STUDIES ON THE PARASITE FAUNA OF THE FISH OF THE RIVER LUGG (A TRIBUTARY OF THE RIVER WYE, HEREFORDSHIRE).

ELIZABETH H. DAVIES.

THESIS FOR THE DEGREE OF Ph.D.

UNIVERSITY OF LIVERPOOL.

TABLE OF CONTENTS.

Studies on the parasite fauna of the fish of the River Lugg, (a tributary of the River Wye, Herefordshire).

Summary

The parasite fauna of five species of fish, Squalius cephalus (L.), Leuciscus leuciscus (L.), Rutilus rutilus (L.), Thymallus thymallus (L.) and Esox lucius L., caught in the River Lugg between January and December 1964, was examined.

1257 fish were examined and 38 species of parasites were recorded; 6 Protozoa (Myxosporidia); 11 Monogenea; 5 Digenea; 4 Cestoda; 5 Nematoda; 5 Acanthocephala; 1 Hirudinea; 1 Mollusca. 8 species of parasites were recorded for the first time in Britain:- Dactylogyrus vistulae, D. folkmanovae, D. prostae, D. cordus, D. tuba, D. nanus, Tetraonchus borealis (Monogenea) and Allocreadium transversale (Digenea).

The seasonal dynamics of commonly recorded parasites were studied. No seasonal variation in incidence was noted for Myxosporidia, and no variation was observed in the shape or size of the spores of Myxobolus species, whereas tailed and tailess spore forms of Henneguya species were recorded at different times of the year. Dactylogyrids (Monogenea) showed a marked seasonal occurrence only being recorded between February and September, and it is postulated that temperature may be the important controlling factor. Annual cycles of development and maturation were present in Allocreadium isoporum, Sphaerostoma bramae (Digenea) and Proteocephalus torulosus (Cestoda), the main reinfection period of the definitive host occurring between September and October, and the peak period of egg production between May and

July. The incidence and intensity of infection of helminth parasites were studied especially in relation to the length and sex of the host.

The parasite faunas of each host were compared and reasons for the different patterns and levels of infection were discussed.

CHAPTER ONE.

INTRODUCTION.

The ecology of the parasites of freshwater fish is a complex subject involving a study of all the factors influencing the host, the parasite and the host-parasite relationship.

Many aspects of the parasites of freshwater fishes have been studied in Britain, all of which contribute to an understanding of the ecology of fish parasites. Lists of parasites from freshwater fish hosts are recorded by Baylis (1928, 39); Rawson (1952); Copland (1956,57) and Kane (1966). The latter author reviews all previous work published on the parasites of freshwater fish in Ireland. The population dynamics of individual parasite species have been studied by Hopkins (1959); Chubb (1963, 64); Paling (1965) and Awachie (1965, 66). The parasites of Salmo trutta L. have been investigated by several authorities, for example, Robertson (1953); Thomas (1964, a and b); Awachie (1963) and Aderounmu (1965, and in progress). Other parasites were only examined when they were found to be the cause of the mass mortality of fish, for example, Duguid and Sheppard (1944); Fraser (1960) and Williams (1964). Investigations of the larval stages and life cycles of parasites, some of which infect freshwater fish were undertaken by Brown (1926); Rees (1932, 55, 57); Erasmus (1958, 59); Iles (1959, 60); Nasir and Erasmus (1964); Awachie (1965). The physiology and in vitro cultivation of Schistocephalus solidus (Müller, 1776) and Ligula intestinalis (L.)

have been studied by Smyth (1946, 56, 59); Hopkins (1950, 52); Hopkins and McCaig (1965); Walkey and Davies (1964); Arme (1966).

In recent years several research workers in the Department of Zoology, University of Liverpool, have investigated the ecology of the parasites of freshwater fishes. This work was initiated by Dr. J.C. Chubb when a preliminary investigation was made of the parasite fauna of the fish of Llyn Tegid (Bala Lake), Merionethshire. Since this investigation, surveys have been undertaken on the parasite faunas of the fish of Rostherne Mere, Cheshire (Rizvi, 1964); the Shropshire Union Canal, Cheshire (Mishra, 1966) and Llyn Padarn, Caernarvonshire (Powell 1966). Awachie (1963) studied the helminths of S. trutta from the Afon Terrig, North Wales, and Aderounmu (work in progress) is comparing the parasites of S. trutta from Chirk Hatchery (Denbighshire) and Llyn Tegid.

The present work involved an investigation of the parasite fauna of the fish of the River Lugg, a tributary of the River Wye (Herefordshire). The aim of this work carried out between 1963 and 1967 was to determine the species of parasites present, the percentage of fish infected, the intensity of the infection and the seasonal dynamics of the parasites. Completion of this work enabled a comparison to be made between the parasite faunas of freshwater fish from differing freshwater habitats in Britain.

The present survey was carried out in conjunction with an investigation by Mr. J.M. Hellawell for the Wye River Authority, on

competition between coarse fish and salmonids. This allowed a study of the biology of the fish and their parasite faunas to be undertaken at the same time and at the same location.

It is hoped that the data from this investigation will provide information on the distribution of parasites of freshwater fishes and their hosts in Britain, and will also be of use in more specialised studies in taxonomy, experimental work on life cycles and seasonal dynamics of these parasites.

The Environment.

The River Lugg is 58.5 miles long. The source of the river is on Rhos Crug (1670' above sea-level) (Montgomeryshire) about seven miles north-west of Knighton. The river flows east and then south to join the River Wye at Mordiford (150' above sea-level) (Herefordshire), five miles south of Hereford. (Figure 1.1.)

Richardson (1935) in his survey of the wells and springs of Herefordshire divided the river into two main sections according to the volume and velocity of water present and to the type of landscape. The first division includes the river above Mortimers Cross Bridge where the river flows through deep valleys of Silurian rock, and is steeply graded, except between Presteigne and Kinsham where the valley is wide and liable to local flooding. The lower part of the river, except where the valley is narrowed at Ford, flows over level open country which is composed mainly of marl deposits of the Downtownian

Figure 1.1

KEY

CARBONIFEROUS LIMESTONE

UPPER AND LOWER OLD RED SANDSTONE (SANDSTONES AND MARLS)

COAL MEASURES

DOWNTONIAN (MAINLY MARLS)

LUDLOW BEDS WITH LIMESTONES

WENLOCK BEDS WITH LIMESTONES

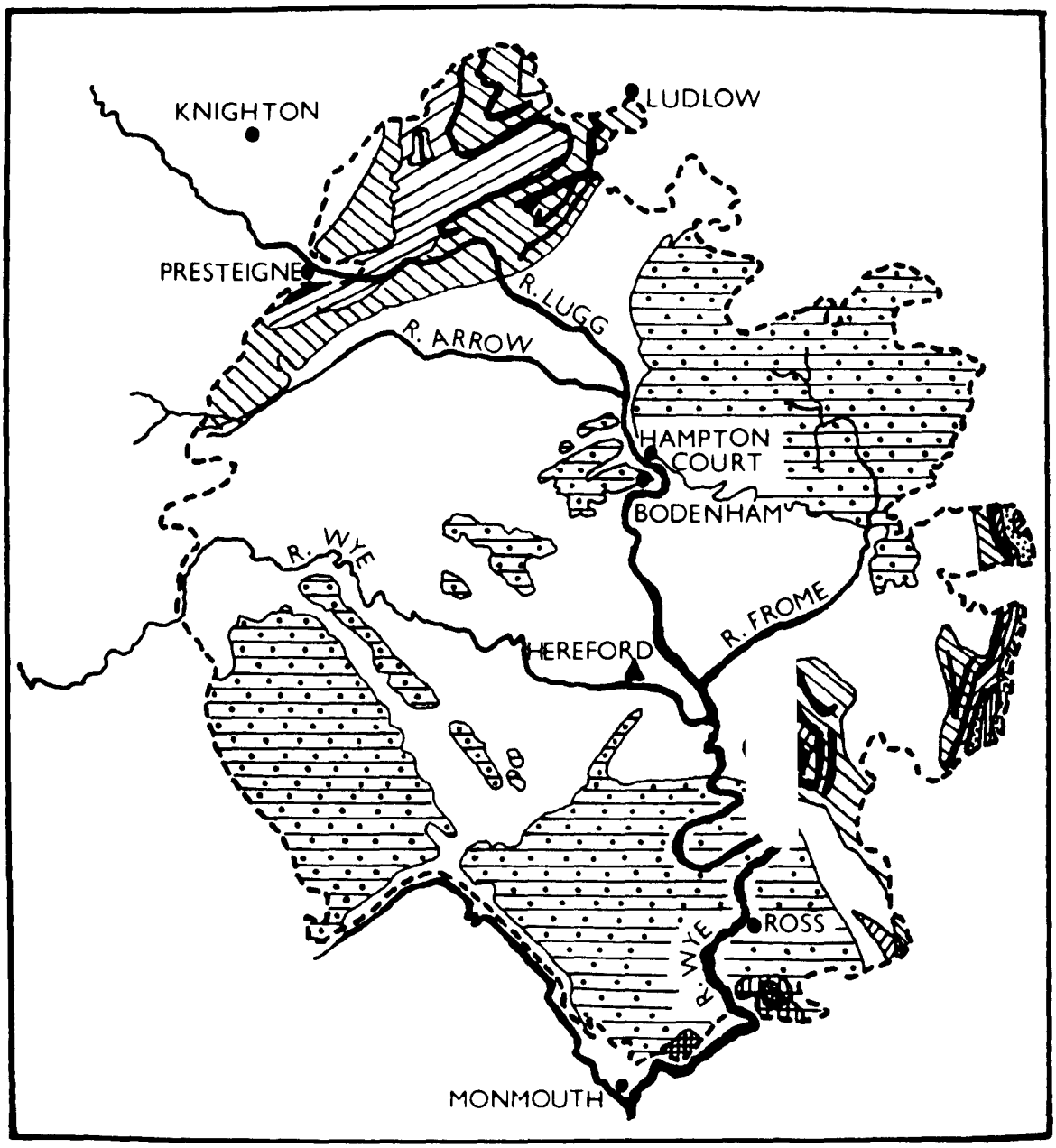
LLANDOVERY BEDS

CAMBRIAN

PRE-CAMBRIAN

COUNTY BOUNDARY

THE GEOLOGY AND MAIN RIVER SYSTEMS OF HEREFORDSHIRE



overlaid locally by gravel. The Downtownian deposits are impervious and water with suspended marl particles colours the river after heavy rain.

The Sampling Site.

Samples were taken from the River Lugg at Bodenham (SO 530509) and Hampton Court (SO 521522) (Herefordshire). In this area the river flows over the Downtownian beds, which are overlaid at the sides by alluvium, and in some places by gravel. The bed of the river consisted of a mixture of small boulders, light shingle, gravel and sands, and the river banks shelved steeply. Plate 1.1. In rivers with this type of bed the average velocity of the current per second should be 24" - 8", (Minnikin, 1920; Ritcher, 1933). When not in flood the greatest depth of the river was 4 - 5 feet, and varied between 15 - 30 feet in width. Both the depth and width of the river varied according to the amount of rainfall, and after heavy rain the water level rose a further 5 - 6 feet. The temperature of the river water was recorded at each sample (Figure 1.2).

Green algae, Fontinalis sp., Ranunculus fluitans and Juncus sp. comprised the main flora of the river. A list of the main invertebrate fauna was compiled from the analysis of bottom samples taken over several months, and from a study of the stomach contents of the fish (Hellawell, pers.comm.) (Table 1.1.) The vertebrate fauna of the river is also listed. (Table 1.2.)

Plate 1.1 The River Lugg, near Bodenham (Herefordshire).

Fig 1.2 The temperature of the River Lugg for each sample

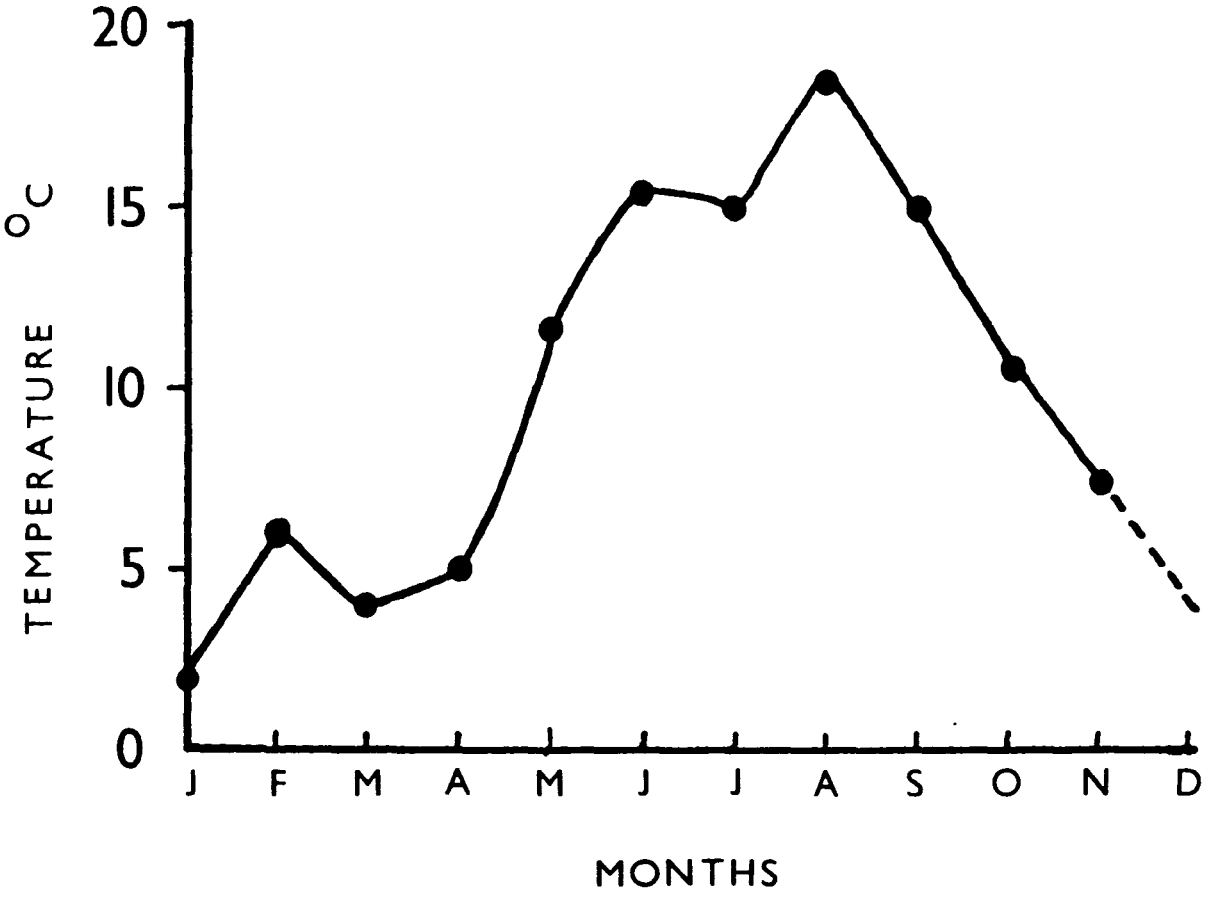

20
15
10
5
0
TEMPERATURE °C
J F M A M J J A S O N D
MONTHS

TABLE 1.1.

INVERTEBRATE FAUNA OF THE RIVER IUGG.

Platyhelminthes:	Tricladida.	
Annelida:	Oligochaeta:	Tubificidae
	Hirudinea:	
Arthropoda:		
Insecta:	Ephemeroptera:	Ecdyonurus sp.
		Leptophlebia sp.
		Baetis sp.
		Ephemera sp.
	Plecoptera:	Capnia bifrons
		Taeniopteryx nebulosa (L)
		Isoperla grammatica (Poda)
		Nemoura sp.
		Protonemoura sp.
	Coleoptera:	Limnius volkmani
		Oolimnius tuberculatis
		Elmis maugellianer
		Dytiscidae.
	Megaloptera:	Sialis sp.
	Hemiptera:	Cryodytes sp.
		Micronecta sp.
	Trichoptera:	Rhyacophila sp.
		Hydropsyche sp.
		3 unidentified species.
	Diptera:	Tipulidae
		Simulidae

Crustacea.

Amphipoda:	Gammarus pulex (L.)
Isopoda:	Asellus aquaticus L.
Decapoda:	Astacus fluviatilis L.

Arachnida:

Hydracarina sp.

Mollusca:

Ancylastrum fluviatele (Müll)
Sphaerium corneum (L.)
Anodonta sp.
Theodorus fluviatilis (L.)
Hydrobia jenkinsi Smith
Limnea peregra Müll
Physa fontinalis (L.)

TABLE 1.2.

VERTEBRATE FAUNA OF THE RIVER IUGG.

Pisces:	Cyprinidae:	Squalius cephalus (L.)
		Leuciscus leuciscus (L.)
		Rutilus rutilus (L.)
		Gobio gobio (L.)
		Phoxinus phoxinus (L.)
	Cottidae:	Cottus gobio (L.)
	Salmonidae:	Thymallus thymallus (L.)
		Salmo salar L.
		Salmo trutta L.
	Esocidae:	Esox lucius L.
	Anguillidae:	Anguilla anguilla (L.)
Amphibia:		Rana temporaria
Aves:	Rallidae:	Gallinula chloropus
	Anatidae:	Anas platyrhynchos
Mammalia:	Rodentia:	Arvicola amphibius

Sampling: Methods and Materials.

The aim was to sample 30 fish a month of each of the main species in the river. Throughout 1964 samples were taken each month from the River Lugg at Lodenham and Hampton Court. The fish were caught non-selectively using an A/C electric fisher fixed in a flat-bottomed boat. All the fish were sorted into species, and then each fish was wrapped separately and packed between layers of CO_2 ice. In the laboratory each species of fish from a sample was placed together and labelled. All those that were not examined fresh were stored under deep-freeze conditions between -5°C and -10°C.

Examination:

Over 1,200 fish belonging to five species were examined (Table 1.3). The species examined were:-

Squaluis cephalus (L.)

Leuciscus leuciscus (L.)

Rutilus rutilus (L.)

Thymallus thymallus (L.)

Esox lucius L.

The following measurements and details were recorded from each fish:-

a) Weight

b) Length (to tip of caudal fin and to the fork)

c) Sex

d) Weight of gonad and stage of development in the female, according to egg size.

e) Age (analysed by Mr. J.M. Hellawell).

Each fish was examined externally for parasites, and then slit ventrally and the parts of the fish and organs, listed below, were examined for parasites:-

a) Body cavity

b) Intestine

c) Swim bladder

d) Urinary ducts

e) Gills

Any parasites found were relaxed and preserved in the appropriate solutions (details are given in the chapter dealing with the different species of parasites) with a record of the number present, details of the host and sample number. The parasites were examined and identified and the following points investigated:-

a) Percentage infection of each host

b) Intensity of infection

c) Variation of percentage and intensity of infection in relation to the length and the sex of the host.

d) Seasonal dynamics.

TABLE 1.3:

THE NUMBER OF FISH EXAMINED.

Month	Fish				
	S.cephalus	L.leuciscus	R.rutilus	T.thymallus	E.lucius
January	32	33	33	-	1
February	31	31	27	11	1
March	29	30	30	18	-
April	30	35	16	25	7
May	31	4	9	8	5
June	30	30	30	17	8
July	30	30	22	30	7
August	30	30	30	5	2
September	28	30	30	-	-
October	27	31	30	25	4
November	30	28	30	30	-
December	31	30	30	30	1
	359	342	317	199	36

Total number of fish examined = 1,257.

Discussion.

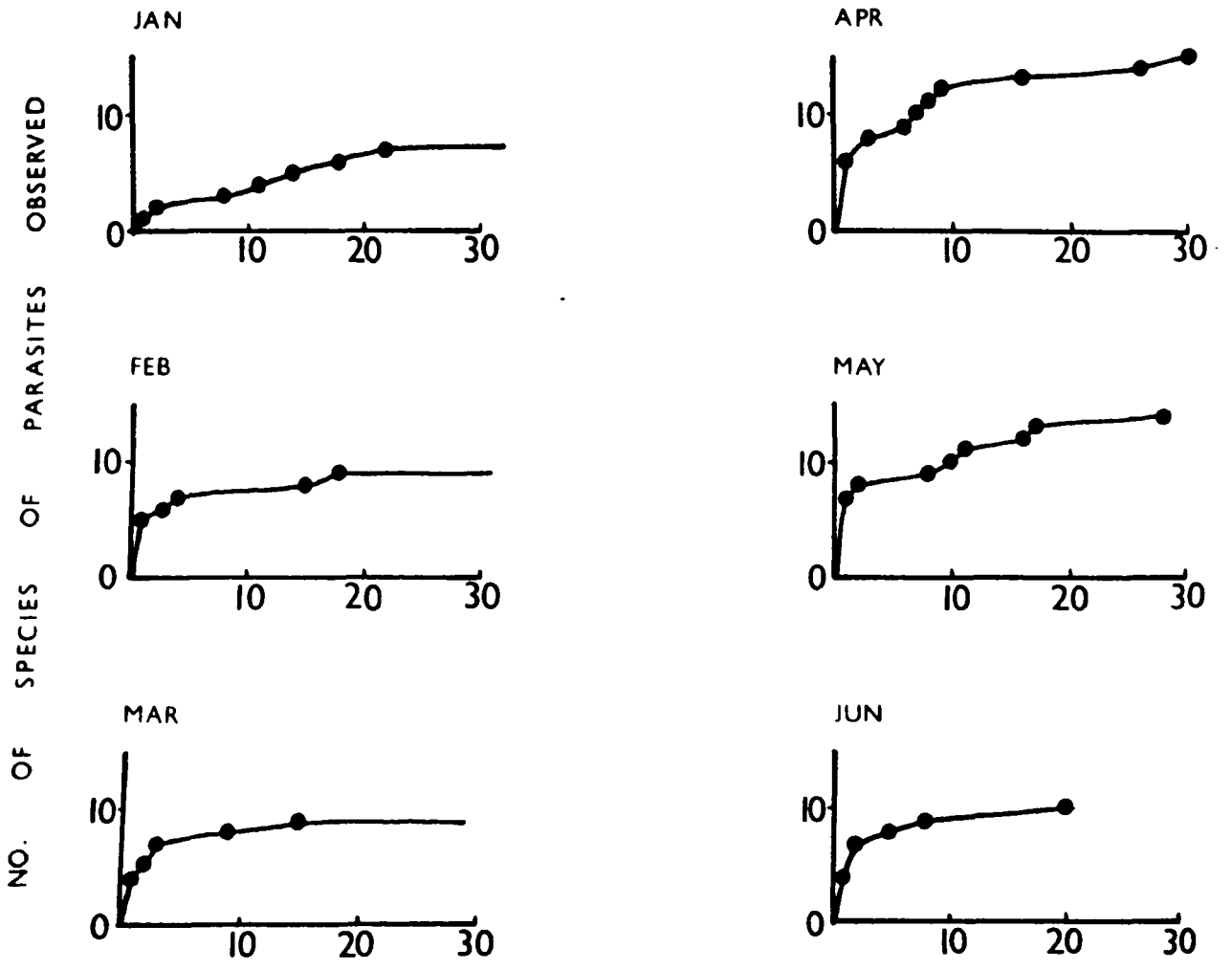
Petrushevsky and Petrushevskaya (1960) state that fifteen fish of each species is an adequate number to examine to give a representative picture of the parasite fauna for a general survey, but for more detailed investigations it is necessary to examine a greater number of fish. The aim of trying to obtain 30 fish of each species, in each sample, was to allow both a general survey as well as studies on the seasonal dynamics of the parasite fauna. Approximately 30 S. cephalus, L. leuciscus and R. rutilus were caught each month, except for poor May samples of L. leuciscus (4 fish) and R. rutilus (9 fish). This led to certain anomalies in the results but these are discussed where they are relevant. Fewer T. thymallus were caught, and samples were missing from January to September, although enough fish were caught to obtain interesting information on the parasite fauna. E. lucius were only caught in small numbers, which prevented any study of the seasonal dynamics of the parasites, but several interesting species were observed.

Petrushevsky and Petrushevskaya (1960) plotted the number of parasite species observed against the number of fish dissected, and they regarded the point at where the graph levelled off as showing the number of dissections necessary to give a true representation of the parasite fauna. This method has been used in the present survey. Figures 1.3, 1.4, 1.5, 1.6. The figures plotted for L. leuciscus and R. rutilus clearly show that nearly all the parasites were recorded

between dissections 1 and 20, the exceptions to this being the uncommon species. S. cephalus showed a similar picture, although most of the graphs did not level out until dissections 20 - 30. Fewer T. thymallus and cyprinids were caught, but Figure 1.6 shows that most of the common parasites were recorded between dissections 1 and 10 for 7 out of 10 samples, and this may result from the less varied parasite fauna recorded from T. thymallus compared to the cyprinids.

From Figures 1.3, 1.4, 1.5 and 1.6 it is possible to conclude that the number of fish in the samples were sufficient to allow a general survey of the parasite fauna, and where the intensity of infection was high a study was made of the seasonal dynamics.

Fig. 1.3 The number of species of parasites observed plotted against the number of S. cephalus dissected in each sample.


S. CEPHALUS
JAN
APR
FEB
MAY
MAR
JUN
NO. OF SPECIES OF PARASITES OBSERVED
NO. OF DISSECTIONS
0
10
20
30

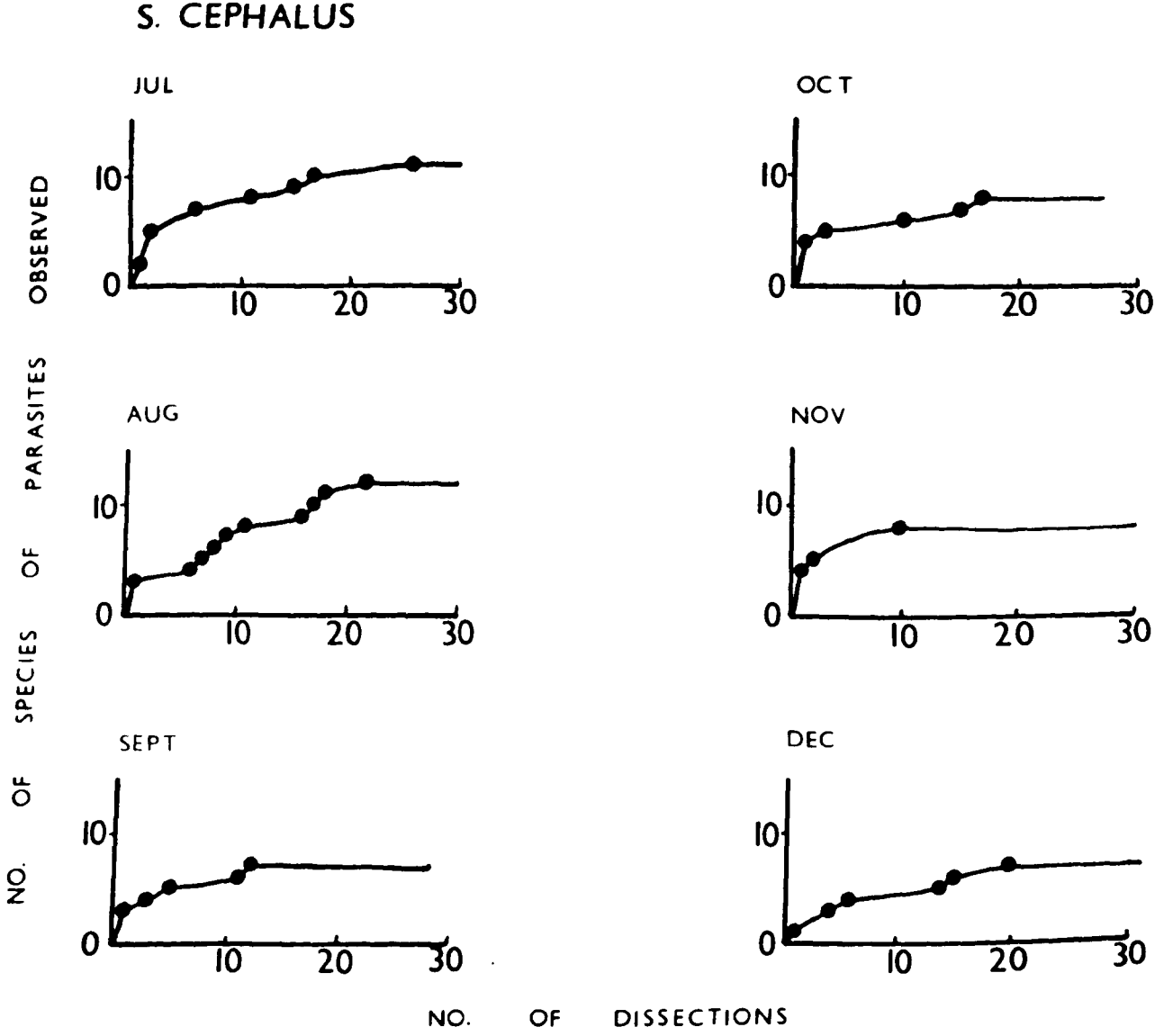
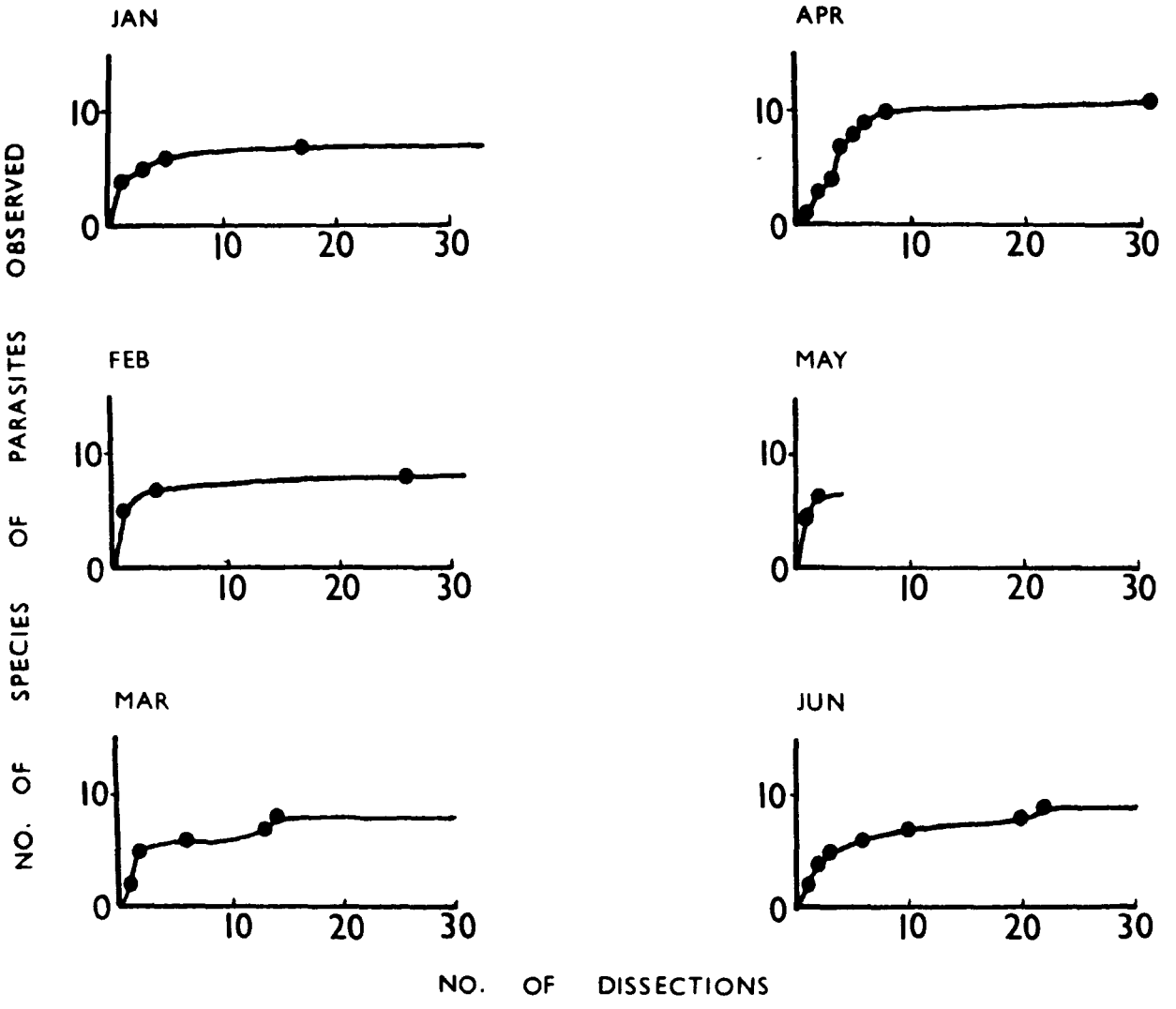

S. CEPHALUS
JUL
AUG
SEPT
OCT
NOV
DEC
NO. OF SPECIES OF PARASITES OBSERVED
NO. OF DISSECTIONS
0
10
20
30

Fig. 1.4 The number of species of parasites observed plotted against the number of L. leuciscus dissected in each sample.


L. LEUCISCUS
JAN
APR
FEB
MAY
MAR
JUN
10
0
10
20
30
NO. OF SPECIES OF PARASITES OBSERVED
NO. OF DISSECTIONS

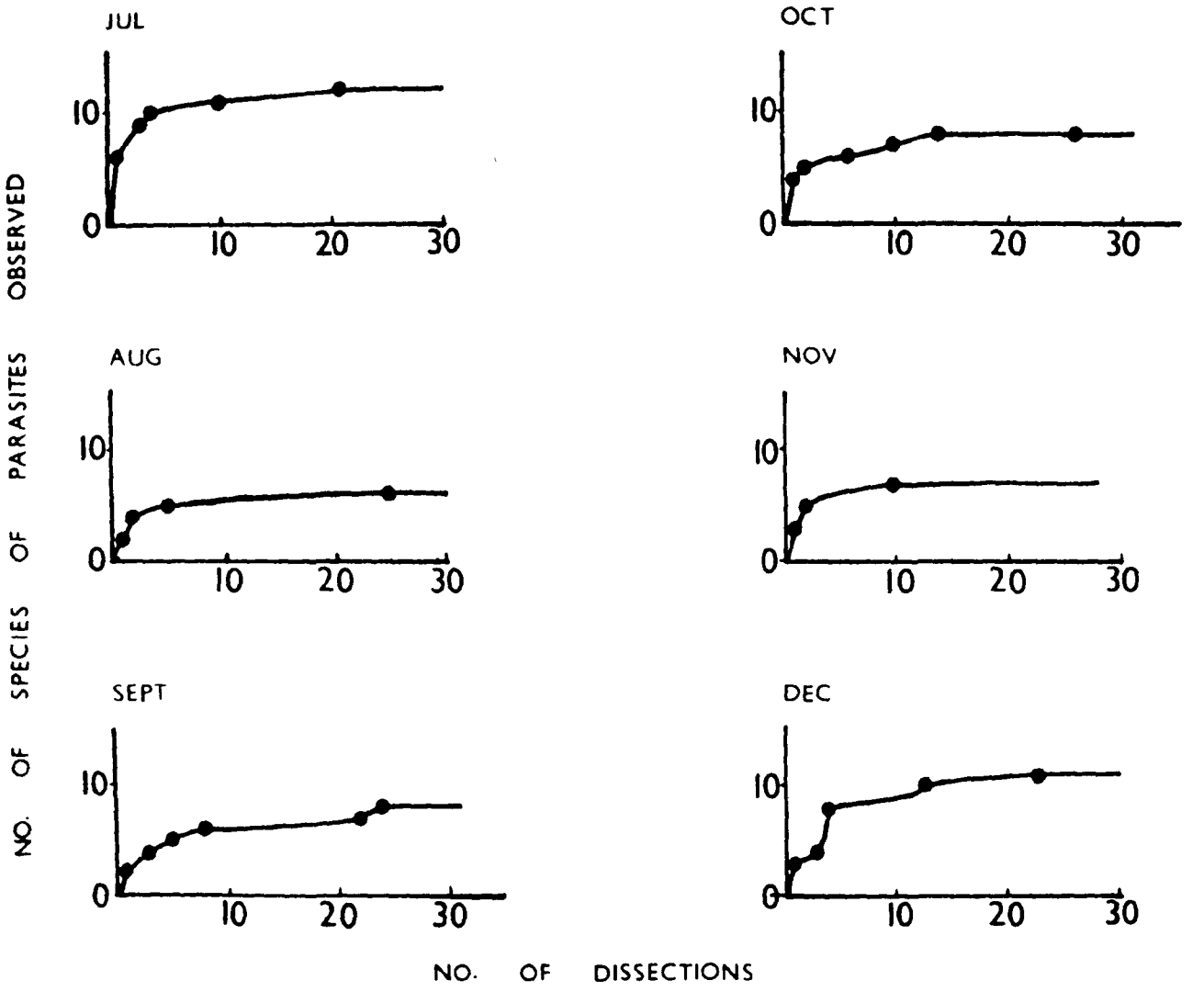
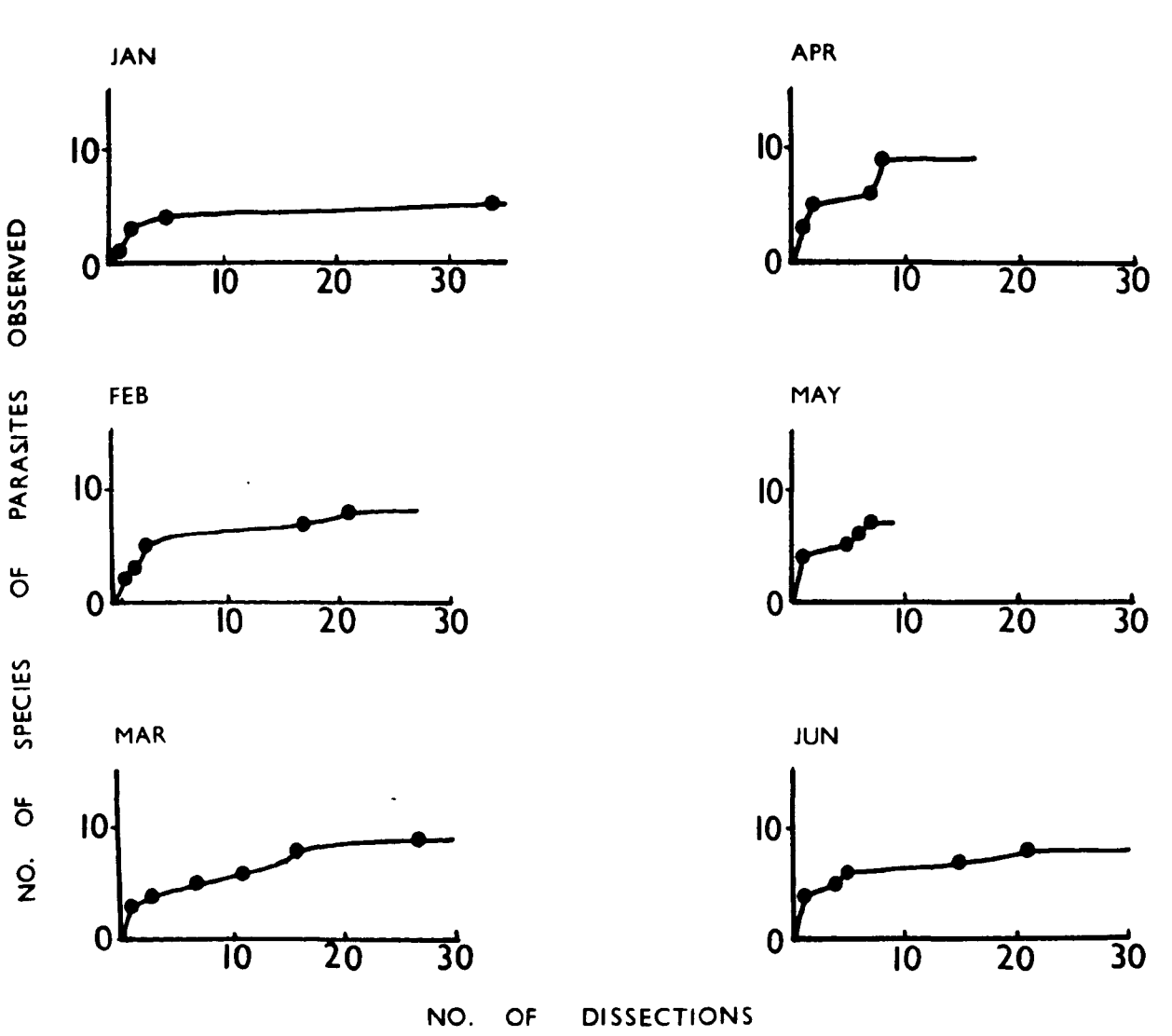

L. LEUCISCUS
JUL
OCT
AUG
NOV
SEPT
DEC
NO. OF SPECIES OF PARASITES OBSERVED
NO. OF DISSECTIONS
0
10
20
30

Fig. 1.5 The number of species of parasites observed plotted against the number of R. rutilus dissected in each sample.


R. RUTILUS
JAN
APR
FEB
MAY
MAR
JUN
10
0
10
20
30
NO. OF SPECIES OF PARASITES OBSERVED
NO. OF DISSECTIONS

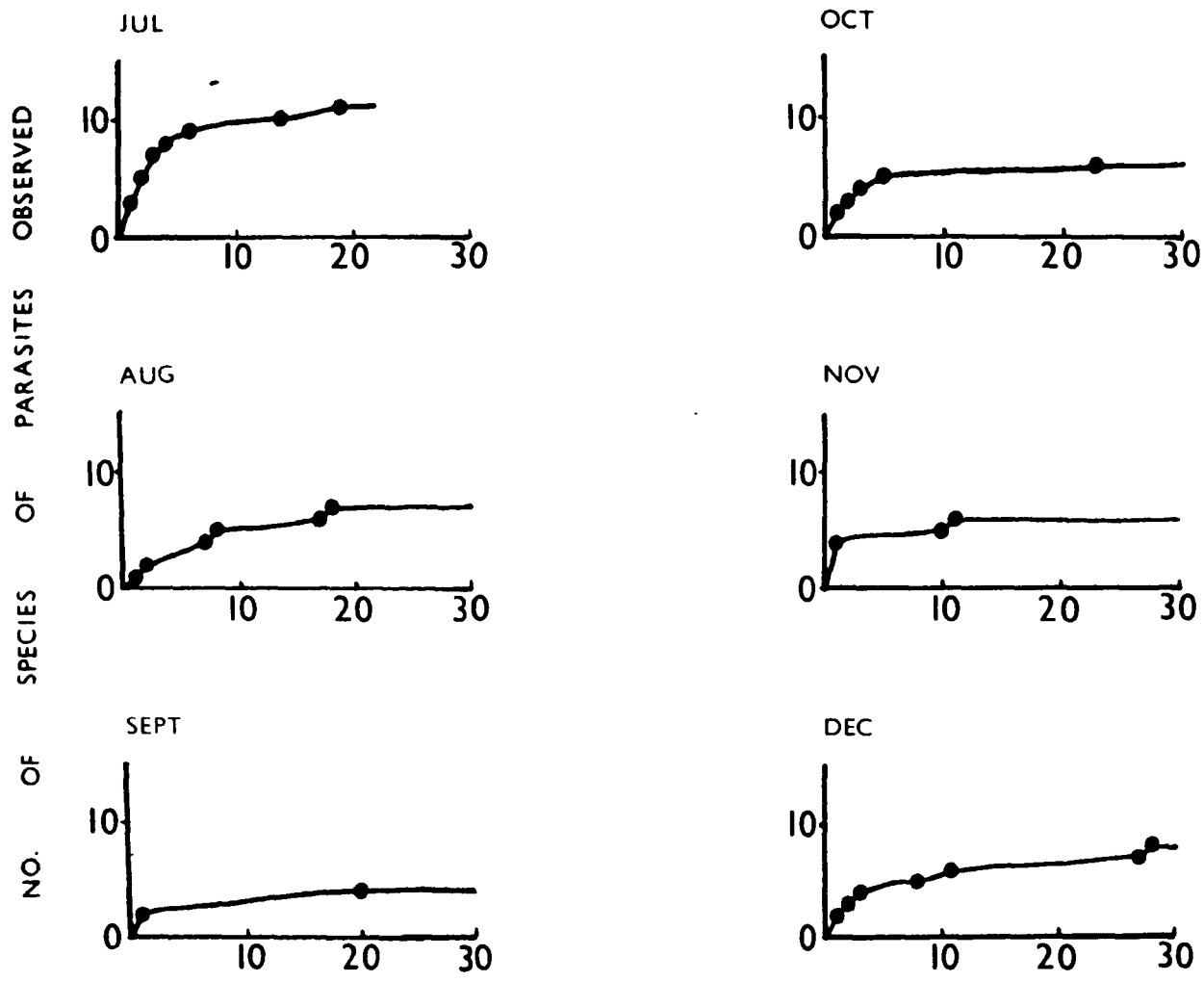
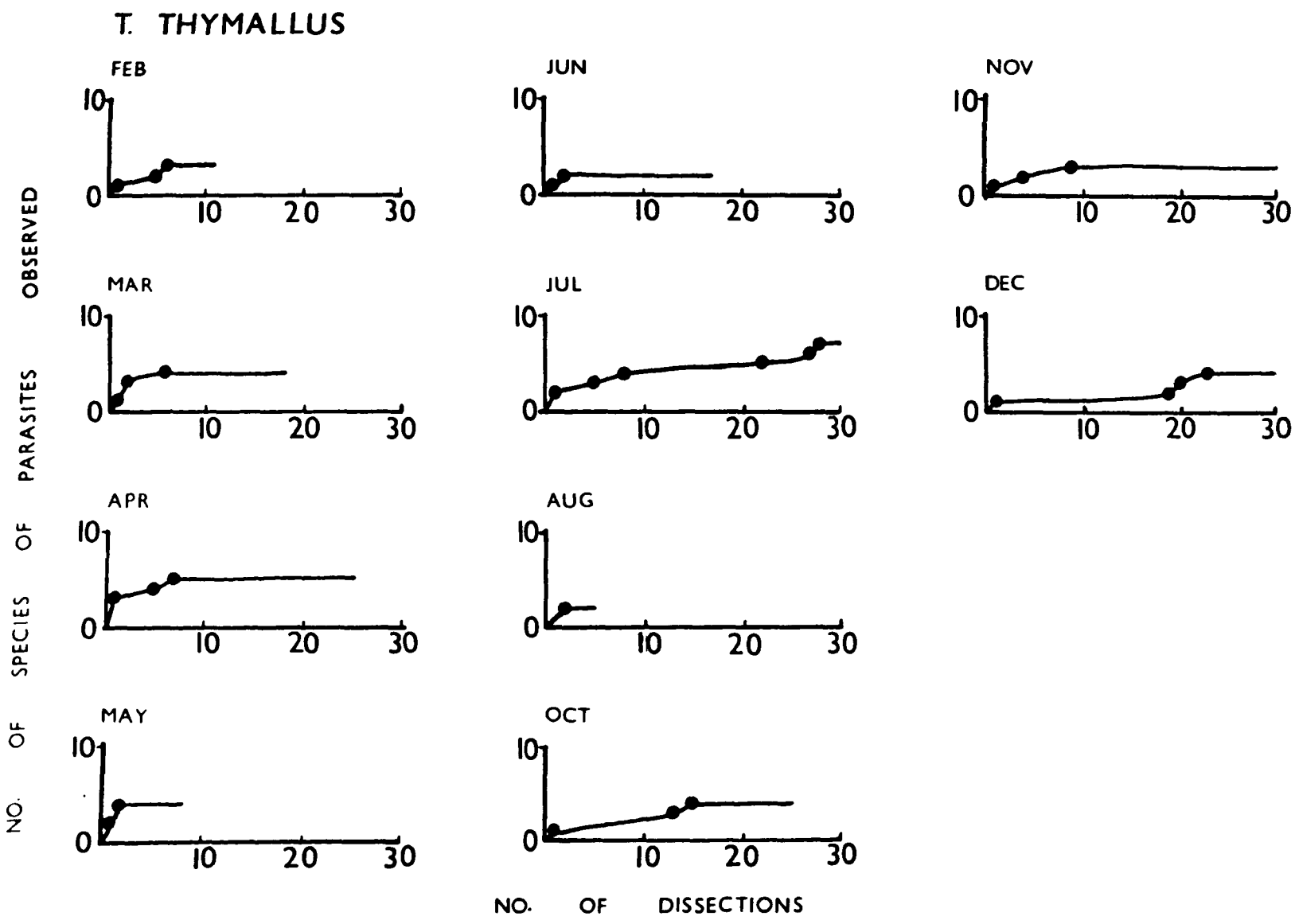

R. RUTILUS
JUL
OCT
AUG
NOV
SEPT
DEC
NO. OF SPECIES OF PARASITES OBSERVED
NO. OF DISSECTIONS
0
10
20
30

Fig. 1.6 The number of species of parasites observed plotted against the number of T. thymallus dissected in each sample.


T. THYMALLUS
FEB
JUN
NOV
MAR
JUL
DEC
APR
AUG
MAY
OCT
10
0
10
20
30
NO. OF SPECIES OF PARASITES OBSERVED
NO. OF DISSECTIONS

List of the parasites recovered from the fish examined from the River Lugg.

Protozoa.

Class Cnidosporidia Doflein 1901.

Order Myxosporidia Butschli, 1881.

Sub-order Bivalvulea Shulman, 1959.

Super family Platysporea Kudo, 1919.

Family Myxo bolidae Thelohan, 1892.

Myxobolus müller̈i Bütschli, 1882.
Myxobolus macrocapsularis Reuss, 1906.
Myxobolus artus Akhmerov, 1960.
Henneguya zschokkei (Gurley, 1894).
Henneguya psorospermica Thelohan, 1895.
Henneguya oviperda (Cohn, 1895).

Platyhelminthes.

Class Monogenoidea (Beneden) Bychowsky, 1937.

Sub-class Polyonchoinea Bychowsky, 1937.

Order Dactylogyridea Bychowsky, 1937.

Family Dactylogytidae Bychowsky, 1933.

Dactylogyrus crucifer Wagener, 1857.
Dactylogyrus sphyrna Linstow, 1878.
Dactylogyrus namus Dogel and Bychowsky, 1934.
Dactylogyrus vistulae Prost, 1957.
Dactylogyrus folkmanovae Ergens, 1956.
Dactylogyrus prostae Molnar, 1964.
Dactylogyrus cordus Nybelin, 1936.
Dactylogyrus tuba Linstow, 1878.

Order Tetraonchidae Bychowsky, 1957.

Family Tetraonchidae Bychowsky, 1937.

Tetraonchus monenteron Diesing, 1858.
Tetraonchus borealis (Olsson, 1893)

Sub class Oligonchoinea Bychowsky, 1937.

Order Mazocraeidea Bychowsky, 1957.

Family Discocotylidae Price, 1936.

Diplozoon paradoxum Nordmann, 1832.

Class Digenea.

Sub class Prosostomata Odhner, 1905.

Order Fasciolata Skryabin and Schul'ts, 1937.

Family Gorgoderidae Looss, 1901.

Phyllodistomum sp.

Family Allocreadiidae Stossich, 1904.

Allocreadium isoporum (Looss, 1894)
Allocreadium transversale (Rudolphi, 1802).
Crepidostomum metoecus (Braun, 1900).
Sphaerostoma bramae (Müller, 1776).

Class Cestoidea Rud. 1808.

Sub class Cestoda.

Order Caryop hyllidea Ben. in Olsson, 1893.

Family Caryophyllaeidae Leuckart, 1878.

Caryophyllaeus laticeps (Pallas, 1781).
Caryophyllaeides fennica (Schneider, 1902).

Order Pseudo phyllidea Carus, 1863.

Family Triaenophoridae Lönnberg, 1889.

Triaenophorus nodulosus (Pallas, 1781) plerocercoid and adult.

Order Proteo cephalidea Wola, 1928.

Family Proteocephalidae La Rue, 1911.

Proteocephalus torulosus (Batsch, 1786).

Aschelminthes.

Nematoda.

Order Ascaridida Skryabin and Shul'ts, 1938.

Sub order Ascaridata Skryabin, 1915.

Family Anisakidae.

Rhaphidascaris acus (Bloch, 1779) juvenile and adult.

Order Spirurida Chitwood, 1933.

Sub order Spirurata Railliet, 1914.

Family Rhabdochonidae Skryabin, 1946.

Spinitectus inermis (Zeder, 1800).

Cystidicola farionis Fischer, 1798.

Sub order Camallanata Chitwood, 1936.

Family Cucullanidae Cobbold, 1864.

Cucullanus sp.

Cucullanus truttae (Fabricius, 1794).

Acanthocephala.

Sub class Neoechinorhynchinea Petrochenko, 1956.

Order Neoechinorhynchida Southwell and Macfie, 1925.

Family Neoechinorhynchidae Van Cleave, 1919.

Neoechinorhynchus rutili (Müller, 1780).

Sub class Echinorhynchinea Petrochenko, 1956.

Order Echinorhynchida Southwell and Macfie, 1925.

Family Echinorhynchinae Meyer, 1931.

Echinorhynchus truttae, Schrank, 1788.
Acanthocephalus lucii (Müller, 1776).

Family Pomphorhynchidae Yamaguti, 1939.

Pomphorhynchus laevis (Müller, 1776).

Order Polymorphidae Meyer, 1931.

Polymorphus minutus (Goeze, 1782) cystacanth.

Annelida.

Class Hirudinea

Order Rhynchobdella Blanchard, 1894.

Family Piscicolidae Johnston, 1865.

Piscicola geometra (L.1761)

Mollusca.

Class Bivalvia.

Anodonta sp. (glochidia)

REFERENCES.

ADEROUNMU, E.A. 1965 The Parasite fauna of the brown trout, Salmo trutta L., from Chirk Hatchery, Denbighshire, and Llyn Tegid (Bala Lake), Merionethshire. M.Sc. Dissertation. University of Liverpool.

ARME, C. 1966. Histochemical and biochemical studies on some enzymes of Ligula intestinalis (Cestoda, Pseudophyllidea). J.Parasit. 52, (1): 63-69.

AWACHIE, J.B.E. 1963 The ecology of intestinal helminth parasites of the fish of Afon Terrig, North Wales. Ph.D. thesis. University of Liverpool.

1965 The ecology of Echinothynchus truttae Schrank, 1788 (Acanthocephala) in a trout stream in North Wales. Parasitology. 55, (4): 747-762.

1966 Observations on Cyathocephalus truncatus Pallas 1871 (Cestoda; Spathebothridia) in its intermediate and definitive hosts in a trout stream, North Wales. J. Helminth. 60, (1/2): 1-10.

BAYLIS, H.A. 1928 Records of some parasitic worms from British vertebrates. Ann.Mag.nat.Hist. (10),1: 329-343.

1939 Further records of parasitic worms from British vertebrates. Ann.Mag.nat.Hist. (11),4: 473-498.

BROWN, F.J. 1926 Some freshwater larval trematodes with contributions to their life histories. Parasitology. 18: 21-34.

BUTCHER, R.W. 1933 Studies on the ecology of rivers. I. On the distribution of macrophytic vegetation in the rivers of Britain. J.Ecol. 21: 58-91.

CHUBB, J.C. 1963 Seasonal occurrence and maturation of Triaenophorus nodulosus (Pallas, 1781) (Cestoda: Pseudophyllidea) in the Pike Esox lucius L. of Llyn Tegid. Parasitology. 53: 419-433.

1964 Occurrence of Echinorhynchus clavula (Dujardin 1845) nec Hamann, 1892 (Acanthocephala) in the fish of Llyn Tegid (Bala Lake) Merionethshire. J.Parasit. 50: 52-59.

COPLAND, W.O. 1956 Notes on the food and parasites of pike (Esox lucius) in Loch Lomond. Glasgow.Nat., 17: 230-235.

1957 The parasites of Loch Lomond Fishes. In studies on Loch Lomond, 1: 128-133. Glasgow.

DUGUID, J.B. & SHEPPARD, E.M. 1944 A Diphyllobothrium epidemic in trout. J.Path.Bact. 56: 73-80.

ERASMUS, D.A. 1958 Studies on the morphology, biology and development of a strigeid cercaria Cercaria X Baylis (Strigeida) within the first intermediate host. Parasitology, 48: 312-335.

1959 The migration of Cercaria X Baylis (Strigeida) within the first intermediate host. Parasitology, 49: 173-190.

FRASER, P. 1960 The occurrence of Diphyllobothrium in trout with special reference to an outbreak in the west of England. J. Helminth 34: 59-72.

HOPKINS, C.A. 1950 Studies on cestode metabolism.1. Glycogen metabolism in Schistocephalus solidus in vivo. J.Parasit. 36: 384-90.

1952 Studies on cestode metabolism.2. The utilization of glycogen by Schistocephalus solidus in vitro. Expl.Parasit. 1: 196-213.

HOPKINS, C.A. 1959 Seasonal variation in the incidence and development of the cestode Proteocephalus filicollis (Rud.1810) in Gasterosteus aculeatus (L.1766). Parasitology, 49: 529-542.

ILES, C. 1959 The larval trematodes of certain freshwater molluscs. Parasitology, 49: 478-504.

1960 The larval trematodes of certain freshwater molluscs.II. Experimental studies on the life cycle of two species of furcocercariae. Parasitology, 50: 401-417.

KANE, M.B. 1966 Parasites of Irish fishes. Scient.Proc.R.Dubl.Soc. Ser.B. 1, (18): 205-220.

McCAIG, M.L.O. and HOPKINS, C.A. 1965 Studies on Schistocephalus solidus. 3. The in vitro cultivation of the plerocercoid. Parasitology, 55: 257-269.

MINNIKIN, R.C. 1920 Practical river and canal engineering. London.

MISHRA, T.W. 1966 Parasite fauna of the fish of the Shropshire Union Canal, Cheshire. Ph.D. thesis, University of Liverpool.

NASIR, P. and ERASMUS, D.A. 1964 A key to the cercariae from British freshwater molluscs. J. Helminth. 38, (3/4): 245-268.

PALING, J.E. 1965 The population dynamics of the monogenean gill parasite Discocotyle sagitta Leuckart on Windermere trout, Salmo trutta L. Parasitology, 55: 667-695.

PETRUSHEVSKY, G.K. & PETRUSHEVSKAYA, M.G. 1960 The accuracy of quantitative indices relating to the study of parasite faunas of fishes. Parazit.Sb. 19: 333-353. Translation by the National Lending Library, Boston Spa. Ref.RTS 2393.

POWELL, A. 1966 A preliminary investigation of the biology and parasitic fauna of the char, (Salvelinus alpinus perisii). Ph.D. thesis, University of Liverpool.

RAWSON, D. 1952 The occurrence of parasitic worms in British freshwater fishes. Ann.Mag.nat.Hist. (12), 5: 877-887.

REES, F.G. 1932 An investigation into the occurrence, structure and life histories of the trematode parasites of four species of Limnea, L.truncatula (Mull.) L.peregra (Mull.), L.palustris (Mull.) and L. stagnalis (Linne) and Hydrobia jenkinsi (Smith) in Glamorgan and Monmouth. Proc.zool.Soc. Lond., 1: 1-32.

1955 The adult and diplostomulum stage (Diplostomulum phoxini (Faust) of Diplostomulum pelmatoides Dubois and an experimental demonstration of part of the life cycle. Parasitology, 45: 295-312.

1957 Cercaria diplostomi phoxini (Faust). A furcocercaria which develops into Diplostomulum phoxini in the brain of the minnow. Parasitology, 47: 126-137.

RIZVI, S.S.H. 1964 The parasite fauna of the fish of Rostherne Mere, Cheshire. Ph.D. thesis. University of Liverpool.

ROBERTSON, J. 1953 The parasites of brown trout (Salmo trutta L.) and other freshwater fishes. Unpublished report of the Brown Trout Reserve Laboratory. Scottish Home Department.

RICHARDSON, 1935. Memoirs of the geological survey, England. Wells and springs of Herefordshire. D.S.I.R. Geological Survey of Great Britain. H.M.S.O.

SMYTH, J.D. 1946 Studies on tapeworm physiology. I. The cultivation of Schistocephalus solidus in vitro.
J.exp. Biol. 23: 47-70.

1956 Studies on tapeworm physiology. IX. A histochemical study of egg shell formation in Schistocephalus solidus (Pseudophyllidea)
Expl. Parasit. 5: 519-540.

1959 Maturation of larval pseudophyllidean cestodes and strigeid trematodes under axenic conditions; the significance of nutritional levels in platyhelminth development.
Ann. N.Y. Acad.Sci. 77: 102-125.

THOMAS, J.D. 1964 Studies on populations of helminth parasites of brown trout (Salmo trutta L.)
J.Anim.Ecol. 33: 83-95.

1964 A comparison between the helminth burdens of male and female brown trout Salmo trutta L., from a natural population in the River Teify, West Wales.
Parasitology, 54: 263-272.

WAIKEY, M. and DAVIES, P.S. 1964 Respiratory studies on Schistocephalus solidus, I. Effect of temperature and worm size.
Parasitology, 54, 6P.

WILLIAMS, H.H. 1964 Some observations on the mass mortality of the freshwater fish Rutilus rutilus (L.)
Parasitology, 54: 155-171.

CHAPTER TWO.

MYXOSPORIDIA.

INTRODUCTION.

Myxosporidia are protozoan parasites of the Class Sporozoa, sub-class Cnidosporidia (sub-phylum, Lom and Vavra, 1962), and are common parasites of many freshwater and marine fish. They inhabit hollow organs, for example, the gall bladder and urinary bladder where they are actively amoeboid, and many other organs and tissues where they often become encysted. Amphibia and reptiles, and more rarely annelids and insects have also been recorded as hosts for Myxosporidia.

The spores are the most conspicuous stage in the life cycle and consist of the shell valves, the polar capsules each of which contain a coiled polar filament and a sporoplasm which often contains an iodinophilous vacuole. Six nuclei are present, two valve nuclei, two polar nuclei and two sporoplasm nuclei which eventually fuse and are often regarded as gametes. The spores have a rigid definite structure and therefore form the basic taxonomic characters for the group. The other stages of the life cycle are passed in various amoeboid or pansporoblast forms. The different stages and sequence of events in the life cycle have been reviewed by Poisson (1953).

The affinities of the Myxosporidia were discussed by Poisson (1953) and he put forward four main points of view:-

(1) The Myxosporidia provide a link between the Protozoa and the Metazoa. Shulman (1964) also held this view, and regarded these

parasites as an example of transition from the unicellular to the multicellular state. Shulman (1964) stated that

> "due to intensive integration of the organism on increasing the cell's size, polymerisation of all organelles including nuclei is the principal direction of the progressive evolution. This may lead to multicellularity. On Protozoa parasitism is often accompanied by the increase of body size. That is why it may also favour polymerisation and the formation of multicellularity".

(2) The Myxosporidia may be regarded as degenerate Cnidaria. The main evidence for this comes from the resemblance of the myxosporidian polar capsules to the nematocysts of the Cnidaria.

(3) The Myxosporidia may have arisen from a hypothetical organism termed by Poisson, a "Procnidiés".

(4) The Myxosporidia may be a completely independent evolutionary line. Shulman (1964) puts forward the idea that the Cnidosporidia originated from parasitic amoebae as a result of the formation of multicellularity with a division of functions of separate nuclei and cells, but Poisson (1953) comments that the Rhizopods may be derived from the amoeboid sporoplasm of Myxosporidia.

As a result of the lack of fossil evidence and of intermediate forms between the Myxosporidia and the Cnidaria, it is probably better to consider the Myxosporidia as an independent evolutionary line.

The aim of the present survey was to investigate the Myxosporidia present on the fish of the River Lugg, with special reference to any variation in seasonal occurrences, spore form and intensity of infection .

METHODS.

The tissues and organs with cysts containing myxosporidian spores were fixed in 5% formalin. Smears of the cyst contents were made of preserved and fresh material. The smears were mounted using two different media:-

1) Glycerine jelly: 7 gms. gelatine in 40 mls. distilled H_2O
40 ml. glycerine
1 granule phenol.

Thin smears were mounted in melted, but cooled, glycerine jelly and a weighted cover slip placed on top to ensure that some spores were flattened in a horizontal plane. Many of the slides mounted in glycerine jelly were too thick to allow a detailed examination using an oil immersion objective which is essential for a detailed study of myxosporidian spores, although it was possible to measure the spores and polar capsules.

2) Polyvinyl lactophenol iodine:
10 mls. polyvinyl lactophenol
A few grains of sublimated iodine.

The iodine dissolves slowly and this process may be accelerated to a certain extent by gentle heating. The mountant may be strengthened by addition of iodine, or diluted by addition of polyvinyl lactophenol. The polyvinyl lactophenol acts as a clearing agent, and the iodine as a stain. Using polyvinyl lactophenol iodine it was possible to determine the two polar capsules, their polar filaments and the two polar nuclei,

the sporoplasm, the two sporoplasm nuclei, occasionally the valve nuclei, and the presence or absence of an iodinophilous vacuole which is an important feature in the taxonomy of the group.

The validity of this vacuole as an important taxonomic character is dubious as some spores appear to take up iodine more readily than others and it is thought that the state of the spore membrane may vary in permeability with the age of the spore.

The Myxosporidia were identified from Shulman and Shtein (1964) and Kudo (1920). The length, breadth and width of the spores and polar capsules were measured (Figure 2.1).

RESULTS:

Six different forms were found, four were definitely identified but difficulties were encountered in the identification of spores from the buccal cavity of S. cephalus, and from the urinary ducts of L. leuciscus and R. rutilus (Table 2.1). Only the most obvious stages (the spores) of myxosporidian life cycles were observed in this investigation.

Myxobolus mülleri Butschli, 1882. This species was recorded from many organs and tissues from S. cephalus and from the gills of R. rutilus and L. leuciscus (Table 2.1).

Infection of S. cephalus.

The percentage of S. cephalus infected each month with M. mülleri from the different infection sites was recorded (Table 2.2). A very high percentage of S. cephalus had infections of M. mülleri on the

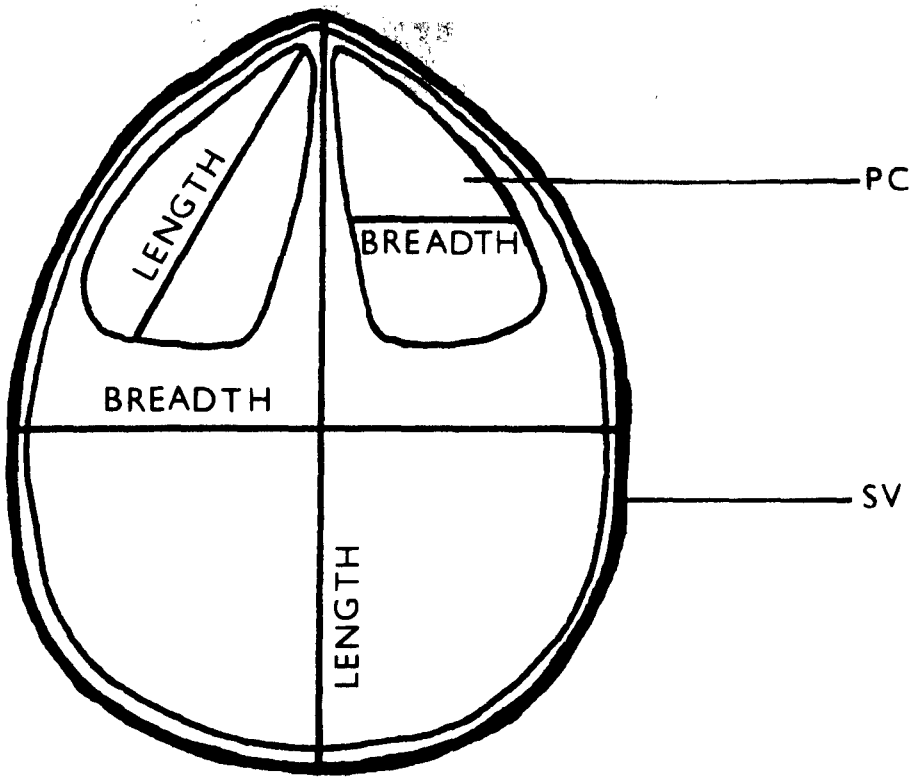
Fig. 2.1 Diagram to show the parameters used in the measurement of myxosporidian spores.

PC - Polar capsule

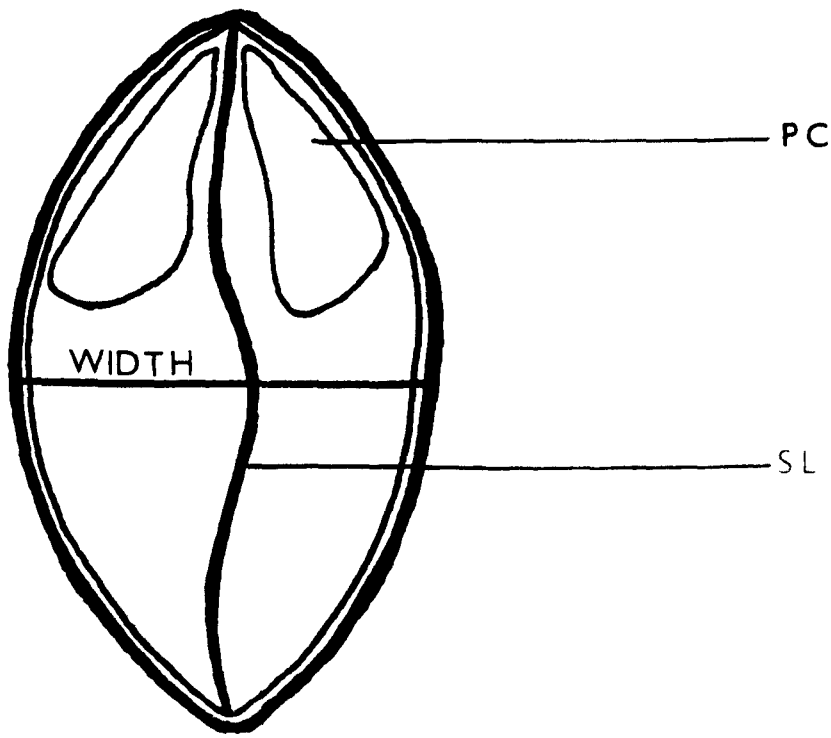
SV - Shell valve

SL - Sutural line

ANTERIOR



POSTERIOR



gills, in the mesenteries of the body cavity and in the urinary ducts, throughout the year, and there was no seasonal variation in occurrence. The lower figures recorded for January result from this being the first sample and many small myxosporidian cysts were overlooked which became obvious in later investigations of this and other samples.

S. cephalus without infected urinary ducts were rare, and for seven months 100% of the S. cephalus were infected. It was extremely difficult to estimate the intensity of infection by Myxosporidia. In the urinary ducts cysts were not observed and only free spores were visible, suggesting that the urinary ducts may not be permanent infection sites for M. mülleri, and the spores may be in transit to some permanent infection site or to the external environment. Estimations of the intensity of infection of M. mülleri in the urinary ducts of chub were made using the following key:-

I.	Rare.	1 spore per 5 x 10 objective fields.
II.	Occasional.	1 spore per x 10 objective field.
III.	Common.	5 spores per x 10 objective field.
IV.	Very common.	10 spores per x 10 objective field.
V.	Abundant.	15+ spores per x 10 objective field.

The infections of M. mülleri in the urinary ducts fall mainly into groups III and IV and less frequently to groups II and V and this pattern was similar each month (Table 2.3). No obvious increase in infection was observed with increase in length or weight of fish.

A high percentage of S. cephalus were infected with M. mülleri

TABLE 2.1.

The Hosts and Sites of Infection of Myxosporidian Parasites from the Fish of the River Lugg.

HOST	SITE OF INFECTION							
	Gills	Urinary ducts	Mesenteries	Intestine	Gonad	Kidney	Buccal cavity	External
S. cephalus	*Myxobolus mülleri*	*Myxobolus mülleri*	*Myxobolus mülleri*	*Myxobolus mülleri*	*Myxobolus mülleri*	*Myxobolus mülleri*	*Myxobolus macro-capsularis?*	
L. leuciscus	*Myxobolus mülleri*	*Myxobolus mülleri*						*Henneguya zschokkei*
R. rutilus	*Myxobolus mülleri*	*Myxobolus mülleri M. artus*						
E. lucius	*Henneguya psorosper-mica*				*Henneguya oviperda*			
T. thymallus								

TABLE 2.2.

The Number and Percentage of S. caphalus infected with M. mülleri from the different infection sites.

		INFECTION SITES											
		Gills		Urinary ducts		Mesenteries		Intestine wall		Kidney		Gonad	
Month	No. fish	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
January	32	16	50.0	6	18.7	13	40.6						
February	31	30	96.7	27	87.0	29	93.5	1	3.2				
March	29	26	89.7	27	93.0	27	93.0			3	10.5	1	3.5
April	30	24	80.3	30	100.0	29	96.6	2	6.6	1	3.3		
May	31	29	93.5	28	90.3	30	96.7	1	3.2	3	9.7	1	3.2
June	30	25	83.3	30	100.0	29	96.6	1	3.3			1	3.3
July	30	27	90.0	30	100.0	27	90.0	2	6.6	3	9.9	2	6.6
August	30	26	86.6	30	100.0	29	96.6			1	3.3	1	3.3
September	28	26	93.0	28	100.0	21	75.0						
October	27	25	92.6	26	96.3	25	92.6	1	3.7			1	3.7
November	30	29	96.6	30	100.0	26	86.6	1	3.3	9	30.0	2	6.6
December	31	25	78.6	31	100.0	29	93.5					1	3.2
Total	359	308	85.8	323	89.9	314	87.5	9	2.5	20	5.6	10	2.8

on the gills, and in the mesenteries of the body cavity. The number of cysts on the gills and in the mesenteries was counted originally. This information was later discarded because it was very inaccurate as a result of the hundreds of cysts present on the gills. Some cysts were visible to the naked eye as small white slightly elongated cysts varying from 1-5 mm. x 1-2 mm., but the majority were only visible microscopically and present in such vast numbers that it was impossible to make any accurate estimate of intensity of infection. The cysts in the mesenteries were less numerous but, instead of being discrete and separate, tended to be diffuse and to spread in an irregular attern, making any estimation of the actual number present, inaccurate.

Only a low percentage infection of M. mülleri was recorded from the intestine wall, gonads and kidneys of S. cephalus.

Spores from each infected tissue and organ were measured from each sample where possible (Table 2.4). The data were examined to determine if there was any seasonal variation in spore shape or size. Solutions used for preserving spores may cause shrinkage of the spore body (Kudo, 1921a), therefore care needs to be exercised in interpretation of data relating to seasonal variation in spore shape and size.

Table 2.4 shows that the smallest spores on the gills were recorded in November, but from any month the greatest difference in spore length did not exceed 1.1μ, and in spore breadth 1μ. Larger spores were recorded from the urinary ducts in March and April than in other months, but overall no seasonal increase in size or seasonal pattern of

TABLE 2.3:

The frequency of each group per month, used as an estimation of the intensity of M.müllerí in the urinary ducts of S.cephalus.

Month	I Rare	II Occasional	III Common	IV Very Common	V Abundant	Not infected
January						
February	1	6	17	6		1
March		3	18	4	2	2
April		3	10	17		
May		5	17	5		
June		8	16	6		
July		4	20	5		
August		3	15	10		
September		6	14	7		
October		3	16	6		
November		4	11	15		
December		6	16	9		
	1	51	170	90	7	7

Plate 2.1 The spores of *Myxobolus müllieri* from infected organs of *S. cephalus*, *L. leuciscus* and *R. rutilus*.

Magnification x1320

M. mulleri

Sites of infection

	Gills	Urinary ducts	Mesenteries	Intestine wall	Kidney	Gonad
S. cephalus						
L. leuciscus						
R. rutilus						

TABLE 2.4:

Comparison of spore dimensions measured in µ of *M.mülleri* from different infection sites in *S.cephalus* each month.

Month	GILLS					URINARY DUCTS					MESENTERIES					INTESTINE WALL					KIDNEY					GONAD				
	Spore			Polar Capsule		Spore			Polar Capsule		Spore			Polar Capsule		Spore			Polar Capsule		Spore			Polar Capsule		Spore			Polar Capsule	
	Length	Breadth	Width	Length	Breadth	Length	Breadth	Width	Length	Breadth	Length	Breadth	Width	Length	Breadth	Length	Breadth	Width	Length	Breadth	Length	Breadth	Width	Length	Breadth	Length	Breadth	Width	Length	Breadth
January	10.2	8.5	5.8	4.4	2.8			+			12.0	9.3		5.5	3.1			0					0					0		
February	9.9	8.8		4.4	2.7	9.8	7.7	4.8	4.4	2.8	15.1	11.4		6.0	3.4	2.2	14.4	11.8	6.6	5.4	3.3			0				0		
March	10.9	9.1		4.5	2.6	12.2	10.2		4.3	2.8	13.9	11.7		5.5	3.4			0			10.5	8.8	5.2	4.3	2.1			+		
April	10.8	8.9		4.4	2.6	12.7	10.1		4.5	2.7	10.3	8.6		4.6	2.6	15.1	11.8		6.1	3.6	10.5	8.7		4.1	2.2			0		
May	9.8	8.3	5.7	4.4	2.5	10.8	8.0		3.8	2.4	15.8	11.3		6.1	3.5	14.7	11.1	5.5	5.5	3.4	10.1	7.8		4.3	2.5	9.9	8.0	5.5	4.4	2.2
June	10.7	9.1	5.7	4.6	2.6	9.9	7.7		4.3	2.2	14.5	11.0		5.7	3.6			+					0					+		
July	10.7	8.8	5.7	4.6	2.7	9.5	7.2	5.5	3.7	2.4	14.6	10.8		5.8	3.4	9.6	8.5	5.6	4.4	2.5			+					+		
August	9.7	8.5	5.2	4.4	2.7	10.7	8.8		4.4	2.5	15.3	11.1	6.0	5.7	3.4	2.6			0					+					+		
September			+					+					+					0					0					0		
October			+			10.4	8.8	6.0	4.4	2.5			+					+					0					+		
November	8.9	8.1		3.5	2.2	10.9	9.3	6.0	3.7	2.3	16.0	10.8		5.4	3.5		10.1	8.8	5.9	4.4	3.1			+			10.6	8.5	5.4	4.3	2.2
December	10.0	8.4	5.7	4.3	2.5			+			15.1	11.6		5.4	3.4	2.6			0					0			10.1	8.1	5.6	4.6	2.7

Key: 0 - No infection. + - Infection present but no measurement available.

TABLE 2.5:

Comparison between the measurements of *Myxobolus mülleri* from different infection sites in *S.cephalus*.

		GILLS			URINARY DUCTS			BODY CAVITY			INTESTINE WALL			KIDNEY			GONAD		
		Mean μ	Range	No. examined	Mean μ	Range	No. examined	Mean μ	Range	No. examined	Mean μ	Range	No. examined	Mean μ	Range	No. examined	Mean μ	Range	No. examined
Spore	Length	10.1	7.7-12.1	103	11.0	9.3-16.5	63	14.4	9.9-18.1	108	12.9	8.8-15.5	52	10.0	9.9-11.0	40	10.2	8.8-11.5	30
	Breadth	8.6	6.6- 8.8	103	8.8	6.6-12.1	63	10.8	8.3-12.1	108	10.5	8.2-12.1	52	8.1	7.3- 9.4	40	8.2	6.6- 8.8	30
	Width	5.6	5.5- 6.6	34	5.3	4.4- 5.5	9	6.5	6.6- 7.1	2	5.9	5.0- 6.6	15	5.2	4.4- 5.5	4	5.5	4.9- 6.0	25
Polar capsule	Length	4.3	3.3- 5.5	186	4.1	2.2- 6.6	107	5.8	4.4- 7.7	192	5.3	3.3- 6.6	85	3.9	3.3- 4.4	66	4.5	3.8- 5.5	47
	Breadth	2.6	1.1- 3.3	187	2.6	2.2- 4.4	106	3.7	2.2- 4.4	185	3.3	2.2- 4.4	82	2.1	1.7- 2.7	63	2.5	2.2- 3.3	40

Infection of L.leuciscus.

M.mülleri was recorded from the gills of L.leuciscus. No seasonal occurrence or variation was very evident in the percentage of fish infected, but overall a much lower percentage of L.leuciscus were infected (30.0%) than S.cephalus (85.8%). (Tables 2.6 and 2.2.) No relationship was apparent between the percentage of fish infected and increase in length of weight of fish.

Infection of R.rutilus.

M.mülleri was recorded from the gills of R.rutilus in all months except February. The percentage of R. rutilus with infected gills (11.4%) was much lower than either S.cephalus (85.8%) or L.leuciscus (30.0%). (Tables 2.7, 2.6 and 2.2.) The percentage of fish infected was greatest in June after which it declined slowly. It is difficult to determine the significance of the data for the two months previous to June as the numbers of fish in the samples were inadequate and it was not possible to draw any conclusions as to the presence or absence of an increase in infection in spring before the highest infection recorded in June.

TABLE 2.6:

The number and percentage of L. leuciscus infected with Myxosporidia.

Month	No.fish	INFECTION SITES: GILLS M.mülleri No.	%	URINARY DUCTS M.mülleri No.	%	EXTERNAL H.zschokkei No.	%
January	33	6	18.0	23	70.0		
February	31	5	16.0	27	89.0	2	6.5
March	30	14	46.6	30	100.0	2	6.6
April	35	5	14.3	34	97.3		
May	4	1	25.0	4	100.0		
June	30	16	53.3	26	86.6	1	3.3
July	30	10	33.3	29	97.0	2	6.6
August	30	14	46.7	30	100.0		
September	30	10	33.3	30	100.0	1	3.3
October	31	12	39.0	31	100.0	4	13.0
November	28	3	10.7	28	100.0		
December	30	7	23.3	30	100.0	1	3.3
Total	342	103	30.1	322	94.2	13	3.8

TABLE 2.7:

The number and percentage of R.rutilus infected with Myxosporidia.

		INFECTION SITES			
		GILLS		URINARY DUCTS	
		M.mülleri		M.mülleri & M.artus	
Month	No.fish	No.	%	No.	%
January	33	1	3.3	19	57.5
February	27	-	-	22	81.5
March	30	7	23.3	26	86.6
April	16	1	6.3	15	93.8
May	9	1	22.2	8	88.9
June	30	12	40.0	30	100.0
July	22	3	13.6	20	90.9
August	30	4	13.3	30	100.0
September	30	1	3.3	28	93.3
October	30	2	6.6	24	80.0
November	30	3	9.9	29	96.6
December	30	1	3.3	29	96.6
Total	317	36	11.4	280	88.3

M.mülleri was recorded from the gills of L.leuciscus, S.cephalus and R.rutilus. Comparisons were made of the dimensions of the spores of M.mülleri from the gills of the different hosts. (Table 2.8.) The spores from the gills of S.cephalus and L.leuciscus have the same mean length, but the breadth of the spores from L. leuciscus and the mean dimensions of the polar capsules are slightly less. The polar capsule dimensions are very similar in the spores from R. rutilus and S.cephalus, but the mean length and breadth of the spore body from R.rutilus are greater than those from S.cephalus.(Plate 2.1. Table 2.8.)

The spores of M.mülleri described by Shulman and Shtein (1964) are extremely variable in form and size. In this investigation the spores ascribed to this species conform in size range, the presence of a prominent intercapsular process, sites of infection, and host species, to the description by Shulman and Shtein (1964). Their key states that extreme variation in spore form has given rise to great confusion in the taxonomy and many new species may have been described without sufficient evidence. Lom (1960) recorded M.mülleri as the most common myxosporidian in Czechoslovakia, and he gave diagrams to show the range of spore variability, and recorded a few tailed forms. The results of this investigation support the evidence for the presence of a great range of spore variability, the presence of tailed forms (on the gills of S.cephalus in January and July) and the common occurrence of M.mülleri in many organs and tissues of cyprinids.

TABLE 2.8:

Comparison between the measurements of Myxobolus mülleri from the gills of L.leuciscus, R.rutilus and S.cephalus.

		L.leuciscus			R.rutilus			S.cephalus		
		Mean	Range	No. examined	Mean	Range	No. examined	Mean	Range	No. examined
Spore	Length	9.9	8.8-11.0	23	11.2	9.9-12.1	30	9.9	7.7-12.1	30
	Breadth	7.8	7.7- 8.8	23	9.1	7.7- 9.9	30	8.7	6.6- 8.8	30
	Width	5.5	5.5-	13	5.8	5.5- 6.6	8	5.7	5.5- 6.6	10
Polar capsule	Length	3.6	2.2- 4.9	42	4.6	3.3- 5.5	55	4.3	3.3- 5.5	60
	Breadth	2.3	1.6- 3.3	37	2.5	2.2- 3.3	52	2.5	1.1- 3.3	60

Myxosporidia from the urinary ducts of L.leuciscus and R.rutilus.

Myxosporidia were found in the urinary ducts of S.cephalus, L.leuciscus and R.rutilus, a high percentage of each host species being infected; L.leuciscus (94.2%); S.cephalus (89.9%); R.rutilus (88.3%). No seasonal variation of occurrence of the spore stage was evident (Tables 2.2, 2.6, 2.7) and the lower percentage infection recorded for January resulted from this being the first sample, and Myxosporidia were not investigated from the first few fish to be examined.

When the smears containing spores from the urinary ducts of L.leuciscus and R.rutilus were examined, some spores were similar in dimensions to M.mülleri recorded from the urinary ducts of S.cephalus, but some were very different. Three spore forms were recorded:-

a) One resembling M.mülleri, length 9.9 - 11.0 μ; breadth 8.8 - 9.9 μ; dimensions of the polar capsules 4.4 - 4.9 x 2.2 - 2.7 μ.

b) A tailed form recorded from 10 L.leuciscus in April and once in both June and September. It is possible that these were tailed forms of M.mülleri.

c) A spore with the following dimensions:- length 6.6 - 8.3 μ; breadth 7.7 - 9.9 μ; polar capsules 2.7 - 4.4 x 2.2 - 3.3 μ. This spore has a greater breadth than length, and the polar capsules nearly filled the spore body. The measurements for this spore and its shape conform to the description of

Myxobolus artus Akhmerov 1960, previously recorded from the intestinal wall and kidney of Cyprinus carpio haematopterus, Temminck and Schlegel, from the Amur River basin.

The frequencies of each group, used as an estimate of intensity of infection in S.cephalus were also recorded to estimate the intensity of infection of the spores present in the urinary ducts of R.rutilus and L.leuciscus (Tables 2.9 and 2.10). These tables included all the spore forms, as it was not until the smears were examined later that the different spore forms were evident. The results from S.cephalus, L.leuciscus and R.rutilus were compared. The most common group frequences in S.cephalus were III and IV, in L.leuciscus II and III, and in R.rutilus I and II (Tables 2.3, 2.9 and 2.10). The same pattern was present in each host, each month, except for one or two months (e.g. February and April for R.rutilus) where the group below was more frequent than the overall common groups. The data show that the highest intensity of myxosporidian infection in the urinary ducts was present in S.cephalus, and the lowest in R.rutilus, although the percentage of fish infected was very similar in S.cephalus, L.leuciscus and R.rutilus. This contrasts with the infection of M.müllerí on the gills where the percentage of S.cephalus infected is markedly higher than the percentage of R.rutilus or L.leuciscus.

TABLE 2.9:

The frequency of each group per month, used as an estimation of the intensity of M.mülleri in the urinary ducts of L.leuciscus.

Month	I Rare	II Occasional	III Common	IV Very Common	V Abundant	VI Not infected
January						
February	6	15	5	1	0	4
March	1	8	14	7	0	0
April	5	11	12	5	1	1
May	1	2	1	0	0	0
June	1	8	12	4	1	4
July	4	16	8	1	0	1
August	6	15	8	1	0	0
September	5	14	11	0	0	0
October	5	21	5	0	0	0
November	2	10	16	0	0	0
December	5	9	13	3	0	0
	41	129	105	22	2	10

TABLE 2.10:

The frequency of each group per month, used as an estimation of the intensity of *M.mülleri* in the urinary ducts of *R.rutilus*.

	I	II	III	IV	V	VI
Month	Rare	Occasional	Common	Very Common	Abundant	Not infected
January						
February	13	8	1	0	0	5
March	2	22	2	0	0	4
April	8	5	2	0	0	1
May	4	4	0	0	0	1
June	6	23	1	0	0	0
July	3	17	1	0	0	1
August	2	18	10	0	0	0
September	7	14	7	0	0	2
October	12	12	0	0	0	6
November	6	23	0	0	0	1
December	12	12	4	0	0	2
	75	158	28	0	0	23

An unidentified species from S.cephalus.

Myxosporidian spores were found in large cysts which were visible when the operculum was raised. The cysts were attached to the roof buccal cavity and were visible without removing the gills. Only three cysts were found, one cyst being recorded from each of the May, August and December samples.

The cysts were large and yellow coloured, approximately 16 mm x 6 mm. and were covered with a thin layer of slightly pigmented tissue, and weighed about 0.8 gms. Spores were measured from each month they were recorded (Table 2.11). The spores tapered towards the anterior end, and the length of the polar capsules was just over one half the length of the spore. The polar filament was coiled 10 - 12 times, and no inter-capsular process was evident. Using poly vinyl lactophenol iodine, an iodinophilous vacuole was shown to be present in all the spores (Plate 2.2).

The total spore and polar capsule length were less in spores from May, compared with the spores from August and December. Only three cysts were found and therefore no definite statement could be made as to the occurrence of any seasonal variation in spore shape or size.

Attempts were made to identify the spores using the previously mentioned keys. The dimensions of the spores from cysts attached to the roof of the buccal cavity correspond in length of spore, and length and breadth of polar capsule to the description of Myxobolus koi Kudo 1919, although the breadth and width of the spore are slightly greater:

Plate 2.2 The spores of Myxobolus macrocapsularis ?

Magnification x1320

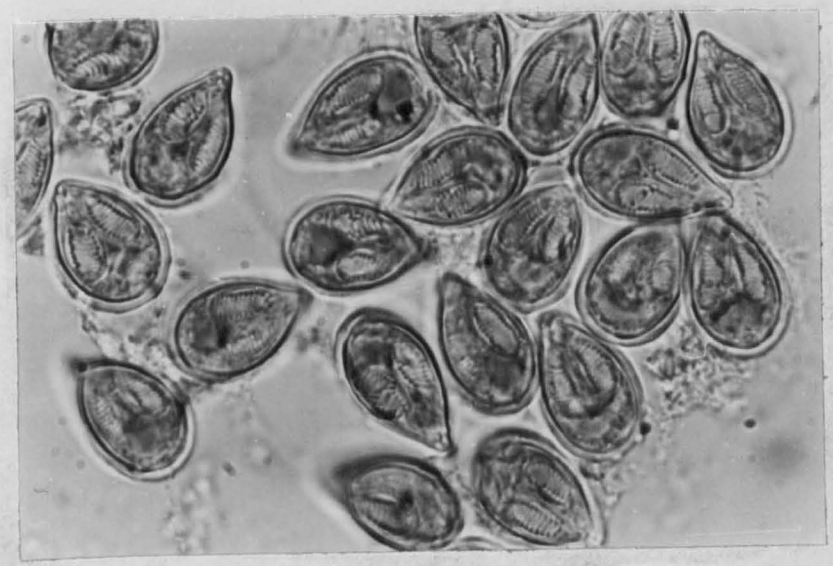


TABLE 2.11:

The dimensions of myxosporidian spores from cysts in the buccal cavity of S.cephalus.

		MAY			AUGUST			DECEMBER			TOTAL		
		Mean	Range	No. examined	Mean	Range	No. examined	Mean	Range	No. examined	Mean	Range	No. examined
Spore	Length	15.3	14.3-15.9	10	16.7	14.3-18.7	11	16.1	14.3-17.6	11	16.1	14.3-18.7	32
	Breadth	9.9	9.9	10	10.0	8.8-11.0	11	10.1	9.4-11.0	11	10.0	8.8-11.0	32
	Width	8.8	8.8	10	7.7	7.7	1	-	-	-	8.6	7.7- 9.9	11
Polar capsule	Length	7.8	7.7- 9.8	20	8.9	6.6- 9.9	11	9.1	7.7- 9.9	15	8.5	6.6- 9.9	46
	Breadth	3.2	2.7- 3.3	20	3.0	2.2- 3.3	15	3.2	2.8- 3.3	12	3.1	2.2- 3.3	47

breadth 8 - 9 μ (Kudo) compared with 8.8 - 11 μ in this investigation; width 5 - 6 μ (Kudo) compared with 7 - 8.8 μ in this investigation. Kudo described this species from the connective tissue of the gill filament of Carpio carpio L. from Tokyo, in April. It is also described by Shulman and Shtein (1964) from the connective tissue of the gill filaments and the subcutaneous tissue of the head of C.carpio haematopterus, Acanthorhodeus asmussi (Dybovskii) and Squaliobarbus curriculus (Richardson) from the Amur River basin. The measurements and shape of the spores correspond in most aspects to the previous descriptions, but the large size and yellow colour of the cysts found in this investigation do not agree with the previous descriptions for M.koi, of small, white spherical cysts up to 0.25 mm in diameter.

Ward (1919) described Myxobolus auratus on the fins of Notropis anogenus from near Put-in-Bay, Lake Erie. The cysts were opaque, and bright orange-yellow in colour, measuring 1 - 1.6 mm x 0.8 - 1.2 mm. The surface of the cysts was spotted with minute but conspicuous black patches of host pigment. The colour of the cyst faded to a dull white or a grayish tone after preservation in alcohol. The spores were ovoid with a slightly pointed anterior end. Two polar capsules, each containing a polar filament which was coiled 6 - 7 times and an iodinophilius vacuole 2 μ in diameter were present. The spore dimensions were:-

Spore	Length	12.4 - 13.5 μ
	Breadth	6.5 - 7.5 μ
	Width	5.0 μ
Polar capsule	Length	6.0 - 7.5 μ

The description of the colour of the cysts and the shape of the spores correspond to the descriptions in the present survey, but discrepancies arise in the size of the cysts, the site of infection and the greater overall spore dimensions. Ward (1919) mentioned a similar species described by Linton (1889) on Notropis megalops from the Black River, Ohio, in which the spores were 17 μ long, 10 μ broad and 6 μ wide. Greater similarity exists between these dimensions and the ones recorded in this investigation. The cysts described by Linton (1889) are larger than those described by Ward (1919) but the colour was described as white with minute patches of black pigment. The fact that all Linton's material was preserved may account for this, but in view of his inadequate description of any internal spore structure, it was not possible to assess any similarity which might exist between these spores and spores from the present survey. Differences in the spore size, cyst size and colour, the location of the infection and the host species have so far prevented the spores recorded from the present survey being identified with any previously described species.

Addendum.

Samples of these spores were sent to Dr. J. Lom in Czechoslovakia, and his findings in relation to this problem were received after the completion of the above section. He stated

> "Your species seems to be rather Myxobolus macrocapsularis Reuss, as pictures in recent Soviet literature. Of course, Reuss's original description is hardly of any use in determination, so that recently described M.macrocapsularis is something taxonomically curious. The difference in cyst size between M.koi and (the Myxobolus from this survey) should not prevent us from taking them for identical species - the same differences can be found in e.g. some Hennegnya or Myxobolus pfeifferi - but my tentative classification as M.macrocapsularis is more based on spore similarity, and this can be of any value, on the same host."

As a result of this communication it has been decided to term these spores from S.cephalus, M. macrocapsularis until further investigations produce evidence to confirm or refute this identification.

Hennegnya zhokkei (Gurley, 1894) from L.leuciscus.

Yellow cysts 5 - 6 mm. x 2 - 4 mm. were found embedded in the subcutaneous tissue and cartilage of the lower jaw, nasal region, opercular regions and the pectoral fins of L.leuciscus. The percentage of fish infected was low, 3.8%, (Table 2.6) and the number of cysts per fish varied between 1 and 6. Six were recorded from one fish in October, five cysts from the head and one from the pectoral fin; two were recorded from the head of one fish in June and only one cyst per fish was recorded for the other infections.

Spores were examined and measured from samples where the infection occurred. The spores from each month were very similar except for the

Plate 2.3 Tailless spores of Henneguya zachokkei

PC - Polar capsules

IV - Iodinophilous vacuole

PCN - Polar capsule nuclei

SN - Sporoplasm nuclei

PS - Posterior spike-like process

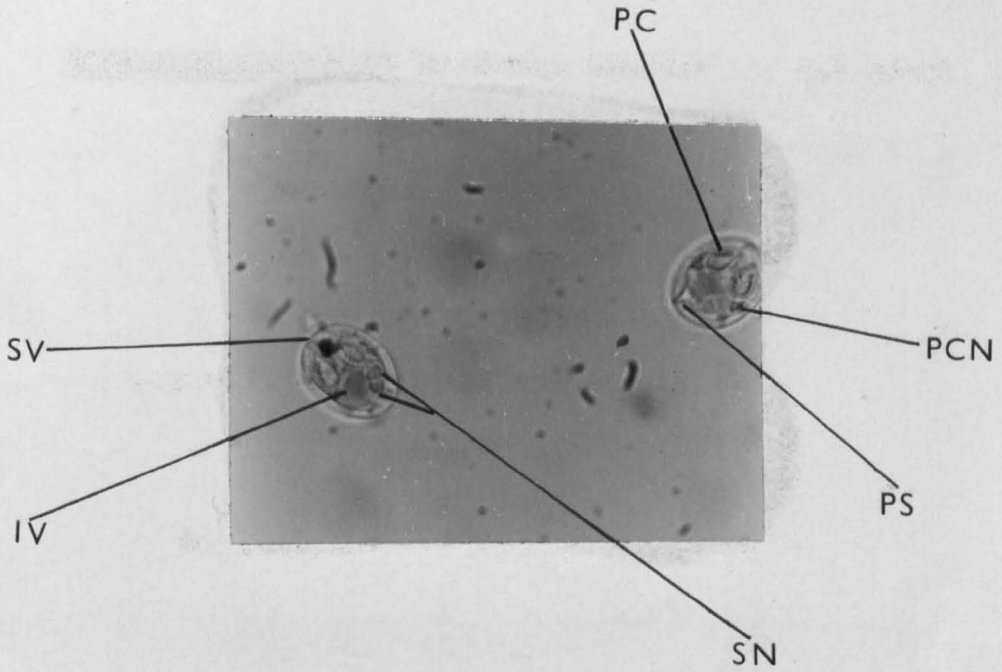
SV - Shell valve

Magnification x 1320

Plate 2.4 Tailless spores of Henneguya zachokkei

BSP - Bifurcate posterior spike-like process.

Magnification x1320


PC
SV
PCN
PS
IV
SN

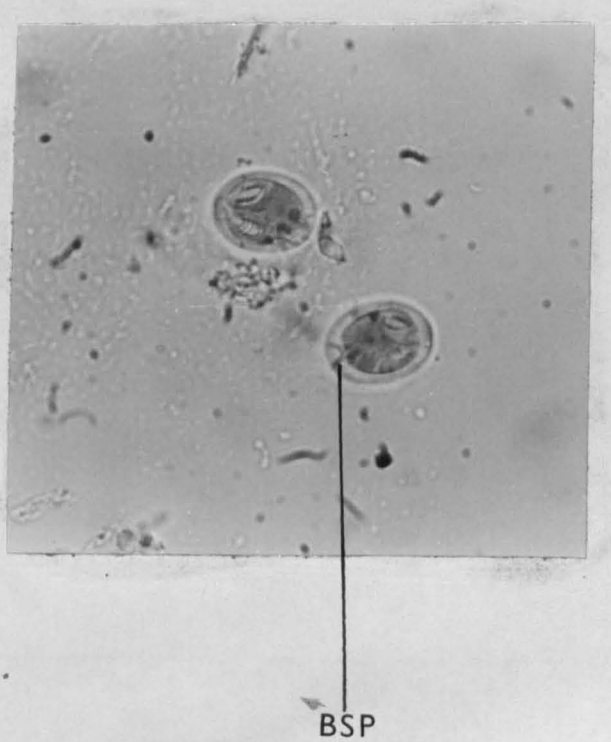

BSP

Plate 2.5 Tailed spore of Henneguya zachokkei with spike-like process at the posterior end of the spore body.

Magnification x1320

Plate 2.6 Tailed spore of Henneguya zachokkei at a different focus showing the spike - like process at the posterior end of the spore body, passing into the caudal processes.

Magnification x1320

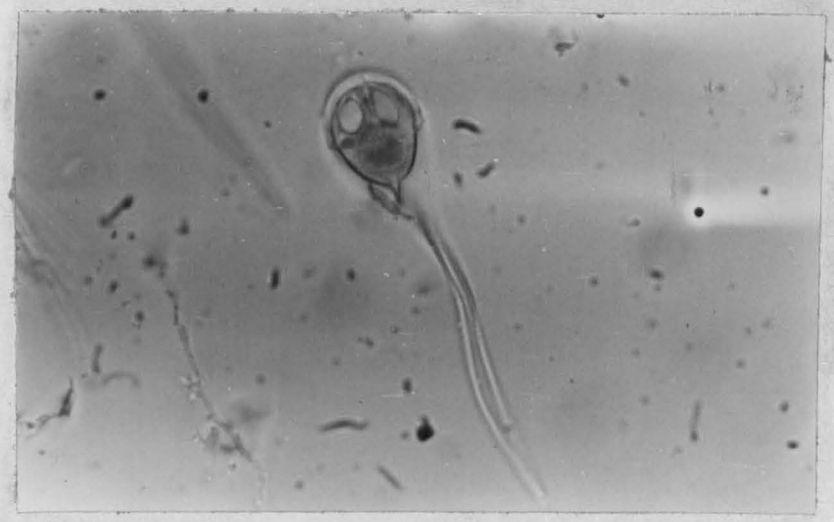


Plate 2.7 A group of tailed spores of Henneguya zschokkei.

PC - Polar capsule with extruded polar filament.

IV - Iodinophilous vacuole.

Magnification x1320

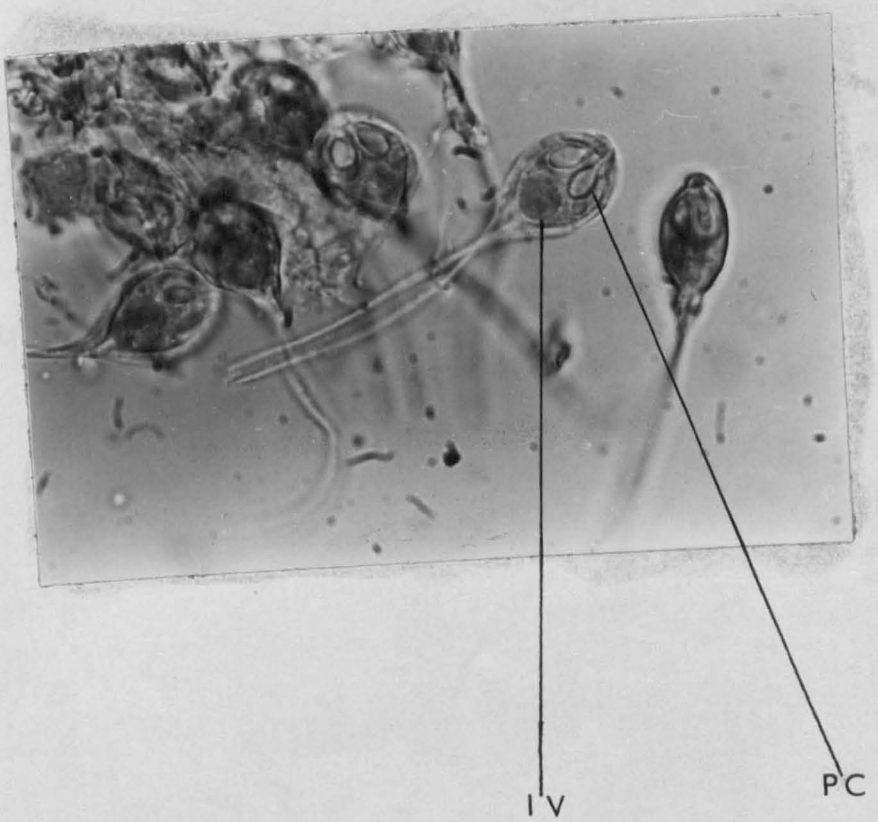

IV
PC

TABLE 2.12:

Comparison between the measurements of the spores of E.zschokkei in the months where infection was present.

		FEBRUARY			MARCH			JUNE			JULY			OCTOBER			TOTAL		
		Mean μ	Range μ	No. examined	Mean μ	Range μ	No. examined	Mean μ	Range μ	No. examined	Mean μ	Range μ	No. examined.	Mean μ	Range μ	No. examined.	Mean μ	Range μ	No. examined.
Spore	Length	11.4	9.9-13.2	30	11.5	11.0-12.6	30	11.6	7.7-13.2	30	12.3	11.0-14.3	30	11.1	8.8-12.1	30	11.6	7.7-14.3	150
	Breadth	8.8	7.7- 9.9	30	9.0	8.8- 9.9	30	8.7	7.1- 9.3	30	9.3	7.6-11.0	30	8.3	7.7- 8.8	30	8.8	7.1-11.0	150
	Width	5.8	5.5- 6.6	14	5.5	-	2	5.6	5.5- 6.0	5		7.7	1	5.5	5.5	9	5.7	5.5- 7.7	31
	Length of Tail	-	-	-	-	-	-		15.4	1	31.7	13.0-40.0	35	-	-	-	31.3	13.0-40.0	36
	Length of tail and spore body	-	-	-	-	-	-		23.1	1	44.0	25.1-52.1	35	-	-	-	45.0	25.1-52.1	36
Polar capsule	Length	4.2	3.3- 4.9	49	4.1	3.3- 4.7	55	4.1	3.3- 5.3	54	4.4	3.3- 5.5	42	4.4	3.3- 5.5	32	4.2	3.3- 5.5	230
	Breadth	2.4	1.7- 3.3	50	2.3	2.2- 2.8	55	2.5	2.2- 3.3	54	2.5	1.7- 3.3	49	2.1	1.7- 2.2	34	2.4	1.7- 3.3	234

Measurements in μ

central spore. Most of the tailed spores had discharged polar filaments, and it is suggested that as these spores are probably in the mature state the sensitivity level for triggering the uncoiling of the polar filaments was higher than in immature tailless spores, and the preserving of mature spores in 5% formalin caused the release of the polar filaments.

H.zschokkei has previously been recorded from Switzerland (Zschokke, 1884, Jenni, 1945); the United States of America (Gurley, 1893, 1894); Norway (Huitfeldt-Kaas, 1912, Grini, 1939 and Vik, 1960) and from the U.S.S.R. (aryschewa and Bauer, 1957). All the records for H. zschokkei were from Coregonus spp. apart from one record from Salvelinus alpinus and the records from Russian investigations which list twelve infected host species, including salmonids and cyprinids. Vik (1960) speculated that there may be two different strains of H. zschokkei, one with a high specificity towards Coregonus spp. and one with a low host specificity. H.zschokkei in this investigation was recorded only from L.leuciscus, and this substantiates the Russian view that H.zschokkei is not specific to coregonids. The manifestation of the infection on L.leuciscus in this investigation differed completely from an infection recorded in this country on Coregonus clupeoides pennanti (Cuvier and Valenciennes) from Lake Bala (Llyn Tegid) Merionethshire. In the latter the cysts were white, large and protruding from the body surface whereas in L.leuciscus the cysts were small and yellow coloured. This may be the result of host reaction to infection, or it may be that instead of H.zschokkei being more specific to Coregonus spp., Coregonus spp. may be more susceptible to

infection than cyprinids. The Henneguya sp. recorded on C.pennanti from Llyn Tegid was named H.tegidiensis (Nicholas and Jones, 1959) being distinguished from other species of Henneguya by having one posterior caudal process longer than the other and this was the main feature used to differentiate it from the very similar H.zschokkei. The data only show the total number of spores measured without stating at what time of year the spores were measured. This is an important point that was overlooked, because as shown in this survey, a great variability in spore shape and size was recorded for H.zschokkei at different times of the year. If spores had been measured each month the differences in the length of the two caudal processes may not have been significant, and it is possible that H.tegidiensis sp.nv. may only be a variation or a synonym of H.zschokkei.

Vik (1960) reviewed the literature on the seasonal occurrence of H.zschokkei. The records from Norway showed that this parasite was found on white fish from the end of September to the end of February. Bauer and Nikolskaja (1957) studied the seasonal occurrence of the parasites of white fish of Ladoga and recorded 7% of the fish from August to November infected with H.zschokkei. In the present investigation H.zschokkei was recorded from L.leuciscus in February, March, June, July and October. No marked pattern of seasonal occurrence was shown in these surveys even though many of the data were incomplete, but a seasonal variation in spore size and shape was present in infections recorded from the L.leuciscus of the River Lugg.

Henneguya spp. from E. lucius.

Henneguya species were recorded from very small cysts on the gills, and from prominent white cysts 2-4 mm. x 2-3 mm. between the eggs in the ovary of E.lucius. Only 36 E.lucius were sampled and the percentage occurrence of Henneguya on the gills was 36.0% and from the gonads 11.0 . (Table 2.13.) The gill species occurred in May, June, July and August, and the gonad species in May and October. The low number of fish sampled did not permit any conclusions as to the presence or absence of any seasonal occurrence.

The species from the gills was identified as Henneguya psorospermica (Thelohan, 1895) and the species from the gonads as Henneguya oviperda (Cohn, 1895). The dimensions of the spores were recorded for both species (Table 2.14). Great variation occurred in spore form. Tailed and tailless spores were recorded from cysts in the gonads in May (Plates 2.8, 2.9) and October (Plate 2.10). Material examined from the gills in July showed only tailless forms (Plate 2.11). The tailless forms from the gonads were compared with tailless forms from the gills; the former had a greater overall spore and polar capsule length but the coils of the polar filaments were less, 10 - 12, compared with 12 - 16 in gill forms. The breadth of the spores and polar capsules were similar (Table 2.14).

Shulman and Shtein (1964) state that H.psorospermica differs relatively little from H.oviperda, and any difference that occurs is a difference in length and width of the spores. Mishra (1966) compared

TABLE 2.13:

The number and percentage of E.lucius infected with H.psorospermica and H.oviperda.

Month	No.fish/sample	H.psorospermica		H.oviperda	
		No.	%	No.	%
January	1	-	-	-	-
February	1	-	-	-	-
March	0				
April	7	-	-	-	-
May	5	2	40.0	1	20.0
June	8	7	87.5	-	-
July	7	3	42.8	-	-
August	2	1	50.0	-	-
September	0				
October	4	-	-	3	75.0
November	0	-			
December	1	-	-	-	-
	36	13	36.1	4	11.0

Plate 2.8 Tailed spore of Kennedya oviperda from the May sample.

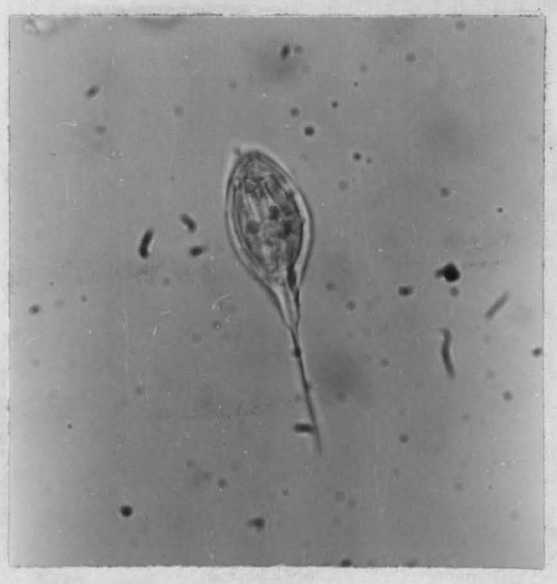
Magnification x1320

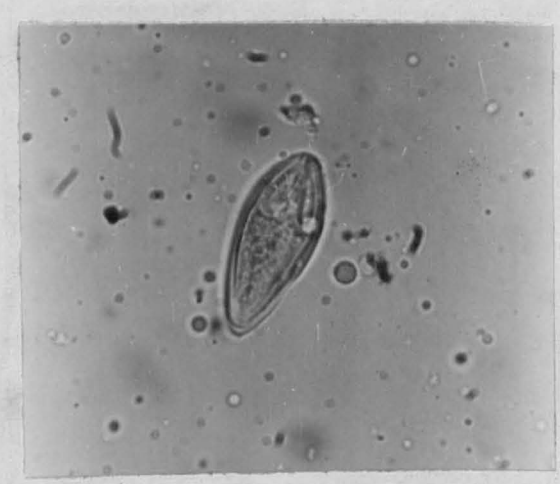
Plate 2.9 Tailless spore of H. oviperda from the May sample.

Magnification x1320

Plate 2.10 Tailed and tailless spores of H. oviperda from the October sample.

Magnification x1320





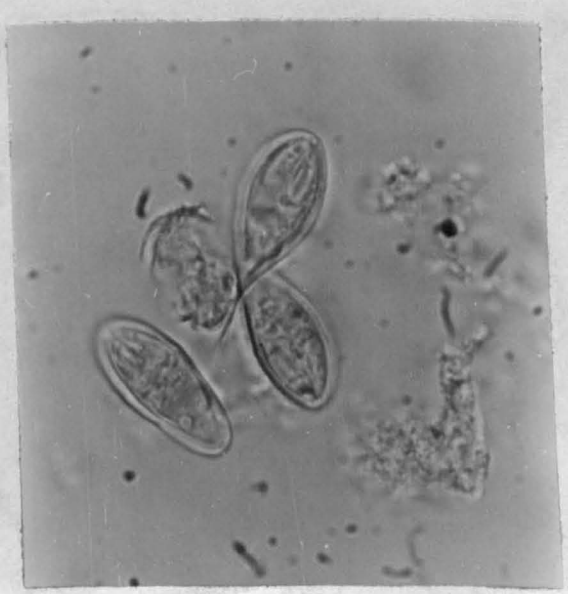


Plate 2.11 Tailless spores of Hennegyya psorospermica from the gills of E. lucius from the July sample.

Magnification x1320

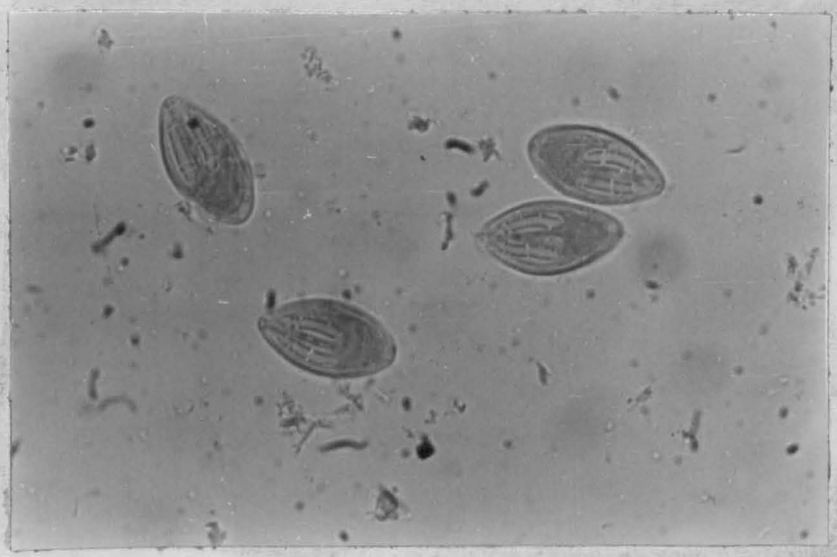


TABLE 2.14:

Comparison between the measurements of H.psorospermica and H.oviperda from S.lucius of the River Tugg.

		GONAD									GILLS		
		MAY			OCTOBER			TOTAL			JUNE		
		Mean	Range	No. examined.	Mean	Range	No. examined	Mean	Range	No. examined	Mean	Range	No. examined
Spore	Length of spore body	17.2	15.4-19.8	20	16.1	14.3-18.7	20	16.6	14.3-19.8	40	15.6	14.3-16.5	20
	Breadth of spore	7.7	6.6- 8.8	20	7.2	6.6- 8.8	20	7.5	6.6- 8.8	40	7.7		20
	Width of spore	5.5	5.5	5	5.5	5.5	3	5.5	5.5	8		-	
	Length of tail	12.8	8.8-16.5	14	13.8	13.3-18.7	16	13.3	3.3-18.7	30	-	-	-
	Length of tail and spore body	29.2	25.3-33.0	14	29.5	22.0-34.2	16	29.4	22.0-34.2	30	-	-	-
Polar capsule	Length	6.1	5.5- 7.0	29	6.0	4.4- 7.7	32	6.1	4.4- 7.7	61	7.3	6.6- 7.7	24
	Breadth	2.0	1.7- 2.2	29	2.0	1.7- 2.2	27	2.0	1.7- 2.2	56	1.8	1.7- 2.2	29

Measurements in μ

the dimensions of H.oviperda from E.lucius of the Shropshire Union Canal with H.oviperda and H.psorospermica of Shulman and Shtein (1964) and found that the caudal processes of H.oviperda were smaller than those of H.psorospermica. From this information and the difference in size of cysts and site of infection Mishra (1966) concluded that H.oviperda and H.psorospermica were probably distinct species. In the present survey a great variability has been recorded in spore shape. Therefore it is necessary to examine spores from each month over at least a year remembering that before any conclusions can be drawn as to the existence of the two species, infection of the different organs may occur at different times of the year and development may take place at different rates in different tissues. When the range of spore variability in relation to the life cycle of H.psorospermica and H.oviperda has been determined, then the importance of cyst size, the different infection sites and the fact that spores on the gills and in the gonads were never recorded from the same individual, must be taken into account when trying to determine the validity of both the species. It is interesting to note that Mishra (1966) only recorded H.oviperda from E.lucius of the Shropshire Union Canal.

Conclusions.

Six different myxosporidian spore forms were recorded in this investigation. Four species were definitely identified; M.mülleri, H.sschokkei, H.psorospermica and H.oviperda; two species were not

given specific names, but were thought to belong to the genus Myxobolus, the one from the buccal cavity of S.cephalus resembling in some features both M.koi and M.aurentus, and tentatively identified by Lom as M.macrocapsularis, and the one from the urinary ducts of L.leuciscus resembling M.artus.

S.cephalus, L.leuciscus and R.rutilus infected with M.mülleri were common, and of these three hosts, S.cephalus had the highest intensity of infection, and the greatest number of infected organs and tissues. M.mülleri was compared from all the different infection sites each month where possible, from the same host (i.e. S.cephalus) and from the same site on different hosts (i.e. from the gills of S.cephalus, L.leuciscus and R.rutilus). No seasonal variation of occurrence or of spore size and shape were evident in the infections of M.mülleri. The spores from the gills of all three hosts were very similar, but the spores from the gills of R.rutilus had a slightly greater overall mean length, and it may be significant to note that the lowest intensity of infection was present on this fish. No seasonal variation of occurrence was evident for H.zschokkei, H.psorospermica and H.oviperda, and although the amount of data available was rather meagre, variation in spore shape and size was very apparent.

Other investigations of the parasites of freshwater fish in this country have revealed myxosporidian infections: H.tegidiensis on C.pennanti from Lake Bala (Merionethshire) (Nicholas and Jones, 1959); H.tegidiensis on C.pennanti and H.psorospermica on E.lucius and

Perca fluviatilis (L.) from Lake Bala (Chubb, 1961); three new species from Scardinius erythrophthalamus, C.carpio and Phoxinus phoxinus (L.) (Quadri, 1962); Myxobolus sp., Myxidium sp. and Chelohanellus sp. on R.rutilus from Brynmill Park, Swansea (Williams, 1963); H.psorospermica and Myxidium lieberkuhni (Butschli, 1882) on E.lucius from Rostherne Mere (Cheshire), (Rizvi, 1964); H.psorospermica and H.oviperda on E.lucius from the Shropshire Union Canal (Cheshire), (Mishra, 1966). No seasonal occurrence in variation in spore shape or size was evident or commented on in any of the above investigations.

Many pathological effects of myxosporidian infections have been recorded by Russian investigators from farms where fish are reared intensively, and from fish in natural waters (Bauer, Petrushevski and Shulman, 1961). Species of Myxobolus have been recorded as causing pernicious anaemia, anaemia and gill rot (Schaperclaus, 1954). M.müllori which was very common in this survey has been reported to cause hypertrophy of the gill epithelium, and to form cysts and tumours. Rupture of the cysts and tumours may damage the host tissue causing extensive haemorrhages and death may follow from asphyxia resulting from damaged gill filaments, and severe loss of blood. H.zschokkei is reported as causing boil diseases. When the cysts rupture the wounds in the musculature bleed and provide the ideal environment for secondary infection by fungi and bacteria.

From investigations carried out in Britain only one observation (Williams, 1963) suggests that infection with Myxosporidia resulted

in the death of the host. In this case it was suggested that Myxosporidia caused the death of over 12,000 R.rutilus between May and July, 1961, at Brynmill Park, Swansea, South Wales. Both M.mülleri, and H.zschokkei were found in the present investigation but no obvious pathological effects in relation to myxosporidian infection were recorded apart from a few small blood clots on the gills with heavy infections.

REFERENCES.

[illegible] and [illegible], T.A. 1957 Die Fischparasiten des Ladogasees. Bull.Inst.freshw.Fish, Leningr.42: 175-226.

[illegible] and [illegible] 1957 Die Dynamik der Parasitenfauna von Coregonus lavaretus baeri n. ladogensis des Ladogasees und ihre epizootologische Bedeutung. Bull.Inst.freshw.Fish, Leningr. 42: 227-242.

BAUER, O.N. 1958 Parasitic diseases of cultured fishes and methods of their prevention and treatment. Parasitology of Fishes. English translation, 1961. Oliver & Boyd Ltd.

CHUBB, J.C. 1961 A Preliminary Investigation of the Parasite Fauna of the Fish of Llyn Tegid (Bala Lake) Merionethshire. Ph.D.thesis, University of Liverpool.

GRINI, O. 1939 Enkelte sykdommer hos fisk Norsk Vet Tidsskr. 6: 5.

GURLEY, R.R. 1891 On the classification of Myxosporidia, a group of protozoan parasites infecting fishes. Bull.U.S. Fish Comm. 11: 407-420.

HUITFELDT-KAAS, H. 1912 Fiskerbiologiske Undersökelser i Vande i Trondhjems-amterne. K.norske vidensk.Selsk.Skr. 14: 75 pp.

JENNI, W. 1945 Zur kenntnis der Fisch parasiten des Zürichsees. Vjschr.naturf.Ges.Zurich 90: 271-275.

KUDO, R. 1920 Studies of Myxosporidia. A synopsis of genera and species of Myxosporidia. Illinois biol.Monogr. 5, 3-4.

KUDO, R. 1921 On the effect of some fixatives upon myxosporidian spores. Trans.am.microsc.Soc. 40: 161-168.

LINTON, E. 1889 Notice of the Occurrence of Protozoan Parasites (Psorosperms) on Cyprinoid fishes in Ohio. Bull.U.S. Fish Comm. 9: 359:361.

LOM, J. 1961 Protozoan parasites in Czechoslovakian Fishes. I. Myxosporidia, Suctoria. Zool.Listy 10 (24),(1): 45-58.

LOM, J. and VAVRA, J. 1962 A proposal to the Classification within the Subphylum Cnidospora. Syst.Zoo. 11, (1-4): 172-175.

MISHRA, T.N. 1966 Parasite fauna of the fish of the Shropshire Union Canal (Cheshire). Ph.D.thesis, University of Liverpool.

NICHOLAS, W.L. and JONES, J.W. 1959 Henneguya tegidiensis sp.nov.(Myxosporidia) from the freshwater fish Coregonus clupeoides pennantii (the gwyniad). Parasitology 49: 1-5.

POISSON, R. 1953 Sous-embranchement des Cnidosporidies. In 'Traité' de Zoologie' I (2):Protozoaires: Rhizopodes, Actinopodes, Sporozoaires, Cnido sporidies. 1006-1041.

QUADRI, S.S. 1962a New Myxosporidia from some British freshwater fishes. Proc.zool.Soc.Lond. 139: 329-335.

RIZVI, S.S.H. 1964 The parasite fauna of the fish of Rostherne Mere, Cheshire. Ph.D.thesis, University of Liverpool.

SCHAPERCLAUS, P.W. 1954 Fisch krankheiten. Berlin Akad.Verl.

SHULMAN, S.S. 1964 Evolution and phylogeny of the Myxosporidia. Report presented at the first International Congress of Parasitology. Acad.Sci.U.S.S.R.Zool.Inst.Leningrad.

SHULMAN, S.S. and SHTEIN 1964 Key to the Parasites of Freshwater Fish of the U.S.S.R.:- Section on Myxosporidia. Translation 1964. Israel Program for Scientific Translations, Jerusalem.

VIK, R. 1960. Henneguya zschokkei (Gurley, 1893). (Sporozoa) in Norway. Nytt.Mag.Zool. 9: 16-22.

WARD, H.B. 1919 Notes on North American Myxosporidia. J.Parasit. 6: 49:64.

WILLIAMS, H.H. 1964. Some observations on the mass mortality of the freshwater fish Rutilus rutilus (L) Parasitology, 54: 155-171.

ZSCHOKKE, F. 1884 Recherches sur L'organisation et la distribution zoologique des vers des poissons d'eau douce. Archs.Biol., Paris. 5: 153-241.

CHAPTER THREE.

MONOGENEA

Introduction.

Eleven species of Monogenea were recorded from the gills of S.cephalus, L.leuciscus, R.rutilus, T.thymallus and E.lucius. These species belonged to three genera, Dactylogyrus and Tetraonchus (sub-class Polyonchoinea Bychowsky 1930) and Diplozoon (sub-class Oligonchoinea Bychowsky 1930).

The parasites were preserved in alcohol-formal-acetic (A.F.A.) (Van Cleave, 1953). The dactylogyrids and tetraonchids were mounted in glycerine jelly and flattened by a weighted cover slip. The opisthaptor and copulatory organ were examined and measured. Diplozoon was examined unstained. The Monogenea were identified from Gussev (1964) and these identifications were later confirmed by Dr. A.V. Gussev. Table 3.1 shows the Monogenea recorded from the fish of the River Lugg. All these Monogenea have previously been recorded from Eastern Europe and the U.S.S.R. D.vistulae, D.prostae, D.folkmanovae, D.cordus, D.tuba, D.nanus and T.borealis are recorded for the first time in Britain. Table 3.2 shows previous records for those Monogenea recorded for the first time in Britain. D.crucifer and D.sphyrna have previously been recorded from R.rutilus in this country (Rizvi, 1964; Mishra, 1966). D.paradoxum has been found on many cyprinid hosts in this country (Sproston 1946; Dawes 1946, 47; Wiles 1965) and T.monenteron has previously been recorded

TABLE 3.1:

Monogenea recorded from the fish of the River Lugg.

Parasite		Host	Total No. parasites
Dactylogyrus crucifer	Wagener, 1847.	R.rutilus	2025
Dactylogyrus sphyrna	Linstow, 1878.	R.rutilus	5
Dactylogyrus namus	Dogiel and Bychowsky, 1934.	R.rutilus	1
Dactylogyrus vistulae	Prost, 1957.	S.cephalus	572
Dactylogyrus prostae	Molnar, 1964.	S.cephalus	753
Dactylogyrus folkmanovae	Ergens, 1956.	S.cephalus	5
Dactylogyrus cordus	Nybelin, 1937.	L.leuciscus	362
Dactylogyrus tuba	Linstow, 1878.	L.leuciscus	10
Tetraenchus borealis	(Olsson, 1893)	T.thymallus	348
Tetraenchus monenteron	Diesing, 1858.	E.lucius	398
Diplozoon paradoxum	Nordmann, 1832	L.leuciscus S.cephalus R.rutilus	464 2 10

TABLE 3.2:

Records from other countries, of those Monogenea recorded for the first time in Britain.

Parasite	Hosts	Location	Author
D.vistulae	L.cephalus R.rutilus	R.Vistulae - Poland	Prost 1957a
	Leuciscus svallize (Heckel) Leuciscus cephalus albus (Bonaparte)	Albania	Ergens 1960a and b.
D.prostae	? L.cephalus L.cephalus orientalis Nordmann	Hungary R. Tisa - U.S.S.R. R. Danube) Czecho- R. Elbe) slovakia R. Oder) Bender-Schach region-Iran.	Volnar 1964. Ergens and Gussev 1965
D.folkmanovae	L.cephalus L.svallize L.cephalus albus	R.Prut - Czecho-slovakia. Albania.	Ergens 1956 Ergens 1960a and b.
D.cordus	L.leuciscus L.idus (L.) Vimba vimba (L). L.cephalus L.leuciscus	Sweden R.Prut.Czechoslovakia. Ponds of the S.R.Trebon System -Czechoslovakia. Basins of the Black and Baltic Seas; North Dvina Basin; Chernyi Irtysh River; Lake Zaisan - U.S.S.R.	Sproston 1946. Rybelin 1957. Kulakovskaya 1960. Ergens, 1962.

TABLE 3.2 (continued)

Parasite	Hosts	Location	Author
D.nanus	Blicca bjoerkna (L.)	Czechoslovakia	Ergens, 1959.
	R.rutilus	Many records from U.S.S.R.	e.g.Dogiel and Bychowsky 1934a
	Abramis brama (L.)	Poland	Prost 1957 b.
	L.cephalus		
	Alburnus alburnus (L.)	Roumania	Sproston 1946 Roman 1953c
D.tuba	L.idus	Roumania	Roman 1953
		Sweden	Nybelin 1937
	Vimba vimba	Czechoslovakia	
	L.cephalus		
	Aspius aspius (L.)	Sweden	
		Poland	Prost 1957b.
	L.leuciscus	All main River Basins of the U.S.S.R	
	L.leuciscus baicalensis (Dybowski)		
	Scardinius erythrophthalmus (L.)		e.g. Agapova 1956.
	E.lucius		
	Carassius auratus gibelio (Bloch)		
	R.rutilus lacustris (Pallas)		
	Tinca tinca (L.)		
T.borealis	T.thymallus	Scandinavia	Olsson 1893.
	Coregonus lavaretus	Rivers flowing to the Arctic Ocean.	Bychowsky 1961.
		Czechoslovakia.	Pacack 1957.

from E.lucius (Sproston 1946; Rawson 1952; Dawes 1947; Chubb 1961; Rizvi 1964; Mishra 1966). Only a few specimens of D.folkmanovae, D.tuba, D.sphyrna and D.nanus were found, whereas D.vistulae, D.prostae, D.cordus, D.crucifer, T.borealis, D.paradoxum and to a certain extent T.monenteron were found in sufficient numbers to allow a study of the intensity of infection and their seasonal dynamics.

Morphological features.

All these Monogenea have previously been described, and only a few relevant and interesting points are mentioned.

Dactylogyridae.

Similarities in the shape of the copulatory apparatus, the hooks, the connecting and supplementary bar, and the presence of a vaginal strut were very evident in D.folkmanovae, D.prostae and D.nanus. These are the main characters used in the taxonomy of the group, and their similarity in these three species, together with the range of morphological variation of the copulatory apparatus and vaginal strut of D.prostae (Ergens and Gussev 1965) made identification difficult. The measurements of these similar characters are shown in Table 3.3. These measurements correspond to those given by Gussev (1964) and Gussev and Ergens (1965). Overall D.prostae was larger in total dimensions than the other two species, but the size and shape of the copulatory apparatus in all three was very similar.

TABLE 3.3:

Comparative measurements in mm. of D.nanus, D.prostae and D.folkmanovae.

	D.nanus	D.prostae	D.folkmanovae
Marginal hook length	0.013	0.026	0.024
Median hook length	0.031	0.045	0.034
Length of connecting bar	0.018	0.028	0.021
Length of copulatory apparatus	0.029	0.031	0.030
Total length of parasite	0.4	0.63	0.42
Breadth of parasite	0.07	0.09	0.07

Tetraonchidae.

Bychowsky (1961) stated that because of the considerable individual variability of the members of the genus Tetraonchus many of the species described from different Salmonidae and Thymallidae may not be valid, and possibly there is only one species of T.monenteron which has different forms on different hosts. T.borealis and T.monenteron were examined with reference to this statement.

The measurements of the most important characters used in the taxonomy of the genus are shown in Table 3.4. All the measurements recorded are less than those stated by Gussev and Strelkov (1964), and this may possibly result from the methods of preservation. In length, breadth and size of copulatory organ T.borealis is larger than T.monenteron, but the dorsal and ventral hooks and connecting bar in T.monenteron are larger than in T.borealis. The differences in the structure of the copulatory apparatus and of the connecting bar are shown in Plates 3.1, 3.2, 3.3 and 3.4 and listed below.

Comparison of the copulatory apparatus and connecting bar in T.borealis and T.monenteron.

T.borealis	T.monenteron
Supporting part of the copulatory apparatus encircles the copulatory tube in open turns 1-1.5 times.	Supporting part of the copulatory apparatus encircles the central copulatory tube in tight turns more than 1-1.5 times.
Connecting bar butterfly shaped with smooth evenly thickened edges.	Connecting bar more X-shaped with unevenly thickened edges.

The differences in these structures which are important taxonomic characters suggests that these two species are quite valid, especially when such small differences in these structures are used to separate D.prostae, D.folkmanovae and D.nanus.

TABLE 3.4:

Comparison of the dimensions (measured in mm.) of important characters used to distinguish T.borealis and T.monenteron.

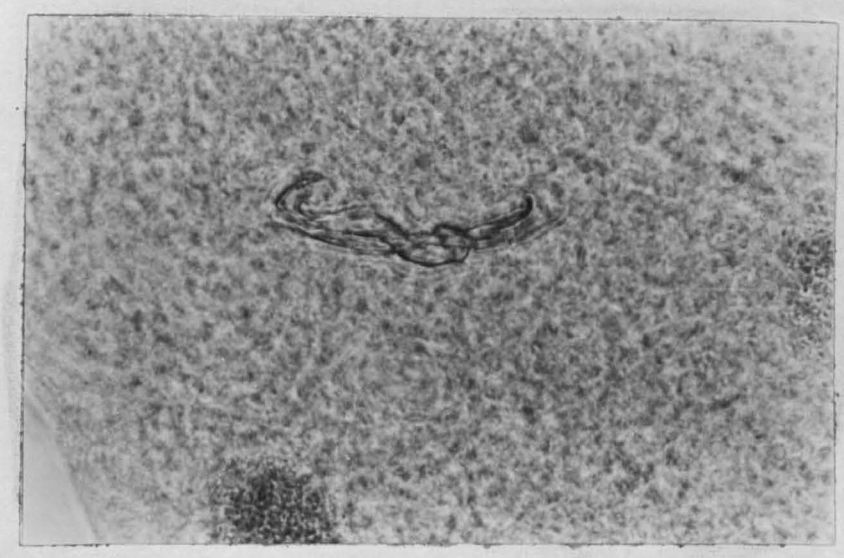
Parasite	Length		Breadth		Copulatory organ		Dorsal hooks		Ventral hooks		Connecting bar	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
T.borealis	1.13	1.04-1.36	0.22	0.15-0.29	0.057	0.066-0.048	0.066	0.064-0.070	0.072	0.064-0.079	0.041	0.035-0.046
T.monenteron	0.86	0.70-1.41	0.12	0.063-1.68	0.043	0.037-0.057	0.071	0.068-0.079	0.076	0.068-0.087	0.056	0.050-0.060

Plate 3.1 The copulatory organ of Tetraonchus borealis.

Magnification x510

Plate 3.2 The copulatory apparatus of Tetraonchus monenteron.

Magnification x510



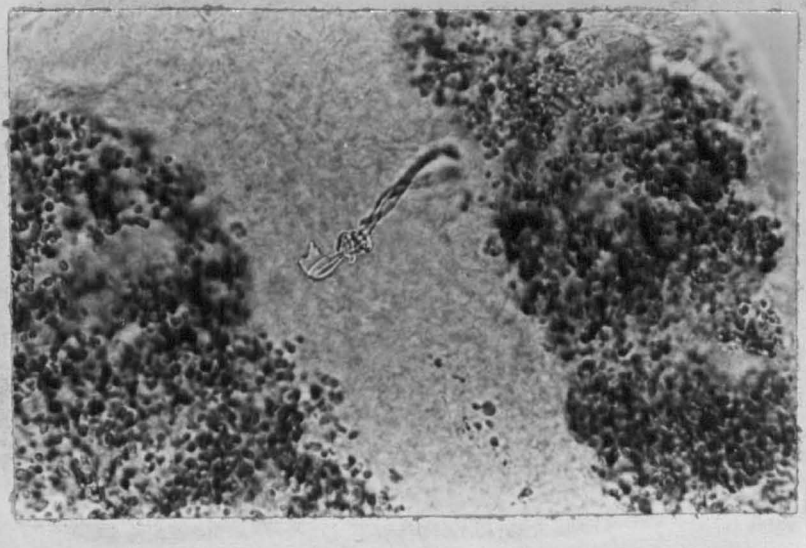
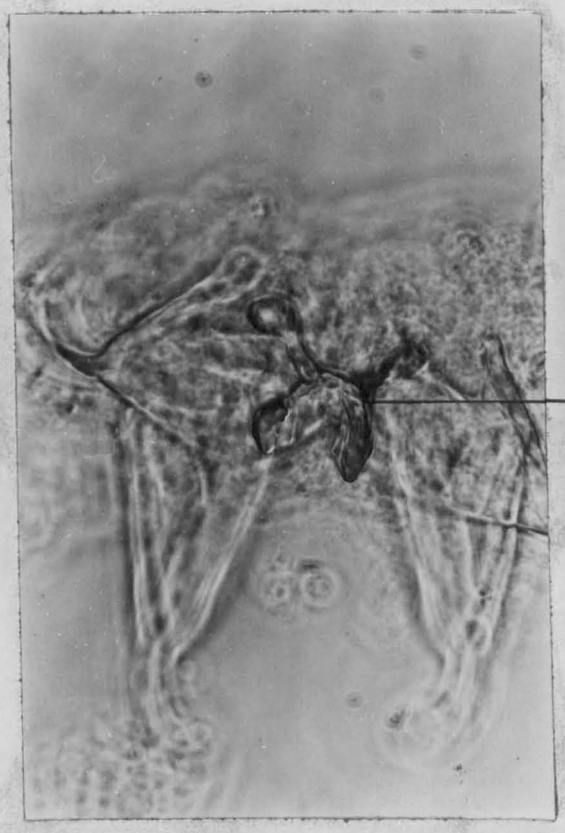


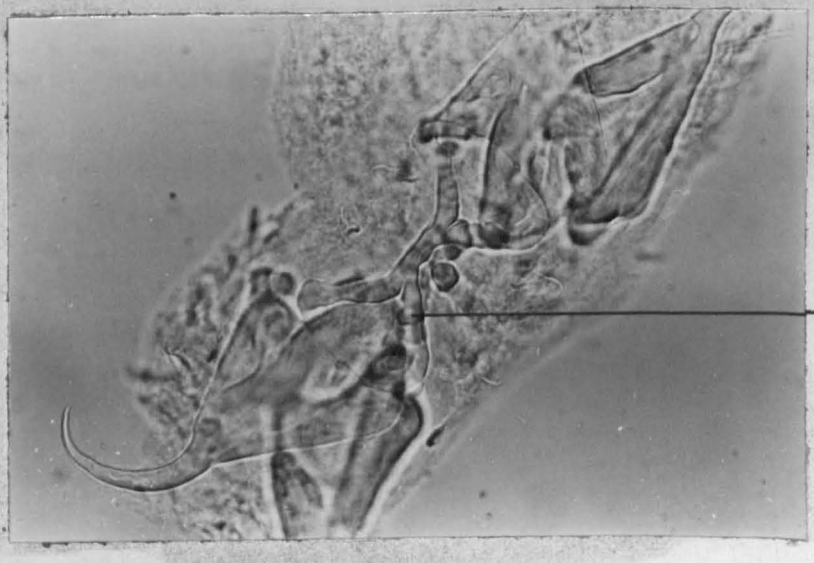
Plate 3.3 The opisthaptor of T. borealis to show the connecting bar (C).

Magnification x510

Plate 3.4 The opisthaptor of T. monenteron to show the connecting bar (C).

Magnification x510


C


C

Occurrence of Infection.

The number and percentage of fish infected each month throughout 1964 with D.crucifer, D.vistulae, D.prostae, D.cordus, T. crealis, T.monenteron and D.paradoxum was recorded (Tables 3.6, 3.7, 3.8, 3.9, 3.11, 3.13, 3.14, 3.15).

Dactylogyridae.

The total percentage of fish infected with dactylogyrids is summarised (Table 3.5) both as a percentage of the fish caught in all months, and as a percentage of the fish caught in the months when infection occurred. The percentage of R.rutilus infected with D.crucifer was much higher than the percentage of S.cephalus infected with D.vistulae and D.prostae, or the percentage of L.leuciscus infected with D.cordus. This pattern of infection was not very evident if only the percentage of the total number of fish was examined.

A marked seasonal occurrence of infection was recorded for the dactylogyrids (Tables 3.6, 3.7, 3.8, 3.9). The percentage of fish infected increased from February, and reached a peak in April in all four species. From April the percentage of fish infected decreased slowly until July after which it decreased rapidly until the infection had disappeared by September. A slight increase in the incidence of infection was recorded in July for all four species but whether this was a real increase throughout the total population or an increase only apparent in the samples, is unknown. Only nine R.rutilus and four L.leuciscus were caught in May. The data from this month were interpreted

cautiously as they resulted from a sampling deficiency.

The life cycle and the influence of the environment on the parasite and the host were examined to try and explain the seasonal occurrence of the dactylogyrids.

The life cycle of dactylogyrids and the influence of the environment.

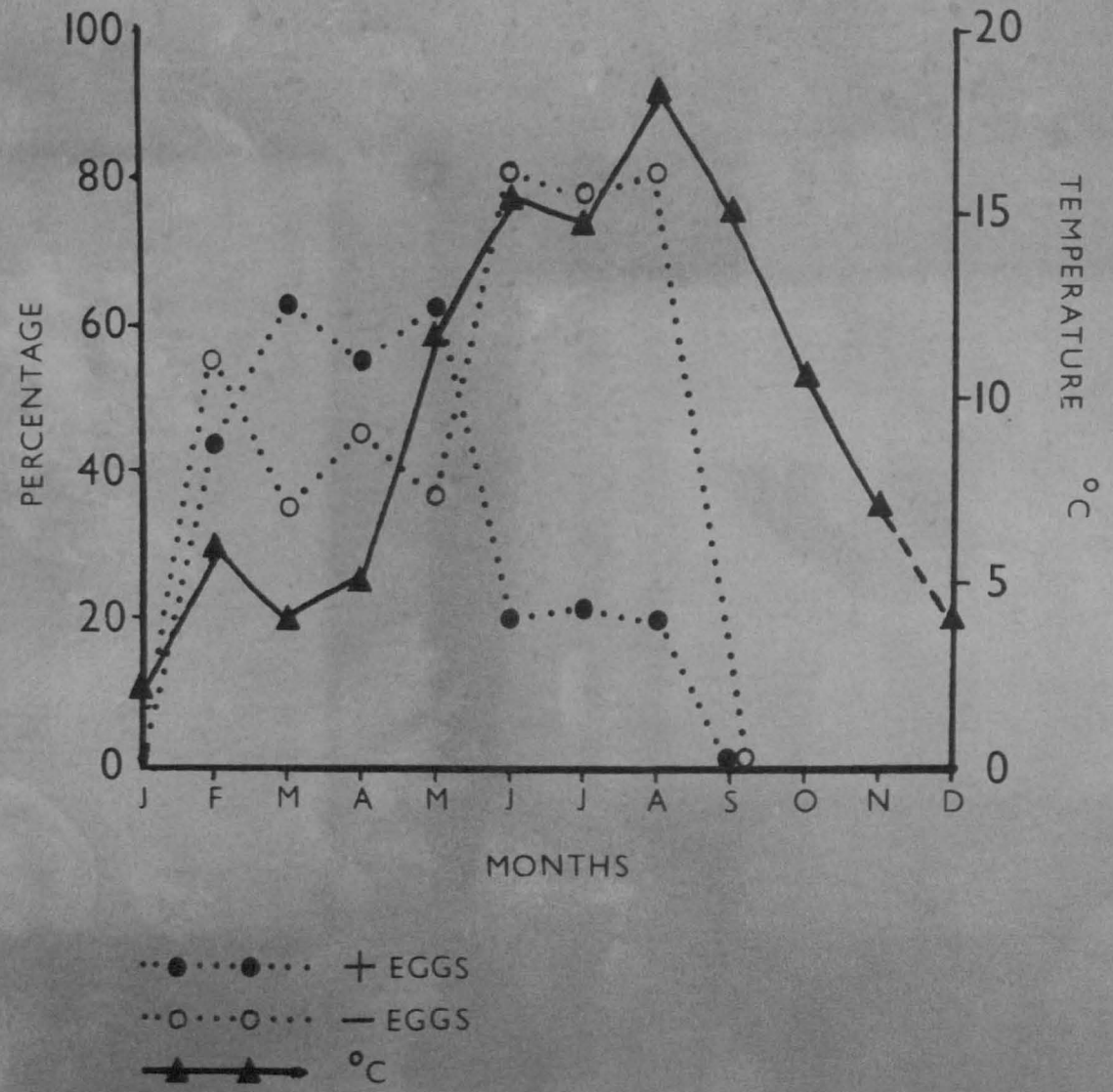
Investigations by Bauer (1954), Izumova (1953, 56) and Paperna (1963 a and b) on the life cycle of Dactylogyrus vastator (Nybelin, 1924) showed that eggs deposited by the adult monogenean developed at different rates depending on the water temperature and oxygen concentration. Lyaiman (1951) stated that egg development did not occur below 4°C, and a severe drop of temperature retarded development for long periods, and eggs produced in late summer remained dormant over the winter. A rise in water temperature in spring caused the dormant eggs to hatch and this provided the spring infection. A low percentage and intensity of infection may therefore be regarded as characteristic of dactylogyrid infections in winter months.

Figure 1.2 shows the water temperature of the River Lugg for each monthly sample. Temperatures below 4°C were recorded in January and December. The fact that the dactylogyrid eggs found by Lyaiman (1951) do not develop below 4°C may provide an explanation for the absence of dactylogyrids from the gills of the fish of the River Lugg in these months. The increase in temperature between February and March would allow the eggs which were dormant over the winter to develop, and this provided an explanation for the sudden appearance of dactylogyrids in

February. The reasons for the disappearance of dactylogyrids in August, September and October is difficult to explain as the temperature in these months varies between 18.3°C and 10.5°C. To try and find an explanation for the disappearance, the percentage of parasites with and without eggs was plotted each month. The results for D.vistulae are shown in Figure 3.1. It was not possible to plot these data for other species as few specimens contained eggs. The life cycle of dactylogyrids previously studied lasted between 20 and 40 days, and to obtain sufficient data for most species about the peak period of egg production it would be necessary to obtain weekly samples of parasites. In March, April and May the percentage of D.vistulae with eggs was greater than the percentage without, but by June the percentage with eggs had rapidly decreased.

The decrease in the production of eggs would result in a decrease in the number of parasites present to infect the hosts, and would explain the fall off in infection between July and September. Reasons for the decrease in egg production after May are unknown, but it is possible that the higher summer temperatures were high enough to have an inhibitory effect on egg production. Although Lyaiman (1951) states that the optimum temperatures for egg production for D.vastator lies between 20 - 25°C, Bauer and Nikolskaya (1954) state that D.solidus Akhmerov,1948 reproduces at temperatures of less than 15°C, and eggs deposited at temperatures over 15°C are mainly inviable and undergo rapid decomposition. Further investigations are required before any statement can be made as to

Fig. 3.1 The percentage of *L. vistulae* with and without eggs in each sample where infection occurred, in relation to temperature.


100
80
60
40
20
0
PERCENTAGE
20
15
10
5
0
TEMPERATURE °C
J F M A M J J A S O N D
MONTHS
+ EGGS
— EGGS
°C

the inhibitory effect of temperatures above 15°C on egg production of the dactylogyrids found in this survey.

TABLE 3.5:

Comparison between the percentage of fish infected with different species of dactylogyrids.

Parasite	Total No.of fish	Total No.fish infected	% of total infected	No.of fish in infected months	% infected in infected months
D.crucifer	317	124	39.1	164	75.6
D.vistulae	359	118	32.9	211	55.9
D.cordus	342	81	23.7	253	32.0
D.prostae	359	52	14.5	211	24.6

TABLE 3.6:

The percentage of R.rutilus infected with D.crucifer.

Month	No.Fish/ sample	No. infected	% infected	No.female infected	% female infected	No. male infected	% male infected
January	33	0	0	0	0	0	0
February	27	17	63.0	9	75.0	8	53.3
March	30	26	86.6	16	100.0	10	71.4
April	16	16	100.0	10	100.0	6	100.0
May	9	1	11.0	1	33.3	0	0
June	30	23	76.6	10	71.4	13	81.2
July	22	21	95.5	11	91.6	10	100.0
August	30	20	66.6	16	76.4	4	50.0
September	30	0	0	0	0	0	0
October	30	0	0	0	0	0	0
November	30	0	0	0	0	0	0
December	30	0	0	0	0	0	0
Total	317	124	39.1	73	47.4	51	32.3
Total for infected months only			75.6		82.0		68.0

TABLE 3.7:

The percentage of S.cephalus infected with D.vistulae.

Month	No.Fish/ sample	No. infected	% infected	No.female infected	% female infected	No. male infected	% male infected
January	32	0	0	0	0	0	0
February	31	16	51.6	9	64.3	7	53.9
March	29	21	72.4	13	72.2	8	72.7
April	30	26	87.0	11	78.5	15	93.7
May	31	20	64.5	16	80.0	4	36.4
June	30	12	40.0	9	47.4	3	27.3
July	30	15	50.0	9	43.0	6	66.6
August	30	6	20.0	2	14.3	4	25.0
September	28	0	0	0	0	0	0
October	27	0	0	0	0	0	0
November	30	0	0	0	0	0	0
December	31	2	0	0	0	0	0
Total	359	118	32.9	69	33.2	47	31.9
Total for infected months only			55.9		57.5		42.9

TABLE 3.8:

The percentage of S.cephalus infected with D.prostae.

Month	No.fish/ sample	No. infected	% infected	No.female infected	% female infected	No. male infected	% male infected
January	32	0	0	0	0	0	0
February	31	7	22.6	4	28.6	3	23.1
March	29	8	27.6	7	38.8	1	9.1
April	30	11	36.6	5	35.7	6	37.5
May	31	7	22.6	7	35.0	0	0
June	30	5	16.6	4	21.1	1	9.1
July	30	6	20.0	3	14.3	3	33.3
August	30	8	26.6	3	21.4	5	31.3
September	28	0	0	0	0	0	0
October	27	0	0	0	0	0	0
November	30	0	0	0	0	0	0
December	31	0	0	0	0	0	0
Total	359	52	14.5	33	15.9	19	13.0
Totals for infected months only.			24.6		27.5		17.3

TABLE 3.9:

The percentage of L.leuciscus infected with D.cordus.

Month	No.fish/ sample	No. infected	% infected	No.female infected	% female infected	No. male infected	% male infected
January	33	1	3.1	1	10.0	0	0
February	31	7	22.6	5	33.3	2	12.5
March	30	16	53.3	7	58.3	9	75.0
April	35	22	62.9	9	64.3	13	92.8
May	4	0	0	0	0	0	0
June	30	11	36.6	3	18.8	8	50.0
July	30	19	63.3	8	61.5	11	84.6
August	30	4	13.3	3	18.8	1	6.3
September	30	1	3.3	1	4.5	0	0
October	31	0	0	0	0	0	0
November	26	0	0	0	0	0	0
December	30	0	0	0	0	0	0
Total	342	81	23.7	37	21.5	44	26.0
Total for infected months only.			32.0		30.3		35.6

Incidence of infection in male and female fish.

Using a χ_2 test the difference between the percentage of male and female R.rutilus infected with D.crucifer was shown to be statistically significant ($p = 0.05$); a greater percentage of male R.rutilus being infected. This difference may show the true picture of what occurs in the population, but it may result from the different number of male and female fish in the sample or from a significant difference in the ratio of male:female fish in each monthly sample. Male or female fish may possibly be more susceptible to infection at certain times of the year. All these issues need to be taken into account, and it is hoped to analyse these results later allowing for these variables.

When all the fish were taken into account little difference was recorded between the percentage of males and females infected with dactylogyrids. If only the fish within the infected months were taken, and the percentage of infected male and female fish recorded, the difference between the percentage of each sex infected, increases for D.vistulae and D.prostae from S.cephalus, but hardly changes for D.cordus from L.leuciscus. (Table 3.10). The smaller increase for D.cordus compared to D.vistulae and D.prostae could be explained by the fact that 1 or 2 L.leuciscus were infected in January and September, months where infections were not recorded from other fish. More fish were therefore taken into account when recording the percentage of male and female L.leuciscus infected within the infective months, making the result closer to that recorded when all L.leuciscus were taken into account.

TABLE 3.10:

The percentage of the total number and the number in infected months of male and female fish infected with dactylogyrids.

Parasite		No.male fish	% male fish infected	No.female fish	% female fish infected
D. crucifer	All fish	163	47.4	154	31.3
	Fish within infected months	75	82.0	89	68.0
D.vistulae	All fish	147	31.9	208	33.2
	Fish within infected months	87	42.9	120	57.5
D.prostae	All fish	147	15.9	208	13.0
	Fish within infected months	87	27.5	120	17.4
D.cordus	All fish	170	21.5	172	26.0
	Fish within infected months	131	30.3	122	33.6

A higher percentage of female fish were infected with D.vistulae and D.cordus, whereas a higher percentage of male fish were infected with D.crucifer and D.prostae. With the exception of R.rutilus it is doubtful whether the difference between the percentage of male and female fish infected is significant. The differences that are recorded in Table 3.10 may result from the presence of different numbers of male and female fish in the samples and the influence of the age or length of the fish in the incidence of infection. Evidence to support this is taken from L.leuciscus which has only a 3% difference between the percentage infection of the sexes, and where nearly equal numbers of each sex (131 male:122 female) within a narrow length range were sampled.

Tetraonchidae.

The percentage of T.thymallus and E.lucius infected with T.borealis and T.monenteron respectively are shown in Tables 3.11 and 3.13. No samples of T.thymallus were obtained in January or September, but the samples obtained in other months showed a seasonal occurrence for T.borealis similar to that recorded for dactylogyrids. The percentage of T.thymallus infected with T.borealis reached a peak in April, and then decreased over the next two months before increasing to a second peak in July. After July the percentage infection decreased rapidly but persisted at a low level in the winter months. The second peak in July may not represent a true picture, but may be a reflection of the

larger number of fish present in this sample in comparison to the previous two months. Only three fish were infected between October and December, and none of the parasites present contained eggs. The percentage of parasites with and without eggs are recorded in Table 3.12. Most parasites did not contain eggs and it was difficult to determine a peak period of egg production. May appeared to be the optimum month, but the small number of parasites recorded reduces the validity of this observation.

No difference was found between the percentage of male and female fish infected in total or within months, approximately 33% of all the male and female fish being infected (Table 3.11).

Only 36 E.lucius were caught, and no samples were obtained in March, September and November. The number and percentage of E.lucius infected with T.monenteron are recorded in Table 3.13. There are certain discrepancies in the literature as to the presence of a seasonal occurrence of infection for T.monenteron. Chubb (1961) recorded T.monenteron from E.lucius at all times of the year from Llyn Tegid (Lake Bala, Merionethshire) and Rizvi (1964) supported this view recording this parasite each month from E.lucius of Rostherne Mere (Cheshire). In contrast to this Rawson (1952) considered T.monenteron as showing marked periodicity, E.lucius only being infected in July and August. This latter statement is not valid as fish were only sampled for two or three months. The small number of E.lucius caught in the present investigation do not allow any conclusions as to the presence

or absence of a seasonal occurrence, but the evidence from other surveys shows that in certain environments T.monenteron is recorded throughout the year.

Diplozoon paradoxum Nordmann, 1832.

L.leuciscus, R.rutilus and S.cephalus were infected by D.paradoxum. The percentage of L.leuciscus infected (53.5%) (Table 3.14) was much higher than the percentage of R.rutilus (3.2) (Table 3.15) or S.cephalus (0.56%). The infection was recorded in all months from L.leuciscus (Table 3.14) and contrasted sharply with the seasonal occurrence of the dactylogyrids and T.borealis. The percentage of L.leuciscus infected throughout the year varied from 30.0% to a peak of 68.0%, but there was no significant build up or fall off in infection at any one time. The figure recorded for May of 75% infection may not be valid as only four fish were sampled that month, of which three were infected.

All the D.paradoxum were examined unstained and they were divided into six main stages, closely related to stages in development:-

I. Single diporpa larvae.

II. United juveniles with 2 - 3 clamps.

III. United pairs with the full number of clamps (4); vitellaria not visible.

IV. Vitellaria partially developed; no eggs.

V. Vitellaria fully developed; no eggs.

VI. Vitellaria fully developed; eggs present.

TABLE 3.11:

The number and percentage of T.thymallus infected with T.borealis.

Month	No.fish/ sample	No. infected	% infected	No.female infected	% female infected	No. male infected	% male infected
January			NO SAMPLE				
February	11	0	0	0	0	0	0
March	18	6	33.3	3	43.0	3	27.2
April	25	20	98.0	8	80.0	12	80.0
May	8	5	62.5	3	60.0	2	66.7
June	17	7	47.1	5	50.0	2	42.9
July	30	24	80.0	10	100.0	14	70.0
August	5	1	20.0	1	33.3	-	-
September			NO SAMPLE				
October	25	1	4.0	0	0	1	9.1
November	30	0	0	0	0	0	0
December	30	2	6.6	2	11.8	0	0
Total	199	66	34.6	32	33.0	34	36.1
Total for infected months only			41.7		51.5		50.8

TABLE 3.12:

The percentage of T.borealis from T.thymallus with and without eggs.

Month	% + eggs	% - eggs	No. parasites
January	NO SAMPLE		
February	0	0	0
March	12.5	87.5	26
April	3.1	96.9	117
May	25.0	75.0	11
June	10.0	90.0	15
July	12.7	87.3	179
August	0	100.0	2
September	NO SAMPLE		
October	0	100.0	3
November	0	0	0
December	0	100.0	4
			357 Total

TABLE 3.13:

The number and percentage of E.lucius infected with T.monenteron.

Month	No. fish sample	No. infected	% infected	No.female infected	% female infected	No. male infected	% male infected
January	1	0	0	0	0	0	0
February	1	1	100.0	1	100.0	0	0
March			N O S A M P L E				
April	7	6	85.7	3	75.0	3	100.0
May	5	4	80.0	2	66.6	2	100.0
June	8	4	50.0	1	33.3	3	60.0
July	7	7	100.0	4	100.0	3	100.0
August	2	2	100.0	1	100.0	1	100.0
September			N O S A M P L E				
October	4	2	50.0	2	50.0	0	0
November			N O S A M P L E				
December	1	0	0	0	0	0	0
Total	36	26	72.3	14	70	12	75.0

TABLE 3.14:

The number and percentage of *L.leuciscus* infected with *D.paradoxum*.

Month	No.fish/ sample	No.infected	% infected	No.female infected	% female infected	No. male infected	% male infected
January	33	10	30.3	3	40.0	6	66.6
February	31	14	45.0	9	64.3	5	35.7
March	30	20	66.6	8	66.6	12	63.2
April	35	20	57.0	7	35.0	13	65.0
May	4	3	75.0	3	100.0	-	-
June	30	14	46.7	7	50.0	7	50.0
July	30	17	56.6	10	76.9	7	41.2
August	30	18	60.0	13	72.2	5	27.8
September	30	12	40.0	8	66.6	4	33.3
October	31	19	61.0	13	68.4	6	31.6
November	28	19	67.8	12	70.6	7	63.6
December	30	17	57.0	8	47.1	9	52.9
Total	342	183	53.5	103	59.8	80	47.1

TABLE 3.15:

The number and percentage of R.rutilus infected with D.paradoxum.

Month	No.fish/ sample	No.infected	% infected	No.female infected	% female infected	No. male infected	% male infected
January	33	-	-				
February	27	-	-				
March	30	1	3.3			1	7.1
April	16	1	6.2	1	10.0		
May	9	-	-				
June	30	2	6.6	1	7.1	1	6.2
July	22	2	9.1	1	8.3	1	10.0
August	30	1	3.3			1	12.5
September	30	-	-				
October	30	1	3.3			1	6.2
November	30	2	6.6	2	18.2		
December	30	-	-				
Total	317	10	3.2	5	3.3	5	3.1

The number of each stage present each month on L.leuciscus was plotted as a percentage of the total number recorded each month, and the results are shown in Figure 3.2. From January to April the percentage of D.paradoxum with partial to fully developed vitellaria increased. The presence of eggs was recorded mainly from April to September, and the peak period of egg production occurred in June (Table 3.16). The figure for May is possibly misleading as only ten parasites were recorded from three fish, and they all contained eggs. From September to December the greater percentage of D.paradoxum had no eggs and the vitellaria was not visible, or only partially visible. Stages I and II were rare and the greater percentage were recorded in July. These young forms probably developed from eggs hatched in April, May and June.

From this data D.paradoxum appears to overwinter on the gills of L.leuciscus in a fairly inactive state, increased development of the vitellaria occurred between January and April and eggs were present from April to September. This information corresponds with work by Zeller (1872) and Bychowsky (1961). They state that the life span of D.paradoxum is three years, the parasite laying eggs only in the second year and usually living for not less than one year after the first eggs have been laid. From this statement it follows that the parasites from this survey, present from September to January in stages III and IV will be composed of parasites in their second year which have laid eggs, and in which the genital system is fully developed even though the

Fig. 3.2 The number of each developmental stage of *D. paradoxum* in *L. leuciscus* expressed as a percentage of the total number examined each month.

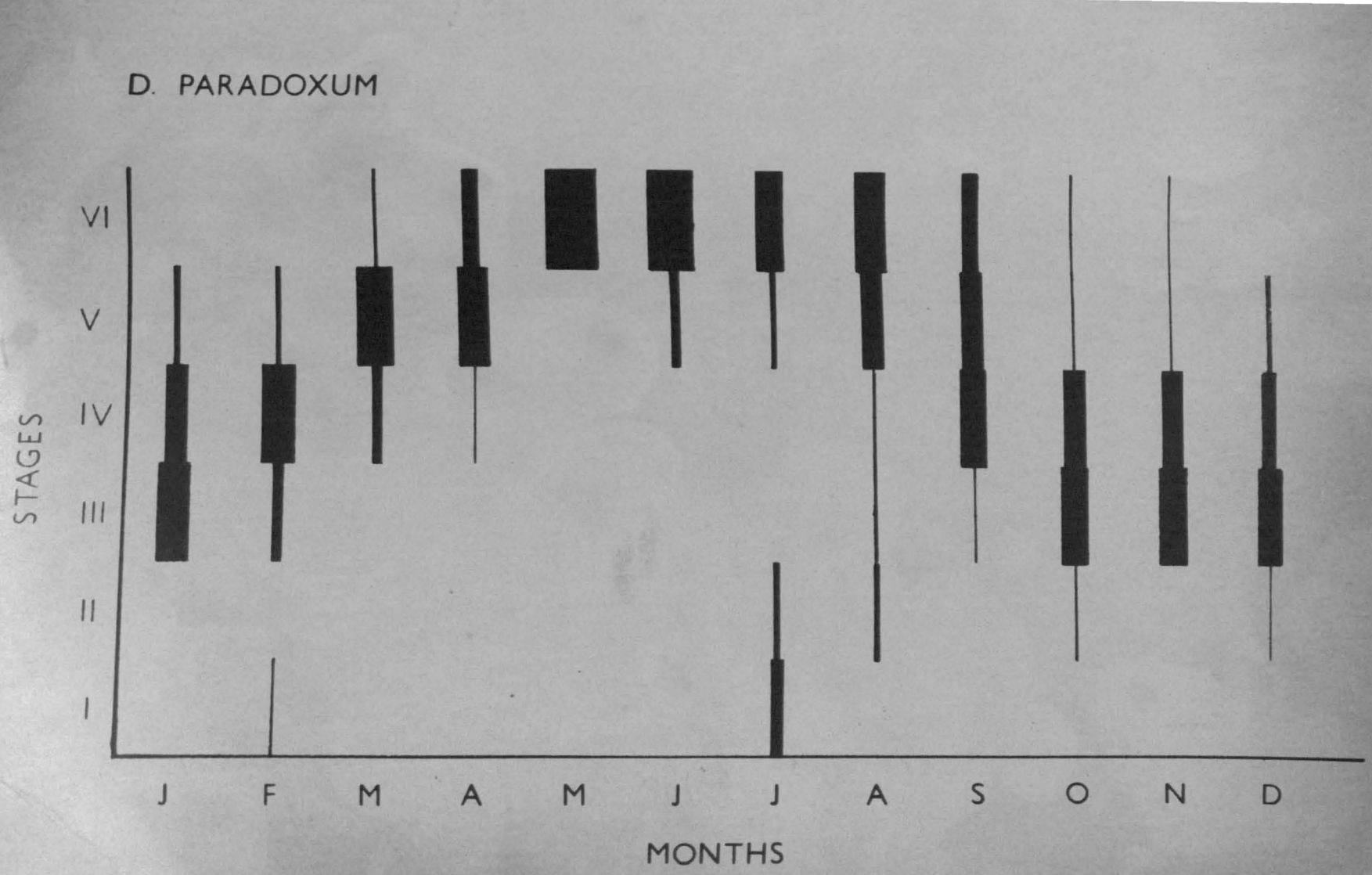

D. PARADOXUM
STAGES
VI
V
IV
III
II
I
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

TABLE 3.16:

The percentage of D.paradoxum with and without eggs each month.

Month	% + eggs	% - eggs	No. of parasites	
January	0	100.0	18	
February	2.5	97.5	40	
March	1.8	98.2	62	
April	35.0	65.0	48	
May	100.0	0	10	
June	88.9	11.1	33	
July	60.0	40.0	29	
August	59.7	40.3	70	
September	28.6	71.4	30	
October	2.7	97.3	43	
November	2.5	97.5	42	
December	0	100.0	41	
			467	Total

vitellaria regresses to an inactive state in the winter. These parasites produced from eggs hatched in May and June also spend the winter in an inactive state and vitellaria and egg cells do not develop until the following spring.

Increase in water temperature has been stated to be the cause of the onset of vitellaria and egg cell development (Zeller, 1872). Another fact is put forward which may cause or work in conjunction with water temperaure to cause the onset of vitellaria and egg cell development. D.paradoxum is a blood and mucus feeder (Halton and Jennings, 1965) and the ingested blood would contain varying levels of reproductive hormones at different times of the year. The peak of maturation of D.paradoxum taken as the months with the greatest percentage of parasites containing eggs (May and June) are the months immediately following the spawning period of L.leuciscus (April) when the level of gonadotrophins in the blood would be high, and could possibly influence the maturation of D.paradoxum.

Intensity of Infection.

Introduction.

The intensity of infection of a parasite is usually recorded as the mean number of parasites per host per sample. This allows a valid comparison between the sample if:-

(a) The same number of host species are present in each sample.

(b) The age and the sex of the host have no influence on the intensity of infection.

The actual level of intensity is shown more accurately by recording the mean number of parasites for only the infected hosts, but comparisons between samples are only valid if (a) and (b) above are true. The mean number of parasites per fish and per infected fish was recorded each month for D.crucifer, D.vistulae, D.prostae, D.cordus, T.borealis and D.paradoxum (last column Tables 3.18, 3.19, 3.20, 3.21, 3.22, 3.23). Approximately 30 of each host species were sampled each month except for deficient samples of R.rutilus in April and May, of L.leuciscus in May and irregular samples of T.thymallus. Where approximately 30 fish per sample were present legitimate comparisons of the mean number of each species of parasite could be made.

Comparison of the overall intensities of infection with each species of parasite.

The dactylogyrids and T.borealis have a seasonal occurrence and therefore the overall mean number for each species was recorded (Table 3.17) as the mean of:-

a) the total number of fish

b) The number of infected fish

c) the number of fish in months where infection occurs.

TABLE 3.17:

Comparison of the overall intensity of infection of six species of Monogenea.

	a	b	c
D.crucifer	6.4	16.3	12.3
D.prostae	2.1	14.5	3.6
T.borealis	1.8	5.4	2.2
D.vistulae	1.6	4.9	2.4
D.paradoxum	1.4	2.5	1.4
D.cordus	1.1	4.5	1.4

The pattern of intensity of infection between a, b and c was similar for each species, but the level of intensity differed according to whether a, b or c were used, therefore it is much easier to determine the patterns than the significance of the intensity of infection. As similar numbers of fish were present in the samples, it is suggested that the most valid figures for comparison of intensities of infection in this survey are those where the mean number of parasites for the fish in infected months was recorded, providing the influence of the age and sex of the fish are taken into account.

D.crucifer showed a greater intensity of infection than the other five species. Each column in Table 3.17 followed a similar pattern, apart from D.cordus which showed a greater intensity of infection than D.paradoxum when only the infected fish were taken into account. This

may be explained by the seasonal occurrence of D.cordus and the fact that fewer fish were involved, whereas D.paradoxum was present throughout the year and a larger number of fish were infected.

Seasonal variation in the intensity of infection.

Comparisons between the mean number of parasites per total number of fish per monthly sample for each species (Tables 3.18, 3.19, 3.20, 3.21, 3.22, 3.23) showed:-

1. The intensity of infection for D.crucifer and D.vistulae rose to a peak in April for the former and May for the latter. The intensity dropped in June but a second peak of doubtful significance occurred in July, before the infection disappeared in September.

2. D.prostae showed a peak period of intensity of infection in March, April and May, this dropped slightly in June, and rose again slightly in July before the disappearance of infection by September.

3. April, June and July was the peak period of intensity of infection for D.cordus, the infection having disappeared by October. No data were available from the May sample.

4. T.borealis showed a similar pattern to D.crucifer and D.vistulae, a peak of intensity of infection being recorded in April, a drop in May and June, and a second peak in July.

5. A slight rise in the intensity of infection was recorded in May and August for D.paradoxum, but no obvious increase occurred at any one time of year.

Relationship of length to the percentage and intensity of infection.

Length was used as some indication of the age of the fish, and also to indicate increase in size and surface area as the surface available for infection was thought to be important when considering intensity of infection. When the age data for the fish are available after the completion of the work on the biology of the fish of the River Lugg, by Mr. J.M. Hellawell, intensity of infection will be correlated with age.

Each host species was divided into four main length groups. For each parasite the following tables and figures were plotted.

(a) The intensity of infection as the mean number of parasites for the total number of fish and for the number of infected fish, for each length group each month. (Tables 3.18, 3.19, 3.20, 3.21, 3.22, 3.23).

(b) The range of the number of parasites as the number of fish in each length group with the same number of parasites (Figures 3.3, 3.4, 3.5, 3.6, 3.7, 3.8).

(c) The percentage of infected and non-infected fish in each length group.

Results.

Only the total results were used as the total number of fish in any length group per month was too small to allow any comparisons between the intensities of infection from fish in different length

groups in the same monthly samples. If it could be shown that the proportions of the different length groups were similar in each month, then conclusions drawn from examining the total figures could be applied to the monthly figures.

Mean number of parasites per length group.

D.crucifer, D.prostae, D.vistulae and T.borealis showed an increase in the mean number of parasites with increase in length, when all the fish and only the infected fish were considered.

When the mean number of T.cordus from L.leuciscus was considered for the total number of fish no increase was observed between 15 - 20 and 20 - 25 cms., but there was an increase in the intensity of infection in the 25 - 30 cm. group. When only the infected fish were considered an increase of intensity was observed between 15 - 20 and 20 - 25 cms. but a decrease between 20 - 25 and 25 - 30 cms. It was difficult to decide which was the true interpretation, and no definite statement could be made unless the same number of infected fish and the same total number of fish were present in each length group.

The pattern of intensity of infection for D.paradoxum was similar when both the total number of fish and only the infected fish were taken into account. There was an increase in intensity of infection between 0 - 15 and 15 - 20 cms., a slight decrease in the 20 - 25 cm. group and a slight increase again by the 25 - 30 cm. group.

The data showed an increase in the intensity of infection with length for D.vistulae and D.prostae from S.cephalus; D.crucifer from

R.rutilus and T.borealis from T.thymallis. No increase of intensity with increase in length was recorded for D.cordus and D.paradoxum from L.leuciscus. S.cephalus and R.rutilus in the samples covered a much wider size range than L.leuciscus, and this may explain why an increase in intensity of infection with increase in length was recorded for S.cephalus and R.rutilus, but not for L.leuciscus. L.leuciscus and T.thymallus have approximately the same size range in this survey, but whereas no increased intensity was recorded for D.cordus with increased length of L.leuciscus, an increase in the intensity of T.borealis was recorded with increase in length of T.thymallus. This observation may be explained by the fact that most L.leuciscus are in one length group i.e. 20 - 25 cm. group, whereas T.thymallus are more distributed over the size range.

Influence of length on the percentage of fish infected.

1. The percentage of R.rutilus, S.cephalus and T.thymallus infected respectively with D.crucifer, D.vistulae and T.borealis increased with an increase in the length of the host (Figures 3.3, 3.4, 3.5).

2. The percentage of S.cephalus infected by D.prostae is approximately the same in the 30 - 40 cm. and 40 - 50 cm. length groups. (Figure 3.6)

3. The percentage of L.leuciscus infected with D.cordus and D.paradoxum increased up to 25 cms., but decreased between 25 - 30 cms. (Figures 3.7, 3.8.)

Range of the number of parasites in relation to the length of the host.

The range of the number of parasites recorded from any one fish tended to increase as the length of the fish increased (Figures 3.3, 3.4, 3.5, 3.6, 3.7, 3.8). This was very apparent for D.crucifer, D.vistulae and D.prostae. In the lower length groups most fish had only a few parasites (especially P.cephalus infected with D.vistulae) whereas in the greater length groups most of the fish had larger numbers of parasites. An increase in the range of the number of parasites was recorded from T.thymallus and L.leuciscus with increase in length up to 25 cms. after which a decrease was recorded, but this may result from the smaller sample of fish in the larger length group. Only low numbers of parasites were present on fish in the shortest length group, but a few fish in all length groups exhibited this phenomenon.

D.paradoxum was recorded in small numbers from fish of all length groups, and no increase in the range of numbers of parasites was noted on larger fish.

Fig. 3.3 The intensity of infection of *D. crucifer* and the percentage of *R. rutilus* infected in relation to the length of the host.

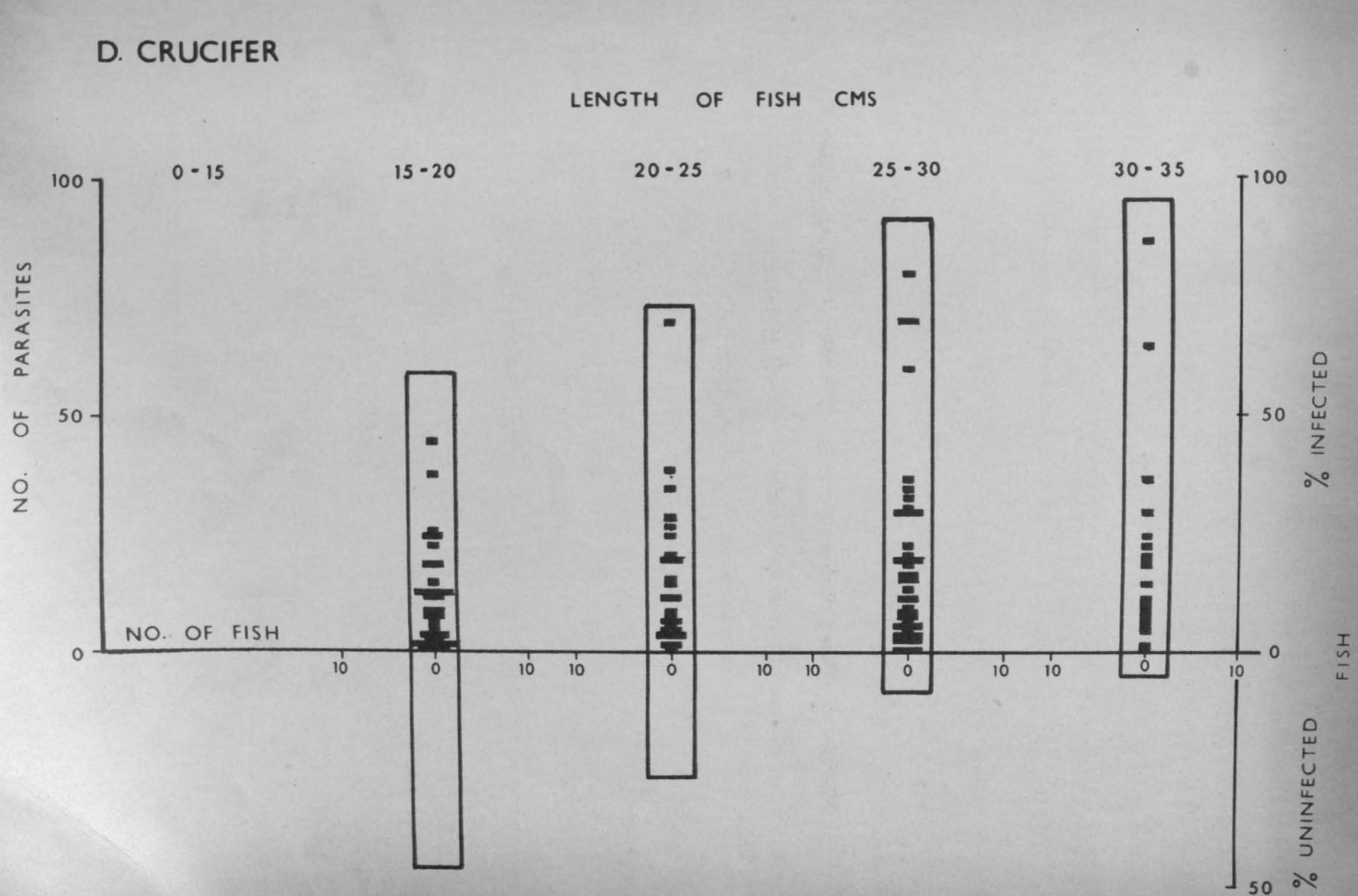

D. CRUCIFER
LENGTH OF FISH CMS
0 - 15
15 - 20
20 - 25
25 - 30
30 - 35
100
50
0
NO. OF PARASITES
NO. OF FISH
10
0
% INFECTED
% UNINFECTED
FISH

Fig. 3.4 The intensity of infection of *D. vistulae* and the percentage of *S. cephalus* infected in relation to the length of the host.

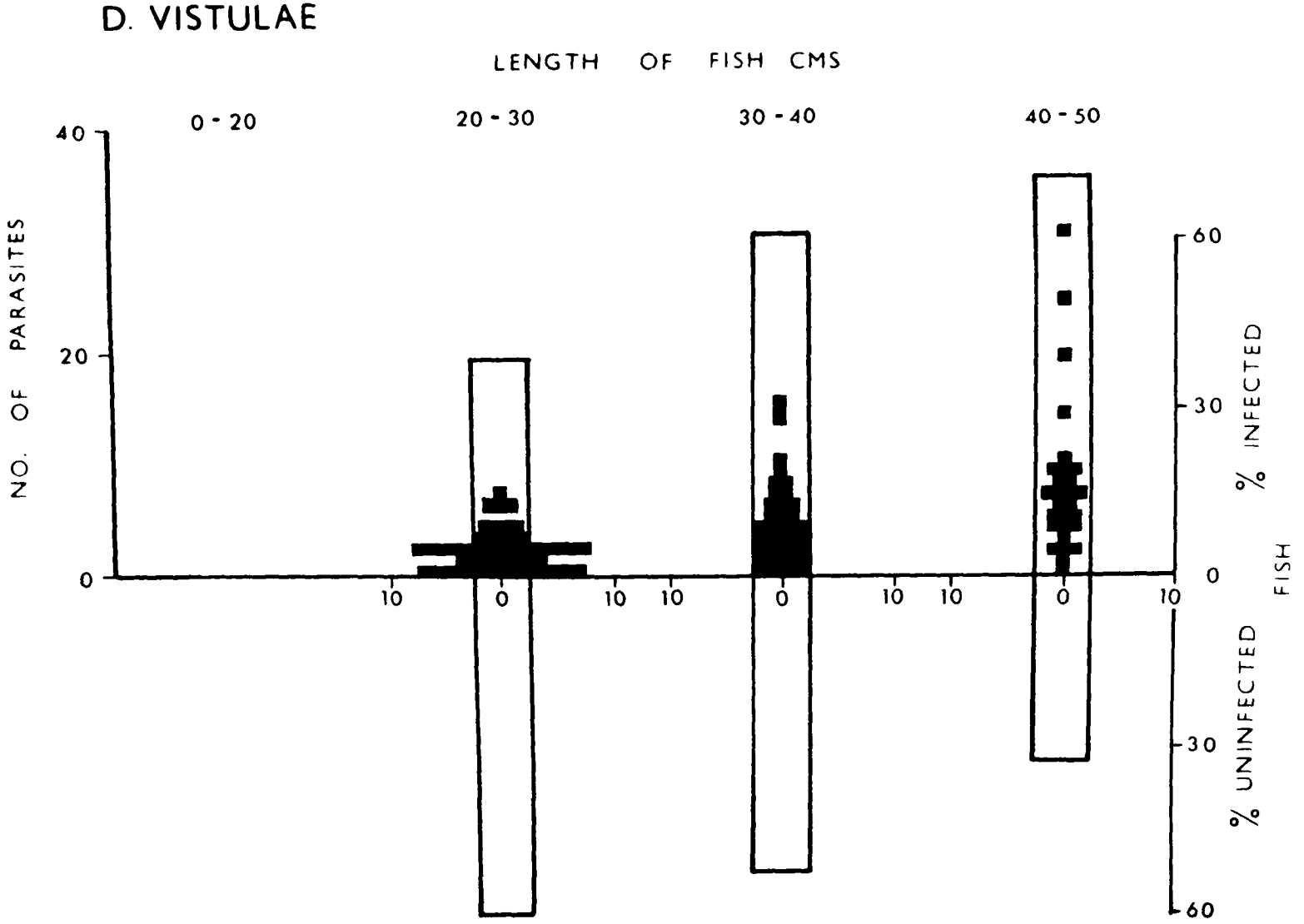

D. VISTULAE
LENGTH OF FISH CMS
0 - 20
20 - 30
30 - 40
40 - 50
NO. OF PARASITES
40
20
0
10
0
10
10
0
10
10
0
10
% INFECTED
% UNINFECTED
60
30
0
30
60
FISH

Fig. 3.5 The intensity of infection of T. borealis and the percentage of T. thymallus infected in relation to the length of the host.

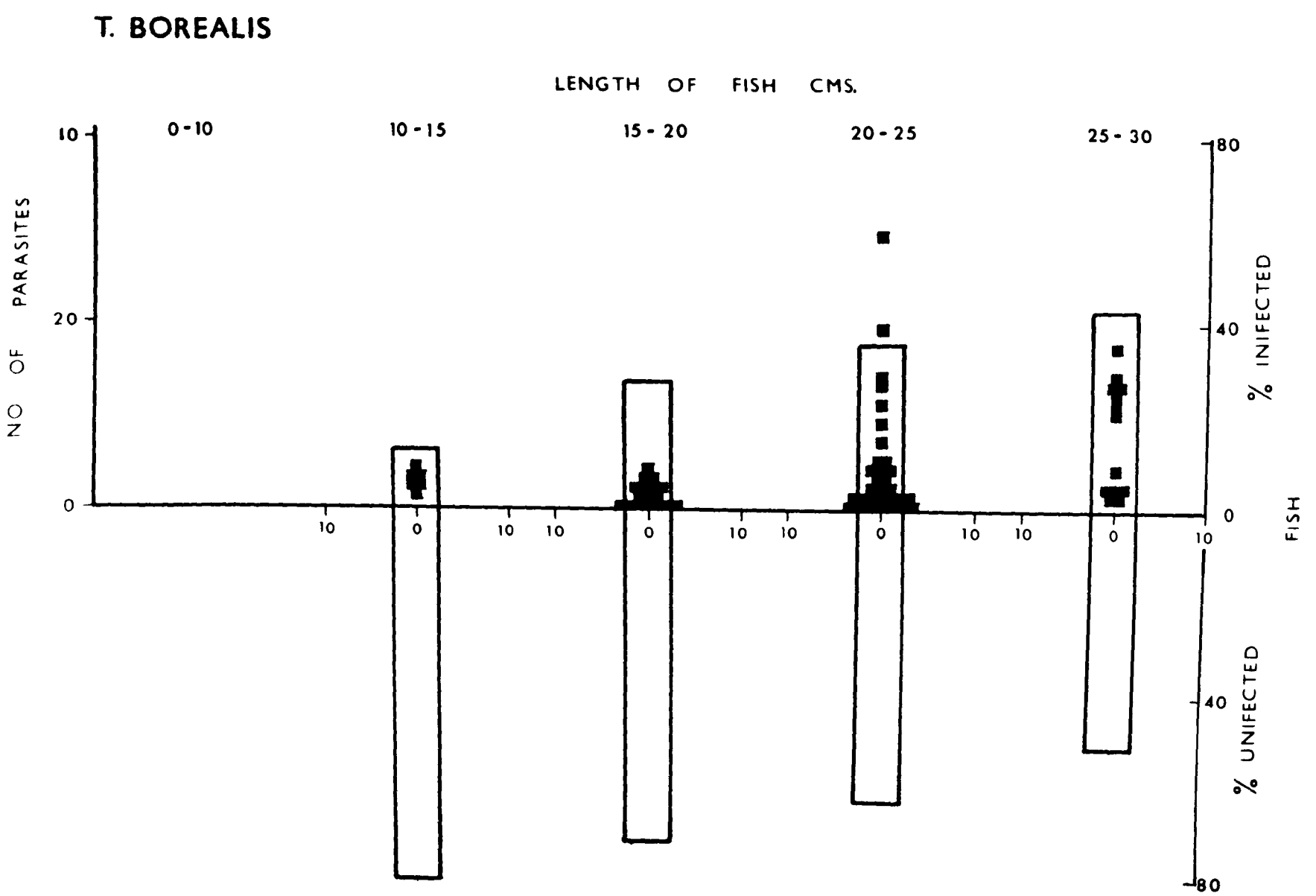

T. BOREALIS
LENGTH OF FISH CMS.
0-10
10-15
15-20
20-25
25-30
NO OF PARASITES
10
20
0
% INIFECTED
% UNIFECTED
80
40
0
FISH
10
0

Fig. 3.6 The intensity of infection of D. prostae and the percentage of S. cephalus infected in relation to the length of the host.

D. PROSTAE

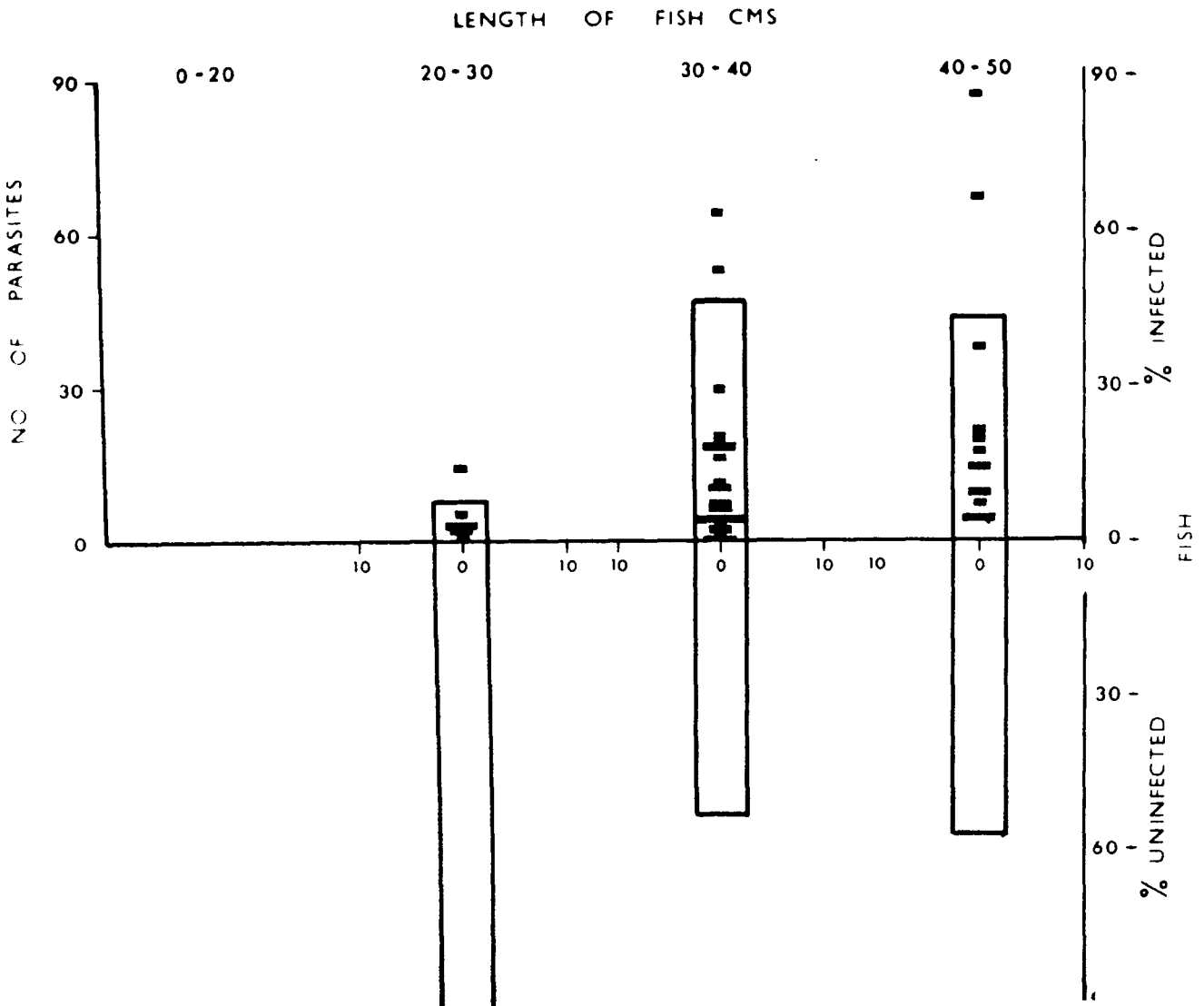

LENGTH OF FISH CMS
0 - 20
20 - 30
30 - 40
40 - 50
NO OF PARASITES
90
60
30
0
% INFECTED
% UNINFECTED
FISH
10
0

Fig. 3.7 The intensity of infection of D. cordus and the percentage of L. leuciscus infected in relation to the length of the host.

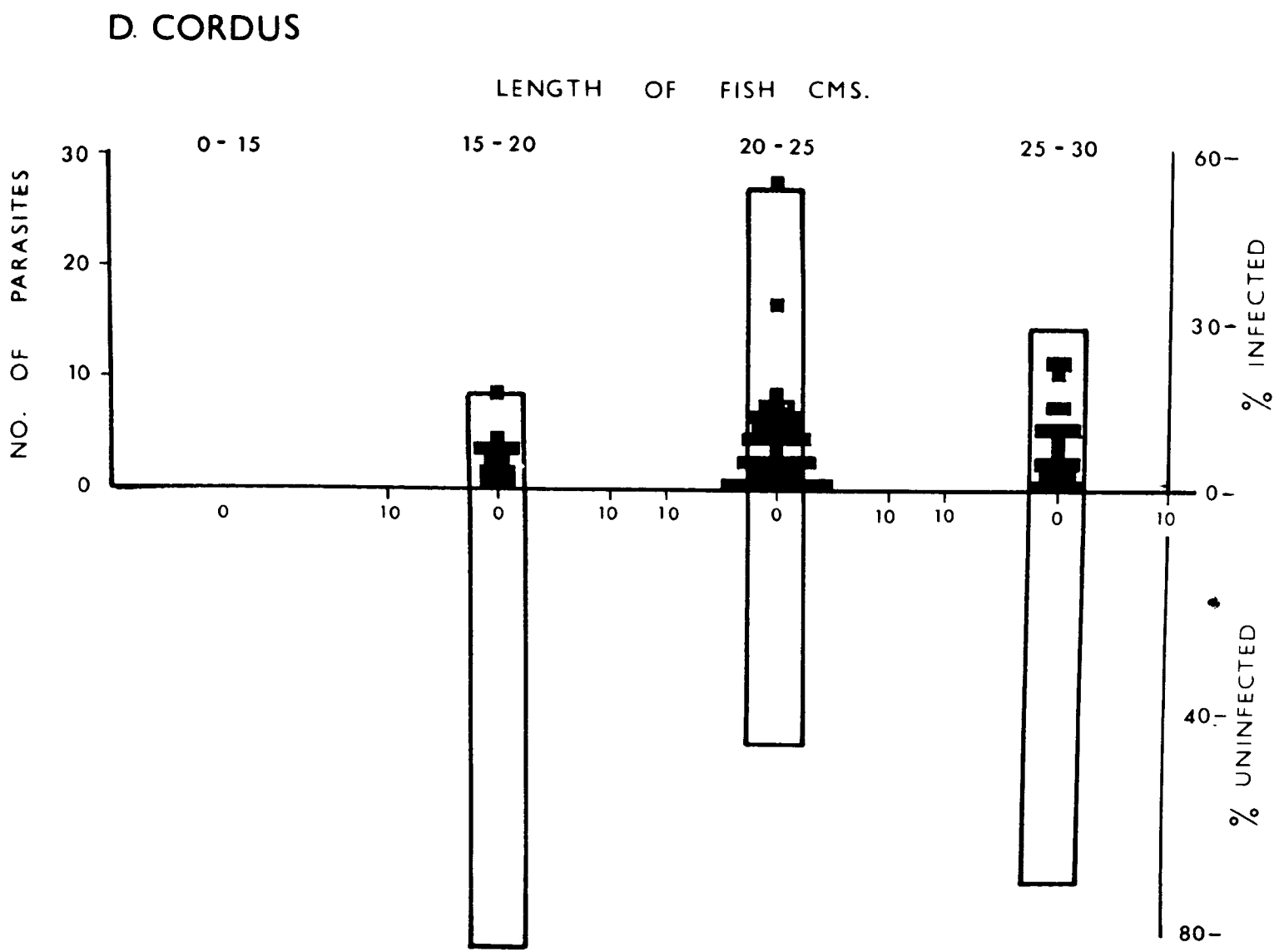

D. CORDUS
LENGTH OF FISH CMS.
0 - 15
15 - 20
20 - 25
25 - 30
NO. OF PARASITES
30
20
10
0
0
10
0
10
10
0
10
10
0
10
60
30
0
% INFECTED
40
80
% UNINFECTED

Fig. 3.3 The intensity of infection of D. paradoxum and the percentage of L. leuciscus infected in relation to the length of the host.

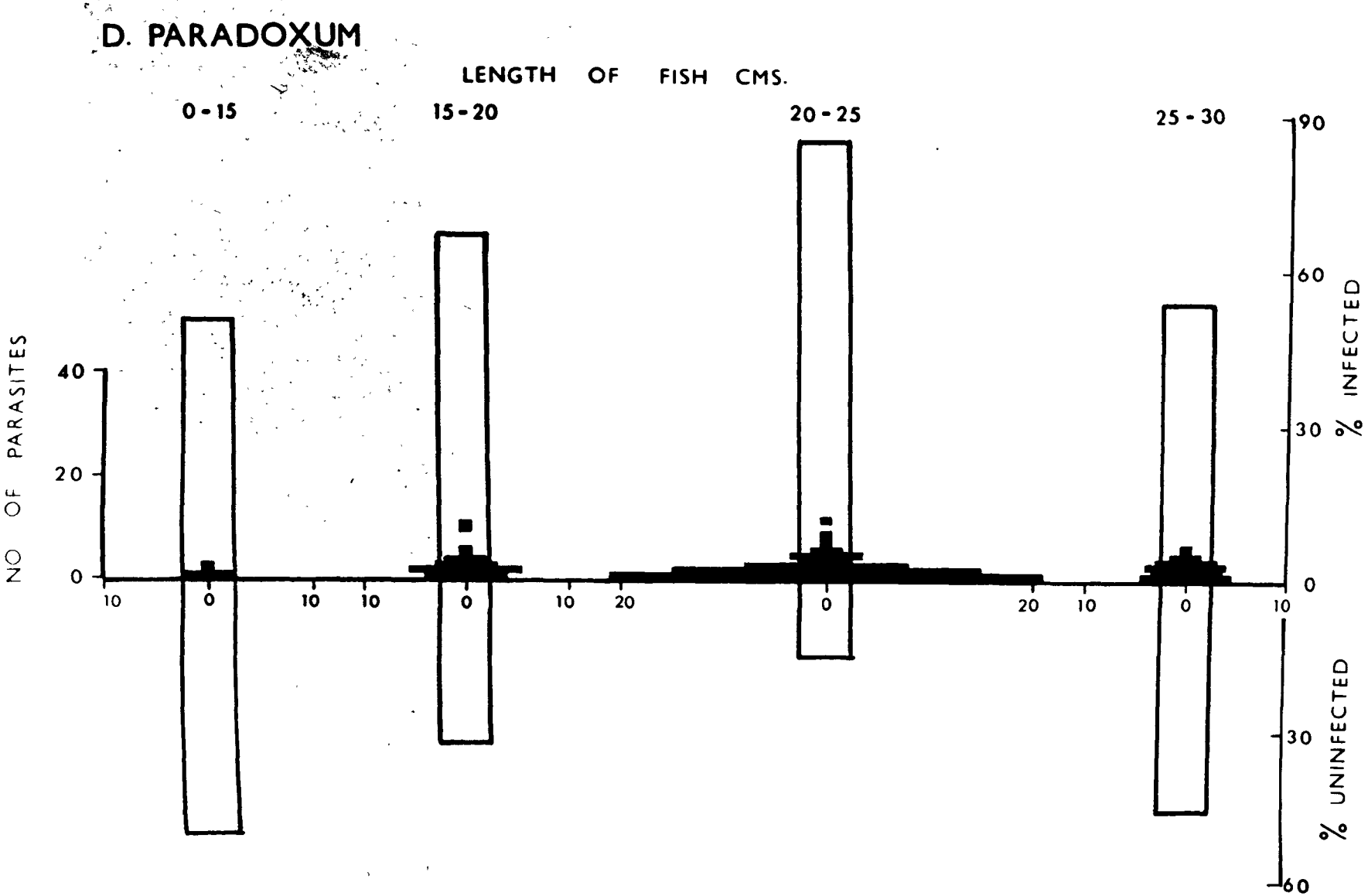

D. PARADOXUM
LENGTH OF FISH CMS.
0 - 15
15 - 20
20 - 25
25 - 30
NO OF PARASITES
40
20
0
% INFECTED
90
60
30
0
% UNINFECTED
30
60
10
0
10
10
0
10
20
0
20
10
0
10

TABLE 3.18:

Intensity of infection of D.crucifer, recorded as the mean number of parasites of the total number of fish and of only infected fish, for each length group from each sample.

	Length in cms.																			
	15-20				20-25				25-30				30-35				All fish			
	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Jan.	0	(20)	0	0	0	3	0	0	0	7	0	0	0	3	0	0	0	33	0	0
Feb.	1.4	9	4.3	3	5.5	8	7.3	6	15.4	7	21.6	5	57.3	3	57.3	3	12.5	27	19.8	17
Mar.	5.1	11	9.3	7	20.8	6	20.8	6	18.6	10	18.6	10	13.3	3	13.3	3	13.9	30	16.0	26
Apr.	2.0	4	2.0	4	16.0	3	16.0	3	28.5	5	28.5	5	25.5	4	25.5	4	18.9	16	18.9	16
May	1.0	8	8.0	1	0	1	0	0	0	0	0	0	0	0	0	0	0.9	9	8.0	1
June	4.1	10	5.2	8	15.0	5	18.7	4	21.6	9	27.6	7	4.5	6	6.7	4	11.2	30	14.6	23
July	22.5	11	22.5	11	18.7	6	20.6	5	17.0	4	17.0	4	2.0	1	2.0	1	19.1	22	20.0	21
Aug.	2.2	6	13.0	1	1.4	8	3.6	3	11.2	12	11.2	12	36.7	4	36.7	4	6.8	30	10.2	20
Sept.	0	8	0	0	0	6	0	0	0	11	0	0	0	4	0	0	0	30	0	0
Oct.	0	15	0	0	0	5	0	0	0	9	0	0	0	1	0	0	0	30	0	0
Nov.	0	7	0	0	0	12	0	0	0	10	0	0	0	1	0	0	0	30	0	0
Dec.	0	8	0	0	0	8	0	0	0	13	0	0	0	1	0	0	0	30	0	0
Total	3.4	117	11.3	35	5.7	71	15.0	27	8.6	97	19.4	43	15.8	31	25.8	19	6.4	317	16.3	124
Total no.of parasites	395				406				834				390				2025			

Key: a - Intensity of infection expressed as the mean number of parasites per fish.

b - Number of fish in each length group.

c - Intensity of infection expressed as the mean number of parasites per infected fish.

d - Number of infected fish in each length group.

TABLE 3.19:

Intensity of infection of D.vistulae, recorded as the mean number of parasites of the total number of fish and of only infected fish, for each length group from each sample.

	Length in cms.																All fish			
	0 - 20				20-30				30-40				40-50							
Month	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Jan.	0	1	0	0	0	19	0	0	0	5	0	0	0	7	0	0	0	32	1.0	1
Feb.	0	0	0	0	0.7	16	1.7	3	6.9	6	6.0	5	9.4	5	9.4	5	2.7	31	4.9	13
Mar.	0	0	0	0	2.2	15	3.3	11	3.6	12	5.4	8	9.5	2	9.5	2	3.3	29	4.5	21
Apr.	0	0	0	0	3.8	16	4.2	15	6.3	11	7.7	9	4.0	3	6.0	2	4.6	30	5.3	26
May	1.0	1	1.0	1	1.3	19	2.5	10	2.2	4	4.5	2	13.3	7	13.3	7	4.1	31	6.4	20
June	0	1	0	0	1.0	15	2.0	3	1.9	7	2.6	5	3.0	7	4.2	5	1.3	30	3.3	12
July	0	0	0	0	0.4	16	3.2	5	3.3	7	3.7	6	4.7	7	8.2	4	2.4	30	4.7	15
Aug.	0	0	0	0	0.3	15	1.3	3	0.8	11	4.0	2	1.0	4	4.0	1	0.5	30	2.6	6
Sept.	0	0	0	0	0	12	0	0	0	10	0	0	0	6	0	0	0	28	0	0
Oct.	0	0	0	0	0	15	0	0	0	7	0	0	0	5	0	0	0	27	0	0
Nov.	0	1	0	0	0	18	0	0	0	6	0	0	0	5	0	0	0	30	0	0
Dec.	0	0	0	0	0	15	0	0	0	9	0	0	0	7	0	0	0	31	0	0
Total	0.2	4	1.0	1	0.7	191	2.9	50	2.1	95	5.2	37	3.5	65	8.8	26	1.6	359	5.1	113
Total no.of parasites	1				148				194				229				572			

Key: a - Intensity of infection expressed as the mean number of parasites per fish.

b - Number of fish in each length group.

c - Intensity of infection expressed as the mean number of parasites per infected fish.

d - Number of infected fish in each length group.

TABLE 3.20:

Intensity of infection of D.prostae, recorded as the mean number of parasites of the total number of fish and of only infected fish, for each length group from each sample.

	Length in cms.																			
	0-20				20-30				30-40				40-50				All fish			
Month	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Jan.	0	1	0	0	0	19	0	0	0	5	0	0	0	7	0	0	0	32	0	0
Feb.	0	0	0	0	0	16	0	0	5.4	6		5	5.0	5	12.5	2	2.0	31	9.0	7
Mar.	0	0	0	0	0.46	15	3.5	2	7.7	12	23.0	4	43.5	2	43.5	2	6.4	29	24.3	8
Apr.	0	0	0	0	0.75	16	4.0	3	11.5	11	18.1	7	3.3	3	10.0	1	4.9	30	13.5	11
May	0	1	0	0	0	19	0	0	1.2	4		1	23.0	7	26.6	6	5.3	31	23.7	7
June	0	1	0	0	0.2	15	3.0	1	0.9	7	3.0	2	1.4	7	5.0	2	0.6	30	3.8	5
July	0	0	0	0	1.2	16	6.3	3	1.3	7	4.5	2	5.4	7	38.0	1	2.2	30	11.0	6
Aug.	0	0	0	0	0	15	0	0	8.1	11	12.7	7	3.7	4	15.0	1	3.5	30	13.0	8
Sept.	0	0	0	0	0	12	0	0	0	10	0	0	0	6	0	0	0	28	0	0
Oct.	0	0	0	0	0	15	0	0	0	7	0	0	0	5	0	0	0	27	0	0
Nov.	0	1	0	0	0	18	0	0	0	6	0	0	0	5	0	0	0	30	0	0
Dec.	0	0	0	0	0	15	0	0	0	9	0	0	0	7	0	0	0	31	0	0
Total	0	4	0	0	0.2	191	4.5	9	3.8	95	13.1	28	5.3	65	23.1	15	2.1	359	14.5	52
Total no.of parasites	0				41				366				346				753			

Key: a - Intensity of infection expressed as the mean number of parasites per fish.

b - Number of fish in each length group.

c - Intensity of infection expressed as the mean number of parasites per infected fish.

d - Number of infected fish in each length group.

TABLE 3.21:

Intensity of infection of D.cordus, recorded as the mean number of parasites of the total number of fish and of only infected fish, for each length group from each sample.

	Length in cms.																			
	0-15				15-20				20-25				25-30				All fish			
Month	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Jan.	0	0	0	0	0	3	0	0	0	21	0	0	0	9	1.0	1	0.33	33	1.0	1
Feb.	0	0	0	0	0	0	0	0	0.6	24	3.5	4	1.1	7	2.6	3	0.7	31	3.3	7
Mar.	0	0	0	0	0.4	9	2.0	2	2.5	10	5.0	5	2.7	11	3.3	9	1.9	30	3.7	16
Apr.	0	5	0	0	2.7	10	3.9	7	2.8	15	3.9	11	4.6	5	5.7	4	2.7	35	4.2	22
May	0	0	0	0	0	1	0	0	0	1	0	0	0	2	0	0	0	4	0	0
June	0	0	0	0	1.4	5	3.5	2	2.3	24	6.9	8	12.0	1	12.0	1	2.5	30	6.7	11
July	0	1	0	0	2.0	3	3.0	2	3.3	21	5.4	13	6.2	5	7.7	4	3.6	30	5.6	19
Aug.	0	0	0	0	0.3	3	1.0	1	0.08	24	1.0	2	0.6	3	2.0	1	0.1	30	1.2	4
Sept.	0	1	0	0	0	3	0	0	0.04	23	1.0	1	0	3	0	0	0.03	30	1.0	1
Oct.	0	2	0	0	0	3	0	0	0	21	0	0	0	5	0	0	0	31	0	0
Nov.	0	3	0	0	0	2	0	0	0	17	0	0	0	6	0	0	0	28	0	0
Dec.	0	3	0	0	0	7	0	0	0	13	0	0	0	7	0	0	0	30	o	0
Total	0	15	0	0	0.9	49	3.2	14	0.92	214	4.7	44	1.6	64	4.6	23	1.1	342	4.5	81
Total no.of parasites						45				210				107				362		

Key: a - Intensity of infection expressed as the mean number of parasites per fish.

b - Number of fish in each length group.

c - Intensity of infection expressed as the mean number of parasites per infected fish.

d - Number of infected fish in each length group.

TABLE 3.22:

Intensity of infection of *T.borealis*, recorded as the mean number of parasites of the total number of fish and of only infected fish, for each length group from each sample.

	Length in cms.																			
	10-15				15-20				20-25				25-30				All fish			
Month	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Jan.								NO	SAMPLE											
Feb.	0	3	0	0	0	2	0	0	0	6	0	0	0	0	0	0	0	11	0	0
Mar.	0	3	0	0	0	3	0	0	22	12	4.3	6	0	0	0	0	1.4	18	4.3	6
Apr.	2.0	3	3.0	2	1.3	3	2.0	2	5.5	18	6.3	16	0	1	0	0	4.04	25	5.2	20
May	-		-		3.0	1	3.0	1	0.8	5	2.0	2	2.0	2	2.0	2	1.4	8	2.5	5
June	3.0	1	3.0	1	1.1	7	2.0	4	0.3	7	1.0	2	0	2	0	0	0.9	17	1.9	7
July	0	0	0	0	3.7	10	4.6	8	4.2	8	5.6	6	9.0	12	10.8	10	5.9	30	7.5	24
Aug.	0	0	0	0	0	0	0	0	0	2	0	0	0.6	3	2.0	1	0.4	5	2.0	1
Sept.								NO	SAMPLE											
Oct.	0	4	0	0	0.18	16	3.0	1	0	4	0	0	0	1	0	0	0.1	25	3.0	1
Nov.	0	7	0	0	0	5	0	0	0	16	0	0	0	2	0	0	0	30	0	0
Dec.	0.3	9	3.0	1	0.2	5	1.0	1	0	2	0	0	0	7	0	0	0.1	30	2.0	2
Total	0.4	30	3.0	4	1.1	52	3.3	17	1.9	87	5.2	32	3.8	30	8.7	13	1.8	199	5.4	66
Total no.of parasites		12				56				166				114				348		

Key :- a - Intensity of infection expressed as the mean number of parasites per fish.

b - Number of fish in each length group.

c - Intensity of infection expressed as the mean number of parasites per infected fish.

d - Number of infected fish in each length group.

TABLE 3.23:

Intensity of infection of D.paradoxum recorded as the mean number of parasites of the total number of fish and of only infected fish, for each length group from each sample.

	Length in cms.																			
	0-15				15-20				20-25				25-30				All fish			
Month	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Jan.	0	0	0	0	0	3	0	0	0.6	21	1.85	7	0.6	9	2.0	3	0.6	33	1.9	10
Feb.	0	0	0	0	0	0	0	0	1.2	24	2.6	11	1.6	7	3.6	3	1.3	31	2.9	14
Mar.	0	0	0	0	2.7	9	4.2	6	1.3	10	1.85	7	2.2	11	3.4	7	2.1	30	3.3	20
Apr.	0	5	0	0	2.2	10	2.4	9	1.1	15	2.0	8	1.6	5	2.6	3	1.3	35	2.3	20
May	0	0	0	0	2.0	1	2.0	1	3.0	1	3.0	1	2.5	2	5.0	1	2.5	4	3.3	3
June	0	0	0	0	1.8	5	3.0	3	0.8	24	1.9	11	3.0	1	0	0	1.1	30	2.4	14
July	0	1	0	0	1.3	3	2.0	2	0.9	21	1.7	11	1.2	5	1.5	4	0.9	30	2.1	17
Aug.	0	0	0	0	1.6	3	2.5	2	2.4	24	4.4	13	2.0	3	2.0	3	2.3	30	3.9	18
Sept.	0	1	0	0	0.6	3	2.0	1	1.2	23	2.5	11	0	3	0	0	1.0	30	2.5	12
Oct.	1.0	2	1.0	2	4.3	3	4.3	3	0.8	21	1.8	10	2.0	5	2.5	4	1.4	31	2.3	19
Nov.	2.0	3	2.0	3	1.5	2	3.0	1	1.5	17	2.1	12	1.3	6	2.6	3	1.5	28	2.3	19
Dec.	0.6	3	1.0	2	1.6	7	2.2	5	1.2	13	2.5	6	1.8	7	3.3	4	1.4	30	2.4	17
Total	0.6	15	1.4	7	1.9	49	2.9	33	1.2	214	2.4	108	1.5	64	2.8	35	1.4	342	2.5	183
Total no.of parasites	10				96				258				100				464			

Key: a - Intensity of infection expressed as the mean number of parasites per fish.

b - Number of fish in each length group.

c - Intensity of infection expressed as the mean number of parasites per infected fish.

d - Number of infected fish in each length group.

Relationship of sex of the host to intensity of infection.

The number and percentage of male and female fish, and the mean number of parasites on each sex in each monthly sample for each length group were recorded for D.crucifer, D.vistulae, D.prostae, D.cordus, T.borealis and D.paradoxum (Tables 3.24 - 3.29 and 3.31 - 3.36).

Results.

D.crucifer, D.vistulae, D.prostae.

(a) Seasonal variation in intensity of infection.

Male and female R.rutilus showed peak intensities of infection with D.crucifer in February and March, and in July (Table 3.24). A peak intensity of infection of D.vistulae was recorded from female S.cephalus in May and July, and from male S.cephalus in April and July (Table 3.25). Peak infections of D.prostae were recorded from female S.cephalus in March and again in July and August, and from male S.cephalus in April and August (Table 3.26).

(b) Relationship of length and sex of the fish to intensity of infection.

Insufficient numbers of fish were sampled each month to allow any extensive comparisons between the number of male and female fish in each length group from each monthly sample, therefore the results were summarised (Tables 3.27, 3.28, 3.29).

The numbers of male and female S.cephalus in each length group were approximately equal except for the 40 - 50 cm. group where most of the fish were female (Tables 3.28, 3.29). More male than female fish

were present in the smallest length group of R.rutilus, whereas the largest length group resembled S.cephalus in having mainly female fish (Table.3.27). An increase in the intensity of infection with increase in length has already been noted for D.crucifer, D.vistulae and D.prostae (Tables 3.18, 3.19, 3.20). As most of the fish in the larger length groups were female, the increase in intensity may not be the result of increase in length, but that female fish may be more susceptible to infection.

No marked difference in the intensity of infection of D.vistulae and D.prostae in male and female S.cephalus was recorded until the 40-50 cm. group, when the mean number of parasites in female fish was much greater than in male fish (Tables 3.28, 3.29). A greater variation in the mean number of D.crucifer was recorded between male and female R.rutilus from each length group, compared with D.vistulae and D.prostae from S.cephalus. Only two male compared to 29 female R.rutilus were present in the greatest length group. The discrepancy between the number of males and females in this group made it difficult to interpret the significance of the different intensities of D.crucifer from the sexes. (Table 3.27).

An overall higher mean number of D.crucifer and D.prostae and to a lesser extent D.vistulae occurred on female R.rutilus and S.cephalus. (Table 3.30).

It was not possible to determine whether these data in Tables 3.27, 3.28, 3.29 showed any significant relationship between the sex

of the host and intensity of infection, and therefore the data was analysed statistically.

(c) Statistical analysis of the data.

The number of parasites in male and female fish was originally plotted against length of fish, and this gave a curvi-linear relationship. To obtain a linear relationship necessary for the analysis, the data was transformed and $\sqrt{x + 1}$ parasites (p) was plotted against weight (w), weight being some indication of increase in size or surface area, factors which are important when studying the intensity of infection of Monogenea.

Regression coefficients (bp.w) were calculated (see appendix. Tables 3.37, 3.38, 3.39) and regressions plotted (Figures 3.9, 3.10, 3.11) for female and male fish infected with D.vistulae, D.prostae and D.crucifer. Each regression was tested to see if it was significantly different from zero and the regressions for female and male fish with each species of parasite were tested to see if they were significantly different from each other.

i) D.vistulae: (Figure 3.9)

The regression bp.w for male and female S.cephalus were both significantly different from zero i.e. the number of parasites increased with increased weight of the fish.

bp.w = Female t_{66} = 5.25 bp.w = Male t_{45} = 3.78

t_{66} at 5% = 3.46 t_{45} at 5% = 3.5

The regression coefficients for female and male were very similar (see appendix) and there was obviously no difference between the two regressions i.e. there was no overall difference in the intensity of infection of female and male S.cephalus with D.vistulae. This information applied to the total number of infected fish, but did not take into account any differences which might occur in intensity of infection from month to month, unless there was no difference in the ratio of female and male fish and the weights of the fish in the different monthly samples. An analysis of variance was performed between the weights of female and male fish in the months where infection occurred. No significant difference was found between either the weight of female or male fish in different months.

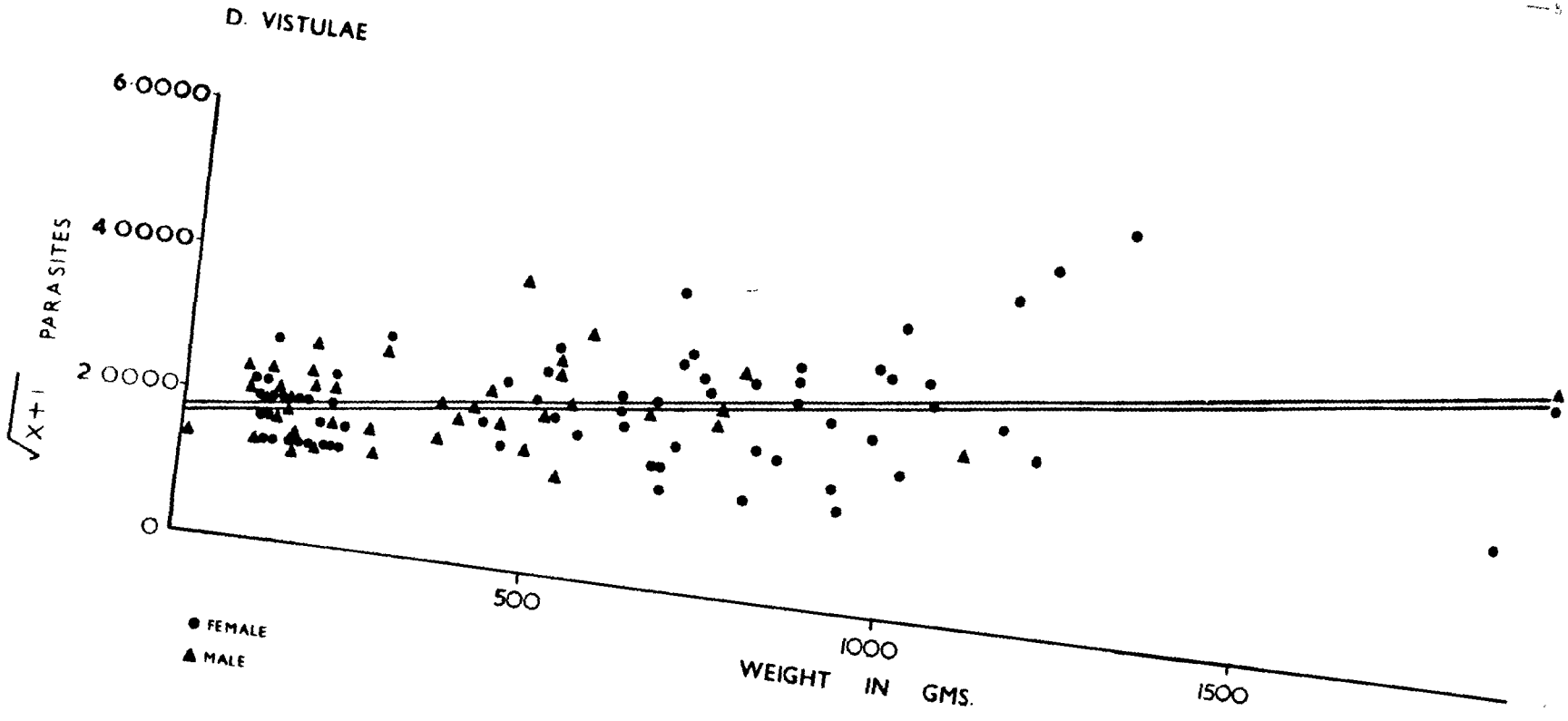
Female $F^{6}_{61} = 1.16$ Male $F^{6}_{41} = 1.04$

F^{6}_{61} at 5% = 2.17 F^{6}_{41} at 5% = 2.34

Homogeneity of female: male fish present in each sample where infection occurred was tested using a chi-squared test. There was no significant difference in the number of females and males in each sample ($p = 0.05$).

The results obtained when the total number of fish were taken into account were also applicable to each monthly sample where infected fish were present.

Fig. 3.9 The relationship between the number of *D. vistulae* and the weight of male and female *S. cephalus*.


D. VISTULAE
6·0000
4·0000
2·0000
0
√X+1 PARASITES
500
1000
1500
WEIGHT IN GMS.
● FEMALE
▲ MALE

ii) D.prostae: (Figure 3.10)

The regression bp.w for female fish was significantly different from zero t_{31} = 3.646; t_{31} at 5% = 2.04, but the regression bp.w for male fish was not significantly different from zero t_{17} = 1.333; t_{17} at 5% = 2.110 i.e. there was an increase in intensity of infection of D.prostae with increase in weight for female but not for male S.cephalus. There was no significant difference between the regression bp.w for female and male fish (p = 0.05) i.e. there was no difference in the intensity of infection of female and male S.cephalus with D.prostae. These results could not be applied to the information from each monthly sample, as although the ratio of females to males were similar in each sample (p = 0.05), there was a significant difference in the weight of female fish, but not in the weight of male fish in infected months.

Female F_{33}^{6} = 3.05 Male F_{19}^{5} = 2.06

F_{33}^{6} at 5% = 2.42 F_{19}^{5} at 5% = 2.74

The difference in weight of female fish in different months may be accounted for by the difference in gonad weight at different times of the year. It was thought that an increase in intensity of infection with increase in weight would occur in male fish if more data were available.

iii) D.crucifer : (Figure 3.11)

The regression bp.w for female R.rutilus was not significantly different from zero.

Female. bp.w = t_{69} = 1.764.

t_{69} at 5 = 1.994.

The regression bp.w for male fish was significantly different from zero

$$\text{Male. bp.w } t_{49} = 2.521.$$

$$t_{49} \text{ at } 5\% = 2.008$$

i.e. an increase of intensity of infection with increase in weight occurred in male but not in female R.rutilus. The regressions bp.w for female and male fish differed significantly from each other ($p = 0.05$) (Figure 3.11) and showed a relationship between intensity of infection and weight in female and male R.rutilus. This information could only be applied to the total sample of fish, as even though there was no difference in the ratio of female and male fish in each sample where the infection occurred ($p = 0.05$) and no significant difference in the weights of the female fish between months ($F_{71}^{6} = 0.176$; F_{71}^{6} at 5% = 2.25), there was a significant difference in the weights of the male fish between months ($F_{51}^{5} = 3.695$; F_{51}^{5} at 5% = 2.45).

T.borealis.

(a) Seasonal variation in intensity of infection.

The intensity of infection of T.borealis on female and male T.thymallus was similar to the pattern shown when the mean number of parasites of all T.thymallus in each sample were considered, and peaks of infection were recorded in April and July (Table 3.31).

(b) Relationship of length and sex of the fish to intensity of infection.

A slightly higher mean number of parasites in male T.thymallus

Fig.3.10 The relationship between the number of *D. prosthe* and the weight of male and female *S. cephalus*.

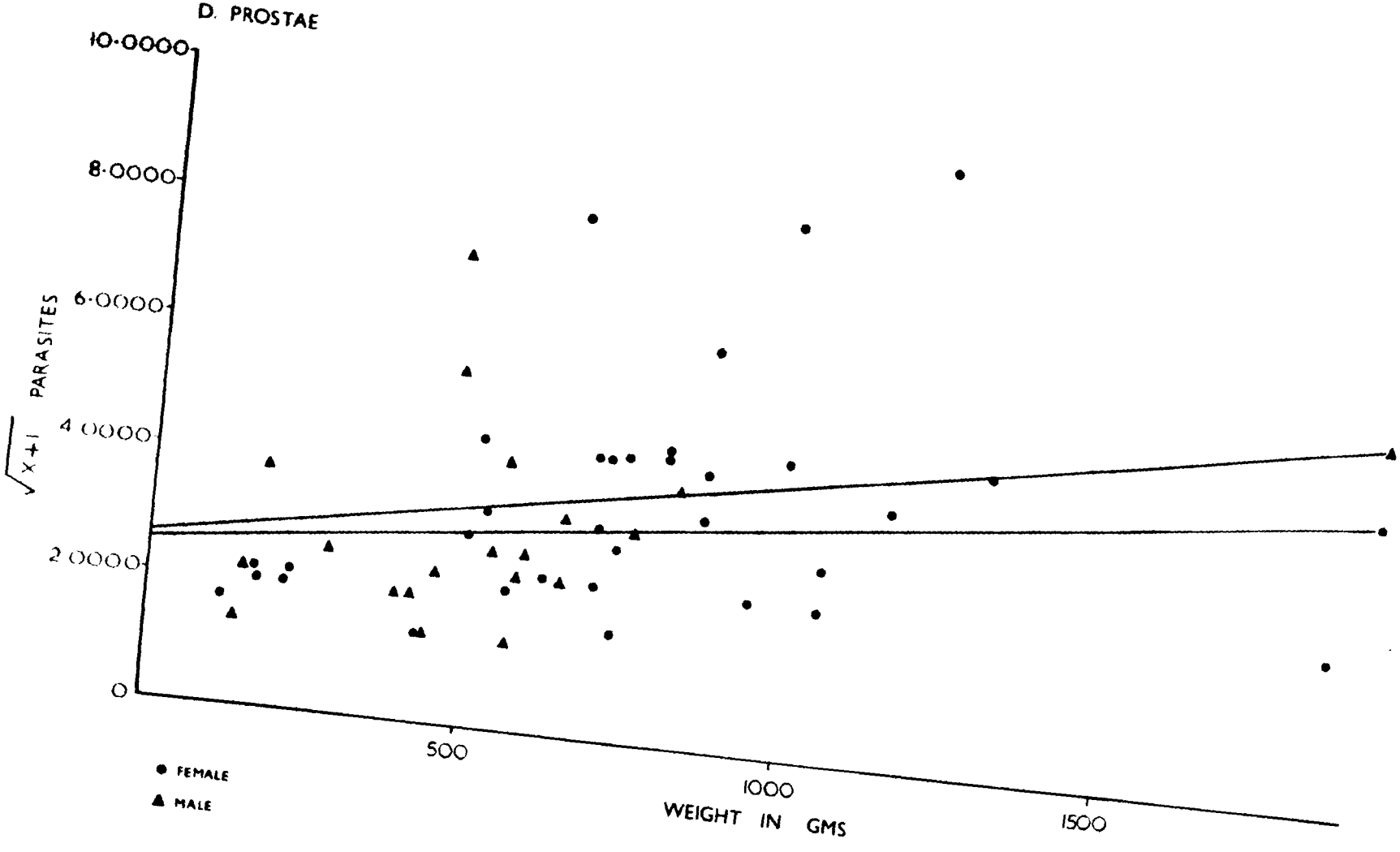

D. PROSTAE
10·0000
8·0000
6·0000
4·0000
2·0000
0
√X+1 PARASITES
500
1000
1500
WEIGHT IN GMS
FEMALE
MALE

TABLE 3.24:

The number of male and female *R.rutilus* (total and infected) and the intensity of infection of each sex with *D.crucifer*.

Month	Total No. parasites	No.parasites in female	No.female fish Total	Infected	Mean no.of parasites in female fish a	b	No.parasites in male	No.male fish Total	Infected	Mean no.of parasites in male fish a	b
Jan.	0	0	12	0	0	0	0	21	0	0	0
Feb.	337	241	12	9	20.1	26.8	96	15	8	6.4	12.0
Mar.	416	246	16	16	15.4	15.4	170	14	10	12.1	17.0
Apr.	302	180	10	10	18.0	18.0	122	6	6	20.3	20.3
* May	8	8	3	1	2.6	8.0	0	6	0	0	0
* June	336	217	14	10	15.5	21.7	119	16	13	7.4	9.1
July	420	217	12	11	18.0	19.7	20[illegible]	10	10	20.3	20.3
Aug.	206	182	22	16	8.3	11.4	24	8	4	3.0	6.0
Sept.	0	0	15	0	0	0	0	15	0	0	0
Oct.	0	0	12	0	0	0	0	18	0	0	0
Nov.	0	0	11	0	0	0	0	19	0	0	0
Dec.	0	0	15	0	0	0	0	15	0	0	0
Total	2025	1291	154	73	8.4	17.7	734	163	51	4.5	14.4

Key: * Spawning period.

a - Intensity of infection expressed as the mean number of parasites per fish.

b - Intensity of infection expressed as the mean number of parasites per infected fish.

TABLE 3.25:

The number of male and female S.cephalus (total and infected) and the intensity of infection of each sex with D.vistulae.

	Month	Total No. parasites	No.parasites in female	No.female fish Total	Infected	Mean no.of parasites in female fish a	b	No.parasites in male	No.male fish Total	Infected	Mean no.of parasites in male fish a	b
	Jan.	0	0	19	0	0	0	0	13	0	0	0
	Feb.	84	64	14	9	4.6	7.1	20	13	7	1.5	2.8
	Mar.	95	64	18	13	3.5	4.9	31	11	8	2.8	3.9
	Apr.	138	65	14	11	4.6	5.9	73	16	15	4.6	4.9
x	May	128	120	20	16	6.0	7.5	8	11	4	0.7	2.0
x	June	40	30	19	9	1.6	3.3	10	11	3	0.9	3.3
	July	71	41	21	9	1.9	4.5	30	9	6	3.3	5.0
	Aug.	16	8	14	2	0.6	4.0	8	16	4	0.5	2.0
	Sept.	0	0	16	0	0	0	0	12	0	0	0
	Oct.	0	0	17	0	0	0	0	10	0	0	0
	Nov.	0	0	20		0	0	0	10	0	0	0
	Dec.	0	0	16	0	0	0	0	15	0	0	0
	Total	572	392	208	69	1.8	5.7	184	147	47	1.2	3.9

Key: x Spawning period.

a - Intensity of infection expressed as the mean number of parasites per fish.

b - Intensity of infection expressed as the mean number of parasites per infected fish.

TABLE 3.26:

The number of male and female S.cephalus (total and infected) and the intensity of infection of each sex with D.prostae.

	Month	Total no. parasites	No.parasites in female	No.female fish Total	Infected	Mean no.of parasites in female fish a	b	No.parasites in male	No.male fish Total	Infected	Mean no.of parasites in male fish a	b
	Jan.	0	0	19	0	0	0	0	13	0	0	0
	Feb.	63	56	14	4	4.0	14.0	7	13	3	0.5	2.3
	Mar.	186	181	18	7	10.1	25.8	5	11	1	0.4	5.0
	Apr.	149	39	14	5	2.8	7.8	110	16	6	6.9	18.3
*	May	166	166	20	7	8.3	23.7	0	11	0	0	0
*	June	19	14	19	4	0.7	3.5	5	11	1	0.4	5.0
	July	66	50	21	3	2.4	16.6	16	9	3	1.8	5.3
	Aug.	104	49	14	3	3.5	16.3	55	16	5	3.4	11.0
	Sept.	0	0	16	0	0	0	0	12	0	0	0
	Oct.	0	0	17	0	0	0	0	10	0	0	0
	Nov.	0	0	20	0	0	0	0	10	0	0	0
	Dec.	0	0	16	0	0	0	0	12	0	0	0
	Total	753	555	208	33	2.7	16.8	198	147	19	1.4	10.4

Key: * Spawning period.

a - Intensity of infection expressed as the mean number of parasites per fish.

b - Intensity of infection expressed as the mean number of parasites per infected fish.

TABLE 3.27:

The number and percentage of male and female *R.rutilus* infected with *D.crucifer* and the mean number of parasites on the total and infected fish from each length group.

Length group in cms.	Sex	No.of fish	No. infected fish	% fish infected	Total no. parasites	Mean no. parasites Total	Mean no. parasites Infected
15 - 20	Female	25	11	44.0	168	6.7	15.3
	Male	92	24	26.1	227	2.5	9.9
	Total	117	35	33.4	395	3.4	12.7
20 - 25	Female	42	11	26.2	160	3.8	14.5
	Male	29	16	55.2	246	8.5	15.4
	Total	71	27	38.0	406	5.7	15.0
25 - 30	Female	57	32	56.1	573	10.05	17.9
	Male	40	11	27.5	261	6.5	23.7
	Total	97	43	44.3	834	8.6	19.4
30 - 35	Female	29	19	65.5	490	16.9	25.8
	Male	2	0	0	0	0	0
	Total	31	19	48.7	390	15.8	25.8

TABLE 3.28:

The number and percentage of male and female S.cephalus infected with D.vistulae, and the mean number of parasites on the total and infected fish from each length group.

Length group in cms.	Sex	No.of fish	No.infected fish	% fish infected	Total no. parasites	Mean no.parasites Total	Mean no.parasites Infected
0 - 20	Female	1	0	0	0	0	0
	Male	3	1	33.3	1	0.3	1.0
	Total	4	1	25.0	1	0.2	1.0
20 - 30	Female	99	24	2'.2	68	0.7	2.7
	Male	92	26	26.0	80	0.86	2.9
	Total	191	50	26.2	148	0.77	2.9
30 - 40	Female	51	21	41.2	106	2.1	5.1
	Male	44	16	36.4	88	2.0	5.5
	Total	95	37	38.9	194	2.04	5.2
40 - 50	Female	57	23	39.6	218	3.7	9.5
	Male	8	3	42.8	11	1.6	3.6
	Total	65	26	40.0	229	3.5	8.8

TABLE 3.29:

The number and percentage of male and female S.cephalus infected with D.prostae, and the mean number of parasites on the total and infected fish from each length group.

Length group in cms.	Sex	No.of fish	No.infected fish	% fish infected	Total no. parasites	Mean no. parasites Total	Mean no. parasites Infected
0 - 20	Female	1	0	0	0	0	0
	Male	3	0	0	0	0	0
	Total	4	0	0	0	0	0
20 - 30	Female	99	5	5.05	16	0.16	3.3
	Male	92	4	4.3	25	0.3	6.2
	Total	191	9	4	41	0.2	4.5
30 - 40	Female	51	15	29.4	218	4.3	14.5
	Male	44	13	29.5	148	3.4	11.4
	Total	95	28	29.5	366	3.9	13.1
40 - 50	Female	57	13	22.4	321	5.5	24.7
	Male	8	2	28.6	25	3.6	12.5
	Total	65	15	23.1	346	4.9	23.1

TABLE 3.29:

The number and percentage of male and female S.cephalus infected with D.vistulae, and the mean number of parasites on the total and infected fish from each length group.

Length group in cms.	Sex	No.of fish	No.infected fish	% fish infected	Total no. parasites	Mean no.parasites Total	Mean no.parasites Infected
0 - 20	Female	1	0	0	0	0	0
	Male	3	1	33.3	1	0.3	1.0
	Total	4	1	25.0	1	0.2	1.0
20 - 30	Female	99	24	2'.2	68	0.7	2.7
	Male	92	26	26.0	80	0.86	2.9
	Total	191	50	26.2	148	0.77	2.9
30 - 40	Female	51	21	41.2	106	2.1	5.1
	Male	44	16	36.4	88	2.0	5.5
	Total	95	37	38.9	194	2.04	5.2
40 - 50	Female	57	23	39.6	218	3.7	9.5
	Male	8	3	42.8	11	1.6	3.6
	Total	65	26	40.0	229	3.5	8.8

TABLE 3.29:

The number and percentage of male and female S.cephalus infected with D.prostae, and the mean number of parasites on the total and infected fish from each length group.

Length group in cms.	Sex	No.of fish	No.infected fish	% fish infected	Total no. parasites	Mean no. parasites Total	Mean no. parasites Infected
0 - 20	Female	1	0	0	0	0	0
	Male	3	0	0	0	0	0
	Total	4	0	0	0	0	0
20 - 30	Female	99	5	5.05	16	0.16	3.3
	Male	92	4	4.3	25	0.3	6.2
	Total	191	9	4	41	0.2	4.5
30 - 40	Female	51	15	29.4	218	4.3	14.5
	Male	44	13	29.5	148	3.4	11.4
	Total	95	28	29.5	366	3.9	13.1
40 - 50	Female	57	13	22.4	321	5.5	24.7
	Male	8	2	28.6	25	3.6	12.5
	Total	65	15	23.1	346	4.9	23.1

TABLE 3.30:

The overall mean number of Monogenea on male and female hosts.

Parasite	Sex of fish	Total no. of fish	Total no. parasites	Mean no. parasites per total no.of fish	Total no. infected fish	Mean no. parasites per infected fish.	Total no.fish in infected months	Mean no.parasites per total no.fish in infected months
D.crucifer	Female	153	1291	8.4	73	17.7	89	14.5
	Male	163	734	4.5	51	14.4	75	9.8
D.vistulae	Female	208	392	1.8	69	5.7	120	3.3
	Male	147	180	1.2	47	3.9	88	2.04
D.prostae	Female	208	555	2.7	33	16.8	120	4.6
	Male	147	198	1.4	19	10.4	88	2.2
D.cordus	Female	172	138	0.8	37	3.7	122	1.1
	Male	170	224	1.3	44	5.1	131	1.7
T.borealis	Female	94	133	1.1	32	4.2	76	1.8
	Male	105	215	2.04	34	6.3	82	2.6
D.paradoxus	Female	172	286	1.7	103	2.8	172	1.7
	Male	170	178	1.04	80	2.2	170	1.04

(Tables 3.30, 3.31). This was fairly evident in all the length groups except the lower (10 - 15 cms.) and quite marked in the higher (25 - 30 cms.) (Tables 3.32).

(c) Statistical analysis of the data.

The regression bp.w for females was not significantly different from zero, whereas that for male T.thymallus was significantly different. (Figure 3.12) (Appendix, Table 3.40).

Female	Male
bp.w = t_{31} = 1.310	bp.w = t_{32} = 2.995
t_{31} at 5% = 2.042	t_{32} at 5% = 2.042

i.e. an increase in intensity of infection with increase in weight was recorded for male but not for female T.thymallus. The regression bp.w for female and male do not differ significantly from each other ($p = 0.05$) and therefore the difference between the intensity of infection of T.borealis on female and male T.borealis was not significant. As in D.crucifer and D.prostae this only applied to the total number of infected fish, as the weights of female T.thymallus in months where infection occurred differed significantly ($F_{26}^{6} = 3.59$; F_{26}^{6} at 5% = 2.47). This is not the result of increased gonad development, as T.thymallus spawned in December, and in the previous two months when the gonads would have been rapidly increasing in weight no infection with T.borealis was recorded. No significant difference was found between the weight of the male fish in the monthly samples where infection was present.

Fig. 3.12 The relationship between the number of *T. borealis* and the weight of male and female *T. thymallus*.

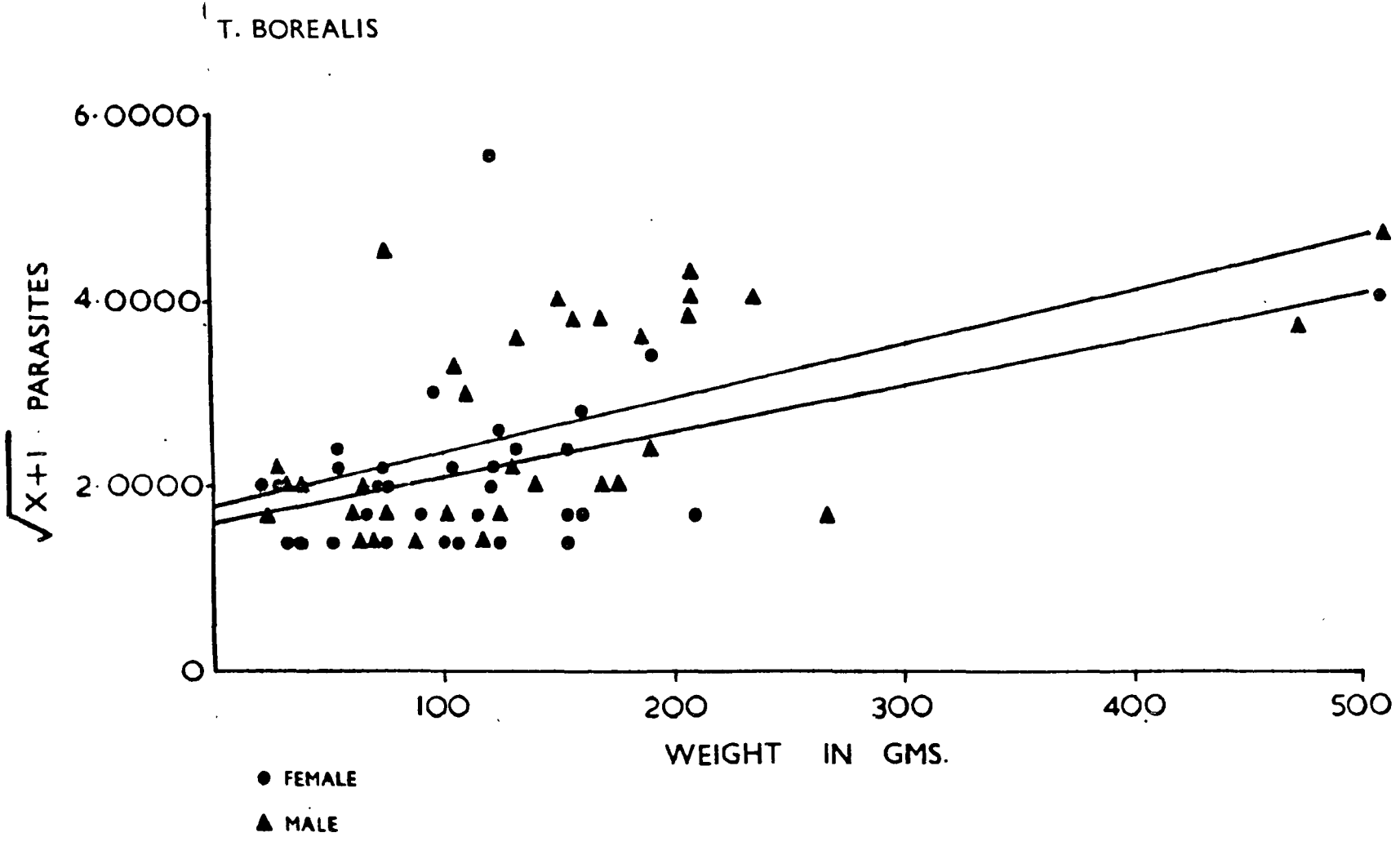

T. BOREALIS
6·0000
4·0000
2·0000
0
√X+1 · PARASITES
100
200
300
400
500
WEIGHT IN GMS.
● FEMALE
▲ MALE

TABLE 3.31:

The number of male and female T.thymallus (total and infected) and the intensity of infection of each sex with T.borealis.

Month	Total No. parasites	No.parasites in female	No.female fish Total	No.female fish Infected	Mean no.of parasites in female fish a	Mean no.of parasites in female fish b	No.parasites in male	No.male fish Total	No.male fish Infected	Mean no.of parasites in male fish a	Mean no.of parasites in male fish b
Jan.		NO SAMPLE									
Feb.	0	0	4	0	0	0	0	7	0	0	0
Mar.	26	11	7	3	1.6	3.6	15	11	3	1.4	5.0
Apr.	110	57	10	8	5.7	7.1	53	15	12	3.5	4.4
May	11	6	5	3	1.2	2.0	5	3	2	1.6	2.5
June	13	11	10	5	1.1	2.2	2	7	2	0.3	1.0
July	179	42	10	10	4.2	4.2	137	20	14	6.8	9.8
Aug.	2	2	3	1	0.6	2.0	0	2	0	0	0
Sept.		NO SAMPLE									
Oct.	3	0	14	0	0	0	3	11	1	0.3	3.0
Nov.	0	0	14	0	0	0	0	16	0	0	0
* Dec.	4	4	17	2	0.2	2.0	0	13	0	0	0
Total	348	133	94	32	1.4	4.2	215	105	34	2.04	6.3

Key: * - Spawning period.

a - Intensity of infection expressed as the mean number of parasites per fish.

b - Intensity of infection expressed as the mean number of parasites per infected fish.

TABLE 3.32:

The number and percentage of male and female T.thymallus infected with T.borealis, and the mean number of parasites on the total and infected fish from each length group.

Length group in cms.	Sex	No. of fish	No. infected fish	% fish infected	Total no. parasites	Mean no. parasites Total	Mean no. parasites Infected
10 - 15	Female	12	2	16.6	6	0.5	3.0
	Male	18	2	11.1	6	0.3	3.0
	Total	30	4	13.3	12	0.4	3.0
15 - 20	Female	30	8	26.6	21	0.7	2.6
	Male	22	9	40.9	35	1.6	3.9
	Total	52	17	32.7	56	1.1	3.3
20 - 25	Female	42	19	45.2	91	2.2	4.8
	Male	45	13	28.8	75	1.6	5.8
	Total	87	32	36.8	166	1.9	5.2
25 - 30	Female	10	3	30.0	15	1.5	5.0
	Male	20	10	50.0	99	4.9	9.9
	Total	30	13	43.3	114	3.8	8.7

(F_{27}^{5} = 1.816; F_{27}^{5} at 5% = 2.57), and no significant difference between the ratio of female and male fish per sample (p = 0.05).

D. cordus.

(a) Seasonal variation in intensity of infection.

The peak period of infection of female L.leuciscus with D.cordus occurred in March, April, June and July. The pattern of intensity of infection was similar in male L.leuciscus, but slightly more prominent peaks, of doubtful significance were present in February and June (Table 3.33).

(b) Relationship of length and sex of the fish to intensity of infection.

The numbers and the intensity of infection of female and male fish overall and in the different length groups were very similar (Tables 3.30, 3.33, 3.34). The difference in the mean number of parasites in the female and male fish was smaller than for the other dactylogyrids and therefore without statistical analysis it was possible to state the sex of L.leuciscus did not influence the intensity of infection of D.cordus.

D.paradoxum.

There was no apparent overall difference in each monthly sample of the mean number of D.paradoxum on the gills of female and male L.leuciscus (Tables 3.30, 3.35). Female and male fish in each length group had similar mean numbers of parasites, and the intensities of infection in all length groups were similar except the 0 - 15 cm. group, where the

intensity of infection was slightly lower (Table 3.36). It was concluded from this data that the sex of the host did not influence the intensity of infection of D.paradoxum.

TABLE 3.33:

The number of male and female L.leuciscus (total and infected) and the intensity of infection of each sex with D.cordus.

Month	Total no. parasites	No.parasites in female	No.female fish Total	No.female fish Infected	Mean no. parasites in female fish a	Mean no. parasites in female fish b	No.parasites in male	No. male fish Total	No. male fish Infected	Mean no. of parasites in male fish a	Mean no. of parasites in male fish b
Jan.	1	1	10	1	0	0	0	23	0	0	0
Feb.	22	12	15	5	0.8	2.4	10	16	2	1.6	5.0
* Mar.	59	29	12	7	2.4	4.1	30	18	9	1.6	3.3
* Apr.	93	37	14	9	2.6	4.1	56	21	13	2.6	4.3
May	0	0	4	0	0	0	0	0	0	0	0
June	74	9	16	3	0.5	3.0	65	14	8	4.6	8.1
July	107	45	13	8	3.4	5.6	62	17	11	3.6	5.6
Aug.	5	4	16	3	0.25	1.3	1	14	1	0.07	1.0
Sept.	1	1	22	1	0.04	1.0	0	8	0	0	0
Oct.	0	0	20	0	0	0	0	11	0	0	0
Nov.	0	0	17	0	0	0	0	11	0	0	0
Dec.	0	0	13	0	0	0	0	17	0	0	0
Total	362	138	172	37	0.8	3.7	224	170	44	1.3	5.1

Key: * - Spawning period

a - Intensity of infection expressed as the mean number of parasites per fish.

b - Intensity of infection expressed as the mean number of parasites per infected fish.

TABLE 3.34:

The number and percentage of male and female L.leuciscus infected with D.cordus, and the mean number of parasites on the total and infected fish from each length group.

Length group in cms.	Sex	No. of fish	No. infected fish	% fish infected	Total no. parasites	Mean no. parasites Total	Mean no. parasites Infected
0 - 15	Female	10	0	0	0	0	0
	Male	5	0	0	0	0	0
	Total	15	0	0	0	0	0
15 - 20	Female	29	7	24.1	26	0.9	3.7
	Male	20	7	35.0	19	0.9	2.7
	Total	49	14	28.6	45	0.9	3.2
20 - 25	Female	101	20	19.8	81	0.8	4.1
	Male	113	24	21.2	129	1.1	5.4
	Total	214	44	20.5	210	0.9	4.7
25 - 30	Female	32	10	37.5	31	0.9	3.1
	Male	32	13	34.4	76	2.4	5.8
	Total	64	23	35.9	107	1.7	4.5

TABLE 3.35:

The number of male and female L.leuciscus (total and infected) and the intensity of infection of each sex with D.paradoxum.

	Month	Total no. parasites	No.parasites in female	No.female fish Total	No.female fish Infected	Mean no. parasites in female fish a	Mean no. parasites in female fish b	No.parasites in male	No.male fish Total	No.male fish Infected	Mean no.of parasites in male fish a	Mean no.of parasites in male fish b
	Jan.	19	7	10	4	0.7	1.7	12	23	6	0.5	2.0
	Feb.	40	32	15	9	2.1	3.5	8	16	5	0.5	1.6
x	Mar.	62	26	12	8	2.2	3.3	36	18	12	2.0	3.0
x	Apr.	46	18	14	7	1.3	2.6	28	21	13	1.3	2.2
	May	10	10	4	3	2.5	3.3	0	0	0	0	0
	June	33	18	16	7	1.1	2.6	15	14	7	1.1	2.1
	July	29	17	13	10	1.3	1.7	12	17	7	0.7	1.7
	Aug.	69	58	16	13	3.6	4.4	11	14	5	0.8	2.2
	Sept.	30	23	22	8	1.1	2.9	7	8	4	0.9	1.7
	Oct.	43	32	20	13	1.6	2.5	11	11	6	1.0	1.8
	Nov.	42	24	17	12	1.4	2.0	18	11	7	1.6	2.6
	Dec.	41	20	13	9	1.5	2.2	21	17	8	1.2	2.6
	Total	464	286	172	103	1.6	2.8	178	170	80	1.1	2.2

Key: x - Spawning period.

a - Intensity of infection expressed as the mean number of parasites per fish.

b - Intensity of infection expressed as the mean number of parasites per infected fish.

TABLE 3.36:

The number and percentage of male and female L.leuciscus infected with D.paradoxum, and the mean number of parasites on the total and infected fish from each length group.

Length group in cms.	Sex	No. of fish	No.infected fish	% fish infected	Total no. parasites	Mean no. parasites Total	Mean no. parasites Infected
0 - 15	Female	10	5	50.0	8	0.8	1.6
	Male	5	2	40.0	2	0.4	1.1
	Total	15	7	46.6	10	0.6	1.4
15 - 20	Female	29	21	72.4	66	2.3	3.1
	Male	20	12	63.2	30	1.5	2.5
	Total	49	23	68.7	96	1.9	2.9
20 - 25	Female	101	58	57.4	158	1.5	2.7
	Male	113	50	44.2	100	0.9	2.0
	Total	214	108	50.4	258	1.2	2.4
25 - 30	Female	32	19	59.4	54	1.7	2.8
	Male	32	16	50.0	46	1.4	2.9
	Total	64	35	54.7	100	1.5	2.8

Conclusions and Discussion.

Eleven species of Monogenea were found in the fishes of the River Lugg, of which seven were recorded for the first time in Britain. The first record of a dactylogyrid in Britain was an undetermined species found on the gills of P.phoxinus from Scotland (Ashworth and Bunnermann, 1927). Vickers (1951) also reported an unidentified species on the gills of S.erythrophthalmus from Ireland. Dactylogyrus species were not recorded from Britain by either Sproston (1946) or Dawes (1946, 1947). Rizvi (1964) described D.crucifer, D.sphyrna and Dactylogyrus similis Wegener, 1909 from R.rutilus and T.monenteron from E.lucius in Rostherne Mere (Cheshire). Mishra (1966) recorded D.suecicdus Nybelin 1937 as well as D.crucifer, D.sphyrna and D.similis from R.rutilus; D.wunderi Bychowsky 1931 and D.crucifer from A.brama; T.monenteron from E.lucius and D.paradoxum from R.rutilus and A.brama. These recent records of Monogenea indicate that further investigation in this field may reveal other species previously unrecorded in this country.

The dactylogyrids and T.borealis from the fish of the River Lugg showed a seasonal occurrence and variation in intensity of infection, the highest percentage and intensity of infection occurring in March and April, and in some species a second peak of infection was present in July, before the infection disappeared in September. The first peak of infection recorded for all species may be explained by the increase in water temperature in February, which caused the eggs which had been dormant over the winter to hatch and this provided the spring infection.

The second peak in July was of doubtful significance, and the data for each species were examined to try and explain this observation. A marked rise in the infection of T.thymallus with T.borealis was noted in July. An examination of the samples showed that in May and June only eight and seventeen fish were sampled, but in July 30 fish were caught of which a larger number than in previous samples were in the greatest length group, these fish having a higher mean number of parasites than fish in lower length groups, and therefore increasing the overall mean number of parasites in the July sample.

Differences in the level of infestation of D.vistulae on S.cephalus were not very apparent in May, June and July and two separate peaks of infection were not recorded. An increase in the intensity of infection of D.prostae on the gills of S.cephalus in May could be explained by the greater number of S.cephalus in the 40 - 50 cm. group of this sample, these fish having a higher mean number of parasites than the smaller fish. No satisfactory explanation is available for the drop in infection in April and June, and it is necessary to test this data statistically to determine if the difference in the level of infection between months is significant.

A decrease in the intensity of infection of D.crucifer from R.rutilus was recorded in May. This could result from the poor May sample of nine fish. All except one were in the lowest length group, and it has been shown that a lower percentage and intensity of infection were recorded from the smaller R.rutilus. The increase in

intensity in June and July was evident in all length groups where a reasonable number of fish were examined. Two possible explanations are put forward:-

a) A second generation of parasites is superimposed on the original infection

b) The movement of fish back from the spawning areas (R.rutilus spawned in May and June) if the spawning areas differ from the normal habitat and are less favourable for infection by dactylogyrids.

A seasonal occurrence with the highest infection in the spring was also recorded for D.crucifer and D.similis on R.rutilus from Rostherne Mere, Cheshire (Rizvi, 1964). D.crucifer was recorded at all times of the year on R.rutilus from the Shropshire Union Canal (Mishra, 1966) although the percentage infection was very low from October to January. A high intensity of infection of Monogenea in the spring and the disappearance of infection in autumn was recorded from the fish of the River Wistula, Poland (Prost, 1957). She stated that the changes throughout the year could be attributed to the low water temperatures and different way of life of the fish in winter, both of which had an adverse effect on the dynamics of the parasites, although the susceptibility to change in temperature was not the same in all Monogenea. This latter fact is illustrated by the effect of temperature on the duration of the life cycle and egg production of D.vastator and D.solidus. Above 15°C egg production in D.vastator is increased

(Lyaiman, 1951a), whereas eggs produced by D.solidus at this temperature are inviable but D.solidus continues to reproduce and develop throughout the winter (Bauer, 1951). The development of D.solidus is similar to that of D.vastator but is slower, the life cycle extending over one year compared to that of a few weeks for D.vastator. Mishra (1966) recorded eggs present in D.crucifer from all months where infection occurred, the percentage of worms with eggs being greater in the winter. The significance of a higher percentage of D.crucifer with eggs in winter is doubtful as only four worms were examined between October and December of which two contained eggs. No dactylogyrids were recorded from the fish of the River Lagg from September to January. Within the months where infection occurred, the peak period of egg production, recorded as the months where the highest percentage of worms containing eggs were present was March to May for D.vistulae and April for D.crucifer, although there was always a greater percentage of D.crucifer without eggs present each month. It is postulated that temperature may effect the viability or development of the eggs of D.vistulae, as the water temperature of the river rises above 15°C by June, and at this time the percentage of D.vistulae containing eggs decreased. This could account for the disappearance of the infection by September, but some explanation is necessary as to how the eggs are produced which overwinter in a dormant condition, and hatch to provide the spring infection when the water temperature rises above 4°C.

An experimental approach is necessary to try and define the

conditions under which the dactylogyrids and T.borealis recorded in this investigation survive and reproduce and the factors responsible for the strict host specificity which was exhibited by all the Monogenea except D.paradoxum.

No seasonal variation of occurrence or intensity of infection was recorded for D.paradoxum on the gills of L.leuciscus in this investigation, or for D.paradoxum on the gills of R.rutilus (Mishra, 1966).

The percentage of R.rutilus, S.cephalus and T.thymallus infected with D.crucifer, D.vistulae and T.borealis increased with increase in length, whereas there was no increase in the percentage of S.cephalus infected with D.prostae in the two greatest length groups. An increase in intensity of infection with increase in length of the host was also recorded for D.crucifer, D.prostae, D.vistulae and T.borealis. This increase was thought to be the result of an increase in the available surface area for infection rather than a specific age or length effect, especially as the parasites had a seasonal occurrence, and there was no cumulative effect from year to year. No increase in the intensity of D.cordus and D.paradoxum was recorded with increase in length of L.leuciscus , and a decrease in the percentage of fish infected was observed from the greatest length group. It was suggested that the narrower size range of L.leuciscus sampled compared to other species may explain the lack of increase of intensity of infection with increase in length.

Mishra (1966) also recorded an increase in the percentage infection

and intensity of infection for dactylogyrids, and a decrease in the number of larger fish infected with D.paradoxum. In contrast with these observations and those of the present survey, Rizvi (1964) recorded a decrease in the percentage of R.rutilus infected with D.crucifer in relation to the age and length of the host.

The influence of host hormones, particularly gonadotrophins on the intensity of infection and maturation of parasites is an important aspect of host parasite relationship. Two main trends are evident from recent work:-

a) The maturation time of the host influences that of the parasite e.g. the genitalia of Polystomum integerrimum Froelich, mature only when the host (frog) enters the water just before copulation, and egg production in P.integerrimum occurs when the frogs are spawning (Lees and Bass, 1960). P.integerrimum feeds on blood (Halton and Jennings, 1965) and would have access to host hormones, and therefore the maturation processes of the fluke may be directly or indirectly under the control of the hormonal activity of the host. D.paradoxum from the gills of L.leuciscus of the River Lugg feeds on blood and mucus, and the peak period of egg production i.e. May and June, occurs just after the spawning time of the host (April). It is postulated that the maturation of D.paradoxum may also be influenced to some extent by the hormones of the host, as well as by an increase in water temperature.

b) A high level of female gonadal hormone may reduce the level of parasitization. Higher levels of infection of P.integerrimum were

recorded from male than female frogs just before breeding. This phenomenon was reported not only for monogeneans but for the total parasite population (Lees and Bass, 1960; Lees, 1962).

The influence of the sex of the fish hosts on the intensity of infection has been investigated by Thomas (1964) and Paling (1965). Thomas (1964) compared the helminth burdens of male and female S.trutta from a natural population in the River Teify, West Wales. Only one statistically significant difference was found between the level of infection in 1 to 2 year old male and female S.trutta. When S.trutta of 3+ and over were spawning or recovering from spawning, the sexually mature females tended to be more heavily infected with some parasites than males. When the gonads were maturing, and the oestrogen levels were high this trend was reversed, or became less prominent. Males were significantly more heavily infected than females in fish that were not spawning, but overall the differences in the levels of infestation were small in mature and female S.trutta.

Paling (1965) investigated the relationship between the sex of S.trutta and the degree of infestation with Discocotyle sagittata (Leuckart, 1842). In the first four years there was little difference in the degree of infestation of male and female fish. In fish between 5+ years and 7, a higher percentage of male S.trutta than female were infected, and the male fish had about twice as many D.sagitta as the females. The difference in percentage and intensity of infection diminished in male and female fish of 8 years or over.

In the present investigation the sex of the host regardless of weight (used as an indication of increase in size) had no influence on the intensity of infection of D.vistulae, D.prostae, T.borealis and D.paradoxum, when all the infected fish were taken into account. The pattern of infection of R.rutilus with D.crucifer differed in female and male fish. The male fish showed a significant increase in the number of parasites with increase in weight, but no significant increase was recorded from females. A significant increase was found between the total percentage of female and male R.rutilus infected with D.crucifer. The results were not tested statistically for the other dactylogyrids but the figures did not show any very apparent differences. The number of male and female fish in each sample was insufficient to allow any valid comparison between the intensity of infection of each sex in each group from each sample, and therefore it was not possible to determine if the pattern of infection differed in males and females of differing lengths at spawning time.

Many problems have been raised in this general ecological survey of the Monogenea of freshwater fishes of the River Lugg. An experimental approach is now required to determine the conditions influencing the life cycle, the physiology of reproduction, the factors responsible for the strict specificity of the dactylogyrids and the effect of the host and the parasite on each other.

TABLE 3.37:

Analysis of covariance: D.crucifer from R.rutilus

Batch	d_f n - 1	Σx^2	Σxy	Σy^2	by.x $\Sigma xy/\Sigma x^2$	d_f n - 2	Deviations from the regression $\Sigma y^2 - (\Sigma xy)^2/\Sigma x^2$	Mean square
Female	n - 1 = 70	1,178,034.15	428.53	236.8117	0.000364	n_1 - 2		
Male	n - 1 = 50	362,445.72	2615.44	145.3863	0.00723	n_2 - 2		
Common	n_1+n_2-2	1540479.87	3043.97	382.1980	0.0019	n_1+n_2-3	i = 376.1832	k= 3.1612
Total	n_1+n_2-1	2,049,675.07	4534.12	386.4857		n_1+n_2-3	j = 376.4557	

TABLE 3.38:

Analysis of covariance: D.vistulae from S.cephalus.

Batch	d_f n - 1	Σx^2	Σxy	Σy^2	by.x $\Sigma xy/\Sigma x^2$	d_f n - 2	Deviations from the regression $\Sigma y^2 - (\Sigma xy)^2/\Sigma x^2$	Mean square
Female	n_1-1 = 67	10,046,959	12,634.53	54.182514	0.00126	n_1- 2		
Male	n_2-1 = 46	2,582,547	3,099.61	15.430106	0.00120	n_2- 2		
Common	n_1+n_2-2	12,629,506	15,734.14	69.612620	0.00125	n_1+n_2-3	i = 50.010652	k=0.4465
Total	n_1+n_2-1	14,736,125.5	17,842.384	72.015828		n_1+n_2-2	j = 50.41290	

TABLE 3.39:

Analysis of covariance: D.prostae from S.cephalus

Batch	d_f n - 1	Σx^2	Σxy	Σy^2	by.x $\Sigma xy/\Sigma x^2$	d_f n - 2	Deviations from the regression $\Sigma y^2 - (\Sigma xy)^2/\Sigma x^2$	Mean square
Female	$n_1 - 1 = 32$	4,222,184.07	8,333.15038	110.0157	0.00197	$n_1 - 2$		
Male	$n_2 - 1 = 18$	656,922.86	1,042.07909	40.31408	0.00158	$n_2 - 2$		
Common	$n_1+n_2 - 2$	4,879,106.93	9,375.22947	150.3298	0.00192	n_1+n_2-3	i = 132.3158	k=2.7003
Total	$n_1+n_2 - 1$	5,697,326.2	11,630.52	166.5297		n_1+n_2-2	j = 142.7877	

TABLE 3.40:

Analysis of covariance: T.borealis from T.thymallus.

Batch	d_f n - 1	Σx^2	Σxy	Σy^2	by. x $\Sigma xy/\Sigma x^2$	d_f n - 2	Deviations from the regression $\Sigma y^2 - (\Sigma xy)^2/\Sigma x^2$	Mean square
Female	$n_1 - 1 = 31$	71,435.16	296.99235	20.69444	0.00416	$n_1 - 2$		
Male	$n_2 - 1 = 33$	241,962.14	1,392.48845	35.06645	0.00575	$n_2 - 2$		
Common	$n_1+n_2 - 2$	313,397.3	1,689.4808	55.76089	0.00539	$n_1+n_2 - 3$	i = 54.85013	k = 7.149
Total	$n_1+n_2 - 1$	773,033.56	10,720.7041	243.36252	0.01387	$n_1+n_2 - 2$	j = 94.684	

Data used in the analysis of covariance for D.crucifer from R.rutilus.

FEMALE				MALE			
Fish		Parasite		Fish		Parasite	
Length	Weight	Number	$\sqrt{X+1}$	Length	Weight	Number	$\sqrt{X+1}$
21.4	113.4	9	3.1623	16.2	53.9	2	1.7321
21.4	130.7	5	2.4495	17.6	56.3	2	1.7321
21.4	122.9	12	3.6056	18.6	72.6	9	3.1623
22.4	163.1	9	3.1623	24.1	188.8	7	2.8284
26.1	259.5	17	4.2426	24.9	215.3	2	1.7321
28.3	297.2	17	4.2426	26.4	247.2	4	2.2361
30.1	364.9	65	8.1240	28.0	295.8	37	6.1644
30.7	438.2	20	4.5826	28.0	344.0	33	5.7446
32.0	390.8	87	9.3808	16.2	52.9	1	1.4142
18.5	84.5	5	2.4495	17.2	64.4	12	3.6056
18.9	82.6	12	3.6056	17.6	73.1	13	3.7417
19.0	91.5	19	4.4721	18.5	80.9	3	2.0000
20.4	126.9	4	2.2361	20.7	121.3	12	3.6056
21.0	125.1	70	8.4261	22.5	170.8	2	1.7321
25.4	231.6	20	4.5826	22.9	159.7	21	4.6904
26.5	269.0	9	3.1623	24.3	197.8	16	4.1231
27.5	317.6	5	2.4495	26.1	247.1	60	7.8102
27.6	309.9	10	3.3166	27.5	351.9	30	5.5678
28.0	353.1	14	3.8730	16.1	49.8	3	2.0000
28.4	338.7	6	2.6458	17.4	62.5	1	1.4142
29.2	342.1	12	3.6056	20.6	121.4	20	4.5826
29.5	383.7	20	4.5826	23.2	156.3	8	3.0000
30.0	325.4	12	3.6056	24.0	188.1	20	4.5826
31.0	500.0	19	4.4721	25.0	200.6	70	8.4261
31.2	512.0	9	3.1623	15.9	44.6	13	3.7417
17.6	74.0	2	1.7321	16.1	50.2	2	1.7321
18.4	86.9	2	1.7321	16.2	49.7	7	2.8284
25.1	181.5	30	5.5678	16.9	53.3	6	2.6458
25.2	-	7	-	17.0	57.1	4	2.2361
26.0	243.9	16	4.1231	17.2	59.0	4	2.2361
26.1	226.6	21	4.6904	17.6	62.5	1	1.4142
30.0	-	25	-	18.0	57.9	4	2.2361
30.1	331.6	10	3.3166	22.6	136.4	5	2.4495
31.0	420.4	30	5.5678	22.9	136.6	29	5.4772
32.0	402.0	37	6.1644	23.3	189.4	26	5.1962
19.2	84.2	8	3.0000	23.7	158.7	15	4.0000
25.4	227.6	70	8.4261	25.0	195.4	3	2.0000
25.8	202.3	23	4.8990	16.0	53.8	15	4.0000
27.0	282.4	9	3.1623	16.8	61.2	25	5.0990
27.3	281.3	4	2.2361	16.9	56.5	45	6.7823
27.7	298.4	80	9.0000	16.9	68.9	9	3.1623
29.0	371.2	4	2.2361	17.2	57.0	25	5.0990
30.3	379.1	15	4.0000	17.2	60.7	8	3.0000

FEMALE

Fish		Parasite	
length	Weight	Number	$\sqrt{x+1}$
30.6	395.1	5	2.4495
31.0	363.4	1	1.4142
32.3	443.9	6	2.6458
16.7	58.5	38	6.2450
18.3	72.1	23	4.8990
19.2	88.7	19	4.4721
19.3	91.1	27	5.2915
21.2	122.3	39	6.3246
21.8	135.6	1	1.4142
26.6	231.8	31	5.6569
26.9	233.3	20	4.5826
27.1	282.7	16	4.1231
29.2	339.4	1	1.4142
32.0	493.8	2	1.7321
19.5	93.4	13	3.7417
20.2	105.7	4	2.2361
20.6	122.0	6	2.6458
21.1	118.8	1	1.4142
27.4	300.7	1	1.4142
28.3	273.8	8	3.0000
28.5	367.5	30	5.5678
28.5	313.8	8	3.0000
28.9	347.6	19	4.4721
29.0	350.8	4	2.2361
29.1	353.7	6	2.6458
29.4	340.5	35	6.0000
30.2	368.8	8	3.0000
30.9	389.6	7	2.8284
32.1	422.9	21	4.6904
32.8	549.0	11	3.4641

Weight	$\sqrt{x+1}$
Σx^2 = 6,229,572.15	Σy^2 = 1,330.002466
Σx = 18,938.3	Σy = 278.4751
$(\Sigma x)^2$ = 358,659,206.89	$(\Sigma y)^2$ = 77,545.5409
n = 71.	n = 71.
C.S.S. = 1,178,034.15.	C.S.S.
C.F. = 5,051,538.0	C.F. = 1,093.1907.
Var. = 16,829.05	Var. = 3.383024
$\bar{x}$ = 266.7	$\bar{y}$ = 3.9222

Σxy = 74706.67616
$\Sigma x \Sigma y$ = 5273748.401
C.Σxy = 428.53
C.F. = 47,278.14
Cov. = 6.121857.

MALE

Fish		Parasite	
Length	Weight	Number	$\sqrt{x+1}$
17.7	70.0	13	3.7417
21.6	129.0	21	4.6904
24.4	196.8	7	2.8284
24.9	178.6	35	6.0000
25.9	226.0	3	2.0000
26.5	216.5	3	2.0000
26.9	247.4	6	2.6458
27.3	271.9	12	3.6056

Weight	$\sqrt{x+1}$
Σx^2 = 1,300,580.72	Σy^2 = 784.002259
Σx = 6,917.0	Σy = 180.4762
$(\Sigma x)^2$ = 47,844,889.0	$(\Sigma y)^2$ = 32569.4209
n = 51	n = 51
C.S.S.=362,445.72	C.S.S.=145.386259
C.F. =938,135.0	C.F. =638.6160
Var. = 7,248.914	Var. = 2.907725
$\bar{x}$ = 135.6	$\bar{y}$ = 3.544

Σxy = 27,092.12236
$\Sigma x \Sigma y$ = 1,248,310.990
C.Σxy = 2,615.44
C.F. = 24,476.68
Cov. = 52.30880

Data used in the analysis of covariance for D.vistulae from S.cephalus.

FEMALE				MALE			
Fish		Parasite		Fish		Parasite	
Length	Weight	Number	$\sqrt{x+1}$	Length	Weight	Number	$\sqrt{x+1}$
22.6	123.4	2	1.7321	24.4	139.9	2	1.7321
23.2	169.8	1	1.4142	25.1	155.5	1	1.4142
35.6	527.4	4	2.2361	26.7	193.9	1	1.4142
39.4	712.1	10	3.3166	31.9	392.0	3	2.0000
40.5	700.0	9	3.1623	32.0	413.5	4	2.2361
43.2	1,040.0	10	3.3166	32.8	435.4	5	2.4495
43.3	1,115.6	3	2.0000	36.4	526.9	4	2.2361
45.0	1,150.0	20	4.5862	20.8	99.2	4	2.2361
46.9	1,200.0	5	2.4495	22.6	132.8	2	1.7321
22.4	123.9	3	2.0000	25.5	185.1	4	2.2361
24.1	157.8	1	1.4142	26.1	214.8	4	2.2361
24.5	169.5	3	2.0000	33.4	452.4	3	2.0000
24.6	173.5	3	2.0000	33.9	494.4	2	1.7321
26.2	208.4	1	1.4142	36.3	530.0	7	2.8284
26.4	222.8	3	2.0000	38.5	660.0	5	2.4495
27.1	221.8	5	2.4495	20.9	88.2	5	2.4495
36.2	505.0	1	1.4142	22.3	113.5	3	2.0000
36.3	565.0	3	2.0000	22.5	116.7	3	2.0000
39.3	675.0	6	2.6458	22.6	135.8	3	2.0000
39.3	695.0	16	4.1231	22.7	112.5	3	2.0000
42.0	800.0	8	3.0000	22.9	133.8	3	2.0000
45.1	970.0	11	3.4641	23.8	158.6	3	2.0000
21.6	111.8	4	2.2361	23.9	149.4	3	2.0000
22.6	115.9	3	2.0000	24.4	155.2	3	2.0000
22.6	120.2	4	2.2361	29.4	284.2	7	2.8284
23.2	128.2	7	2.8284	32.2	367.5	4	2.2361
24.5	140.2	3	2.0000	36.4	530.0	8	3.0000
36.4	525.0	9	3.1623	36.5	473.2	15	4.0000
37.8	620.0	5	2.4495	39.0	785.0	9	3.1623
38.4	625.0	4	2.2361	41.1	755.0	5	2.4495
39.1	730.0	8	3.0000	11.4	10.4	1	1.4142
39.3	740.0	7	2.8284	21.9	113.4	1	1.4142
47.5	1,150.0	7	2.8284	21.9	120.4	5	2.4495
22.1	117.0	2	1.7321	22.4	124.8	1	1.4142
23.0	133.8	1	1.4142	27.4	266.8	2	1.7321
23.0	124.4	1	1.4142	31.3	357.1	2	1.7321
24.2	-	3	-	41.9	760.0	6	2.6458
26.8	219.2	1	1.4142	23.5	153.0	1	1.4142
26.8	233.5	2	1.7321	24.8	178.5	5	2.4495
28.0	285.8	8	3.0000	25.2	178.7	7	2.8284
37.9	620.0	6	2.6458	35.6	550.0	5	2.4495
39.0	700.0	3	2.0000	36.2	535.0	1	1.4142
40.4	860.0	10	3.3166	37.0	570.0	11	3.4641

FEMALE

Fish		Parasite	
Length	Weight	Number	$\sqrt{x+1}$
41.4	985.0	10	3.3166
41.4	910.0	6	2.6458
42.7	1,050.0	8	3.0000
44.2	1,200.0	25	5.0990
48.0	1,300.0	31	5.6569
49.1	1,850.0	3	2.0000
22.8	143.8	3	2.0000
24.5	181.8	1	1.4142
32.1	425.6	3	2.0000
32.6	456.9	6	2.6458
39.6	680.0	2	1.7321
40.2	930.0	1	1.4142
40.4	920.0	2	1.7321
41.4	970.0	5	2.4495
42.0	860.0	7	2.8284
24.9	211.1	1	1.4142
24.9	195.3	2	1.7321
32.3	454.8	2	1.7321
37.4	675.0	2	1.7321
38.4	685.0	1	1.4142
40.6	810.0	6	2.6458
41.0	840.0	3	2.0000
41.9	860.0	9	3.1623
43.6	1,000.0	15	4.0000
34.4	511.0	7	2.8284
38.2	800.0	1	1.4142

Weight		$\sqrt{x+1}$	
Σx^2	34,086,518.01	Σy^2	453.03545
Σx	40,431.3	Σy	164.6232
$(\Sigma x)^2$	1,634,690,019.69	$(\Sigma y)^2$	27,100.7979
C.F.	24,039,559.0	C.F.	398.85294
C.S.S.	10,046,959.01	C.S.S.	54.18251
Var.	149,954.61	Var.	1
$\bar{x}$	594.578	$\bar{y}$	2.4
n	68	n	68

Σxy	110,511.71746
$\Sigma x \Sigma y$	6,655,929.98616
C.F.	97,881.320
C.S.S.	12,630.397
Cov.	188.513

MALE

Fish		Parasite	
Length	Weight	Number	$\sqrt{x+1}$
21.8	113.6	1	1.4142
26.4	212.9	2	1.7321
28.7	276.1	1	1.4142
43.2	1,100.0	4	2.4495

Weight		$\sqrt{x+1}$	
Σx^2	7,373,037.43	Σy^2	232.001866
Σx	15,005.1	Σy	100.8904
$(\Sigma x)^2$	225,153,026.01	$(\Sigma y)^2$	10,178.8728
C.F.	4,790,489.9	C.F.	216.5717
C.S.S	2,582,547.53	C.S.S.	15.430106
Var.	56,142.33	Var.	0.3354
$\bar{x}$	319.257	$\bar{y}$	2.1466
n	47	n	47

Σxy	35,309.62294
$\Sigma x \Sigma y$	1,513,870.54104
C.F.	32,210.01
C.S.S.	3,099.61
Cov.	67.383

Data used in the analysis of covariance for D.prostae from S.cephalus.

FEMALE				MALE			
Fish		Parasite		Fish		Parasite	
Length	Weight	Number	+1	Length	Weight	Number	+1
39.4	712.1 Feb	19	4.4721	31.9	392.0 Feb	3	2.0000
39.5	860.0	12	3.6056	32.0	413.5	3	2.0000
40.5	700.0	10	3.3166	32.8	435.1	1	1.4142
45.0	1,150.0	15	4.0000	33.4	452.5 March	5	2.4495
24.6	173.5 March	3	2.0000	23.9	149.4 April	4	2.2361
26.4	222.8	4	2.2361	29.4	284.2	6	2.6458
36.3	565.0	4	2.2361	35.3	465.6	53	7.3485
38.6	645.0	64	8.0623	36.4	530.0	7	2.8284
39.3	695.0	19	4.4721	36.5	473.2	30	5.5678
42.0	800.0	20	4.5326	41.1	755.0	10	3.3166
45.1	970.0	67	8.2462	35.2	650.0 June	5	2.4495
22.6	115.9 April	2	1.7321	22.4	139.5 July	1	1.4242
36.4	525.0	11	3.4641	24.8	178.5	14	3.8730
37.8	620.0	5	2.4495	37.0	570.0	1	1.4142
39.1	730.0	2	1.7321	35.8	555.0 Aug.	17	4.2426
39.3	740.0	19	4.4721	36.1	650.0	11	3.4641
39.0	700.0 May	5	2.4495	36.5	580.0	5	2.4495
40.4	860.0	18	4.3589	37.0	590.0	7	2.8284
41.1	985.0	21	4.6904	40.8	820.0	15	4.0000
42.7	1,050.0	8	3.0000				
44.2	1,200.0	87	9.3808				
48.0	1,300.0	22	4.7958				
49.1	1,850.0	5	2.4495				
26.1	212.4 June	3	2.0000				
32.1	425.6	1	1.4142				
43.0	1,050.0	5	2.4495				
43.1	940.0	5	2.4495				
24.4	165.8 July	4	2.2361				
32.0	500.0	8	3.0000				
41.9	860.0	38	6.2450				
34.4	511.0 Aug.	20	4.5826				
38.0	730.0	8	3.0000				
38.2	800.0	21	4.6904				

FEMALE		MALE	
Weight	$\sqrt{X+1}$	Weight	$\sqrt{X+1}$
Σx^2 = 22,210,346.07	Σy^2 = 587.99998	Σx^2 = 4,999,839.76	Σy^2 = 217.0006
Σx = 24,364.1	Σy = 124.2718	Σx = 9,083.8	Σy = 57.9424
$(\Sigma x)^2$ = 593,609,368.81	$(\Sigma y)^2$ = 15,443.48027	$(\Sigma x)^2$ = 82,515,422.44	$(\Sigma y)^2$ = 3357.0436
C.F. = 17,988,162.00	C.F. = 467.9842	C.F. = 4,342,916.9	C.F. = 176.6865
C.S.S. = 4,222,184.07	C.S.S. = 110.0157	C.S.S. = 656,922.86	C.S.S = 40.31408
Var. = 131,943.25	Var. = 6.1119	Var. = 36,495.7	Var. = 2.23967
$\bar{x}$ = 738.306	$\bar{y}$ = 3.7658	$\bar{x}$ = 478.0947	$\bar{y}$ = 3.0496
Σxy = 100,083.770738		Σxy = 28,743.03509	
$\Sigma x \Sigma y$ = 3,027,770.56238		$\Sigma x \Sigma y$ = 526,337.17312	
C.F. = 91,750.62		C.F. = 27,701.956	
C.S.S. = 8,333.1504		C.S.S. = 1,042.07909	
Cov. = 260.4109		Cov. = 57.89328	

Data used in the analysis of covariance for T.borealis from T.thymallus.

FEMALE				MALE			
Fish		Parasite		Fish		Parasite	
Length	Weight	Number	$\sqrt{x+1}$	Length	Weight	Number	$\sqrt{x+1}$
20.8	115.5 March	2	1.7321	20.4	125.0 March	2	1.7321
20.7	122.9	4	2.2361	22.2	-	1	-
20.9	154.9	5	2.4495	20.6	133.9	12	3.6056
19.9	73.0 Apr.	3	2.0000	14.0	24.1 Apr.	2	1.7321
20.1	74.5	3	2.0000	14.6	28.8	4	2.2361
20.1	75.9	1	1.4142	19.6	65.0	1	1.4142
21.2	91.3	2	1.7321	20.3	76.3	2	1.7321
21.9	97.3	8	3.0000	21.0	106.3	10	3.3166
22.1	104.5	4	2.2361	21.4	89.4	1	1.4142
22.8	122.5	30	5.5678	22.1	113.3	8	3.0000
24.0	125.8	6	2.6458	22.1	103.2	2	1.7321
22.8	125.4 May	1	1.4142	22.7	118.6	1	1.4142
23.4	121.4	3	2.0000	22.7	141.1	3	2.0000
26.9	209.2	2	1.7321	23.1	130.2	4	2.2361
14.8	28.9 June	3	2.0000	24.4	151.2	15	4.0000
15.7	37.2	1	1.4142	15.6	32.9 May	3	2.0000
18.4	54.0	5	2.4495	30.1	267.7	2	1.7321
21.9	102.1	1	1.4142	19.4	66.4 June	1	1.4142
22.2	107.8	1	1.4142	19.8	71.3	1	1.4142
17.6	52.1 July	1	1.4142	18.4	76.5 July	2	1.7321
17.8	54.8	4	2.2361	18.9	77.1	20	4.5826
19.1	67.5	2	1.7321	19.0	68.9	3	2.0000
19.5	74.9	4	2.2361	19.1	72.0	1	1.4142
24.2	133.9	5	2.4495	24.8	159.7	14	3.8730
24.3	155.0	1	1.4142	25.3	170.0	3	2.0000
24.4	161.5	7	2.8284	25.4	169.8	14	3.8730
24.5	132.7	5	2.4495	26.2	187.1	12	3.6056
24.5	154.3	2	1.7321	26.3	177.8	3	2.0000
26.2	190.3	11	3.4641	27.1	207.4	14	3.8730
25.3	161.4 Aug.	2	1.7321	27.2	190.3	5	2.4495
13.3	21.0 Dec.	3	2.0000	27.4	208.9	18	4.3589
15.3	32.0	1	1.4142	29.9	235.5	15	4.0000
				36.5	470.9	13	3.7417
				17.2	39.8 Oct.	3	2.0000

FEMALE				MALE			
Weight			$\sqrt{X+1}$	Weight			$\sqrt{X+1}$
Σx^2 =	419,108.91	Σy^2 =	165.00198	Σx^2 =	817,059.74	Σy^2 =	247.002605
Σx =	3,335.5	Σy =	67.9547	Σx =	4,356.4	Σy =	83.6295
$(\Sigma x)^2$ =	11,125,560.25	$(\Sigma y)^2$ =	4,617.84125	$(\Sigma x)^2$ =	18978,220.96	$(\Sigma y)^2$ =	
n =	32	n =	32	n =	33		6,993.89327
C.F. =	347,673.75	C.F. =	144.30754	C.F. =	575,097.60	n =	33
C.S.S. =	71,435.16	C.S.S. =	20.69444	C.S.S. =	241,962.14	C.F. =	211.93616
Var. =	2,304.36	Var. =	0.66756	Var. =	7,561.3168	C.S.S. =	35.06645
$\bar{x}$ =	104.2344	$\bar{y}$ =	2.1236	$\bar{x}$ =	132.012	Var. =	1.0958
						$\bar{y}$ =	2.5342

Σxy =	7,380.2073	Σxy =	12,432.5961
$\Sigma x \Sigma y$ =	226,662.9018	$\Sigma x \Sigma y$ =	364,323.5538
C.F. =	7,083.2156	C.F. =	11,040.1076
C.S.S. =	296.9923	C.S.S. =	1,392.4894
Cov. =	9.5804	Cov. =	43.5153

FORMULAE.

Analysis of variance

$$\text{Var. } x = \frac{\Sigma(x)^2 - \frac{(\Sigma x)^2}{n_1}}{n_1 - 1} \qquad \text{Var. } y = \frac{\Sigma(y)^2 - \frac{(\Sigma y)^2}{n_2}}{n_2 - 1}$$

$$\text{Covariance} = \frac{\Sigma(xy) - \frac{(\Sigma x \Sigma y)}{n}}{n - 1}$$

Significance of the regression

$$\Sigma dy^2.x = [\Sigma y^2 - (\Sigma xy)/\Sigma x^2]$$

$$S^2_{y.x} = \frac{\Sigma dy^2.x}{n - 2}$$

$$Sb = \frac{\sqrt{S^2_{y.x}}}{\sqrt{\Sigma x^2}}$$

$$t_{n-2} = \frac{b_{y.x}}{Sb}$$

To test the difference between the two regressions.

$$t = \frac{(b_{y.x_1} - b_{\ 2})\sqrt{\frac{(N_1-1)(N_2-1)S^2_{x1}\ S^2_{x\ 2}}{(N-1)S^2_{x\ 1} + (N-1)S^2_{x\ 2}}}}{\sqrt{\frac{(N-2)S_y{}^2{}_{x_1} + (N-2)S_y{}^2{}_{x_2}}{N_1 + N_2 - 4}}}$$

REFERENCES.

AGAPOVA, A.I. 1956 Parasites of fish in reservoirs of western Kazakhstan (Russian text). Trudy Inst.Zool.Akad.nauk.Kazakhskoi S.S.R. 5: 5-60.

ASHWORTH, A.W. and BANNERMAN, K.W. 1927 On a Tetracotyle (T.phoxini) in the brain of the minnow. Trans.R.Soc.Edinb. 55 1 (8): 159-172.

BAUER, O.N. 1951 K voprosu o patogennosti: Dactylogyrus solidus Achmerov (Russian text) Dokl.Akad.Nauk S.S.S.R., 78 4:825-827

BAUER, O.N. 1954 Biology of D.vastator Nybelin (Russian text). Trudi Leningradskogo Obscherva Estestvospitatelei Otdelenie Zodogii 72 (4): 9-15.

BAUER, O.N. and NIKOL'SKAIA, N.P. 1954 Dactylogyrus solidus Achmerov: ego biologiia razvihe i rybokhoziaitvennoe znachenie Trudy probl.temat.Soveshch.zool.Inst. 4: 99-110.

BYCHOWSKY, B.E. 1961 Monogenetic Trematodes, their Systematics and Phylogeny (English translation) American Institute of Biological Sciences Washington, D.C.

CHUBB, J.C. 1961 A preliminary investigation of the parasite fauna of the fish of Llyn Tegid (Bala Lake) Merionethshire. Ph.D.thesis, University of Liverpool.

DAWES, B. 1946 The Trematoda. Cambridge.

DAWES, B. 1947 The Trematoda of British Fishes. Ray Society, London.

DOGIEL, V.A. and BYCHOWSKY, B.E.	1934a	Die Fisch parasiten des Aral-Seas (Russian text - German summary). Parazit.Sb.Zool.Akad.Nauk SSR. Leningrad. 4: 241-346.
ERGENS, R.	1956	Výsledky výzkumu monogenetických motolic rodu Dactylogyrus Diesing,1850. Pr.brn.Zakl.csl.Akad.Ved. 28,(7)346-376.
ERGENS, R.	1959	Nálezy dalších druhů rodu Dactylogyrus diesing (Monogenoidea) v ČSR a vliv lokalisace na morfologické změny chitinových castitiaptoru Dactylogyrus hermiamphi bothrium. Ceskosl.parasit. 6, (1) 187-92.
ERGENS, R.	1960a	Neue bisher beschriebene Dactylogyrus Arten (Monogenoidea) aus der Tschechoslowakei Helminthologia 2, (1): 3-8.
ERGENS, R.	1960b	Helminthofauna nekotoryx ryb Albanii (Russian text). Ceskosl.parasit. 7: 49-90.
ERGENS, R.	1962	Helminthefauna ryb dvou jihočeských rybničních soustav.II. Trematoidea, Monogenoidea Nematoda,Acanthocephala a Hirudinea Ceskosl.parasit. 9: 167-190.
ERGENS, R. and GUSSEV, A.V.	1965	Dactylogyrus prostae Molnar, 1964 (Monogonoidea) aus den kiemen von Leuciscus cephalus (L.) und Leuciscus cephalis orientalis Nordmann. Ceskosl.parasit. 12: 323-325.
GUSSEV, A.V.	1962	'Key to the Parasites of Freshwater Fish of the U.S.S.R.' - Dactylogyridae. Translation. 1964. Israel Program for Scientific Translations; 1964.
GUSSEV, A.V. and STREIKOV, Yu.A.	1962	'Key to the Parasites of Freshwater Fish of the U.S.S.R.' Tetraonchidae. Translation, 1964. Israel Program for Scientific Translations, 1964.

HALTON, D.W. and JENNINGS, J.B.	1965	Observations on the nutrition of monogenetic trematodes. Biol.Bull.biol.Lab., Woods Hole, 129: 257-272.
IZUMOVA, N.A.	1953	Biologiia Dactylogyrus vastator Nybelin i Dactylogyrus solidus Achmerov v karpovykh khoziaistvakh. Zoolog.inst.AN SSSR.autoref.diss: 1-17.
IZUMOVA, N.A.	1956a	Materialy po biologii Dactylogyrus vastator Nybelin. Parazit.Sb. (Zoolog.inst.AW SSSR) 16: 229-244.
KULAKOVSKAYA, O.P.	1960	Parasites of fish of the upper reaches of the River Prut. Naukove Zapysky Navkoho - Pryrodez-navchoho Muzeyu AN URSR 8: 70-82.
LEES, E.	1962	The incidence of helminth parasites in a particular frog population. Parasitology, 52: 95-102.
LEES, A. and BASS, L.	1960	Sex hormones as a possible factor influencing the level of parasitization in frogs. Nature, Lond. 188: 1207-1208.
LYAIMAN, E.M.	1951	Vliiarue temperatury vody na razmnoztenie monogeneticcheskogo sosal'shchika D.vastator. Trudy mosk.tekhnol.Inst.ryb Prom.Khoz. 4: 190-196.
MISHRA, T.N.	1966	Parasite fauna of the fish of the Shropshire Union Canal (Cheshire). Ph.D.thesis, University of Liverpool.
MOLNAR, K.	1964	Über die Parasitenfauna der Fische in Ungarn.II. Bekannte und neue Dactylogyrus - Arten an einheimischen Fischen. Acta vet.hung. 14: 455-467.
NYBELIN, O.	1937	Kleine Betrage zur kenntnis der Dactylogyren. Ark.Zool. 29: 1-29.

OLSSON, P.	1893	Bidrag till scandinaviens Helmintho-fauna II. Svenska AK Handl. 25: 1-41.
PACAK, S.	1957	Príspevok k stúdiu parazitofauny salmonidov v potaku Demänová. Ceskosl.parasit. 4: 239-247.
PALING, J.E.	1965	The population dynamics of the monogenean gill parasites Discocotyle sagitta Leuckart on Windermere trout, Salmo trutta, L. Parasitology, 55: 667-695.
PAPERNA, I.	1963a	Some observations on the biology and ecology of Dactylogyrus vastator in Israel. Bamidgeh. Israel, 15: 8-28.
PAPERNA, I.	1963b	Dynamics of Dactylogyrus vastator Nybelin (Monogenea) population on the gills of carp fry in fish ponds. Bamidgeh. Israel, 15: 31-50.
PROST, M.	1957a	Dactylogyrus sp.n and Gyrodactylus raabei sp.n - new species of Monogenoidea of gills of fishes. Acta.parasit.pol. 5: 107-114.
PROST, M.	1957b	Monogenoidea of gills of fishes of Vistula. Acta.parasit.pol. 5: 299-395.
RAWSON, D.	1952	The occurrence of parasitic worms in British freshwater fishes. Ann.Mag.nat.Hist. 12 (5): 877-887.
RIZVI, S.S.H.	1964	The parasite fauna of the fish of Rostherne Mere, Cheshire. Ph.D.thesis, University of Liverpool.
ROMAN, E.	1953	Contributii la cunoasterea faunei de monogenee din R.P.R. Bull.Stiintific 5: 807-831.

SPROSTON, N.G. 1946 A Synopsis of the monogenetic trematodes. Trans.zool.Soc.Lond. 4: 185-600.

THOMAS, J.D. 1964 A comparison between the helminth burdens of male and female brown trout Salmo trutta L., from a natural population in the River Teify, West Wales. Parasitology. 54: 263-272.

VAN CLEAVE, H.J. 1953 Acanthocephala of North American Mammals. Illinois biol.Monogr. 23: 1-179.

VICKERS, K.V. 1951 Some trematodes from freshwater fish of north-east Ireland. Ir.Nat.J. 10 (7): 189-190.

WILES, M. 1965 Reproduction in the gill fluke Diplozoon paradoxum v Nordmann, 1832. Parasitology, 55: 4-5P.

ZELLER, A. 1872 Untersuchungen über die Entwicklung des Diplozoon paradoxum. Z.wiss.Zool. 22: 168-180.

CHAPTER FOUR.

DIGENEA.

Introduction.

Digenetic trematodes in the larval and adult stages are common parasites of many freshwater fishes. The larval forms for which the fish acts as an intermediate host may be encysted in the skin or the fins, or occur unencysted in a more stable environment such as the vitreous humor of the eye. The adults usually occur in the intestine which allows easy passage of the eggs to the exterior for continuation of the life cycle, but some adults also occur in the urinary bladder, urinary ducts and in the circulatory system.

The occurrence and seasonal dynamics of three species of adult Digenea, and preliminary observations on two other adult Digenea were investigated in the present survey.

Methods.

Fresh and frozen material was fixed and preserved in A.F.A. The fresh material was relaxed in water prior to fixation. Material was examined stained and unstained, Digenea being stained with acetic haematoxylin (Chubb, 1962). Each species was identified as far as possible, and the occurrence, intensity of infection and state of maturity recorded.

Results.

Species recorded.

Five species of adult Digenea were recorded from five species of

fish, four species were found in the alimentary canal and one in the urinary bladder (Table 4.1).

All the Digenea, with the exception of A.transversale, have previously been recorded in Britain. A.transversale was recorded from the intestine of T.thymallus in the present investigation. This was the first record of this species in Britain, and from T.thymallus. A.transversale (syn. Fasciola transversalis, Rudolphi, 1802; Distoma transversale Rudolphi, 1819) was first described by Rudolphi in 1802. Previous records of A.transversale are shown in Table 4.2.

Szidat (1938) redescribed the species from a single specimen in Cobitis taenia L. from East Prussia, and this was the first specimen found for 130 years after the original discovery. Markevich (1963) stated that the metacercaria of this species were believed to encyst in C.pulex, and are possibly the forms known as Distomum agamos Linstow, which is a progenetic form eaching sexual maturity in C.pulex.

Measurements of the specimens of A.transversale in T.thymallus from the River Lugg are shown in Table 4.3. These measurements were compared with those of Bychowskaya-Pavlovskaya (1964). The measurements for A.transversale found in Britain fall within the range recorded by Russian workers. The most characteristic feature was the large dimension of the ventral sucker compared to the oral sucker. The overall dimensions of A.transversale from the present survey were smaller than those recorded from Russia. The differences in size may be the result of most specimens from the River Lugg being immature and being recorded from a thymallid instead of a cyprinid host.

TABLE 4.1:

The hosts and site of infection of Digenea from the fish of the River Lugg.

Hosts	Parasites				
	Allocreadium isoporum	Sphaerostoma bramae	Crepidostomum metoecus	Allocreadium transversale	Phyllodistomum sp.
S.cephalus	Intestinal bulb and intestine	Intestinal bulb and intestine			
L.leuciscus	Intestinal bulb and intestine	Intestinal bulb and intestine			
R.rutilus	Intestinal bulb and intestine	Intestinal bulb and intestine			
T.thymallus			Pyloric coccae and upper intestine	Intestine	Urinary bladder
E.lucius					Urinary bladder

TABLE 4.2:

Previous records of A.transversale

Host	Location	Author
Barbus barbus L.	Zagreb	Babic, 1935.
Nemachilus spp.	Ili Basin	Gvozdev et al.1953.
Tinca tinca	Kustanai Oblast	Agapova, 1960.
Leuciscus idus	Kustanai Oblast	Agapova, 1960.
L.l.baicalensis	Kustanai Oblast	Agapova, 1960.
Carassius carassius (L.)	U.S.S.R., Moscow and Kiev Regions.	x
Misgurnus fossilis (L.)	Berlin U.S.S.R., Moscow and Kiev Regions.	Odhner, 1901.
Cobitis taenia L.	East Prussia U.S.S.R., Moscow and Kiev Regions.	Szidat, 1938. x

x Many records from these hosts have been made from the U.S.S.R., and they are listed in the Index Catalogue of Medical and Veterinary Zoology.

TABLE 4.3:

Comparison between the measurements of A.transversale recorded in the present investigation and in the U.S.S.R.

Measured parameters		Measurements in mm. Length Mean	Length Range	Width Mean	Width Range	Breadth Mean	Breadth Range	No.examined
Whole specimen	B	1.41	1.24 -1.62		0.31 -0.37		0.5 -0.6	10
	R		1.7 -2.6				0.5 -0.8	
Ventral sucker	B	0.29	0.25 -0.32		0.20 -0.24	0.25	0.20 -0.31	10
	R						0.30 x0.43	
Oral sucker	B	0.14	0.12 -0.17		0.12	0.14	0.12 -0.17	10
	R		0.16 -0.26				0.20 x0.26	
Pharynx	B	0.06	0.05 -0.07			0.08	0.06 -0.09	9
	R		0.07 -0.15					
Eggs	B	0.07	0.063-0.085			0.05	0.042-0.063	8
	R		0.086-0.115				0.045-0.098	

Key: B = Measurements for A.transversale in T.thymallus from the River Lugg, Herefordshire.

R = Measurements for A.transversale from Bychovskaya-Pavlovskaya (1964).

The species of Phyllodistomum recorded from the urinary bladder of E.lucius is probably either Phyllodistomum simile Nybelin, 1926, or Phyllodistomum folium (Olfers, 1916). The dimensions of the species found in the present survey are compared with those of P.simile and P.folium recorded from the U.S.S.R. (Table 4.4.) The dimensions of the measured parameters overlap to such an extent that it is impossible to separate the species. As a result of the great variation in dimensions, the separation of P.simile and P.folium on the differences of the size ratio between the oral and ventral suckers (Bychowskaya-Pavlovskaya,1964) would not appear to be valid. Dawes (1946) states in relation to this problem

> "that in the ultimate analysis P.simile is likely to prove identical with P.folium".

Incidence of Infection.

Of the five species of Digenea, A.isoporum and S.bramae were recorded from S.cephalus, L.leuciscus and R.rutilus. Phyllodistomum sp. occurred in T.thymallus (1 record) and E.lucius, and C.metoecus and A.transversale were recorded only from T.thymallus.

Seasonal variation of incidence.

The incidence of infection was expressed as the percentage of each host infected with each species of Digenea (Tables 4.6 - 4.11).

Allocreadium isoporum (Looss, 1894).

The percentage of fish infected by A.isoporum was greater than in

TABLE 4.4:

Measurements of Phyllodistomum spp. recorded from the urinary bladder of E. lucius.

	Specimens from the present investigation	Russian specimens. P.simile	P.folium
	Measurements in mm.		
Length	1.87 - 2.57	0.8 - 2.5	1.2 - 3.2.
Width anterior	0.32 - 0.53	0.5 - 1.3	0.6 - 0.8
Width posterior	0.61 - 0.97		
Oral sucker	0.21 -0.26 x 0.17 -0.21	0.12 - 0.26	0.16 -0.18 x 0.18 -0.20
Ventral sucker	0.24 -0.39 x 0.26 -0.35	0.18 -0.34 x 0.22 -0.40	0.16 -0.30 x 0.25 -0.26
Ovary	0.15 -0.29 x 0.15 -0.20	0.14 -0.22 x 0.16 -0.26	0.12 x 0.16
Vitellaria	0.11 -0.21 x 0.06 -0.11	0.12 -0.14 x 0.06 -0.08	0.36 -0.44 x 0.16 -0.24
Testes	0.24 -0.36 x 0.16 -0.28	0.16 -0.36 x 0.12 -0.36	0.26 -0.34 x 0.16 -0.22
Eggs	0.034-0.042 x 0.021-0.025	0.033-0.039 x 0.022-0.029	0.023-0.033 x 0.016-0.023

the case of infection by other Digenea. Of the infected fish a higher percentage of S.cephalus were infected (67.4%), compared to L.leuciscus (51.2%) and R.rutilus (12.6%). The incidence of A.isoporum was recorded in each of the monthly samples from each infected host (Tables 4.5, 4.6, 4.7). With slight variations a similar pattern of incidence for A.isoporum was present in S.cephalus, L.leuciscus and R.rutilus. From January to February an increase in infection occurred, but after this the incidence of infection remained fairly constant until July, except in R.rutilus where infection increased gradually to reach a peak in June. Lower figures recorded in May from L.leuciscus and R.rutilus were the result of poor samples of four and nine fish respectively. A marked drop in incidence was recorded in August from all three hosts, after which an increase was recorded in September and October from S.cephalus and L.leuciscus, but only in October from R.rutilus, no infection being recorded from the latter in September. A decrease from 85.0% to 30.0% was recorded from October to November from S.cephalus, but an increase to 61.0% occurred in December. A decrease in incidence in November though less marked was also recorded from infections in L.leuciscus and R.rutilus both of which were followed by a slight increase in December.

Sphaerostoma bramae (Müller, 1776).

S.bramae occurred in S.cephalus, L.leuciscus and R.rutilus, and in all three hosts the incidence of infection was low compared to A.isoporum. A greater incidence of S.bramae was recorded from R.rutilus compared to S.cephalus and L.leuciscus (Tables 4.8, 4.9, 4.10) and this

contrasted with infection by A.isoporum where the lowest incidence was recorded from R.rutilus.

The percentage of R.rutilus infected increased from January to June with the exception of a slight decrease in May which was the result of the poor May sample. After June the incidence of infection decreased, and between August and October only three R.rutilus were infected, and infection was absent in September. An increase in incidence occurred between October and December but this had not reached the level of the previous January in the December sample.

The incidence of infection in L.leuciscus and S.cephalus was very sporadic (Tables 4.9, 4.10). In the former S.bramae was recorded in March, April and May, and again in October and December. Infection of S.cephalus occurred in all months except those between June and October, and nearly 50.0% of the February and April samples were infected. S.bramae was absent from all three hosts between June and October and the seasonal variation of incidence was therefore similar to that recorded for A.isoporum.

Crepidostomum metoecus (Braun, 1900).

Approximately 33.0% of all T.thymallus sampled were infected with C.metoecus. With the exception of June and August infection was recorded in all months from which samples were obtained (Table 4.11). No samples were obtained in January and September. The highest incidences of infection were recorded in February (91.0%) and April (88.0%), after

which there was a fall to 50.0% in May. With the exception of a low grade infection in July (6.6%) no further infection was recorded until October. The incidence of infection between October and December was much lower than that recorded from the previous January.

The lack of infection in the summer months indicated that a similar pattern of seasonal variation may exist to that observed for A.isoporum and S.branae.

Allocreadium transversale (Rudolphi, 1802).

The occurrence of this parasite was rare. It was recorded from only eleven T.thymallus (5.6%) (Table 4.12); three times in February, three times in April; once in May, twice in July and twice in December. Clearly it was impossible to state from these few records whether there was any seasonal variation in the incidence of infection.

Phyllodistomum sp.

Incidence in E.lucius.

Phyllodistomum sp. was recorded from the urinary bladder of seven E.lucius. However only small numbers of E.lucius were caught throughout the year, therefore it was impossible to learn anything about the seasonal variation in incidence of Phyllodistomum sp. except that it was only recorded in June (75% incidence) and July (14.3% incidence).

Incidence in T.thymallus.

Only one specimen of Phyllodistomum sp. was recorded from the urinary bladder of T.thymallus (0.5% incidence), and this specimen was recorded in a female fish in the 20-25 cm. group from the July sample.

TABLE 4.5:

The incidence of A.isoporum in S.cephalus.

Month	No.fish/sample	Infected fish		Female fish		Infected female fish		Male fish		Infected male fish	
		No.	%	No.	%	No.	%	No.	%	No.	%
Jan.	32	15	46.8	19	59.4	6	31.6	13	40.6	9	69.2
Feb.	31	28	88.3	*14	52.0	14	100.0	*13	48.0	14	92.8
Mar.	29	23	79.3	18	62.1	15	83.3	11	37.9	8	72.7
Apr.	30	28	93.3	14	46.6	12	85.7	16	53.4	16	100.0
May	31	19	61.3	20	64.5	11	55.0	11	35.5	8	72.7
June	30	25	83.3	19	63.3	15	78.9	11	36.7	10	90.9
July	30	27	90.0	21	70.0	19	90.5	9	30.0	8	88.8
Aug.	30	7	23.3	14	46.6	3	21.4	16	53.4	4	25.0
Sept.	28	19	67.8	16	57.0	10	62.5	12	43.0	9	75.0
Oct.	27	23	85.2	17	63.0	15	88.2	10	37.0	8	80.0
Nov.	30	9	30.0	20	66.7	3	15.0	10	33.3	6	60.0
Dec.	31	19	61.3	16	51.6	10	62.5	15	48.4	9	60.0
Total	359	242	67.4	208	58.0	133	63.9	147	42.0	109	73.5

Key: * Sex of 4 fish undetermined.

TABLE 4.6:

The incidence of A.isoporum in L.leuciscus.

Month	No.fish/sample	Infected fish		Female fish		Infected female fish		Male fish		Infected male fish	
		No.	%	No.	%	No.	%	No.	%	No.	%
Jan.	33	14	42.4	10	30.0	4	40.0	23	70.0	10	43.5
Feb.	31	21	67.7	15	48.0	11	73.3	16	52.0	10	62.5
Mar.	30	19	66.7	12	40.0	7	58.3	18	60.0	12	66.6
Apr.	35	21	60.0	14	40.0	6	43.0	21	60.0	15	71.4
May	4	1	25.0	4	100.0	1	25.0	0		0	
June	30	16	53.3	16	53.3	8	50.0	14	46.7	8	57.0
July	30	12	40.0	13	43.0	6	46.0	17	57.0	6	35.3
Aug.	30	3	10.0	16	53.3	1	6.3	14	46.7	2	14.6
Sept.	30	15	50.0	22	73.0	10	45.4	8	27.0	5	62.5
Oct.	31	23	71.0	20	64.5	16	80.0	11	35.5	7	63.6
Nov.	28	13	42.8	17	61.0	9	52.9	11	39.0	4	36.3
Dec.	30	17	57.0	13	43.0	9	69.2	17	57.0	3	47.0
Total	342	175	51.2	172	56.3	88	51.2	170	49.7	87	51.2

TABLE 4.7:

The incidence of A.isoporum in R.rutilus.

Month	No.fish/sample	Infected fish		Female fish		Infected female fish		Male fish		Infected male fish	
		No.	%	No.	%	No.	%	No.	%	No.	%
Jan.	33	1	3.0	12	36.4	1	8.3	21	63.6	0	
Feb.	27	3	11.1	12	44.4	3	25.0	15	55.6	0	
Mar.	30	2	6.6	16	53.4	2	12.5	14	46.6	0	
Apr.	16	3	18.8	10	62.5	2	20.0	6	37.5	1	16.6
May	9	1	22.2	3	33.3	0	0	6	66.7	1	16.6
June	30	14	46.6	14	46.6	8	57.0	16	53.4	6	37.5
July	22	5	22.5	12	54.5	3	25.0	10	44.5	2	20.0
Aug.	30	2	6.6	22	76.6	1	4.5	8	23.4	1	12.5
Sept.	30	0		15	50.0	0		15	15.0	0	
Oct.	30	4	13.2	12	40.0	4	33.3	18	60.0	0	
Nov.	30	2	6.6	11	36.6	2	18.1	19	63.4	0	
Dec.	30	3	9.9	15	50.0	3	20.0	15	50.0	0	
Total	317	40	12.6	154	48.6	29	15.0	163	51.4	11	6.7

TABLE 4.8:

The incidence of S.brawae in R.rutilus.

Month	No.fish/sample	Infected fish		Female fish		Infected female fish		Male fish		Infected male fish	
		No.	%	No.	%	No.	%	No.	%	No.	%
Jan.	33	9	27.0	12	36.4	5	41.7	21	63.6	4	19.0
Feb.	27	10	37.0	12	44.4	5	41.7	15	55.6	5	33.3
Mar.	30	11	36.6	16	53.4	7	43.7	14	46.6	4	28.5
Apr.	16	8	50.0	10	62.5	6	60.0	6	37.5	2	33.3
May	9	2	44.4	3	33.3	1	33.3	6	66.7	1	16.6
June	30	16	50.0	14	46.6	8	50.0	16	53.4	8	50.0
July	22	6	27.0	12	54.5	6	50.0	10	44.5	0	0
Aug.	30	2	6.6	22	76.6	2	9.1	8	23.4	0	0
Sept.	30	1	3.3	15	50.0	1	6.6	15	50.0	0	0
Oct.	30	6	16.6	12	40.0	5	33.3	18	60.0	1	5.5
Nov.	30	4	13.3	11	36.6	2	18.2	19	63.4	2	10.5
Dec.	30	8	26.6	15	50.0	7	46.6	15	50.0	1	6.6
Total	317	83	26.2	154	48.6	55	17.4	163	51.4	28	17.2

TABLE 4.9:

The incidence of S.bramae in S.cephalus.

Month	No.fish/sample	Infected fish		Female fish		Infected female fish		Male fish		Infected male fish	
		No.	%	No.	%	No.	%	No.	%	No.	%
Jan.	32	3	9.4	19	59.4	1	5.3	13	40.6	2	15.4
Feb.	31	13	41.9	14	52.0	5	35.7	13	48.0	8	61.5
Mar.	29	5	17.2	18	62.1	4	22.2	11	37.9	1	9.1
Apr.	30	14	46.6	14	46.6	5	35.7	16	53.4	9	56.2
May	31	6	19.4	20	64.5	4	20.0	11	35.5	2	18.2
June	30	0		19	63.3	0		11	36.7	0	
July	30	0		21	70.0	0		9	30.0	0	
Aug.	30	0		14	46.6	0		16	53.4	0	
Sept.	28	0		16	57.0	0		12	43.0	0	
Oct.	27	0		17	63.0	0		10	37.0	0	
Nov.	30	2	6.6	20	66.7	0		10	33.3	2	20.0
Dec.	31	5	16.1	16	51.6	2	12.5	15	48.4	3	20.0
Total	359	48	13.4	208	58.0	21	10.1	147	42.0	27	18.4

TABLE 4.10:

The incidence of S.bramae in L.leuciscus.

Month	No.fish/sample	Infected fish		Female fish		Infected female fish		Male fish		Infected male fish	
		No.	%	No.	%	No.	%	No.	%	No.	%
Jan.	33	0		10	30.0	0		23	70.0	0	
Feb.	31	0		15	48.0	0		16	52.0	0	
Mar.	30	2	6.6	12	40.0	1	8.3	18	60.0	1	5.5
Apr.	35	4	11.4	14	40.0	2	14.3	21	60.0	2	9.5
May	4	1	25.0	4	100.0	1	25.0	0		0	
June	30	0		16	53.3	0		14	46.7	0	
July	30	0		13	43.0	0		17	57.0	0	
Aug.	30	0		16	53.3	0		14	46.7	0	
Sept.	30	0		22	73.0	0		8	27.0	0	
Oct.	31	1	3.2	20	64.5	1	5.0	11	35.5	0	
Nov.	28	0		17	61.0	0		11	39.0	0	
Dec.	30	2	6.6	13	43.0	2	15.4	17	57.0	0	
Total	342	10	2.9	172	56.3	7	4.1	170	49.7	3	1.8

TABLE 4.11:

The incidence of C.metoecus in T.thymallus.

Month	No.fish/sample	Infected fish		Female fish		Infected female fish		Male fish		Infected male fish	
		No.	%	No.	%	No.	%	No.	%	No.	%
Jan.		NO SAMPLE									
Feb.	11	10	91.0	4	36.4	4	100.6	7	63.6	6	85.7
Mar.	18	11	61.0	7	38.9	5	71.4	11	61.1	6	54.5
Apr.	25	22	88.0	10	40.0	8	80.0	15	60.0	14	93.3
May	8	4	50.0	5	62.5	3	60.0	3	37.5	1	33.3
June	17	0		10	58.8	0		7	41.2	0	
July	30	2	6.6	10	33.3	0		20	66.7	2	10.0
Aug.	5	0		3	60.0	0		2	40.0	0	
Sept.		NO SAMPLE									
Oct.	25	9	36.0	14	56.0	5	35.7	11	44.0	4	36.3
Nov.	30	6	23.3	14	46.6	2	14.3	16	53.4	4	25.0
Dec.	30	9	30.0	17	56.6	6	35.3	13	43.4	3	23.1
Total	199	73	36.7	94	47.2	33	35.1	105	52.8	40	38.1

Incidence in relation to the length of the host.

The fish were divided into length groups (Tables 4.35,-4.38). The number of fish infected with each digenean was recorded for each length group, and for each sex per length group, in each monthly sample and for the total sample (Tables 4.13 - 4.19).

Splitting of the information as above resulted in an insufficient quantity of data in each length group per monthly sample to determine the presence or absence of any relationship between incidence of infection and length. The data for each length group was therefore summarized, and as different numbers of fish were present in the different length groups the number of infected fish per length group was expressed as a percentage of the total number of fish examined per length group (Table 4.12).

Three patterns of incidence of infection were observed in relation to the length of the host.

a) An increase in the incidence of infection occurred with increase in length. This was shown in the infection of L.leuciscus and R.rutilus with both A.isoporum and S.bramae. The incidence of infection of A.isoporum for each length group in L.leuciscus was greater than that for R.rutilus, whereas the incidence of R.rutilus from each length group with S.bramae was greater than the incidence in L.leuciscus.

b) An increased incidence of infection occurred until the greatest length group, where a decrease in incidence was observed. This pattern was observed in the incidence of S.bramae in S.cephalus and C.metoecus

in T.thymallus. Infection of S.cephalus with S.bramae was uncommon and from the small amount of data no definite statement could be made about the relationship of incidence to length. The incidence of C.metoecus decreased in the 25 - 30 cm. group of T.thymallus. 100.0% incidence was recorded from the 30 - 35 cm. group but this information was misleading, as only one fish was sampled from this length group, and it was infected. The largest sample of fish in the 25 - 30 cm. group were caught in July. Two infected fish occurred in this length group in July, when the incidence of C.metoecus was low, and where fish in other length groups were uninfected. If as many 25 - 30 cm. fish were caught in months where infection was common, as were caught in July, a different relationship between incidence and length might have been observed. A more accurate interpretation of this data would be possible if similar and adequate numbers of fish in each length group in each monthly sample were present. This is the ideal situation which rarely exists, but plotting of the number of infected fish as a percentage of the total number of fish for each length group from each monthly sample would give data for a valid comparison, providing that if any seasonal variation occurred, the same variation was present in each length group. The data from T.thymallus showed that fish infected with C.metoecus in the 20 - 25 cm. group appeared to have a greater incidence of infection than other length groups from February to April, whereas 15 - 20 cm. fish appear to have a greater incidence from October to November. This may mean that the smaller fish are more susceptible to infection at this time of year than

larger fish, but until more data are available the significance of these observations is doubtful.

c) No apparent relationship between incidence and length of the host.

The above observation was made for A.isoporum infections from S.cephalus and A.transversale infections from T.thynallus. The incidence of A.isoporum increased in S.cephalus between the 0 - 20 and 20 - 30 cm. groups, reaching a maximum in the latter. Incidence declined in the 30 - 40 cm. group and then increased slightly in the 40 - 50 cm. group.

The incidence of A.isoporum in S.cephalus was the highest digenean incidence recorded. It is suspected that the apparent lack of any relationship between incidence and length of host where most data were present might be the case for other infections if a similar quantity of data were available.

A.transversale was uncommon. It is only possible to state that the greatest percentage of infected fish occurred in the 0 - 15 cm. group and to a lesser extent in the 25 - 30 cm. group. The only fish recorded from the 30 - 35 cm. group was infected with both A.transversale and C.metcecus.

Incidence in relation to the sex of the host.

The data present in each category when each sample was split into the number of infected fish of each sex in each length group were

insufficient to draw any conclusions as to the presence or absence of any relationship between the sex of the host and incidence of infection (Tables 4.13 - 4.19). The data for each sex in each length group were summarized (Table 4.12) and the following observations made.

a) In the lowest length groups where both female and male fish were present i.e. A.isoporum infections in the 0 - 15 cm. group of L.leuciscus and C.metoecus infections in the 0 - 15 cm. group of T.thymallus, a similar incidence was present in each sex. The exception was A.transversale where a greater incidence of female T.thymallus in the 0 - 15 cm. group were infected. The validity of this observation was very doubtful as the overall incidence of A.transversale was extremely low.

b) A.isoporum infections.

The incidence of infection in male and female L.leuciscus was similar in all length groups except the 25 - 30 cm. group where there was a greater incidence of infected males (Table 4.14).

A similar percentage of male and female R.rutilus were infected except in the 25 - 30 cm. group where a greater percentage of females were infected, and in the 30 - 35 cm. group where only infected females were present (Table 4.15).

A greater percentage of female S.cephalus were infected in the 20 - 30 cm. group, whereas the difference between the incidence of female and male fish in the 30 - 40 and 40 - 50cm. groups was negligible (Table 4.13).

c) S.bramae infections.

Only a few data were available from S.cephalus and L.leuciscus. The difference in the incidence of infection of female and male S.cephalus was negligible except in the 20 - 30cm. group where a greater percentage of male fish were infected (Table 4.17). Infection of both male and female L.leuciscus with S.bramae only occurred in the 20 - 25cm. group, and the low incidence does not permit any conclusions as to any relationship between the sex of L.leuciscus and the incidence of S.bramae (Table 4.18).

A greater percentage of female R.rutilus were infected in the 15 - 20 and 25 - 30cm. groups, but in the 20 - 25cm. group the percentage of infected male and female fish was approximately the same. Thirty-one female and two male R.rutilus were present in the 30 - 35 cm. group (Table 4.37) and only females (12) were infected (Table 4.16).

d) C.metoecus infection.

Only in the 20 - 25cm. group were more females infected than males. In the 30 - 35cm. group only one male T.thymallus was recorded and this was infected, giving rise to the misleading figure of 100.0% incidence (Table 4.19).

The data from all the length groups were summarized (last column Table 4.12), and this showed that a marked difference between the percentage of infected male and female fish only occurred in R.rutilus, where a higher percentage of females were infected with A.isoporum and S.bramae.

TABLE 4.12:

The number of infected fish in each length group expressed as a percentage of the total number of fish in each length group.

		Length in cms.																		
		0-20			20-30			30-40			40-50						Totals		
		F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
S.cephalus	A.isoporum	0	66.6	50.0	68.7	80.8	74.2	68.3	58.7	58.5	62.5	57.1	61.8				63.9	72.6	67.4
	S.bramae	0	0	0	8.1	18.1	12.8	13.3	19.6	16.0	10.4	14.3	10.9				10.0	18.0	13.4
		0-15			15-20			20-25			25-30						Totals		
		F	M	T	F	M	T	F	M	T	F	M	T				F	M	T
L.leuciscus	A.isoporum	50.0	40.0	33.3	48.3	45.0	46.9	52.3	45.1	48.5	56.3	78.1	67.2				51.2	51.2	51.2
	S.bramae	0	0	0	0	5.0	2.0	3.0	1.8	2.3	12.5	0	6.3				4.1	1.8	2.9
		0-15			15-20			20-25			25-30			30-35			Totals		
		F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
R.rutilus	A.isoporum	0	0	0	8.0	6.4	6.7	9.3	7.1	8.5	26.3	7.7	18.7	27.6	0	25.8	18.8	6.8	12.6
	S.bramae	0	0	0	8.0	1.7	15.1	3.3	25.0	23.9	15.6	25.6	17.5	11.4	0	38.7	35.7	17.2	26.2
		0-15			15-20			20-25			25-30			30-35			Totals		
		F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
T.thymallus	C.metoecus	33.3	33.3	33.3	40.0	36.4	36.5	48.1	48.9	43.7	14.3	18.2	17.2		100.0	100.0	36.2	37.0	36.7
	A.transversale	16.6	5.5	10.0	3.3	4.5	3.8	7.1	0	3.5	0	9.1	6.9		100.0	100.0	6.4	4.8	5.6

Key: T = total
F = Female
M = Male

TABLE 4.13:

The number of S.cephalus of each sex in each length group infected with A.isoporum.

	Length in cms.														
	0-20			20-30			30-40			40-50			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				5	9	14				1	0	1	6	9	15
Feb.				6	11	17	3	3	6	5	0	5	14	14	28
Mar.				8	6	14	6	2	8	1	0	1	15	8	23
Apr.				6	10	16	5	5	10	1	1	2	12	16	28
May	0	1	1	6	7	13	3	0	3	2	0	2	11	8	19
June	0	1	1	7	6	13	4	2	6	4	1	5	15	10	24
July				10	4	14	4	3	7	5	1	6	19	8	27
Aug.				1	2	3	1	1	2	1	1	2	3	4	7
Sept.				5	3	8	2	6	8	3	0	3	10	9	19
Oct.				7	6	13	4	2	6	4	0	4	15	8	23
Nov.				2	5	7	0	1	1	1	0	1	3	6	9
Dec.				5	7	12	3	2	5	2	0	2	10	9	19
Total	0	2	2	68	76	144	35	27	62	30	4	34	133	109	242
% total no. of male and female fish in each length group.		66.6	50.0	80.7	80.8	74.2	58.3	58.7	58.5	62.5	57.1	61.8	63.9	72.6	67.4

Key: T = total
F = Female
M = Male

TABLE 4.14:

The number of *L.leuciscus* of each sex in each length group infected with *A.isoporum*.

Month	Length in cms. 0-15 F	0-15 M	0-15 T	15-20 F	15-20 M	15-20 T	20-25 F	20-25 M	20-25 T	25-30 F	25-30 M	25-30 T	Totals F	Totals M	Totals T
Jan.							1	7	8	3	3	6	4	10	14
Feb.							8	8	16	3	2	5	11	10	21
Mar.				2	2	4	4	2	6	1	8	9	7	12	19
Apr.	0	1	1	3	3	6	3	8	11	0	3	3	6	15	21
May										1	0	1	1	0	1
June				1	1	2	7	6	13	0	1	1	8	8	16
July							5	4	9	1	2	3	6	6	12
Aug.							1	2	3				1	2	3
Sept.				1	0	1	8	4	12	1	1	2	10	5	15
Oct.				2	0	2	10	6	16	4	1	5	16	7	23
Nov.	1	0	1	1	1	2	5	1	6	2	2	4	9	4	13
Dec.	2	1	3	4	2	6	1	3	4	2	2	4	9	8	17
Total	3	2	5	14	9	23	53	51	104	18	25	43	88	87	175
% total no. of male and female fish in each length group.	30.0	40.0	33.3	48.3	45.0	46.9	52.3	45.1	48.5	56.3	78.1	67.2	51.2	51.2	51.2

Key: T = total
F = Female
M = Male

TABLE 4.15:

The number of R.rutilus of each sex in each length group infected with A.isoporum.

Month	Length in cms. 0-15 F	0-15 M	0-15 T	15-20 F	15-20 M	15-20 T	20-25 F	20-25 M	20-25 T	25-30 F	25-30 M	25-30 T	30-35 F	30-35 M	30-35 T	Totals F	Totals M	Totals T
Jan.													1	0	1	1	0	1
Feb.				1	0	1				1	0	1	1	0	1	3	0	3
Mar.										1	0	1	1	0	1	2	0	2
Apr.				1	0	1				0	1	1	1	0	1	2	1	3
May				0	1	1										0	1	1
June				0	4	4	1	1	2	5	1	6	2	0	2	8	6	14
July				0	1	1	2	1	3	1	0	1				3	2	5
Aug.										0	1	1	1	0	1	1	1	2
Sept.																		
Oct.										3	0	3	1	0	1	4	0	4
Nov.							1	0	1	1	0	1				2	0	2
Dec.										3	0	3				3	0	3
Total				2	6	8	4	2	6	15	3	18	8	0	8	29	11	40
% of total no.of male and female fish in each length group				8.0	6.4	6.7	9.3	7.1	8.5	26.3	7.7	18.7	27.6	0	25.8	18.8	6.8	12.6

Key: T= Total
F= Female
M= Male

TABLE 4.16:

The number of *R.rutilus* of each sex in each length group infected with *S.bramae*.

Month	Length in cms. 0-15 F	0-15 M	0-15 T	15-20 F	15-20 M	15-20 T	20-25 F	20-25 M	20-25 T	25-30 F	25-30 M	25-30 T	30-35 F	30-35 M	30-35 T	Totals F	Totals M	Totals T
Jan.				2	1	3	0	0	0	1	3	4	2	0	2	5	4	9
Feb.				0	2	2	4	0	4	1	3	4				5	5	10
Mar.				1	1	2	1	3	4	4	0	4	1	0	1	7	4	11
Apr.				1	0	1	0	1	1	3	1	4	2	0	2	6	2	8
May				1	1	2										1	1	2
June				0	5	5	0	3	3	3	0	3	5	0	5	8	8	16
July				1	0	1	1	0	1	4	0	4				6	0	6
Aug.										1	0	1	1	0	1	2	0	2
Sept.										1	0	1				1	0	1
Oct.				1	1	2				3	0	3	1	0	1	5	1	6
Nov.							2	0	2	0	2	2				2	2	4
Dec.							2	0	2	5	1	6				7	1	8
Total				7	11	18	10	7	17	26	10	36	12	0	12	65	28	93
% of total no.of male and female fish in each length group.				38.0	11.7	15.1	23.3	25.0	23.9	45.6	25.6	37.5	41.4		28.7	35.7	17.2	26.2

Key: T = Total
F = Female
M = Male

TABLE 4.17:

The number of S.cephalus of each sex in each length group infected with S.bramae.

Month	Length in cms. 0-20 F	0-20 M	0-20 T	20-30 F	20-30 M	20-30 T	30-40 F	30-40 M	30-40 T	40-50 F	40-50 M	40-50 T	Totals F	Totals M	Totals T
Jan.				1	1	2	0	1	1	0	0	0	1	2	3
Feb.				2	7	9	1	1	2	2	0	2	5	8	13
Mar.				2	0	2	2	1	3	0	0	0	4	1	5
Apr.				1	4	5	3	4	7	1	1	2	5	9	14
May				1	2	3	2	0	2	1	0	1	4	2	6
June				0	0	0	0	0	0	0	0	0			
July				0	0	0	0	0	0	0	0	0			
Aug.				0	0	0	0	0	0	0	0	0			
Sept.				0	0	0	0	0	0	0	0	0			
Oct.				0	0	0	0	0	0	0	0	0			
Nov.				0	1	1	0	1	1	0	0	0	0	2	2
Dec.				1	2	3	0	1	1	1	0	1	2	3	5
Total				8	17	25	8	9	17	5	1	6	21	27	48
% of total no. of male and female fish in each length group.				8.1	18.1	12.8	13.3	19.6	16.0	10.4	14.3	10.9	10.0	18.0	13.4

Key: T = Total
F = Female
M = Male

TABLE 4.18:

The number of L.leuciscus of each sex in each length group infected with S.bramae.

Month	Length in cms. 0-15 F	0-15 M	0-15 T	15-20 F	15-20 M	15-20 T	20-25 F	20-25 M	20-25 T	25-30 F	25-30 M	25-30 T	Totals F	Totals M	Totals T
Jan.															
Feb.															
Mar.							0	1	1	1	0	1	1	1	2
Apr.				0	1	1	2	1	3				2	2	4
May										1	0	1	1	0	1
June															
July															
Aug.															
Sept.															
Oct.							1	0	1				1	0	1
Nov.															
Dec.										2	0	2	2	0	2
Total				0	1	1	3	2	5	4	0	4	7	3	10
% of total no. of male and female fish in each length group.				0	5.0	2.0	3.0	1.8	2.3	12.5	0	6.3	4.1	1.8	2.9

Key: T = Total
F = Female
M = Male

TABLE 4.19:

The number of T.thymallus of each sex in each length group infected with C.metoecus.

Month	Length in cms. 0-15 F	0-15 M	0-15 T	15-20 F	15-20 M	15-20 T	20-25 F	20-25 M	20-25 T	25-30 F	25-30 M	25-30 T	30-35 F	30-35 M	30-35 T	Totals F	Totals M	Totals T
Jan.	NO SAMPLE																	
Feb.	2	1	3	1	1	2	1	4	5							4	6	10
Mar.			0	1	1	2	4	5	9							5	6	11
Apr.	1	2	3	1	1	2	6	10	16	0	1	1				8	14	22
May			0			0	2	0	2	1	0	1	0	1	1	3	1	4
June			0			0			0			0			0			0
July			0			0			0	0	2	2			0	0	2	2
Aug.			0			0			0			0			0			0
Sept.	NO SAMPLE																	
Oct.	1	1	2	4	3	7			0			0			0	5	4	9
Nov.	0	1	1	2	0	2	0	3	3			0			0	2	4	6
Dec.	0	1	1	3	1	4	3	0	3	0	1	1				6	3	9
Total	4	6	10	12	7	19	16	22	38	1	4	5	0	1	1	33	40	73
% of total no.of male and female fish in each length group.	33.3	33.3	33.3	40.0	36.4	36.5	38.1	48.9	43.7	14.3	18.2	17.2		100.0	100.0	36.2	37.0	36.7

Key: T = Total
F = Female
M = Male

Intensity of Infection.

Total intensity of infection.

The intensity of infection of each species of Digenea from each infected host is recorded as the mean number of parasites per infected fish (Tables 4.20, 4.22, 4.24, 4.26, 4.28, 4.30, 4.32).

A.isoporum:

i) The greatest intensity of infection was recorded from R.rutilus (Table 4.24) where although the occurrence of infection was lower than in either S.cephalus or L.leuciscus (Tables 4.5, 4.6, 4.7), one or two exceptionally heavy infections were encountered (Table 4.25).

ii) A greater actual number of A.isoporum were recorded from S.cephalus (Table 4.21), but a greater number of fish were infected (Table 4.5) making the mean number of parasites (Table 4.20) less than in R.rutilus.

iii) The actual number of A.isoporum in L.leuciscus was less than in either R.rutilus or S.cephalus (Table 4.23). The number of infected L.leuciscus was greater than the number of infected R.rutilus but less than the number of infected S.cephalus (Table 4.6). This resulted in a lower mean number of parasites per total infected L.leuciscus (Table 4.22) than in either R.rutilus or S.cephalus.

S.bramae.

The greatest mean number of parasites was recorded from R.rutilus (Table 4.26) where the occurrence of infection and the number of parasites present (Tables 4.7, 4.27) were greater than in either

S.cephalus (Tables 4.5, 4.21) or L.leuciscus (Tables 4.6;4.23). Where A.isoporum and S.bramae were present in the same host, a greater mean number of A.isoporum was present.

C.metoecus.

The mean number of C.metoecus for infected T.thymallus was approximately the same as the mean number of A.isoporum in S.cephalus (Tables 4.32, 4.20), but the occurrence of C.metoecus (Table 4.11) and the number of parasites recorded (Table 4.33) were less than the records for A.isoporum in S.cephalus (Tables 4.5, 4.21) as a result of the smaller number of T.thymallus sampled.

A.transversale, Phyllodistomum sp.

The mean number of A.transversale in infected T.thymallus was 2.6, and the mean number of Phyllodistomum sp. in E.lucius was 23.0 (Table 4.34). The low occurrence of infection of these two species invalidated the significance of these records of intensity.

Seasonal variation in intensity of infection.

A.isoporum.

The overall pattern of seasonal variation in intensity of infection was similar in S.cephalus, L.leuciscus and R.rutilus (Tables 4.20, 4.22, 4.24). An increase in intensity occurred between January and February, and was most apparent in S.cephalus and L.leuciscus.

Between February, June and July there was a slight increase in intensity in S.cephalus and L.leuciscus, but this was of doubtful significance. A marked increase in intensity occurred between February and July in R.rutilus. The lower figure recorded in May was the result of the poor sample of only nine fish. A conspicuous fall in the intensity of infection occurred in July and August in S.cephalus, in August in L.leuciscus and August and September in R.rutilus, no infection being recorded in R.rutilus from the latter month. In September and October an increase in intensity of infection followed by a decrease in November was recorded from L.leuciscus and S.cephalus. The intensity of infection had risen again by December in L.leuciscus but remained low in S.cephalus. Infection reappeared in R.rutilus by October and there was an increase in intensity of infection between October and December.

S.bramae.

The pattern of seasonal variation in intensity of infection was similar to that recorded for A.isoporum. The intensity of S.bramae in R.rutilus was fairly uniform between January and July. A marked decrease in intensity occurred in August and September, after which an increase was recorded in October followed by a decrease in November but a further increase in December (Table 4.26).

The intensity of infection of S.bramae in S.cephalus (Table 4.28) was low when ever infection was present. The absence of S.bramae in R.rutilus between June and October was also noted in the other two hosts

although in the latter case the parasites were absent until November.

C.metoecus.

The intensity of infection increased between February and April, after which a decrease occurred in May and with the exception of two fish in July with a mean number of two parasites, no infection was recorded again until October. The intensity of infection between October and December remained fairly constant although the number of parasites and the mean number per infected fish decreased slightly by December (Tables 4.33, 4.32).

Intensity of infection in relation to the length of the host.

Mean number of parasites for the total number of fish in each length group.

A.isoporum.

An increase in intensity of infection with increase in length of the host was recorded for A.isoporum infections in all three cyprinid hosts (Table 4.34), although the increase recorded between the 25-30 and 30-35cm. groups in R.rutilus was negligible.

S.bramae.

Increased intensity of infection with increased length was recorded for S.bramae from R.rutilus and S.cephalus (Table 4.34). The infrequent records of S.bramae from L.leuciscus prevented any analysis of the mean number of parasites in relation to the length of the host.

C.metoecus.

An increase in the intensity of infection was recorded between the 0 - 15cm. and 20 - 25cm. groups, after which the mean number of parasites decreased in the 25 - 30cm. and 30 - 35cm. groups. (Table 4.34) The decrease in the two latter groups coincided with a decrease in both the occurrence of infection and the total number of fish sampled in these groups. (Tables 4.11, 4.38).

Seasonal variation in the intensity of infection in each length group.

A.isoporum.

The intensity of infection in each length group followed a pattern similar to the seasonal variation in intensity recorded for the total number of infected fish in each monthly sample i.e. the gradual increase in intensity up to June and July, the disappearance of infection in September or October which may be followed by a drop in infection in November before another slight increase in December. This pattern is clearly seen in each length group of S.cephalus where most data were available (Table 4.20). The pattern is also apparent in the length groups of L.leuciscus (Table 4.22) but is obscured in R.rutilus (Table 4.24) when the infected fish were split into the different length groups.

S.bramae.

Only the data from the number of infected R.rutilus in the 25-30cm. length group were sufficient to show a pattern of seasonal variation in intensity of infection, and this was similar to the pattern recorded

when all the infected R.rutilus were examined. (Table 4.26). It is probable that a similar pattern of intensity would be recorded from the other length groups if sufficient data were available. With regard to the seasonal variation in intensity of S.bramae in relation to the length of S.cephalus, it was only possible to state that a low intensity of infection was present between January and May, and November and December in the 20 - 30cm. and 30 - 40cm. groups, and in February, April, May and December in the 40 - 50cm. group. In L.leuciscus low intensities of S.bramae were recorded in March, April and October in the 20 - 25cm. group, in March, May and December in the 25 - 30cm. group and a relatively higher intensity (although this data came from one infected fish) in the 15 - 20cm. group.

C.metoecus (Table 4.32).

The 0 - 15cm., 15 - 20cm. and 20 - 25cm. length groups showed an increase in intensity of infection from February to April, a more or less complete disappearance of infection between June and October, and the reappearance of a slightly lower intensity of infection between October and December. This pattern was similar to the one recorded when all the infected fish were taken into account. Few fish were caught in the 25 - 30cm. and 30 - 35cm. groups, and low intensities were recorded in April, May and July in the 25 - 30cm. group and in May in the 30 - 35cm. group.

Intensity of infection in relation to the sex of the host.

A.isoporum from S.cephalus. (Table 4.20).

Examination of the mean number of parasites per infected male and female fish from each length group in each monthly sample showed that in the 25 - 30cm. group little difference was present between the intensity of infection in male and female S.cephalus. In the 30 - 40cm. group, female fish had a greater intensity of infection than male fish in each monthly sample, with the exception of November where no infected female fish and only one infected male were recorded. In the four months that infected male S.cephalus were recorded in the 40 - 50cm. group, they had a greater mean number of parasites than female fish (Table 4.20).

The mean number of parasites for the total numbers of infected female and male S.cephalus in each length group was calculated (Tables 4.20, 4.34). The same observations were recorded as when each monthly sample was considered, almost an equal intensity of infection was present in female and male fish in the 20 - 30cm. group, a greater intensity in infected female than male fish in the 30 - 40cm. group and a greater intensity in males than females in the 40 - 50cm. group. The comparison of intensity of infection between female and male fish in the 40 - 50cm. group is not really valid as infected females were present in each monthly sample whereas infected males were only present in four samples, two of which were months where the intensity of infection was at its highest (April and June).

Overall when the total number of infected male and female fish were taken into account a higher intensity of infection was recorded from female fish (Table 4.34). An increase in intensity of infection has already been recorded with increase in length of the host (Table 4.20). As most of the larger fish are female (Table 4.35) it is possible that it is the larger size of female fish and not just the fact that as females they are more susceptible to infection, that accounts for the greater intensity of infection. No evidence is available yet to confirm which, if either, of the above suppositions is true.

A.isoporum from L.leuciscus (Tables 4.22, 4.34).

The data from the monthly samples of each length group were summarized (Table 4.34). The difference between the intensity of infection of male and female fish in the 15 - 20 cm. group was negligible i.e. 0.3. Female fish from the 20 - 25cm. and 25 - 30cm. groups had a greater intensity of infection than males, and this was still apparent when the data from the total numbers of infected male and female fish were summarized. The total numbers of male and female L.leuciscus with A.isoporum was 88:87 respectively (Table 4.14), and as these numbers are approximately the same, the difference in intensity of infection between the two sexes may be significant. 53 females to 51 males were infected in the 20 - 25cm. group and, as mentioned above, a higher intensity was recorded from the females. Before any definite statement to the effect that females overall and of any length have a greater intensity of infection than males it is

necessary to sample equal numbers of male and female fish in each length group each month because of the seasonal occurrence of the parasite, or to treat the data by a statistical method to eliminate all other variables that might influence intensity of infection.

A.isoporum from R.rutilus. (Tables 4.24, 4.34).

Splitting the data from each monthly sample into the different length groups obscured the pattern of seasonal variation in intensity of infection shown when all infected fish were examined. The splitting of each monthly sample into different sexes per length group would therefore reveal no further information about seasonal variation in the intensity of infection. Therefore the data from all the samples were summarized for each sex in each length group. No great difference in intensity was recorded from male and female fish in the 15 - 20cm. and 20 - 25cm. groups. However a greater intensity was recorded from male fish in the 25 - 30cm. group, but no infected males were present in the 30 - 35cm. group. When the data from the total number of infected fish were examined, male R.rutilus had a greater overall intensity of infection. This result is probably misleading, and may arise from the heavy infection in June of one male in the 25 - 30cm. group. This heavy infection together with the data from the two other infected male R.rutilus in this length group, one from May and the other from August, gave a very high mean number of parasites per infected male fish for this group, and probably gives an unbalanced picture of the intensity of infection of male R.rutilus in June, in the overall sample

and in the total population.

S.bramae (Tables 4.26, 4.28, 4.30, 4.34).

No apparent difference occurred in the intensity of infection in the length groups where both male and female R.rutilus were present. Only two male R.rutilus out of a total of 31 fish were present in the 30 - 35cm. group, and neither were infected. No difference was recorded between the intensity of infection for the total numbers of male and female R.rutilus infected with S.bramae. (Table 4.26.)

The same observation was made for S.bramae when the data from each sex and length group for all the samples were summarized for S.cephalus.

The few observations of S.bramae infections in L.leuciscus were insufficient to draw any conclusions as to the presence or absence of any relationship between intensity of infection and the sex of the host (Table 4.30).

C.metoecus (Tables 4.32, 4.34).

As for other species the data for each sex and length group for all samples was insufficient to merit any valid conclusions, and therefore the data were summarized for each sex and length group, and for each sex and the total number of infected fish. In T.thymallus a slightly greater intensity was present in females in the 0 - 15cm. group, and in males in the 15 - 20cm. group. In the 20 - 25cm. group no difference in intensity was recorded between the sexes. The same observation was made in the 25 - 30cm. group, although the data were insufficient. The

observations showed that the female fish appeared to have a greater intensity of infection than male fish when they are younger. As the fish grow older the male fish become more heavily infected, until the fish reach a certain age where both sexes have an equal intensity of infection. Until more data becomes available for all length groups it is impossible to determine the significance of the above observation. No difference in intensity of infection between the sexes was found when the total numbers of infected male and female T.thymallus were examined.

Seasonal variation of development and maturation of adult Digenea in the definitive host.

The data on the incidence and intensity of infection recorded for A.isoporum, S.bramae and C.metoecus suggested the presence of an annual life cycle. All the individuals of each species were examined and it was possible to separate the adult Digenea into four main stages of development and maturation:-

Stage I : Parasites small, the gut and rudimentary gonads present, vitellaria absent.

Stage II : Gonads well developed; vitellaria present.

Stage III : Gonads and vitellaria well developed. Eggs present in uterus.

Stage IV : Regression of the gonads; eggs still present.

The number of each stage present each month, was plotted as a percentage of the total number present each month for:-

TABLE 4.20:

The mean number of *A.isoporus* in each sex and length group for the samples of *S.cephalus*.

	Length in cms.														
	0 - 20			20-30			30-40			40-50			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				8.2	7.3	7.6				12.0	0	12.0	8.8	7.3	7.9
Feb.				5.3	7.9	7.6	24.3	9.6	17.0	21.2	0	21.2	15.1	8.3	11.7
Mar.				8.9	4.7	7.1	23.2	2.5	18.0	2.0	0	2.0	14.1	4.1	10.6
Apr.				8.0	8.2	8.1	21.2	8.8	15.0	2.0	65.0	33.5	13.0	11.9	12.4
May.			1.0	4.5	6.9	5.8	25.3	0	25.3	6.5	0	6.5	10.5	6.9	9.2
June	0	5.0	5.0	5.0	4.8	4.9	46.0	17.0	36.3	40.5	63.0	45.0	25.4	14.5	21.3
July				2.2	6.0	3.3	20.5	2.0	12.6	3.2	4.0	3.3	6.3	4.3	5.7
Aug.				1.0	2.5	2.0	18.0	1.0	9.5	1.0	3.0	2.0	6.6	2.2	4.1
Sept.				14.0	6.0	11.0	16.5	11.0	12.4	11.3	0	11.3	13.7	9.3	11.6
Oct.				6.7	17.5	11.7	33.7	3.0	23.5	50.0	0	50.0	25.5	13.9	21.4
Nov.				17.0	7.6	10.3	0	6.0	6.0	2.0	0	2.0	12.0	7.3	8.8
Dec.				3.8	3.9	3.8	9.3	1.5	6.4	3.0	0	3.0	5.4	3.3	4.4
Total	0	5.0	6.0	6.6	7.3	6.9	25.0	7.4	17.3	18.5	33.7	20.3	14.1	8.4	11.6

Key: T = Total
F = Female
M = Male

TABLE 4.21:

The number of *A.isoporum* in each sex and length group for the samples of *S.cephalus*.

	Length in cms.														
	0-20			20-30			30-40			40-50			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				41	66	107				12	0	12	53	66	119
Feb.				32	87	119	73	29	102	106	0	106	211	116	327
Mar.				71	28	99	139	5	144	2	0	2	212	33	245
Apr.				48	82	130	106	44	150	2	65	67	156	191	347
May	0	1	1	27	48	75	76	0	76	13	0	13	116	49	165
June	0	5	5	35	29	64	184	34	218	162	63	225	381	131	512
July				22	24	46	82	6	88	16	4	20	120	34	154
Aug.				1	5	6	18	1	19	1	3	4	20	9	29
Sept.				70	18	88	33	66	99	34	0	34	137	84	221
Oct.				47	105	152	135	6	141	200	0	200	382	111	493
Nov.				34	38	72	0	6	6	2	0	2	36	44	80
Dec.				19	27	46	29	3	32	6	0	6	54	30	84
Total	0	6	6	447	557	1004	875	200	1075	556	135	691	1888	898	2776
% of total no.of parasites		100.0		44.5	55.5		81.4	18.6		80.5	19.5		67.8	32.2	

Key: T = Total
F = Female
M = Male

TABLE 4.22:

The mean number of *A.isoporum* in each sex and length group for the samples of *L.leuciscus*.

	Length in cms.														
	0-15			15-20			20-25			25-30			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.							1.0	1.9	1.8	1.3	1.3	1.3	1.2	1.7	1.6
Feb.							12.4	2.4	7.4	6.6	1.5	4.6	10.8	2.2	6.7
Mar.				7.5	3.5	5.5	4.2	9.5	6.0	2.0	9.9	9.0	4.9	8.7	7.3
Apr.		2.0	2.0	3.3	2.3	2.8	17.3	1.3	5.6	0	8.0	8.0	10.6	2.9	5.1
May										22.0	0	22.0	22.0	0	22.0
June				8.0	7.0	7.5	5.1	4.3	4.8	0	11.0	11.0	5.5	5.5	5.5
July							7.0	22.2	13.8	54.0	3.0	20.0	14.8	15.8	15.3
Aug.							1.0	2.0	1.3				1.0	2.0	1.3
Sept.				4.0	0	4.0	12.5	12.0	12.3	30.0	16.0	23.0	13.4	12.8	13.2
Oct.				1.5	0	1.5	14.9	5.3	11.3	14.3	15.0	14.4	13.1	6.7	11.1
Nov.	1.0	0	1.0	1.0	3.0	2.0	4.6	2.0	4.2	2.0	1.5	1.7	3.2	2.0	2.8
Dec.	1.0	3.0	1.6	2.0	2.0	2.0	1.0	5.6	4.5	43.0	3.5	23.2	10.8	3.9	7.5
Total	1.0	2.5	1.6	3.6	3.1	3.4	9.8	5.5	7.7	15.5	6.7	10.4	9.6	5.5	7.6

Key: T = Total

F = Female

M = Male

TABLE 4.23:

The number of *A.isoporum* in each sex and length group for the samples of *L.leuciscus*.

	Length in cms.														
	0-15			15-20			20-25			25-30			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.							1	13	14	4	4	8	5	17	22
Feb.							99	19	118	20	3	23	119	22	141
Mar.				15	7	22	17	19	36	2	79	81	34	105	139
Apr.	0	2	2	10	7	17	52	10	62	0	24	24	64	43	107
May							0	0	0	22	0	22	22	0	22
June				8	7	15	38	26	64	0	11	11	46	44	90
July							35	89	124	54	6	60	89	95	184
Aug.							1	4	5				1	4	5
Sept.				4	0	4	100	48	148	30	16	46	134	64	198
Oct.				3	0	3	149	32	181	57	15	72	209	47	256
Nov.	1	0	1	1	3	4	23	2	25	4	3	7	29	8	37
Dec.	2	3	5	8	4	12	1	17	18	86	7	93	97	31	128
Total	3	5	8	49	28	77	516	279	795	279	168	447	849	480	1329
% of total no.of parasites	37.5	62.5		60.5	39.4		64.9	35.1		62.6	37.4		63.9	36.1	

Key: T = Total
F = Female
M = Male

TABLE 4.24:

The mean number of *A.isoporum* in each sex and length group for the samples of *R.rutilus*.

	Length in cms.																	
	0-15			15-20			20-25			25-30			30-35			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.													7.0	0	7.0	7.0	0	7.0
Feb.				14.0	0	14.0				1.0	0	1.0	11.0	0	11.0	8.6	0	8.6
Mar.										1.0	0	1.0	28.0	0	28.0	14.5	0	14.5
Apr.				19.0	0	19.0				0	43.0	43.0	336.0	0	336.0	177.5	43.0	132.6
May				0	31.0	31.0										0	31.0	31.0
June				0	13.2	13.2	27.0	27.0	27.0	39.4	487.0	114.0	13.0	0	13.0	31.3	94.5	58.4
July				0	9.0	9.0	43.5	68.0	51.6	59.0	0	59.0				48.6	38.5	44.6
Aug.										0	2.0	2.0	2.0	0	2.0	2.0	2.0	2.0
Sept.																		
Oct.										16.3	0	16.3	7.0	0	7.0	14.0	0	14.0
Nov.							40.0	0	40.0	9.0	0	9.0				24.5	0	24.5
Dec.										83.0	0	83.0				83.0	0	83.0
Total				16.5	15.5	15.6	38.5	47.5	41.5	26.6	177.3	51.7	52.1	0	52.1	34.6	65.4	43.1

Key: T = Total

F = Female

M = Male

TABLE 4.25:

The number of *A.isoporum* in each sex and length group for the sample of *R.rutilus*.

	Length in cms.																	
	0-15			15-20			20-25			25-30			30-35			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.													7	0	7	7	0	7
Feb.				14	0	14				1	0	1	11	0	11	26	0	26
Mar.										1	0	1	28	0	28	29	0	29
Apr.				19	0	19				0	43	43	336	0	336	335	43	398
May				0	31	31										0	31	31
June				0	53	53	27	27	54	197	487	684	26	0	26	250	567	817
July				0	9	9	87	68	155	59	0	59				146	77	223
Aug.										0	2	2	2	0	2	2	2	4
Sept.																		
Oct.										49	0	49	7	0	7	56	0	56
Nov.							40	0	40	9	0	9				49	0	49
Dec.										83	0	83				83	0	83
Total				33	93	126	154	95	249	399	532	931	417	0	417	1003	720	1723
% of total no. of parasites.				26.2	73.8		61.8	38.2		42.9	57.1		100.0		100.0	58.2	41.8	

Key: T = Total
F = Female
M = Male

TABLE 4.26:

The mean number of S.bramae in each sex and length group for the samples of R.rutilus.

	Length in cms.																	
	0-15			15-20			20-25			25-30			30-35			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				1.0	4.0	2.0				5.0	5.0	5.0	13.5	0	13.5	6.5	4.7	5.9
Feb.				0	1.5	1.5	2.5	0	2.5	4.0	5.0	4.7				2.8	3.6	3.2
Mar.				1.0	1.0	1.0	2.0	9.3	7.5	3.5	0	3.5	1.0	0	1.0	2.6	7.2	4.3
Apr.				8.0	0	8.0	0	2.0	2.0	7.0	15.0	9.0	5.5	0	5.5	6.6	8.5	7.1
May				4.0	6.0	5.0										4.0	6.0	5.0
June				0	4.4	4.4	0	2.0	2.0	7.3	0	7.3	6.6	0	6.6	6.9	3.5	5.2
July				2.0	0	2.0	1.0	0	1.0	11.7	0	11.7				8.3	0	8.3
Aug.										1.0	0	1.0	1.0	0	1.0	1.0	0	1.0
Sept.										1.0	0	1.0				1.0	0	1.0
Oct.				5.0	2.0	3.5				6.6	0	6.6	1.0	0	1.0	5.2	2.0	4.7
Nov.							1.0	0	1.0	0	1.5	1.5				1.0	1.5	1.2
Dec.							7.5	0	7.5	6.6	2.0	5.8				6.9	2.0	6.3
Total				3.1	3.4	3.3	3.0	5.1	3.9	6.5	5.0	6.1	6.2	0	6.2	5.3	4.4	5.0

Key: T = Total

F = Female

M = Male

TABLE 4.27:

The number of S.brama in each sex and length group for the samples of R.rutilus.

	Length in cms.																	
	0-15			15-20			20-25			25-30			30-35			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				2	4	6				5	15	20	27	0	27	34	19	53
Feb.				0	3	3	10	0	10	4	15	19				14	18	32
Mar.				1	1	2	2	28	30	14	0	14	1	0	1	18	29	47
Apr.				8	0	8	0	2	2	21	15	36	11	0	11	40	17	57
May				4	6	10										4	6	10
June				0	22	22	0	6	6	22	0	22	33	0	33	55	28	83
July				2	0	2	1	0	1	47	0	47				50	0	50
Aug.										1	0	1	1	0	1	2	0	2
Sept.										1	0	1				1	0	1
Oct.				5	2	7				20	0	20	1	0	1	26	2	28
Nov.							2	0	2	0	3	3				2	3	5
Dec.							15	0	15	33	2	35				48	2	50
Total				22	38	60	30	36	66	168	50	218	74	0	74	294	124	418
% of total no.of parasites in each length group.				36.6	63.3		45.5	54.5		77.1	22.9		100.0		100.0	70.3	29.6	

Key: T = Total
F = Female
M = Male

TABLE 4.28:

The mean number of S.bramae in each sex and length group for the samples of S. cephalus.

	Length in cms.														
	0-20			20-30			30-40			40-50			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				1.0	1.0	1.0	0	1.0	1.0				1.0	1.0	1.0
Feb.				1.5	2.0	1.9	3.0	7.0	5.0	7.0	0	7.0	4.0	2.6	3.2
Mar.				1.5	0	1.5	2.5	1.0	2.0				2.0	1.0	1.8
Apr.				1.0	1.5	1.4	5.0	4.0	4.4	3.0	4.0	3.5	3.8	2.9	3.2
May				3.0	1.0	1.7	1.0	0	1.0	12.0	0	12.0	4.2	1.0	3.2
June															
July															
Aug.															
Sept.															
Oct.															
Nov.				0	1.0	1.0	0	1.0	1.0				0	1.0	1.0
Dec.				4.0	14.0	10.7	0	1.0	1.0	1.0	0	1.0	2.5	9.6	6.8
Total				1.9	3.1	2.7	3.1	3.0	3.1	6.0	4.0	5.6	3.3	3.1	3.2

Key: T = Total

F = Female

M = Male

TABLE 4.29:

The number of S.bramae in each sex and length group for the samples of S.cephalus.

	Length in cms.														
	0-20			20-30			30-40			40-50			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				1	1	2	0	1	1				1	2	3
Feb.				3	14	17	3	7	10	14	0	14	20	21	41
Mar.				3	0	3	5	1	6				8	1	9
Apr.				1	6	7	15	16	31	3	4	7	19	26	45
May				3	2	5	2	0	2	12	0	12	17	2	19
June															
July															
Aug.															
Sept.															
Oct.															
Nov.				0	1	1	0	1	1				0	2	2
Dec.				4	28	32	0	1	1	1	0	1	5	29	34
Total				15	52	67	25	27	52	30	4	34	70	83	153
% of total no.of parasites in each length group.				22.4	77.6		48.0	52.0		88.2	11.8		45.8	54.2	

Key: T = Total
F = Female
M = Male

TABLE 4.30:

The mean number of S.bramae in each sex and length group for the samples of L.leuciscus.

	Length in cms.														
	0-15			15-20			20-25			25-30			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.															
Feb.															
Mar.								1.0	1.0	1.0	0	1.0	1.0	1.0	1.0
Apr.				0	23.0	23.0	1.0	4.0	2.0				1.0	13.5	7.2
May										4.0	0	4.0	4.0	0	4.0
June															
July															
Aug.															
Sept.															
Oct.							1.0	0	1.0				1.0	0	1.0
Nov.															
Dec.										2.5	0	2.5	2.5	0	2.5
Total				0	23.0	23.0	1.0	2.5	1.6	2.5	0	2.5	1.9	9.3	4.1

Key: T = Total

F = Female

M = Male

TABLE 4.31:

The number of S.bramae in each sex and length group of the samples of L.leuciscus.

Month	Length in cms. 0-15 F	M	T	15-20 F	M	T	20-25 F	M	T	25-30 F	M	T	Totals F	M	T
Jan.															
Feb.															
Mar.							0	1	1	1	0	1	1	1	2
Apr.					23	23	2	4	6				2	27	29
May										4	0	4	4	0	4
June															
July															
Aug.															
Sept.															
Oct.							1	0	1				1	0	1
Nov.															
Dec.										5	0	5	5	0	5
Total				0	23	23	3	5	8	10	0	10	13	28	41
% of total no.of parasites in each length group.					100.0			3.8	6.2		100.0			31.7	68.3

Key: T = Total
F = Female
M = Male

TABLE 4.32:

The mean number of C.metoecus in each sex and length group for the samples of T.thymallus.

	Length in cms.																	
	0-15			15-20			20-25			25-30			30-35			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.						NO	SAMPLE											
Feb.	13.0	7.0	11.0	15.0	11.0	13.0	9.0	5.5	6.2							12.5	6.6	9.0
Mar.				4.0	26.0	15.0	8.5	6.8	7.5							7.6	10.0	8.9
Apr.	7.0	7.5	7.3	15.0	54.0	34.5	25.0	22.4	23.4	0	12.0	12.0				21.5	21.8	21.7
May							6.5	0	6.5	4.0	0	4.0	0	3.0	3.0	5.7	3.0	5.0
June																		
July										0	2.0	2.0				0	2.0	2.0
Aug.																		
Sept.						NO	SAMPLE											
Oct.	4.0	4.0	4.0	4.2	10.3	6.8										4.2	8.7	6.2
Nov.	0	11.0	11.0	4.0	0	4.0	0	7.3	7.3							4.0	8.2	6.8
Dec.	0	2.0	2.0	5.6	0	5.6	0	2.0	2.0							5.3	2.0	4.4
Total	9.3	6.5	7.6	6.3	15.5	10.5	13.8	13.7	13.7	4.0	4.5	4.4	0	3.0	3.0	10.2	12.1	11.3

Key: T = Total

F = Female

M = Male

TABLE 4.33:

The number of C.metoecus in each sex and length group for the samples of T.thymallus.

	Length in cms.																	
	0-15			15-20			20-25			25-30			30-35			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.							NO SAMPLE											
Feb.	26	7	33	15	11	26	9	22	31							50	40	90
Mar.				4	26	30	34	34	68							38	60	98
Apr.	7	15	22	15	54	69	150	224	374	0	12	12				172	305	477
May							13	0	13	4	0	4	0	3	3	17	3	20
June																		
July										0	4	4				0	4	4
Aug.																		
Sept.							NO SAMPLE											
Oct.	4	4	8	17	31	48										21	35	56
Nov.	0	11	11	8	0	8	0	22	22							8	33	41
Dec.	0	2	2	17	2	19	15	0	15	0	2	2				32	6	38
Total	37	39	76	76	124	200	221	302	523	4	18	22	0	3	3	338	486	824
% of total no.of parasites in each length group.	48.7	51.3		38.0	62.0		42.3	57.7		18.2	81.8		100.0			41.0	59.0	

Key: T = Total
F = Female
M = Male

TABLE 4.34:

The mean number of each digenean from each host for:-

a) the number of infected male and female fish in each length group.

b) the total number of infected male and female fish

c) the total number of infected fish

Host	Parasite	Length in cms.																	
		0-20			20-30			30-40			40-50						Totals		
		F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
S.cephalus	A.isoporum		5.0	6.0	6.6	7.3	6.9	25.0	7.4	17.3	18.5	33.7	20.3				14.1	8.4	11.6
	S.brama				1.9	3.1	2.7	3.1	3.0	3.1	6.0	4.0	5.6				3.3	3.1	3.2
		0-15			15-20			20-25			25-30						Totals		
		F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
L.leuciscus	A.isoporum	1.0	2.5	1.6	3.6	3.1	3.4	9.8	5.5	7.7	15.5	6.7	10.4				9.6	5.5	7.6
	S.brama				0	23.0	23.0	1.0	2.5	1.6	2.5	0	2.5				1.9	9.3	4.1
		0-15			15-20			20-25			25-30			30-35			Totals		
		F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
R.rutilus	A.isoporum				16.5	15.5	15.6	38.5	47.5	41.5	26.6	177.3	51.7	52.1	0	52.1	34.6	65.4	43.1
	S.brama				3.1	3.4	3.3	3.0	5.1	3.9	6.5	5.0	6.1	6.2	0	6.2	5.3	4.4	5.0
		0-15			15-20			20-25			25-30			30-35			Totals		
		F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
T.thymallus	C.metoecus	9.3	6.5	7.6	6.3	15.5	10.5	13.8	13.7	13.7	4.0	4.5	4.4	0	3.0	3.0	10.2	12.1	11.3
	A.transversale	1.5	2.0	1.7	3.0	1.0	2.0	1.7	0	1.7	0	7.0	7.0	0	1.0	1.0	1.8	3.6	2.6
		0-20			20-30			30-40			40-50						Totals		
		F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
E.lucius	Phyllodistomum sp.				16.0	45.0	37.7	1.0	0	1.0	4.5	0	4.5				6.5	45.0	23.0

TABLE 4.35:

The total number of S.cephalus of each sex in the different length groups.

	Length groups in cms.														
	0-20			20-30			30-40			40-50			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.	0	1	1	9	10	19	9	2	11	1	0	1	19	13	32
Feb.			0	* 6	12	19	7	4	11	1	0	1	* 14	16	31
Mar.			0	9	6	15	7	5	12	2	0	2	18	11	29
Apr.			0	6	10	16	6	5	11	2	1	3	14	16	30
May	0	1	1	10	9	19	3	1	4	7	0	7	20	11	31
June	0	1	1	9	6	15	4	3	7	6	1	7	19	11	30
July			0	11	5	16	4	3	7	6	1	7	21	9	30
Aug.			0	8	7	15	5	6	11	1	3	4	14	16	30
Sept.			0	6	6	12	4	6	10	6	0	6	16	12	28
Oct.			0	8	7	15	4	3	7	5	0	5	17	10	27
Nov.	1	0	1	11	7	18	3	3	6	5	0	5	20	10	30
Dec.			0	6	9	15	4	5	9	6	1	7	16	15	31
Total	1	3	4	* 99	94	194	60	46	106	48	7	55	* 208	150	359
% of each sex	25.0	75.0		51.0	48.5		56.6	43.4		87.3	12.7		58.2	41.8	

* 1 fish sex undetermined

Key: T = Total
F = Female
M = Male

TABLE 4.36:

The total number of *L.leuciscus* of each sex in the different length groups.

Length groups in cms.

Month	0-15			15-20			20-25			25-30			Totals		
	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				2	1	3	3	18	21	5	4	9	10	23	33
Feb.						0	10	14	24	5	2	7	15	16	31
Mar.				5	4	9	4	6	10	3	8	11	12	18	30
Apr.	3	2	5	5	5	10	5	10	15	1	4	5	14	21	35
May				1	0	1	1	0	1	2	0	2	4	0	4
June				3	2	5	13	11	24	0	1	1	16	14	30
July	0	1	1	1	2	3	11	10	21	1	4	5	13	17	30
Aug.				1	2	3	13	11	24	2	1	3	16	14	30
Sept.	1	0	1	3	0	3	16	7	23	2	1	3	22	8	30
Oct.	1	1	2	3	0	3	12	9	21	4	1	5	20	11	31
Nov.	3	0	3	1	1	2	10	7	17	3	3	6	17	11	28
Dec.	2	1	3	4	3	7	3	10	13	4	3	7	13	17	30
Total	10	5	15	29	20	49	101	113	214	32	32	64	172	170	342
% of each sex	66.7	33.3		59.2	40.8		47.2	52.8		50.0	50.0		50.3	49.7	

Key: T = Total
F = Female
M = Male

TABLE 4.37:

The total number of R.rutilus of each sex in the different length groups.

	Length groups in cms.																
	0-15			15-20			20-25			25-30			30-35			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				6	14	20	2	2	4	2	4	6	2	1	3	12	21	33
Feb.				1	8	9	6	2	8	2	5	7	3	0	3	12	15	27
Mar.				3	8	11	2	4	6	8	2	10	3	0	3	16	14	30
Apr.				2	2	4	0	3	3	4	1	5	4	0	4	10	6	16
May				2	6	8	1	0	1							3	6	9
June				0	10	10	1	4	5	7	2	9	6	0	6	14	16	30
July				4	7	11	3	3	6	4	0	4	1	0	1	12	10	22
Aug.				3	3	6	7	1	8	8	4	12	4	0	4	22	8	30
Sept.				2	7	9	3	3	6	7	4	11	3	1	4	15	15	30
Oct.				1	14	15	3	2	5	7	2	9	1	0	1	12	18	30
Nov.				0	8	8	9	2	11	1	9	10	1	0	1	11	19	30
Dec.				1	7	8	6	2	8	7	6	13	1	0	1	15	15	30
Total				25	94	119	43	28	71	57	39	96	29	2	31	154	163	317
% of each sex				21.0	79.0		60.6	39.4		59.4	40.6		93.5	6.5		48.6	51.4	

Key: T = Total

F = Female

M = Male

TABLE 4.38:

The total number of *T.thynnallus* of each sex in the different length groups.

	Length groups in cms.																	
	0-15			15-20			20-25			25-30			30-35			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.							NO SAMPLE											
Feb.	2	1	3	1	1	2	1	5	6							4	7	11
Mar.	0	3	3	1	2	3	6	6	12							7	11	18
Apr.	1	2	3	2	1	3	7	11	18	0	1	1				10	15	25
May			0	0	1	1	4	1	5	1	1	2				5	3	8
June	1	0	1	5	2	7	4	3	7	0	2	2				10	7	17
July			0	4	6	10	5	3	8	1	10	11	0	1	1	10	20	30
Aug.			0			0	0	2	2	0	3	3				0	5	5
Sept.							NO SAMPLE											
Oct.	3	1	4	9	7	16	2	2	4	0	1	1				14	11	25
Nov.	2	5	7	4	1	5	6	10	16	2	0	2				14	16	30
Dec.	3	6	9	4	1	5	7	2	9	3	4	7				17	13	30
Total	12	18	30	30	22	52	42	45	87	7	22	29	0	1	1	91	108	199
% of each sex	40.0	60.0		57.7	42.3		48.3	51.7		24.1	75.9			100.0		45.7	54.3	

Key: T = Total
F = Female
M = Male

a) A.isoporum from S.cephalus, L.leuciscus and R.rutilus (Tables 4.39, 4.40, 4.41; Figures 4.1, 4.2, 4.3.)

b) S.bramae from R.rutilus and S.cephalus (Tables 4.42, 4.43; Figure 4.4.)

c) C.metoecus from T.thymallus (Table 4.44; Figure 4.5.)

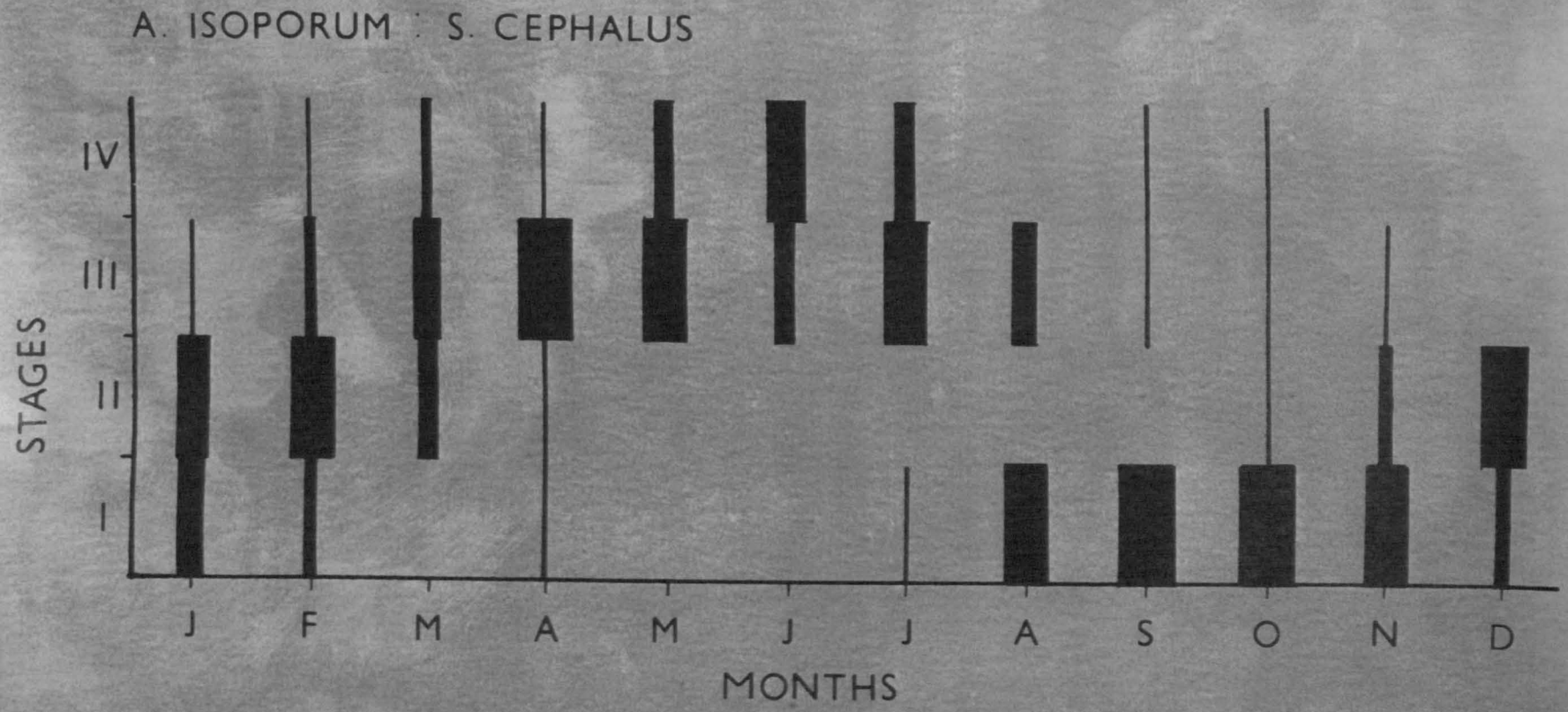
Observations on the state of maturation were made in the months where infection was present for A.transversale from T.thymallus; S.bramae from L.leuciscus and Phyllodistomum sp. from E.lucius.

A.isoporum: infection in S.cephalus (Table 4.39, Figure 4.1.)

Stages I and II were prominent in the January sample. Stage II was most prominent by February, and Stage III by April and May. Small numbers of Stage IV were present in February, but they did not reach a maximum until May, June and July. By August Stage I was again prominent and increased to a maximum in September and October. A small number of Stage II were present in October, after which the presence of this stage increased until by December it was more prominent than Stage I.

From this information it appeared that an increase in development of the vitellaria occurred between January and May; the main egg producing period lay between March and July; regression of the gonads occurred between May and July and by August and September nearly all the mature adults had disappeared. From the disappearance of the mature forms it is suggested that after egg production the parasites degenerate and pass out of the definitive host, the eggs either being liberated with the faeces or passing out with the adult. Young stages predominated

Fig. 4.1 The number of each developmental stage of *A. isoporum* in *S. cephalus* expressed as a percentage of the total number examined each month.


A. ISOPORUM : S. CEPHALUS
STAGES
IV
III
II
I
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

between August and November. In August only 18 specimens were present, but by September and October 216 and 473 specimens respectively were recorded. The months where large numbers of immature flukes were found were probably the period of reinfection. By November the number of worms present was reduced to 62, and it is suggested that during the period of reinfection many of the parasites are lost, but those that become established mature and produce eggs in the following spring and early summer.

A.isoporum: infection in L.leuciscus (Table 4.40; Figure 4.2)

Stage II predominated between January and April. A gradual increase in Stage III occurred from February and reached a maximum in June. The data for the May sample were disregarded as it contained only four fish of which only one was infected. Stage IV, omitting the May sample, appeared in June and reached a peak in July. By August 100.0% of the infection belonged to Stage I, but Table 4.23 shows that only five specimens were found. By September and October an increase in numbers was recorded, 148 and 181 specimens respectively, before a decrease to 25 in November. Stage II reappeared in September and gradually increased up to December. This information showed that A.isoporum infections in L.leuciscus followed a seasonal cycle of maturation similar to that recorded from S.cephalus.

A.isoporum: infection from R.rutilus (Table 4.41; Figure 4.3).

The cycle of development of A.isoporum in R.rutilus was similar to

Fig. 4.2 The number of each developmental stage of *A. isoporum* in *L. leuciscus* expressed as a percentage of the total number examined each month.

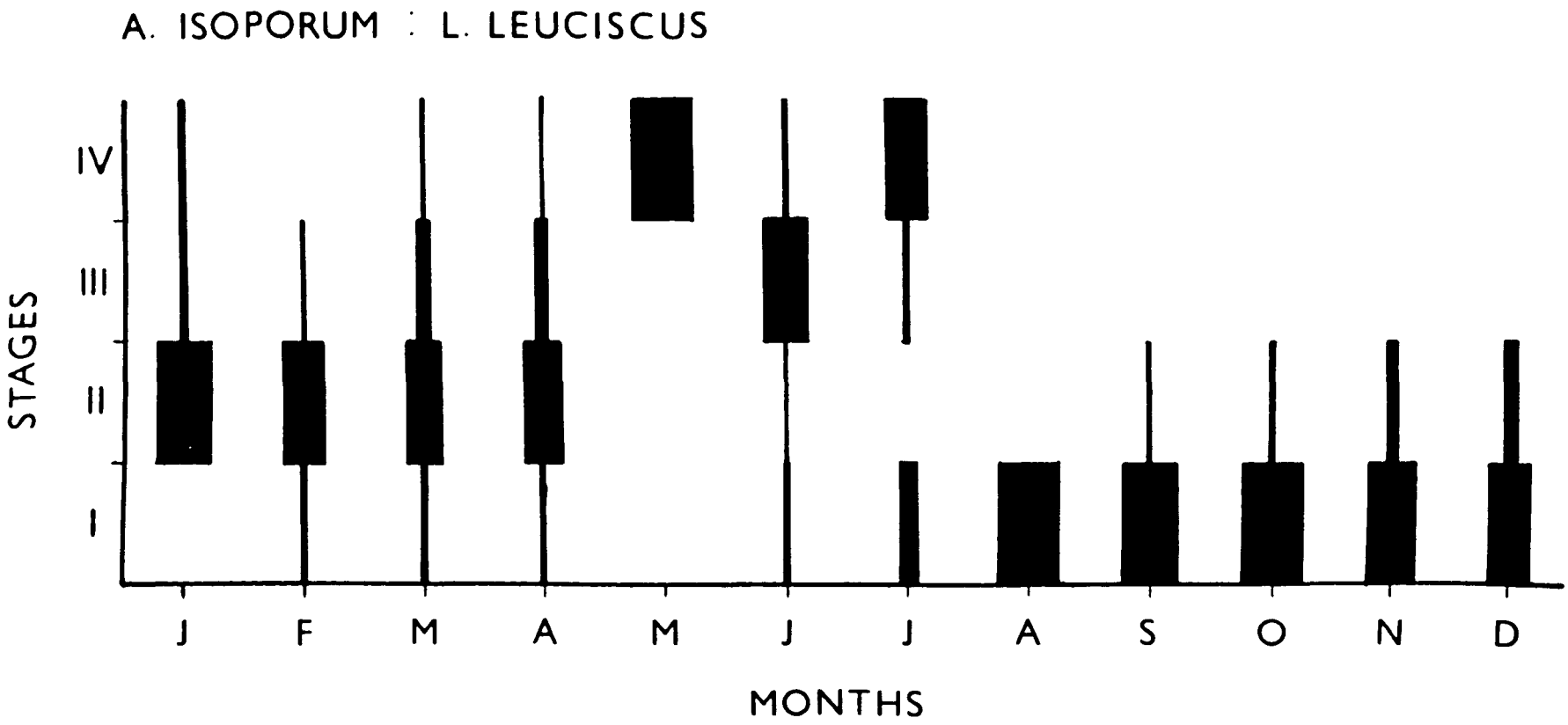
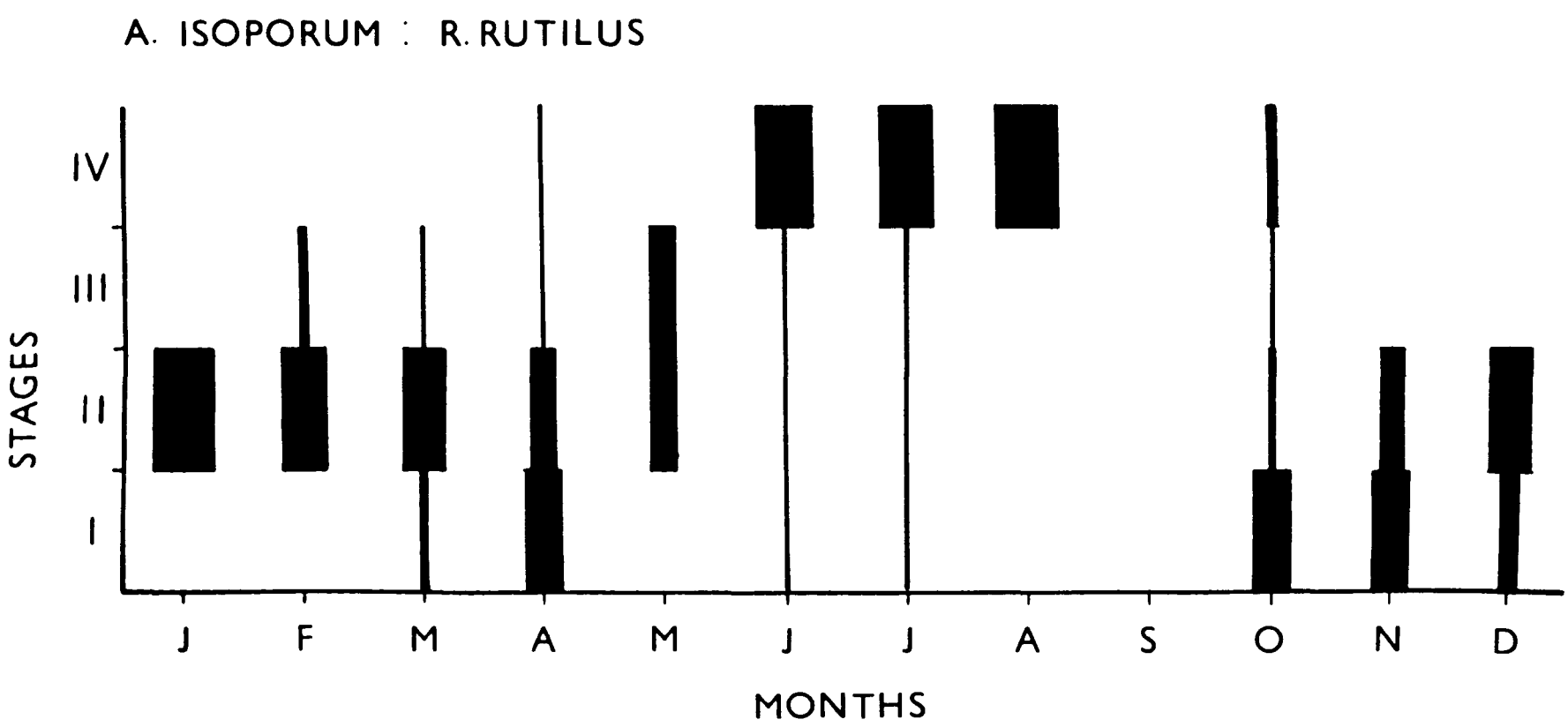

A. ISOPORUM : L. LEUCISCUS
STAGES
IV
III
II
I
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

Fig. 4.3 The number of each developmental stage of *A. isocorum* in *R. rutilus* expressed as a percentage of the total number examined each month.


A. ISOPORUM : R. RUTILUS
STAGES
IV
III
II
I
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

that recorded from L.leuciscus and S.cephalus with the following variations:-

i) Stage II was predominant over a slightly longer period at the beginning of the year i.e. from January to May, compared with January to April in L.leuciscus and January and February in S.cephalus.

ii) Stage III was only prominent in May, compared with March to June in L.leuciscus, and March to July in S.cephalus.

iii) Stage IV was more or less the only stage recorded between June and August, whereas Stage III was still present in June and July in L.leuciscus and between June and August in S.cephalus.

iv) Stage I did not reappear until October in R.rutilus, two months later than in L.leuciscus and S.cephalus.

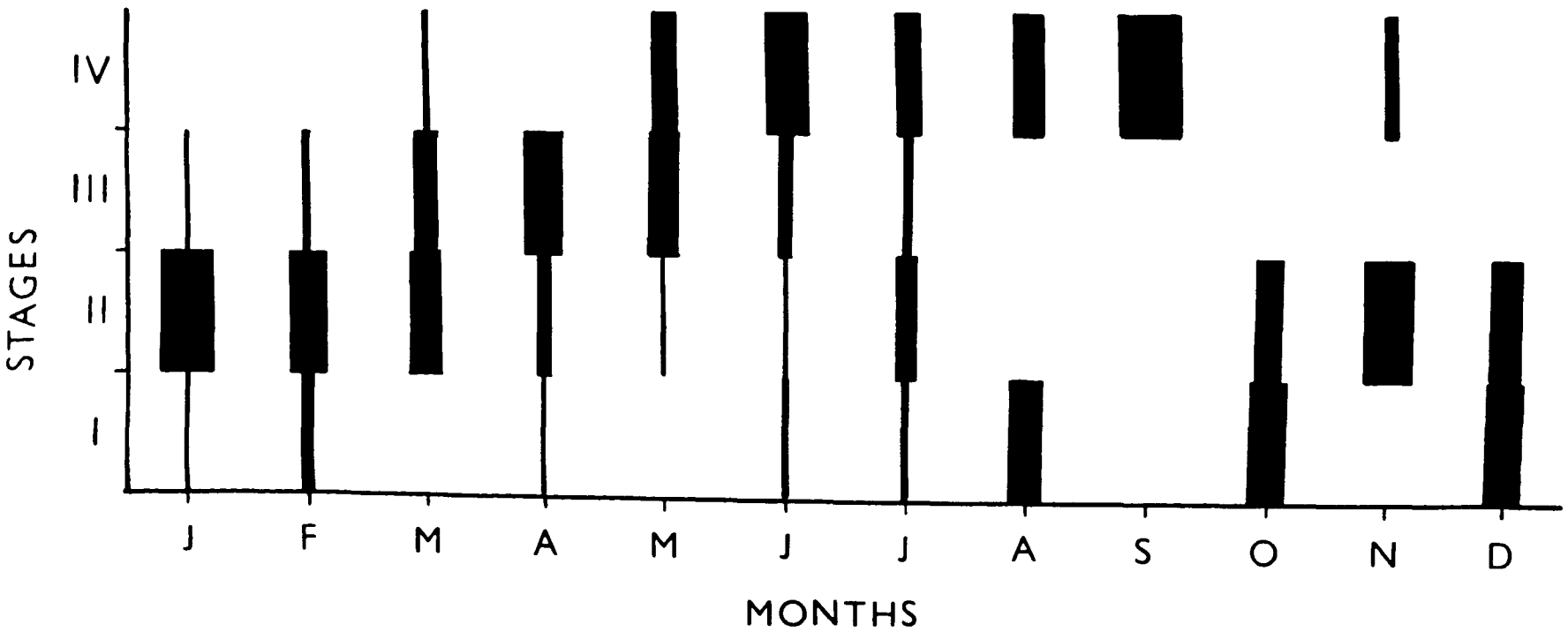
v) No loss of infection was recorded between November and December from R.rutilus.

S.bramae: infection in R.rutilus (Table 4.42; Figure 4.4).

Stage II was prominent between January and March; Stage III in April and May and Stage IV where the parasites were packed with eggs, from June to September. The intensity of infection was very low in August and September (Table.4.26). Stages I and II reappeared in October. A drop in infection occurred in November, only five fish were infected by five specimens, 80.0% of these being Stage II. It is suggested that a similar situation exists as for A.isoporum infections in S.cephalus, and that many young S.bramae are lost at the initial period of reinfection i.e. November, before a balance is maintained between the host, and the

Fig. 4.4 The number of each developmental stage of *L. brevis* in *R. rutilus* expressed as a percentage of the total number examined each month.

S. BRAMAE : R. RUTILUS



number of parasites that will mature to produce eggs. Reinfection continues at a slower rate after October and November, and an increase in the numbers of Stage I and II were recorded in December.

S.bramae: infection in S.cephalus (Table 4.43).

The occurrence and intensity of infection were low and it was only possible to state that Stage III was dominant between February and May; no infection was recorded between June and November, after which Stage I was present in December.

The information available for S.bramae indicated that the pattern of seasonal variation and maturation was similar to that of A.isoporum.

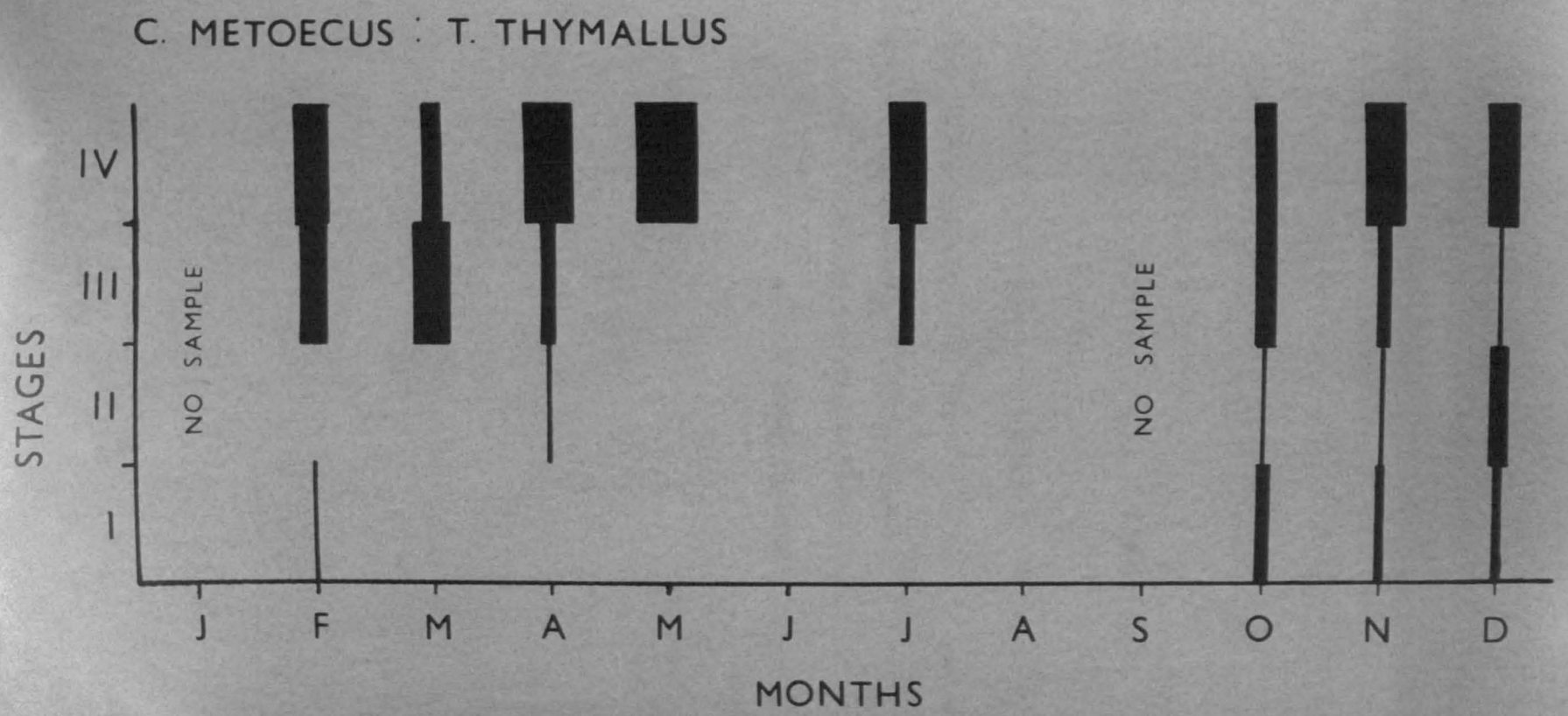
C.metoecus. (Table 4.44; Figure 4.5).

C.metoecus also appeared to have a seasonal cycle of development. Mature forms and forms where the gonads were beginning to regress were recorded between February and May. Infection was not recorded between May and October apart from four specimens (Stage IV) in the July sample. Between October and November young forms (Stages I and II) were present as well as parasites in Stages III and IV.

A.transversale.

In February and April six parasites were recorded at Stage II and one at each of Stages II and III. In May seven specimens were found between Stages III and IV. Although insufficient data were available to determine accurately the presence of any pattern of seasonal

Fig. 4.5 The number of each developmental stage of *C. metoecus* in *T. thymallus* expressed as a percentage of the total number examined each month.


C. METOECUS : T. THYMALLUS
STAGES
IV
III
II
I
NO SAMPLE
NO SAMPLE
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

maturation the small amount of information suggested that the pattern of seasonal maturation for A.isoporum, S.bramae and C.metoecus may also occur for A.transversale.

Phyllodistomum sp.

160 specimens of Phyllodistomum sp. were recorded from E.lucius in June, and one in July. In June 69.8% of the specimens belonged to Stage III and 30.2% to Stage IV. The specimen recorded in July belonged to Stage III. Phyllodistomum sp. from E.lucius contained eggs at the same time of year as A.isoporum and S.bramae, but two months later than the peak period of egg production in C.metoecus.

TABLE 4.39:

The number of each developmental stage of A.isoporum in S.cephalus as a percentage of the total number examined each month.

Month	Total no. parasites recorded.	No. and % of each stage examined. I No.	I %	II No.	II %	III No.	III %	IV No.	IV %
Jan.	119	52	43.4	64	54.1	3	2.5		
Feb.	327	45	13.9	211	65.3	62	19.3	5	1.5
Mar.	245			73	31.6	112	48.5	46	19.9
Apr.	347	3	0.9	5	1.5	329	97.0	2	0.6
May	165					114	72.2	44	27.8
June	512					146	29.7	345	70.3
July	154	2	1.3			96	62.3	56	36.4
Aug.	29	18	75.0	6	25.0				
Sept.	221	216	97.7			4	1.8	1	0.5
Oct.	493	473	96.0	10	2.0	5	1.0	5	5.0
Nov.	80	62	77.5	16	20.0	2	2.5		
Dec.	84	16	20.0	65	80.0				
Total	2776	888		446		879		504	

TABLE 4.40:

The number of each developmental stage of A.isoporum in L.leuciscus as expressed as a percentage of the total number examined each month.

Month	Total no. parasites recorded	No. and % of each stage examined. I No.	I %	II No.	II %	III No.	III %	IV No.	IV %
Jan.	22			19	82.6	2	8.7	1	
Feb.	141	29	20.6	106	75.2	6	4.2		
Mar.	139	21	15.9	80	60.6	29	22.0	2	1.5
Apr.	107	8	7.7	67	64.4	26	25.0	2	1.9
May	22								100.0
June	90	11	12.2	5	5.5	63	70.0	11	12.2
July	184	43	23.6			22	12.1	117	64.3
Aug.	5	5	100.0						
Sept.	198	181	91.4	17	8.6				
Oct.	256	240	94.5	14	5.5				
Nov.	37	28	75.5	9	24.5				
Dec.	128	89	69.5	39	30.5				
Total	1329	655		356		148		133	

TABLE 4.41:

The number of each developmental stage of A.isoporum in R.rutilus expressed as a percentage of the total number examined each month.

Month	Total no. parasites recorded	No. and % of each stage examined							
		I		II		III		IV	
		No.	%	No.	%	No.	%	No.	%
Jan.	7			7	100.0				
Feb.	26			23	88.5	3	11.5		
Mar.	29	5	17.2	22	75.8	2	6.9		
Apr.	398	240	60.7	155	38.9	2	0.5	1	0.02
May	31			16	51.6	15	48.4		
June	817	23	2.8	16	2.0	21	2.6	757	92.6
July	223	1	0.5	5	2.2	10	4.5	207	92.4
Aug.	4							4	100.0
Sept.	0								
Oct.	56	36	64.3	8	14.3	2	3.6	10	17.8
Nov.	49	32	65.3	17	34.7				
Dec.	83	26	31.3	57	68.7				
Total	1723	363		326		55		979	

TABLE 4.42:

The number of each developmental stage of *S.bramae* in *R.rutilus* expressed as a percentage of the number examined each month.

Month	Total no. parasites recorded	No. and % of each stage examined. I		II		III		IV	
		No.	%	No.	%	No.	%	No.	%
Jan.	53	2	3.8	50	94.3	1	1.9		
Feb.	32	7	21.0	20	62.5	5	15.6		
Mar.	47			28	59.6	16	34.0	3	6.4
Apr.	57	3	5.3	15	26.3	39	68.4		
May	10			1	1.0	5	50.0	4	40.0
June	83	4	4.8	3	3.6	18	21.6	58	69.8
July	50	3	6.0	19	38.0	8	16.0	20	40.0
Aug.	2			1	50.0			1	50.0
Sept.	1							1	100.0
Oct.	28	17	60.7	11	39.3				
Nov.	5			4	80.0			1	20.0
Dec.	50	32	64.0	18	56.0				
Total	418	68		170		92		88	

TABLE 4.43:

The number of each developmental stage of S.bramae in S.cephalus expressed as a percentage of the total number examined each month.

Month	Total no. parasites recorded	No. and % of each stage examined. I No.	%	II No.	%	III No.	%	IV No.	%
Jan.	3			2	66.7	1	33.3		
Feb.	41			1	2.4	33	80.5	7	17.1
Mar.	9					3	33.3	6	66.7
Apr.	45					45	100.0		
May	19					14	73.7	5	26.3
June									
July									
Aug.									
Sept.									
Oct.									
Nov.	2	1	50.0					1	50.0
Dec.	34	31	91.2					3	8.8
Total	153	32		3		96		22	

TABLE 4.44:

The number of each developmental stage of C.metoecus in T.thymallus expressed as a percentage of the total number examined.

Month	Total no. parasites recorded	No. and % of each stage examined: I No.	I %	II No.	II %	III No.	III %	IV No.	IV %
Jan.									
Feb.	90	2	2.2			42	46.7	46	51.1
Mar.	98					64	65.3	34	34.7
Apr.	477			1	0.2	111	23.3	365	76.5
May	20							20	100.0
June	0								
July	4					1	25.0	3	75.0
Aug.	0								
Sept.									
Oct.	56	12	21.4	2	3.6	21	37.5	21	37.5
Nov.	41	4	9.8	1	2.4	8	19.5	28	68.3
Dec.	38	4	10.3	13	34.3	2	5.4	19	50.0
Total	824	22		17		249		536	

Mixed infections of A.isoporum and S.bramae.

The number of S.cephalus, L.leuciscus and R.rutilus with infections of A.isoporum only, S.bramae only and with mixed infections of both species were recorded (Tables 4.45 - 4.47).

Infections in S.cephalus (Table 4.45).

The number of fish infected with only A.isoporum was greater than the number infected only with S.bramae or the number with mixed infections. A.isoporum infections were common, and mixed infections were encountered more frequently than only S.bramae infections.

Infections in L.leuciscus. (Table 4.46).

A pattern of occurrence for A.isoporum infections only, S.bramae infections and mixed infections was similar to that recorded for S.cephalus.

Infections in R.rutilus (Table 4.47).

The number of R.rutilus infected with only S.bramae was greater than either the number with only A.isoporum or only mixed infections, although the number with mixed infections was less than the number with only A.isoporum. S.bramae infections occurred more frequently in R.rutilus than infections of A.isoporum.

Where mixed infections of A.isoporum and S.bramae were present, the numbers of A.isoporum in each of the infections were arranged in descending order, and the number of S.bramae present recorded in the

TABLE 4.45:

The number of S.cephalus infected with:- a) Only A.isoporum

b) Only S.bramae

c) Only mixed infections

	Infected with only A.isoporum			Infected with only S.bramae			Infected with only A.isoporum & S.bramae		
Month	F	M	T	F	M	T	F	M	T
Jan.	6	8	14	1	1	2	0	1	1
Feb.	9	8	17	0	2	2	5	6	11
Mar.	11	7	18	0	0	0	4	1	5
Apr.	7	7	14	0	0	0	5	9	14
May	7	6	13	0	0	0	4	2	6
June	15	10	25			0			0
July	19	8	27			0			0
Aug.	3	4	7			0			0
Sept.	10	9	19			0			0
Oct.	15	8	23			0			0
Nov.	3	4	7	0	0	0	0	2	2
Dec.	9	8	17	1	2	3	1	1	2
Total	114	87	201	2	5	7	19	22	41

Key: T = Total

F = Female

M = Male

TABLE 4.46:

The number of L.leuciscus infected with:- a) Only A.isoporum

b) Only S.bramae

c) Only mixed infections

Month	Infected with only A.isoporum			Infected with only S.bramae			Infected with only A.isoporum & S.bramae		
	F	M	T	F	M	T	F	M	T
Jan.	4	10	14						
Feb.	11	10	21						
Mar.	7	11	18	1	0	1	0	1	1
Apr.	5	14	19	1	1	2	1	1	2
May	1	0	1	1	0	1			
June	8	8	16						
July	6	6	12						
Aug.	1	2	3						
Sept.	10	5	15						
Oct.	15	7	22				1	0	1
Nov.	9	4	13						
Dec.	7	8	15				2	0	2
Total	84	85	169	3	1	4	4	2	6

Key: T = Total

F = Female

M = Male

TABLE 4.47:

The number of R.rutilus infected with:- a) Only A.isoporum

b) Only S.bramae

c) Only mixed infections

Month	Infected with only A.isoporum			Infected with only S.bramae			Infected with only A.isoporum & S.bramae		
	F	M	T	F	M	T	F	M	T
Jan.			0	4	4	8	1	0	1
Feb.	2	0	2	4	5	9	1	0	1
Mar.	1	0	1	6	4	10	1	0	1
Apr.			0	4	1	5	2	1	3
May	0	1	1	1	1	2			0
June	5	4	9	5	6	11	3	2	5
July	1	2	3	4	0	4	2	0	2
Aug.	1	1	2	2	0	2			0
Sept.			0	1	0	1			0
Oct.	1	0	1	2	1	3	3	0	3
Nov.	2	0	2	2	2	4			0
Dec.	2	0	2	6	1	7	1	0	1
Total	15	8	23	41	25	66	14	3	17

Key: T = Total

F = Female

M = Male

adjacent column (Table 4.48). The data were investigated to see if the number of A.isoporum present had any effect on the number of S.bramae. No increase in the number of S.bramae with a decrease in the number of A.isoporum or vice versa, in any of the hosts where mixed infections were present. It was concluded that the presence of A.isoporum did not influence the establishment of S.bramae in the host species studied, and that the lower incidence and intensity of infection of S.bramae was the result of factors other than competition between two parasites in the same environment.

Variation in the size of A.isoporum from different hosts.

An obvious size difference was immediately apparent between A.isoporum from S.cephalus and L.leuciscus on the one hand, and those from R.rutilus on the other. The range of measurements in mm. was recorded for several parameters from mature specimens of A.isoporum from all three hosts (Table 4.49). A.isoporum from S.cephalus were slightly larger, except in breadth, than those from L.leuciscus, whereas A.isoporum from R.rutilus were much smaller than specimens from the other two hosts. A proven explanation for this phenomenon is not available at the present time, but two reasons are suggested for the smaller size of A.isoporum in R.rutilus:-

i) The environment of the intestine of R.rutilus may not be as favourable for the development of A.isoporum as that of other hosts.

TABLE 4.48:

The number of parasites in mixed infections of A.isoporum, and S.bramae, from S.cephalus, R.rutilus and L.leuciscus.

S.cephalus		S.cephalus		R.rutilus		L.leuciscus	
A.isoporum	S.bramae	A.isoporum	S.bramae	A.isoporum	S.bramae	A.isoporum	S.bramae
68	1	10	1	336	8	85	4
65	4	10	4	85	1	16	1
50	2	10	1	59	8	13	1
50	10	10	1	49	5	6	1
40	1	9	2	43	15	3	4
33	3	8	1	26	5	1	1
32	1	6	1	20	5		
27	12	6	1	19	8		
24	4	6	12	11	17		
23	4	6	1	8	11		
22	5	6	4	7	1		
20	1	5	2	7	8		
18	1	4	2	3	6		
17	4	4	1	1	4		
14	3	4	1	1	7		
13	1	3	7	1	5		
13	3	2	3	1	1		
12	2	1	1				
11	1	1	1				
10	1	1	1				
10	1						

TABLE 4.49:

Comparison between the dimensions of mature A.isoporum from S.cephalus, L.leuciscus and R.rutilus.

Parasite	Hosts		
A.isoporum	S.cephalus	L.leuciscus	R.rutilus
Length	1.79-4.17	2.96 -3.74	1.67 - 2.24
Breadth	0.59-1.05	0.71 -1.13	0.45 - 0.69
Oral Sucker	0.25-0.44 x 0.33-0.44	0.32 -0.39 x 0.32 -0.41	0.25 - 0.32 x 0.24 - 0.30
Pharynx	0.15-0.21 x 0.15-0.18	0.14 -0.17 x 0.12 -0.17	0.12 - 0.15 x 0.11 - 0.15
Ventral Sucker	0.35-0.48 x 0.40-0.51	0.34 -0.44 x 0.31 -0.48	0.26 - 0.32 X 0.28 - 0.35
Ovary	0.17-0.25 x 0.24-0.28	0.19 -0.22 x 0.22 -0.24	0.15 - 0.18 x 0.13 - 0.18
Eggs	0.08-0.09 x 0.06-0.07	0.085x 0.059-0.068	0.08 - 0.09 x 0.05 - 0.07
Testes	0.48-0.75 x 0.44-0.61	0.37 -0.69 x 0.32 -0.66	0.16 - 0.28 x 0.13 - 0.21

Measurements in mm.

ii) The mean number of A.isoporum in R.rutilus was much greater than the mean number recorded in the other two hosts (Table 4.34). It was thought at first that a 'crowding effect' might exist where the presence of many parasites results in a decrease in size and weight (Read, 1951; Holmes, 1961). Further observations revealed that flukes of similar dimensions were also recorded from low infections in R.rutilus and therefore the above phenomenon does not explain the presence of smaller A.isoporum in R.rutilus.

The identification of A.isoporum.

The validity of the identification of the Allocreadium recorded from S.cephalus, L.leuciscus and R.rutilus as A.isoporum was raised. (Mr. L. Chappell pers.comm.)

The first character used to separate the species of Allocreadium in Bychowskaya-Pavlovskaya (1964) was the relative position of the bifurcation of the intestine. In many of the specimens examined the intestinal bifurcation was posterior to the anterior margin of the ventral sucker, and following Bychowskaya-Pavlovskaya (1964) this parasite should be identified as Allocreadium laymani Bychowskaya sp.nov.

The only differences between A.isoporum and A.laymani from the descriptions in the key are:-

a) The level of bifurcation of the intestine which is stated to be anterior to the anterior edge of the ventral sucker in A.isoporum, and between mid-way and the posterior edge of the ventral sucker in A.laymani.

b) The slight difference in the extent of the vitellaria; the vitellaria not extending beyond the level of the posterior margin of the ventral sucker in A.isoporum, and reaching only to the posterior margin of the ovary in A.laymani.

c) The greater size range of A.isoporum.

Each of the above points was examined:-

a) A great variation in the relative position of the bifurcation of the intestine existed in the specimens examined in the present investigation, and in eight other specimens from three different localities and hosts (Dr. Chubb pers.comm.). The level of bifurcation is not shown in Slusarski's figure of A.isoporum in the Russian Key, Looss (1894) showed the bifurcation just on the anterior edge of the ventral sucker, and in his diagram of a more juvenile form the intestine bifurcates at the posterior margin of the ventral sucker and Ergens (1962) gave a figure of A.isoporum in which the intestine appeared to bifurcate between the middle and the posterior edge of the ventral sucker. It is possible that these variations may result from the methods used for relaxation and fixation of the specimens, and if this is so the validity of the bifurcation of the intestine as an important taxonomic character is questionable.

b) Looss (1894) showed the vitellaria extending to the anterior edge of the ovary, whereas in Ergens (1962) the vitellaria extended as far as the middle of the ventral sucker. Personal observations showed that the vitellaria extended from the level of the ovary to the middle

of the ventral sucker, the variation de ending on the relaxation of the specimen and the state of maturity.

c) A great variation in size was observed in the Allocreadium from S.cephalus, L.leuciscus and R.rutilus (Table 4.49), the range being much greater than that recorded for A.laymani.

From the confusion that exists it was impossible to come to any definite conclusions, but it is suggested that there is no real justification for recording A.laymani as a separate species, especially as Lyaiman (1933) thought that this species may have been confused with A.isoporum in the past.

Discussion.

With the exception of A.transversale all other Digenea found in this survey have previously been recorded from Britain (Dawes, 1946). From the present survey a similar seasonal variation of occurrence, intensity of infection and maturation were observed for A.isoporum, S.bramae and C.metoecus. No reference was found to any previous data on the seasonal variation of A.isoporum. The data collected in the present survey showed that A.isoporum had an annual life cycle. Eggs were produced mainly in June, after which the reproductive organs began to degenerate and the parasites disappeared from the host. It was presumed that the parasites died, and that the eggs were either liberated with the host faeces, or when the parasites passed out of the host. When the eggs hatch the miracidia penetrate an intermediate host, Cyclas

cornea L. or Cyclas rivicola Leach according to Looss, 1894, or S.corneum (see Markevich, 1963). Linstow (1897) reported numerous encapsulated Distomum larvae in the larvae of Ephemera vulgata L., Chaetopteryx villosa (Fabricius, 1798) and Anabolia nervosa (Curtis, 1834) which he likened to that described by Looss (1894) as Distomum isoporum now known as A.isoporum. Markevich (1963) stated that these insect larvae are complementary hosts for A.isoporum in which the cercariae encyst, and these parasites enter the definitive host when the insect larvae are eaten. Insect larvae formed an important part of the diet of S.cephalus and L.leuciscus from the River Lugg. The main diet of R.rutilus appeared to be aquatic weeds and algae and S.corneum, and only small numbers of insect larvae were present which may account for the sporadic occurrence of A.isoporum in this host. The common occurrence of S.corneum (the suspected intermediate host of A.isoporum) in the diet of R.rutilus suggests that it may be possible for A.isoporum to mature in fish without having to encyst in an aquatic insect larva, and thus a more direct and rapid development may be the cause of the smaller size of A.isoporum in R.rutilus.

The part of the life cycle passed in the intermediate host was thought to occur between July and September when the occurrence and intensity of infection of A.isoporum in the definitive host were low, and the stages present were either stage IV with degenerating gonads or stage I (small immature worms). Samples of S.corneum were examined from these months for evidence of rediae of A.isoporum but so far the

results have been negative.

By September and October the occurrence and intensity of infection began to increase and most of the parasites were young with immature gonads, and none or only partially developed vitellaria. This was the period of reinfection, when if infected intermediate hosts were eaten by cyprinids, the parasites were released in the definitive host. After the period of increase of infection a decrease in intensity was apparent in November in S.cephalus and L.leuciscus. The significance of this was doubtful, but it was possible after the initial reinfection, many of the parasites were lost, and only a certain number became established or can be supported by the host. A certain amount of reinfection still appeared to occur between November and February.

A similar annual life cycle was recorded for S.bramae. The main period of egg production occurred from May to July, the development of the young stages in August and September, and the reinfection of the definitive host in October. Bithynia tentaculata (L.) is recorded as the first intermediate host for S.bramae after which the cercariae are said to penetrate and encyst under the skin of a leech (Herpobdella sp.) (See Markevich, 1963). Few specimens of B.tentaculata were recorded from the River Lugg, although an extensive survey of the invertebrate fauna was not undertaken. Large numbers of leeches were present in the river, but few were recorded from the food of the fish, and this could explain the low incidence and intensity of infection recorded for S.bramae.

The seasonal variation of S.bramae under the conditions of the

Karelo-Finnish A.S.S.R. was discussed by Malakhova (1963) but at the present time a translation of this work is not available and the summary only stated that:-

1. The trematodes were divided into six different groups according to the development of their genital organs.

2. Measurements of the genital system were taken in specimens collected monthly.

The only results given in the summary showed that the rate of growth varied according to season, and that some information was available in relation to the longevity and egg production under the temperature conditions of the Karelian lake.

In the present survey the onset of vitellaria development and egg production coincided with the increase of water temperature between March and August, but this may not be the only factor to influence egg production in the parasite.

The life cycle of S.bramae in relation to the stages in the intermediate hosts were described by Chernogorenko-Bidulina and Bliznyuk (1960) and they concluded that the developmental cycle in nature may follow one of two routes:-

"1. With 2 hosts (intermediate and accessory) mollusc and leech. The cercaria within the mollusc may be inside or outside the sporocysts.

2. With only one intermediate host, mollusc, which also acts as the accessory host, in this case short tailed, tailless and encysted cercariae develop within the mollusc.

A third route of development may exist in which the intermediate and accessory hosts are molluscs of the same species."

The information from Russian investigations and the present survey combines to form a general picture of the life cycle and the seasonal dynamics of S.bramae.

The present survey showed a similar pattern of seasonal variation in occurrence and intensity of infection for C.metoecus in T.thymallus to that recorded for A.isoporum and S.bramae. Recent studies in this country on C.metoecus were made by Thomas (1958) and Awachie (1963). Thomas (1958) studied C.metoecus and Crepidostomum farionis (Müller, 1784) parasitic in S.trutta and S.salar from rivers in Mid-Wales. Awachie (1963) also reviewed the occurrence and seasonal periodicity of C.metoecus and C.farionis found by other authors, and made an extensive study of the life cycle of these parasites and found

> "not only clear cyclical changes in the final host, but marked and correlated seasonal rhythms of occurrence in all 3 hosts involved in the life cycle of Crepidostomum spp".

Nöller (1928) postulated that the larval stage of C.metoecus was Cercaria arhopalocerca from a Pisidium sp. which was reported to encyst in a chironomid larva of the genus Chironomus or Corethra. Awachie (1963) recorded L.pereger and G.pulex as intermediate hosts in the life cycle of C.metoecus and Pisidium sp. probably P.casertanum Poli and G.pulex as intermediate hosts for C.farionis. In the present investigation no rediae or cercariae of any kind were recorded from any of the S.corneum, L.pereger or T.fluviatilis that were examined. As

L.pereger and G.pulex were present in the River Lugg it is quite possible that further investigations will show that they do act as intermediate hosts for C.metoecus, T.fluviatilis was also common in the river and as a component of the diet of T.thymallus, and was also a suspect intermediate host. This latter fact supposes that metacercariae of C.metoecus are capable of forming in the molluscan host, and that G.pulex is not always an essential intermediate host. This situation if proven would be similar to that recorded for S.bramae in B.tentaculata (Chernogorenko-Bidulina and Bliznyuk, 1960).

No overlap in the digenean fauna was recorded from the Cyprinidae and Thymallidae in this investigation. A.isoporum and S.bramae were recorded from S.cephalus, L.leuciscus and R.rutilus, and C.metoecus and A.transversale from T.thymallus. Previous records of A.transversale showed that it was commonly present in cyprinid hosts. Markevich (1963) stated that the metacercarial forms of A.transversale had been found encysted in G.pulex which is also recorded as an intermediate host for C.metoecus (Awachie, 1963). G.pulex was much commoner in the diet of T.thymallus than in any of the cyprinids, and this could explain the presence of A.transversale and C.metoecus only in T.thymallus.

In many investigations by Russian workers A.isoporum and S.bramae which are common parasites of cyprinids have been recorded from E.lucius. Only a few E.lucius were sampled in this investigation, and Phyllodistomum sp. was the only digenean recorded. From other evidence (Bychowskaya-Pavlovskaya, 1964) it appears that E.lucius may be

infected by parasites common to either Cyprinidae and to a lesser extent Thymallidae and Salmonidae. It is uncertain whether many of the parasites recorded from E.lucius have been acquired via the intermediate host, or secondarily by E.lucius feeding on infected fish where the parasites are already in their definitive host (Chubb, 1964).

Conclusions.

1. Five species of adult Digenea were recorded from five species of fish. Four species were located in the alimentary canal and one in the urinary bladder.
2. A.transversale was recorded for the first time in Britain, and for the first time from T.thymallus.
3. Seasonal variation in the incidence and intensity of infection was recorded for A.isoporum and S.bramae from L.cephalus, L.leuciscus and R.rutilus, and for C.metoecus from T.thymallus.
4. An annual life cycle was proposed for A.isoporum, S.bramae and C.metoecus. The seasonal dynamics and development and maturation of each parasite were examined in the definitive host.
5. The greatest intensity of infection of A.isoporum was recorded from R.rutilus, where the incidence of A.isoporum was lowest. The greatest intensity of S.bramae was recorded from R.rutilus, and in this case the incidence was also greatest.
6. a) i) Increase in incidence and intensity of infection with increase in length of the host was recorded for A.isoporum from L.leuciscus and R.rutilus.

ii) No increase in incidence with length, but an increase of intensity of infection with length of the host was recorded for A.isoporum infections from S.cephalus.

b) i) Increase in incidence and intensity of infection with increase in length was recorded for S.bramae from R.rutilus.

ii) Increase in incidence, but no increase of intensity with increase in length was recorded for S.bramae from L.leuciscus.

iii) A decrease in incidence, but an increase in intensity with increase in length was recorded for S.bramae from S.cephalus.

c) i) A decrease in incidence and intensity of infection in the two greater length groups was recorded for C.metoecus from T.thymallus.

7. a) A marked difference between the percentage of infected male and female fish only occurred in A.isoporum and S.bramae infections from R.rutilus.

b) A higher intensity of A.isoporum was recorded from female S.cephalus and L.leuciscus, but from male R.rutilus.

c) No apparent difference was recorded in the intensity of infection of male and female R.rutilus and S.cephalus with S.bramae.

d) No apparent difference was recorded in the intensity of infection of male and female T.thymallus with C.metoecus.

The significance of the results on the relationship between incidence and intensity of infection and the length and sex of the host is doubtful, as in some cases insufficient data were available for each sex in each length group.

8. The presence of A.isoporum appeared to have no influence on the establishment of S.bramae in S.cephalus, L.leuciscus and R.rutilus, and therefore the overall lower incidence and intensity of infection of S.bramae must be the result of factors other than that of competition between the two species.

9. The dimensions of A.isoporum from S.cephalus and L.leuciscus were greater than those of A.isoporum from R.rutilus.

10. The validity of the identification of A.isoporum was questioned. From the confusion that exists in the literature it was impossible to reach any conclusions. It is suggested that at the moment there is no real evidence to justify recording A.claymani as a separate species.

11. The seasonal dynamics of the Digenea in the fish of the River Lugg have been examined. It is suggested that future work should involve an examination of the stages in the intermediate host, and an analysis of the factors responsible for the specificity of these parasites, especially in relation to their presence in either cyprinid or thymallid hosts, but rarely in both.

REFERENCES

АСАРОВА, А.І. 1960 Parasites of fish of waters of Kustani oblast (Russian text). Trudy Inst.Zool.Akad.Nauk.Kazakhsk. S.S.R.V.14: 71-87.

AWACHIE, J.B.E. 1963 The Ecology of Intestinal Helminth Parasites of the Fish of Afon Terrig, North Wales. Ph.D. thesis, University of Liverpool.

BABIC, I. 1935 O nalazima entopara_zitičkih crva kod slatkovodnih riba./ Russian text, German summary_/ Vet.Archiv. Zagreb 5 (8):356-357.

BYCHOWSKAYA-PAVLOVSKAYA, 1964 'Key to the Parasites of Freshwater Fish of the U.S.S.R.' Section on Digenea, and List of parasites of freshwater fish of the U.S.S.R. Translation 1964. Israel Program for Scientific Translation, Jerusalem.

CHERNOGORENKO-BIDULINA, M.I. & BLIZNYUK, I.D., 1960 Life cycle of Sphaerostoma bramae (Müller, 1776) Dokl.Akad.Nauk.S.S.S.R. 134:(1) 237-240. Transl.

CHUBB, J.C. 1962 Acetic acid as a diluent and dehydrant in the preparation of whole, stained helminths. Stain Techn. 37: (3): 179-187.

CHUBB, J.C. 1964 Occurrence of Echinorhynchus clavula (Dujardin 1845) nec Hamann, 1892 (Acanthocephala) in the Fish of Llyn Tegid (Bala lake), Merionethshire. J.Parasit. 50: (1), 52-59.

DAWES, B. 1946 The Trematoda. C.U.P.

ERGENS, R. 1962 Helminto fauna ryb dvou jihočeských rybničních soustav. II. Trematoidea, Monogenoidea, Nematoda, Acanthocaphala a Hirudinea. Ceskosl.parasit. 9: 167-190.

GVOZDEV, E.V., AGAPOVA, A.N. and MARTYKHOV, P.F. 1953 Parasites of fish in the Ili river basin. (Russian text) Izvest.Akad.Nauk.Kazaksk.SSR. (125) s.Biol.(8): 92-114.

HOLMES, J.C. 1961 Effects of concurrent infections on Hymenolepis diminuta (Cestoda) and Moniliformis dubius (Acanthocephala). I. General effects and comparison with crowding. J.Parasit. 47: 209-216.

LYAIMAN, E.M. 1933 Parasitic worms of Lake Baikal Fish (In Russian). Trudy baikal. limnol.Sta. 4: 5 - 99.

LINSTOW, O. 1897 Helminthologische Mittheilungen Arch.mikr.Anat. 48: 375-397.

LOOSS, A. 1894 Die Distomen unserer Fische und Frösche. Stuttgart.

MALAKHOVA, R.P. 1963 Seasonal variation of Bunodera luciopercae (Müller, 1776) and Sphaerostoma bramae (Müller, 1776) under conditions of the Karelo-Finnish A.S.S.R. Zool.Zh. 42 (10): 1453-1461.

MARKEVICH, A.P. 1951 Parasitic Fauna of Freshwater Fish of the Ukranian S.S.R. (Translation, 1963). Israel Program for Scientific Translations Ltd. Jerusalem.

NÖLLER, W. 1928 Zu welchem Trematoden gehört Cercaria ar hopalocerca Nöller, 1925. S.B. Ges.naturf.Fr.Berl. 8-10:162-164.

ODHNER, T.	1901	Revision einiger Arten Distomengattung Allocreadium Lss. Zool.Jahrb.,Jena, Abt.Syst. v 14 (6): 483-520.
READ, C.P.	1951	The "crowding effect" in tapeworm infections. J.Parasit. 37 : 174-178.
RUDOLPHI, C.A.	1802	Fortsetzung der Beobachtungen über die Eingeweidewürmer. Arch.Zool.u.Zoot. 2(1): 1:67 3(1): 61-125.
SZIDAT	1938	Ueber Allocreadium transversale Rud., aus Misgurnus fossilis L. Z.Parasiten Kde. 10 (4), 468-475.
THOMAS, J.D.	1958	Studies on Crepidostomum metoecus (Braun) and Crepidostomum farionis (Muller), parasitic in Salmo trutta L. and Salmo salar L. in Britain. Parasitology, 48: 336-352.

CHAPTER FIVE

CESTODA.

Methods:

Cestodes were removed from the intestine. Fresh material was relaxed in water. Both fresh and deep-frozen material were fixed and preserved in 5% formalin.

The specimens were stained in Mayers paracarmine for identification and determination of the state of maturity. Mayers paracarmine was diluted with 45% acetic acid, and the procedures followed for dehydration and clearing were those given by Chubb (1962). Creosote was used as a final clearing medium as it made the material pliable and easier to mount.

The occurrence, intensity of infection and state of maturity were recorded for each species.

Results: Species recorded.

Four species of adult cestodes were recorded from the intestine of fish of the River Lugg (Table 5.1).

Incidence of infection.

The incidence of each species of cestode was recorded as the number of fish infected expressed as a percentage of the total number of fish in:-

i) the total sample

ii) each monthly sample

iii) each length group and each sex per length group.

Proteocephalus torulosus (Batsch, 1786).

When the total samples were considered the incidence of P.torulosus in L.leuciscus was greater than that in S.cephalus. The incidence of infection in both hosts increased from February to the beginning of July. P.torulosus was not recorded from L.leuciscus in August and September. A high incidence was present in October, but this decreased markedly in November and December. Such a marked pattern of incidence was not present in S.cephalus. In the latter, infection was absent in August, a low incidence was present in September which increased slightly in October, but then fell to zero in November and December (Tables 5.2 and 5.3).

A slight increase in incidence was recorded with increase in length of L.leuciscus, whereas a decrease in incidence with increase in length occurred in S.cephalus (Tables 5.5, 5.6)

As the incidence of infection in S.cephalus was low the data were insufficient to merit any conclusion on any possible relationship between length of host and incidence. This statement also applied to the data for the total incidence recorded from each sex from all the length groups. When the total number of infected male and female fish were expressed as a percentage of all the male and female S.cephalus sampled, no great difference was evident in the incidence of infection between the two sexes. (Table 5.6.) In L.leuciscus where more data were available no apparent difference in incidence was recorded between infected male and female fish when they were considered from each length

group, and from the total sample. (Table 5.5.)

Caryophyllaeides fennica.

The incidence of infection in all three cyprinid hosts was low, but of these three, S.cephalus had the higher and L.leuciscus the lower incidence (Tables 5.2, 5.3, 5.4). The incidence appeared to increase between September and December in S.cephalus and to some extent in R.rutilus, but the low incidence of C.fennica made it difficult to determine any significant seasonal variation. The low incidence also prevented the collection of any valid information on incidence in relation to the length and sex of the host, except in the case of R.rutilus and S.cephalus where the presence of slightly more data suggested a possible increase in incidence with length in R.rutilus and between the 20 - 30cm. and 30 - 40cm. groups in S.cephalus (Tables 5.7, 5.8, 5.9.).

Caryophyllaeus laticeps. (Tables 5.10, 5.11, 5.12).

A low incidence of C.laticeps was also recorded from the three cyprinid hosts. The absence of infected fish from some of the samples may be the result of either the low incidence of infection and a seasonal variation in infection, or a combination of both factors. An increase in incidence was present in June in S.cephalus, and in July for both R.rutilus and L.leuciscus.

Tables 5.10 and 5.11 suggest that a possible increase in incidence occurs with increase in length, but the low incidence of infection as in C.fennica does not permit any valid conclusions as to the presence

or absence of a relationship between incidence and the length and sex of the host.

Triaenophorus nodulosus.

The total number of E.lucius sampled was small and only eight (22.2%) of the total sample of 36 were infected. T.nodulosus was only recorded in April (4:57.1%), August (1:50.0%) and October (3:75.0%), the figures in brackets referring to the number and percentage of infected fish.

TABLE 5.2:

The occurrence of P.torulosus, C.fennica and C.laticeps in L.leuciscus.

Month	No.fish/ sample	No.and % of L.leuciscus infected with each cestode.					
		P.torulosus		C.fennica		C.laticeps	
		No.	%	No.	%	No.	%
Jan.	33	0	-	0	-	0	-
Feb.	31	1	3.2	1	3.2	0	-
Mar.	30	1	3.3	0	-	0	-
Apr.	35	7	20.0	2	5.7	3	9.9
May	4	0	-	0	-	0	-
June	30	18	60.0	0	-	1	3.3
July	30	13	43.3	1	3.3	7	23.3
Aug.	30	0	-	0	-	0	-
Sept.	30	0	-	1	3.3	0	-
Oct.	31	22	71.0	2	6.4	6	19.4
Nov.	28	3	10.7	3	10.7	0	-
Dec.	30	5	16.6	0	-	1	3.3
Total	342	70	20.5	10	2.9	18	5.3

TABLE 5.3:

The occurrence of P.torulosus, C.fennica and C.laticeps in S.cephalus.

Month	No.fish/ sample	No.and % of S.cephalus infected with each cestode. P.torulosus		C.fennica		C.laticeps	
		No.	%	No.	%	No.	%
Jan.	32	0	-	1	3.1	0	-
Feb.	31	1	3.2	0	-	2	6.5
Mar.	29	1	3.4	2	6.9	1	3.5
Apr.	30	3	10.0	5	16.6	1	3.3
May	31	1	3.0	1	3.2	0	-
June	30	11	36.6	2	6.6	7	23.3
July	30	8	26.6	2	6.6	2	6.6
Aug.	30	0	-	2	6.6	1	3.3
Sept.	28	1	3.6	8	28.6	0	-
Oct.	27	3	11.1	5	18.5	1	3.7
Nov.	30	0	-	8	26.6	0	-
Dec.	31	0	-	4	12.9	0	-
Total	359	29	8.1	40	11.1	15	4.2

TABLE 5.4:

The occurrence of C.fennica and C.laticeps in R.rutilus.

Month	No.fish/ sample	No.and % of R.rutilus infected with each cestode. C.fennica		C.laticeps	
		No.	%	No.	%
Jan.	33	0	-	0	-
Feb.	27	1	3.7	0	-
Mar.	30	3	9.9	1	3.3
Apr.	16	0	-	1	6.3
May	9	1	11.1	1	11.1
June	30	2	6.6	3	9.9
July	22	1	4.5	4	18.2
Aug.	30	4	13.2	0	-
Sept.	30	3	9.9	0	-
Oct.	30	5	16.6	0	-
Nov.	30	5	16.6	0	-
Dec.	30	3	9.9	1	3.3
Total	317	28	8.8	11	3.5

TABLE 5.5:

The number of L.leuciscus of each sex in each length group infected with P.torulosus.

	Length in cms.														
	0-15			15-20			20-25			25-30			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.			0			0			0			0	0	0	0
Feb.							0	1	1				0	1	1
Mar.								1	1				0	1	1
Apr.				2	0	2	0	4	4	0	1	1	2	5	7
May						0							0	0	0
June				1	2	3	8	6	14	0	1	1	9	9	18
July				1	1	2	3	4	7	1	3	4	5	8	13
Aug.													0	0	0
Sept.													0	0	0
Oct.				1	0	1	11	6	17	4	0	4	16	6	22
Nov.							1	0	1	1	1	2	2	1	3
Dec.				0	1	1	0	1	1	1	2	3	1	4	5
Total				5	4	9	23	23	46	7	8	15	35	35	70
Infected fish expressed as a % of the total no. of fish.				17.2	20.0	18.4	22.8	20.3	21.5	21.9	25.0	23.4	20.3	20.6	20.5

Key: T = Total
F = Female
M = Male

TABLE 5.6:

The number of S.cephalus of each sex in each length group infected with P.torulosus.

	Length in cms.														
	0-20			20-30			30-40			40-50			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.															0
Feb.							1	0	1				1	0	1
Mar.															1*
Apr.				0	2	2	1	0	1				1	2	3
May				0	1	1							0	1	1
June		1	1	6	4	10							6	5	11
July				4	3	7	1	0	1				5	3	8
Aug.															0
Sept.				1	0	1							1	0	1
Oct.				0	1	1	2	0	2				2	1	3
Nov.															
Dec.															
Total		1	1	11	11	22	5	0	5				16	12	29*
Infected fish expressed as a % of the total no. of fish		33.3	25.0	11.1	11.7	11.3	8.3		4.7				7.7	8.0	8.0

Key: * = sex and length of one fish not recorded.
T = Total
F = Female
M = Male

TABLE 5.7:

The number of S.cephalus of each sex in each length group infected with C.fennica.

	Length in cms.														
	0-20			20-30			30-40			40-50			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				1	0	1							1	0	1
Feb.															0
Mar.				1	0	1	0	1	1				1	1	2
Apr.				0	4	4	0	1	0				0	5	5
May				0	1	1							0	1	1
June				1	0	1	0	1	1				1	1	2
July				1	0	1	1	0	1				2	0	2
Aug.				0	1	1				0	1	1	0	2	2
Sept.				1	2	3	0	4	4	1	0	1	2	6	8
Oct.				0	1	1	3	0	3	1	0	1	4	1	5
Nov.				2	2	4	1	1	2	2	0	2	5	3	8
Dec.				1	2	3	0	1	1				1	3	4
Total				8	13	21	5	9	13	4	1	5	17	23	40
Infected fish expressed as a % of the total no. of fish.				8.0	13.8	10.8	8.3	19.6	12.3	8.3	14.3	9.1	8.2	15.3	11.1

Key: T = Total
F = Female
M = Male

TABLE 5.8:

The number of *L.leuciscus* of each sex in each length group infected with *C.fennica*.

	Length in cms.														
	0-15			15-20			20-25			25-30			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.															0
Feb.							0	1	1				0	1	1
Mar.															0
Apr.				0			1	1	2				1	1	2
May															0
June															0
July							0	1	1				0	1	1
Aug.															0
Sept.				1	0	1							1	0	1
Oct.	1	0	1	1	0	1							2	0	2
Nov.							1	2	3				1	2	3
Dec.															0
Total	1	0	1	2	0	2	2	5	7				5	5	10
Infected fish expressed as a % of the total no.of fish.	10.0		6.6	6.9		4.1	2.0	4.4	3.3				2.9	2.9	2.9

Key: T = Total
F = Female
M = Male

TABLE 5.9:

The number of R.rutilus of each sex in each length group infected with C.fennica.

Month	Length in cms. 0-15 F	0-15 M	0-15 T	15-20 F	15-20 M	15-20 T	20-25 F	20-25 M	20-25 T	25-30 F	25-30 M	25-30 T	30-35 F	30-35 M	30-35 T	Totals F	Totals M	Totals T
Jan.																		0
Feb.							1	0	1							1	0	1
Mar.				0	1	1	0	1	1	1	0	1				1	2	3
Apr.																		0
May							1	0	1							1	0	1
June				0	1	1							1	0	1	1	1	2
July				0	1	1										0	1	1
Aug.				1	0	1				2	1	3				3	1	4
Sept.				0	1	1				2	0	2				2	1	3
Oct.				1	1	2				3	0	3				4	1	5
Nov.				0	2	2	1	0	1	0	2	2				1	4	5
Dec.				0	1	1	1	0	1	1	0	1				2	1	3
Total				2	8	10	4	1	5	9	3	12	1	0	1	16	12	28
Infected fish expressed as a % of the total no. of fish.				3.0	8.5	8.4	3.3	3.6	7.0	15.8	7.7	12.5	3.4		3.2	10.4	7.4	8.8

Key: T = Total
F = Female
M = Male

TOTAL 5.10:

The number of S.cephalus of each sex in each length group infected with C.laticeps.

	Length in cms.														
	0-20			20-30			30-40			40-50			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.															0
Feb.							2	0	2				2	0	2
Mar.				0	1	1							0	1	1
Apr.										0	1	1	0	1	1
May															0
June							3	1	4	2	1	3	5	2	7
July				1	1	2							1	1	2
Aug.										1	0	1	1	0	1
Sept.															0
Oct.										1	0	1	1	0	1
Nov.															0
Dec.															0
Total				1	2	3	5	1	6	4	2	6	10	5	15
Infected fish expressed as a % of the total no. of fish				1.01	2.1	1.5	8.3	2.2	5.7	8.3	28.6	10.9	4.8	3.3	4.2

Key: T = Total
F = Female
M = Male

TABLE 5.11:

The number of *L.leuciscus* of each sex in each length group infected with *C.laticeps*.

	Length in cms.														
	0-15			15-20			20-25			25-30			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.															0
Feb.															0
Mar.															0
Apr.				0	2	2				0	1	1	0	3	3
May															0
June										0	1	1	0	1	1
July							1	4	5	1	1	2	2	5	7
Aug.															0
Sept.															0
Oct.							3	2	5	1	0	1	4	2	6
Nov.															0
Dec.										0	1	1	0	1	1
Total				0	2	2	4	6	10	2	4	6	6	12	18
Infected fish expressed as a % of the total no. of fish.					10.0	4.1	3.9	5.3	4.7	6.3	12.5	9.4	3.5	7.1	5.3

Key: T = Total
F = Female
M = Male

TABLE 5.12:

The number of *R.rutilus* of each sex in each length group infected with *C.laticeps*.

	Length in cms.														
	0-15			15-20			20-25			25-30			30-35			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.																		0
Feb.																		0
Mar.										1	0	1				1	0	1
Apr.										1	0	1				1	0	1
May				1	0	1										1	0	1
June				0	1	1	1	0	1				1	0	1	2	1	3
July				2	0	2	1	1	2							3	1	4
Aug.																		
Sept.																		
Oct.																		
Nov.																		
Dec.										1	0	1				1	0	1
Total				3	1	4	2	1	3	3	0	3	1	0	1	9	2	11
Infected fish expressed as a % of the total no. of fish				12.0	1.1	3.4	4.6	3.6	4.2	5.3		3.1	3.4		3.2	5.8	1.2	3.5

Key: T = Total
F = Female
M = Male

Intensity of Infection.

The intensity of infection was measured as the mean number of parasites per infected fish. The intensity was recorded for:-

(i) the total sample

(ii) each monthly sample

(iii) each length group

(iv) each sex in:- a) each length group

b) the total sample

Proteocephalus torulosus.

A greater intensity of infection of P.torulosus was recorded from L.leuciscus than from S.cephalus. The seasonal variation in intensity of infection in L.leuciscus was similar to that of incidence, one peak of intensity occurring in June, and a second in October. A drop in intensity was recorded in July and no infection was recorded in August and September. A drop in intensity was also recorded between October and December. As with incidence a slight increase in intensity of infection was also present in June and July in S.cephalus. No P.torulosus was recorded from S.cephalus in August, but infection reappeared in September and October, although no evidence of infection was recorded in November and December. From the information it is suggested that a similar seasonal variation in intensity of infection is probably present in both L.leuciscus and S.cephalus, but the low incidence and intensity in the latter are too low to show a significant pattern (Table 5.13).

In L.leuciscus an increase of intensity of infection was recorded with

increase in length of fish (Table 5.14 . The low intensity recorded in S.cephalus prevented any conclusion as to any such relationship. The only fact to emerge was that most infected S.cephalus and most parasites were recorded from the 20 - 30cm. group, none being present in the 40 - 50cm. group (Table 5.15).

Female L.leuciscus had a greater intensity of infection than males in the larger length group, and this was reflected in the result when the intensity was examined for the total numbers of infected males and females. Although a difference was recorded it is not certain from the data that this difference was significant (Table 5.14).

The data were insufficient to justify any comment on the presence or absence of any relationship between intensity of infection and sex of the host in S.cephalus (Table 5.15).

Caryophyllaeides fennica.

When the total sample was considered a similar intensity of infection was present in allthree cyprinid hosts, the intensity in both S.cephalus and R.rutilus being 1.7 (Table 5.16). A peak of intensity was recorded in October from all three hosts. A similar peak was recorded in April from L.leuciscus but as a result of the low infection no significance could be attached to the observations from L.leuciscus (Table 5.16).

As a result of low incidence and intensity of infection insufficient data were available from which to draw any valid conclusions as to any relationship between intensity and the length and sex of the host. Examination of the number of parasites from the total number of infected

TABLE 5.13:

Intensity of infection of P.torulosus in L.leuciscus and S.cephalus.

Month	L.leuciscus			S.cephalus		
	No. infected fish	No. parasites	Mean no.	No. infected fish	No. parasites	Mean no.
Jan.	0	0	0	0	0	0
Feb.	1	2	2.0	1	1	1.0
Mar.	1	1	1.0	1	1	1.0
Apr.	7	31	3.5	3	4	1.3
May	0	0	0	1	R	R
June	18	130	7.2	11	30	2.7
July	13	22	1.7	8	20	2.5
Aug.	0	0	0	0	0	0
Sept.	0	0	0	1	1	1.0
Oct.	22	207	9.4	2	4	2.0
Nov.	3	26	2.5	0	0	0
Dec.	5	62	12.4	0	0	0
Total	70	481	6.7	28	61	2.2

Key: R = Rare.

TABLE 5.14:

The number of P.torulosus in L.leuciscus.

L e n g t h i n cms.

Month	0-15			15-20			20-25			25-30			Totals		
	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.			0			0			0			0			0
Feb.								2	2					2	2
Mar.								1	1					1	1
Apr.				6	0	6	0	6	6	0	19	19	6	25	31
May						0									0
June				2	2	4	22	34	56	0	67	67	24	103	127
July				2	1	3	2	6	8	9	2	11	13	9	22
Aug.															0
Sept.															0
Oct.				4	0	4	81	18	99	104		104	189	18	207
Nov.							3	0	3	21	2	23	24	2	26
Dec.				0	1	1	0	1	1	26	34	60	26	36	62
Total				14	4	18	108	68	176	160	124	284	282	196	478
Mean no.of parasites				2.8	1.0	2.0	4.7	3.0	3.8	22.8	15.5	18.9	8.1	5.6	6.7

Key: T = Total
F = Female
M = Male

TABLE 5.15:

The number of P.torulosus in S.cephalus.

	Length in cms.														
	0-20			20-30			30-40			40-50			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.															0
Feb.															1[x]
Mar.															1[x]
Apr.				0	3	3	1	0	1				1	3	4
May				0	R	R							0	R	R
June		R	R	7	23	30							7	23	30
July				12	4	16	4	0	4				16	4	20
Aug.															
Sept.				1	0	1							1	0	1
Oct.				0	1	1	3	0	3				3	1	4
Nov.															
Dec.															
Total		R	R	20	31	51	8	0	8				28	31	61
Mean no. parasites				1.8	2.8	2.3	1.6		1.6				1.7	2.6	2.1

Key: x - length and sex of fish unrecorded.
R - Rare
T - Total
F - Female
M - Male

male and female fish suggested that no difference in intensity existed between sexes in L.leuciscus and S.cephalus (Tables 5.17, 5.18). More female than male R.rutilus were infected in the 25 - 30 cm. fish sampled. If equal numbers of both sexes were present in each length group a valid comparison of intensity between sexes could be made. From the present results it is impossible to say whether the slightly higher intensity in female R.rutilus (Table 5.19) results from females being more susceptible to infection rather than to any other factors.

Caryophyllaeus laticeps.

The intensity of infection was low in each of the cyprinid hosts when the total samples were examined, ranging from 1.3 in S.cephalus to 3.6 in R.rutilus (Table 5.20).

No apparent seasonal variation was recorded. The highest intensity was recorded in June for R.rutilus, and July and October for L.leuciscus.

The low incidence and intensity of infection did not permit investigations into the relationships between intensity and length and sex of the host. Tables 5.21, 5.22, 5.23 show that a greater intensity of C.laticeps was recorded from the 15 - 20cm. group of R.rutilus and the 20 - 25cm. group of L.leuciscus, but uniform intensity was present in the length groups of S.cephalus. These observations reflect the results of the July sample for R.rutilus and the July and September samples for L.leuciscus, where the greatest number of C.laticeps were recorded, and where the infected fish nearly all fall within the same length groups i.e. 15-20cm. in R.rutilus and 20-25cm. in L.leuciscus.

TABLE 5.16:

The intensity of infection of C.fennica in S.cephalus, L.leuciscus and R.rutilus.

Month	S.cephalus			L.leuciscus			R.rutilus		
	No. infected fish	No. parasites	Mean no.	No. infected fish	No. parasites	Mean no.	No. infected fish	No. parasites	Mean no.
Jan.	1	1	1.0	0	0	0	0	0	0
Feb.	0	0	0	1	1	1.0	1	1	1.0
Mar.	2	3	1.5	0	0	0	3	3	1.0
Apr.	5	9	1.8	2	5	2.5	0	0	0
May.	1	1	1.0	0	0	0	1	1	1.0
June	2	2	1.0	0	0	0	2	2	1.0
July	2	2	1.0	1	1	1.0	1	1	1.0
Aug.	2	3	1.5	0	0	0	4	9	2.2
Sept.	8	15	1.9	1	1	1.0	3	3	1.0
Oct.	5	11	2.7	2	5	2.5	5	18	3.6
Nov.	8	15	1.9	3	6	2.0	5.	6	1.2
Dec.	4	4	1.0	0	0	0	3	4	1.3
Total	40	66	1.7	10	19	1.9	28	48	1.7

TABLE 5.17:

The number of C.fennica in S.cephalus.

Length in cms.

Month	0-20			20-30			30-40			40-50			Totals		
	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.				1	0	1							1	0	1
Feb.															0
Mar.				2	0	2	0	1	1				2	1	3
Apr.				0	5	5	0	4	4				0	9	9
May				0	1	1							0	1	1
June				1	0	1	0	1	1				1	1	2
July				1	0	1	1	0	1				2	0	2
Aug.				0	1	1				0	2	2	0	3	3
Sept.				1	4	5	0	9	9	1	0	1	2	13	15
Oct.				0	1	1	9	0	9	1	0	1	10	1	11
Nov.				4	3	7	5	1	6	2	0	2	11	4	15
Dec.				1	2	3	0	1	1				1	3	4
Total				11	17	28	15	17	32	4	2	6	30	36	66
Mean no. parasites				1.4	1.3	1.3	3.0	1.9	2.5	1.0	2.0	1.2	1.7	1.5	1.6

Key: T = Total
F = Female
M = Male

TABLE 5.18:

The number of C.fennica in L.leuciscus.

	length in cms.														
	0-15			15-20			20-25			25-30			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.															
Feb.							0	1	1				0	1	1
Mar.															0
Apr.							3	2	5				3	2	5
May															0
June															0
July							0	1	1				0	1	1
Aug.															0
Sept.				1	0	1							1	0	1
Oct.	3	0	3	2	0	2							5	0	5
Nov.							1	5	6				1	5	6
Dec.															0
Total	3	0	3	3	0	3	4	9	13				10	9	19
Mean no. parasites	3.0	0	3.0	1.5	0	1.5	2.0	1.8	1.9				2.0	1.8	1.9

Key: T = Total
F = Female
M = Male

TABLE 5.19:

The number of C.fennica in R.rutilus.

Length in cms.

Month	0-15			15-20			20-25			25-30			30-35			Totals		
	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.																		
Feb.							1	0	1							1	0	1
Mar.				0	1	1	0	1	1	1	0	1				1	2	3
Apr.																		0
May							1	0	1							1	0	1
June				0	1	1							1	0	1	1	1	2
July				0	1	1										0	1	1
Aug.				2	0	2				6	1	7				8	1	9
Sept.				0	1	1				2	0	2				2	1	3
Oct.				1	1	2				16	0	16				17	1	18
Nov.				0	3	3	1	0	1	0	2	2				1	5	6
Dec.				0	2	2	1	0	1	1	0	1				2	2	4
Total				3	10	13	4	1	5	26	3	29	1	0	1	34	14	48
Mean no. parasites				1.5	1.2	1.3	1.0	1.0	1.0	2.9	1.0	2.4	1.0	0	1.0	2.1	1.2	1.7

Key: T = Total
F = Female
M = Male

TABLE 5.20:

The intensity of C.laticeps in S.cephalus, L.leuciscus and R.rutilus.

Month	S.cephalus			L.leuciscus			R.rutilus.		
	No. infected fish	No. parasites	Mean No.	No. infected fish	No. parasites	Mean No.	No. infected fish	No. parasites	Mean No.
Jan.	0	0	0	0	0	0	0	0	0
Feb.	2	2	1.0	0	0	0	0	0	0
Mar.	1	1	1.0	0	0	0	1	1	1.0
Apr.	1	2	2.0	3	4	1.3	1	1	1.0
May	0	0	0	0	0	0	1	1	1.0
June	7	11	1.6	1	1	1.0	3	3	1.0
July	2	2	1.0	7	26	2.0	4	35	8.7
Aug.	1	1	1.0	0	0	0	0	0	0
Sept.	0	0	0	0	0	0	0	0	0
Oct.	1	1	1.0	6	19	3.2	0	0	0
Nov.	0	0	0	0	0	0	0	0	0
Dec.	0	0	0	1	4	4.0	1	1	1.0
Total	15	20	1.3	18	54	2.3	11	42	3.6

TABLE 5.21:

The number of C.laticeps in S.cephalus.

Length in cms.

Month	0-20 F	0-20 M	0-20 T	20-30 F	20-30 M	20-30 T	30-40 F	30-40 M	30-40 T	40-50 F	40-50 M	40-50 T	Totals F	Totals M	Totals T
Jan.															0
Feb.							2	0	2				2	0	2
Mar.				0	1	1							0	1	1
Apr.										0	2	2	0	2	2
May															0
June							4	1	5	5	1	6	9	2	11
July				1	1	2							1	1	2
Aug.										1	0	1	1	0	1
Sept.															0
Oct.										1	0	1	1	0	1
Nov.															0
Dec.															0
Total				1	2	3	6	1	7	7	3	10	14	6	20
Mean no. parasites				1.0	1.0	1.0	1.2	1.0	1.1	1.7	1.5	1.6	1.4	1.2	1.3

Key: T= Total
F= Female
M= Male

TABLE 5.22:

The number of C.laticeps in L.leuciscus.

Length in cms.

Month	0-15			15-20			20-25			25-30			Totals		
	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.															0
Feb.															0
Mar.															0
Apr.				0	3	3				0	1	1	0	4	4
May															0
June										0	1	1	0	1	1
July							17	7	24	1	1	2	18	8	26
Aug.															0
Sept.															0
Oct.							16	3	19	1	0	1	17	3	20
Nov.															0
Dec.										0	4	4	0	4	4
Total				0	3	3	33	10	43	2	7	9	35	20	55
Mean no. parasites					1.5	1.5	8.3	1.6	4.3	1.0	1.7	1.5	5.8	1.7	3.1

Key: T = Total
F = Female
M = Male

TABLE 5.23:

The number of *C.laticeps* in *R.rutilus*.

	Length in cms.																	
	0-15			15-20			20-25			25-30			30-35			Totals		
Month	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T	F	M	T
Jan.																		0
Feb.																		0
Mar.										1	0	1				1	0	1
Apr.										1	0	1				1	0	1
May				1	0	1										1	0	1
June				0	1	1	1	0	1				1	0	1	2	1	3
July				32	0	32	2	1	3							34	1	35
Aug.																		0
Sept.																		0
Oct.																		0
Nov.																		0
Dec.										1	0	1				1	0	1
Total				33	1	34	3	1	4	3	0	3	1	0	1	40	2	42
Mean no. parasites				11.0	1.0	8.5	1.5	1.0	1.3	1.0		1.0	1.0	0	1.0	4.4	1.0	3.8

Key: T = Total
F = Female
M = Male

Seasonal dynamics.

Proteocephalus torulosus.

Three specimens of P.torulosus were recorded in February and March but it was not until April that many specimens were recorded. Most of the specimens in April were mature, and the absence of younger forms in any number from previous months was thought to be unusual. It was suspected that the immature forms had been overlooked either because they were very small or because they were situated in a different location. The intestinal bulb of the fish was being examined by Mr. J. Hellawell in connection with the diet of the fish. As a result of the observation on the incidence of P.torulosus the intestinal bulb was examined for the presence of this species each month after April. Table 5.24 shows the presence of more P.torulosus in the intestinal bulb than in the intestine in June and July and from October to December, and therefore it is probable that P.torulosus was present in the intestinal bulb from January to April. No P.torulosus were recorded from the inadequate sample of only four L.leuciscus in May. Five P.torulosus were recorded on the gill filaments, probably as a result of regurgitation from the stomach, while the fish were being caught.

The specimens from L.leuciscus and S.cephalus were examined and a record kept of their state of development and maturation.

Five main stages of development and maturation were recorded:-

I. Plerocercoid under 1cm.; no strobilation.

II. Plerocercoid 1 - 3cm.; no strobilation.

III. Strobilation and genital rudiments present.

IV. Mature proglottids; no eggs.

V. Mature proglottids; with eggs.

The mean and the range of length of each stage is recorded in Table 5.25. A fact which may or may not prove to be significant if more specimens had been measured, is that mature P.torulosus (Stage V) from L.leuciscus were longer than those from S.cephalus, indicating that L.leuciscus may be a more suitable host for P.torulosus. The presence of fewer specimens in S.cephalus may also tend to support this suggestion.

The number of each stage of P.torulosus from each sample were expressed as a percentage of the total number of P.torulosus from each sample for infections in L.leuciscus and S.cephalus (Tables 5.26, 5.27).

L.leuciscus (Table 5.26).

The three specimens found in February and March were at Stage III. In April the first four stages were present, the greater percentage being either Stage III or Stage IV. All five stages were recorded in June and an increase in Stage I was noted. By July the occurrence and intensity of infection had decreased, and the greater percentage of P.torulosus present were Stage V. No infection was recorded in August and September. In October a sudden increase of occurrence and intensity were recorded, all the specimens being categorised as Stage I. A drop

in occurrence and intensity was present in November and all the parasites were recorded as Stage II, as was the case in December.

From this data and the incidence and intensity of infection it was concluded that P.torulosus had an annual life cycle. A gradual increase occurrence, intensity of infection and maturation occurred between February and June. In July the occurrence and intensity of infection decreased and most of the parasites were full of eggs, and by August the infection had completely disappeared. This suggested that when the worms are mature and full of fertilised eggs they pass out of the host i.e. in July. In August and September the eggs probably hatch and the eggs are ingested by the intermediate host, usually a species of Cyclops. The onchosphere bores through the intestine wall, and develops into a procercoid in the haemocoel.

In October a great increase in occurrence and intensity of infection of Stage I was recorded. Although some Stage I were recorded in June, it is postulated that this is the main period of reinfection, and that P.torulosus procercoids from any infected Cyclops that are ingested become established in the definitive host. A limit on the number of worms which can be supported by each definitive host may account for the decrease of infection in November. The specimens from this sample were beginning to increase in size, and this may represent the stable level of infection.

S.cephalus (Table 5.27).

The number of parasites recorded from S.cephalus was lower, and infection was recorded only between April and July, and September and October. In spite of the low incidence, when the specimens were examined to determine the stages of maturation, it was possible to see that P.torulosus had a similar annual life cycle in L.leuciscus and S.cephalus. Data obtained from S.cephalus in February 1965 supported this statement, the expected stages for this time of year, Stages II and III being present.

C.fennica and C.laticeps.

Five main stages of development were proposed for C.fennica and C.laticeps in the definitive host (C.Kennedy, pers.comm.):-

I. No genitalia present.

II. Genitalia just appearing.

III. Genitalia fully developed.

IV. Egg production just commencing.

V. Many eggs present.

The number of each stage present each month was expressed as a percentage of the total number of C.fennica or C.laticeps present each month (Tables 5.28, 5.29).

C.fennica from S.cephalus. (Table 5.28).

Between January and August, Stages III, IV and V were present. From

TABLE 5.24:

The distribution of P.torulosus in the alimentary canal of L.leuciscus.

Month	Number of Parasites			
	Intestinal bulb	Intestine	Gills	Total
Jan.	X	0	0	0
Feb.	X	2	0	2
Mar.	X	1	0	1
Apr.	X	29	2	31
May	0	0	0	0
June	96	31	3	130
July	22	0	0	22
Aug.	0	0	0	0
Sept.	0	0	0	0
Oct.	190	17	0	207
Nov.	17	9	0	26
Dec.	41	21	0	62
Total	366	110	5	481

Key: X = not examined.

TABLE 5.25:

The length in mm. of the stages of development of P.torulosus.

Stage	Mean	Range	No.examined
I D	0.75	0.55 - 1.03	11
II D	2.46	1.26 - 4.68	29
C	2.68	1.49 - 4.00	12
III D	17.4	17.4	1
C	11.8	6.5 - 22.0	3
IV D	142.3	80.0 -182.0	3
V D	189.3	104.0 -282.0	11
C	157.2	101.0 -193.0	8

Key: D = L.leuciscus.

C = S.cephalus.

TABLE 5.26:

The number of each stage of P.torulosus in L.leuciscus expressed as a percentage of the total number in each sample.

Month	Stages of development. I No.	I %	II No.	II %	III No.	III %	IV No.	IV %	V No.	V %
Jan.										
Feb.					2	100.0				
Mar.					1	100.0				
Apr.	2	6.5	13	41.9	6	19.4	10	32.2		
May										
June	19	15.4	6	4.6	16	12.3	21	16.9	65	50.8
July	2	14.3			2	14.3			10	71.4
Aug.										
Sept.										
Oct.	207	100.0								
Nov.			26	100.0						
Dec.			23	100.0						

TABLE 5.27:

The number of each stage of *P.torulosus* in *S.cephalus* expressed as a percentage of the total number in each sample.

	Stages of development.									
	I		II		III		IV		V	
Month	No.	%	No.	%	No.	%	No.	%	No.	%
Jan.										
Feb.										
Mar.										
Apr.			1	50.0			1	50.0		
May									1	100.0
June			1	3.3	1	3.3	6	20.0	22	73.4
July	1	5.0			1	5.0	3	15.0	15	75.0
Aug.										
Sept.	1	100.0								
Oct.	3	100.0								
Nov.										
Dec.										
Jan.										
Feb.			56	18.3	26	31.7				

August to December Stage II was recorded each month. Stages III to V were recorded from September to Dece-ber with the exception of Stage IV in December. Stage V was the most common between October and December. From the data it was not possible to estimate the duration of the life cycle. Reinfection of the host may occur between August and December when most Stage II were recorded. The possibility that either C.fennica matures rapidly and produces eggs for nearly a year, or that reinfection at all times of year followed by rapid maturation which is of short duration, or that lasts for nearly a year, may account for the presence of Stage V in most months of the year.

C.fennica from L.leuciscus (Table 5.28).

Infection of L.leuciscus with C.fennica resembled that in S.cephalus until the July sample. No Stage II were recorded between July and December, and Stages III and IV were only present in October. Stage V was the most common stage and was recorded over the whole year.

C.fennica from R.rutilus (Table 5.28).

Only three records of C.fennica occurred in R.rutilus between January and July. Stage V was the only stage present in the previously mentioned samples but was also present in each sample from August to December. Stages II and III were present in August, Stage III was also present in November and Stage IV in December. As in S.cephalus reinfection of R.rutilus with C.fennica may occur between August and December, although mature worms were present in all months except January and March.

C.laticeps from S.cephalus (Table 5.29).

Table 5.29 shows that Stages III and V were present between February and June. Stages II - V were present in June, after which only Stage V was recorded in July, August and October.

C.laticeps from L.leuciscus (Table 5.29).

The occurrence of C.laticeps in L.leuciscus was very erratic. The first record was present in April, of Stages II to IV. Infection with Stages IV to V were recorded in June and July, more Stage V being present in the latter sample. Records of Stage III were present in October and December and also of Stage V in the former month.

C.laticeps from R.rutilus (Table 5.29)

The occurrence of C.laticeps in R.rutilus was rare. Stage III in April, Stages IV and V in June and Stages I to V in July were recorded, but no further occurrence was noted until December (Stage V). This infection showed an increase in maturation of C.laticeps between April and July and a reinfection of the definitive host in July with a greater number of small parasites.

The length of C.fennica and C.laticeps in the definitive hosts.

The length of adult C.fennica and C.laticeps at different stages of maturation were measured in mm. (Tables 5.30, 5.31). Comparisons were made between Stage V from all three cyprinid hosts.

A greater mean length was recorded for C.fennica from L.leuciscus

although a greater range was recorded from R.rutilus. The difference between the lengths from each host were small and probably of no significance. The less mature stages in L.leuciscus were smaller than in either of the other hosts. Both the mean length and the range of length of C.laticeps from L.leuciscus were greater than those from either R.rutilus and S.cephalus.

Mishra (1966) measured the length of C.fennica and C.laticeps from R.rutilus taken from the Shropshire Union Canal, Cheshire. He stated that

> "Egg formation starts in the worm when it acquires the minimum size of 10 mm. The worm of maximum size e.g. 33mm x 3 mm. was noticed in the month of May".

In the present survey all Stage IV C.fennica were over 10mm. except those from L.leuciscus but only one Stage IV specimen was examined in this case. A maximum length of 29mm. was recorded for C.fennica from R.rutilus. Mishra (1966) recorded a length of 14.4mm. for C.laticeps from R.rutilus. In the present investigation a range of 23 - 40mm. was recorded, and this coincided with the range given by Dubinina (1964).

TABLE 5.28:

The number of each stage of C.fennica in each sample, from S.cephalus, L.leuciscus and R.rutilus, expressed as a percentage of the total number in each sample.

		Stages of development.									
		I		II		III		IV		V	
Month	Host	No.	%	No.	%	No.	%	No.	%	No.	%
Jan.	C							1	100.0		
	D										
	R										
Feb.	C										
	D									1	100.0
	R									1	100.0
Mar.	C					3	100.0				
	D										
	R										
Apr.	C					1	11.1			8	88.9
	D					2	40.0			3	60.0
	R										
May	C									1	100.0
	D										
	R									1	100.0
June	C									2	100.0
	D										
	R									2	100.0
July	C									2	100.0
	D									1	100.0
	R									1	100.0
Aug.	C			1	33.3	2	66.7				
	D										
	R			1	12.5	2	25.0			5	62.5
Sept.	C			1	6.2	1	6.2	8	50.0	6	37.6
	D									1	100.0
	R									3	100.0
Oct.	C			1	10.0	3	30.0	3	30.0	3	30.0
	D					1	20.0	1	20.0	3	60.0
	R									18	100.0
Nov.	C			2	6.7	1	13.3	4	26.7	8	53.3
	D									6	100.0
	R					1	16.6			5	83.4
Dec.	C			1	25.0					3	75.0
	D										
	R							1	25.0	3	75.0

Key: C = S.cephalus; D = L.leuciscus; R = R.rutilus.

TABLE 5.29:

The number of each stage of C.laticeps in each sample, from S.cephalus, L.leuciscus and R.rutilus expressed as a percentage of the total number in each sample.

		Stages of development.									
		I		II		III		IV		V	
Month	Host	No.	%	No.	%	No.	%	No.	%	No.	%
Jan.	C										
	D	0									
	R										
Feb.	C					1	50.0	1	50.0		
	D	0									
	R										
Mar.	C									1	100.0
	D	0									
	R										
Apr.	C					2	100.0				
	D			1	25.0	1	25.0	2	50.0		
	R			1	100.0						
May	C										
	D										
	R									1	100.0
June	C			1	9.1	1	9.1	2	18.2	17	63.6
	D							1	100.0		
	R							1	33.3	2	66.7
July	C									2	100.0
	D							2	7.7	24	92.3
	R	26	74.3	3	8.6	1	2.8			5	14.3
Aug.	C									1	100.0
	D										
	R										
Sept.	C										
	D										
	R										
Oct.	C									1	100.0
	D					13	68.4			6	31.6
	R										
Nov.	C										
	D										
	R										
Dec.	C										
	D					4	100.0				
	R									1	100.0

Key: C = S.cephalus; D = L.leuciscus; R = R.rutilus.

TABLE 5.30:

The length in mm. of the stages of development of C.fennica in the definitive host.

	DEFINITIVE HOSTS.					
	S.cephalus		L.leuciscus		R.rutilus	
Stage	Mean	Range	Mean	Range	Mean	Range
I	4.2	3.5 - 5.0				
II	4.5	2.5 - .5				
III	7.3	6. - 8.0	3.7	3.0 - 4.5	6.2	5.5 - 7.0
IV	11.1	9.5 -13.0	5.7		11.4	11.4 -13.8
V	18.3	13.7 -22.5	21.2	17.0 -25.5	18.5	12.6 -29.0

TABLE 5.31:

The length in mm. of the stages of development of C.laticeps in the definitive host.

	DEFINITIVE HOSTS.					
	S.cephalus		L.leuciscus		R.rutilus.	
Stage	Mean	Range	Mean	Range	Mean	Range
I					1.6	
II					5.7	
III	8.5		12.8	11.5 -12.1	9.9	
IV	14.5		14.8			
V	24.0	23.0 -25.0	30.5	23.5 -40.0	26.8	25.4 - 33.5

Discussion.

Previous records of the hosts and location of Proteocephalus spp. and C.fennica, and investigations of the life cycles have been reviewed by Chubb (1961).

P. torulosus was recorded for the first time in Britain, in the present survey from L.leuciscus and S.cephalus. A Proteocephalus sp. in S.cephalus from the Rivers Avon, Test, Itchen and Stour (Hampshire) was tentatively identified as P.torulosus (Stranack, pers.comm.) La Rue (1914) describes and reviews the previous records and hosts of P.torulosus. The description by La Rue (1914) agrees with that given for specimens from the U.S.S.R (Dubinina, 1964). The records stated by the two previous authors, and those from the present survey show P.torulosus to occur in Europe, the U.S.S.R. and Britain. Recent European records are reported by Ergens (1960 and 1961) from L.cephalus albus, and Lucky and Dyk (1964).

Other species of Proteocephalus recorded in Britain are shown in Table 5.32.

All the species of Proteocephalus from this country examined with respect to their seasonal dynamics exhibited an annual life cycle, (Hopkins, 1959; Rizvi, 1964; Mishra, 1966 and the present survey). Chubb (1961) reported that there was an indication of a seasonal cycle of maturation in the Proteocephalus from Llyn Tegid, but this was not investigated. As well as a seasonal cycle of maturation Hopkins (1959) showed a "strongly marked seasonal cycle in the incidence". This was

TABLE 5.32:

Records of *Proteocephalus* spp. from Britain.

	Parasite	Host	Location	Author	Comments
1.	*Proteocephalus* ? *percae* (Müller, 1780)	*Perca fluviatilis* L.	R. Severn.	Rawson, 1952.	Scolex missing.
2.	*Proteocephalus* sp.	*Salvelinus alpinus* (L.)	Windermere and neighbouring becks.	Rawson, 1952.	Immature.
3.	*Proteocephalus filicollis* (Rud. 1810).	*Gasterosteus aculeatus* (L.)	Bellshill, N. Lanarkshire.	Hopkins, 1959.	
4.	*Proteocephalus* sp.	*Coregonus clupeoides pennanti*	Llyn Tegid (L. Bala) Merionethshire.	Chubb, 1961.	*
5.	*Proteocephalus* sp.	*S. trutta*	Fish hatchery, Chirk, Denbighshire.	Chubb, 1961. **	Resembles *P. neglectus*, La Rue, 1911.
6.	*P. percae*	*P. fluviatilis*	Rostherne Mere, Cheshire.	Rizvi, 1964.	
7.	*P. percae*	*P. fluviatilis*	Shropshire Union Canal, Cheshire.	Mishra, 1966.	
8.	*Proteocephalus* ? *neglectus*	*S. trutta*	Fish Hatchery, Chirk, Denbighshire.	Aderounmu, 1965.	**
9.	*P. torulosus*	*S. cephalus* *L. leuciscus*	River Lugg, Herefordshire.	Present investigation.	
10.	*P. torulosus* ?	*S. cephalus*	Rivers Avon, Itchen, Test and Stour (Hampshire)	Stanack (pers. comm.)	

* These specimens are similar to *P. percae*, *P. fallax* La Rue, 1911, and *P. pollanicola* Cresson, 1952, but "because of the great variation in size, number and form of parts of these worms, for the present a name has not been given to the Llyn Tegid cestodes". (Chubb, 1961).

** Almost certainly both the same species i.e. *P. neglectus*.

the result of gravid worms being shed at a particular time of year, and fish building up infection shortly after, or several months later.

In the present survey a seasonal cycle of maturation and a seasonal variation in incidence was recorded for P.torulosus. The incidence decreased markedly in July, and the parasites were absent from L.leuciscus in August and September, after which a high incidence of young forms was recorded in October. The level of incidence was lower when the samples from November were analysed. If this pattern of incidence is studied in relation to the maturation of P.torulosus in the definitive host, the explanations put forward by Hopkins (1959) for P.filicollis also apply for P. torulosus. Hopkins (1959) states

> "the significant point in the host/parasite relationship, which has been overlooked, is that the incidence throughout the year is a dynamic equilibrium between loss and gain .... incidence does not just rise while fish are eating infected copepods and then remain static until the worms become gravid and are lost, but shows considerable changes long before the worms are mature. In fact, in P.filicollis the lost of 'spent' worms accounts for the death of an insignificant fraction of the total. Less than 1% of the worms become established survive to become gravid....."

Rizvi (1964) recorded no marked seasonal variation in incidence of P.percae although an increase in the mean number of parasites was present in July and August, the months where reinfection may occur. A much lower incidence of P.percae was recorded by Mishra (1966). From this data no seasonal variation in incidence was recorded, but the number of fish infected in September and October was slightly higher, although this is of doubtful significance.

Wagner (1917) gave an account of the life cycle of P.torulosus,

and this appeared to coincide with what Hopkins (1959) termed the direct cycle where

> "procercoids develop through the plerocercoid stage to the adult in the intestine of the definitive host".

This statement is supported by the present investigation, where very small (under 1mm.) unstrobilated pro-plerocercoids were recorded from the intestinal bulb of the definitive host. The intermediate host in the life cycle of P.torulosus has not been identified in the present survey, but Cyclops caudatus - Gruber (1878), and Diaptomus castor and Cyclops strenuus F. (Wagner, 1917) have been recorded as intermediate hosts.

C.fennica has been recorded from Europe, the U.S.S.R. and Britain. The previous records in Britain have all been made from R.rutilus, by Copland (1957) from Loch Lomond; Chubb (1961) from Llyn Tegid; Rizvi (1964) from Rostherne Mere, Cheshire, and Mishra (1966) from the Shropshire Union Canal, Cheshire. In the present investigation C.fennica was recorded from S.cephalus and L.leuciscus as well as R.rutilus. Stranack (1966) also recorded C.fennica in L.leuciscus from rivers in Hampshire.

Chubb (1961) recorded no recognisable change of incidence or intensity of infection and worms containing eggs were present in all months of the year. The data did show an increase in the number of small worms without eggs, as well as worms with eggs in October and in December,

whereas in February and June a slight increase in just the worms with eggs was recorded. In the present survey an increase in the number of smaller worms was noticed in S.cephalus and R.rutilus between August and December, and mature worms were present in all months except January and March. No periodic occurrence or seasonal variation was recorded by Mishra (1966), most of the worms examined were recorded between January and May, only nine worms being examined between June and November. From the data for this country no seasonal variation in occurrence or intensity of infection has been recorded for C.fennica, but it is suggested that reinfection of the definitive host may occur between August and December.

C.laticeps has also been recorded from Europe, (e.g. Sekutowicz, 1932; Wunder, 1939; Lucky and Dyk, 1964); the U.S.S.R. (Dubinina, 1964) and Britain (Mishra, 1966; Stranack, 1966; the present investigation). Mishra (1966) recorded a very low infection from R.rutilus (2.8%) and the absence of any seasonal variation in incidence. He proposed three main stages of development for the adult in the definitive host:-

I. Sex organs not developed.

II. Sex organs developed.

III. Eggs present in the uterus.

Stage I was present from June to November with the exception of October, a peak occurring in November. Stage II was present from August to November (excluding October) and from January to April (excluding March) with a peak in April. Only one mature worm was recorded in May. From

this evidence Mishra (1966) proposed that C.laticeps had an annual life cycle, reinfection of the definitive host occurring between June and December, these worms maturing the following spring and summer. In the present survey Stages I and II correspond to the Stage I of Mishra (1966). Stage I was rare and was only recorded in July from R.rutilus, and this is the only indication that this may be the period of reinfection. An increase in the maturation of C.laticeps occurred between April and July, and the greatest number of worms all of which contained eggs were present in June and July. From this data it is not possible to confirm or refute the proposal of an annual life cycle for C.laticeps (Mishra, 1966) and further investigations are required.

Investigations on the life cycle and occurrence of Caryophyllaeidae are being undertaken in the U.S.A. Mackiewicz (1965) redescribed Glaridacris catostomi, Cooper 1920 (Cestoidea: Caryophyllaeidae) and collected specimens in all months except March and September, but gravid forms were only found in February, April and May. Mackiewicz and McCrae (1962) suggested that Hunterella nodulosa CEN.N.SP.N. (Cestoidea:Caryophyllaeidae) did not show any seasonal variation in incidence. The work in the U.S.A. is of little relevance to the situation that may exist for British Caryophyllaeidae, as in the U.S.A. different parasite and host species are being investigated in a country where a continental climate predominates, and the extremes of temperature encountered provide a very different environment to that found in temperate countries. This latter statement would have immense bearing on the seasonal dynamics and the life cycle of the species in

question.

As the incidence of infection is low in all investigations of C.fennica and C.laticeps in this country to date, it is difficult to try and determine the duration of the life cycle and the seasonal dynamics of these species in their definitive hosts. From the available information it is suggested that reinfection may occur any time between July and December. If such a long period of reinfection occurred, this would account for the presence of mature forms each month e.g. young forms present in August may mature by October or November while reinfection is continuing and young forms present in December may not mature until the summer. The longer time taken to mature for those becoming established in December could be explained by a drop in water temperature and the onset of maturation not occurring until the spring rise in temperature.

At the present time the life cycle of C.fennica is not fully understood. Stylaria lacustris which is ubiquitous in the western parts of the U.S.S.R. and Nais proboscidea are postulated as the intermediate host for C.fennica (see Yamaguti, 1959; Dubinina, 1964). Tubifex tubifex, T.barbatus and Limnodrilus claparedeanus are cited as intermediate hosts for C.laticeps (see Yamaguti, 1959; Dubinina, 1964). Aquatic oligochaetes were not examined for the juvenile stages of these caryophyllaeids in the present survey. Future work on these species should involve a study of the occurrence and intensity of infection in the intermediate hosts with a view to clarifying the dynamics of infection in the definitive host.

REFERENCES.

ADKROUKEU, E.A. 1965 The parasite fauna of the brown trout, Salmo trutta, L., from Chirk Hatchery, Denbighshire, and Llyn Tegid (Bala Lake) Merionethshire. M.Sc. Dissertation. University of Liverpool.

CHUBB, J.C. 1961 A preliminary investigation of the parasite fauna of the fish of Llyn Tegid (Bala Lake) Merionethshire. Ph.D.Thesis, University of Liverpool.

1962 Acetic acid as a diluent and dehydrant in the preparation of whole stained helminths. Stain Techn. 37: (3): 179-187.

COPLAND, W.O. 1957 The parasites of Loch Lomond Fishes In Studies on Loch Lomond. I. 128-133. Glasgow.

DUBININA, M.N. 1964 Key to the Parasites of Freshwater Fish of the U.S.S.R. English translation. Israel Program for Scientific Translation.

ERGENS, R. 1960 Helminthofauna nekotoryx ryb Albanii Ceskosl.parasit. 7: 49-90.

1961 Helmintofauna ryb dvou jihočeských rybničních soustav. 1. Cestoidea-Tasemnice. Ceskosl.parasit. 8: 137-150.

GRUBER, A. 1878 Ein neuer Cestodenwirt. Zool.Anz. S : 74-75.

HOPKINS, C.A. 1959 Seasonal variation in the incidence and development of the cestode Proteocephalus filicollis (Rud.1810) in Gasterosteus aculeatus (L.1766). Parasitology. 49, (3-4): 529-542.

LA RUE, G.R. 1914 A revision of the cestode family Proteocephalidae. Illinois biol.Monogr. 1: 7-350.

LUCKY, Z. and DYK, V.	1964	Cizopasníci ryb v řekách a rybnicích povodí odry a dyje. Sb.vys.Sk.zemed. les Fac. Brno. 7:49-75.
MACKEWICZ, J.S. and McCRAE, R.	1962	Hunterella nodulosa GEN.N.,SP.N. (Cestoidea: Caryophyllaeidae) from Catostomus commesoni (Lacépède) (Pisces.Catostomidae) in North America. J.Parasit. 48: 798-806.
MACKIEWICZ, J.S.	1965	Redescription and distribution of Glaridacris catostomi Cooper, 1920 (Cestoidea:Caryophyllaeidae). J.Parasit. 51: 554-560.
MISHRA, T.N.	1966	Parasite fauna of the fish of the Shropshire Union Canal (Cheshire). Ph.D. thesis. University of Liverpool.
RAWSON, D.	1952	The occurrence of parasitic worms in British freshwater fishes. Ann.Mag. nat.Hist. 12,(5): 877-887.
RIZVI, S.S.H.	1964	The parasite fauna of the fish of Rostherne Mere, Cheshire. Ph.D.thesis. University of Liverpool.
SEKUTOWICZ, S.	1932	Etudes sur le développement et sur la biologie de Caryophyllaeus laticeps (Pallas). C.R.Soi.Math.nat.Acad. Polon.(8) p.4.
STRANACK, F.R.	1966	Some helminths of fish from Hampshire Rivers. Parasitology. 56, (4) : 10 P.
WAGNER, O.	1917	Ueber Entwicklungsgang und Bau einer Fisch taenie (Ichthyotaenia torulosa Batsch). Jena. Z. Naturw. 55 : 1-66.
WUNDER, W.	1939	Das Jahreszeitliche Auftreten des Bandwurmes (Caryophyllaeus laticeps Pall.) im Darm des Karpfens (Cyprinus carpio L.) Z.ParasitKde. 10 : 704-713.
YAMAGUTI, S.	1959	Systema Helminthum. Vol.2. Cestodes of Vertebrates. Interscience Publishers, New York and London.

CHAPTER SIX.

NEMATODA.

Introduction.

Five species of Nematoda were recorded from the fishes of the River Lugg. All the adult forms were found in the intestine apart from Cystidicola farionis which was recorded in the swim bladder. Juvenile forms were found encysted in the intestine wall, mesenteries and the liver of cyprinids.

Living adult nematodes were dropped into glacial acetic acid, which killed them in an extended condition, (Berland, 1961.) Freshly killed and deep frozen material was preserved in 70% alcohol.

Results.

The species of nematodes recorded, their hosts and their site of infection are recorded in Table 6.1.

Rhaphidascaris acus (Bloch, 1779).

R.acus was found in the intestine of E.lucius caught in the April, May, June and July samples, three (43.0%); four (80.0%); one (12.5%) and three (43.0%) fish in each sample were infected. Only 36 E.lucius were caught over the whole year, and 75% of these were caught between the April and July samples. Because of the small number of fish caught in other months it is impossible to say whether or not R.acus infects E.lucius in months other than April to July. 54 adult R.acus were found,

TABLE 6.1:

The hosts and site of infection of nematode parasites from the fishes of the River Lugg.

PARASITE	HOST				
	S.cephalus	L.leuciscus	R.rutilus	T.thymallus	E.lucius
Rhaphidascaris acus (juvenile)	Intestine wall Mesenteries Liver	Intestine wall Mesenteries Liver	Intestine wall Mesenteries Liver		
Rhaphidascaris acus (adult)					Intestine
Spinitectus inermis					Intestine
Cucullanus sp.					Intestine
Cucullanus truttae				Intestine	
Cystidicola farionis				Swim bladder	

a mean number of 4.1 per infected fish, and a mean number and actual number in each sample of 5.0 (15) April; 6.7 (27) May; 1.0 (1) June and 3.6 (11) July. Of the 54 specimens 15 were female; 20 male and 19 immature adults in which the sex was unrecognisable. The number of female, male and immature worms in each sample where the infection occurred are recorded in Table 6.2. Immature adults were present in April and May, but not in June or July. Only one male was recorded in June. The range of length and the mean length of *L.acus* in each sample except June are shown in Table 6.3. The size of male and female worms increases from April to July, and by July the females are full of ova.

From Tables 6.2 and 6.3 it appears that more immature adults were present in May than April, and that the worms in May were smaller than those in April. As only a small sample was involved the above statement is of doubtful significance. If further investigations also revealed larger numbers of smaller worms in May compared to April, one suggested explanation is that May is the optimum time for reinfection of the definitive host, where a greater number of smaller worms are recorded.

Juvenile forms.

Many small cysts were recorded from the intestine wall, the mesenteries and the liver of *S.cephalus*, *L.leuciscus* and *R.rutilus*. When these cysts were squashed they revealed small juvenile nematodes. The number and percentage of each host infected are recorded in Tables 6.4, 6.5 and 6.6. These tables indicate that a greater infection in each sample and overall was found in *S.cephalus* than in either

TABLE 6.2:

The number of female, male and immature adult R.acus in each sample where infection occurred.

Months	Female	Male	Immature adults
April	4	6	5
May	3	10	14
June		1	
July	8	3	
	15	20	19

Total = 54.

TABLE 6.3:

The length of female, male and immature adult R.acus from April, May and July samples.

Month	Female		Male		Immature adult	
	Range	Mean	Range	Mean	Range	Mean
April	12-17mm.	15mm.	15mm.		6-14.5mm.	11.3mm.
May	18-38mm.	21.7mm.	13-25.5mm.	20.8mm.	7.5-10mm.	8.7mm.
July	26-40mm.	32.4mm.	25-29mm.	27mm.		

TABLE 6.4:

Juvenile nematodes in the intestine wall, the mesenteries and the liver of S.cephalus.

Month	No. fish	No. infected	% infected	No. female infected	% female infected	No. male infected	% male infected
Jan.	32						
Feb.	31	31	100.0	14	100.0	13	100.0
Mar.	29	23	79.3	15	83.3	8	72.7
Apr.	30	30	100.0	14	100.0	16	100.0
May	31	30	96.8	20	100.0	10	90.9
June	30	24	80.0	15	78.9	9	81.8
July	30	16	53.3	11	52.4	5	55.5
Aug.	30	19	63.3	9	64.3	10	62.5
Sept.	28	23	83.7	14	87.5	9	75.0
Oct.	27	23	85.2	14	82.3	9	90.0
Nov.	30	30	100.0	20	100.0	10	100.0
Dec.	31	31	100.0	16	100.0	15	100.0
Total	359	280	78.0	164	78.8	116	78.9

TABLE 6.5:

Juvenile nematodes in the intestine wall, mesenteries and the liver of L.leuciscus.

Month	No. fish	No. infected	% infected	No. female infected	% female infected	No. male infected	% male infected
Jan.	33	14	42.4	6	60.0	8	34.8
Feb.	31	16	52.0	12	80.0	4	25.0
Mar	30	11	36.6	3	25.0	8	44.4
Apr.	35	12	34.3	7	50.0	5	23.8
May	4	4	100.0	4	100.0	-	-
June	30	8	26.6	6	37.5	2	14.3
July	30	10	33.3	3	23.1	7	41.2
Aug.	30	5	16.6	3	18.7	2	14.3
Sept.	30	9	30.0	6	27.3	3	37.5
Oct.	31	23	74.2	14	70.0	9	81.8
Nov.	28	28	100.0	17	100.0	11	100.0
Dec.	30	23	76.6	11	84.7	12	70.6
Total	342	163	47.7	92	53.5	71	41.8

TABLE 6.6:

Juvenile nematodes in the intestine wall, mesenteries and liver of *R.rutilus*.

Month	No. fish	No. infected	% infected	No. female infected	% female infected	No. male infected	% male infected
Jan.	33	10	30.6	4	33.3	6	28.6
Feb.	27	6	22.2	4	33.3	2	13.3
Mar.	30	16	53.3	9	56.2	7	50.0
Apr.	16	3	18.7	3	30.0	-	-
May	9						
June	30	1	3.3	1	7.1		
July	22	7	31.8	5	41.6	2	20.0
Aug.	30	1	3.3	1	4.5		
Sept.	30						
Oct.	30	8	26.6	4	33.3	4	22.2
Nov.	30	24	80.0	11	100.0	13	92.2
Dec.	30	24	80.0	10	66.6	14	93.3
Total	317	100	31.5	52	21.3	48	29.4

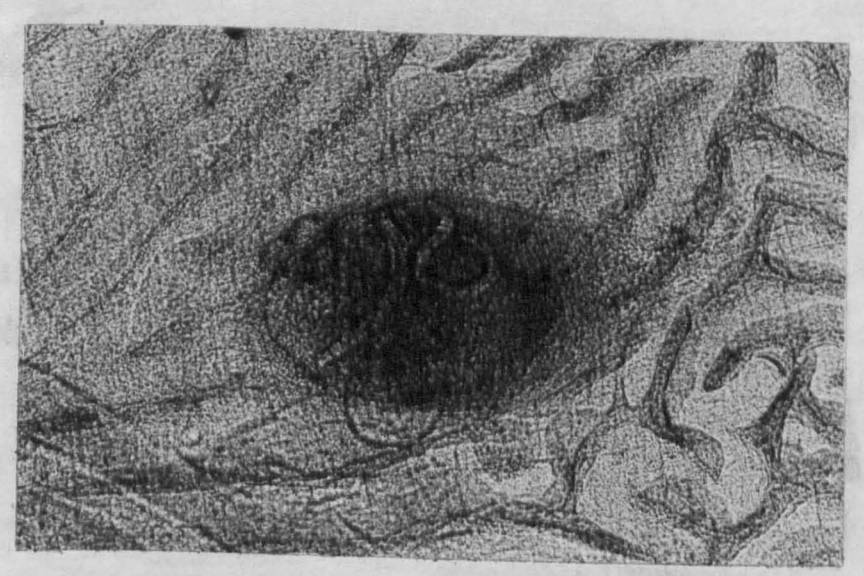
L.leuciscus or R.rutilus, 75.0% S.cephalus being infected compared to 50.0% L.leuciscus and 33.0% R.rutilus. A slight decrease in the percentage of S.cephalus infected occurred in July and August. The absence of any record from this host in January results from the fact that these juvenile nematodes were not recognised until the subsequent examination of L.leuciscus and R.rutilus in this sample. No obvious pattern of seasonal infection was present in L.leuciscus, although the minimum percentage of infected fish (16.6%) occurred in August. In R.rutilus no infection was recorded from the May and September samples, and only one fish was infected in the June and August samples, but a high infection for R.rutilus (31.8%) was present in July. Although a slight decrease of the percentage of fish infected was present in the summer months, the significance of this is doubtful, and until the parasite is identified and the life cycle known, it is not possible to state whether the larvae develop and pass out of the cyprinids, whether they are eventually absorbed by the host or whether they accumulate and no further development occurs until they enter another host.

Portions of the gut wall containing cysts cleared in Curr's Creosote Beechwood, revealed small coiled nematodes surrounded by a cyst wall (Plate 6.1). Many of the cysts appeared to be calcified especially in S.cephalus. This indicates two important points about the life cycle:-

1. Juvenile forms need to enter another host before they develop to the adult form.

Plate 6.1 A juvenile *R. gaug* encysted in the intestine wall of *S. cephalus*.

Magnification x51



2. If the juveniles remain for over a certain period of time in the cyprinid host, they either die or are killed by the host.

No definite structure to aid identification was present in the juvenile form.

A series of experiments were performed to try and obtain the adult nematode, both for purposes of identification and for further information on the life cycle.

Experiments: Series I.

Method.

S.cephalus from the River Lugg were maintained in the laboratory. These fish were killed by a blow on the head. The intestine and liver containing encysted nematodes were dissected, and the intestine washed free of food remains. Three-quarters of the intestine and part of the liver of each fish were fed in water to six two-week old Aylesbury ducklings. Two ducks were killed after periods of 4, 11 and 15 days. The gut from each animal was divided into four regions approximating to the proventriculus, small intestine, large intestine and the rectum and rectal caeca. Each section was examined for parasites.

To ensure that the juvenile nematodes in the cysts were living, portions of the gut and liver of S.cephalus used in the experiment were placed in a pepsin digest:-

3.5 gm pepsin
2 mls. HCl
} in 500 ccs. H_2O

The solution in a 500 ml.flask was placed in a water bath at a temperature between 37° and 40°C, which corresponded to the body temperature of the ducks.

Results:

a) No parasites were recovered from any portion of the duck intestine after either the 4th, 11th or 15th day.

b) Living excysted nematodes were recovered from the pepsin digest.

Series II.

Method:

Encysted nematodes in the gut and liver of S.cephalus were fed to a duckling placed in a separate cage under which was a removable tray. The faeces of this animal were examined after a period of three hours up to a period of eight hours after feeding with infected intestine, by which time the remains of digested fish intestine should have passed through the duck.

Results:

No nematodes were recovered from any of the faecal deposits.

Conclusion:

Nematodes are either digested before they can pass along the length of the duck intestine, or they undergo a migration from the intestine.

To try and test these two suggestions, two further examinations were made:-

1) Squashes of the duck liver were made of those ducks killed 4 and 11 days after being fed infected intestine and liver. No nematodes were present in the liver, but this is not conclusive that the nematodes did not migrate from the intestine, as they could easily have passed beyond the liver in four days.

2) Encysted juvenile nematodes were fed to a duck which was killed after one hour, with the result that no nematodes were recorded on examination of the gut, and the presence of fish intestine was unrecognisable.

From these results it was concluded that the nematodes were probably digested, and the conditions in the duck intestine were not favourable for the development of juvenile to adult.

To try and determine more specifically the factors that might be detrimental to the juveniles three flasks were set up:-

1. Pepsin digest at 37°C.
2. Saline solution at 37°C.
3. Water at 37°C.

Encysted nematodes from the intestine of S.cephalus were placed in each flask, and each flask was examined at 15 minute intervals, and the number of living encysted nematodes was recorded (Table 6.7).

From this preliminary investigation it is possible to say that rapid excystment occurs in pepsin digest, slow excystment is present

in saline, but hardly any excystment occurs in water. After one hour, most of the excysted nematodes recovered from any flask were dead. This suggested that temperature may be the detrimental factor as nematodes are usually capable of surviving several hours in saline or water.

Subsequently encysted nematodes were incubated in pepsin digest at 25°C. The excysted nematodes survived for a greater length of time and were still alive after 5½ hours. This indicated that the body temperature of the duck was too high, and therefore a definitive host with a lower body temperature was sought.

In the River Lugg, E.lucius was the main predatory fish. Examination of E.lucius revealed three species of nematode R.acus, S. inermis and C.dogieli. The juveniles of R.acus are reported from the mesenteries, liver and intestine wall of cyprinid fishes (Izyumova, 1964) and therefore it was decided to try and infect E.lucius with the encysted nematodes from the intestine wall and liver of S.cephalus.

Experiments: Series III.

Introduction:

As E.lucius from the River Lugg were infected with R.acus, they could not be used in these infection experiments. E.lucius were obtained from Llyn Tegid (Lake Bala, Merionethshire), as previous investigation by Chubb (1961) showed that R.acus was not recorded in

TABLE 6.7:

Minutes	Flask 1.		Flask 2.		Flask 3.	
	No. of excysted nematodes					
	Living	Dead	Living	Dead	Living	Dead
15	0	0	0	0	1	0
30	2	0	1	0	0	0
45	11	0	1	0	0	0
60	2	2	0	3	0	0
75	0	3	0	2	0	0
90	1	3	0	5	0	0
105	0	10	0	0	0	0
120	0	10	0	0	0	0

in any of the 104 E.lucius examined.

Methods:

One E.lucius was anaesthetised in MS_{222}; stock = 1 gm in 250 ml. and this was diluted x 8 to a working concentration i.e. 5gms. in 10 litres in this case. Infected S.cephalus intestine and liver was cut into small pieces and pushed into the stomach of the anaesthetised fish with a piece of rubber tubing. A pepsin digest containing pieces of infected gut and liver was prepared to determine if the nematodes were

alive. It was intended to examine the E.lucius after seven days, but the air in the aquarium failed and the fish died between the third and fourth day after infection.

Results:

1) Examination of the intestine of E.lucius revealed the following nematodes:-

Parasite	No.of parasites	Location
Cucullanus sp.	1	Lower intestine.
Juvenile nematodes	43	Lower intestine.

2) Living nematodes were recovered from the pepsin digest.

The young worms from the lower intestine of E.lucius were killed in glacial acetic acid, and mounted temporarily in lactophenol. These worms were approximately the same size as the nematodes excysted from the intestine wall of S.cephalus, but the oesophageal structure was more defined, the oesophagus forming a bulb and a posteriorly directed caeca. (Figure 6.1, Plates 6.2, 6.3). This arrangement is typical of the rhaphidascarid arrangement, and further examination of larger forms, excysted in the pepsin digest revealed the same structure. Pepsin digests of infected intestines and livers from L.leuciscus and R.rutilus revealed nematodes with the same oesophageal structure as that found in S.cephalus. From this information it is suggested that the encysted nematodes in the intestine wall, liver and mesenteries of S.cephalus, L.leuciscus and R.rutilus are the juvenile forms of R.acus.

Plate 6.2 The juvenile of *R. aequa*.

Magnification x120

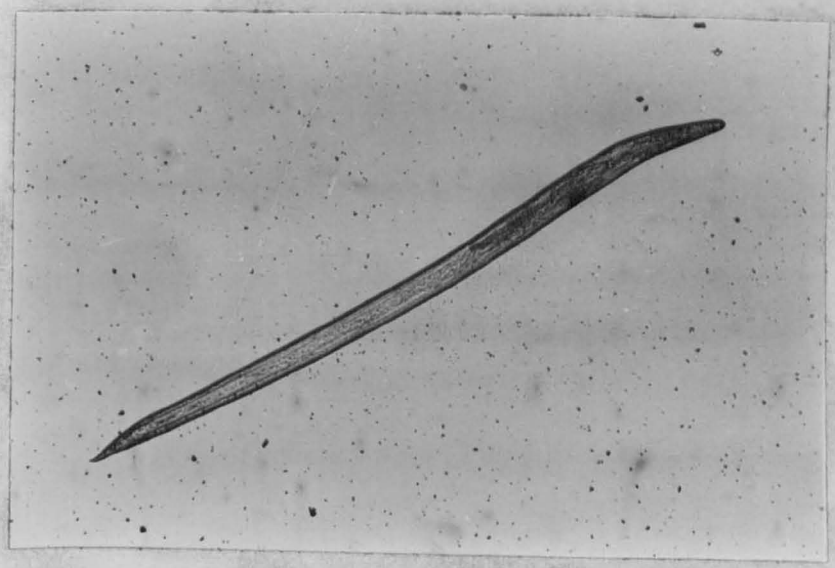


Fig. 6.1 The arrangement of the oesophageal structures in *R. agus* juveniles.

O - Oesophagus (muscular part).

OB - Oesophageal bulb (glandular part).

OC - Oesophageal caecum.

I - Intestine.

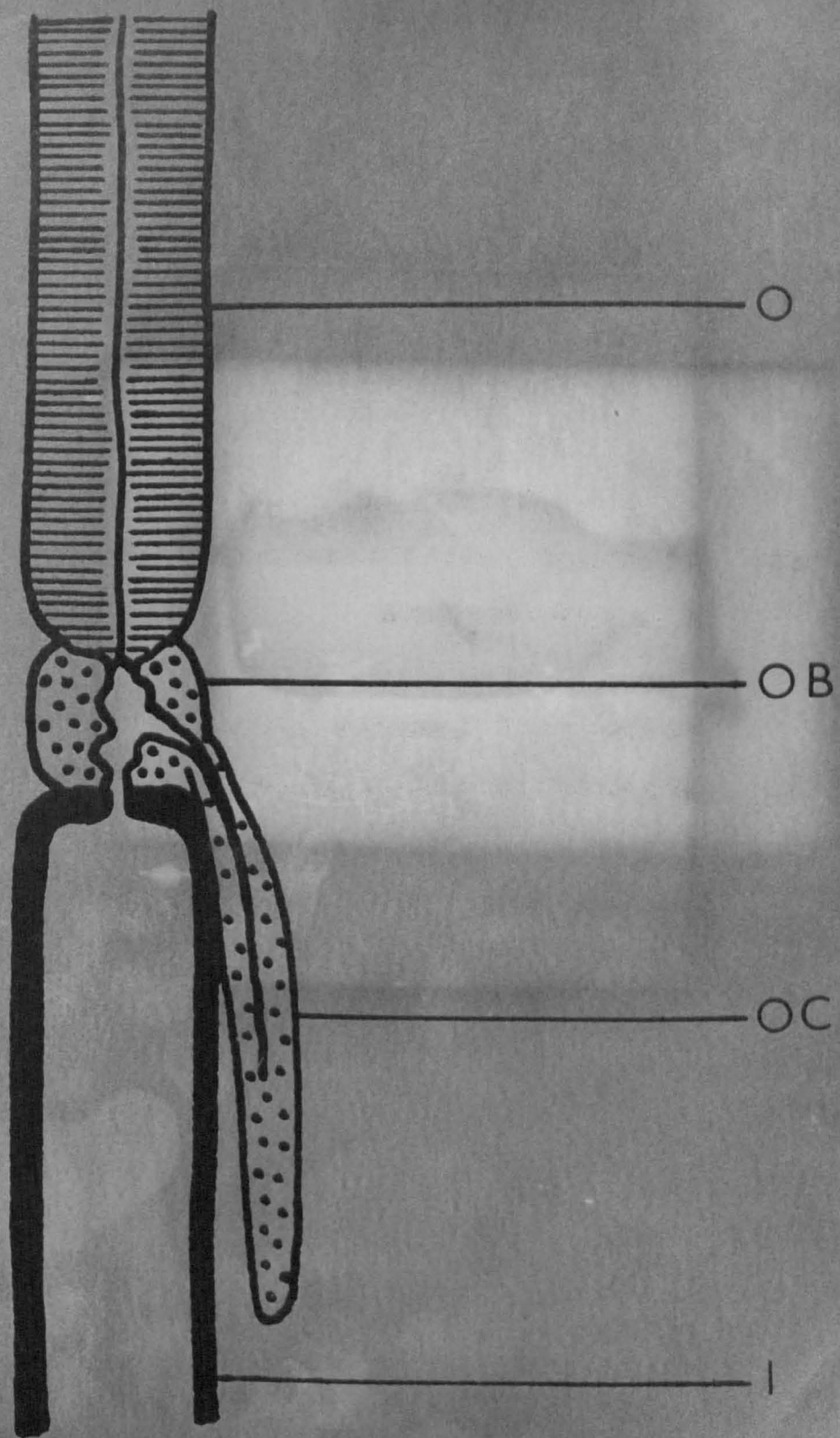

O
OB
OC
I

Plate 6.3 The oesophageal structures of a juvenile *R. aegus*.

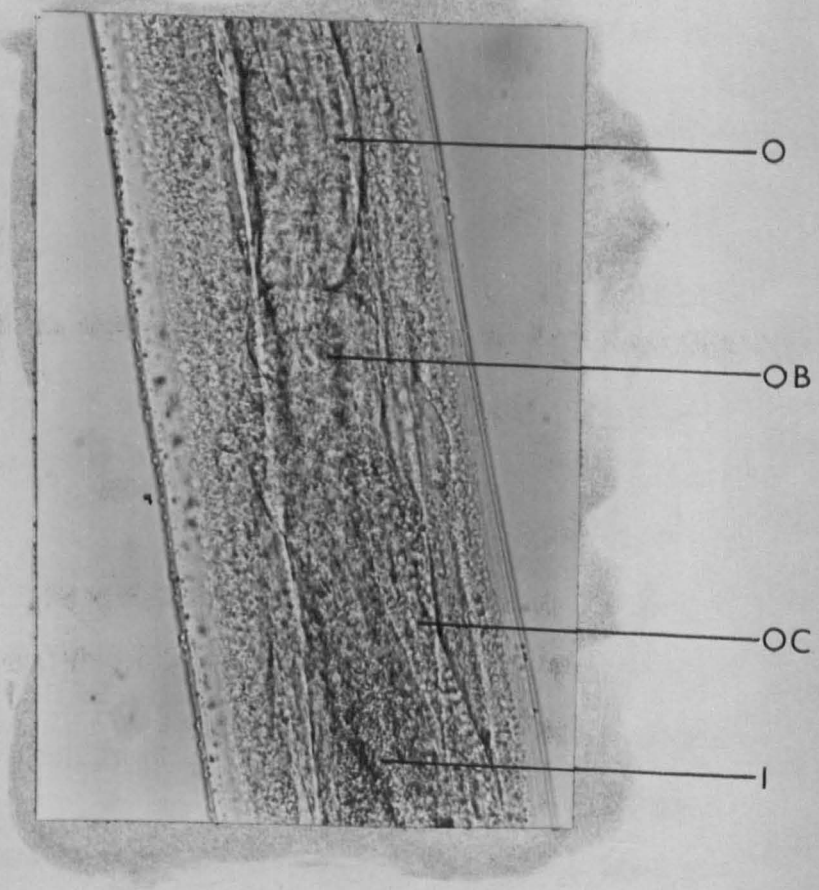
Magnification x510

O - Oesophagus (muscular part)

OB - Oesophageal bulb (glandular part)

OC - Oesophageal caecum

I - Intestine


O
OB
OC
I

Life Cycle.

The presence of encysted juveniles in cyprinids, and the presence of adult R.acus in E.lucius, as well as the recovery of excysted forms after the infection of E.lucius with encysted forms, suggests that cyprinids act as the intermediate host, and the juveniles do not mature until the cyprinids are eaten by E.lucius. Further support for this suggestion comes from Thomas (1937) who examined the life cycle of Rhaphidascaris canadensis, Smedley, 1933, from E.lucius. From experiments and observations Thomas (1937) showed that R.canadensis laid its eggs in the intestine of E.lucius in the morula stage. The eggs passed to the water in the faeces, and became embryonated within eight hours at 75-80°F. After one moult the eggs became infective to Phoxinus spp. and P.fluviatilis (bottom feeders) and in these fish the nematodes became encysted in the mesenteries and the liver, and do not grow further until ingested by E.lucius.

The apparent similarity in the life cycle and intermediate and definitive hosts, led to an examination of the descriptions of both species to see if despite the more or less identical life cycles and hosts, the species were really separate.

The features listed by Smedley (1934) in the description of R.canadensis are shown in Table 6.8 and similar features in R.acus from the present survey, and where the data were available, from R.acus from the U.S.S.R. are compared (Table 6.8). The table shows that mature males of R.canadensis are slightly smaller than those of R.acus, but the

significance of this for differentiating species is extremely suspect. Smedley (1934) recorded unequal spicules in the male, but only one measurement is quoted in the text, no distinction being made between the two spicules either in length or width. No difference was apparent between the spicule dimensions of R.acus and R.canadensis. Plate 6.4 shows the spicules of R.acus. The vulva is in the same position in both 'species', and the uteri do not appear to pass anteriorly to the vulva. Differences in the size of the ova may be accounted for by differences in the stage of development, or by the type of fixative used to preserve the nematodes. In the present survey ova were not surrounded by a hard shell, and would therefore be susceptible to osmotic changes, and a great variation in size and shape of ova was recorded. Narrow lateral alae of unequal breadth were recorded as running the whole length of the body in R.canadensis. It is uncertain whether lateral alae are present in R.acus.

So far no definite feature is present which definitely distinguishes R.canadensis from R.acus, and with the similarity of the life cycle and the hosts involved it is suggested that at the present time no valid reasons exist for differentiating between R.canadensis and R.acus.

Doubt has also been raised as to whether Rhaphidascaris cristata (von Linstow, 1872) is really a valid species. Apart from the original record, all other records have been made from Britain, Bayliss (1928, 1939) from A.anguilla, Frost (1946) in A.anguilla from the Windermere

TABLE 6.8:

Comparisons of the features of R.canadensis and R.acus.

	R.canadensis Smedley, 1933.	R.acus Bloch(1779) Russia (Izuymova, 1964)	R.acus Bloch(1779) River Lugg, Britain Range	Mean	R.cristata(Linstow, 1872)
Gap between striations	15 μ		13-15 μ	14 μ	
Oesophagus	$\frac{1}{8}$ body length		1/7 - $\frac{1}{8}$ body length		
Pre-anal papillae	Depend on size and development of worm Mature - 21 prs.	Up to 17 prs.			
Length mature male	Up to 23mm.	Up to 33mm.	25-29mm.	27.0mm.	
Spicules	Sub-equal; slender sharply curved 0.65 x 0.0125mm.	0.64 - 1.02mm.	0.56-0.63mm. x 0.01 0.02mm. broad at base Usually equal.	0.61mm.	
Length mature female	Up to 50mm.	Up to 45mm.	26-40mm.	32.4mm.	
Vulva	Slit in cuticle, 1/5 of body length from anterior end.	Between 1st & 2nd thirds of body.	1/6 - 1/7 of body length from anterior end.		
Uteri	Directed posteriorly, do not extend beyond vulva anteriorly.		Directed posteriorly, do not appear to extend anterior to the vulva.		
Ova	0.06 x 0.04mm.		0.074-0.085mm. x 0.053-0.064mm.	0.079mm x 0.057mm.	

Plate 5.4 The pair of extruded spicules at the posterior end of a male *R. aqua*.

Magnification x120

catchment area; Rawson (1952) in E.lucius from the River Severn in August; Chubb (1961) in A.anguilla and P.fluviatilis from Llyn Tegid and in P.phoxinus, S.trutta, S.salar and P.fluviatilis from Llyn Padarn (Caernarvonshire) (Chubb pers.comm.). Frost (1946) states

> "The nematode was R.cristata ... Dr. H.A. Baylis of the British Museum (Natural History), informs me that the identity of the species of Rhaphidascaris commonly referred to as R.acus (Bloch) is very uncertain, as it is insufficiently described. He has examined some of the material on which Yorke and Maplestone's (1926) figures of 'R.acus' were based and believes that it is actually R.cristata. Unless Linstow's description of this species is inaccurate it appears to be distinct from R.acus."

It is hoped to obtain Linstow's original description (Linstow, 1872) of R.cristata and to compare it with the descriptions of R.acus and R.canadensis. I have examined R.cristata collected by Dr. J.C.Chubb from Llyn Padarn. All the worms were free in the intestine of the fish apart from a few encysted forms on the swim bladder of P.phoxinus (Chubb, pers.comm.). Although the sexes were recognisable, the worms were immature and it was impossible to make a significant comparison with the data from mature R.canadensis and R.acus. General observations on immature R.cristata showed a great similarity existed between all three species. Comparison between immature forms is however unjustified on the basis that the mature forms of a species may be different even if the juveniles are similar. Before any further statements can be made it is necessary to examine some mature R.cristata and to study Linstow's original description.

A wider host range is quoted for R.cristata from Britain, than for R.acus, although Senk (1953) in an investigation of cyathocephalosis,

recorded R.acus in S.trutta. Adult parasites were found in the stomach, duodenum, intestine, body and nasal cavities. Encysted juveniles were found in the liver, the pyloric caecae and the mesentery, and tiny free juveniles were present in the body cavity. The stomachs of a number of S.truttae contained a few P.phoxinus full of adult R.acus. In May, June and August S.trutta contained adult R.acus, whereas free or encysted juveniles were recorded in April, May, June, August and October. S.trutta caught in other months were not infected with these parasites, and only fish over two years old were infected.

Pathogenicity.

Severe infestations of R.acus were recorded from E.lucius, L.idus, S.erythrophthalmus, A.aspius, T.tinca, C.carassius, Lucioperca lucioperca (L.) and C.carpio, from Lake Sudochye and near Muynak near the delta of the Amu Daria (Osmanov, 1953). A.brama was the most severely affected, the worms being found in the intestine walls and the liver. The latter organ was severely damaged

> "only isolated patches remained, like islands connected with one another by strands of tissue".
>
> (Osmanov, 1953, p.42).

From the intensity of infection normal function of the liver, gut, gonads and other organs was impossible, and the fish were very emaciated and died over the winter of 1951-52.

Heavy infections of juvenile R.acus were recorded in the present survey, especially from S.cephalus, but so far no pathogenic effects are apparent.

Spinitectus inermis (Zeder, 1800).

Ten specimens of S.inermis, four female and six male, were recorded from the stomach of one female E.lucius caught in February. This was the only time this species was recorded. S.inermis was first recorded in Britain by Chubb (1961), seven specimens, four male and three female being found in the stomach of A.anguilla from the Afon Lyfrdwy, which flows into Llyn Tegid (Merionethshire). Two of the females were damaged but a provisional redescription of the species, and a list of all previous records of the species were given (Chubb, 1961).

All previous records of S.inermis with the exception of a juvenile found in the intestine of Alburnus lucidus (von Linstow,1878) were from the stomach of A.anguilla. E.lucius appeared to be the definitive host in the present survey. This indicates that E.lucius as well as A.anguilla may act as the definitive host, or that S.inermis may be able to use E.lucius as a definitive host if A.anguilla is ingested as part of the diet of E.lucius, E.lucius in this case being an accidental host.

The range of measurements recorded for S.inermis from A.anguilla and E.lucius are shown in Table 6.9. Mature female and male S.inermis are longer in E.lucius than in A.anguilla. No detailed description is available of the female system of S.inermis from A.anguilla. Although the uteri were full of eggs which obscured some of the detail, a general description of the female system of S.inermis from E.lucius

is given. The male system appears identical to that described by Chubb (1961).

The vagina has thick muscular walls 0.026 - 0.037mm. thick, and approaches the external pore from an anterior direction. The pore is situated in these specimens 1.6 - 2.5mm. from the posterior tip of the worm. A duct arises from the vagina which runs slightly anteriorly for about 0.3mm. and then divides into two, each of these ducts running a further 0.3mm. before opening out into a wider tube or uterus which is full of eggs. The eggs are oval and surrounded by a thick shell, and measure 0.032 x 0.023mm. Each uterus passes anteriorly first of all in a straight line, and then in a coiled, twisted manner. The uteri extend approximately as far as the muscular portion of the oesophagus. Thinner strands of tissue 0.037 - 0.057mm. wide are present and are most prominent in the region between the vagina and the posterior tip, although the same structure was present between the coils of the uteri in the more anterior part of the body. This structure was thought to be part of the ovary as two uteri are present, two ovaries should also be present. In the specimens examined only one terminal part of an ovary was visible, in the region between the vagina and the posterior end of the worm. The ovary appeared to be divided into two portions, a proximal short rounded portion posterior to the vagina, and a long distal rope-like coiled portion which joined the uterus. The pathway of this coiled portion was traced until it ran anterior to the vagina and became lost among the coiled uteri. (Figure 6.2). It is thought that the beginning of the second ovary lay anterior to the vagina and

Fig.6.2 The posterior end of a female *Spinitectus inermis*.

O - Ovary.

U - Uterus.

I - Intetine.

TO - Terminal part of the ovary.

CS - Cuticular spines.

A - Anus.

BW - Body wall.

VP - Vaginal pore.

V - Vagina.

UV - Uterine vagina.

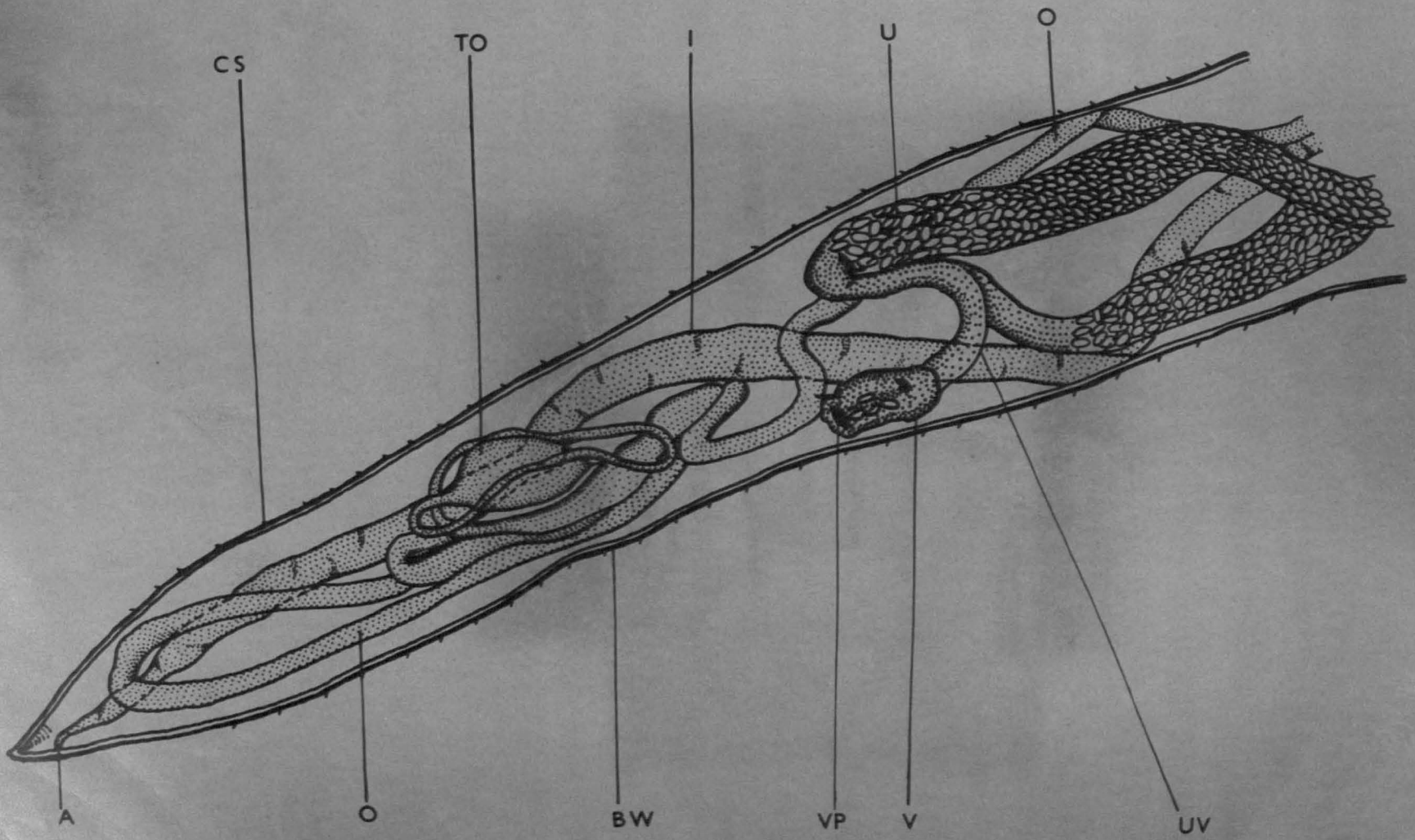

CS
TO
I
U
O
A
O
BW
VP
V
UV

TABLE 6.9:

Comparison of the features of *S.inermis* from *A.anguilla* and *E.lucius*.

	S.inermis from *A. anguilla*, Llyn Tegid (Chubb 1961)	*S.inermis* from *E.lucius* River Lugg. Present survey.
Oesophagus into body length		5 - 6 times
Muscular: glandular oesophagus	1:5.7 - 1.42	1: 3.6
Junction of muscular and glandular oesophagus	7th-8th cuticular ring	5th-6th cuticular ring.
Junction of glandular oesophagus and intestine	Range 1.13-1.22mm. Mean 1.19mm.	Range 1.81-2.22mm. Mean 1.93mm.
No.of spines on 2nd cuticular ring.	56 - 60	56 - 62
Length mature female	12mm.	Range 16-19mm. Mean 18mm.
Size of eggs	0.034 x 0.020mm.	0.032 x 0.023mm.
Direction in which the vagina approaches the pore.	?	From the anterior end.
Length of vagina	?	0.21mm.
Length of mature male	4.5 - 6.5mm.	10.7mm.
Long spicule	Hollow half way along length	?

was obscured by the eggs in the uteri.

In the Russian Key (Isuymova, 1964) the eggs of S.inermis are recorded as possessing polar filaments. Polar filaments are not recorded on eggs from this species either by Chubb, 1961, or in the present survey. It is suggested that the eggs of S.inermis may have been confused with those of Spinitectus oviflagellis Fourment, 1883, which possesses filaments on the eggs and is the type species.

Cucullanus spp.

Four specimens of Cucullanus sp., three female and one male were recorded from E.lucius, and three specimens, two male and one which was damaged were recorded from T.thymallus. It is not certain whether all these specimens are C.truttae, or whether the ones from E.lucius are C.dogieli. C.truttae and C.dogieli could be accidental parasites of E.lucius being released after the ingestion of T.thymallus or cyprinids as food.

Cystidicola farionis Fischer, 1798.

Only two specimens, both female and full of eggs were found in the swim bladder of T.thymallus in March.

Conclusions.

1) The adult forms of S.inermis, Cucullanus sp., C.farionis and the adult and juvenile forms of R.acus were recorded from the fish of the River Lugg.

2) Adult S.inermis, R.acus and Cucullanus sp. were recorded from the intestine of E.lucius. Adult C.farionis were recorded from the swim bladder of T.thymallus, whereas the only nematodes recorded in the cyprinids were juvenile R.acus encysted in the intestine wall, the liver and the mesenteries.

3) R.acus is the only nematode found in this survey, for which E.lucius has been reported as the definite definitive host. The presence of S.inermis and Cucullanus sp. may result from the predatory habit of E.lucius, these two parasites being released from ingested food.

4) The validity of R.canadensis. R.acus and R.cristata as separate species was questioned, and the evidence so far available suggests they may be synonyms.

5) The female system of S.inermis is described. The male system and other features of the nematodes were identical to those described by Chubb (1961).

6) The small number of all adult nematodes recorded, prevented any conclusions as to the presence or absence of any seasonal variation in the percentage of fish infected, the intensity of infection and the maturation of the parasites in the definitive host. A slight decrease of doubtful significance was noted in the summer, for the number of cyprinids with juvenile R.acus.

7) This preliminary survey of the nematode fauna of fishes of the River Lugg has revealed several interesting problems, and further investigation is required into the taxonomy and the life cycles of *Rhaphidascaris* sp. and *S.inermis*.

REFERENCES.

BAYLIS, H.A. 1928 Records of some parasitic worms from British vertebrates. Ann.Mag.nat.Hist.(10) 1: 329-343.

BAYLIS, H.A. 1939 Further records of parasitic worms from British vertebrates. Ann.Mag.nat.Hist.(11) 4: 473-498.

BERLAND, B. 1961 Use of glacial acetic acid for killing parasitic nematodes for collection purposes. Nature, 191 : 1320-1.

BLOCH, M.E. 1779 Beitrag zur Naturgeschichte der Würmer, welche in anderen Thieren leben. Beschaft.d.Berl.Gesellsch.naturf.Fr. 4: 534.

CHUBB, J.C. 1961 A Preliminary Investigation of the parasite fauna of the fish of Llyn Tegid (Bala Lake) Merionethshire. Ph.D.thesis, University of Liverpool.

FROST, W.E. 1946 Observations on the food of eels (Anguilla anguilla) from the Windermere catchment area. J.anim.Ecol. 15: 43-53.

IZYUMOVA, N.A. 1964 In 'Key to the Parasites of Freshwater Fish of the U.S.S.R.' Nematoda. English Translation. Israel Program for Scientific Translation.

LINSTOW, O von 1872 Über Ascaris cristata nov.spec. Arch.Naturg. 38, J 1(2): 148-155 (unseen).

LINSTOW, O von 1878 Neue Beobachtungen an Helminthen. Arch.Naturg.I : 218-245.

OSMANOV, S.U. 1953 Rhaphidascarosis of bream in the delta of Amu - Daria. Fish Ind., Moscow. 8.

RAWSON, D.	1952	The occurrence of parasitic worms in British freshwater fishes. Ann.Mag.nat.Hist. 12 (5): 877-887.
SENK, O.	1953	Rhaphidascaris acus - Bloch entero parazit Salmoni da rijeke Zujevine. Veterinaria 2: 311-316.
SMEDLEY, E.M.	1934	Nematode parasites from Canadian Marine and Freshwater Fishes. Contr.Canad.Biol. VIII : 169-179.
THOMAS, L.J.	1937	Life cycle of Rhaphidascaris canadensis Smedley 1933, a nematode from pike Esox lucius L. J.parasit. 23 : 372.
YORKE, W. and MAPLESTONE, P.A.	1926	The Nematode Parasites of Vertebrates. London.

CHAPTER 7.

ACANTHOCEPHALA.

Introduction:

Four species of adult Acanthocephala and one juvenile species were recovered from the fish of the River Lugg.

Methods:

Fresh material was removed from the intestine of the fish and placed in cold water until the proboscides were fully extended. Both relaxed fresh material and deep frozen material were fixed in alcohol-formal-acetic (A.F.A.) (Van Cleave, 1953). For identification and determination of sex and the stage of development, the specimens were cleared in pure creosote.

Acanthocephala which had been deep frozen differed from Monogenea, Digenea and Cestodes, in that they were not recovered in a relaxed condition.

Results:

The species of Acanthocephala recovered, their hosts and the site of infection are recorded in Table 7.1.

Neoechinorhynchus rutili (Müller, 1780).

N.rutili was found in the intestine of all the species of cyprinids and E.lucius. N.rutili was never found in large numbers, only 33 being

TABLE 7.1:

The hosts and sites of infection of Acanthocephala from the fishes of the River Lugg.

PARASITE	HOST				
	S.cephalus	L.leuciscus	R.rutilus	T.thymallus	E.lucius
Neoechinorhynchus rutili	Intestinal bulb and intestine	Intestine	Intestine		Intestine
Acanthocephalus lucii	Intestinal bulb and intestine	Intestine	Intestine		Intestine
Pomphorhynchus laevis	Intestine	Intestine			
Echinorhynchus truttae				Intestine	Intestine
Polymorphus minutus (cystacanth)		Intestine	Intestine	Intestine	

recorded, 27 of these from S.cephalus (Table 7.2), two from one R.rutilus in March, three from E.lucius (two in April and one in June), and one from L.leuciscus in January.

The average intensity of infection was 1.0 parasites per infected fish, with the exception of the S.cephalus in the June sample where the intensity was 1.4. Table 7.2 shows a higher percentage of S.cephalus infected between June and August than in other months, but the intensity of infection was the same in all months, except for the slight increase in June from 1.0 to 1.4 parasites per infected fish.

The different stages of development of the female N.rutili are recorded in Table 7.3.

Young female Acanthocephala have a single or a double ovary, and the formation of egg cells, fertilisation and development of the embryo has been described by Hyman (1951). The original ovary breaks up into fragments which are called ovarian balls and these float freely in the ligament sac, until this ruptures and the contents are released to the pseudocoel. The ovarian balls consist of a central syncitium from which the egg cells separate and pass to the periphery. After the eggs are fertilised, a fertilisation membrane arises inside the original egg membrane, and the eggs escape from the ovarian balls and continue to develop in the pseudocoel. A third membrane is eventually formed between the two membranes already present, and is called the shell. When the shell is formed the juveniles are called shelled acanthors (Van Cleave, 1935, 1947). Acanthors may be released at intervals from

TABLE 7.2:

Infection of S.cephalus with N.rutili.

Month	No. fish	Infected fish No.	%	Infected female fish No.	%	Infected male fish No.	%	No. parasites	Parasites in female fish No.	%	Parasites in male fish No.	%	No.female fish No.	%	No.male fish No.	%
Jan.	32	0	0	0	0	0	0	0	0	0	0	0	19	59.4	13	40.0
Feb.	31	0	0	0	0	0	0	0	0	0	0	0	14	52.0	13	48.0
Mar.	29	0	0	0	0	0	0	0	0	0	0	0	18	62.1	11	37.9
Apr.	30	2	6.6	2	14.3	0	0	2	2	100.0	0	0	14	46.6	16	53.4
May	31	2	6.4	0	0	2	18.2	2	0	0	2	100.0	20	64.5	11	35.5
June	30	7	23.3	5	26.3	2	18.2	10	8	80.0	2	20.0	19	63.3	11	36.7
July	30	5	16.6	4	19.1	1	11.1	5	4	80.0	1	20.0	21	70.0	9	30.0
Aug.	30	4	13.3	2	14.3	2	6.3	4	2	50.0	2	50.0	14	46.6	16	53.4
Sept.	28	2	7.1	2	6.3	0	0	2	2	100.0	0		16	57.0	12	43.0
Oct.	27	0	0	0	0	0	0	0	0	0	0	0	17	63.0	10	37.0
Nov.	30	1	3.3	0	0	1	0	1	0		1	100.0	20	66.7	10	33.3
Dec.	31	1	3.2	1	5.0	0	0	1	1	100.0	0		16	51.6	15	48.4
Total	359	24	6.7	16	7.7	8	5.4	27	19	70.4	8	29.6	208	58.0	147	42.0

TABLE 7.3:

The state of development of female N.rutili.

Month	HOST			
	S.cephalus	L.leuciscus	R.rutilus	E.lucius
Jan.		Shelled acanthors.		
Feb.				
Mar.			Intact ovary.	
Apr.				?
May				
June	Shelled acanthors			Ovarian balls
July	Ovarian balls			
Aug.	Ovarian balls			
Sept.	Shedding			
Oct.				
Nov.	Ovarian strand			
Dec.	Ovarian balls			

the female worm to the intestine of the host, or they may not be released until the female passes out of the host.

Specimens of N.rutili were recorded with the intact ovary, ovarian balls and shelled acanthors. When acanthors were present all other structures in the pseudocoel were obscured. The acanthors in the two specimens recorded from September were not so densely packed and it is suggested that acanthors were being released from the worms at this time, and the term shedding is used in Table 7.3.

No obvious seasonal pattern of development was present, but because of the small number of specimens found, it was impossible to determine the length of time that adult N.rutili remain in the host, or the time when infection occurred. Acanthors were recorded in the females in January and June, and one worm which appeared to be losing acanthors was present in September. It is possible that reinfection may only occur at one time of year, or that it may occur continuously, and therefore a detailed investigation of the seasonal dynamics of N.rutili in both the intermediate and the definitive hosts is necessary before any conclusions can be drawn.

Acanthocephalus lucii (Müller, 1776).

A.lucii was recorded from the same infection sites and the same hosts as N.rutili (Table 7.1). Tables 7.4, 7.5, 7.6 show the months where infection was recorded in S.cephalus, L.leuciscus and R.rutilus. One male E.lucius was infected with one male A.lucii in April. Only 34 specimens were recorded altogether, 26 of these being from

TABLE 7.4:

Infection of S.cephalus with A.lucii.

Month	No. fish	Infected fish		Infected female fish		Infected male fish		No. parasites	Parasites in female fish		Parasites in male fish	
		No.	%	No.	%	No.	%		No.	%	No.	%
Feb.	31	1		1		0		1	1		0	
Mar.	29	2		1		1		2	1		1	
Apr.	30	2		1		1		2	1		1	
Oct.	27	3		3		0		20	20		0	
Nov.	30	1		0		1		1	0		1	
Total		9	2.6	6	2.9	3	2.0	26	23	88.5	3	11.5

TABLE 7.5:

Infection of L.leuciscus with A.lucii.

Month	No. fish	Infected fish		Infected female fish		Infected male fish		No. parasites	Parasites in female fish		Parasites in male fish	
		No.	%	No.	%	No.	%		No.	%	No.	%
Apr.	35	1		0		1		1	0		1	
June	30	1		0		1		1	0		1	
July	30	2		2		0		2	2		0	
Total		4	1.2	2	1.2	2	1.2	4	2	50.0	2	50.0

TABLE 7.6:

Infection of R.rutilus with A.lucii.

Month	No. fish	Infected fish		Infected female fish		Infected male fish		No. parasites	Parasites in female fish		Parasites in male fish	
		No.	%	No.	%	No.	%		No.	%	No.	%
Jan.	33	1				1		1			1	
Feb.	27	1		1				1	1			
May	9	1		1				1	1			
Total		3	0.9	2		1		3	2		1	

S.cephalus, four from L.leuciscus, three from R.rutilus and the one from E.lucius. A mean number of one parasite per infected fish was present in each sample from all hosts, except in October where a mean of 6.6 parasites was recorded from S.cephalus. In S.cephalus 42.3% were female and 57.7% were male. In L.leuciscus and R.rutilus all the parasites were female, and the only specimen recorded from E.lucius was male. Examination of the stage of development of female A.lucii at different times of the year, revealed no information as to the presence or absence of a seasonal pattern of development.

Pomphorhynchus laevis (Müller, 1776).

One specimen of P.laevis was recorded from the intestine of a female S.cephalus in January. P.laevis was also recorded from the intestine of L.leuciscus in January and December. In January two male fish were infected, one with 29 parasites (15 female and 14 male), and one with one male parasite. In December two male fish were each infected with one P.laevis, one of which was female and the other male. Of the female parasites 83.4% contained ovarian balls, and 16.6% contained acanthors.

Echinorhynchus truttae (Schrank, 1788)

E.truttae was recorded from the intestine of T.thymallus and E.lucius. The number and percentage of T.thymallus infected and the number of parasites present are recorded in Table 7.7. Infections from E.lucius were only recorded in April and July, three E.lucius

infected in April and one in July. The number and sex and the stage of development of female E.truttae from T.thymallus and E.lucius are recorded in Tables 7.8 and 7.9, but the small number of E.truttae recorded prevents any study of their seasonal dynamics.

Polymorphus minutus (Goeze, 1782) cystacanth.

The cystacanth stage of P.minutus was recorded from the intestine of L.leuciscus, R.rutilus and T.thymallus.

P.minutus was recorded from L.leuciscus in July, September and November, six, one and four fish being infected respectively with six, one and four P.minutus. One one male R.rutilus was infected with one P.minutus cystacanth in July. Infections were present in T.thymallus in April, May and July, one, one and two fish infected respectively, each fish with only one parasite.

The adult P.minutus is found in the intestine of many aquatic birds (Crompton & Harrison, 1965) but the juvenile forms or cystacanths are often found in freshwater fish, although the real intermediate host is a Gammarus sp.

Discussion.

In the present survey although five species of Acanthocephala were recorded, they were only present in small numbers and it was imporsible to study their life cycles and seasonal dynamics.

All five species have previously been recorded in this country

TABLE 7.7:

Infection of T.thymallus with E.truttae.

Month	No. fish	Infected fish		Infected female fish		Infected male fish		No. parasites	Parasites in female fish		Parasites in male fish	
		No.	%	No.	%	No.	%		No.	%	No.	%
Jan.					NO SAMPLE							
Feb.	11	0	0	0	0	0	0	0	0	0	0	0
Mar.	18	0	0	0	0	0	0	0	0	0	0	0
Apr.	25	1	4.0	1	10.0	0	0	1	1	100.0	0	0
May	8	1	12.5	1	20.0	0	0	1	1	100.0	0	0
June	17	4	23.5	2	20.0	2	28.6	4	2	50.0	2	50.0
July	30	10	33.3	2	20.0	8	40.0	16	2	12.5	14	87.5
Aug.	5	0	0	0	0	0	0	0	0	0	0	0
Sept.					NO SAMPLE							
Oct.	25	1	4.0	1	7.1	0	0	1	1	100.0	0	0
Nov.	30	0	0	0	0	0	0	0	0	0	0	0
Dec.	30	0	0	0	0	0	0	0	0	0	0	0
Total	199	17	8.5	7	7.4	10	9.5	23	7	30.4	16	69.6

TABLE 7.8:

The number, sex and stage of development of female E.truttae in T.thymallus.

Months where infection recorded	No.Parasites	Sex of Parasite Female	Male	Stage of development of female
Apr.	1	0	1	
May	1	0	1	
June	4	3	1	
July	16	8	8	Ovarian balls and acanthors.
Oct.	1	1	0	Disintegrating.

TABLE 7.9:

The number, sex and stage of development of female E.truttae in E.lucius.

Months where infection recorded	No.Parasites	Sex of Parasite Female	Male	Stage of development of female
Apr.	12	7	5	Ovarian balls (5) Acanthors (2)
July	1	0	1	

TABLE 7.10:

Records of N.rutili in Britain.

Host	Location	Authority
S.trutta	River Severn	Rawson, 1952.
S.trutta T.thymallus E.lucius N.rutilus	Llyn Tegid (Bala Lake) Merionethshire.	Chubb, 1963, 1964, 1965.
S.trutta	Llyn Padarn, (Caernarvonshire)	Chubb, 1964.
S.trutta	Cheshire	Chubb, 1965.
S.trutta	River Teify (West Wales)	Thomas, 1964.
S.cephalus L.leuciscus N.rutilus E.lucius	River Lugg (Herefordshire)	Present survey.

TABLE 7.11:

Records of A.lucii in Britain.

Host	Location	Authority
A.anguilla		Baylis, 1928.
P.fluviatilis	Swithland Reservoir (Leicestershire). Windermere, N. Basin.	Rawson, 1952.
E.lucius P.fluviatilis R.rutilus Pleuronectes flesus L. Coregonus clupeoides Lacépède	Loch Lomond.	Copland, 1956,1957.
R.rutilus E.lucius P.fluviatilis A.anguilla	Shropshire Union Canal - Shropshire Cheshire	Kennedy & Chubb (1963 unpublished) in Chubb (1965) Mishra, 1966.
R.rutilus E.lucius P.fluviatilis	Rostherne Mere, Cheshire.	Rizvi, 1964.
S.cephalus L.leuciscus R.rutilus E.lucius	River Lugg, Herefordshire.	Present survey.

TABLE 7.12:

Records of E.truttae in Britain.

Host	Location	Authority
S.trutta	Buckinghamshire; Hampshire; Hertfordshire; Derbyshire etc.	Baylis, 1928.
S.trutta	Scandale Beck, (Windermere Catchment area) Swithland Reservoir (Leicestershire).	Rawson, 1952.
T.thymallus	Llyn Tegid (Bala Lake) Merionethshire.	Chubb, 1963, 1964.
S.trutta	Afon Terrig (North Wales)	Awachie, 1965.
T.thymallus E.lucius	River Lugg, Herefordshire.	Present survey.

TABLE 7.13:

Records of P.laevis in Britain.

Host	Location	Authority
R.rutilus	Oxfordshire.	Baylis, 1928.
S.cephalus L.leuciscus	River Avon (Hampshire)	Walker, 1964. Chubb, 1965. Chubb, 1966. Stranack, 1966. Chubb, 1967. Kennedy, pers.comm.
	River Lugg, Herefordshire.	Present survey.

and Tables 7.10 - 7.13 list the definitive hosts and the location of the records for all the species except P.minutus.

Investigations into the life cycles and seasonal dynamics of these Acanthocephala have been made in Britain, Europe, the U.S.S.R. and the U.S.A.

Villot (1885) reported the occurrence of juvenile stages of Echinorhynchus clavaeceps (= N.rutili) in the larvae of Sialis niger. Robin (1871) previously reported the young stages of this parasite in Nephelis octoculata (Annelida), but Villot regarded this as a case of accidental parasitism. Levander (1905) reported them from a collection of ostracods near Helsingfors (Finland). Ward (1940) investigated the life history of Neoechinorhynchus cylindratus (Van Cleave, 1913) which is stated to be similar to the European N.rutili. After the shelled acanthors of N.cylindratus were passed out in the faeces of the definitive host, Huro salmoides they are eaten by ostracods, Cypria (Physacypria) globula, and the acanthors develop until they closely resemble the adult except in size and sexual maturity. If infected ostracods are eaten by Lepomis pallidus, the juvenile acanthocephalan encysts in the liver. The parasite develops to maturity in the intestine of the definitive host when L.pallidus is ingested by H.salmoides.

N.rutili has not been found encysted in the liver of any fish in the present survey, and further investigations are required before the intermediate host and details of the life cycle can be determined.

Some of the first observations on the development of Acanthocephala were made by Leuckart (1876), and among these he described observations on the development of Echinorhynchus angustatus (= A.lucii) in Asellus aquaticus. Kaiser (1893) also studied the developmental stages of A.lucii. Gammarus sp. as well as A.aquaticus is also reported as an intermediate host for A.lucii (Komarova, 1950).

The development and life history of E.truttae, is described by Awachie (1965), C.pulex acting as the intermediate host.

Gammarus sp. are also thought to act as the intermediate host for P.laevis. Linstow (1892) found P.laevis encysted in small fish and thought that these served as the first intermediate host, and that the presence of this parasite in Gammarus sp. was abnormal. Encysted juveniles of P.laevis in Tinca vulgaris were fed to E.lucius from which the adults were recovered (Riquier, 1909). No encysted P.laevis were noted in the present survey, and without a more detailed description of the type of encystment it is not possible to state if this is the result of host reaction to infection, or whether the juveniles were incapable of developing in the adult in these hosts, or that it is a normal part of the life cycle. The latter is thought to be unlikely as no other reports of encysted forms are available.

The adult P.minutus is a parasite of many aquatic birds (Lühe, 1911; Meyer, 1933; Lundström, 1942). Greef (1864) identified this parasite from C.pulex, and after feeding these to ducks, he obtained the adult form. Luther (1904) observed juvenile forms of Echinorhynchus

polymorphus (= P.minutus) in G.locusta, Hynes (1955) also showed that G.duebeni Lilljeborg and G.lacustris Says are also intermediate hosts. As in the present survey, Meyer (1933) also recorded juveniles in several species of fish, and the crayfish, and it is suggested that they may serve as transport hosts. An extensive study of juvenile and adult stages of the life cycle of P.minutus were made by Nicholas and Hynes (1957) and Hynes and Nicholas (1958), and Crompton and Harrison (1965).

The presence of a well defined seasonal periodicity of development has been recorded for some Acanthocephala e.g. Echinorhynchus gadi Müller, 1776 (Shulman, and Shulman-Albova, 1953); Neoechinorhynchus gracilisentis (Van Cleave); Neoechinorhynchus longirostris (Van Cleave) in Dorosoma cepidianum (Le Sueur) (Van Cleave, 1916); N.rutili (Steinstrasser, 1936) and A.lucii (Komarova, 1950). No seasonal periodicity of development has been reported for Neoechinorhynchus emydis (Leidy, 1851), (Van Cleave, 1916); E.gadi (Polyanski, 1955); Echinorhynchus clavula Dujardin, 1845 nec Hamann, (1892), (Chubb, 1964); A.lucii (Rizvi, 1964; Mishra, 1966). Both E.gadi and A.lucii are recorded by some authorities to possess a seasonal periodicity of development whereas others state this does not occur. Chubb (1964) postulated that as no seasonal periodicity appears to occur if the body of water investigated does not freeze over for any length of time,

> "temperature may play a major part in determining the presence or absence of a well defined seasonal periodicity of development for some of the Acanthocephala".

As previously stated the small number of each species of Acanthocephala recorded in the present survey only allowed their presence to be reported. It is interesting to note that N.rutili and A.lucii were recorded from the same hosts and in approximately the same numbers. The presence of both species in one individual host was uncommon. The significance of this is unknown, but it is an interesting field for further study as interaction between Acanthocephala and other intestinal parasites has previously been recorded (Cross, 1934 a, b; Beck 1951; Holmes 1961, 1962 a & b; Thomas 1964).

The fish hosts become infected with Acanthocephala by eating the intermediate host, and the variation in the intensity of feeding and the type of food ingested influences the chance of infection. This may go some way to explain why P.laevis was recorded from two of the cyprinids, S.cephalus and L.leuciscus, but not from R.rutilus, the latter commonly feeding on plants and algae. E.truttae was only recorded from T.thymallus and E.lucius. Previous studies on life cycles have shown that G.pulex can act as intermediate host for A.lucii (Komarova, 1950), P.laevis (Von Linstow, 1892) and E.truttae (Awachie, 1963) and therefore factors other than that of variation in diet must operate in determining the suitability of the host for the continued development of the parasite. E.lucius was infected by Acanthocephala which were recorded from both the cyprinids and T.thymallus, and it is postulated (Chubb, 1964) that these infections

may be acquired secondarily by E.lucius ingesting fish already infected with the adult parasite.

OTHER PHYLA

Annelida : Hirudinea

One species of leech Pisicola geometra L. was recorded from S.cephalus, L.leuciscus, R.rutilus and T.thymallus. Fresh material was relaxed in water, and both fresh and deep frozen material were preserved in 70% alcohol.

P.geometra was found mainly on the body surface attached to the scales, but six specimens (five from S.cephalus, one from L.leuciscus) were recovered from the branchial cavity, and were usually gorged with blood.

Only 49 specimens were recorded, and of these a greater number were found on S.cephalus i.e. 37 on S.cephalus (see Table 7.14); compared to three on L.leuciscus, six on R.rutilus and four on T.thymallus (Table 7.15). L.leuciscus, R.rutilus and T.thymallus never had more than one leech per fish, and although a greater number of parasites were recorded from S.cephalus, a greater number of fish were infected and the intensity of infection only rose slightly in the February, October and November samples to 1.6. The small number of P.geometra recorded prevented any study of their seasonal dynamics although the slight rise of incidence in winter months agrees with findings in the U.S.S.R.

Bauer (1958) states that P.geometra appears on fish in autumn. If

TABLE 7.14:

Infection of S.cephalus with P.geometra.

Month	No.fish/ sample	No.infected	% infected	No.parasites.
Jan.	32	2	6.3	2
Feb.	31	7	22.6	11
Mar.	29			
Apr.	30			
May	31	2	6.5	2
June	30			
July	30	4	13.3	4
Aug.	30	1	3.3	1
Sept.	28	2	7.1	2
Oct.	27	3	11.1	5
Nov.	30	5	16.6	8
Dec.	31	2	6.5	2
Total	359	28	7.8	37

TABLE 7.15:

Infection of L.leuciscus, P.rutilus and T.thymallus with P.geometra.

Host	Month	No.fish infected	No. parasites
L.leuciscus	February	1	1
	April	1	1
	September	1	1
Total		3	3
R.rutilus	February	1	1
	June	1	1
	July	1	1
	September	1	1
	December	2	2
Total		6	6
T.thymallus	November	2	2
	December	2	2
Total		4	4

there is a high intensity of infection they cause irritation, and excessive movement of the fish, which results in loss of weight and death in exceptional cases. In the summer the leeches leave the fish and deposit cocoons full of eggs. The eggs hatch in late summer, and the young leeches reinfect the fish in autumn. P.geometra also serves as a vector for trypanosomes e.g. Trypanoplasma cyprini Plehn, 1903. Infection of fish with these parasites may produce a greater pathogenic effect than infection with only P.geometra.

Mishra (1966) recorded P.geometra on R.rutilus, P.fluviatilis and E.lucius. As in the present survey this parasite was only present in small numbers and no pathogenic effects were observed.

Mollusca.

Glochidia were recorded from the gills of T.thymallus, S.cephalus and L.leuciscus. The occurrence of glochidia was rare, and all records are shown in Table 7.16.

TABLE 7.16:

Infection of T.thymallus, S.cephalus and L.leuciscus with glochidia.

Host	Month	No.fish infected	No.parasites
T.thymallus	April	3	3
S.cephalus	April	2	3
	May	1	1
	August	1	1
L.leuciscus	May	1	1

More than one glochidia on one fish was only recorded once i.e. on S.cephalus in April. April and May appear to be the months when glochidia are produced, but no significance can be attached to this observation until further investigations are undertaken. The structure of the beak of the glochidia and the size of the valves suggest it may be Anodonta cygnea L.

Zhadin (1938) reported mass shedding of glochidia from swan mussels in May and June. If the identification of glochidia in the present survey is correct, the presence of glochidia mainly in April and May, even though only in small numbers, corresponds with the above report.

REFERENCES

AWACHIE, J.B. 1965 The ecology of Echinorhynchus truttae Schrank, 1788. (Acanthocephala) in a trout stream in North Wales. Parasitology. 55: 747-762.

BAUER. O.N. 1958 Parasitic diseases of cultured fishes and methods of their prevention and treatment. Parasitology of Fishes. Translation 1961. Oliver and Boyd Ltd.

BAYLIS, H.A. 1928 Records of some parasitic worms from British vertebrates. Ann.Mag.nat.Hist. 1 (10), 329-343.

BECK, J.W. 1951 Effect of diet upon singly established Hymenolepis diminuta in rats. Expl.Parasit. 1: 46-59.

CHUBB, J.C. 1963 On the characterization of the parasite fauna of the fish of Llyn Tegid. Proc.zool.Soc.Lond. 141, (3): 609-621.

1964a Occurrence of Echinorhynchus clavula Dujardin, 1843 nec Hamann, 1892 (Acanthocephala) in the fish of Llyn Tegid (Bala Lake) Merionethshire. J.Parasit. 50 (1): 52-59.

1964b A preliminary comparison of the specific composition of the parasite fauna of the fish of Llyn Padarn, Caernarvonshire, an oligotrophic lake, and Llyn Tegid (Bala Lake) Merionethshire, a late oligotrophic or early mesotrophic lake. Wiad. paraszyt. 10, (4-5): 499-510.

1965a Report on the parasites of freshwater fishes of Lancashire and Cheshire. Lancashire and Cheshire Fauna Committee Publ. No.50. 35th report.

1965b Mass occurrence of Pomphorhynchus laevis (Müller, 1776) Monticelli 1905 (Acanthocephala) in the chub, Squalius cephalus (L.) of the River Avon, Hampshire. Parasitology, 55: 5P.

CHUBB, J.C. 1966 The 'orange peril' of the Avon. Fishing. 156 : 17-18.

1967 The parasites of the Avon. Fishing. 163: 10-12.

COPLAND, W.O. 1956 Notes on the food and parasites of pike (E.lucius) in Loch Lomond. Glasgow Nat. 17 : 230-235.

1957 The parasites of Loch Lomond fishes. In studies of Loch Lomond. I. Glasgow : 128-133.

CROMPTON, D.W.T. and HARRISON, J.C. 1965 Observations on Polymorphus minutus (Goeze, 1782) (Acanthocephala) from wild fowl in a reserve in Kent. Parasitology. 55: 345-355.

CROSS, S.X. 1934a Two mutually limiting parasites of ciscoes. Proc.helminth.Soc. Wash. 1:7.

1934b A probable case of non-specific immunity between two parasites of ciscoes of the Trout Lake region of northern Wisconsin. J.Parasit. 20 : 244-245.

GREEF, R. 1864 Untersuchungen über den Bau und die Naturgeschichte von Echinorhynchus miliarius Zenker (E.polymorphus). Arch.Naturgesch. Jg. (30) 1: 98-140.

HAMANN, O. 1891 Monographie der Acanthocephalen (Echinorhynchen). Ihre Entwicklungsgeschichte Histogenie und Anatomie nebst Beiträgen zur Systematik und Biologie. Jen. Zeit. Nat. 18 : 113-231.

HOLMES, J.C. 1961 Effects of concurrent infections on Hymenopepis diminuta (Cestoda) and Moniliformis dubius (Acanthocephala). I. General effects and comparison with crowding. J.Parasit. 47 : 209-216.

HOLMES, J.C.	1962a	Effects of concurrent infections on Hymenolepis diminuta (Cestoda) and Moniliformis dubius (Acanthocephala). II. Effects on growth. J.Parasit. 48 : 87-96.
	1962b	Effects of concurrent infections on Hymenolepis diminuta (Cestoda) and Moniliformis dubius (Acanthocephala). III. Effects in hamsters. J.Parasit. 48 : 97-100.
HY'AN, L.H.	1951	The Invertebrates: Acanthocephala, Aschelminthes and Entoprocta. McGraw-Hill Book Co., New York.
HYNES, H.B.N.	1955	The reproductive cycle of some British freshwater Gammaridae. J.Anim.Ecol. 24 : 352 -
HYNES, H.B.N. and NICHOLAS, W.L.	1958	The development of Polymorphus minutus (Goeze, 1782) (Acanthocephala) in the intermediate host. Ann.trop.Med.Parasit. 51 : 380 - 391.
KAISER, J.	1893	Die Acanthocephalen und ihre Entwicklung. Bibl. Zool. 7.
KOMAROVA, M.S.	1950	K voprosy o zhiznennom tsikle akre bnya Acanthocephalus lucii Müll. Dokl.Akad.Nauk.SSSR Novaya Seriya 70 (2) : 359-360.(Translation).
LEUCKART, R.	1876	Die menschlichen Parasiten und die von ihnen herrührenden krankheiten. Bd.2, Leipzig u.Heidelberg.
LEVANDER, K.M.	1905	Nogra zoologiska notiser, Meddn.Soc.Fauna Flora.fenn. 31: 66-67.
LINSTOW, O. von	1892	Beo-bach-tungen an Helminthen larven. Arch.mikrosk.Anat.Entwmech. 39: 325-343.
LÜHE, M.	1911	Acanthocephalen. Brauer, Suswasserfauna Deutschlands. H.16.

LUNDSTROM	1942	Die Acanthocephalen Schwedens mit Ausnatime der Fischacanthocephalen von Susswasserstandorten. Lund.238 pp.
LUTHER, A.	1904	Larver of Echinorhynchus polymorphus; Gammarus locusta. Meddn.Soc.Fauna Flora fenn. 31: 31.
MEYER, A.	1933	Acanthocephala. Bronn's Klassen und Ordnungen des Tierreichs. 4 (II,2), 582 p.p.
MISHRA, T.N.	1966	The parasite fauna of the fish of the Shropshire Union Canal, Cheshire. Ph.D. thesis. University of Liverpool.
NICHOLAS, W.L. and HYNES, H.B.N.	1958	Studies on Polymorphus minutus (Goeze, 1782) (Acanthocephala) as a parasite of the domestic duck. Ann.trop.Med.Parasit. 52 : 36-47.
POLYANSKI, Yu.I.	1955	Materiali po parazitologii ryb severnich morei SSSR. Parasiti ryb Barentsova mo rya. Trudy zool.Inst.,Leningr. 19: 5-170.
RAWSON, D.	1952	The occurrence of parasitic worms in British freshwater fishes. Ann.Mag.nat.Hist. 5(12): 877-887.
RIQUIER, J.K.	1909	Die Larve von Posphorhynchus laevis Zoega (= Echinorhynchus proteus Westr.) in der Tinca vulgaris und dessen experimentell erzielte Entwicklung in Esox lucius. Zentbl.Bakt.Parasit Kde. Ong.52:248-252.
RIZVI, S.H.H.	1964	The parasite fauna of the fish of Rostherne Mere, Cheshire. Ph.D. thesis. University of Liverpool.
ROBIN, Ch.	1871	Traité du Microscope. p.777 (Citation from Villot, 1885).

SHULMAN, S.S. and SHULMAN-ALBOVA, R.E. 1953 Parazit ryb Belogo morya. Izdatel. Akademii Nauk SSSR., Moscow.

STEINSTRASSER, W. 1936 Acanthocephalen als Forellenparasiten. Z. Fisch. 34 : 177-212.

STRANACK, F.R. 1966 Some helminths of fish from Hampshire Rivers. Parasitology 56 : 10 P.

THOMAS, J.D. 1964 Studies on populations of helminth parasites in brown trout (Salmo trutta L.) J.Anim.Ecol. 33 : 83-95.

VAN CLEAVE, H.J. 1916 Seasonal distribution of some Acanthocephala. J.Parasit. 2: 106-110.

1935 The larval stages of Acanthocephala. J.Parasit., 21: 435-436.

1947 A critical review of terminology for immature stages in acanthocephalan life histories. J.Parasit. 33 : 118-125.

1953 Acanthocephala of North American Mammals. Illinois biol.Monogr. 23, (1 & 2): 1-179.

VILLOT, A. 1885 Sur l'état larvaire et l'hôte intermédiare de l'Echinorhynchus clavaeceps Zeder. Zool. Anz. 8: 19-22.

WALKER, R. 1964 Killer parasites of the Avon. Fishing. 92 : 14-16.

WARD, H.L. 1940 Studies on the life history of Neoechinorhynchus cylindratus (Van Cleave, 1913) (Acanthocephala). Trans.Am.microsc.Soc., 59 : 327-347.

ZHADIN, V.I. 1938 Semeistvo Unionidae. Fauna SSSR (The Family Unionidae). Fauna SSSR 4 (1) : 1-169.

CHAPTER EIGHT.

Comparison of the parasite faunas of the fish of the River Lugg.

92.1% of all the fish examined were infected with parasites. 100.0% of E.lucius; 98.8% L.leuciscus; 98.3% S.cephalus; 95.6% R.rutilus, and 63.8% T.thymallus were infected. The total number and percentage of each species of fish infected overall and each month are shown in Table 8.1. Explanations are postulated for the levels of incidence of infection in the different hosts.

E.lucius has a distinctive parasite fauna, the parasites often being specific to the Esocidae e.g. T.monenteron, T.nodulosus (adult), R.acus (adult) and H.oviperda. As well as this typical parasite fauna the predatory habit of E.lucius often leads to the accumulation of parasites from other fish which form part of its diet. E.lucius feeds on cyprinids and salmonids and was infected in the present investigation by Phyllodistomum sp., C.truttae, E.truttae (found in salmonids); A.lucii, N.rutili (found in cyprinids) and S.inermis which has been previously recorded from A.anguillae (see Chapter 6). The presence of the typical parasite fauna as well as superimposed infections resulting from the predatory habit may explain the high incidence of infection and varied nature of the parasite fauna of E.lucius.

The high percentage of cyprinids infected with Myxosporidia especially M.mülleri (see Chapter 2) and juvenile R.acus, and the absence of Myxosporidia and juvenile nematodes in T.thymallus may

TABLE 8.1:

The total number and percentage of fish infected overall, and in each sample.

Month	E.lucius			S.cephalus			L.leuciscus			R.rutilus			T.thymallus		
	No. fish	Infected fish No.	%	No. fish	Infected fish No.	%	No. fish	Infected fish No.	%	No. fish	Infected fish No.	%	No. fish	Infected fish No.	%
Jan.	1	1	100.0	32	26	81.3	33	30	90.9	33	27	81.8	NO SAMPLE		
Feb.	1	1	100.0	31	31	100.0	31	31	100.0	27	27	100.0	11	10	90.9
Mar.	0	0	0	29	29	100.0	30	30	100.0	30	30	100.0	18	15	83.3
Apr.	7	7	100.0	30	30	100.0	35	34	97.1	16	16	100.0	25	25	100.0
May	5	5	100.0	31	31	100.0	4	4	100.0	9	9	100.0	8	7	87.5
June	8	8	100.0	30	30	100.0	30	30	100.0	30	30	100.0	17	10	58.8
July	7	7	100.0	30	30	100.0	30	30	100.0	22	22	100.0	30	26	86.6
Aug.	2	2	100.0	30	30	100.0	30	30	100.0	30	30	100.0	5	2	40.0
Sept.	0	0	0	28	28	100.0	30	30	100.0	30	28	93.3	NO SAMPLE		
Oct.	4	4	100.0	27	27	100.0	31	31	100.0	30	25	83.3	25	10	40.0
Nov.	0	0	0	30	30	100.0	28	28	100.0	30	30	100.0	30	9	30.0
Dec.	1	1	100.0	31	31	100.0	30	30	100.0	30	29	96.6	30	13	43.3
Total	36	36	100.0	359	353	98.3	342	338	98.8	317	303	95.6	199	127	63.8

explain the difference in the levels of incidence of infection between cyprinids and T.thymallus. The lower incidence recorded in January for all cyprinids reflects inadequate observations of Myxosporidia in this sample. A decrease in the percentage infection of T.thymallus was recorded from August to December (Table 8.1). Examination of the parasite fauna showed that the decrease coincided with an almost complete disappearance of T.borealis from the gills, as well as a drop in the occurrence of C.metaecus from the pyloric caeca. The lower percentage infection recorded in June also results from a decrease in the incidence of T.borealis, and subsequent increased incidence results in a rise in percentage infection again in July. The pattern of the percentage of T.thymallus infected appears to be controlled by the seasonal dynamics of monogean and digenean parasites.

No seasonal occurrence or development was recorded for Myxosporidia and juvenile R.acus, in the present survey. These parasites are excluded from Table 8.2 where the percentage of cyprinids infected with all other species of parasites are recorded. The percentage of S.cephalus and L.leuciscus infected is still higher than for T.thymallus, but the percentage of infected R.rutilus is now lower. A marked increase in the percentage of cyprinids infected occurred between January and February, and this is explained by the appearance of dactylogyrids on the gills in February (see Chapter 3). From February to July a high level of percentage infection is maintained,

one exception being noted from R.rutilus in May, but this is attributable to a sampling deficiency, only nine fish being examined. A decrease in percentage infection was recorded from all three hosts in August. Examination of the parasite fauna showed that this coincided with the loss of dactylogyrids and A.isoporum from the hosts. The subsequent rise in incidence again between September and October resulted from reinfection of the hosts with small immature A.isoporum (see Chapter 4). The decrease again in November has already been noted and is attributed to the stabilisation of the number of A.isoporum in the hosts, after the period of heavy reinfection where not all the parasites become established. The lower figures recorded for R.rutilus result from the fewer reinfection records for A.isoporum in these months. If it was not for the presence of dactylogyrids especially D.crucifer between February and July a much lower percentage infection corresponding to that found between August and December would be recorded for R.rutilus.

The pattern of percentage infection recorded in the cyprinids and T.thymallus results from the seasonal occurrence of the dactylogyrids and tetraonchid Monogenea, and is emphasised by the loss of A.isoporum from cyprinid hosts in August and September. The presence or absence of any seasonal variation in percentage infection of E.lucius with T.monenteron could not be determined from the small samples obtained.

The bottom line of Table 8.3 shows the total number of parasites recorded from each host species, and the mean number of parasites in

TABLE 8.2:

The incidence of infection in cyprinids excluding Myxosporidia and juvenile R.acus.

Month	S.cephalus			L.leuciscus			R.rutilus		
	No. fish	Infected fish No.	%	No. fish	Infected fish No.	%	No. fish	Infected Fish No.	%
Jan.	32	20	62.5	33	22	66.7	33	9	27.3
Feb.	31	30	96.8	31	28	90.3	27	22	81.5
Mar.	29	27	93.1	30	29	96.6	30	27	90.0
Apr.	30	29	96.6	35	30	85.7	16	16	100.0
May	31	26	83.9	4	4	100.0	9	5	55.5
June	30	29	96.6	30	29	96.6	30	30	100.0
July	30	29	96.6	30	26	86.6	22	22	100.0
Aug.	30	19	63.3	30	19	63.6	30	20	66.7
Sept.	28	21	75.0	30	22	73.3	30	4	13.3
Oct.	27	24	88.9	31	31	100.0	30	10	33.3
Nov.	30	15	50.0	28	25	89.3	30	11	36.6
Dec.	31	25	80.6	30	24	80.0	30	14	46.6
Total	359	294	81.9	342	289	84.5	317	190	59.9

each infected fish species (excluding Myxosporidia and juvenile nematodes). The total number of infected fish of each species are recorded in Table 8.1. The greatest mean number of parasites per infected fish was recorded for R.rutilus, where the lowest percentage infection was present. This may be explained by the large numbers of D.crucifer and A.isoporum recorded in the months where infection occurred. Greater numbers of D.crucifer were found than any other dactylogyrid. E.lucius had a mean number of 18.5 parasites per infected fish, compared to 15.3 in S.cephalus; 9.8 in T.thymallus and 9.7 in L.leuciscus. The intensity of infection in T.thymallus and L.leuciscus is therefore similar, although a much greater percentage of L.leuciscus were infected.

The composition of the parasite fauna varied as to whether the hosts belonged to the Cyprinidae Salmonidae or Esocidae (Table 8.3). Protozoa (Myxosporidia) were present in the Cyprinidae and E.lucius, but not in T.thymallus. A more varied monogenean and cestode fauna were present in the cyprinids compared to E.lucius and T.thymallus whereas a greater variety of nematodes were present in E.lucius and T.thymallus. Hirudinea and glochidia were absent from E.lucius in the present survey, but a similar number of species of Digenea and Acanthocephala were present in all the hosts.

Altogether 38 different species of parasite were recorded from the present survey. 25 species were recorded from the cyprinids, 12 from E.lucius and 10 from T.thymallus. From the cyprinid hosts

TABLE 8.3:

The number and percentage of infected fish of each species from the River Lugg, and a record of the total number and intensity of infection of each species of parasite.

	Parasites	S.cephalus				L.leuciscus				R.rutilus				E.lucius				T.thymallus			
		Infected fish		Parasites		Infected fish		Parasites		Infected fish		Parasites		Infected fish		Parasites		Infected fish		Parasites	
		No.	%	No.	Mean	No.	%	No.	Mean	No.	%	No.	Mean	No.	%	No.	Mean	No.	%	No.	Mean
PROTOZOA	Myxobolus macrocapsularis	3	0.7	3cysts	1.0																
	Myxobolus mülleri (kidney)	20	5.6																		
	Myxobolus mülleri (gonads)	10	2.8																		
	Myxobolus mülleri (intestine wall)	9	2.2																		
	Myxobolus mülleri (mesenteries)	314	87.5																		
	Myxobolus mülleri (gills)	308	85.8			103	30.1			36	11.4										
	Myxobolus mülleri (urinary ducts)	323	89.9			322	94.2			280	88.3										
	Henneguya zschokkei					13	3.8														
	Myxobolus artus									Rare											
	Henneguya psorospermica											13		13	36.1						
	Henneguya oviperda													4	11.0						
MONOGENEA	Diplozoon paradoxum	2	0.6	2	1.0	183	53.5	464	2.5	10	3.2	10	1.0								
	Dactylogyrus vistulae	116	33.1	572	4.9																
	Dactylogyrus prostae	52	14.5	753	14.5																
	Dactylogyrus folkmanovae	5	1.4	6	1.2																
	Dactylogyrus cordus					81	23.7	362	4.5												
	Dactylogyrus tuba					6	1.8	10	1.6												
	Dactylogyrus crucifer									124	39.1	2026	16.3								
	Dactylogyrus sphyrna									3	0.9	3	1.0								
	Dactylogyrus namus									1	0.3	1	1.0								
	Tetraonchus monenteron													26	72.3	398	15.3				
	Tetraonchus borealis																	66	34.6	348	5.4
DIGENEA	Allocreadium isoporum	242	67.4	2776	11.6	175	51.2	1329	7.6	40	12.6	1725	43.0								
	Sphaerostoma bramae	48	13.4	153	3.2	10	2.9	41	4.1	83	26.2	418	5.0								
	Phyllodistomum sp.													7	19.4	167	23.0	1	0.5	1	1.0
	Crepidostomum metoecus																	73	36.7	824	11.3
	Allocreadium transversale																	11	5.6	29	2.6
CESTODA	Proteocephalus torulosus	29	8.1	61	2.1	70	20.5	481	6.7												
	Caryophyllaeides fennica	40	11.1	66	1.6	10	2.9	19	1.9	28	8.8	48	1.7								
	Caryophyllacus laticeps	15	4.2	20	1.3	18	5.3	54	2.3	11	7.3	42	3.6								
	Triaenophorus nodulosus													8	22.2	16	2.0				
NEMATODA	Rhapidascaris acus (juvenile)	280	78.0			163	47.7			100	31.5										
	Rhaphidascaris acuè (adult)													11	30.5	54	4.1				
	Spinitectus inermis													1	2.8	10	10.0				
	Cucullanus sp.													3	8.3	4	1.3				
	Cucullanus truttae																	3	1.5	3	1.0
	Cystidicola farionis																	1	0.5	2	2.0
ACANTHOCEPHELA	Pomphorhynchus laevis	1	0.3	1	1.0	4	1.2	32	8.0												
	Acanthocephalus lucii	9	2.6	26	2.9	4	1.2	4	1.0	3	0.9	3	1.0	1	2.8	1	1.0				
	Neoechinorhynchus rutili	24	6.7	27	1.1	1	0.3	1	1.0	1	0.3	2	2.0	3	8.3	3	1.0				
	Echinorhynchus truttae													4	11.1	13	3.2	17	8.5	23	1.4
	Polymorphus minutus (cystacanth)					11	3.2	11	1.0	1	0.3	1	1.0					4	2.0	4	1.0
HIRUDINEA	Piscicola geometra	28	7.8	37	1.3	3	0.9	3	1.0	6	1.9	6	1.0					4	2.0	4	1.0
MOLLUSCA	Anodonta sp. (glochidia)	5	1.4	5	1.0	1	0.3	1	1.0									3	1.5	3	1.0
	Total			4505	15.3			2812	9.7			4313	22.7			666	18.5			1241	9.8

17 species were present in both S.cephalus and L.leuciscus and 15 in R.rutilus. Ten species were common to all three cyprinids i.e. M.mülleri, D.paradoxum, A.isoporum, S.bramae, C.fennica, C.laticeps, R.acus (juvenile), A.lucii, N.rutili and P.geometra, although a great variation occurred in the percentage and intensity of infection in each host. These variations are recorded in the chapters dealing with the individual parasites, and the results are summarised in Table 8.3 and below.

1. M.mülleri infected a wider range of tissues and organs, and a greater percentage of S.cephalus, though similar percentage infections were recorded for M.mülleri in the urinary ducts of all three cyprinid hosts.

2. D.paradoxum was very common on the gills of L.leuciscus, but was rare on R.rutilus and S.cephalus.

3. A.isoporum was much commoner in S.cephalus and L.leuciscus than in R.rutilus, but when A.isoporum was present in the latter host the overall intensity of infection was greater than in the other two hosts.

4. The percentage of R.rutilus infected with S.bramae was greater than either S.cephalus or L.leuciscus, but the intensity of infection was similar in all three hosts.

5. C.fennica and C.laticeps were never present in large numbers. C.fennica was commoner in S.cephalus and R.rutilus, but the intensity was similar in all three cyprinids. C.laticeps occurred more

frequently in R.rutilus and L.leuciscus, where the intensity of infection was slightly higher than in S.cephalus.

6. R.acus juveniles were most common in S.cephalus.

7. A.lucii and N.rutili were only recorded in small numbers, but were much commoner in S.cephalus than in either L.leuciscus or R rutilus.

8. The intensity of infection with P.geometra was similar in all the cyprinids, but this species was recorded more frequently from S.cephalus.

The only monogenean common to all three cyprinids was D.paradoxum. All the dactylogyrids appeared to be host specific, the reasons for this being unknown.

With the exception of P.geometra, D.paradoxum, M.mulleri and R.acus (the latter using cyprinids as an intermediate host) all the other parasites which the cyprinids have in common require an intermediate host. It is thought that food items which act as intermediate hosts for these parasites are ingested by all these cyprinids and the difference in percentage and intensity of infection is related to the number of these infected organisms in the diet, although other factors affecting the establishment of the parasite e.g. the microenvironment of the host intestine, will be superimposed on the initial infection.

The cyprinids and T.thymallus have three species of parasite in common i.e. P.minutus, P.geometra and Anodonta sp. (glochidia). The two latter species are both external parasites where the initial

function served by the host is one of attachment, and one which is served by many species of fish, thereby explaining the lack of specificity shown by these parasites. P.minutus acanthellae develop in C.pulex, and when these are eaten by the definitive host (aquatic birds) they develop to the adult. If infected C.pulex are ingested by fish, the cystacanth is released to the lumen of the fish intestine, but no further development ensues unless the fish is ingested by an aquatic bird, and probably the cystacanth eventually passes out with the faeces. The cystacanths of P.minutus are therefore accidental parasites and are not specific to any fish host. The parasites that T.thymallus and cyprinids have in common are, therefore, those in which no special requirements are essential for their survival, or young stages which accidentally occur in many fish.

E.truttae and Phyllodistomum sp. were the only two parasites in common between E.lucius and T.thymallus, and it is uncertain whether the Phyllodistomum belonged to the same species. E.lucius may be accidentally infected with E.truttae by the ingestion of salmonid fishes. Both fish are infected by species of Tetraonchus, and although it has been suggested that if cross-infection experiments were carried out both species may appear identical, differences in the structure of the connecting bar and copulatory organ of T.monenteron and T.borealis from the present survey, seem to justify the existence of two species.

A.lucii and E.rutili were found in E.lucius and the cyprinids

The infections in E.lucius may again result from ingestion of cyprinids. A.lucii and E.truttae both have G.pulex as an intermediate host, and although this organism is ingested by T.thymallus and the cyprinids, A.lucii was never recovered from T.thymallus and E.truttae never recovered from cyprinids. This suggests that both Acanthocephala need requirements which are specific to the host in which they mature. It seems unlikely that E.lucius should possess the requirements shown by both hosts, and the above argument is put forward to support the hypothesis that these Acanthocephala are accidental or secondarily acquired parasites of E.lucius.

P. laevis and P.torulosus were recorded from S.cephalus and L.leuciscus but not from R.rutilus. The occurrence of P.laevis in the present survey was rare. A.lucii which was recorded from R.rutilus and P.laevis both use G.pulex as an intermediate host. P.laevis has been reported in R.rutilus from other investigations and further studies may reveal this parasite in R.rutilus of the River Lugg. The absence of P.torulosus in R.rutilus may result from the feeding habits of this fish. R.rutilus is mainly a bottom feeder, and the intermediate host of P. torulosus is probably a species of cyclops which is found in the phytoplankton nearer the water surface.

Summary of the parasite fauna of fish from different freshwater habitats.

Recent studies on the parasite fauna of freshwater fishes by several research workers in the Department of Zoology, University of

TABLE 8.4:

The parasite fauna of freshwater fishes recorded from four surveys in Britain.

Parasites	S.cephalus R.Lugg	L.leuciscus R.Lugg	R.Lugg	R.rutilus Llyn Tegid	R.rutilus Rostherne Mere	Shropshire Union Canal	Abramis brama Shropshire Union Canal	Phoxinus phoxinus Llyn Padarn	P.fluviatilis Llyn Tegid	P.fluviatilis Rostherne Mere	Shropshire Union Canal	Gasterosteus aculeatus Llyn Padarn	R.Lugg	E.lucius Llyn Tegid	E.lucius Rostherne Mere	Shropshire Union Canal	T.thymallus R.Lugg	T.thymallus Llyn Tegid	S.trutta Llyn Tegid	S.trutta Llyn Padarn	S.salar Llyn Tegid	S.salar Llyn Padarn	Salvelinus alpinus perissi Llyn Padarn	Coregonus clupeoides pennanti Llyn Tegid	A.anguillae Llyn Tegid	A.anguillae Shropshire Union Canal	A.anguillae Llyn Padarn
Myxobolus müller Butschli, 1882	x	x	x																								
Myxobolus artus, Akhmerov, 1960.			x																								
Myxobolus macrocapsularis, Reuss, 1906.	x																										
Myxidium lieber kühni, Bütschli, 1082.															x												
Henneguya zschokkei, (Gurley, 1894)		x																									
Henneguya tegidensis sp.nov.(Nicholas & Jones 1959)																								x			
Henneguya psorospermica, Thelohan, 1895.									x				x	x	x												
Henneguya oviperda, (Cohn, 1895)													x			x											
Ichthyophthirius multifiliis, Fouquet, 1876.						x													x								
Trichodina domerquei sub.sp.domerquei Haider,1964.												x															
Trichodina temidens Faure-Fremiet												x															
Tetraonchus monenteron Diesing, 1858.													x	x	x	x											
Tetraonchus borealis (Olsson, 1893)																	x										
Dactylogyrus crucifer Wagener, 1857.			x		x	x	x																				
Dactylogyrus sphyrna Linstow, 1878.			x		x	x																					
Dactylogyrus nanus Dogiel & Rychowsky, 1934.			x																								
Dactylogyrus similis (Wegener, 1909)					x	x																					
Dactylogyrus suecicus (Nybelin, 1937)						x																					
Dactylogyrus wunderi (Rychowsky, 1931)							x																				
Dactylogyrus cordus Nybelin, 1936.		x																									
Dactylogyrus tuba Linstow, 1878.		x																									
Dactylogyrus vistulae Prost, 1957.	x																										
Dactylogyrus folkmanovae Ergens, 1956.	x																										
Dactylogyrus prostae Molnar, 1964.	x																										
Dactylogyrus sp.								x																			
Gyrodactylus? arcuatus? Rychowsky, 1933.												x															
Gyrodactylus pungitii n.nom.												x															
Gyrodactylus laevis, Malmberg, 1957.								x																			
Gyrodactylus limneus, Malmberg, 1964.								x																			
Gyrodactylus macronychus, Malmberg, 1957.								x																			
Gyrodactylus aphyae, Malmberg, 1964.								x																			
Ancyrocephalus paradoxus, (Cuplin, 1839)									x																		
Discocotyle sagitta, (Leuckart, 1842).																											
Diplozoon paradoxum (Nordmann, 1832.	x	x	x	x		x	x											x		x							

TABLE 8.4: (Continued)

Parasites	S.cephalus	L.leuciscus	R.rutilus			Abramis brama	Phoxinus phoxinus	P.fluviatilis			Gasterosteus aculeatus	E.lucius		T.thymallus		S.trutta		S.salar		Salvelinus alpinus perissi	Coregonus clupeoides pennanti	A.anguillae		
	R.Lugg	R.Lugg	R.Lugg	Llyn Tegid	Rostherne Mere	Shropshire Union Canal	Shropshire Union Canal	Llyn Padarn	Llyn Tegid	Rostherne Mere	Shropshire Union Canal	Llyn Padarn	R.Lugg	Llyn Tegid	Rostherne Mere	Shropshire Union Canal	R.Lugg	Llyn Tegid	Llyn Padarn	Llyn Tegid	Llyn Padarn	Llyn Padarn	Llyn Tegid	Llyn Tegid	Shropshire Union Canal	Llyn Padarn
Allocreadium isoporum (Looss,1894)	x	x	x					x																	
Allocreadium transversale (Rudolphi, 1802)																x									
Sphaerostoma bramae (Müller, 1776)	x	x	x																						
Bunodera lucioperca, Müller, 1776.								x	x	x		x	x												
Diplostomulum spathaceum Rudolphi,1819 (Metacercaria)					x	x	x		x	x		x	x												
Diplostomulum clavatum Nordmann, 1832 (metacercaria)					x				x			x													
Tetracotyle sp.									x																
Asymphylodora kubanicum, Isaichikov, 1923.						x	x																		
Crepidostomum farionis (Müller, 1784)														x	x	x									
Crepidostomum metoecus (Braun, 1900)														x	x	x									
Phyllodistomum folium (Olfers, 1816)								x			x	x		x		x				x					
Prohemistomulum sp. (Ciurea, 1933)																									
Metacercaria (undetermined)								x			x					x									x
Proteocephalus torulosus (Batsch, 1786)	x	x																							
Proteocephalus neglectus La Rue, 1911.																									
Proteocephalus percae (Müller, 1780)									x	x		x										x			
Proteocephalus sp.																							x		
Proteocephalus filicollis, (Rudolphi, 1802)											x											x	x		x
Triaenophorus nodulosus (Pallas, 1781)								juv.	juv.	juv.			x	x	x	x									
Caryophyllaeides fennica (Schneider, 1902)	x	x	x	x	x	x																			
Caryophyllaeus laticeps (Pallas, 1781)	x	x	x			x																			
Ligula intestinalis (L.)				x	x																				
Schistocephalus solidus, (Müller, 1776)											x														
Cyathocephalus truncatus (Pallas, 1781)																x		x							x
Eubothrium crassum (Bloch, 1779)											juv.					x		x		x					
Eubothrium salvelini (Schrank, 1790)											x					x		x							
Diphyllobothrium ditremum (Creplin, 1825)											x			x	x	x		x							
Diphyllobothrium dendriticum (Nitzsch, 1824)																									
Bothriocephalus claviceps (Goeze, 1782)											x														
Rhaphidascaris acus (Bloch, 1779)	x juv.	x juv.	x juv.																				x		
Rhaphidascaris cristata (Linstow, 1872)								x	x		x		x			x									
Spinitectus inermis (Zeder, 1800)													x										x		
Cucullanus truttae (Fabricius, 1794)														x									x		
Cucullanus sp.					x								x										x		
Camallanus lacustris (Zoega, 1776)								x		x													x		
Haplonema tenerrimum (Linstow, 1878)														x	x	x									
Cystidicola farionis Fischer, 1798.																							x		x
Philometra rischta Skryabin, 1917.						x																			
Capillaria sp.																x									

TABLE 8.4:[3] (Continued)

Parasites	S.cephalus R.Lugg	L.leuciscus R.Lugg	R.lugg	R.rutilus Llyn Tegid	R.rutilus Rostherne Mere	Shropshire Union Canal	Abramis brama Shropshire Union Canal	Phoxinus phoxinus Llyn Padarn	P.fluviatilis Llyn Tegid	P.fluviatilis Rostherne Mere	Shropshire Union Canal	Gasterosteus aculeatus Llyn Padarn	R.lugg	E.lucius Llyn Tegid	E.lucius Rostherne Mere	Shropshire Union Canal	T.thymallus R.lugg	T.thymallus Llyn Tegid	S.trutta Llyn Tegid	S.trutta Llyn Padarn	S.solar Llyn Tegid	S.solar Llyn Padarn	Salvelinus alpinus perissi Llyn Padarn	Coregonus clupeoides pennanti Llyn Tegid	A.anguillae Llyn Tegid	A.anguillae Shropshire Union Canal	A.anguillae Llyn Padarn
Neoechinorhynchus rutili (Müller, 1780)	x	x	x	x									x	x				x	x	x		x					
Acanthocephalus lucii (Müller, 1776)	x	x	x		x	x				x	x		x		x	x										x	
Pomphorhynchus laevis (Müller, 1776)	x	x																									
Echinorhynchus truttae, Schrank, 1788.													x				x	x		x							
Echinorhynchus clavula Dujardin, 1845.				x					x			x		x				x		x				x	x		x
Polymorphus minutus (Goeze, 1782)cystacanth.		x	x														x										
Helobdella stagnalis (L.)						x									x												
Hemiclepsis marginata (Müller, 1774).					x					x					x												
Piscicola geometra (L.)	x	x	x			x	x				x					x	x										
Glochidia	x	x				x	x										x										
Argulus coregoni																			x								
Argulus foliaceus (L.)					x	x	x			x	x				x	x		x									
Actheres percarum. Nordmann, 1832.										x																	
Salmincola salmonea (L.)																					x						

TABLE 8.5:

The parasites of R.rutilus from four surveys in Britain, and the presence of these parasites from surveys in the U.S.S.R.

Parasites	R.LUGG			LLYN TEGID			ROSTHERNE MERE			SHROPSHIRE UNION CANAL			Mouth of R.Neman	Nevskaya Guba	Konchosero	R. Ob	R. Kama	Lake Zaysan	R.Yenisey	R. Lena	Aral Sea	Caspian Sea	R. Chu.
	Infected fish No.	%	Intensity of Infection	Infected fish No.	%	Intensity of Infection	Infected fish No.	%	Intensity of Infection	Infected fish No.	%	Intensity of Infection											
Myxobolus müller	Very common																	x					
Myxobolus artus	Uncommon																						
Ichyophthirius multifilius											Present												
Dactylogyrus crucifer	124	39.1	16.3				199	59.2	4.1	578	62.6	13.4	x	x	x	x	x	x	x	x	x	x	
Dactylogyrus sphyrna	3	0.9	1.0				Present (rare)			36	5.9	1.1	x	x	x		x				x	x	
Dactylogyrus nanus	1	0.3	1.0												x		x						x
Dactylogyrus similis							53	15.8	1.4	5	1.7	1.2		x									x
Dactylogyrus suecicus										1	0.17	1.0											
Dactylogyrus wunderi																							
Diplozoon paradoxum	10	3.2	1.0	Uncommon						98	16.2	1.5	x	x		x	x	x	x	x	x	x	
Allocreadium isoporum	40	12.6	43.0										x	x		x	x	x	x				
Sphaerostoma bramae	83	26.2	5.0				194	56.7	3.9	2	0.34	2.5	x		x		x						
Diplostomulum spathaceum (metacercaria)							Present			594	98.5	136.9	x	x	x	x	x		x	x	x	x	
Diplostomulum clavatum (metacercaria)							Present																
Asymphylodora kubanicum										173	28.6	8.2				x					x	x	
Caryophyllaeides fennica	28	8.8	1.8	61	15.6	2.3	Present			32	5.3	2.1					x	x	x	x			
Caryophyllaeus laticeps	11	7.3	3.6							16	2.8	10.4		x	x	x							
Ligula intestinalis				1	0.3	1.0	Present											x			x	x	
Rhaphidascaris acus (juvenile)	100	31.5											x	x	x						x	x	
Cucullanus sp.							Present																
Philometra rischta											Present												
Neoechinorhynchus rutili	1	0.3	2.0	2	0.6	1.0									x	x			x	x			
Acanthocephalus lucii	3	0.9	1.0				22	6.4	1.8	16	2.8	1.4											
Echinorhynchus clavula				63	16.1	3.0									x								
Polymorphus minutus	1	0.3	1.0																				
Helobdella stagnalis										2	0.34	1.5											
Hemiclepsis marginata							Present																
Pisicola geometra	6	1.9	1.0							13	2.1	1.0											
Argulus foliaceus							107	31.3		38	6.3	1.2		x						x			
Anodonta sp. (glochidia)											Present			x									
	Personal observations			Chubb, 1961.			Rizvi, 1964.				Mishra, 1966.		Taken from Dogiel (1958) "Parasitology of Fishes".										

hosts' geographical distribution e.g. Russian workers found Neascus cuticola only in southern regions i.e. the Caspian and Aral Seas and lake Zaysan; Pa-laeorchis unicus, P.incognitus and Coitocoecum skryabini were only found in rivers draining to the Black Sea, the Neman and the West Dvina. A decrease in the number of parasites in R.rutilus was noted from the Yenisey (west) to the Lena (east). This fact has been noticed in other Siberian cyprinids which also seem to lose certain species the further eastwards they were found. A relationship between latitude and distribution of fish parasites was noted by Petrushevski and Bauer (1948), and they divided the parasites occurring in Siberian rivers into three groups:-

1. Parasites present along the length of the river.
2. Parasites only present in the northern regions, i.e. near the mouth of the river
3. Parasites present only in the southern regions i.e. near the source of the river.

The small area of Britain compared to the U.S.S.R. makes it impossible to study the influence of latitude and longitude on the composition of the parasite fauna of fish in this country. It was possible, however, from the surveys in this country and those in the U.S.S.R. to place the parasites of R.rutilus into two main categories:-

1. Parasites distributed throughout most of the localities where the host is found. These may be subdivided:-

a) Non specific, widely distributed species, e.g

M.mülleri (M.bramae)

D.paradoxum

A.isoporum

S.bramae

D.spathaceum

C.fennica

C.laticeps

R.acus (juvenile)

N.rutili

A.lucii

b) Species strictly specific to R.rutilus, e.g.

D.crucifer

D.sphyrna

2. Parasites that are only present when the host is found in the fringe areas of its distribution, or in unusual environments e.g. N.cuticola; P.unicus, P.incognitus, C.skryabini.

It may therefore be stated that the typical parasite fauna of R.rutilus would be that found in those hosts located in the centre of the geographical range, and that the typical parasite fauna is modified in proportion to the distance of the host from this central range, making a proviso for the effects of human intervention.

The effect of the position of the host within its geographical

range is one of the many factors influencing the parasite fauna. These many factors may be collectively termed the host specificity which has been defined by Shulman (1964) as being

> "historically formed, ecologically modified, maintained by natural selection and fixed by heredity".

Chubb (1963) supported the statement by Wisniewski (1958) that the parasite fauna of a body of water may be related to the character of the body of water, but also pointed out

> "the importance of the degree of host specificity of the parasites throughout their life cycle .... for it is this intimate relationship between host and parasite and host and environment which determines the character of both free living and parasitic fauna".

This conception of the phenomenon of host specificity as the complex interrelationships between host, parasite and environment therefore forms the basis, and must be of primary consideration in all investigations on the ecology of parasites. The present survey examines the incidence, intensity of infection and the seasonal dynamics of parasites from five species of fish. This is only one aspect of a complex situation, but this information does provide a basis for further studies on more specialised aspects of the subject.

REFERENCES

DOGIEL, V.A. 1958 Ecology of the parasites of freshwater fishes, in 'Parasitology of Fishes'. Oliver and Boyd Ltd. Translation, 1961.

PETRUSHEVSKI, G.K. and BAUER, O.N. 1948 Zoogeography of fish parasites of Siberia. Bull.Inst.Freshw.Fish, Leningr. 27.

SHULMAN, S.S. 1954 On the specificity of fish parasites. Zool.Zh. 33 (1) : 14-25.

CHUBB J.C. 1963 On the characterization of the parasite fauna of the fish of Llyn Tegid. Proc.zool.Soc. Lond. 141 : 609-621.

WISNIEWSKI, W.L. 1958 Characterization of the parasitofauna of an eutropic lake (Parasitofauna of the biocoenosis of Druzno lake - part I. Acta. Parasit. Polon. 6: 1-64.

ACKNOWLEDGEMENTS

I would like to thank Professor R. J. Pumphrey in whose Department this work was undertaken. I am also greatly indebted to my supervisor Dr. J. C. Chubb for all his advice and encouragement.

I would also like to thank Mr. Staite and the bailiffs of the Wye River Authority for the organisation of the sampling trips, without which this work would not have been possible, and Lord Hereford for permission to fish the River Lugg at Hampton Court.

I am also grateful to Mr. J. M. Hellawell for help in sampling and for data he supplied on the biology of the fish; Mr. W. Irvine for the excellent production of plates and figures; Dr. P. Hull (Genetics Department, University of Liverpool) for his patience and valuable assistance with the statistical analyses; Dr. T. Pearson and Dr. E. Korn (Department of Zoology, University of Liverpool) for the translation of foreign literature; Dr. Z. Kabata (University of British Columbia, Vancouver) and Dr. J. Lom (Institute of Parasitology, Academy of Sciences, Czechoslovakia) for help in the identification of Myxosporidia; Dr. A. V. Gussev (Zoological Institute, Academy of Sciences Leningrad) for the confirmation of the identification of dactylogyrids; Dr. C. K. Kennedy (Department of Zoology, University of Exeter) for the identification of caryophyllaeids.

I am also grateful to the S.R.C. for the provision of a grant for three years during which time this research was undertaken.