Within-lake dynamics in the similarity of parasite assemblages of perch (*Perca fluviatilis*)

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SUMMARY

Although parasite communities have been studied extensively in recent years, spatial and temporal variation in factors affecting the communities has received less attention. This paper examined the similarity of parasite assemblages of perch (*Perca fluviatilis*) in 18 locations within a single lake in relation to geographical distance and temporal dynamics in the host and parasite populations. We expected that in the present study-scale where distinct but potentially interacting host subpopulations could occur, similarity of the assemblages could be affected by seasonal dynamics in host movements particularly during the spawning period. Parasite species showed differences in infection levels between the sampling locations and similarity of the assemblages of autogenic parasite species in winter, measured inversely as difference in parasite numbers, was negatively affected by geographical distance between the locations. However, no such relationship was observed in the allogenic species *Ichthyocotylurus variegata*. Furthermore, no relationship was found either in autogenic parasites when the locations were re-sampled in summer, after the spawning period of perch. We concluded that the effect of geographical distance on the similarity of parasite assemblages is a dynamic process, which is affected by seasonal dynamics in host and parasite populations.

Key words: parasite communities, within-lake dynamics, autogenic-allogenic species concept, similarity, distance, transmission, seasonality.

INTRODUCTION

During recent years, considerable research interest has been focused on parasite communities (e.g. Esch, Bush and Aho, 1990; Janovy, Clopton and Percival, 1992; Sousa, 1994; Poulin, 1998, 2001; Carney and Dick, 2000; Valtonen *et al.* 2001; Valtonen, Pulkkinen and Julkunen, 2003*a*), which has revealed a range of factors affecting their formation and structure. However, much less emphasis has been put on the effects of spatial and temporal variation, and short-term and local processes, on community structure, which is why it is difficult to draw general conclusions on the significance of these factors. Although some recent studies have tackled spatial and temporal variation influencing repeatability in parasite community structure (Poulin and Valtonen, 2002; Timi and Poulin, 2003; Vidal-Martinez and Poulin, 2003), more studies are needed to obtain a better understanding of the patterns operating in different systems and study scales. One important factor influencing the similarity of parasite communities is geographical distance (Poulin and Morand, 1999; Poulin, 2003; Karvonen and Valtonen, 2004), which has generally been studied at the level of host populations. However, the effect of distance on the similarity of parasite communities has not been considered at a scale of a single host population i.e. between potentially interacting subpopulations where host movements may directly influence the similarity in relation to geographical distance. Furthermore, it is not known how temporal dynamics in host populations (movement or migration) or in parasite occurrence (seasonality of transmission) may change this relationship. In this study, we examined spatial and temporal dynamics in the structure of metazoan parasite assemblages of perch (*Perca fluviatilis*).

In a recent study, Karvonen and Valtonen (2004) examined parasite assemblages of whitefish in a cluster of lakes connected by a common waterway. They found that similarity in autogenic parasite species assemblages was negatively affected by geographical distance and concluded that this was due to long colonization distances between the lakes (see also Poulin and Morand, 1999; Poulin, 2003). Perch is a widespread and abundant freshwater fish species, which is found in various types of environments and is known to harbour a considerable number of helminth parasites (Valtonen, Holmes and Koskivaara, 1997; Valtonen *et al.* 2003*b*). Perch is also considered a relatively sessile species and in this respect provides a different type of study object compared to

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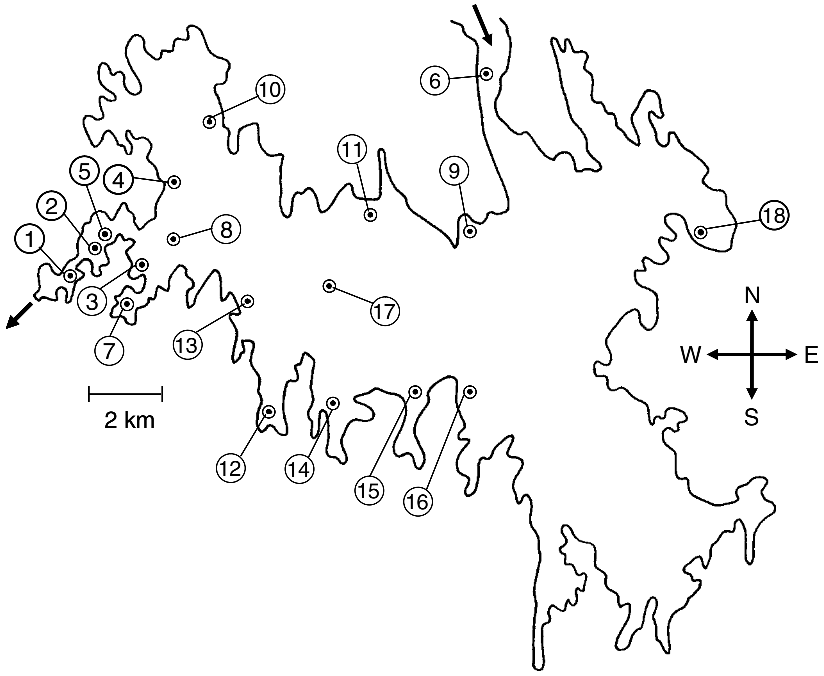

Fig. 1. Map of the Lake Konnevesi (Central Finland) indicating the 18 locations sampled for perch (*Perca fluviatilis*) in winter and summer 2004. Arrows indicate direction of water flow.

migratory whitefish. However, perch may still move long distances (Johnson, 1978; Valkeajärvi, 1983) and this is particularly likely during the spawning period in spring when the fish gather to certain spawning areas within a lake in high numbers (Treasurer, 1981; Koli, 1990; Craig, 2000). During this period some degree of interaction and mixing between subpopulations could be expected, which could provide a seasonal component affecting the relationship between geographical distance and similarity of parasite assemblages.

In the present paper, we studied the similarity of parasite assemblages of perch in an oligotrophic lake in Central Finland. Our study scale was small enough for factors such as trophic status, lake size and altitude (e.g. Wisniewski, 1958; Esch, 1971; Kennedy, 1978; Esch *et al*. 1988, Marcogliese and Cone, 1991; Karvonen and Valtonen, 2004) to become negligible, but large enough to allow examination on the similarity of parasite assemblages in subpopulations of perch in relation to geographical distance. Our aim was to examine how geographical distance affected the similarity of autogenic and allogenic parasite assemblages in a temporal scale by sampling a number of locations in the lake before and after the spawning period of perch during which more extensive movement of fish could occur. We expected that (1) similarity would be negatively influenced by increasing geographical distance particularly in autogenic parasite species and (2) this relationship could be different between seasons if mixing of fish individuals between subpopulations took place.

MATERIALS AND METHODS

The study was conducted at Lake Konnevesi (62°N 26°E), which is an oligotrophic lake in Central Finland (Fig. 1) with an area of 113 km^2 and mean depth of 13 m (max depth 56 m). Eighteen locations were selected from the lake and the distance between the locations varied from 0·25 to 21 km (Fig. 1). Two samples of perch were caught from each location using fish traps placed to the depth of 2–3 m (Table 1). First samples were taken in mid-winter (January–February 2004), during the ice cover, when water temperature reaches as low as 1–2 °C and there is very little, if any, parasite transmission taking place. Second samples were taken in June 2004, well after the ice melt and the spawning period of perch in May. Live fish were transferred to the laboratory where they were killed, measured for length and dissected. Each time, the purpose was to obtain best possible homogeneity in the size of fish (see Fig. 2). Mean size of the studied fish ranged from 10·33 ± 0·15 cm to 13·86 ± 0·52 cm (mean ± S.E.) and this did not differ between the seasons (*t*-test: $t_{34} = -1{\cdot}18$, $P = 0{\cdot}25$; Fig. 2).

Instead of studying the whole parasite fauna, we focused on metazoan species found in the viscera. These species included metacercariae of the trematode *Ichthyocotylurus variegata*, which are found in heart, liver, swim bladder and kidney of perch. These organs were removed from each fish and studied for *I. variegata* infection by compressing the organs separately between 2 glass plates under a microscope. Other species included those found in the

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Table 1. Number of perch (*Perca fluviatilis*) studied for metazoan endoparasites from 18 locations in Lake Konnevesi (Central Finland) during winter and summer 2004

Location	Winter	Summer
1	44	31
2	31	31
3	34	30
4	44	31
5	30	31
6	34	30
7	48	31
8	31	31
9	27	31
10	38	31
11	34	31
12	31	31
13	36	31
14	10	31
15	33	30
16	30	30
17	32	33
18	35	31
Total	602	556

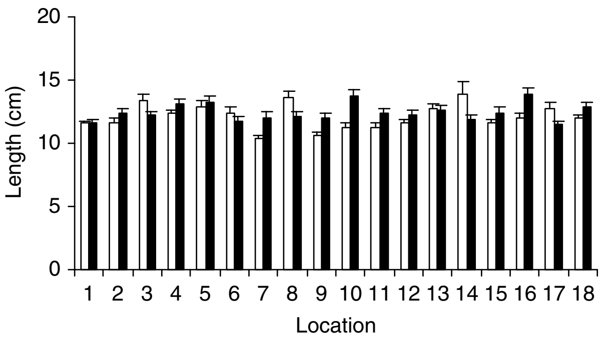

Fig. 2. Mean length (+S.E.) of perch (*Perca fluviatilis*) caught from 18 locations in Lake Konnevesi (Central Finland) in winter (□) and summer (■) 2004. Numbers of studied fish are indicated in Table 1.

intestine: cestode *Proteocephalus percae*, trematode *Bunodera lucioperca*, nematode *Camallanus lacustris* and acanthocephalan *Acanthocephalus lucii*. Infection of these parasites was studied by removing the intestine from each fish and studying the contents using the method described above.

For the data analysis, we measured 2 geographical distances between the sampling locations (all possible pairs) from a map: the straight distance and the distance via waterway, which corresponded to the colonization distance for allogenic and autogenic parasites, respectively (see Karvonen and Valtonen, 2004). Absolute values of difference in the mean parasite abundance between the locations were then calculated for each parasite species and used as an inverse measure of similarity in parasite assemblages. For the autogenic species (*P. percae*, *B. lucioperca*, *C. lacustris* and *A. lucii*) differences were summed across species yielding one value for each pair of locations. We also calculated the absolute difference in the mean length of fish between the locations, which could be compared with the similarity values for corresponding location pairs. Values for allogenic (*I. variegata*) and autogenic parasite species were then plotted against the corresponding values of geographical distance, and fish length, and the relationships were analysed using linear stepwise regression analysis. Differences in parasite abundance between the locations and seasons were analysed using non-parametric tests. All analyses were conducted in SPSS statistical package.

RESULTS

The most prevalent and abundant parasite species was *I. variegata*, which was observed in 99·5% of the studied fish and had high abundances throughout the lake comprising 83·2% of the parasite individuals observed (Fig. 3). Prevalences of other parasite species were lower ranging from 32·2% to 72·1%. Abundances varied significantly between the locations in all parasite species (Fig. 3): *P. percae* (Kruskall-Wallis test on data combined across seasons: $\chi^2 = 242{\cdot}46$, D.F. $= 17$, $P < 0{\cdot}001$), *B. lucioperca* ($\chi^2 = 137{\cdot}56$, D.F. $= 17$, $P < 0{\cdot}001$), *C. lacustris* ($\chi^2 = 76{\cdot}55$, D.F. $= 17$, $P < 0{\cdot}001$), *A. lucii* ($\chi^2 = 35{\cdot}81$, D.F. $= 17$, $P < 0{\cdot}001$) and *I. variegata* ($\chi^2 = 403{\cdot}99$, D.F. $= 17$, $P < 0{\cdot}001$). However, a seasonal component was observed only in *A. lucii* whose abundances were higher at all locations in summer (Mann-Whitney U-test: $Z = -5{\cdot}06$, $P < 0{\cdot}001$; Fig. 3). Parasite abundance was significantly correlated between the seasons in *P. percae* (Spearman correlation: $r_s = 0{\cdot}68$, $n = 18$, $P < 0{\cdot}01$), *C. lacustris* ($r_s = 0{\cdot}60$, $n = 18$, $P < 0{\cdot}01$) and *I. variegata* ($r_s = 0{\cdot}82$, $n = 18$, $P < 0{\cdot}001$).

The analysis of the relationships between geographical distance and similarity in parasite assemblages between the locations indicated that in winter the difference in abundance of autogenic parasite species was increased, i.e. similarity was decreased, with increasing distance (stepwise linear regression: $r^2 = 0{\cdot}17$, $F = 31{\cdot}37$, $P < 0{\cdot}001$; Fig. 4). The effect of fish length was non-significant and was excluded from the analysis. However, no relationship between similarity and distance was observed with the allogenic *I. variegata*, but similarity was decreased with increasing difference in fish length ($r^2 = 0{\cdot}09$, $F = 14{\cdot}44$, $P < 0{\cdot}001$). In summer, no relationship was observed either in autogenic or allogenic species (Fig. 4), but fish length had the same effect on the similarity in *I. variegata* ($r^2 = 0{\cdot}10$, $F = 17{\cdot}51$, $P < 0{\cdot}001$). Exclusion of each autogenic parasite species at a time from the analysis did not affect the result.

DISCUSSION

This paper examined the structure of parasite assemblages of perch (*P. fluviatilis*) in a large lake

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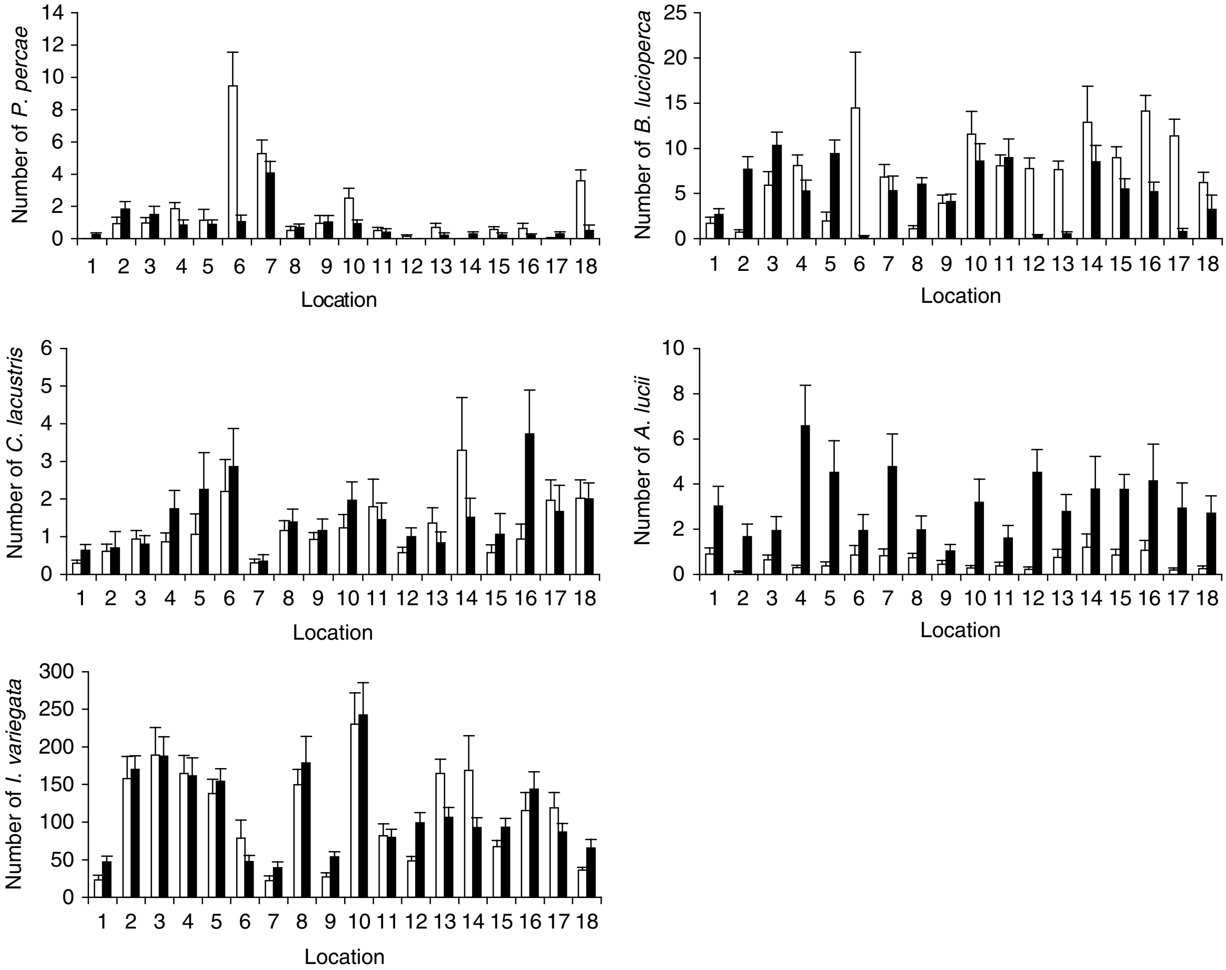

Fig. 3. Mean abundance (+S.E.) of 5 metazoan parasite species in perch (*Perca fluviatilis*) caught from 18 locations in Lake Konnevesi (Central Finland) in winter (□) and summer (■) 2004. Note differences in Y-axis scales. Numbers of studied fish are indicated in Table 1.

in Central Finland. Our aim was to explore how geographical distance affected the similarity of the assemblages and if this relationship had a seasonal component in respect to expected movement and mixing of individuals among the host subpopulations. Parasite species showed considerable variation in the infection levels between the 18 sampling locations and the abundance of *A. lucii* differed also between the seasons. Difference in parasite assemblages of autogenic species was increased with increasing distance between the sampling locations in winter, distance accounting for 17% of the variance, but the relationship was no longer observed in summer after the spawning period of perch. No such relationship was observed either in allogenic *I. variegata*. This study was conducted at the scale of a single large lake and we recognize that this may cast a doubt on the independency of the fish samples between different locations. However, as the purpose was to explore how the structure of parasite assemblages changed in spatial and temporal scale, each of the samples was considered a snapshot of the assemblage at one particular location and time providing a reasonable estimate of parasite occurrence for the purpose of this study. Furthermore, although winter sampling was conducted within a period of 2 months, we assumed that there was little movement of fish between the locations during that time, which seems reasonable since the activity of fish is generally low in winter as a result of low water temperature (1–2 °C) and low light intensity caused by the ice cover (Wootton, 1990).

The species composition in terms of parasite prevalence and abundance was typical for perch and resembled that described in other lakes in Central Finland (Valtonen *et al*. 1997, 2003*b*). However, the mean abundances of *I. variegata*, although highly variable between the locations, were substantially higher than those reported by Valtonen *et al*. (1997, 2003*b*). This is likely to be caused by specific local circumstances such as differences in the composition and abundance of intermediate hosts, which generate variation in the transmission rates of *I. variegata*, and also the other parasite species investigated in this study. Moreover, the lack of seasonality in parasite infection during the period between January and June, except that for *A. lucii* (see also Brattey, 1988), probably reflects specific transmission dynamics of

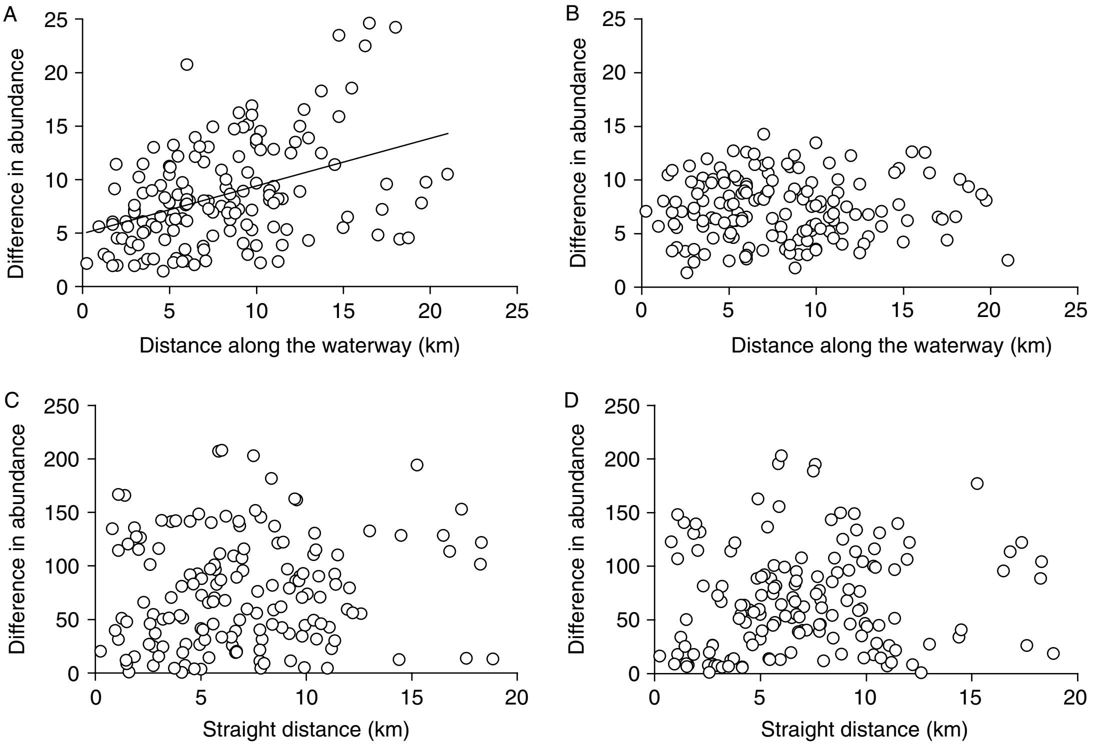

Fig. 4. Relationships between geographical distance and similarity in parasite assemblages of perch (*Perca fluviatilis*) between 18 locations in Lake Konnevesi (Central Finland) in 2004. Absolute differences in parasite abundances were used as inverse measures of similarity. The relationships were calculated separately for the autogenic parasite species (summed value of difference in *P. percae*, *B. lucioperca*, *C. lacustris* and *A. lucii*) and the corresponding measure of distance in winter (A) and summer (B), and for the allogenic parasite species *I. variegata* in winter (C) and summer 2004 (D).

these species, which are discussed in more detail below.

The difference in parasite assemblages of autogenic parasite species was increased with geographical distance, which is consistent with previous findings (Karvonen and Valtonen, 2004; see also Poulin and Morand, 1999; Poulin, 2003) and indicates that distance may have a major role in shaping parasite assemblages even in the scale of a single lake. Apparently, distances in this system were long enough to allow the formation of distinct subpopulations of perch, which were characterized by different infection levels. In summer, the relationship between similarity and geographical distance was no longer observed. It could be speculated that the disappearance of the relationship was caused by changes in the transmission rate of the autogenic parasite species between January and June. This is unlikely, however, since temporal change in transmission was observed only in *A. lucii* and the exclusion of the parasite species one by one from the analysis indicated that the relationship was not caused by any of the species alone. However, significant positive correlations in the abundances of *P. percae* and *C. lacustris* between seasons might imply that these species have a lesser role in causing the result.

The more likely explanation for the observed result is the increased activity and movement of fish with increasing water temperature after the ice melt, which was expected to mix fish individuals between the subpopulations. This would be particularly evident during the spawning period of perch, which took place in May between our sampling periods and generally concentrates large numbers of fish to certain areas (Treasurer, 1981; Koli, 1990; Craig, 2000). Tagging-recapture experiments in Lake Konnevesi also indicate that perch can move distances up to 10 km (Valkeajärvi, 1983). It is possible that the best spawning sites attract fish from long distances, which could allow the mixing of the subpopulations to the extent that differences in the assemblages of these relatively short-lived (up to 1 year) and non-accumulative autogenic parasite species (e.g. Rahkonen, Valtonen and Gibson, 1984; Brattey, 1988; Valtonen and Rintamäki, 1989) have disappeared. It is also possible that seasonal differences in parasite transmission become important in late summer and autumn (after our sampling period in June), which could again cause subpopulations to diverge in terms of structure of parasite assemblages. For example, transmission of the most abundant autogenic species *B. lucioperca* takes place in late summer and autumn (Rahkonen *et al.* 1984).

We observed no relationship between geographical distance and difference in abundance of the allogenic *I. variegata*. The same phenomenon has also been observed in the related species *I. erraticus* infecting whitefish in lakes in north-eastern Finland (Karvonen and Valtonen, 2004). The lack of the relationship is probably caused by higher movement rate of the avian definitive hosts of these species compared to autogenic parasites (Esch *et al.* 1988; Criscione and Blouin, 2004), which leads to effective dissemination of parasite infective stages and steady infection in the populations of intermediate molluscan hosts. On the other hand, differences in the infection level between the locations are likely to be due to different composition of molluscan hosts. Moreover, these parasites tend to accumulate in fish and can probably live for an extended period of time as metacercarial stages, which is likely to obscure seasonal patterns in parasite occurrence but cause the observed relationship between the difference in the parasite abundance and fish length.

To conclude, we observed that the difference in parasite assemblages of perch increased with geographical distance, which indicates that distance is an important factor contributing to the structure of these assemblages even on the scale of a single lake. The relationship was different for autogenic and allogenic parasite species, which supports the role of their different colonization and transmission patterns in shaping the structure of parasite assemblages in fish. Moreover, observed seasonality in the effects of distance on similarity of parasite assemblages, despite of the positive correlations in the occurrence of some parasite species between seasons, suggests that this relationship is dynamic i.e. the effect may be observed at one time but not at other. This could be due to factors such as host movements and seasonal patterns in parasite transmission although the latter was not supported by the present data. Nevertheless, dynamic patterns in host and parasite populations may be important in determining the occurrence or magnitude of relationships between parasite community structure and geographical distance.

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