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PARASITES OF TROUT AND PERCH IN MALHAM TARN

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Introduction

Malham Tarn, by virtue of its isolation, altitude, climate and water chemistry, is in many respects an unusual lake, and thus of particular interest to limnologists. It has a small catchment area, one main inflow (Tarn Beck), and an outflow stream that disappears underground (Holmes, 1965) and thus prohibits colonization upstream. It is very alkaline, with high concentrations of calcium carbonate which precipitates out, accumulates on the bottom and encrusts the aquatic plants (Lund, 1961; Holmes, 1965). Several aspects of the biology of its flora and fauna have already been studied and documented, and a general account of its natural history has been given by Holmes (1965). In this and an earlier paper (Holmes, 1960*a*) data on the biology of the fish, together with notes on their parasites, were presented. At that time, however, no stocking of trout had taken place for several years and the trout population was being maintained by natural spawning only: the information presented on the perch related almost exclusively to numbers caught and their fluctuations, and the data on the fish parasites were fragmentary and incomplete. Since then a management programme for the fishery has been implemented, and trout have been stocked regularly (see Burrough and Kennedy, 1978), so that the condition of the fishery now may be very different to that at the time of Holmes' publications.

Although six species of fish occur in the Tarn, the two most interesting from a biological and angling viewpoint are the brown trout *Salmo trutta* and perch *Perca fluviatilis*. The other four species, bullhead (*Cottus gobio*), stoneloach (*Noemacheilus barbatulus*), stickleback (*Gasterosteus aculeatus*) and minnow (*Phoxinus phoxinus*), are of no angling interest and have not been examined for parasites. In order therefore to ascertain the current state of the fishery, a survey of the trout and perch was carried out during the summer of 1977. The results of the studies on the fish themselves are presented elsewhere (Burrough and Kennedy, 1978 and *in press*): this present paper is concerned with the parasites of the fish.

The parasite community forms an integral part of any ecosystem. The parasites live within or upon the free-living animals, their hosts, and rely upon the feeding or spatial relationships between the host species for transfer from one to the other. Any deleterious effects they have upon individual hosts will have an influence upon the host population. Knowledge of the parasite community is as essential to an understanding of an ecosystem as is knowledge of the free-living community. The paper aims to introduce the fish parasites to fishermen and biologists working on the Tarn who would otherwise be unfamiliar with this component of the fauna, and to indicate how a knowledge of the fish parasites can provide information about the biology of the fish themselves, about the feeding relationships between various members of the free-living community, and about the overall productivity of the lake.

COLLECTION OF MATERIAL

All fish were caught in July 1977. The majority were taken in gill nets, and a few by rod and line. Nets were set, generally overnight, in all parts of the lake, but especially off the eastern boathouse on the north shore. Altogether 30 trout and 62 perch were examined for parasites. Fish were taken back to the Field Centre as soon as possible after capture, and examined immediately. They were searched thoroughly for parasites, particular attention being paid to the external surface, gills, eyes, swim bladder, body cavity, bladder and alimentary tract. Blood was not examined.

COMPOSITION OF THE FISH PARASITE FAUNA

The parasites found in the fish in Malham Tarn are listed in Table 1. On the whole the parasite fauna is a very poor one. Only nine species were found altogether, significantly fewer than in the other British lakes for which data are given in Table 5. Trout harboured only six species, which is less than in any other British lake (in Table 5) except Slapton Ley. In the Ley, however, the trout are not regular and permanent members of the lake fauna, but only enter the lake for short periods in summer and spend the rest of the year in the feeder streams (Kennedy, 1975). Perch at Malham harboured only five species of parasite, which is also less than for every other lake (in Table 5) except Slapton Ley. Malham Tarn has the poorest fish parasite fauna in terms of diversity and number of species of all the British lakes studied to date. Some parasite species that might be expected do not occur at all. No protozoans or monogeneans were found. There is a complete absence of intestinal digeneans, including such species as *Crepidostomum farionis* and *C. metoecus* which are otherwise widespread and common in trout throughout the British Isles. *Proteocephalus percae*, a widespread and common parasite of perch, is also absent. No acanthocephalans were found in perch, and this whole group is represented in Malham Tarn by only a single species.

Table 1. *The fish parasites of Malham Tarn*

Parasite species	Site in host	Incidence (%) of fish	
		Trout	Perch
Platyhelminthes, Digenea			
Diplostomum spathaceum (Rud.)	Lens of eye	66·6	66·1
Diplostomum gasterostei Williams	Humour of eye	76·6	85·4
Tylodelphys clavata (Nordmann)	Humour of eye	0	100·0
Tylodelphys podicipina Kozicka and Niewiadomska	Humour of eye	0	87·0
Platyhelminthes, Cestoda			
Diphyllobothrium dendriticum (Nitzsch.)	Body cavity	46·6	0
Eubothrium crassum Bloch	Intestine	83·3	0
Nematoda			
Cystidicola farionis Fischer	Swim bladder	23·3	0
Camallanus lacustris (Zoega)	Intestine	0	64·7
Acanthocephala			
Neoechinorhynchus rutili (Muller)	Intestine	6·7	0
Total species		6	5

This paucity of fish parasite species and the absence of particular species is not associated with the absence or scarcity of intermediate hosts in most instances, since both the plankton and molluscan fauna of the Tarn are rich in species and abundant in individuals (Holmes, 1965). The absence of some species of acanthocephalans may, however, be related to the absence of *Asellus* spp., their intermediate hosts, from the lake. The most likely explanations for the paucity of fish parasite species are the small size of the Tarn and its isolation. In a study of the factors influencing the composition of the parasite fauna of trout, Kennedy (*in press*) has shown that the size of the water body is one of the most important. The smaller the lake, the fewer the number of parasite species harboured by trout. Malham Tarn is the smallest of the lakes listed in Table 5, and so would be expected to contain the least number of parasites in trout. This would be further accentuated by the fact that the great majority of trout are stocked fish: they have been reared in hatcheries where parasites are controlled, and thus parasites that are more characteristic of young trout, such as protozoans and some monogeneans, would not occur in the Tarn. The isolation of the Tarn, however, is probably also an important factor in determining its parasite fauna. Dissemination of parasites in space is achieved far more often by the movements of the host containing the parasite than by the movements of the parasites themselves (Kennedy, 1976). Thus, in an isolated lake such as Malham Tarn where there is little possibility of fish containing parasites invading the lake from other water bodies, most parasite invaders are likely to be species maturing in birds. It is very significant in this context that over 50% of the parasite species in Malham Tarn complete their life cycle in bird hosts (Table 5). The peculiarities of the composition of the fish parasite fauna in Malham Tarn can thus largely be explained in terms of the nature and isolation of the lake.

The majority of the species present in Malham Tarn shows a distinct preference for a particular host species, and only two species, *Diplostomum spathaceum* and

Table 2. *The life histories of the fish parasites of Malham Tarn*

(a) Parasites with three hosts

Parasite species	First intermediate host	Second intermediate host	Definitive bird host
Diplostomum spathaceum	*Lymnaea peregra* (wandering snail)	Trout, perch	Laridae (gulls)
Diplostomum gasterostei	*L. peregra*	Trout, perch	Anseridae (ducks) and Laridae
Tylodelphys clavata	*L. peregra*	Perch	*Podiceps* spp. (Gt. crested and other grebes)
Tylodelphys podicipina	Unknown (probably *Lymnaea*)	Perch	*Podiceps* spp.
Diphyllobothrium dendriticum	*Cyclops* sp. (Copepod)	Trout	Laridae

(b) Parasites with only two hosts

Parasite species	Intermediate host	Definitive fish host
Eubothrium crassum	*Cyclops* sp.	Trout
Cystidicola farionis	*Gammarus pulex*	Trout
Camallanus lacustris	*Cyclops* sp.	Perch
Neoechinorhynchus rutili	Ostracoda	Trout

D. gasterostei, occur in both fish. The occurrence of these two species at such a high incidence in trout is very unusual. In Slapton Ley neither species occurs in trout (Kennedy, 1975). In Hanningfield Reservoir both species occur in trout (*D. gasterostei* was not identified as such, but specimens of *Diplostomum* occurring in the humour of the eye and presumed to belong to this species were recorded separately from those occurring in the lens, which were identified as *D. spathaceum*), but at a very much lower incidence level than in perch (Wootten, 1974) and experimental investigations have shown that brown trout is not a suitable host for *D. spathaceum* (Betterton, 1974). In other localities *D. gasterostei* is regarded primarily as a parasite of perch and/or stickleback (*Gasterosteus aculeatus*). The specimens from trout and perch of Malham Tarn are morphologically similar to *D. gasterostei* from Slapton Ley and have been presumed to be the same species, but in view of the current uncertainty about the taxonomic criteria to be used in classification of Diplostomulids the possibility remains that they do in fact represent a different species. With the exception of these two species, however, it is possible to recognize within the lake a distinct trout element and a distinct perch element.

The Life Histories of the Fish Parasites

The life histories of the parasites are well known, and are summarized in Table 2. They fall clearly into two groups: that of parasites with three hosts for which the fish is an intermediate host, and that of parasites with two hosts for which fish is the definitive host. Into the first group fall all four species of eye fluke. The first intermediate host for them is a species of pond snail, generally *Lymnaea peregra*. Eggs released by the parasites within the definitive bird host pass into the water with the bird faeces. When the eggs hatch, the released miracidium larva penetrates a snail, where the parasite then undergoes a series of developmental stages. At the conclusion of these another larval stage, the cercaria, is released, and these penetrate fish and locate in their eyes. Within the eye the metacercaria or displostomulum stage remains alive, although unencysted, for long periods (from one to several years). It cannot escape from the fish, and so either dies within the eye or, if the fish is eaten by a suitable bird host, develops into the adult in the intestine of the bird to complete the life cycle. The life cycle of *Diphyllobothrium dendriticum* is similar in some respects. It differs in that the first intermediate host is a planktonic copepod (which ingests the larva) and not a snail, and that fish become infected by eating the infected copepods and not as a result of the parasite escaping into the water and infecting the fish. The life cycles of the species in the second group are very similar. Eggs released from adult parasites in infected fish pass into the water, and are either eaten by the intermediate host or hatch to liberate a larval stage that is eaten by the intermediate host. The parasite then develops within the intermediate host, and the infective larval stage remains within it until the host is eaten by a fish.

Since these parasite life cycles are well known, it is possible to use this knowledge to provide information about some aspects of the biology of the hosts themselves. The high levels of incidence and large numbers of *Diphyllobothrium dendriticum* and *Eubothrium crassum* in trout of all ages (Table 3) indicates that the trout feed intensively upon copepods, the only intermediate host of these parasites. Analysis of the stomach contents of trout (Holmes, 1960*a*, 1965), however, provides no

Table 3. *Changes in the parasite infection levels in relation to the age of the trout*

	Fish age (years)				
	Stocked fish				Native fish
	1+	3+	4+	5+	2+
No. of fish examined	12	11	1	3	3
Diplostomum gasterostei					
% infected	50·0	100·0	100·0	100·0	66·6
Mean worm burden	3	58·7	20	53·6	1·5
Variance	4	1866	–	–	–
Diplostomum spathaceum					
% infected	25·0	90·9	100·0	100·0	100·0
Mean worm burden	3·7	5·3	5·0	8·6	1·6
Variance	9·3	17·3	–	–	–
Diphyllobothrium dendriticum					
% infected	8·3	81·8	100·0	66·6	33·3
Mean worm burden	1·0	15·2	3·0	25·5	5·0
Variance	–	118	–	–	–
Eubothrium crassum					
% infected	100·0	81·8	0	66·6	66·6
Mean worm burden	63·1	19·5	0	5	55·0
Variance	1591	995	–	–	–
Cystidicola farionis					
% infection	50·0	0	0	0	33·3
Mean worm burden	3·6	0	0	0	4·0
Variance	8·6	–	–	–	–
Neoechinorhynchus rutili					
% infection	0	0	0	0	66·6
Mean worm burden	0	0	0	0	2·0
Variance	–	–	–	–	–

indication of this at all as copepods were not recorded in their diet. The presence of *Cystidicola farionis*, by contrast, confirms Holmes' observations that trout do feed extensively upon *Gammarus*. Similarly, the high incidence of *Camallanus lacustris* in perch indicates that these fish are also feeding intensively upon copepods. *Neoechinorhynchus rutili* is found only in naturally spawned fish and never in stocked fish (Table 3). This would suggest that either only native fish feed on ostracods or, and more likely, that infected ostracods do not occur in the Tarn itself but only in the feeder stream, where they are only available to the native trout which are hatched and live in the stream before entering the lake. The high levels of infection with the four species of eye flukes reveal nothing about the diets of the fish, but are consistent with the high mollusc densities in the lake.

The life histories of the parasites also indicate extensive predation upon fish by the birds of the Tarn. Several species of gull can serve as hosts to *Diplostomum spathaceum*. The herring gull, *Larus argentatus*, is the commonest definitive host of this parasite, but as they are not very common on the Tarn it may be that common gulls, *L. canus*, or other species which are more common (Holmes, 1960*b*) are serving instead. Both ducks and black-headed gulls *L. ridibundus* can serve as hosts for *D. gasterostei*, and both are common on the Tarn. Thus the high levels of infection of fish by these two species of parasite indicate extensive predation or scavenging upon both trout and perch by gulls. This is confirmed by the high incidence and levels of *Diphyllobothrium dendriticum*, which also uses gulls as its definitive host. Equally interesting is the absence of *Diphyllobothrium ditremum* from the lake. This species uses particularly divers (*Gavia* spp.) as its definitive host, and its absence from the Tarn can be associated with the virtual absence of this group of birds (Holmes, 1960*b*). The presence at high levels of *Tylodelphys clavata* and *T. podicipina* in perch indicates intensive predation upon perch by grebes. In this locality it must be by great crested grebes, *Podiceps cristatus*, since this species breeds regularly upon the Tarn whereas other species are rare visitors (Holmes, 1960*b*). Some measure of the extent of this predation can be gained from the fact that no more than three pairs of grebes breed upon the Tarn and numbers have varied only between four and nine pairs, i.e. a maximum of 18 birds, yet all the 62 perch examined were infected with *T. clavata* (Table 4) and 87% with *T. podicipina*, whilst the average number of *T. clavata* per fish varies from ten in young fish to 94 in older ones: the whole population being maintained and circulated through between 8 and 18 grebes. Thus the levels of parasitization in the fish reveal extensive predation by birds upon fish, and so an extensive interaction between the fish and avian fauna.

Dispersion of Fish Parasites within the Fish Populations

Within any species of fish the infection by parasites is seldom spread uniformly, as both incidence of infection and abundance of parasites may alter with fish age. The changes in the parasite infection levels in relation to the age of the trout of Malham Tarn are shown in Table 3. The distribution of the parasites here reflects not only the fish age, but also the fish management policy. The majority of trout

Table 4. *Change in the parasite infection levels in relation to the age of the perch*

	Fish age (years)					
	1+	2+	3+	4+	6+ and 7+	8+ to 12+
No. of fish examined	12	11	12	13	10	4
Diplostomum gasterostei						
% infected	83·3	63·6	91·6	92·3	90·0	100·0
Mean worm burden	2·7	2·5	3·4	3·6	3·9	4·0
Variance	2·5	3·6	3·2	3·6	5·7	12·2
Diplostomum spathaceum						
% infected	41·6	63·6	66·6	69·2	80·0	100·0
Mean worm burden	2·0	1·0	1·4	1·6	2·2	3·2
Variance	1·4	0	0·2	0·2	1·7	4·2
Tylodelphys clavata						
% infected	100·0	100·0	100·0	100·0	100·0	100·0
Mean worm burden	10·4	51·4	69·1	84·3	77·5	94·0
Variance	14·4	259·2	566·4	1089	566·4	1169
Tylodelphys podicipina						
% infected	100·0	90·9	100·0	100·0	50·0	50·0
Mean worm burden	13·4	6·6	3·9	3·7	1·0	1·0
Variance	13·7	7·8	7·8	6·2	0	0
Camallanus lacustris						
% infected	0	100·0	50·0	75·0	71·4	33·0
Mean worm burden	0	1·0	1·0	2·6	2·2	7·0

in the Tarn is stocked, as opposed to native, fish. They are obtained from a hatchery, and stocked into the Tarn in spring when they are already 1+* years old. In 1977 stocking of 1,000 trout took place in April: thus fish aged 1+ had only spent about 3 months in the Tarn at the time of the survey. It is clear that the trout become infected with *Diplostomum gasterostei* and *D. spathaceum* soon after stocking, but the infection remains at a low level. There are two periods of infection with both species, in autumn and in spring (Kennedy and Burrough, 1977; Burrough, *in press*). The low levels of infection in the 1+ trout must therefore have arisen from the spring infection. By the time the trout are 3+ (2+ fish were absent in 1977 since no fish were stocked in 1976), they have experienced two autumn periods of infection and three spring ones and since both species of parasite survive in fish for at least a year, both the incidence of infection and the mean parasite burden have increased considerably. In the case of *D. spathaceum*, which lives for several years, the mean parasite burden continues to rise as the fish get older, are exposed to more infection periods and so accumulate parasites. *D. gasterostei*, however, probably does not live as long, and the mean parasite burden does not continue to increase as infection by new parasites is balanced by mortality of old ones. *Diphyllobothrium dendriticum* shows a similar pattern to *Diplostomum spathaceum*. The main period of infection by this parasite is in late summer, so that at the time of the survey the 1+ fish had not been exposed to much infection and both incidence and mean parasite burden were low. After fish have spent two full years in the lake and are 3+, they have been exposed to infection twice and both the percentage infection and mean parasite burden have increased dramatically. Thereafter, since the parasites live for several years, the mean parasite burden continues to rise.

The distribution of *Eubothrium crassum* in trout is in marked contrast to these three species. The infection period is earlier, since 100% of the 1+ fish were infected by the time of the survey, and the percentage infected and the mean parasite burden decrease with the age of the fish. This parasite lives for only a year or less (Wootten, 1972), so that by the time they are 3+ the fish will have lost all of the parasites they acquired in the first year. The lower levels in subsequent years is almost certainly due to the fact that the older the trout are, the less they feed upon planktonic copepods, the intermediate host of the tapeworm. Very similar patterns of distribution of both *Diplostomum spathaceum* and *Eubothrium crassum* respectively were found in brown trout in Hanningfield Reservoir (Wootten, 1972, 1974), where the fish were stocked into the lake at an age of 2. The distribution of *Cystidicola farionis* is more puzzling, as it appears to occur only in native trout and in trout in their first year in the Tarn but in other localities it also infects older fish. Its presence in native trout indicates that it does occur in the Tarn or in its feeder stream and has not been introduced into the lake with the stocked fish. Its intermediate host in Britain is *Gammarus pulex*, which is very local in distribution within the Tarn where the common fresh water shrimp is *G. lacustris*, (Holmes, 1965). *G. lacustris* is also commoner in the diet of trout at Malham (Holmes, 1965), and it may be that the unusual distribution of *C. farionis* is a reflection of spatial and dietary differences between young and old trout. The occurrence of *Neoechinorhynchus rutili* in native trout exclusively suggests that the infection takes place only in the inflow stream to the Tarn, where the native fish spend their first

* The convention for referring to fish ages is 0+ = all fish up to the age of 1, 1+ = all fish aged between 1 and 2 years, etc.

two years of life before entering the lake. Thus the changes in the parasite infection levels in trout of different ages relate closely to the period of infection by the parasite, its life span, and the stocking policy in operation.

The changes in the parasite infection levels in relation to the age of perch are shown in Table 4. The perch in the Tarn are an entirely native population. Perch apparently become infected with *Diplostomum gasterostei* in their first year of life, and thereafter parasite infection and mean parasite burden continue to rise. It can be presumed that the rate of new infections each year is higher than the parasite mortality, perhaps because as the fish increases in size it presents a larger target to the invasive cercarial stage of the parasite. Such a change in the distribution pattern of this species is unusual. In general, although the percentage infection increases throughout the life of the fish, the mean parasite burden rises to a peak in medium-sized fish and then declines (Wootten, 1974; Kennedy and Burrough, 1977). Furthermore, in other localities the overdispersion, indicated by the variance to mean ratio, is very high, whereas in Malham Tarn it is close to unity. These differences add further support to the suggestion that the *D. gasterostei* in the Tarn may in reality not be the same entity as that also called *D. gasterostei* in Slapton Ley and presumed to be *D. gasterostei* in Hanningfield Reservoir. The increase in both incidence and mean parasite burden of *D. spathaceum* with age of perch is similar to the pattern found in perch in other localities and in trout at Malham Tarn, and has a similar explanation.

Perch also clearly become infected with *Tylodelphys clavata* in their first year of life. Thereafter the mean worm burden continues to rise. This species is believed to have a life span of only one year (Kennedy and Burrough, 1977; Burrough, *in press*), and so the higher levels in older fish cannot be due to the continued survival of parasites that infected the fish in previous years. It must instead be due to higher levels of infection in fish of each year-class, presumably again because the older and larger fish present a better target for the infective stages. In other localities the infection level may fall in older fish (Wootten, 1974), or even be more or less independent of fish age (Kennedy and Burrough, 1977; Burrough, *in press*). By contrast, *T. podicipina* is clearly a parasite of young fish. Although fish of all ages are infected, both incidence and especially mean parasite burden decline with fish age. Such a pattern has been reported elsewhere (Wootten, 1974; Sweeting and Powell, 1977). In other localities the infection has often disappeared in fish of 3+ or 4+, but in these localities the overall infection level was much lower than in Malham Tarn. Sweeting and Powell (1977) have suggested selective mortality amongst infected perch as the most likely explanation for this situation, but this explanation does not appear to be very likely at Malham, since the perch population is dominated by older fish (Burrough and Kennedy, 1978) and these still contain the parasites.

The changes in infection with *Camallanus lacustris* follow a different pattern again. Fish only become infected in their third year of life. Thereafter the percentage infection falls, but the mean parasite burden rises. It can only be presumed that this relates in some way to the feeding habits of the perch. It seems likely that as the perch grow older, fewer individuals feed upon copepods, and hence the percentage infection declines: but those that do feed upon them do so more intensively, and hence the mean worm burden increases.

Although the majority of the parasite species increased in abundance with age of the fish, there was no evidence that any of the fish were in any way deleteriously affected by the presence of the parasites. *Diphyllobothrium dendriticum* is known to be harmful to trout at high densities; *Diplostomum spathaceum* is known to be a serious pathogen of trout in fish farm conditions; *D. gasterostei* is thought to be possibly capable of causing host death; and *Tylodelphys podicipina* has also been suggested as a fish mortality agent. In no cases, however, did the changes in parasite infections in relation to the age of the fish in Malham Tarn suggest that there was selective mortality amongst the older and more heavily infected fish.

Comparison with Other British Lakes

Although Holmes (1960*a*; 1965) makes reference to the presence of *Diphyllobothrium norvegicum* (now known to be a synonym of *D. dendriticum*) and *Eubothrium crassum* in the trout of Malham Tarn, he does not provide sufficient information to enable any meaningful comparison to be made between the occurrence of the parasites then and now.

A comparison of the parasite fauna of Malham Tarn with that of some other British lakes is given in Table 5. The most obvious characteristic of the fish parasite fauna of the Tarn, and one that it shares with Slapton Ley, is the paucity of species. The principal reasons for this are probably the same in both cases: both lakes are small and geographically isolated, and both have been subjected to considerable disturbance in the way of management regimes. In the case of Slapton, this is accentuated by the lake being very recent in geological terms (see Kennedy, 1975). There is very little similarity in species composition between the parasite fauna in the two lakes. None of the parasites found in the trout at Malham occur in the trout at Slapton, or vice versa. This undoubtedly relates to the different status of the trout in the two lakes. In the Tarn the trout are a major element of the lacustrine fauna, and contain parasites whose life cycle is completed in the lake itself. In the Ley the trout are primarily inhabitants of the inflow streams: they enter the lake only for short periods in summer, and they contain parasites whose life cycle is completed in the inflow streams and not in the lake itself. The perch contain two species in common, *Diplostomum gasterostei* and *Tylodelphys clavata*. At Malham the perch are also infected with *D. spathaceum*, but although this parasite is abundant in Slapton Ley it does not appear to infect perch there (Kennedy, 1975). The reason for this is not known. The absence of *T. podicipina* from Slapton Ley is probably fortuitous. The parasite could only enter the lake with great crested grebes: the grebe population has only recently become re-established there (Kennedy and Burrough, 1977): and it would appear to be a matter of chance that the original colonizers brought with them *T. clavata* but not *T. podicipina*, whereas the grebes at Malham contain both species.

The parasite fauna of Malham Tarn is unusual in other respects. Attention has already been drawn to the fact that there is extensive interaction between the fish and the birds of the Tarn and that the proportion of helminth species completing their life cycle in birds in the Tarn is very high indeed when compared with other British lakes (Table 5). It has been suggested that this is not surprising, in that this must be one of the primary ways in which fish parasites can invade isolated lakes. The situation is surprising, however, in another context: that of the characterization of a lake by its parasite fauna. This concept is discussed in some

Table 5. *Comparison of the metazoan fish parasite fauna of Malham Tarn with that of some other British lakes*

	Malham Tarn (Yorks)	Slapton Ley eutrophic (Devon)	Loch Leven eutrophic (Kinross)	Hanningfield Reservoir eutrophic/ mesotrophic (Essex)	Rostherne Mere eutrophic (Cheshire)	Bala Lake mesotrophic (Merioneth)	Llyn Padarn oligotrophic (Caerns.)
No. of species in trout	6	4	16	13	A	15	16
No. of species in perch	5	4	10	10	10	9	A
Total no. of helminth species	9	15	25	27	16	30	32
No. completing cycle in birds	5	4	9	10	4	5	5
% completing cycle in birds	55·5	26·6	36·0	37·0	25·0	16·6	15·6
Data from	Present survey	Kennedy, 1975	Campbell, 1974	Wootten, 1973	Chubb, 1970		

detail by Kennedy (1975) in relation to Slapton Ley. The basic argument is that just as it is possible to recognize an oligotrophic lake fauna and a eutrophic lake fauna, so also is it possible to recognize an oligotrophic and eutrophic parasite fauna and therefore if the trophic status of the lake is known, it should be possible to predict the species of parasite present (Chubb, 1970). A development of this concept was proposed by Esch (1971), who considered that the nature of the predator-prey relationships served as the best biological index for predicting the structure of a parasite fauna in any given lake. He demonstrated that in oligotrophic lakes there was a greater diversity of parasite species, but that the majority of the parasites utilized fish as their definitive hosts since these were the major predators in this type of lake. In eutrophic lakes, parasite diversity was less but because of the high level of interaction between fish and bird predators, a greater proportion of fish parasites utilized birds as their definitive hosts. It can be seen in Table 5 that although the data from other British lakes support the concepts of Esch (1971), those from Malham at first sight do not. Thus the proportion of parasites completing their life cycle in birds is higher in eutrophic lakes such as Slapton Ley and Loch Leven than in oligotrophic lakes such as Llyn Padarn. The diversity of some eutrophic lakes such as Slapton Ley and Rostherne Mere is indeed lower than that of oligotrophic ones, but there are exceptions to this such as Loch Leven. Of particular interest to the present account, however, is the position of Malham Tarn. The diversity of the parasite fauna is lower and the proportion of parasites completing their life cycle in birds is higher than in any other British lake, and this would suggest that Malham is more eutrophic than any of the other lakes. This is certainly not what would be expected for a high altitude moorland tarn, in view of its geographical situation. It is not, however, too unexpected in view of the peculiar characteristics of Malham Tarn. It is shallow, does not stratify, has a water nitrogen content similar to that of Lake Windermere, and has a very high alkalinity level (Lund, 1961; Holmes, 1965). Both the flora and the fauna are rich and varied, and the variety of phytoplankton, molluscs and leeches, for example, are typical of a eutrophic lake. Thus, the free-living biota of the Tarn reveal it to be far more productive than its location and climatic features would suggest. The features of the fish parasite fauna thus strongly support the characterization of Malham Tarn as a productive lake: one more similar to eutrophic lowland lakes such as Loch Leven, Slapton Ley and Hanningfield Reservoir than to oligotrophic mountain lakes such as Llyn Padarn. This serves further to emphasize the individuality of lakes, and the particular interest of Malham Tarn.

Conclusions

The results of this survey have demonstrated yet again the value of studying the parasite fauna of a lake as well as the free-living animals. Knowledge of the fish parasite fauna of Malham Tarn has illuminated several aspects of the interrelationships between the free living animals that are important to an understanding of the ecosystem as a whole. The most significant of these, and one not noted in other publications on the lake, is the extensive predation upon fish that must take place by birds. Not only were birds considered to be a major agent in the introduction of some of the parasitic, and probably also therefore of free-living, animals into the Tarn, but they clearly use the Tarn extensively for obtaining food as well as for roosting. This extensive bird-fish interaction emphasizes the point that no lake, however isolated geographically, can really be considered a closed system: through both the input of nutrient material from inflow streams and surrounding vegetation, and the bird fauna, it is closely interrelated to the surrounding terrestrial ecosystem. The distribution of the parasite fauna has also revealed extensive predation by both trout and perch upon zooplankton, a feature of the biology of these species in the Tarn that has not hitherto been noted. The study has equally confirmed the conclusions based upon a survey of the parasites of the other lake managed by the Field Studies Council, Slapton Ley, that there is considerable variation in the parasite fauna between lakes, and that it is very difficult to characterize lakes on the basis of their parasite faunas. It emphasizes instead the individuality of lakes. Thus, although there is no species of fish parasite unique to Malham Tarn, the particular combination of species present and several aspects of their specificity are not found in any other lake. The parasite fauna clearly indicates that Malham Tarn is more productive and more similar to eutrophic lakes than would have been expected from its situation and climate, but in terms of species composition it is dissimilar to many of the eutrophic lakes, and especially Slapton Ley. Thus, the individual features in the hydrology, history and free-living fauna of a lake determine and are reflected in the individuality of its parasite fauna.

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