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Patterns of trematode parasitism in lymnaeid snails from northern and central Finland

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A species rich and prevalent larval digenean fauna was found in lymnaeid snail populations from two lakes in northern Finland (Kuivasjärvi and Pyykösjärvi populated by *L. stagnalis* and *L. peregra*, respectively) and ten years later in a third lake in central Finland (Kuuhankavesi populated by *L. stagnalis*). Echinostomes were common to all lakes, one species overlapping between Pyykösjärvi and Kuuhankavesi (*Echinostoma revolutum*). All three lymnaeid populations also harboured xiphidiocercariae of *Plagiorchis elegans*, furcocercariae of *Diplostomum pseudospathaceum* and *Trichobilharzia ocellata* and the monostome *Notocotylus attenuatus*. A consistent seasonal pattern of infection was recorded for four of the parasites in Pyykösjärvi, although annual variation in mean prevalence was generally significant. Annual parasite species composition within the three lakes was relatively stable despite the long dormant winter. This may be due to the over-wintering of larval digeneans in infected snails that then act as a source of reinfection of bird definitive hosts each spring.

1. Introduction

Snail-trematode systems have recently attracted considerable interest from evolutionary ecologists studying the evolution of sexual reproduction (reviewed by Lively 1996), host-parasite co-evolution (Lively 1989, Dybdahl & Lively 1998), the effect of parasitism on life-history evolution (Jokela & Lively 1995) and host resistance (Webster & Woolhouse 1998). They are also of enormous medical importance as 113 digenean species have been reported from human hosts and the schistosomes alone infect in excess of 200 million people (Crompton 1999). Despite this, however, long-term changes in snail-trematode systems and the digenean fauna of northern snail populations have been poorly studied.

Knowledge of larval digenean trematodes in Finland is particularly limited with only two previously published studies (Wikgren 1956, Niewiadomska *et al*. 1997). Wikgren (1956) described twenty-three species of cercariae and Tetracotyle metacercariae from four freshwater snail species, including *Lymnaea stagnalis* and *L. peregra*, collected in the Tvärminne archipelago of southern Finland. Niewiadomska *et al.* (1997) observed nine cercarial species infecting a population of *L. stagnalis* from lake Kuuhankavesi in central Finland.

L. stagnalis and *L. peregra* are widely distributed throughout Europe and Asia, their geographical ranges extending to North America and North Africa for *L. stagnalis* and *L. peregra*, respectively. Both species serve as intermediate hosts to a considerable number of digenean parasites, particularly for species maturing in aquatic birds (Erasmus 1972). The extreme seasonality in climate in Finland has not restricted the distribution of *L. stagnalis* or *L. peregra*, both of which occur throughout the country (Hubendick 1949).

This article examines material collected from three separate lakes in Finland: two in the Oulu region of northern Finland, which are in close proximity but populated by different *Lymnaea* species (*L. stagnalis* and *L. peregra*), and a third lake in central Finland with an abundant population of *L. stagnalis*. In addition to the geographical and host species differences, a period of approximately ten years separated the sampling of the two northern lakes (1982–1984) from that in central Finland (1993–1995). The aims were to examine the effects of host species difference and geographical separation on the lymnaeid parasite fauna within the lakes and to study how the long dormant winter period influences the seasonality and annual stability of larval digenean populations.

2. Material and methods

2.1. Study lakes

Lakes Pyykösjärvi and Kuivasjärvi are situated to the north of the city of Oulu in northern Finland (Fig. 1). They are interconnected, with waters from Pyykösjärvi flowing through Kuivasjärvi and into the Gulf of Bothnia. Both lakes were eutrophic during this study. At the time of sampling, Pyykösjärvi contained a population of *L. peregra* but no *L. stagnalis* were present, while Kuivasjärvi contained mostly *L. stagnalis* and very few *L. peregra*.

Pyykösjärvi and Kuivasjärvi are middle-sized lakes, approximately 1–1.5 km^2 in area, with aquatic vegetation consisting mainly of *Equisetum fluviatile*, *Schoenoplectus lacustris* and *Nuphar lutea*. The lakes are ice-covered on average from October/November until May and water temperatures reach a maximum in excess of 20 °C in July and August. Many thousands of birds stop off to feed in the lakes as they leave Finland on their winter migrations, particularly gulls (*Larus* spp.). The lake areas are also important nesting locations for aquatic birds and a variety of bird species feed in the lake throughout the open water period.

Kuuhankavesi is a mesotrophic lake north-east of the city of Jyväskylä (Fig. 1). Sampling took place in a hypereutrophic bay opposite a wood processing plant. The bay contained an abundant population of *Lymnaea stagnalis* but very few *L. peregra*. The lake is ice-covered from November until early May and water temperatures reach a maximum in excess of 20 °C in July and August. The aquatic vegetation in the sampling area consisted of *Calla palustris*, *Menyanthes trifoliata*, *Nymphaea candida*, *N. tetragona*, *Nuphar lutea*, *Equisetum fluviatile*, *Utricularia vulgaris*, *Myriophyllum* sp. and several *Potamogeton* species. A variety of aquatic birds feed and nest in the area including gulls, several species of Anatidae and swans.

2.2. Snail collection

L. peregra were collected monthly from Pyykösjärvi during the open-water period between May and October in 1982, 1983 and 1984. Random grab sampling throughout the lake was initially attempted but was unsuccessful. Snails were therefore collected by hand along a 50 m stretch of sandy beach, in parallel lines approximately 1 m wide and extending from the shoreline to a water depth of 1 m. Between 30 and 50 snails were collected along each line depending on their population density, which was greatest in June and July and at a minimum in May and October.

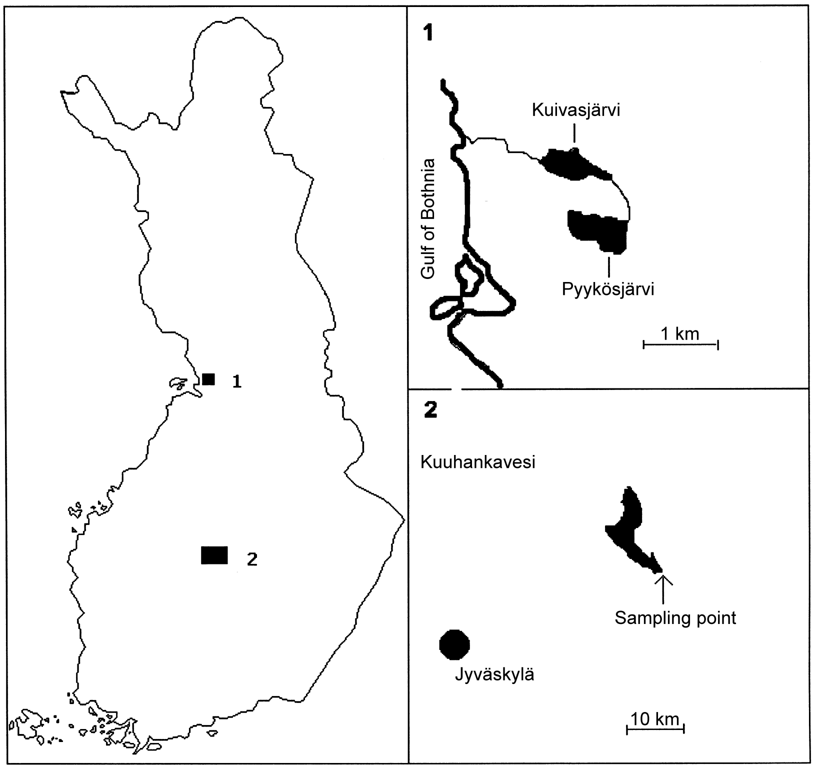


Fig. 1. Study lakes and their location in Finland.

L. stagnalis were collected monthly from Kuivasjärvi between June and September 1982 and two further samples were taken in June and September 1983. Sample sizes depended on the availability of snails but mostly exceeded 30 and were maximal from June to August. Sampling was carried out from a boat, the snails being picked by hand from the water surface and the aquatic vegetation along the shoreline.

Kuuhankavesi was sampled for *L. stagnalis* monthly from June to September 1993. A further sample was collected in July 1995 to confirm the identification of particular parasite species. Sampling was carried out from a boat, the snails being picked by hand from the water surface and the aquatic vegetation along a 50-m stretch of the bay. Monthly samples in 1993 exceeded 200 snails, whilst the single sample in 1995 comprised 122 individuals.

2.3. Parasite identification

Shell length (mm) was measured for each snail apart from the June 1993 and July 1995 samples from Kuuhankavesi. The soft tissues were either teased apart or compressed between two glass plates and examined under a dissecting microscope for intramolluscan stages of digenean parasites (sporocysts or rediae, cercariae and Tetracotyle metacercariae). The morphology of cercariae was studied using newly emerged, live individuals observed under a light microscope immersion objective. Measurements were taken as an aid to identification from cercariae killed by heat, in water, or fixed in ethanol. For some species of cercariae chaetotaxy was studied after impregnation with $AgNO_3$.

2.4. Statistical analysis

Proportions of infected snails were compared within and among the three lakes with the χ^2-test. Seasonal and annual variability in infection were examined statistically only for Pyykösjärvi, from which adequate data were available for all three years of sampling. The effect of month and year on the prevalence of infection was tested separately for each of the parasite species using logistic regression analysis. Only 'old' over-wintered snails that were born in the previous summer were used to avoid variance caused by recruitment of the new, uninfected cohort from July to August. The binomial variable 'infection' (infected, non-infected) was used as a dependent variable in a stepwise logistic regression model. 'Year' (1982, 1983 and 1984) and 'month' (May, June, July and August) were used as categorical covariates. Deviation contrasts were used for both of these, and the first class was treated as a reference class. The model that provided the best fit to the data among all possible models, including models with interaction terms, was selected using a forward stepwise procedure. The significance of the effects was estimated with the likelihood ratio statistics.

3. Results

3.1. Life history of the snails

The life span of *L. peregra* in Pyykösjärvi was approximately one year with egg-laying from the end of June until mid-July. The first juveniles (< 5 mm shell length) appeared in August and the oldest individuals (> 20 mm shell length) began to disappear around the same time. Some of the juveniles successfully over-wintered and survived to breed during their second summer. Consequently there were two distinct cohorts of *L. peregra* sampled from Pyykösjärvi during any particular year: over-wintered and young-of-year snails.

L. stagnalis from Kuivasjärvi and Kuuhankavesi were able to over-winter a second winter and reach a maximum age of 2–2.5 years and a maximum shell length exceeding 50 mm. Egg laying was observed from June until late August. However, it was not possible to separate the snail population into age cohorts on the basis of the length-frequency distribution of sampled snails.

3.2. Levels of infection

The overall prevalence of larval digeneans, including Tetracotyle metacercariae, was extremely high in both *L. peregra* of Pyykösjärvi and *L. stagnalis* of Kuivasjärvi in each of the years studied, reaching in excess of 70% and 85% in Pyykösjärvi and Kuivasjärvi, respectively (Fig. 2). Metacercarial cysts formed a large component of the overall parasite burden in Pyykösjärvi (pooled prevalence 37.8%) and Kuivasjärvi (64.0%) and frequently occurred in joint infections with cercarial species (prevalence 6.8% and 24.9% in Pyykösjärvi and Kuivasjärvi, respectively). However, no metacercariae were observed in *L. stagnalis* from Kuuhankavesi where infection was only with cercarial species and the total prevalence was somewhat lower (Fig. 2). If metacercarial infections are excluded, the prevalence of cercarial species did not differ significantly between the pooled data of Pyykösjärvi (38.9%) and Kuivasjärvi (42.3%) (χ^2-test, $P > 0.05$) but was significantly higher in each these lakes than in Kuuhankavesi (28.6%) (χ^2-test, $P < 0.001$ in both cases).

Levels of infection were compared between Kuivasjärvi and Pyykösjärvi separately for 1982 and 1983, pooling the data for months when the lakes were concurrently sampled (June to September). The overall prevalence of infection as well as the prevalence of Tetracotyle metacercariae and of cercarial infections was higher in Kuivasjärvi than Pyykösjärvi in both 1982 and 1983. However, the only significant differences between the two lakes were for overall infection and for metacercarial infection in 1982 (χ^2-test, $P < 0.001$ in both cases). Comparing pooled data from June to September for all years sampled, the prevalence of cercarial infections in Kuuhankavesi was significantly lower than in Kuivasjärvi and Pyykösjärvi (χ^2-test, $P < 0.001$ in both cases).

3.3. Parasite species in the study lakes

Cercariae of nine species of digenean parasites were recorded from *L. peregra* of Pyykösjärvi and also from *L. stagnalis* of Kuuhankavesi (Table 1). The cercariae from Kuuhankavesi were identified and described by Niewiadomska *et al.* (1997). Echinostomes were not identified to species in Kuivasjärvi but were recorded as a group. However, *L. stagnalis* in this lake were infected with a further four cercarial species and Tetracotyle metacercariae.

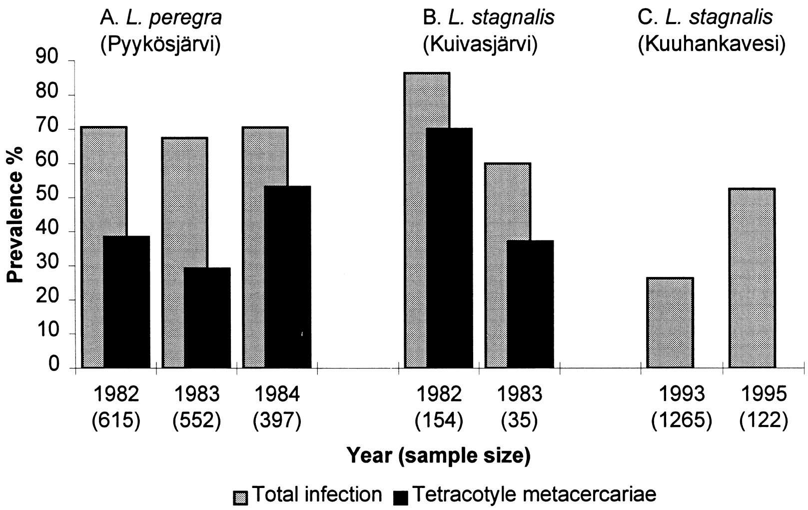


Fig. 2. Annual variation in overall prevalence of larval digeneans and infection with Tetracotyle metacercariae in the three study lakes.

Echinostomes were common to all three lakes, one species overlapping between Pyykösjärvi and Kuuhankavesi (*Echinostoma revolutum*). In addition, all three snail populations harboured xiphidiocercariae of *Plagiorchis elegans*, furcocercariae of *Diplostomum pseudospathaceum* and *Trichobilharzia ocellata* and the monostome *Notocotylus attenuatus* (Table 1).

The prevalence of most individual cercarial species was low (Table 1 and Fig. 3). Of the nine cercarial species in Kuuhankavesi, only two exceeded 1% in prevalence (*E. aconiatum* and *P. elegans*). However, there were interesting differences between lakes in the dominant cercarial species. Monostomes (*N. attenuatus*) were the most common type in *L. peregra* from Pyykösjärvi (15.7%), echinostomes were highly prevalent in *L. stagnalis* from Kuivasjärvi (30.2%) and xiphi-

Table 1. Species occurrence and total prevalence (%) of digenean parasites of *Lymnaea peregra* and *L. stagnalis* from three lakes in northern (Pyykösjärvi and Kuivasjärvi) and central Finland (Kuuhankavesi). Sampling years and numbers of snails examined are in parentheses.

Cercarial type	Species	Pyykösjärvi (1982–1984) *L. peregra* (1564)	Kuivasjärvi (1982–1983) *L. stagnalis* (189)	Kuuhankavesi (1993–1995) *L. stagnalis* (1387)
Echinostome	All echinostomes	6.0[a]	30.2[a]	10.2
	Echinoparyphium aconiatum	0.0		9.7
	Echinostoma revolutum	+		0.3
	Hypoderaeum conoideum	0.0		0.1
	Echinoparyphium recurvatum	+		0.0
	Echinostome cercaria sp. II	+		0.0
Xiphidiocercaria	*Plagiorchis elegans*	10.3	3.7	17.3
Furcocercaria	*Diplostomum pseudospathaceum*	0.8	4.2	0.6
	Australapatemon minor	1.2	0.0	0.2
	Trichobilharzia ocellata	4.2	1.6	0.1
	Cotylurus sp.	0.0	0.0	0.1
Monostome	*Notocotylus attenuatus*	15.7	3.2	0.1
Metacercaria	*Tetracotyle* sp.	37.8	64.0	0.0
	Total Infection (%)	69.4	81.5	28.6

[a] Echinostomes recorded only as a group in Pyykösjärvi and Kuivasjärvi and not identified to species in Kuivasjärvi.
+ Present but prevalence not recorded.

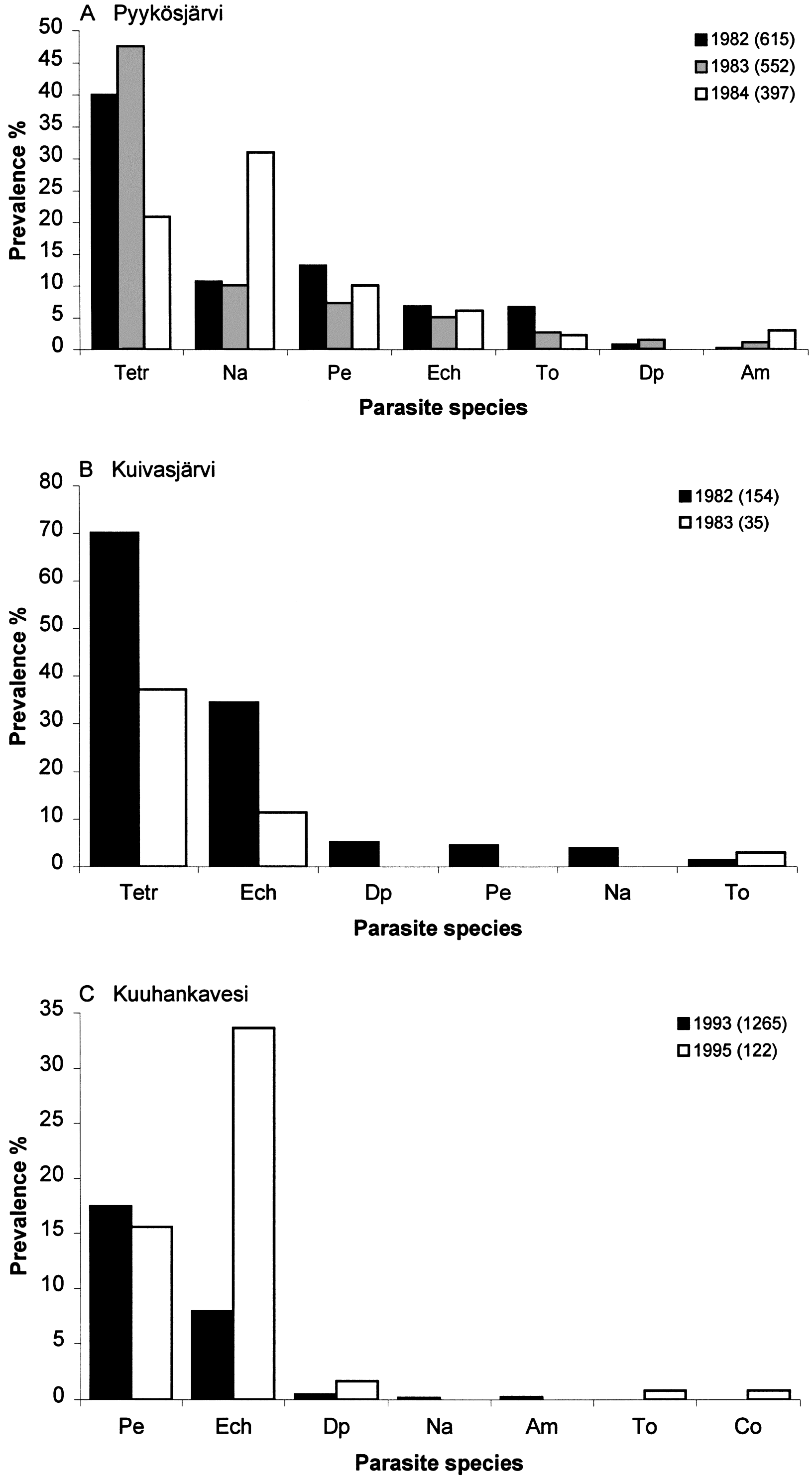


Fig. 3. Prevalence of individual parasite species in *L. peregra* from Pyykösjärvi (A) and *L. stagnalis* from Kuivasjärvi (B) and Kuuhankavesi (C) in each year studied. Sample sizes are in parentheses in the figure legends. Species recorded were Tetracotyle metacercariae (Tetr), *N. attenuatus* (Na), *P. elegans* (Pe), echinostomes (Ech), *T. ocellata* (To), *D. pseudospathaceum* (Dp), *A. minor* (Am) and *Cotylurus* sp. (Co).

diocercariae of *P. elegans* were dominant in the *L. stagnalis* population from Kuuhankavesi (17.3%). The proportion of snails infected with echinostomes, *P. elegans*, *N. attenuatus*, *T. ocellata*, *D. pseudospathaceum* and *A. minor* varied significantly among the three snail populations (χ^2-test on pooled data from all years, $P <$ 0.01 for each species). Only *Cotylurus* sp., which was recorded from a single snail from Kuuhankavesi but absent from the other two lakes, did not differ significantly in prevalence between sites (χ^2-test, $P > 0.05$).

No multiple infections of more than one digenean species were observed in *L. stagnalis* from Kuuhankavesi. However, joint infections were recorded in 7.4% of *L. peregra* from Pyykösjärvi and 28.0% of *L. stagnalis* from Kuivasjärvi, in most cases between Tetracotyle metacercariae and a cercarial species. In Pyykösjärvi, Tetracotyle co-occurred with all cercarial species and in three combinations the prevalence was significantly higher than that expected by chance: with *P. elegans* (2.30%), *N. attenuatus* (1.73%) and echinostomes (0.9%) (χ^2-test, $P < 0.001$ in all cases). However, only 1% of *L. peregra* from Pyykösjärvi were concurrently infected with two cercarial species (*T. ocellata* with *P. elegans*, *T. ocellata* with *N. attenuatus* or *P. elegans* with *D. pseudospathaceum*) and in no cases were the numbers of joint infections significantly greater than or less than expected by chance (χ^2-test, $P > 0.05$).

3.5. Seasonality and annual variability of infection

Logistic regression analysis of over-wintered *L. peregra* from Pyykösjärvi revealed a significant effect of both month and year on the prevalence of Tetracotyle metacercariae, echinostomes and *T. ocellata*, but no significant interaction between month and year (Table 2). This indicates that there were similar seasonal profiles in each year but significant differences between years in the mean prevalence (Figs. 3 and 4d). *T. ocellata* peaked in infection in July but the maximum prevalence in old snails in this month was lower in 1983 (5.6%) than in 1982 (21.2%) or 1984 (25.0%).

In the case of *D. pseudospathaceum*, only month had a significant influence on prevalence and no difference was found between years (Table 2). Neither the seasonal profile nor the mean prevalence therefore differed significantly between years. However, this was a rare parasite in Pyykösjärvi (Table 1), as was *A. minor*, for which both the seasonal profile and the mean level of infection did differ significantly between years (Table 2). The peak prevalence of *A. minor* in over-wintered *L. peregra* was only 1.0% and 1.3% in July of 1982 and 1983, respectively, but 25.0% (n = 4) in August 1984.

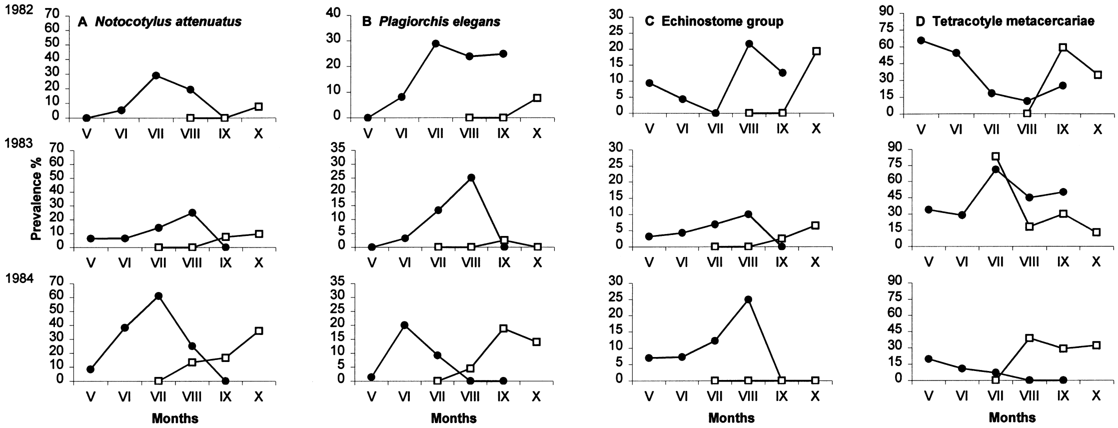
For both xiphidiocercariae and *N. attenuatus* there was a significant month effect and a significant interaction between the effects of month and year, indicating that the seasonal profile differed significantly between years (Table 2 and Fig. 4). However, the effect of year on the prevalence of infection was a significant only for *N. attenuatus*.

Therefore, of the seven trematode species or groups in Pyykösjärvi, four had consistent seasonal patterns of infection (Tetracotyle metacercariae, echinostomes, *T. ocellata* and *D. pseudospathaceum*) while annual variability was significant for all species except xiphidiocercariae and *D. pseudospathaceum*.

In *Lymnaea stagnalis* from both Kuivasjärvi and Kuuhankavesi, the cercarial infection increased from the spring to a maximum in September when the last samples were collected (Fig. 5). A significantly higher prevalence of cercarial infection than in June was recorded in September in Kuivasjärvi (χ^2-test, $P < 0.05$) and in September in Kuuhankavesi (χ^2-test, $P < 0.001$). The prevalence of Tetracotyle in Kuivasjärvi was highest in June and July but there was no significant variation in prevalence among sampling months (χ^2-test, $P > 0.05$). It was not possible to distinguish separate age cohorts of *L. stagnalis* from length-frequency distributions in either lake, but the greater the shell length size class the higher was the prevalence of infection. In the largest and oldest snails from Kuuhankavesi (shell length > 45 mm) the prevalence of cercarial infection was 96.6% while that of *P. elegans* exceeded 70%.

L. stagnalis were collected from Kuivasjärvi in only June and September of 1983. When comparing the pooled data from June and September of 1982 (n = 48) with that of 1983 (n = 35) there was no significant difference between years in the prevalence of any cercarial species (χ^2-test, $P >$ 0.05 in all cases) but the prevalence of Tetracotyle metacercariae was significantly lower in 1983 than in 1982 (χ^2-test, $P < 0.001$).

For Kuuhankavesi there was no significant difference between the single sample of *L. stagna-*



	V	VI	VII	VIII	IX	X
1982	32, 0	321, 0	104, 0	88, 19	8, 17	0, 26
1983	94, 0	93, 0	233, 6	20, 33	2, 40	0, 31
1984	71, 0	55, 0	98, 3	4, 67	2, 48	0, 50

Fig. 4. Monthly variation in prevalence of the main cercarial species and Tetracotyle metacercariae in over-wintered (filled symbols) and young-of-year (open symbols) *L. peregra* from Pyykösjärvi in each year studied (1982–1984). Numbers of over-wintered and young-of-year snails examined in each month are indicated at the bottom of the figure.

lis collected in July 1995 ($n = 122$) and the July data from 1993 ($n = 206$) in the prevalence of the dominant *P. elegans* (χ^2-test, $P > 0.05$) but a large and significant difference in the prevalence of echinostomes (χ^2-test, $P < 0.001$) (Fig. 3c). Many of the rare cercarial species in Kuuhankavesi were observed in only one of the two years that samples were collected.

Table 2. Logistic regression models for the probability of infection by various trematode species in relation to study year and month in Pyykösjärvi. The likelihood ratio gives a test statistic (χ^2) for the statistical significance of the change in the fit of the model if the particular term is removed. The difference in the degrees of freedom (df) between the corresponding models (with and without the term in question) is indicated.

Term	Change in log likelihood if term removed	Likelihood ratio	df	*P*
Tetracotyle metacercariae				
Year	–801	126.0	2	< 0.0001
Month	–758	41.57	3	< 0.0001
T. ocellata				
Year	–207	21.01	2	< 0.0001
Month	–243	93.86	3	< 0.0001
Xiphidiocercariae				
Month	–410	61.91	3	< 0.0001
Year × Month	–395	30.63	6	< 0.0001
N. attenuatus				
Year	–453	9.53	2	0.0085
Month	–485	73.30	3	< 0.0001
Year × Month	–459	20.70	6	0.0021
Echinostomes				
Year	–291	6.63	2	0.0363
Month	–301	26.95	3	< 0.0001
D. pseudospathaceum				
Month	–72	27.97	3	< 0.0001
A. minor				
Year	–74	17.03	2	0.0002
Year × Month	–77	22.56	6	0.0010

4. Discussion

A high prevalence of larval digenean infections was recorded in the two lakes of northern Finland, which are in close proximity but populated by different *Lymnaea* species, although overall *L. stagnalis* from Kuivasjärvi was more heavily infected than *L. peregra* from Pyykösjärvi. In both lakes, the parasite fauna was dominated by Tetracotyle metacercariae, which were absent from the population of *L. stagnalis* of lake Kuuhankavesi in central Finland. However, when excluding Tetracotyle, the prevalence of cercarial infections was significantly higher in northern Finland than in central Finland, or in the Tvärminne archipelago of southern Finland studied by Wikgren (1956) between 1946–1952. Interestingly, Wikgren also recorded a greater prevalence of cercarial infections in *L. stagnalis* than in *L. peregra*.

The present data for Finland as a whole demonstrate species-rich and prevalent lymnaeid parasite faunas when compared to earlier studies in other countries reviewed by Erasmus (1972) and more recent investigations in Europe and North America (e.g. Mangagonzalez *et al.* 1994, Toledo *et al.* 1998, Yoder and Coggins 1998). This is likely in part to reflect the type of freshwater habitat. Erasmus (1972) noted that the prevalence of infection in snail populations is typically higher in still waters such as Finnish lakes than in flowing waters such as the stream investigated by Yoder and Coggins (1998) or the river basin sampled by Mangagonzalez *et al.* (1994). Furthermore, prevalence has been observed to be lower in larger waterbodies (Erasmus 1972). This could account for the higher levels of infection in the two smaller northern Finnish lakes as compared with the larger Kuuhankavesi. It is also consistent with the observations of Wikgren (1956), who recorded a higher prevalence in snails from pools than those from shoreline areas of the Tvärminne archipelago.

The parasite species composition of the three lakes showed a considerable degree of overlap despite the difference in host species between Pyykösjärvi (*L. peregra*) and the other two lakes (*L. stagnalis*). This reflects a relatively low specificity of the digenean larvae for their molluscan intermediate host and also the fact that all the species recorded mature in aquatic birds, including migratory ducks. Furthermore, only one species (*D. pseudospathaceum*) utilises fish as obligatory second intermediate hosts. Metacercariae of this digenean locate in the eyes of various fish species and the adults are intestinal parasites of fish-eating birds, particularly those of the order Lariformes (Niewiadomska 1996). Five of the larval digeneans of the present study (*E. revolutum*, *E. recurvatum*, *H. conoideum*, *A. minor* and *N. attenuatus*) were earlier recovered as adults from ducks (*Anas* spp. and *Aythya* spp.) collected from Hailuoto Island in the Bothnian Bay (Brglez & Valtonen 1987). The same population of birds also harboured a separate *Plagiorchis* species (*P. laricola*) and *Cotylurus cornutus*. Due to the close proximity of Kuivasjärvi and Pyykösjärvi it is inevitable that cross-infection of the lakes with larval digeneans will occur as birds move between them.

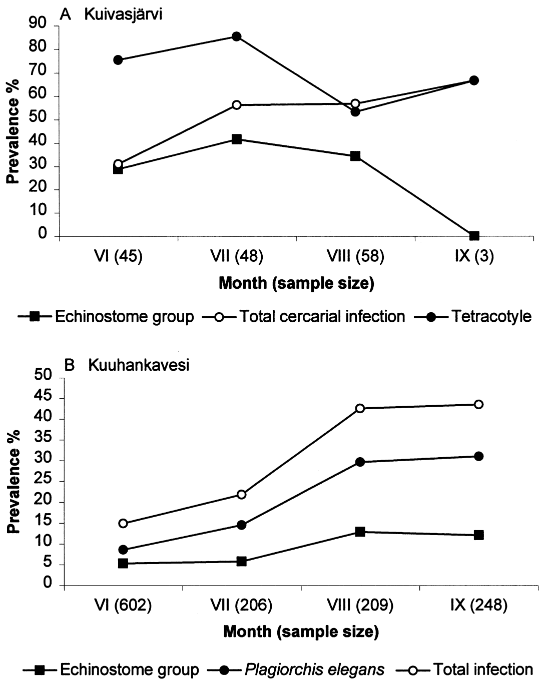


Fig. 5. Monthly variation in prevalence of the dominant cercarial species and Tetracotyle metacercariae in *L. stagnalis* from (A) Kuivasjärvi in 1982 and (B) Kuuhankavesi in 1993.

The parasites which did not overlap between the two species of lymnaeid hosts included those known to be host specific, such as *Echinoparyphium recurvatum*, which is restricted to *L.*

peregra, and the morphologically similar *Hypoderaeum conoideum* found only in *L. stagnalis*. However, considering echinostomes as a group, all the cercariae of northern Finland were also present in the central Finnish lake. Previous investigations of parasite communities in lymnaeids conducted elsewhere in Europe and North America have rarely achieved the level of identification of this study and frequently identified the parasites only to type or genus. It is therefore difficult to make general conclusions about whether the high parasite overlap recorded here is a typical pattern or characteristic of palearctic lakes.

It was notable that the dominant cercarial species was different in each lake (*N. attenuatus* in Pyykösjärvi, echinostomes in Kuivasjärvi and *P. elegans* in Kuuhankavesi). However, without knowing the actual bird definitive hosts for these larval digeneans it is not possible to determine whether variations in their prevalence between lakes are accidental or related to bird host distribution.

Tetracotyle metacercariae dominated the parasite fauna of the lymnaeids from both lakes in northern Finland although the prevalence was higher in *L. stagnalis* from Kuivasjärvi (64.0%) than in *L. peregra* from Pyykösjärvi (37.8%). The metacercariae were not identified but may have represented more than one Strigeid species. However, as adults of *C. cornutus* were noted to be highly prevalent in Anatidae from the same area (Brglez & Valtonen 1987) the metacercariae in lymnaeids from Pyykösjärvi and Kuivasjärvi may have been partly of the same *Cotylurus* species.

Several freshwater snail species, including lymnaeids, can serve as first intermediate hosts to *Cotylurus* species. Curiously, no *Cotylurus* cercariae were observed in either *L. peregra* of Pyykösjärvi or *L. stagnalis* of Kuivasjärvi, despite the high prevalence of Tetracotyle metacercariae in both of these lakes. Similar results also troubled Wikgren (1956), who commonly found Tetracotyle cysts in all *Lymnaea* species he dissected but rarely observed the cercarial stage. Yoder and Coggins (1998) also noted that metacercariae of *Cotylurus flabelliformis* were highly prevalent in *L. stagnalis* from a stream in southeastern Wisconsin but sporocysts and cercariae of this species were rarely found. A solution to this puzzle may have been found by Campbell (1997) who studied the host-finding behaviour of *C. flabelliformis* cercariae for five species of snail host. The cercariae displayed chemo-positive attraction to the snails, especially to *L. stagnalis*, were host-specific and did not penetrate the snail which produced them. Therefore, the Tetracotyle species in Pyykösjärvi and Kuivasjärvi are likely to use lymnaeids only as second intermediate hosts and alternative snail species as the first intermediate hosts.

The seasonal profile of cercarial infections differed between the two *Lymnaea* species but followed very similar patterns to those reported previously (Erasmus 1972). In Pyykösjärvi, the prevalence of cercarial species in over-wintered *L. peregra* increased from spring to late summer, when this cohort of snails died out, and there was a subsequent accumulation of infection in young-of-year snails born in the summer. Furthermore, logistic regression analysis revealed a consistent seasonal pattern of infection in each of the three years studied for four of the seven species or groups of parasites in this lake. For the longer-lived *L. stagnalis* in Kuivasjärvi and Kuuhankavesi there was no complete disappearance of adult molluscs in late summer and cercarial prevalence continued to increase throughout the open-water period.

There was significant annual variation in infection in Pyykösjärvi with all larval digeneans except *D. pseudospathaceum* and xiphidiocercariae. However, the parasite community structure and species composition remained approximately constant during the three years of study. This stability in the parasite communities is quite remarkable considering the long dormant winter period, which breaks the transmission cycle of the parasites each year. Migratory birds gradually lose their parasite infections during the winter migration and the time spent in the wintering area (Erasmus 1972). However, there was clear evidence in this study that larval digeneans can overwinter in their snail hosts. This must help to both maintain infections within the mollusc population and also act as a 'seed' for re-infection of aquatic birds returning to breed in the spring, who will then begin to deposit parasite eggs into the lakes in early summer. The complete re-establishment of parasite life-cycles each spring via the adult birds must therefore be a very rapid process.

However, it is probably the juvenile population of birds in each year that plays the key role in maintaining the stability of the lymnaeid parasite communities. According to Brglez and Valtonen (1987), the Anatidae of Hailuoto Island acquire trematode infections as juveniles in the nesting areas. The juvenile birds will therefore not only obtain parasites of local origin but they will also rapidly infect the young-of-year snails as they live in close proximity along the shoreline among the vegetation. The rate at which the young snails accumulate larval digenean infections indicates that large numbers of miracidia are present in the water at the time. Juvenile birds therefore facilitate the high parasite prevalence of infection in lymnaeids each summer and also help to maintain the composition of the larval digenean community from one year to the next. However, this is only possible because the parasites themselves exhibit a low specificity for their bird definitive hosts (Brglez & Valtonen 1987) and are therefore unaffected by annual variations in the migratory bird populations.

This low specificity of the parasites for their avian hosts enables a variety of migratory bird species to become infected and transmit infection from one waterbody to another. As Finland has a vast number of lakes, many of which are interconnected, the parasites will eventually spread to colonise any aquatic habitats where the appropriate intermediate hosts are present and where infected birds continue to visit.

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