Ann. Zool. Fennici 34: 47–59 ISSN 0003-455X
Helsinki 28 February 1997

Aspects of the biology of diplostomid metacercarial (Digenea) populations occurring in fishes in different localities of northern Finland

E. Tellervo Valtonen & David I. Gibson

Valtonen, E. T., Department of Biological and Environmental Science, University of Jyväskylä, FIN-40100 Jyväskylä, Finland
Gibson, D. I., Department of Zoology, The Natural History Museum, London SW7 5BD, UK

Received 16 May 1996, accepted 20 October 1996

Diplostomid metacercariae were found at a high prevalence and in large numbers in the eyes of a wide variety of fish species from widely differing freshwater and brackish water environments in northern Finland. These parasites were found to infect the following: 21 of 25 fish species, some of which were marine, studied in the oligohaline, brackish waters of the Bothnian Bay, Baltic Sea; all nine fish species studied from a large, oligotrophic lake in NE Finland (Yli-Kitka); and all five studied fish species in a small, hypereutrophic lake (Kuivasjärvi). Diplostomids in the lens of the fishes of the Bothnian Bay, studied during two periods extending over seven years, suggest the presence of a stable and predictable system, despite the extremely narrow transmission window between the first (snail) and second (fish) intermediate hosts. Diplostomids in the lens of fishes from the Bothnian Bay and Lake Kuivasjärvi predominated (> 50% infection in 14 of 21 species) over those from the vitreous body of the eye in most cases, but were much lower (< 18%) in Lake Yli-Kitka. The situation in the vitreous body was quite the reverse, since diplostomids in this site predominated over those in the lens in fishes of Lake Yli-Kitka (> 80% prevalences in five of nine fish species). This difference is considered to be dependent on differences in the piscivorous bird fauna. The fact that diplostomid metacercariae accumulated in the fish, together with the lack of any real seasonal variation, confirms the longevity of these larvae in their fish intermediate hosts. Thus metacercariae form a reservoir which is mainly responsible for the maintenance of diplostomid suprapopulations in these northern latitudes.

1. Introduction

The parasitic mode of existence is very common; in fact, Keymer and Gregory (1992) have estimated that more than 50% of all animals are parasitic in at least some stage during their life-history. Many parasitic organisms have complex life-cycles, which have developed independently in diverse groups (e.g. the phyla Platyhelminthes, Nematoda and Acanthocephala). These complex life-cycles, which may involve one, two or more intermediate hosts, a definitive (final) host and sometimes paratenic hosts, have evolved to facilitate transmission. However, the parasites encounter considerable hazards in harmonising the co-occurrence of larval stages and host in time and space, especially in highly seasonal environments.

Diplostomids, digenean parasites of piscivorous birds, are distributed throughout the Holarctic region and have a complex, three-host life-cycle which involves: i) a free-living larva (miracidium) which hatches from the egg; ii) two asexual generations (parthenitae) in an aquatic snail; iii) a second free-living, motile larva (cercaria) which is released in huge numbers and is involved in transmission to the second intermediate fish host which it penetrates, usually through the gills; iv) an unencysted larva (metacercaria) usually in the eyes (lens, humour or under the retina) of fishes; and v) a sexually mature, hermaphroditic adult in the intestine of piscivorous birds. Metacercariae in the eyes of freshwater fishes can become major pathogens, since infection may lead to a severe ocular pathology associated with cataracts or blindness (Shariff *et al.* 1980, Ieshko & Shustov 1982, Chappell *et al.* 1994) or even death (Bauer *et al.* 1964). Heavily infected fish are lost from the population either through disease or selective predation (Pennyquick 1971, Lester 1977, Kennedy 1981a, 1984).

Some of the mechanisms which have been evolved to enable helminth parasites to survive in sub-Arctic regions have been touched upon by Gibson and Valtonen (1984). Esch and Fernandez (1993) have suggested that complex life-cycles are adaptations to prevent extinctions at the level of a metapopulation (i.e. all of the infrapopulations from a single host species within an ecosystem), although local extinctions may occur. One could speculate that the local extinction of parasites with complex life-cycles could quite easily happen; in the life-cycle of diplostomids in northern latitudes, for example, the transmission window between the first (snail) and second (fish) intermediate hosts is narrow, because cercarial production is regulated primarily by temperature. Cercariae of species of the genus *Diplostomum* emerge into water only at temperatures above 10°C (Berrie 1960, Wootten 1974, Brassard *et al.* 1982, Stables & Chappell 1986) and, according to the latter authors, the optimum temperature for the establishment of metacercariae in rainbow trout *Oncorhynchus mykiss* is 17.5°C, a temperature which tends to occur in the Bothnian Bay region of the Baltic Sea only between mid-July and mid-August. Although we would expect some adaptation in temperature thresholds to suit local conditions, as found by Rahkonen *et al.* (1984) in relation to *Bunodera luciopercae*, this temperature-limited window is supported by observations of the release of *Diplostomum* cercariae at this time from the snail intermediate hosts, *Lymnaea stagnalis* and also *L. peregra,* in two small lakes connected to the Bothnian Bay (Väyrynen 1996). The successful transmission of the parasite to the second intermediate host also requires that these fish be found in the littoral zone where the lymnaeid snails occur during the time of cercarial emission. Furthermore, in northern latitudes, the final hosts (piscivorous birds) are annual migrators, being present only for a limited period of the year during the open water (ice-free) period.

In this study we examine the occurrence, stability and predictability of diplostomid metacercarial metapopulations in the eyes of freshwater fishes in two areas from northern Finland: i) a brackish water area, the Bothnian Bay, NE Baltic Sea, where the salinity is low (2–3‰) and conditions lacustrine, using material collected on a seasonal basis during two periods spanning 7 years (1977–79 and 1983); and ii) a large, oligotrophic lake situated close to the Arctic Circle in NE Finland (1980–1981). Comparative material was also collected from a small hypereutrophic lake connected to the Bothnian Bay (1979–1980). In total, 26 fish species and almost 5 000 fishes were studied. Most previous investigations of diplostomid metacercariae have involved only one or a small number of fish species in a single locality (see e.g. Chubb 1979).

2. Materials and methods

2.1. Study areas

The Bothnian Bay is the most northerly part of the Gulf of Bothnia. It is the least saline (0.5–3.5‰) and most oligotrophic part of the Baltic Sea (Alasaarela 1979). The study

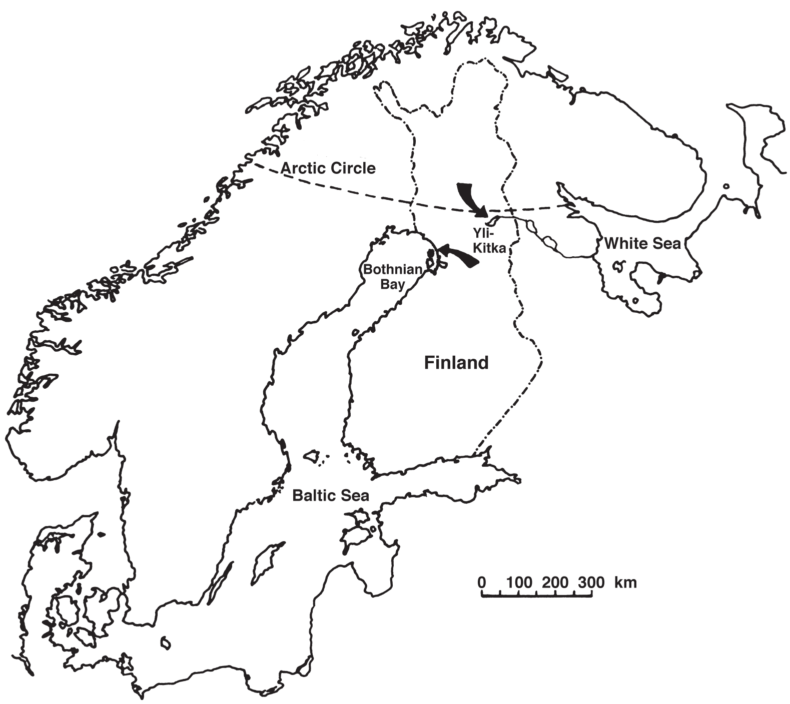

Fig. 1. Map showing the study areas.

area in the north-eastern region of the bay is ice-covered for six months of each year from mid-November to mid-May (Fig. 1). The fish fauna of the Bothnian Bay includes 52 recorded species of which about 30 spawn in the region (Andreasson & Petersson 1982). Most species are of freshwater origin, but some marine species, such as *Zoarces viviparus, Clupea harengus, Myoxocephalus scorpius, Ammodytes tobianus* and *Pomatoschistus minutus*, are able to complete their life-cycles in the Bothnian Bay. Migrating species, such as *Gadus morhua* and *Lampetra fluviatilis*, and occasional visitors also occur (see also Valtonen *et al*. 1989, Valtonen & Crompton 1990).

Lake Yli-Kitka is a 235 km^2 large, oligotrophic lake still in its natural state. It is located at 240 m above sea-level close to the Arctic Circle in NE Finland. This lake is ice-covered for 7–8 months (October–May) of each year. At least 15 freshwater fish species typical of oligotrophic waters may be found in the lake, of which *Coregonus albula* is the most abundant. *C. lavaretus acronius* and brown trout *Salmo trutta* m. *lacustris* also occur here (Hyytinen & Valtonen 1984). The waters of Lake Yli-Kitka drained into the Bothnian Bay in early post-glacial times, but reversed direction to flow into the White Sea following a bifurcation phase. The western outflow route dried up ca. 8 400 BP (Heikkinen & Kurimo 1977).

Lake Kuivasjärvi is located close to the Bothnian Bay and connected to it by a small river of about 2 km in length. It is small (0.84 km^2), shallow (mean depth 1.9 m), covered by ice from late October until early May, and almost hyper-eutrophic (Myllymaa 1978). The fish species inhabiting the lake are perch *Perca fluviatilis*, roach *Rutilus rutilus*, ruffe *Gymnocephalus cernuus*, pike *Esox lucius* and Crucian carp *Carassius carassius*. Fish populations suffer anoxic conditions in winter during the period covered by this study.

2.2. Fish studied

A total of 3 132 fish belonging to 25 fish species was studied from the Bothnian Bay (Table 1) during two periods, 1977–79 and 1983. Samples of the most common species were caught at monthly (open water periods) or bimonthly intervals where possible. The fish were caught by local fishermen working in the relatively shallow NE coastal region (mean depth 11 m) (Valtonen 1983). During the winter months fish were caught using seine nets under the ice. At other times, trawls and occasionally fyke nets were used, together with fingerling traps for sticklebacks.

In Lake Yli-Kitka, 1 026 fish belonging to the nine most common species were studied (Table 1). Monthly or bimonthly samples were collected between March 1980 and May 1981, using seine nets both in open water and under the ice.

In Lake Kuivasjärvi, all of the fish species present, totalling 698 specimens, were studied between May 1979 and August 1980. With the exception of January and February 1980, equal numbers of fish were collected monthly (about 20 perch and roach, but fewer of the other species). However, for the Lake Kuivasjärvi material, only the pooled monthly prevalence and abundance data for each fish species are used.

Both the vitreous body and the lens were examined for diplostomid metacercariae in all fish, except for the period

1977–79 when, in fish from the Bothnian Bay, the lens only was examined. Metacercariae from all the non-lens parts of the eye, including the retina, are included with those from the vitreous body.

The data were analysed using Systat Version 5.0.

3. Results

3.1. Parasite identity

The identification of members of the genus *Diplostomum* Von Nordmann, 1832 has been, and continues to be, a real problem. The majority of species are morphologically very similar and often distinguishable only if processed in a similar manner and by utilizing combinations of metrical data in statistical analyses. The problems are further complicated by nomenclatural difficulties and differences of opinion by authorities on the group: compare, for example, Shigin (1986, 1987) and Niewiadomska (1984, 1986, 1989). In addition, the cercariae, metacercariae and adults have each been the focus of separate taxonomic treatments, and only occasionally have these been related successfully.

The present material was collected at a time when it was usual to consider metacercarial specimens from the lens as "*D. spathaceum*" and those from the rest of the eye (vitreous body and retina) as "*D. gasterostei*" or "*Diplostomum* sp.". Preliminary investigations, using multivariate analysis on metacercariae from a wide range of hosts in the Bothnian Bay region carried out by undergraduate students at The Natural History Museum in London (Gibson *et al.* 1985) indicated the presence of three groups, two from the lens and one from the vitreous body. The majority of the specimens from the lens appeared to resemble the form described by Shigin as "*D. indistinctum*", which would appear to be *D. spathaceum* (Rudolphi,

Table 1. Species and number of fishes examined.

Fish species	Habitat	Bothnian Bay 1977–1979	Bothnian Bay 1983	L. Yli-Kitka 1980–1981	L. Kuivasjärvi 1979–1980
Lampetra fluviatilis	Marine	25	0	–*	–
Clupea harengus	Marine	172	153	–	–
Esox lucius	FW	34	0	35	88
Salmo trutta	FW	37	0	0	–
Coregonus albula	FW	144	133	155	–
Coregonus lavaretus lavaretus	FW	9	0	–	–
Coregonus widegreni/acronius	FW	59	149	232	–
Osmerus eperlanus	Euryh.	222	135	–	–
Rutilus rutilus	FW	192	139	65	209
Leuciscus leuciscus	FW	56	136	0	0
Leuciscus idus	FW	8	0	0	0
Phoxinus phoxinus	FW	32	0	68	0
Alburnus alburnus	FW	42	31	–	–
Carassius carassius	FW	5	0	–	133
Gadus morhua	Marine	8	0	–	–
Lota lota	FW	97	0	18	0
Zoarces viviparus	Marine	20	0	–	–
Gasterosteus aculeatus	Euryh.	156	163	–	–
Pungitius pungitius	FW	47	22	54	–
Myoxocephalus quadricornis	Euryh.	66	46	–	–
Myoxocephalus scorpius	Marine	24	0	–	–
Perca fluviatilis	FW	153	58	171	262
Gymnocephalus cernuus	FW	194	163	228	66
Ammodytes tobianus	Marine	15	0	–	–
Pomatoschistus minutus	Marine	12	0	–	–
Total		1 829	1 329	1 026	658

*0, not studied; –, not present.

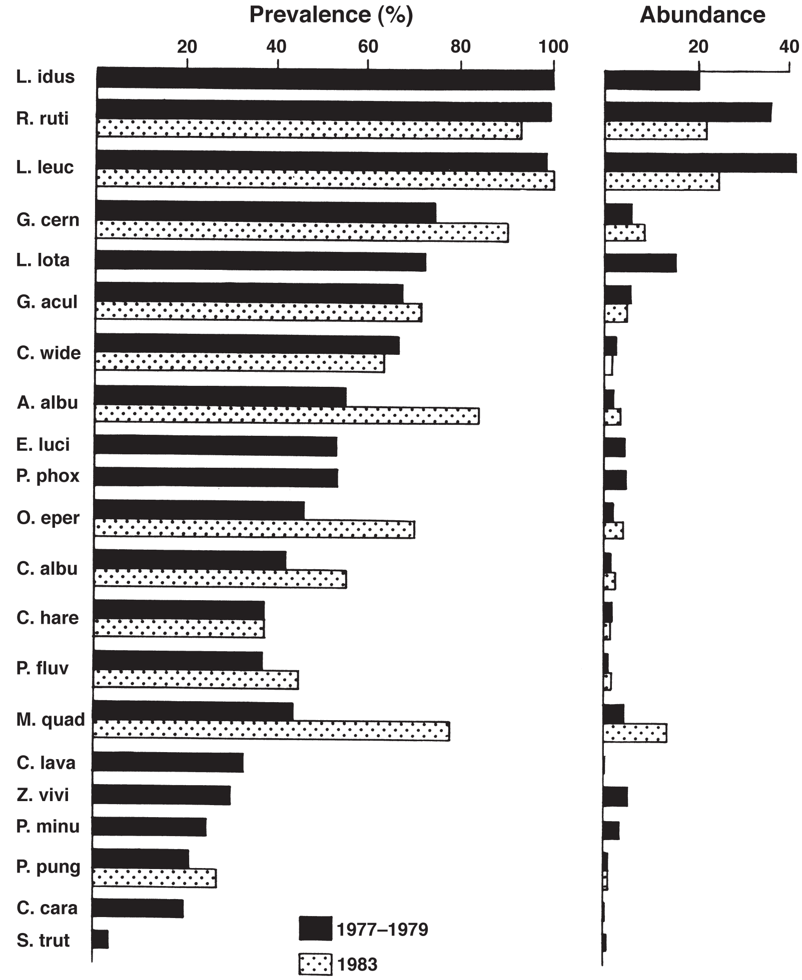

Fig. 2. Prevalence (left) and abundance (right) of diplostomid metacercariae in the lens of fishes from the Bothnian Bay collected during the periods 1977–79 and 1983. The abbreviations for the fish names are in the form of the generic abbreviation plus the first four letters of the specific name, e.g. R. ruti for *Rutilus rutilus* (see Table 1).

1819) (see Niewiadomska 1984, 1986). The remainder of the specimens from the lens appeared to be *D. commutatum* (Diesing, 1850), a species which we have recovered as an adult in the tern *Sterna hirundo* in northern Finland: the latter form represented only a small percentage (6.5%) of the lens metacercariae. For the purpose of this study, both species were grouped together. Taxonomic and nomenclatural problems preclude naming of the form or forms from the vitreous body, but metacercariae from the non-lens regions of the eye have been referred to by several names in recent years, including *D. baeri* Dubois, 1937 and *D. volvens* (Nordmann, 1932). Certainly at least some of our material is likely to be conspecific with the form from perch in Sweden called *D. baeri* by Høglund and Thulin (1992). Diplostomid metacercariae in the vitreous body, especially in percids, also include *Tylodelphys clavata* (Nordmann, 1832). A detailed analysis of diplostomid specimens from the vitreous body showed that, in fishes examined from the Bothnian Bay, *T. clavata* represented only 7.5% of the diplostomid population and in Lake Yli-Kitka only 5.3%, the only exception being *Lota lota*, in which they were the majority. For the purpose of this study, *T. clavata* and *Diplostomum* spp. in the vitreous body were grouped together.

3.2. Comparison of hosts, sites and localities

As indicated in Fig. 2. and Table 1, in the Bothnian Bay diplostomids were found in 21 of the 25 species studied: those uninfected were marine and migratory species studied in only small numbers. All nine species studied in Lake Yli-Kitka and all five studied in Lake Kuivasjärvi were infected

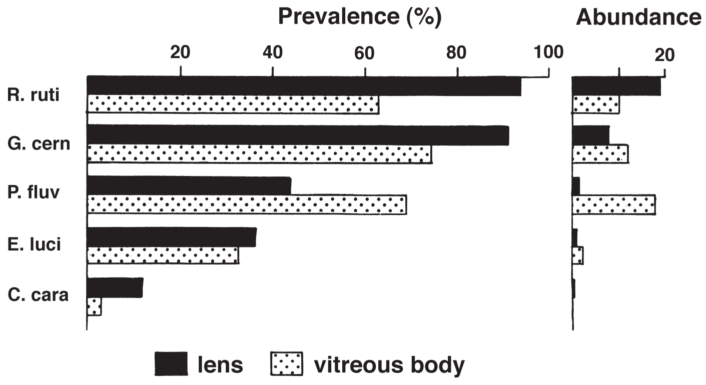

Fig. 3. Prevalence (left) and abundance (right) of diplostomid metacercariae in the lens and vitreous body of fishes from Lake Kuivasjärvi during 1979–1980. The abbreviations for the fish names are as for Fig. 2.

with diplostomids. High prevalences (> 50%) of diplostomids were found in the lenses of 13 species of fish in the Bothnian Bay, i.e. five species of cyprinids, plus *Gymnocephalus cernuus*, *Lota lota*, *Gasterosteus aculeatus*, *Myoxocephalus quadricornis*, *Esox lucius*, *Coregonus lavaretus widegreni*, *Osmerus eperlanus* and *Coregonus albula*, and relatively high prevalences (≥ 20%) were found in the remainder of the fishes studied, except for *Salmo trutta* (Fig. 2). A slight tendency for increased prevalences in the lens during the second period of study (1983) was found, and

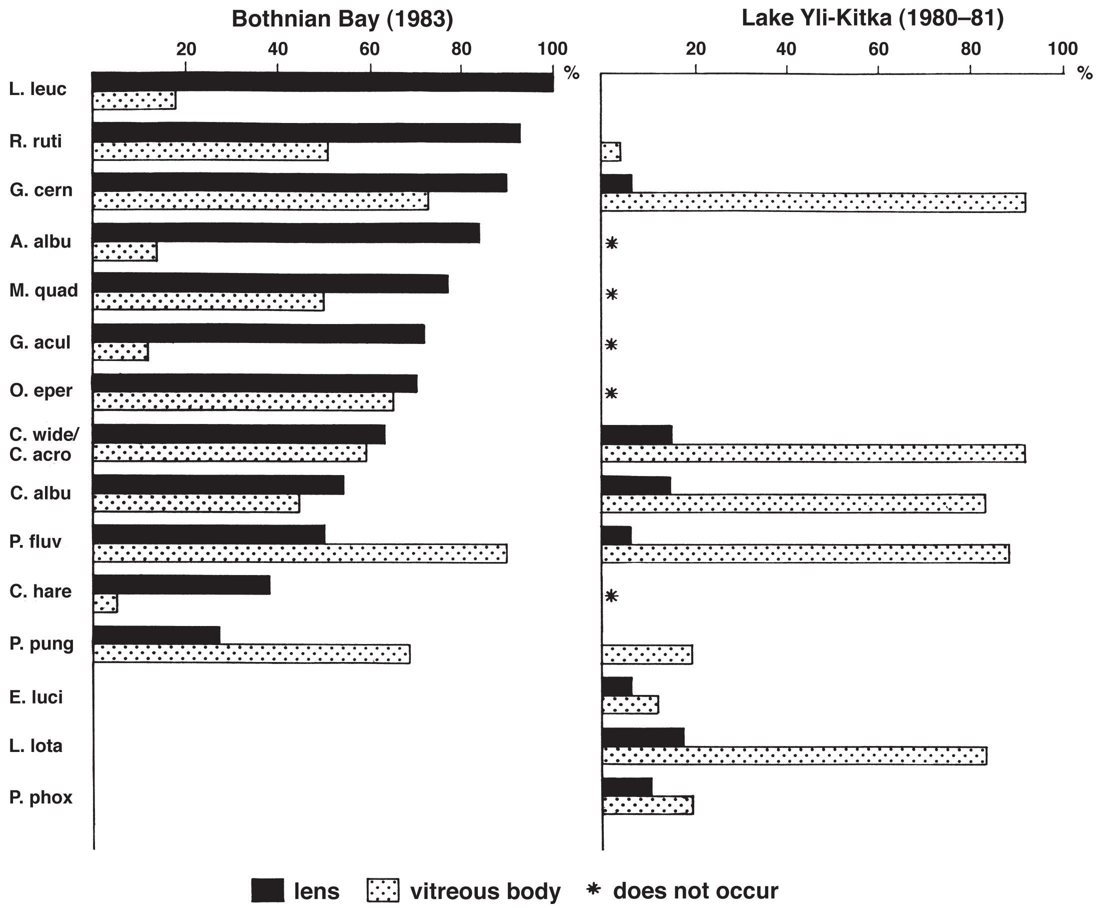

Fig. 4. Prevalence of diplostomid metacercariae in the lens and vitreous body of fishes of the Bothnian Bay during 1983 and from Lake Yli-Kitka during 1980–81. The abbreviations for the fish names are as for Fig. 2.

these differences were statistically significant in five cases, i.e. *G. cernuus*, *Alburnus alburnus*, *O. eperlanus*, *C. albula* and *Rutilus rutilus* (*G*-test, $p < 0.001, 0.007, 0.001, 0.037, 0.003$, respectively) and seven species showed little or no variation (Fig. 2). Comparison of material from the eutrophic Lake Kuivasjärvi reveals very similar infection patterns as occur in the same fish species in the Bothnian Bay, both in the lens and vitreous body: diplostomids in the lens dominated in all fish species with the exception of *P. fluviatilis* (Fig. 3). Consequently, the data for this lake are not dealt with in detail below.

The occurrence of *Diplostomum* in the lens of fishes of Lake Yli-Kitka was much lower than that encountered in the Bothnian Bay, the prevalence being < 18% in all of the fish species studied (Fig. 4). In terms of abundance (the total number of parasites of a given species divided by the total number of hosts studied: Williams & Jones 1994)) (Fig. 2), in the Bothnian Bay only three cyprinid species, i.e. *Leuciscus leuciscus*, *Rutilus rutilus* and *L. idus*, had figures > 20 in at least one or other of the periods of study and *Lota lota* and *M. quadricornis* had figures > 10 (Fig. 2). In Lake Yli-Kitka, only *L. lota* had an abundance greater than 1 (i.e. 5.8, Fig. 5).

The situation in the vitreous body is quite different. In the Bothnian Bay material for 1983, very high prevalences (> 70%) occurred in percids (*G. cernuus* and *P. fluviatilis*), high prevalences (> 50%) occurred in *Phoxinus phoxinus, R. rutilus*, *O. eperlanus* and *C. l. widegreni*, and a low prevalence (< 10%) occurred only in *Clupea harengus*. In Lake Yli-Kitka very high prevalences (> 80%) occurred in all the species studied apart from *P. phoxinus*, *Pungitius pungitius, E. lucius* and *R. rutilus* (Fig. 4). The abundance data were similar to those of prevalence (Fig. 5). In the Bothnian Bay the abundance in the vitreous body was always < 10, whereas in Lake Yli-Kitka an abundance > 30 occurred in *G. cernuus* and *Coregonus acronius* and > 15 in *C. albula*, *P. fluviatilis* and *Lota lota*; in all other species it was < 1 (Fig. 5).

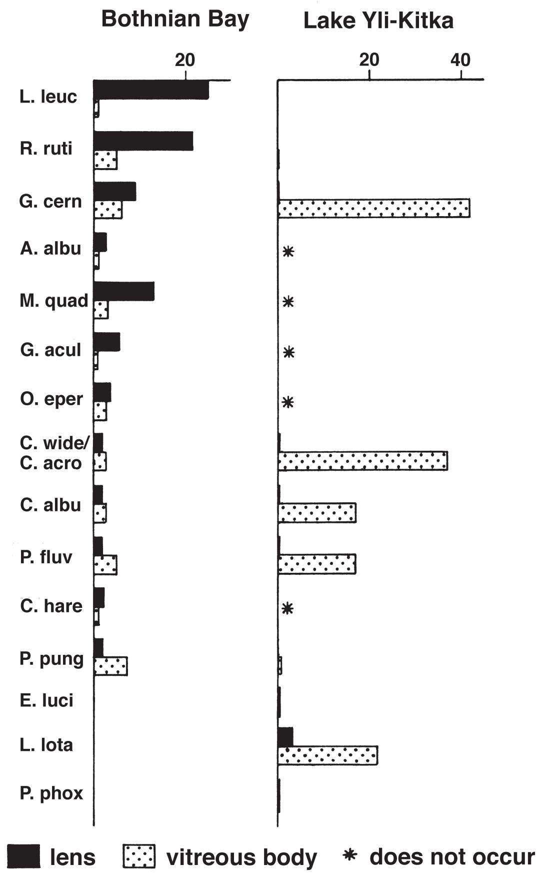

Fig. 5. Abundance of diplostomid metacercariae in the lens and vitreous body of fishes from the Bothnian Bay during 1983 and from Lake Yli-Kitka during 1980–81. The abbreviations for the fish names are as for Fig. 2.

3.3. Associations

The occurrence of concurrent infections of diplostomids in the vitreous body and in the lens did not differ from the expected frequencies, except in *L. lota* from Lake Yli-Kitka (Independence test, *G statistic* = 5.1, $p = 0.025$) and *G. cernuus*, *G. aculeatus*, *C. l. widegreni* and *M. quadricornis* from the Bothnian Bay (Table 2). In all these cases concurrent occurrences were found more often than might have been expected. In all of these species, plus *O. eperlanus* and *P. pungitius*, positive correlations between numbers in the lens and vitreous body were also significant (Table 2). Only in *Leuciscus leuciscus* was the correlation negative.

3.4. The effects of host-size

It was very apparent from the results that, in the majority of cases where large numbers of fishes were studied, there was little or no association between the prevalence of infection and host-size, but there was a distinct accumulation in the number of parasites. The most clear examples of this in the lens material from the Bothnian Bay (combined data for all years studied) occurred in the cyprinids *R. rutilus* and *L. leuciscus* (Fig. 6), although it was also apparent in *G. cernuus* and *C. albula*. Cases where an increase in prevalence occurred with increasing size were *G. aculeatus* and *O. eperlanus* (Fig. 6). In the material from the vitreous body of fishes from the Bothnian Bay (data for 1983), again only in *G. cernuus* and *O. eperlanus* did the smallest size-group of fish have a lower prevalence compared with other fishes, but a general trend of an accumulation of specimens in the larger fish was noted. In Lake Yli-Kitka, the prevalence of the lens material was too low to exhibit any clear trends, but, in the case of the material from the vitreous body, there was evidence of an increase in prevalence with increasing size in *P. pungitius*, *P. phoxinus*, *P. fluviatilis* and *C. albula,* where a decrease in prevalence in the largest fish was also apparent. By contrast, in *C. l. acronius* and *G. cernuus* the prevalence remained relatively level in fish of all sizes, although a clear accumulation of specimens with increasing size was noted in *G. cernuus* especially.

3.5. Seasonality

Seasonal results for the more heavily infected fish species tended not to exhibit any clear patterns, but generally maintained high levels of prevalence throughout the year in all study areas. However, in the cases of *G. aculeatus* and *C. albula* in the Bothnian Bay during 1978–79, there was an increase in the prevalence of diplostomids in the lens during the late summer and early autumn in comparison with the levels during the remainder of the year (Fig. 7). Great changes in the prevalence in *C. harengus* might be explained by the migration of this host to more southern and deeper areas during winter. Fish from March and May are recent immigrants into the Bothnian Bay area, which become infected in the shallow waters during the summer. There was also an apparent seasonal effect in the prevalence of diplostomids in the vitreous body of *C. albula* in Lake Yli-Kitka, where the prevalence was lowest during the spring (ca. 60%) and then increased during the summer, after which all fish were infected. A similar pattern in other fish species from the lake was not so apparent.

4. Discussion

One of the most obvious features of these results, at least with regard to metacercariae in the lens of Bothnian Bay fishes, is the consistent infection pattern between two periods spanning seven years; this suggests a reasonably stable, predictable system, despite the fact that diplostomids are highly seasonal in relation to their transmission patterns between the first (snail) and second (fish) intermediate hosts. Cercariae of *Diplostomum* do not emerge from the snails in water temperature below 10°C (see Introduction) and in the present study areas only during the time of the warmest water temperatures, from mid-July to mid-August

Table 2. Concurrent infections of diplostomids in the lens and vitreal body of fishes from the Bothnian Bay during 1983 in cases where they occur more often than they ought to according to expected frequencies (Likelihood Ratio Test , *G*). Spearman correlations (r_s) of the numbers of diplostomids in the two sites are also given.

Fish species	*G*	*p*	r_s	*p*
Coregonus widegreni acronius	21.9	< 0.001	0.39	< 0.001
Gasterosteus aculeatus	7.6	0.01	0.18	0.02
Gymnocephalus cernuus	4.6	0.03	0.21	0.01
Myoxocephalus quadricornis	9.2	0	0.42	0
Pungitius pungitius			0.47	0.03
Osmerus eperlanus			0.19	0.03
Leuciscus leuciscus			– 0.18	0.04

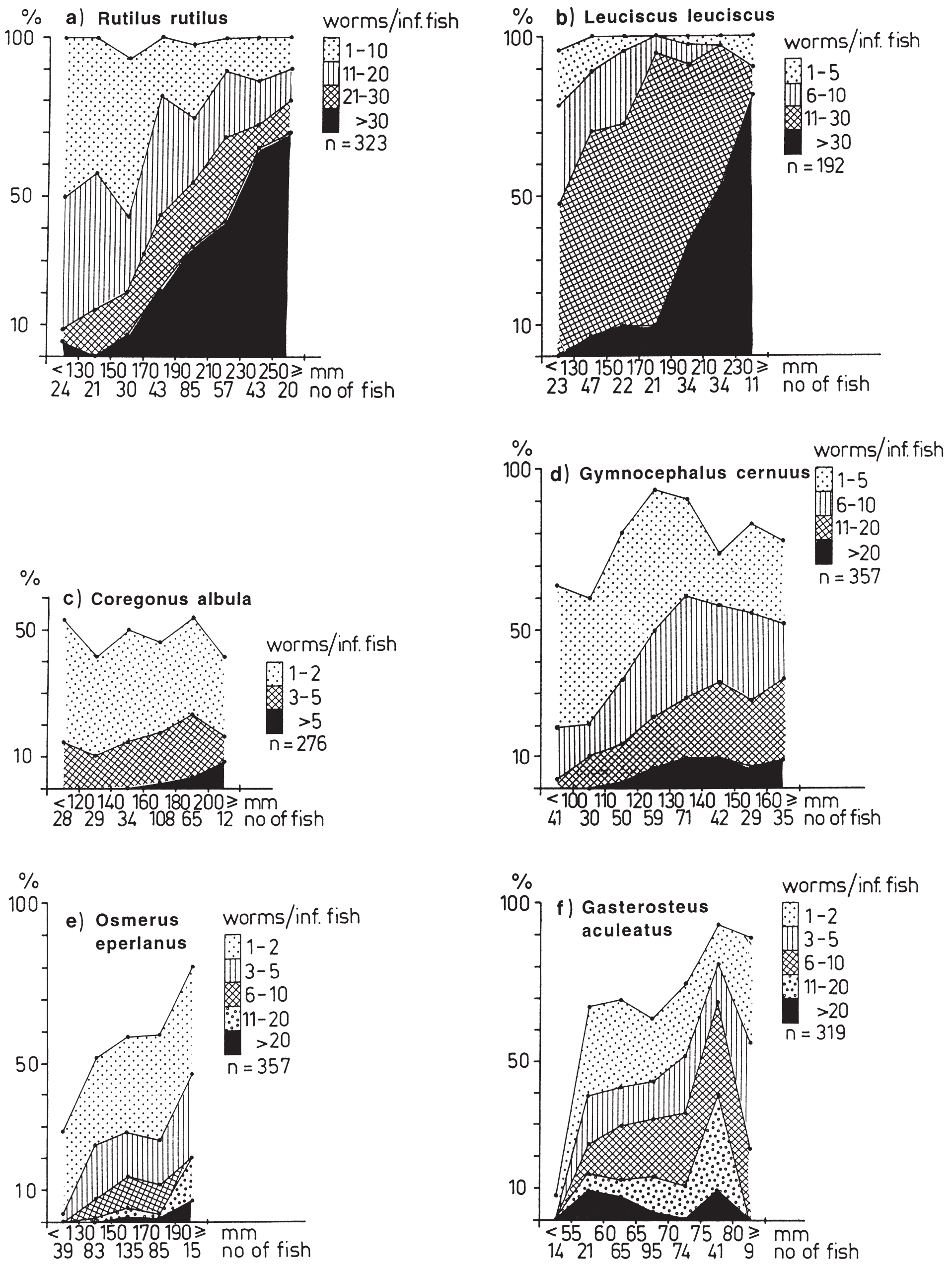

Fig. 6. Prevalence and levels of intensity of diplostomid metacercariae from the lens of fishes from the combined material from the Bothnian Bay and in relation to fish size.

when water temperatures vary from 15–18°C (Water Statistics, Bothnian Bay Research Station) and apparently during an even shorter period in Lake Yli-Kitka, where the ice-cover lasts 1–2 months longer than in the Bothnian Bay. Stables and Chappell (1986) indicated that the optimum temperature for cercarial emission is 17.5°C. Furthermore, the definitive hosts of diplostomids are annual migrators, present only for the limited period of open water. Diplostomids are, however, among the most common and abundant metazoan parasites in all three study areas (e.g. Valtonen *et al.* 1988, Valtonen & Julkunen 1995). Indeed, results from the Bothnian Bay suggest that robust,

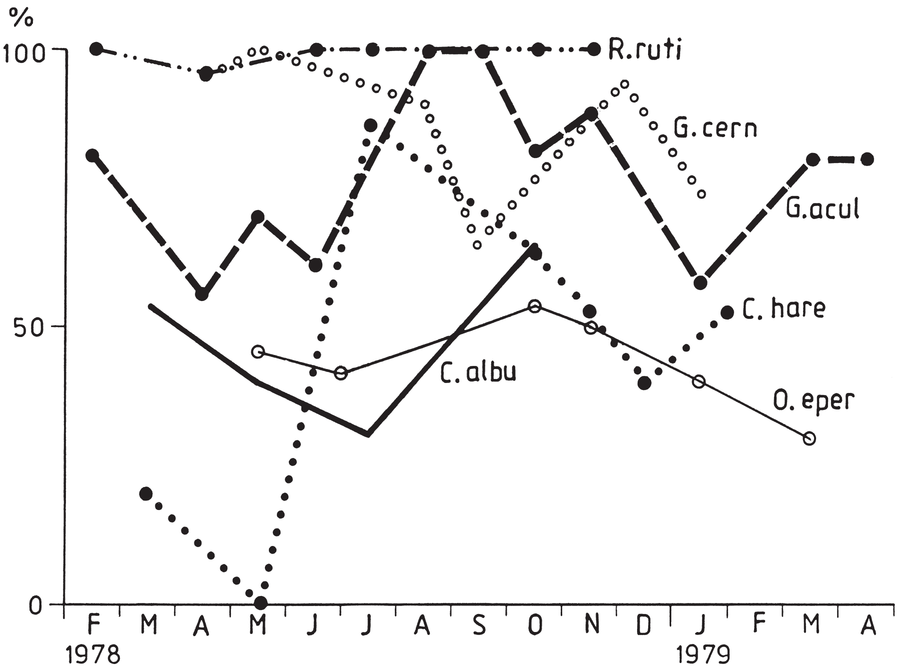

Fig. 7. Seasonal prevalence of diplostomid metacercariae in the lens of certain fish species from the Bothnian Bay during 1979. The abbreviations for the fish names are as for Fig. 2. The average sample-sizes were 13, 21, 14, 16, 27 and 21 for *R. rutilus*, *G. cernuus*, *G. aculeatus*, *C. harengus*, *O. eperalanus* and *C. albula*, respectively.

well-established suprapopulations of diplostomids are maintained in these northern latitudes, even in brackish water. Key to the maintenance of stable diplostomid suprapopulations, especially in northern latitudes, are the reservoirs of metacercariae in the fish intermediate hosts. The larval stages in snails may also help maintain the stability of diplostomid populations. Furthermore, they overwinter as sporocysts in two species of *Lymnaea* in the region (Väyrynen 1996). Metacercariae in fish may live for up to four years (Shigin 1964) and perhaps until their fish host dies; this longevity is seen in the present material in the accumulation of the worms in older and larger fishes of several species. The accumulation of *Diplostomum* spp. (but not *Tylodelphys clavata*) in the lens and vitreous humour have also been reported by Pennycuick (1971), Sweeting (1974), Wootten (1974) and Burrough (1978).

The longevity of diplostomid metacercariae in fishes may also explain the lack of seasonal variation observed in most fishes in the Bothnian Bay material during the study and also in the majority of fishes in the lake material. The winter temperatures in all of the study areas are low, close to 0°C during most winter months (T. Valtonen, personal communication), which must surely further extend the longevity of the larvae. Similarly, further south (in the UK), no seasonal variation in diplostomid metacercarial prevalences was reported by Chappell (1969) or Wootten (1974), although their intensities have been reported to increase during the period of cercarial emission (Chappell 1969, Burrough 1978).

The great variation in the level of diplostomid infection in the lenses of different fish species in the Bothnian Bay was maintained between the two study periods in most cases. Also, variation was found in the prevalences and abundances of infections between fish species in the two lakes. It has been suggested that such variation is due to differences in host specificity (e.g. Wootten 1974, Burrough 1978, Ching 1984, Moravec & Scholz 1984, Kalfa-Papaioannou & Sinis 1985). Of the freshwater fishes of the Bothnian Bay, cyprinids were the most susceptible to lens diplostomids. It has previously been shown (Betterton 1974) that brown trout *Salmo trutta* are much less susceptible to the transmission of *Diplostomum spathaceum* than rainbow trout *Oncorhynchus mykiss*. Our results also showed that sea trout had the lowest *D. spathaceum* prevalence in the Bothnian Bay. Furthermore, when brown trout were experimentally exposed to cercariae of one species of *Diplostomum* from Central Finland (up to 94 cercariae per litre) only a few larvae were able to migrate to the lenses of these fish, which responded to the exposure by simultaneous increases in activity and heart rate (Laitinen *et al.* 1996). Similar differences in susceptibility may explain some of the other differences found in the prevalences and abundances of these parasites in the fishes of the present study.

Nevertheless, ecological factors, such as host habitat selection, must also be important in determining the transmission and infection levels of diplostomids in the eyes of fishes. For example, only three of the six marine fish species in the Bothnian Bay were infected, with prevalences of < 40% and low abundances. This can be explained by the facts that marine species prefer to stay in deeper waters (Andreasson & Petersson 1982), while snails occur in the littoral zone. In addition, since cercariae are able to live for only 24 hours and are probably infective for an even shorter period, they cannot migrate long distances (Erasmus 1959). However, it is interesting to note that any fish coming into the region, even marine species whose ranges extend into the Bothnian Bay where the salinity is only 2–3‰, do indeed become infected with diplostomids. Buchmann (1986) has even reported a *Diplostomum spathaceum* infection of 22.5% in cod *Gadus morhua* from the Bornholm Basin in the southern regions of the Baltic proper, where the salinity is 15‰.

In Lake Yli-Kitka, the levels of infection in the lens are considerably lower than in both the Bothnian Bay and Lake Kuivasjärvi which is connected to it. When diplostomids in the vitreous body are considered, the position is reversed. The most likely explanation for this is the difference in the piscivorous bird fauna between Lake Yli-Kitka and the Bothnian Bay area: larids (gulls), especially *Larus canus*, a major host of *D. spathaceum* (the main lens metacercaria) (see Bakke 1972) and *L. ridibundus*, are very common in the Bothnian Bay, but form a smaller proportion of the piscivorous bird population in Lake Yli-Kitka where *L. canus* does occur but not in great numbers. In this lake, piscivorous anatids (the sawbills, mergansers and goosanders, i.e. *Mergus* spp.) and gaviids (divers) form a greater proportion of the piscivorous bird population than in the Bothnian Bay. Indeed, it is worth noting that *Gavia arctica* is relatively common in Lake Yli-Kitka but does not occur in the Bothnian Bay. That some degree of bird host-specificity is involved was demonstrated by experimental life-history studies carried out by Brady (1989) in Scotland, who showed that one of the four species of *Diplostomum* that she studied was unable to produce viable eggs in gulls, and Høglund and Thulin (1992) considered that the anatid *Mergus merganser* made a better definitive host for "*D. baeri*" from the vitreous body of perch. So it seems likely that differences in the bird fauna explain some of the qualitative differences in the diplostomid fauna of the two regions. This is also supported by the similarity of diplostomid infections in the Bothnian Bay and Lake Kuivasjärvi, since the proximity of the lake to the sea (2 km) means that the bird-fauna is likely to be similar. Although all fish species present in Lake Kuivasjärvi are spring-spawners and are known to immigrate from the Bothnian Bay, there is still a local fish population in the lake, judging from the common occurrence of the metacercariae of the digenean *Rhipidocotyle campanula* in roach and adults of the same species in perch (T. Mäkela, personal communication), which have not been encountered in the Bothnian Bay (E. Tellervo Valtonen, unpublished).

It is also possible that the diplostomid fauna may reflect differences in the molluscan fauna. The major first intermediate host of diplostomids in European waters are *Lymnaea* spp. According to the Host–Parasite Data-base at The Natural History Museum, London, most recent records of *D. spathaceum* have been from *L. peregra* (includes *L. ovata*) and *L. stagnalis*, whereas some other species of the genus appear to have been recorded more often in other species of *Lymnaea*, such as *L. auricularia* and *L. palustris*. The non-lens species, *D. baeri*, for example appears especially prevalent in *L. auricularia*. In the Bothnian Bay, *L. peregra* is very common in shallow, coastal waters and *L. palustris* and *L. stagnalis* do occur (Kangas 1976), and Väyrynen (1996) has found *D. spathaceum* in both *L. peregra* and *L. stagnalis* in Lake Kuivasjärvi. In Lake Yli-Kitka, the presence of limestone rocks might favour a much wider variety of molluscs, but *L. peregra*, for example, is not so common as in the Bothnian Bay. Unfortunately, no detailed studies of the benthic community of Lake Yli-Kitka have been undertaken.

Positive associations between the occurrence of diplostomids in the lens and vitreous body may well be linked to the fact that the species involved use the same species of molluscan host. Association may also reflect the fact that individual fishes which frequent shallows, where the molluscan hosts occur, are more likely to be infected with these parasites than those which tend to feed in deeper waters.

The results of this study have shown that diplostomid metacercariae can occur, often with a high prevalence and in large numbers, in the eyes of a wide variety of fish species from widely differing freshwater environments and brackish water, and can even infect essentially marine fishes whose range extends into brackish water. In view of their known pathogenicity, which may result in direct host mortality (Brassard *et al.* 1982) or indirect host mortality through increased vulnerability to predation, and also their apparent ubiquity in freshwater fishes in northern regions, these parasites as a group must be considered important factors in terms of aquaculture, fisheries management and also as a potential regulator of wild fish populations.

Acknowledgements. We are grateful to the Board of Natural Sciences of the Finnish Academy for financial support to ETV. We are also indebted to Prof. J. C. Holmes, University of Alberta, for helpful suggestions with regard to the text, to Dr. R. A. Bray (The Natural History Museum, London) for reading the manuscript, to Dr. P. Tikkanen for discussions on benthic communities and to Mr. E. Merilä M.Sc. and J. Mäkelä M.Sc. for discussions in bird communities of the Bothnian Bay and Lake Yli-Kitka, respectively. Mr. M. Julkunen helped with the statistics. We are extremely grateful to Mrs. Päivi Rintamäki-Kinnunen (Phil. lic.), Mrs. Riitta Rahkonen (Phil. lic.) and to Mrs. Marjatta Lappalainen for their kind help with the collection of material from Kitkajärvi and Kuivasjärvi, respectively.

References

Alasaarela, E. 1979: Phytoplankton and environmental conditions in central and coastal areas of the Bothnian Bay. — Ann. Bot. Fennici 16: 241–274.

Andreasson, A. & Petersson, B. 1982: The fish fauna of the Gulf of Bothnia. — In: Miiller, E. (ed.), Coastal research in the Gulf of Bothnia. Monogr. Biol. 45: 301–315.

Bakke, T. A. 1972: Studies of the helminth fauna of Norway. XXII. The common gull, Larus canus L., as a final host for Digenea (Platyhelminthes). 1. The ecology of the common gull and the infection in relation to season and the gull's habitat, together with the distribution of the parasites in the intestine. — Norw. J. Zool. 20: 165–188.

Bauer, O. N., Vladimirov, V. L. & Mindel, N. V. 1964: New knowledge about the biology of Strigeata causing mass diseases of fishes. — In: Ergens, R. & Rysavy, B. (eds.), Parasitic worms and aquatic conditions: 77–82. Czech. Acad. Sci., Prague.

Berrie, A. D. 1960: Two Diplostomulum larvae (Strigeida, Trematoda) in the eyes of sticklebacks (Gasterosteus aculeatus L.). — J. Helminth. 34: 211–216.

Betterton, C. 1974: Studies on the host specificity of the eyefluke, Diplostomum spathaceum, in brown and rainbow trout. — Parasitology 69: 11–29.

Brady, A. 1989: Studies on the taxonomy and biology of Diplostomum species (Digenea). — Ph.D.-thesis, University of Stirling, 277 pp.

Brassard, P., Curtis, M. A. & Rau, M. E. 1982: Seasonality of Diplostomum spathaceum (Trematoda: Strigeidae) transmission to brook trout (Salvelinus fontinalis) in northern Quebec, Canada. — Can. J. Zool. 60: 2258–2263.

Buchmann, K. 1986: Prevalence and intensity of infection of Cryptocotyle lingua (Creplin) and Diplostomum spathaceum (Rudolphi) – parasitic metacercariae of Baltic cod (Gadus morhua L.) — Nord. Vet.-Med. 38: 303–307.

Burrough, R. J. 1978: The population biology of two species of eyefluke, Diplostomum spathaceum and Tylodelphys clavata, in roach and rudd. — J. Fish Biol. 13: 1932.

Chappell, L. H. 1969: The parasites of the three-spined stickleback Gasterosteus aculeatus L. from a Yorkshire pond. II. Variation of parasite fauna with size, and sex of fish. — J. Fish Biol. 1: 339–347.

Chappell, L. H., Hardie, L. J. & Secombes, C. J. 1994: Diplostomiasis: the disease and host-parasite interactions. — In: Pike, A. W. & Lewis, J. W. (eds.), Parasitic diseases of fish: 59–86. Samara Publishing Ltd., Tresaith, Dyfed.

Ching, H. L. 1985: Occurrence of the eyefluke, Diplostomum baeri bucculentum Dubois et Rausch, 1948, in salmonid fishes of northern British Columbia. — Can. J. Zool. 63: 396–399.

Chubb, J. C. 1979: Seasonal occurrence of helminths in freshwater fishes. Part II. Trematoda. — Adv. Parasit. 17: 141–313.

Erasmus, D. A. 1959: The migration of Cercaria X Baylis (Strigeida) within the fish intermediate host. — Parasitology 49: 173–190.

Esch, G. W. & Fernandez, J. C. 1993: A functional biology of parasitism. Ecological and evolutionary implications. — Chapman & Hall, London. 337 pp.

Gibson, D. I., Oliver, S. E. & Shaw, K. 1985: Can different species of Diplostomum metacercariae be distinguished by principal components analysis? — Abstracts, Spring Meeting of the Brit. Soc. Parasit., Nottingham, 26–28 March, 1985: 63.

Gibson, D. I. & Valtonen, E. T. 1984: How do the helminth-parasites of fishes survive in the frozen north? — Parasitology 89: xlix.

Gregory, R. D. & Keymer, A. E. 1989: The ecology of host parasite interactions. — Sci. Prog., Oxf. 73: 67–80.

Heikkinen, O. & Kurimo, H. 1977: The post-glacial history of Kitkajärvi, north-eastern Finland, as indicated by trend-surface analysis and radio-carbon dating. — Fennica 153: 1–32.

Høglund, J. & Thulin, J. 1992: Identification of Diplostomum spp. in the retina of perch Perca fluviatilis and the lens of roach Rutilus rutilus from the Baltic Sea, an experimental study. — Syst. Parasit. 21: 1–19.

Hyytinen, L. & Valtonen, E. T. 1984: Fishing and fish breeding in the Koillismaa region. — Oulanka Rep. 5: 41–44.

Ieshko, E. P. & Shustov, Y. A. 1982: (Effect of diplostomose infection (Trematoda, Diplostomatidae) on the visual activity of fish.) — Parazitologiya 16: 81–83. (In Russian.)

Kalfa-Papaioannou, A.-M. & Sinis, A. I. 1985: Metacercariae of Diplostomum spathaceum in freshwater fish of the lake system Koronia and Volvi (Macedonia, Greece). — Zentralblatt Vet. Reiche B 32: 65–70.

Kangas, P. 1976: Littoral stony-bottom invertebrates in the Krunnit area of the Bothnian Bay. — Acta Univ. Oul. Ser. A. No. 42. Biol. 3: 97–106.

Kennedy, C. R. 1981: Long term studies on the population biology of two species of eyefluke, Diplostomum gasterostei and Tylodelphys clavata (Digenea: Diplostomatidae), concurrently infecting the eyes of perch, Perca fluviatilis. — J. Fish Biol. 19: 221–236.

Kennedy, C. R. 1984: The use of frequency distributions in an attempt to detect mortality induced by infections of diplostomid metacercariae. — Parasitology 89: 209–220.

Laitinen, M., Siddall, R. & Valtonen, E. T. 1996: Bioelectronic monitoring of parasite-induced stress in brown trout and roach. — J. Fish Biol. 48: 228–241.

Lester, R. J. G. 1977: An estimate of the mortality in a population of Perca flavescens owing to the trematode Diplostomum adamsi. — Can. J. Zool. 55: 64–73.

Moravec, F. & Scholz, T. 1984: First record of the trematode Tylodelphys podicipina Kozicka & Niewiadomska, 1960 in Czechoslovakia. — Folia Parasit. 31: 331–332.

Myllymaa, U. 1978: (The state of the lakes at Oulu district.) — Vesihallituksen monistesarja 141: 1–31. (In Finnish.)

Niewiadomska, K. 1984: Present status of Diplostomum spathaceum (Rudolphi, 1819) and differentiation from Diplostomum pseudospathaceum nom. nov. (Trematoda, Diplostomidae). — Syst. Parasit. 6: 81–86.

Niewiadomska, K. 1986: Verification of the life-cycle of Diplostomum spathaceum (Rudolphi, 1819) and D. pseudospathaceum Niewiadomska, 1984 (Trematoda, Diplostomidae). — Syst. Parasit. 8: 23–31.

Niewiadomska, K. 1989: On the synonymy of Diplostomum pseudospathaceum Niewiadomska, 1984 (Digenea, Diplostomidae). — Acta Parasit. Pol. 34: 103–106.

Pennycuick, L. 1971a: Seasonal variations in the parasite infections in a population of three-spined sticklebacks, Gasterosteus aculeatus L. — Parasitology 63: 373–388.

Pennycuick, L. 1971b: Frequency distributions of parasites in a populations of three-spined sticklebacks, Gasterosteus aculeatus L., with particular reference to the negative binomial distribution. — Parasitology 63: 389–406.

Rahkonen, R., Valtonen, E. T. & Gibson, D. I. 1984: Trematodes of northern Finland. II. The occurrence of Bunodera luciopercae (Müller, 1776) [Trematoda] in three different water bodies in northern Finland. — Bothnian Bay Rep. 3: 55–66.

Shariff, M., Richards, R. H. & Sommerville, C. 1980: The histopathology of acute and chronic infections of rainbow trout Salmo gairdneri Richardson with eye flukes, Diplostomum spp. — J. Fish Dis. 3: 455–465.

Shigin, A. A. 1964: (The life-span of Diplostomum spathaceum in the intermediate host.) — Trudy Gelmint. Lab. 14: 262–272. (In Russian.)

Shigin, A. A. 1986: (Trematodes of the USSR. Genus Diplostomum. Metacercariae.) — Nauka, Moscow. (In Russian.)

Shigin, A. A. 1987: (Morphology, biology and taxonomy of the maritae of Diplostomum chromatophorum (Brown, 1931) Shigin, 1986 (Trematoda: Diplostomidae).) — Trudy Gelmint. Lab. 35: 176–182. (In Russian.)

Stables, J. N. & Chappell, L. H. 1986: The epidemiology of diplostomiasis in farmed rainbow trout from north-east Scotland. — Parasitology 92: 699–710.

Sweeting, R. A. 1974: Investigations into natural and experimental infections of freshwater fish by the common eyefluke Diplostomum spathaceum Rud. — Parasitology 69: 291–300.

Valtonen, E. T. 1983: On the ecology of Echinorhynchus salmonis and two Corynosoma species (Acanthocephala) in the fish and seals of the northern Gulf of Bothnia. — Acta Univ. Oul. A 156. Biol. 22: 1–48.

Valtonen, E. T. & Crompton, D. W. T. 1990: Acanthocephala in fish from the Bothnian Bay, Finland. — J. Zool., London 220: 619–639.

Valtonen, E. T. & Julkunen, M. 1995: The influence of the transmission of parasites from prey fishes on the composition of the parasite community of a predatory fish. — Can. J. Fish. Aquat. Sci. 52 (suppl. 1): 233–245.

Valtonen, E. T., Rintamäki, P. & Lappalainen, M. 1989: Triaenophorus nodulosus and T. crassus in fish from Northern Finland. — Folia Parasit. 36: 351–370.

Valtonen, E. T., Brummer-Korvenkontio, H. & Rahkonen, R. 1988: A survey of the parasites of coregonids from three water bodies in Finland. — Finn. Fish. Res. 9: 313–322.

Väyrynen, T. 1996: Occurrence of digenean larvae in Lymnaea peregra in a small lake in Northern Finland. — Phil. lic. thesis., Univ. Oulu.

Williams, H. H. & Jones, A. 1994: Parasitic worms of fish. — Taylor & Francis, London. 593 pp.

Wootten, R. 1974: Observations on strigeid metacercariae in the eyes of fish from Hanningfield Reservoir, Essex, England. — J. Helminth. 48: 73–83.