accordance with the experimental observations at 4-8°C, where

egg production and the appearance of gravid flukes was not dependent

on an increase in temperature. Cannon (1972) stated that gravid

B. luciopercae are shed from the fish. In the water they swell,

rupture and release their eggs. Many of the above authors have

suggested that this loss of gravid worms from perch in the spring-

summer was a result of increasing water temperatures. The loss of

B. luciopercae from perch at Lake Seliger (U.S.S.R.) (Layman, 1940),

Lake Opeongo (Canada) (Cannon, 1972) and Hanningfield Reservoir (Essex)

(Wootten, 1973b) was similarly timed (Wootten, 1973c). In these lakes

the temperature reached 10-15°C in May-June, at which time the gravid

parasites were shed. In the River Yenisey (U.S.S.R.) (Dogiel, 1958)

and Lake Ontario (Canada) (Tedla & Fernando, 1969) the water temperature

did not reach 10-15°C until June-July, and the loss of gravid

B. luciopercae from the fish was consequently delayed for 2-3 months.

At Llyn Tegid, the loss of gravid flukes primarily occurred between

May-July, when the lake temperature at 6m was 8.5-13.5°C. Cannon (1972)

found that gravid B. luciopercae were shed from yellow perch after

11-20 days at 20°C and 25°C, but not after 40 days at 4°C.

The timing of cercarial emergence from pisidia, and the seasonal

feeding habits of the fish, are important in determining the appearance

of juvenile stage (I) B. luciopercae in perch. Infective plankton

may be available from May onwards. Wootten (1973c) considered that

infective metacercariae were available for several months after cercarial

emergence in June, at Hanningfield Reservoir (Essex). At Llyn Tegid, perch did not ingest appreciable numbers of planktonic crustaceans until July, and planktonic crustaceans were then important dietary components until October (see Chapter III). Consequently, juvenile stage (I) B. luciopercae were predominant in perch from July (Table XIX). The incidence of infection rose in August, and remained high until the following March-April. The incidence of infection was lowest in July (Table XIX). The intensity of infection was at a minimum in June. It then increased and reached a prominent peak in August and September (Table XIX). In October there was a marked fall in the intensity of infection, and then the intensity remained fairly constant until the following April, when it began to fall (Table XIX).

The marked fall in the intensity in October suggested that during the preceeding months of August and September the constant, high intensity of infection was a result of a high input and output of parasites from perch. The high input was provided by the extensive plankton feeding habits of the fish at this time and may also be a result of the seasonal abundance of metacercariae in the second intermediate host. In October, when the occurrence of zooplankton in the stomachs of perch fell, input also decreased and the intensity of infection dropped as a result of the continued output of parasites. From Fig. 21 it appears that during July-September the juvenile B. luciopercae did not establish or develop beyond stage (I).

Hopkins (1959), Chubb (1963b), Chubb et al. (1964) and Kennedy (1968) have all demonstrated the existence of dynamic conditions within populations of fish parasites. Kennedy (1970) pointed out that the input in such systems is influenced by the availability of infective larvae and the feeding habits of the host, and went on to consider

the factors affecting output. According to Kennedy (1970) output is influenced by the failure of parasites to establish the host rejection of established parasites, and the natural mortality of parasites at the end of their life. In addition, all of these factors may be influenced by inter- or intra-specific competition, and abiotic factors such as temperature (Kennedy, 1970). The effect of temperature on the establishment of Crepidostomum farionis and C. meteocus in trout (Salmo trutta) was noted by Awachie (1968), when the parasites failed to establish at temperatures above 10°C. Kennedy & Walker (1969) found that there was a temperature dependent host rejection of the cestode Caryophyllaeus laticeps by dace (Leuciscus leuciscus), and reported that the parasite could establish more readily and survive longer at cooler temperatures. Kennedy (1969, 1970) considered that temperature dependent responses by the fish are a major control of the flow of parasites through this type of system, since it permits establishment only in the winter months when the ability of the fish to respond is lowest. In laboratory fish kept at 16-20°C, the infection of B. luciopercae established and developed normally for 80-90 days. By day 130 the infection had disappeared. This result suggested that the high output of flukes from perch during August-October is not produced directly by high summer-autumn temperatures, or by a simple host rejection response. Unless there are other factors involved, it would appear that there may be the involvement of a density dependent process, causing the loss of B. luciopercae stage (I) at high intensities. Since lake temperatures are high during August and September, the influence of temperature on this density dependent process may require investigation. Stromberg & Crites (1975) have suggested that there may be a density dependent mortality of the nematode Camallanus oxycephalus from white bass

(M*o*rone chrysops).

The presence of zooplankton in the stomachs of perch (and the occurrence of stage (I) B. luciopercae) in most months of the year indicated that recruitment was not restricted to a single season. However, the results suggested the following patterns of input and output of B. luciopercae from adult perch at Llyn Tegid. During July the incidence and intensity of infection had begun to rise after a seasonal minimum. This was a result of the acquisition of stage (I) flukes from infected zooplankton. There may have been little output of juvenile flukes at this time. As a result of extensive plankton feeding the incidence and intensity of infection was high in August and September. During this period the input and output were both relatively high and resulted in a constant intensity of infection. In October, as a result of the decrease in plankton feeding, input fell though output continued and produced a marked fall in intensity. Between November-February input and output continued at a reduced level and maintained the intensity of the overwintering population fairly constant. The output increased during April-July as a result of the loss of gravid worms. During these months incidence and intensity fell as a result of the very low input.

Kennedy (1970) stated that the patterns of population change may not necessarily be characteristic of a parasite species or a host-parasite system. Whilst the overall pattern of seasonal changes in occurrence and maturation of B. luciopercae was similar in a range of widely varying geographical areas, there may exist discrete differences in the dynamics of the infection from locality to locality, and from year to year. In contrast to the condition observed at Llyn Tegid, Wootten (1973c) found a significant increase

in the intensity of infection during December-February 1968/69

at Hanningfield Reservoir (Essex). This presumably resulted from

either a decrease in output and/or an increase in input of

parasites from the system. In addition, Campbell (1974) has

recorded an annual difference in the infection of perch with

B. luciopercae at Loch Leven (Scotland).

The lack of experimental studies on the seasonal maturation of

the digenetic trematode parasites of fish has been indicated. The

results from the experiments performed on laboratory infected fish

in this study are considered below. The incidence of infection in

experimantal fish was usually high, though in each experiment only

20-22% of the original 150 flukes were recovered. This may have

been a result of several factors, including the damage of the

parasites during dissection and transfer and the unfavourable

nature of the perch stomach into what they were initially introduced.

Nonetheless, these results do allow some tentative conclusions

to be drawn.

The development of B. luciopercae proceeded normally at 16-20°C

reaching stage (III) by day 83. However, the infection had disappeared

by day 135 and 165. It seems unlikely that the parasite had matured

and disappeared from the fish between day 84-135, or that all of the

fish examined on day 135 and 165 were (by chance) uninfected. Whilst

the results from this experiment require further investigation by the

examination of larger numbers of fish between day 80-130, it appeared

that stage (I) - early stage (II) B. luciopercae were unable to develop

beyond stage (III) at 16-20°C.

At 4-8°C the development of B. luciopercae may be initially retarded.

Development did not proceed beyond stage (II) until after day 92.

However, there was a complicating factor in this experiment. Between

day 35-120 the experimental fish kept at 4-8°C refused food, and

stomachs of the fish dissected on day 35 and 92 were empty. Therefore

the lack of initial development of B. luciopercae in this experiment

may have been influenced by the lack of food (or associated digestive

substances) from the intestine of the fish. With the onset of feeding

on day 120, the flukes apparently matured rapidly and reached stage (III)

and stage (IV) by day 137 and stage (IV) and stage (V) by day 158.

Under natural conditions at Llyn Tegid, B. luciopercae developed over

the winter in perch (Fig. 15), at a time when feeding activity is

reduced (Chapter III). With the increased feeding activity of perch

in March-April there is a coincident appearance of flukes at stages (IV)

and (V) (Fig. 15). Ananichev (1959) has shown that there was a

seasonal variation in the patterns of activity of the digestive

enzymes of some fish, and this could markedly effect physiological

conditions within the intestine (Williams et al. 1970). Therefore,

it may be enlightening to study the development of B. luciopercae

in perch that were maintained at various temperatures and either

starved, or fed a constant amount of food, throughout the experiment.

It is interesting to note that the production of gravid flukes

at 4-8°C, and at natural environmental temperatures, occurred after

a similar period of time (day 158-168). Between day 10-160 the range

of air temperatures under the natural environmental conditions was

0-16°C, though it is unlikely that water temperatures fluctuated so

widely. However, these results showed that at low temperatures (16°C,

or less) the development and maturation of B. luciopercae resulted in the

production of gravid flukes (from stage (I) - early stage (II) parasites)

after 158-168 days. It is likely that the gravid parasites produced

at 4-8°C after 158 days would have remained in the fish for some time.

Cannon (1972) found that gravid B. luciopercae were present in

yellow perch after 40 days at 4°C, though they were shed after

11-20 days at 20°C.

Whilst the dynamic nature of the B. luciopercae infection of perch

at Llyn Tegid has been indicated, it was suggested that the overwintering

levels of input and output were relatively low. This, along with

the fact that stage (I) - early stage (II) B. luciopercae can survive

and develop into gravid flukes after 158-168 days in experimental

fish, suggested that at least some of the parasites present in perch

during October-November at Llyn Tegid may have survived and matured

the following spring. Because of the loss of parasites from perch

during August-October, it is thought that few of the parasites acquired

in July-September survived to attain subsequent maturity. The details

of the dynamic aspects of the B. luciopercae infection have been

discussed elsewhere.

The failure of parasites to mature at a temperature of 16-20°C,

even after exposure to 4-8°C for 43 days, suggested that B. luciopercae

in its definitive requires an extended period of "vernalisation" in

order to develop and mature normally. Kennedy (1969) and Kennedy &

Walker (1969) stated that egg production in Caryophyllaeus laticeps

(a cestode with a progenetic larva) was not stimulated by a rise in

temperature, and it was suggested that maturation in this parasite

might be related to host endocrine levels. A similar explanation

was offered to explain the seasonal maturation of Proteocephalus

torulosus (Cestode) by Kennedy & Hine (1969). The presence of

gravid B. luciopercae in juvenile, non-spawning perch (aged 0++),

along with the maturation of flukes in experimental perch whose gonads

did not develop beyond early stage III on the Nikolsky (1963) scale,

strongly suggests that maturation in this parasite is not dependent upon

the normal seasonal changes in gonadotrophin levels in adult perch.

VII. 3.5   SUMMARY

It appeared that the life cycle of B. luciopercae at Llyn
Tegid involved Pisidium lilljeborgii as the first intermediary,
cladoceran and/or copepod crustaceans as the second intermediaries,
and perch as the only definitive host.

The distribution of the parasite in the adult perch population
was markedly overdispersed. There were no signs of pathogenic
effects, even at very high intensities.

The infection was similar in adult male and female perch.

Perch acquired the infection during their first few weeks of
life in Llyn Tegid. The infection was prevalent in fish aged 0++
and above. In perch older than 6++ there was a marked increase
in the intensity of infection. This was attributed to the cannibalistic
feeding habits of the older fish.

The infection was similar at a shallow and deeper water site
during June-July.

B. luciopercae was found in the pyloric caeca and intestine of
perch. The parasite was recorded from the gall bladder of a single
perch. Aspects of intra- and inter- specific competition were
discussed.

The intramolluscan development was studied at three temperatures
in laboratory infected pisidia, and compared to the seasonal development
within the natural intermediate host at Llyn Tegid. B. luciopercae
did not develop beyond the sporocyst stage at 4-8°C. At 16-21°C the
development was similar to that reported by previous workers. The
experiment at natural environmental temperatures failed as a result
of the high summer temperatures during 1976. At Llyn Tegid, the

development was similar to the experimental studies at 16-21°C until
the second generation rediae were reached. It was suggested that
falling autumn-winter temperatures may have initiated the production
of immature cercariae. Cercariae matured and were shed in a short
period of time between March-May.

A technique was described for the successful transfer of
B. luciopercae from infected, recently killed perch into uninfected,
live laboratory fish. The effect of temperature on the development
of B. luciopercae in its definitive host was examined at four thermal
regimes. A 16-20°C the development of B. luciopercae did not proceed
normally and the infection had disappeared by day 130. At 4-8°C
and at natural environmental conditions, gravid flukes were produced
after 158-168 days. It was suggested that in order to develop normally
B. luciopercae requires an extended period at low temperatures. Whilst
an increase of temperature on infected fish maintained at 4-8°C for
43 days did not stimulate maturation, the effect of a longer
"vernalisation period" (prior to an increase in temperature) was not
investigated.

In perch at Llyn Tegid there was a distinct seasonal cycle of
incidence, intensity and maturation.

Life history of B. luciopercae at Llyn Tegid. In view of the
large amount of literature available on this parasite, the life
history at Llyn Tegid is summarised below.

Gravid flukes were shed from perch in response to increasing lake
temperatures during April-July. Eggs hatched and miracidia infected
P. lilljeborgii. Other pisidia were relatively scarce in Llyn Tegid.
Sporocysts were present during May and July. Two generations of rediae
were produced, the latter of which contained immature cercariae by
January. Falling lake temperatures may have stimulated the production

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of immature cercariae. Cercariae were shed over a short period between
March-May. Cercariae may infect a number of species of littoral and
pelagic Cladocera and Copepoda. Juvenile newly acquired B. luciopercae
were most abundant during July-September, when plankton feeding was
prevalent. However, during August-September the intensity of
infection was high and the flukes did not become established.
Consequently, in October when plankton feeding decreased, the
intensity of infection fell and remained constant during the
overwintering maturation of B. luciopercae. Recruitment appeared
to occur in most months and the dynamic aspects of the infection
were considered.

Temperature is clearly a major influence on the life history
and development of B. luciopercae. Further investigations should be
aimed at elucidating the details of this relationship, and similar
studies made on other digenean parasites of ecto-thermic hosts.

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