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THE NATURAL HISTORY OF SLAPTON LEY NATURE RESERVE

VIII. THE PARASITES OF FISH, WITH SPECIAL REFERENCE TO THEIR USE AS A SOURCE OF INFORMATION ABOUT THE AQUATIC COMMUNITY

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INTRODUCTION

ALTHOUGH the flora and fauna of Slapton Ley Nature Reserve has been fairly well documented, most attention has so far been directed towards the most conspicuous elements of the natural history. Even amongst the fish in the Ley, only perch, *Perca fluviatilis*, have been investigated in any detail. The parasite community of the reserve as a whole, including both aquatic and terrestrial species, has been examined by Canning et al. (1973), who have provided a useful species list, with notes on the life histories of many species. Although their study includes many of the fish parasites, it was not, and was not intended to be, comprehensive. It recorded only those parasites found on field courses at one time of year, the findings were selective, and the section on the fish parasites formed only a part of a much wider study.

The parasite community, however, forms an integral part of any ecosystem. It is superimposed upon the free-living community, and the parasites utilize the free-living animals as their intermediate and definitive hosts, frequently relying upon the feeding relationships between the hosts for transfer from one to the other. A detailed study of the parasite fauna should therefore be as essential a part of the study of the dynamics of any community as is the study of the free-living members of the community themselves. Primarily for this reason, regular monthly observations on the parasites of the fish of Slapton Ley were started at the same time as the studies on their fish hosts were being intensified.

A knowledge of the parasite community of a habitat can, however, be very informative for other reasons. If the life cycles and ecology of the parasites are reasonably well known, then it is possible to deduce information about the free-living community. At its simplest, the presence of a parasite provides information about the spatial and feeding relationships of its host species. It may further provide evidence of host movements and behaviour, and about the inter-relationships between the community under study and neighbouring communities. Knowledge of the parasite community may also assist in the classification and characterization of the habitat under study, in revealing its history and the changes that have taken place within it.

The aim of this paper is to show how a knowledge of the fish parasites of Slapton Ley can be used to provide information about the fish of the Ley and about the free-living community of the lake. During the study it became apparent that some of the information also shed light upon the history of the Ley. The results of the regular observations on the fish parasites will be published elsewhere; this account is intended only to introduce the fish parasites to workers on the Ley and to indicate some of the ways in which a study of the parasite community can be of much wider interest and significance to students.

COLLECTION OF MATERIAL

The fish were captured in various ways. Some specimens of all species were obtained from anglers' catches. Perch were caught in perch traps as part of the regular trapping programme. Pike, *Esox lucius*, were taken in gill nets set at irregular intervals throughout the year. The majority of roach, *Rutilus rutilus*, and rudd, *Scardinius erythrophthalamus*, were captured by seine netting. The rest were taken in traps. Eels, *Anguilla anguilla*, were captured by electric fishing. *Gasterosteus aculeatus*, three-spined sticklebacks, were caught in stickleback traps. Trout, *Salmo trutta*, were caught in seine hauls in small numbers throughout the summer.

The fish were caught throughout the year, though chiefly in summer. Most perch traps were set in the Higher Ley and in the Graveyard. Pike nets were set off the shores E_1 and E_2 (Mercer, 1966), near the boathouse or in Ireland Bay. Seine netting was along the stony part of the E_2 shore. Electro-fishing was by the boathouse and sticklebacks were trapped in the area of the causeway, E_3 and G_1.

Wherever possible, fish were taken back to Slapton Ley Field Centre or to the laboratory and either examined at once or deep-frozen. They were then searched thoroughly for parasites, particular attention being paid to the external surface, gills, eyes and alimentary tract, as described by Chubb (1963).

THE COMPOSITION OF THE FISH PARASITE FAUNA

The list of parasites recorded from the fish of Slapton Ley is in Table 1. This includes all the records published by Canning et al. (1973), many of which have been confirmed and amplified, as well as new records resulting from the present study. The parasitic leeches have been omitted. Both *Piscicola geometra* and *Hemiclepsis marginata* are known to occur in the Ley, but they have nearly always been found on stones and not on the fish themselves. They are known, however, to be able to occur on all the fish species present in the Ley (Kennedy, 1974).

The identification of the larval digeneans (a sub-class of flatworms) merits further comment. Canning et al. (1973) recorded only *Diplostomum spathaceum*, but reported it in a wide range of species, in both the lens and humour of the eye. They recognized, however, that perch were infected only in the humour and roach only in the lens. Identification of diplostomulids is notoriously difficult, and none of those in the Ley have had their life history studied experimentally at all stages. Nevertheless, current opinion (Sweeting, 1971; Blair, pers. comm.) inclines to the view that *D. spathaceum* occurs only in the lens of fish, whereas the species occurring in the humour is *D. gasterostei*. The two species are otherwise apparently indistinguishable in the larval stage in fish. The site of occurrence alone has therefore been accepted as evidence of specific identity in this study. *Tylodelphys*[*clavata*] is here reported from the Ley for the first time, and there is clear evidence (p. 184) that it has only recently appeared in the lake. Precise identification of species within this genus can again only be made as a result of experimental studies, which have not been carried out. Whilst there is no doubt that the species belongs in the genus *Tylodelphys*, it differs in some respects from *T. clavata* as found in other parts of Britain and is more like *T. conifera*. Because of the uncertainty of specific identification, the specimens have been ascribed to *T. clavata* until evidence to the contrary is forthcoming.

This list of parasites shows several interesting features. The majority of parasites are fairly specific; 57 per cent are monospecific and occur in one species of host only, and a further 26 per cent occur only in two species of fish. Only a few species occur in more than two fish and even these may show preferences. Rudd is clearly not a suitable host for *D. spathaceum*, and *D. gasterostei* prefers perch. Only *Argulus foliaceus* show little preference, apart from being absent from eels, and this species will be considered elsewhere (Towner, in press). Whereas the parasite fauna of some fish is similar, roach and rudd for example having 6 species in common, the fauna of others is very characteristic. Thus, apart from *A. foliaceus*, all the species found in trout occur in no other fish. Despite the widespread occurrence of both the fish and the parasite species throughout the lake, the parasites show distinct preferences for particular hosts. Since in this habitat this is unlikely to be due in most cases to lack of opportunity for host and parasite to make contact, it is probably due to differences in the susceptibility of the fish themselves to parasitic infection. It is thus possible within the lake to recognize clearly a trout element in the parasite fauna, comprising *Crepidostomum metoecus*, *Cystidicoloides tenuissima* and *Echinorhynchus truttae*, and an eel element comprising *Acanthocephalus lucii* and *Ergasilus gibbus*. The majority of the remaining parasites form a coarse fish or cyprinid element, although some species such as *Proteocephalus filicollis* are clearly associated with other fish families. The situation in Slapton Ley is therefore very similar to that in Lake Bala, where Chubb (1963) was also able to recognize salmonid, anguillid and cyprinid elements in the parasite fauna.

The other interesting features of the list in Table 1 are the general paucity of the

Table 1. *The fish parasites of Slapton Ley*

Parasite species	Fish species						
	Trout	Perch	Pike	Rudd	Roach	Stickle-back	Eel
Protozoa							
Trichodina sp.	A	P	A	A	P	A	A
Trypanosoma remaki	A	A	P	A	A	A	A
T. percae	A	P	A	A	A	A	A
T. granulosum	A	A	A	A	A	A	P
Cryptobia borelli	A	A	A	A	P	A	A
Myxobolus sp.	A	A	A	P	P	A	A
Monogenea							
Dactylogyrus vistulae Prost.	A	A	A	P	P	A	A
Neodactylogyrus sp.	A	A	A	P	P	A	A
Tetraonchus monenteron	A	A	P	A	A	A	A
Digenea							
Crepidostomum metoecus	100%	A	A	A	A	A	A
Diplostomum spathaceum L.	A	A	33%	19%	77%	A	80%
D. gasterostei L.	A	98%	A	A	A	42%	A
Tylodelphys clavata L.	A	70%	P	A	42%	A	A
Cestoda							
Proteocephalus filicollis L.	A	A	A	A	A	28%	A
Caryophyllaeus laticeps	A	A	A	A	1%	A	A
Caryophyllaeides fennica	A	A	A	3%	11%	A	A
Ligula intestinalis L.	A	A	A	A	3%	A	A
Nematoda							
Cystidicoloides tenuissima	100%	A	A	A	A	A	A
Acanthocephala							
Acanthocephalus clavula	A	P	P	A	P	P	A
A. lucii	A	A	A	A	A	A	P
Echinorhynchus truttae	P	A	A	A	A	A	A
Crustacea							
Ergasilus gibbus	A	A	A	A	A	A	95%
Argulus foliaceus	70%	75%	90%	70%	70%	14%	A
Totals 23	4	6	6	6	12	4	4

L = larval stage; P = present but incidence not determined; A = absent parasite fauna and the absence of certain species. If the total number of species from Slapton Ley is compared with the totals from fish from some other British Lakes (Table 2), it is found to be smaller than for all except Rostherne Mere. In Rostherne, however, only 3 of the 10 fish species were examined for parasites, whereas at Slapton all species present were examined, and it seems likely that the total of parasites at Rostherne will be found to be greater. When it is also considered that four of the species found in roach are either specific to this fish or clearly prefer it and so have probably been introduced into the Ley with the roach in recent years, the parasite fauna of the indigenous Slapton fish is probably poorer still. Thus Slapton Ley has the poorest fish parasite fauna in terms of species diversity of all the British lakes studied to date. Some parasite species that might be expected do not occur. In addition to the complete absence of intestinal digeneans and nematodes from all fish except trout, there is a dearth of cestodes that utilize planktonic intermediate hosts. This latter group is represented only by *Proteocephalus filicollis* and *Ligula intestinalis*, which has appeared in the lake only very recently (p. 184). The cestode *Triaenophorus nodulosus* is commonly found in localities where pike and perch occur together, including Lake Bala and Rostherne Mere, but is absent from Slapton Ley despite the presence of both these fish. *Bothriocephalus claviceps*, a common parasite of eels in both river and lake habitats, is also absent. The proteocephalid tapeworms are also poorly represented in the Ley: *Proteocephalus percae* and *P. macrocephalus*, common parasites of lake perch and eels respectively, are not present.

Whilst the absence of many digeneans may be associated with the general poverty of molluscs, their intermediate hosts, in the Ley (Chatfield, 1972), the absence of cestodes cannot readily be associated with any absence of zooplankton, which is both rich and varied. The absence of nematodes is also not easily explicable in terms of absence of intermediate hosts. The one factor that these three groups do share in common is that all reach the adult stage in fish. It is noteworthy that, apart from *C. metoecus* in trout, all the digeneans in the Ley have their adult stage in birds, and one of the two cestodes utilizing planktonic hosts, *Ligula intestinalis*, also reaches sexual maturity in birds. The most probable explanation lies elsewhere than in the absence

Table 2. *The number of parasite species occuring in fish in some British lakes*

Fish	Slapton	Hanning-field	Lake Rostherne	Bala	Padarn	Total for Britain
Brown trout	4	13	A	16	16	63
Perch	6	10	11	10	A	42
Pike	6	A	10	7	A	48
Roach	12	9	10	7	A	53
Rudd	6	A	A	A	A	17
Eel	4	4	A	6	7	23
3-spine stickleback	4	A	A	A	10	40
Other fish species	0	18	0	15	18	
Total parasite species	23	30	20	35	34	
Total fish species	7	8	10	12	6	
Total fish species examined for parasites	7	8	3	8	6	
Data from	Present survey	Wootten, 1973	Chubb, 1970			Kennedy, 1974

The above table excludes leeches and, in the case of Hanningfield, protozoans.

of suitable invertebrate intermediate hosts from Slapton Ley. In geological terms, the lake is very young, having been formed only about 1,500 years ago (Morey, pers. com.), and so it has not had much time to acquire a rich parasite fauna. It has been shown in other countries that young habitats generally have less diverse parasite faunas than older ones (Dogiel, 1961). Slapton Ley is also an isolated body of water. There are few lakes of any size in Devon and Cornwall from which colonization of the Ley could take place and most of those nearest to the Ley contain predominantly salmonid fish. So the Ley is additionally isolated in the sense that it contains a coarse fish fauna in a region dominated by salmonids. Thus only those species of parasite maturing in birds are likely to reach the Ley easily and colonize it. Those maturing in fish are more likely to reach the Ley by the deliberate introduction of fish from other localities, as has happened with the roach and its parasites. The pecularities in the composition of the fish parasite fauna in Slapton Ley can thus be explained in terms of its location and history.

The Life Cycles of the Fish Parasites

The life histories of most of the fish parasites are well known and have been described by Canning et al. (1973). It is therefore possible to use this information to elucidate some aspects of the biology of the hosts. That all the fish trypanosomes utilize the leech *Hemiclepsis marginata* as their vector confirms the fact that this leech feeds on most of the fish species, even though it has not yet been found on any fish in the Ley. The wide diet of roach is revealed by the presence of the parasites *Caryophyllaeus laticeps*, *Caryophyllaeides fennica*, *Ligula intestinalis* and *Acanthocephalus clavula*, which employ benthic oligochaetes, oligochaetes associated with algae, planktonic crustaceans and benthic crustaceans respectively as their intermediate hosts. The presence of *A. clavula* in a wide variety of fish suggests that its intermediate host, *Asellus meridianus*, is preyed upon extensively.

The parasite fauna also indicates extensive predation upon fish by the birds of the Ley. The high levels of infection of fish by the three species of larval digeneans can only be maintained by correspondingly high levels of infections in birds, and this in turn can only be achieved by intensive predation. The high incidence and intensity of infection of *Diplostomum spathaceum* in roach suggests that this fish is an important part of the diet of herring gulls, *Larus argentatus*, the normal definitive hosts of this species. Its presence in herring gulls has been confirmed by Canning et al. (1973). Similarly, the presence of *D. gasterostei* indicates predation on perch by black headed gulls, *Larus ridibundus*. The case of *Tylodelphys clavata* is less clear; its normal hosts are reported to be herons, *Ardea cinerea*, and marsh harriers, *Circus aeruginosus*, the former found on the Ley, but not the latter. If, however, the true identity of this species is *T. conifera*, then great crested grebes, *Podiceps cristatus*, are the normal hosts and must be feeding upon perch. *Ligula intestinalis* can use almost any aquatic bird as host and so provides no information about food pathways. The parasite fauna provides no information about cormorant, *Phalacrocorax carbo*, predation upon fish, despite the large number of cormorants on the Ley. Those examined have been free of any freshwater parasites and have contained only marine species. Whilst this does not prove that they are not feeding on fish in the Ley, it does indicate that they still feed extensively on marine fish. When it is considered that many of the water birds of the Ley also contain parasites that use invertebrates in the lake as their intermediate hosts, then it is clear that, as revealed by the parasite fauna, there is considerable interaction between the avian and the permanently aquatic fauna and the Ley cannot be regarded as a closed aquatic system. Indeed the presence of some of the fish parasites in the Ley also indicates (pp. 184–185) interchange between the avian fauna of the Ley and that of other bodies of water in the region.

The presence of *Acanthocephalus lucii* in eels suggests that the eels sometimes move out of the Ley and into its feeder streams. The intermediate host of this parasite is the crustacean *Asellus aquaticus*, which does not occur in the Ley itself but is known to occur in the River Gara. The parasites of the trout also appear to have been acquired in the streams. As its intermediate host, *Cystidicoloides tenuissima* utilizes mayflies of the genus *Leptophlebia* which do not occur in the Ley but only in fast, stony streams. *Crepidostomum metoecus* may utilize *Gammarus pulex* as intermediate host; it also uses mayflies of the genus *Ephemera*, which are not found in the Ley but only in streams. *Echinorhynchus truttae* also uses *G. pulex*. Although *G. pulex* does occur in the lake, it is much commoner in the streams, and *E. truttae* is normally regarded as a stream species. Thus, apart from *Argulus foliaceus*, all the parasites of trout are probably acquired in the streams flowing into the lake rather than in the lake itself. Within the lake trout do not acquire any parasites except *Argulus*, and this species is not only the least specific but also one of the easiest parasites to acquire. The parasite evidence would therefore suggest that the trout are not permanent residents of the Ley, and, in view of the short life span of their stream parasites and the failure to acquire many lake parasites, that they only spend a short time in it. Probably they move into the lake for part of the summer and return to the streams at other seasons—a fairly common migratory pattern for lake trout.

Dispersion of the Fish Parasites Within Host Populations

Within each species of fish the infection of parasites is not spread uniformly. Both the incidence of infection and the abundance of the parasites may alter with age of the fish; this can clearly be seen amongst the eye flukes, (Table 3). Almost 100 per cent of the fish above 1 year old are infected with the larval digeneans, but the average number per fish continues to rise as the fish ages. These parasites have a life span as long as that of the fish, and so the older the fish, the longer it has been exposed to infection and the more parasites it therefore contains. In addition, the older the fish, the larger it is, and so the greater the chances of the active free-swimming stages of the parasite making contact with it. This rate of increase in parasite numbers tends to decline as the fish grows older as the oldest, and therefore most heavily infected, fish die. The data in Table 3 would thus suggest that roach tend to die off after 3 years old.

Table 3. *Changes in the average number of parasites per fish in relation to the age of the fish*

Host and parasite	Fish age (years)				
	under 1	1+	2+	3+	4+
Perch					
Diplostomum gasterostei	1·1	7·6	9·5	16·2	22·0
Tylodelphys clavata	2·6	1·9	9·8	8·8	15·0
Roach					
Diplostomum spathaceum	1·7	5·9	7·4	35·9	36·5
Tylodelphys clavata	0·7	2·1	2·8	3·9	0·7

Even within a single age class of fish, the infection is not dispersed uniformly. This again is clearly exemplified by the frequency distribution of *Diplostomum gasterostei* in perch (Table 4). Sixty-six per cent of the fish harboured less than 10 parasites each,

Table 4. *The frequency distributions of infections of Diplostomum gasterostei in one age class of perch in autumn 1973*

	Number of parasites per fish							
	0–4	5–9	10–14	15–19	20–24	25–30	31–34	Total fish
Frequency of occurrence	45	10	12	8	3	2	2	82

but 2·4 per cent contained over 30. This sort of frequency distribution is common amongst fish parasites, but the reasons for it are not clear. It may be that some fish are more susceptible to infection than others, either because their behaviour brings them more often into the vicinity of the parasites or because they are physiologically different in some way. In either case, it indicates that not all perch can be regarded as similar in behaviour and physiology but that individual differences do occur. These differences may be of considerable importance. Although only 8·4 per cent of the fish contained over 20 parasites, the parasites in these fish comprised 30 per cent of the total parasite population. Thus, from the point of view of the perpetuation of the parasite population, it is more advantageous for this 8·4 per cent to be the proportion that is preyed upon by the birds. In other words, a large proportion of the parasite population is contained in a small proportion of the fish population, and so the small number of heavily infected fish play a disproportionately large part in the maintenance of the parasite population. If one of these is eaten by a bird, then the fish population is scarcely affected whereas a large part of the parasite population may have succeeded in completing its life cycle. Thus the parasites not only reveal the existence of individual variation within the fish population but rely upon it and indicate the importance of the individual as opposed to the population.

Temporal Changes in the Parasite Fauna

Seasonal changes

The parasite fauna is seldom constant in either incidence or intensity of infection throughout the year. Often it changes in a regular pattern. Such changes are clearly seen in the infection of perch by *Diplostomum gasterostei* (Table 5). Both incidence and intensity of infection are at their highest in summer, decline to a minimum in late

Table 5. *Seasonal changes in the infection of perch with Diplostomum gasterostei*

	Year and month			
	1973		1974	
	June–Sept.	Oct.–Dec.	Jan.–Mar.	Apr.–June
% of fish infected	98	80	72	95
Mean no. of parasites per fish	19·7	7·1	4·0	14·4
Maximum no. of parasites per fish	92	33	22	85

winter, and then rise again in spring. The rise in spring and summer may be due to new infections, since most cercariae are released from their snail hosts only in the warmer months. The decline in winter is less easy to explain. It is not due to the death of the parasites within the fish, since they are able to live as long as the fish and no dead eye flukes have been found. The decrease in the mean and maximum number of parasites per fish would suggest that the decline is due to the disappearance in winter of the larger and more heavily infected perch. This could in turn be due either to natural mortality at the most difficult season, or to some change in the behaviour of these fish such that they were no longer being caught in the traps. Neither explanation is to be preferred at present, but the change in the parasite fauna provides conclusive evidence for a seasonal change of some sort amongst the older members of the perch population.

Long term changes

Since the Ley has been studied by the London University Parasitology field course for a number of years, some of the longer term changes in the parasite fauna have been recorded. The most conspicuous concern *Ligula intestinalis* and *Tylodelphys clavata* (Table 6). Neither species was present in the fish of the Ley until 1973, when

Table 6. *Long term changes in the abundance of some fish parasites*

	Date and month			
	until 1972	1973	1974	
			Jan.–Mar.	Apr.–June
Ligula intestinalis No. of infected fish found	0	1	3	5

	until 1972	1973		1974	
		Jan.–June	July–Dec.	Jan.–Mar.	Apr.–June
Tylodelphys clavata					
% infection	0	0	70	47	54
Mean no. of parasites per fish	0	0	8·3	3·5	3·7

both species were first found,—a single *Ligula* in 1973, followed by three in February 1974 and 5 specimens since*. The infection is thus clearly establishing itself and building up, and there seems every likelihood that it will continue to increase and may even reach epidemic proportions. In view of its pathogenic effects, it is likely to have a pronounced effect upon the fish population in time. *Tylodelphys* also first appeared in fish in 1973, although it must have entered the Ley at some time previous in order to have completed its development stages in the snails. From the rapid rise in incidence it must have been widely dispersed throughout the lake, either by the initial introduction of eggs at several points or by the cercaria dispersion. In either case, it has built up rapidly, and the changes since have been largely seasonal in nature. Thus, somewhere about the end of 1972, two new species of parasite have been introduced into the Ley.

* 1975 samples show an average of 40% roach infected.

Since no fish were introduced at this time (roach having been introduced some years earlier), the source of the introduction must have been birds. Some change must therefore have taken place in the bird population to cause birds from another locality to move to the Ley. Unfortunately the bird population has not been monitored and so we are not sure what the change was. There are however two possibilities. The cormorant population has increased in the past few years, but, as mentioned earlier (p. 181), neither of the parasites, nor any other freshwater ones, have been found in them. The other possibility relates to the great crested grebes. Whilst these have often visited the lake, in 1973 and again in 1974 a pair bred there for the first time for many years. If it could be shown that either parasite matures in grebes in Slapton Ley, or that *T. clavata* is in fact *T. conifera**, for which grebes are the normal host (p. 181), then the circumstantial evidence for the grebes as the source of the introduction would be very strong. Even in the present state of knowledge, the synchronous timing of the introduction and the grebes taking up residence is very suggestive.

Characterization of the Parasite Fauna of Slapton Ley and Comparison with Other British Lakes

The concept of the characterization of a lake by its parasite fauna was propounded by Wisniewski (1958). In his view, the character of the water body influences and determines the parasite species present. The most important feature is the availability of oxygen, i.e. the trophic status of the lake. Just as it is possible to recognize an oligotrophic (no oxygen deficit) or eutrophic (oxygen deficit) fauna, so also is it possible to recognize an oligotrophic or eutrophic parasite fauna. Wisniewski therefore believes it possible to predict the species of parasites in lakes if the trophic status of the lake is known. This view has received considerable support from the studies of Chubb (1963, 1970) on some British lakes. Accepting that the combination of the available host species and the degree of specificity shown by the parasites will be largely responsible for the presence or absence of a parasite in a habitat, Chubb goes on to show that oligotrophic and eutrophic parasite faunas can be recognized as such and can be distinguished in mesotrophic (some oxygen deficiency) lakes such as Lake Bala. He recognizes, however, that some species, such as *Argulus foliaceus* and *Acanthocephalus clavula*, occur on a wide range of fish species in all types of lakes and that the absence of a species may be due to the absence of a host or to its inability to colonize the lake.

This concept has been challenged by Halvorsen (1971). He believes that the parasite fauna of fish contributes little to the characterization of lakes, since the same fish species has similar parasites in water bodies of widely different trophic status. In his view the parasite fauna depends upon the fish species present, and the relationship between hosts and parasites is constant despite limnological and geographical differences. His view is supported by Wootten (1973), who showed that in Hanningfield reservoir the parasite fauna is not characteristic of the basically eutrophic nature of the water body because of the presence of trout and hence of a large oligotrophic component of the parasite fauna. The composition of the parasite fauna in this locality was influenced chiefly by the composition of the fish species and by the presence of invertebrates capable of acting as intermediate hosts.

An alternative approach to this problem has been proposed by Esch (1971).

* *T. conifera* has just been reduced to synonomy with *T. clavata*.

After studying the parasites in a range of lakes of differing trophic status, he concluded that the nature of the predator-prey relationships should serve as the best potential biological index for predicting the structure of a parasite fauna in any given aquatic ecosystem. He showed that in oligotrophic lakes there was a greater diversity of parasite fauna, but that the majority of parasites reached maturity in fish hosts since fish were the most important tertiary predators in this type of system. In eutrophic lakes by contrast, parasite species diversity was lower, but, because of the much greater degree of interaction between the aquatic and terrestrial communities, a greater proportion of the parasites attained maturity in birds, which were here the dominant tertiary predators.

If we examine the parasite fauna of Slapton Ley to see how this fits into these current ideas on lake characterization, we find that, as judged by its physicochemical features and by the flora and fauna of the free-living community, Slapton Ley must be considered a eutrophic lake. The extent of the interaction between the birds and the fish of the lake has already been emphasized, and this also is typical of its eutrophic condition. The proportion of helminth parasites completing their life cycle in birds is compared with that of other British lakes in Table 7. Few species in the Ley complete their cycle in pike, the only tertiary fish predator, and this proportion is higher in the eutrophic lakes Hanningfield and Rostherne than in lakes Bala and Padarn, and the proportion in Slapton is very close to that of the eutrophic Rostherne Mere. In Hanningfield, Wootten (1973) specifically notes that the dominant group of parasites is the larval digeneans that complete their cycle in birds. The diversity of the parasite fauna is also low in Slapton and in Rostherne Mere, compared to that in lakes Bala and Padarn (Table 2) and to Britain as a whole. The high diversity in Hanningfield is due in part to the presence of trout, and, in this context, it should be considered mesotrophic. Thus the characteristics of the fish parasite fauna in Slapton Ley support the views of Esch (1971) that the predator-prey relationships are of crucial importance in determining the composition of the parasite fauna in each type of water body.

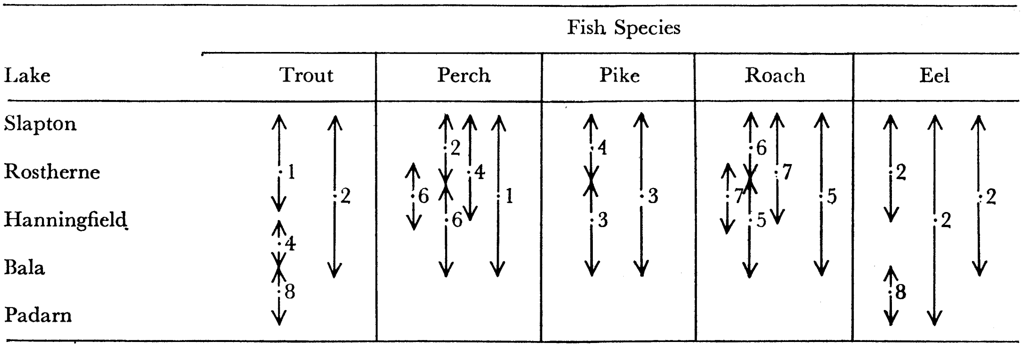
The situation in Slapton supports the views of Chubb (1963) in so far as it is possible to recognize an oligotrophic element, the parasite fauna of trout, and an eel element and a remaining eutrophic or cyprinid element (p. 179). If, however, the parasite fauna of each species of fish in the British lakes is compared on the bases of length of species list (Table 2) and similarity in the composition of their parasite fauna

Table 7. *The proportion of fish helminth parasite species completing their life cycles in birds in some British lakes*

	Lake and status				
	Slapton eutrophic	Hanningfield eutrophic	Rostherne eutrophic	Bala mesotrophic	Padarn oligotrophic
Total no. of helminth species	15	27	16	30	32
No. completing cycle in birds	4	10	4	5	5
% completing cycle in birds	26·6	37	25	16·6	15·6
Data from	Present survey	Wootten, 1973	Chubb, 1970		

(Table 8), then the situation is less clear. Lakes Bala and Padarn are undoubtedly similar, yet have different trophic status, thus supporting the view of Halvorsen (1971). It is clear also that the fauna of roach is reasonably similar in all the habitats, again supporting Halvorsen and contradicting Chubb (1970). On the other hand, the parasite fauna of eels and trout, and to a lesser extent pike and perch, is dissimilar, thus denying Halvorsen's contention that the same fish has similar parasites in water bodies of different trophic status. It is also clear from Table 8 that the parasite fauna of Slapton is not particularly similar to that of Rostherne Mere, despite the similar trophic status of the two lakes. This table does show, however, that the degree of similarity between any two lakes will depend to a very large extent upon which species of fish are present, and to this extent only it supports the views of Halvorsen (1971) and Wootten, (1973), and denies those of Chubb (1970) and Wisniewski (1958).

Table 8. *The index of similarity of the parasite fauna of selected species of fish in some British lakes*



$$\text{Index of similarity} = \frac{\text{No. of species of parasite common to each fish species in both lakes}}{\text{Total no. of species present in each fish species in both lakes}} \times 2$$

Conclusions

The use of parasites to provide information about the free-living community is not new. They have been used extensively by Margolis (1965) to provide additional information about the Pacific salmons and in the many studies using parasites as biological tags (e.g. Gibson, 1972). It adds substantially to our knowledge of Slapton Ley. A study of the fish parasites confirms ideas on the recent origin and isolation of the lake, has clarified the role of trout in the fish community, has indicated the extensive interaction between the lake and the bird fauna, has emphasized the importance of individual fish as opposed to the whole fish population, and has provided evidence for changes in the bird fauna in recent years.

Above all, perhaps, the study has emphasized the variation in fauna between lakes and the individuality of Slapton Ley. Whilst the parasite fauna indicates clearly that it is a eutrophic lake, it is not very similar to the other British eutrophic lakes studied to date, and it does appear that in general terms Halvorsen (1971) was correct in his view that the parasites of fish contribute little to the characterization of lakes. That this is true for Slapton Ley is not due to the same fish species having similar parasites in different bodies of water as Halvorsen suggests, but rather to the parasite fauna of Slapton being so different from that of other lakes. This peculiarity of the Ley can probably be related to its history and isolation, and it is difficult to escape the conclusion that these have played a more important part in the formation of its fish parasite fauna than the presence of particular fish species, the specificity of the parasites or the fact that the lake is eutrophic.

The relative poverty of the parasite fauna is consistent with both the recent age of the lake and its isolation, and the fact that the coarse fish, which are the dominant fish group, are on the very edge of their British distribution range. The parasite fauna of every indigenous species of fish in the lake is poorer than the fauna of the same species in all the other lakes with which it was compared, and this is entirely consistent with what is known about the parasite fauna of hosts at the limits of their distribution (Dogiel, 1964). Halvorsen (1971) did not find this to apply in the River Gloma, where the cyprinids were again at the limits of their range, but in Slapton this trend must perforce be reinforced and amplified by the isolation and age of the habitat. The fish parasite fauna of Slapton Ley thus seems to have been determined very largely by the chance introductions of species. Some have been effected by birds, and the progress of two of them has been recorded in this study.

Others have been effected by fish, and the four species specific to roach, and possibly also some of those found in rudd, must have been introduced with the roach. This investigation has also indicated the extent to which a parasite fauna can change over a very short period as a result of chance introductions, since six species at least, the four specific to roach and the two bird introductions, have only colonized the lake in the past few years. This, together with the peculiarities of the indigenous parasite fauna, and its individuality, casts doubt upon the advisability, value and validity of attempts to characterize the parasite fauna of lakes. It emphasizes instead the importance in the development of a parasite fauna, stressed by Dogiel (1964), of the history and location of the water body and the place of the hosts within their own distribution range.

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