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The biogeography of parasitism in sticklebacks: distance, habitat differences and the similarity in parasite occurrence and abundance

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Similarity in parasite community composition often decreases with both increasing geographic distance and environmental dissimilarity between localities, though it is unknown whether similarity in local abundance of selected parasite species follows similar rules. We tested this using data on metazoan parasites in 126 stickleback (*Gasterosteus aculeatus*) populations, with locations from Eurasia, eastern North America, and western North America treated separately. Similarity values were regressed against pairwise distances between localities; after correcting for distance, the effect of environmental dissimilarity was assessed by splitting similarity values into those between pairs of localities with either similar, moderately different or very different salinity (freshwater, marine or brackish). For selected parasite species, pairwise similarity in abundance (mean no. parasites per host) were computed across all localities, and treated as above. Similarity in parasite community composition decreased with increasing distance between localities in all three geographic regions. A significant effect of environmental difference was found in all regions: for a given distance between two sites, their parasite communities were more similar if they were of the same salinity. Slopes for distance decay in similarity were consistently higher for eastern North America than for Eurasia. Among the 12 parasite species for which sufficient data were available, only 4 showed the expected relationship, i.e. the greater the geographical separation between host populations, the greater the difference in parasite abundance; also, significant effects of environmental differences in salinity were only found for 3 of these species. Our findings show that parasite communities of sticklebacks are structured by geographical distance and local salinity conditions. The results indicate that strong effects at the community level do not translate into corresponding effects at the population level, suggesting that parasite dispersal and population dynamics are controlled by different processes.

The geography of parasitism is attracting increasing attention in the context of emerging diseases, biological invasions and environmental change (Rohde 2002, Poulin and Morand 2004, Morand and Krasnov 2010). At large spatial scales, much attention has been paid to the composition of parasite communities, which vary widely across host populations of the same species. Typically, a suite of predictable parasite species occurs across most of a host's geographical range, whereas others only exploit the host in some parts of its range; this has been well-documented in freshwater fish (Carney and Dick 1999, Nelson and Dick 2002). Host specificity resulting from vicariance events or a long coevolutionary history between some parasites and their host, the ability of generalist parasites to exploit different host species with similar ecological attributes, and the susceptibility of many hosts to colonization by new parasites after their introduction to new localities, all combine to create a mosaic of parasite assemblages across the geographical range of any host species (Barker et al. 1996, Carney and Dick 1999, 2000, Choudhury and Dick 2001, Nelson and Dick 2002, Poulin and Mouillot 2003). Not only the composition of parasite communities, but also the abundance of particular parasite species may change across the geographical range of the host. Indeed, parasite abundance, measured as the mean number of conspecific parasites per individual host, can vary by more than one order of magnitude among host populations (Poulin 2006).

Recent studies suggest a recurrent pattern in the geographic variation in the composition of parasite communities. The distance between different parasite communities, i.e. between different host populations, is emerging as the key determinant of their similarity (Poulin and Morand 1999). As a rule, the similarity in species composition between any two parasite communities of the same host species decreases exponentially with increasing distance between them. This is true for freshwater fish hosts inhabiting fragmented and physically isolated habitats such as lakes and rivers (Poulin 2003, Seifertova et al. 2008), but also for marine fish (Oliva and Gonzalez 2005, Pérez-del-Olmo et al. 2009, Thieltges et al. 2010) and other organisms (Poulin 2003, Krasnov et al. 2005, Thieltges et al. 2009) living in more-or-less continuous habitats. This distance decay of similarity is an almost universal phenomenon in biogeography (Nekola and White 1999, Soininen et al. 2007). It results from three non-exclusive types of processes: species-sorting along environmental gradients, dispersal constraints imposed by topography, and intrinsic species differences in dispersal abilities (Soininen et al. 2007). The limited dispersal abilities of most parasites can certainly contribute to distance decay in community similarity, but so can the influence of environmental gradients across geographic space. For instance, environmental factors determine the distribution of all intermediate or definitive hosts necessary for the completion of a parasite's life cycle. More directly, the free-living infective stages of parasites can only survive and successfully infect a host within narrow and species-specific sets of environmental conditions (Pietrock and Marcogliese 2003). Beyond its effect on community composition, the fact that two nearby localities share many biotic and abiotic features, whereas distant ones are more likely to differ, should also influence the similarity in abundance of particular parasite species between two host populations (Poulin and Dick 2007).

Although previous studies have documented the influence of distance between localities on either parasite community similarity or abundance of given parasite species, there have been few attempts to use distance decay relationships to test specific hypotheses about either the processes causing the decay, or biogeographical differences in rates of decay. Among communities of ectoparasites on mammalian hosts, for instance, differences in environmental variables between localities are often more important than distance per se in explaining variation in species composition between communities (Krasnov et al. 2005, Vinarski et al. 2007). For parasite communities of fish hosts, this possibility, as well as many other important issues, remain completely unexplored. In fish species occurring along an environmental gradient, such as that from marine to freshwater habitats, similarity in parasite communities between any two fish populations might depend more on environmental similarity than on pure distance (Thieltges et al. 2010). The same is true of similarity in the abundance of specific parasite species. Comparisons of the rate at which similarity decreases with distance among host populations inhabiting the same or distinct types of environments would allow us to distinguish between the effects of environmental variables versus distance itself. In addition, decay in parasite community similarity might vary across the geographical range of the host. Such variation could reveal heterogeneous patterns in beta-diversity, which is the rate of change in species composition across localities that is used to estimate the level of endemism, i.e. the proportion of species restricted to one or few localities. However, when the same parasite species or related parasite taxa infect a host species across its entire range, we would predict similar decay rates in community similarity in different parts of the host's range if biological features, such as dispersal abilities, are not outweighed by physical factors such as major biogeographic barriers.

Here, we address these biogeographical issues related to the effects of distance using the metazoan parasite communities of the threespine stickleback *Gasterosteus aculeatus* (Pisces: Gasterosteidae). This is an ideal host species for such a study, for a number of reasons. First, it lives in a wide range of aquatic habitats (Wootton 1984). Some populations are resident in freshwater habitats ranging from large lakes to small ponds and streams. Others are anadromous, migrating to the sea in autumn and then back into rivers, salt marshes or tidal pools in the spring to breed; these anadromous populations generally live their entire life in habitats ranging from brackish to fully marine. Second, the threespine stickleback has a broad circumpolar geographical distribution, occurring along most coastal habitats of North America and Eurasia above about 35°N (Wootton 1984). Its presence in freshwater habitats far inland from the coast results mostly either from Pleistocene glaciations or from invasion along riverine routes (Wootton 1984). Speciation is occurring in some regions (Rundle et al. 2000, Colosimo et al. 2005), but all lineages remain closely-related sibling species. Third, the biology of the threespine stickleback has been very well-studied, since it has been a very popular laboratory model for behavioural and evolutionary studies (Wootton 1984, Bell and Foster 1994, Foster and Baker 2004, Ostlund-Nilsson et al. 2006). Finally, several parasite species are known to exert strong selective pressures on threespine sticklebacks. The cestode *Schistocephalus solidus* can induce drastic reductions in stickleback reproductive output (Heins and Baker 2008), as well as cause marked alterations in the behaviour and phenotype of its fish host (LoBue and Bell 1993, Ness and Foster 1999, Barber et al. 2004). Larval stages of the trematode *Diplostomum* spp. can cause partial blindness in sticklebacks (Owen et al. 1993) and select for strong investments in immune defences (Kalbe and Kurtz 2006). The ectoparasitic crustaceans *Argulus* spp. cause changes in schooling and habitat selection by threespine sticklebacks (Poulin and FitzGerald 1989a, b), as well as increasing their mortality (Poulin and FitzGerald 1987). It is therefore important to identify the forces acting on the geographic distribution of these and other parasites in order to better understand their possible role in the rapid phenotypic diversification of threespine sticklebacks (Bell and Foster 1994, Foster and Baker 2004, Ostlund-Nilsson et al. 2006).

Our specific objectives are 1) to determine whether the similarity in species composition of parasite communities between populations of threespine sticklebacks *G. aculeatus* decays significantly with increasing geographical distance; 2) to assess whether parasite community similarity is influenced by habitat similarity independently of spatial distance; 3) to compare rates of decay in similarity among different regions within the stickleback geographical range; and 4) to evaluate whether differences in local abundance of specific parasite species between host populations follow similar spatial decay patterns. This last objective represents the first application of distance decay models to intraspecific variation in parasite abundance across geographical space. We take advantage of a model host species that occurs in different salinities to assess whether habitat similarity plays an equally important role compared to spatial distances between localities in shaping parasite assemblages.

Materials and methods

Data compilation

Data on parasite communities in threespine stickleback populations were obtained from the literature and from unpublished studies made available to us following a request for data made to numerous colleagues worldwide (Supplementary material Appendix 1, 2 for the data, and Appendix 3 for the sources). We only included data from complete metazoan parasite surveys, that is, those in which it was clear that the authors searched for both internal and external parasites. In addition, we only retained surveys in which both the locality of sampling and the type of aquatic habitat were specified. For each survey, i.e. each stickleback sample, we recorded: 1) the name of the sampling locality and its longitude and latitude; 2) the habitat type, i.e. either freshwater, brackish or marine, which had to be inferred from the location in many cases; 3) the number of individual fish examined for parasites, if available; 4) the list of parasite taxa found that were identified at least to the genus level, with corrections made for all known synonymies; and 5) the abundance of each parasite species, i.e. the mean number of individual parasites of a given species per individual host, for the subset of surveys providing this information or allowing its computation from data on prevalence and intensity of infection. The month and year of sampling were also recorded; most localities were sampled during summer months, sometimes over two or more years.

Parasite species richness, or the number of parasite species, generally correlates positively with sampling effort: the more individual hosts are examined for parasites, the more parasites are found, up to an asymptote corresponding to the actual parasite species richness in the host population (Walther et al. 1995). To verify that stickleback populations could all be included in our analyses regardless of how many fish were examined for parasites in each case, we tested for correlations between parasite species richness and host sample size (both log-transformed) across the different localities. Since the number of fish examined for parasites was not available for all surveys, we also compared parasite species richness between surveys with known and unknown sample sizes, using a Wilcoxon two-sample test. Finally, the analyses were also repeated after exclusion of localities for which the number of fish examined for parasites was not available.

The localities were clustered into three distinct geographical regions: Eurasia, northeastern North America and northwestern North America (Fig. 1). There are clear genetic differences between threespine sticklebacks from these three areas, suggesting that they represent distinct lineages with no recent gene flow (Colosimo et al. 2005, Mäkinen and Merilä 2008). For these reasons, the three regions are hereafter treated separately. In addition, we prepared the data as matrices of parasite species (columns) by localities (rows), with data on presence/absence of species and data on species abundance placed in different matrices. Thus, we ended up with five different data matrices on which subsequent analyses are performed: parasite presence/absence matrices for each of the three geographical regions, and parasite abundance matrices for Eurasia and NE North America (abundance data were available for an insufficient number of localities from NW North America). Because abundance data are not available from all sites, fewer localities are included in the parasite abundance matrices than in the parasite presence/absence matrices.

Distance and similarity measurements

For any given number of localities, n, the number of possible pairwise comparisons among them is $n(n-1)/2$.

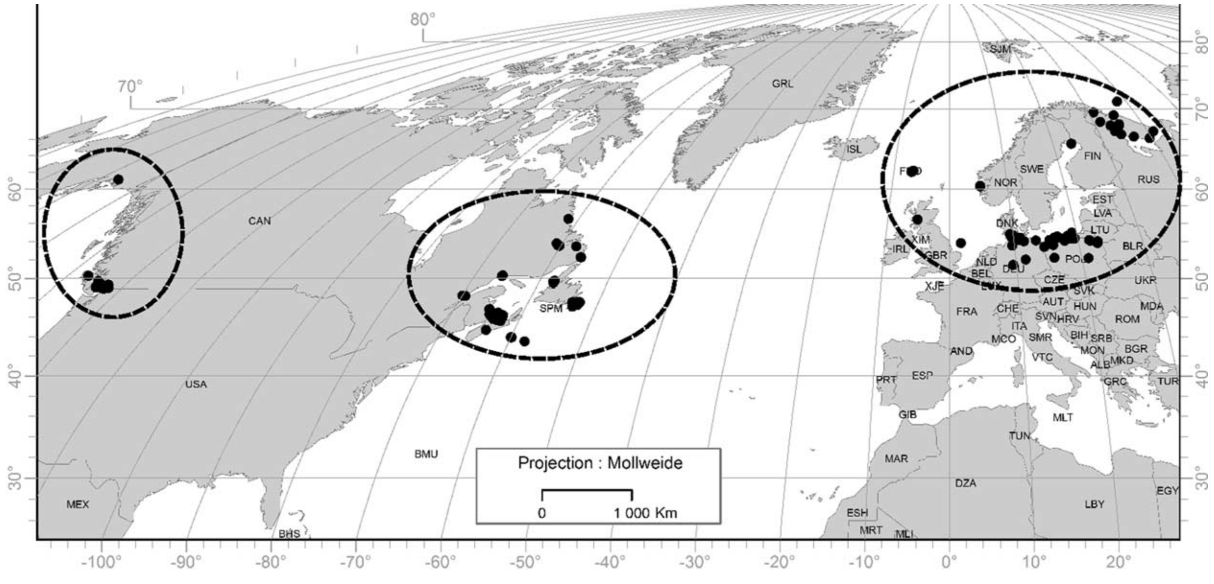

Figure 1. Map showing the location of the 126 localities from which parasite communities of threespine sticklebacks were sampled. The three ellipses indicate the three geographical regions (Eurasia, northeastern North America and northwestern North America) treated separately in the analyses.

For each pair of locality within a geographical region, we calculated the shortest linear distance ('as the crow flies') between localities using great circle calculations (<http://gc.kls2.com>) based on the coordinates of each locality. Small errors are possible in cases where coordinates for a locality were not given in the original source, and had to be obtained from a map. In such cases, a conservative estimate of the maximum error of these distance estimates is ±500 m for sites <20 km apart, and 10 km for sites >20 km apart; given that most distances are in the range of hundreds or thousands of km, these potential errors are insignificant. In addition, each pair of localities was classified as either from the same habitat type based on salinity (both from either freshwater, brackish or marine habitats), from moderately different habitat types (one locality is brackish and the other is either marine or freshwater), or from very different habitats (one is freshwater and the other is marine).

Similarity in parasite community composition between all pairs of sites within a geographical region was calculated using the software EstimateS (Colwell 2006). Parasite taxa identified only to genus level were treated as distinct from those identified to species level. Thus, *Gyrodactylus* sp. was treated as a different species from *G. pungitii*, although in reality they may be the same. Since these few cases of poor taxonomic resolution were probably equally likely to result in overestimates of similarity than in underestimates, they were left in the main analyses. For parasite presence/absence matrices, we used the Jaccard similarity index, which corresponds to the proportion of shared parasite species out of the total from two localities. Its value ranges from 0 when two localities have no parasite species in common, to 1 when they both have exactly the same parasite species. For parasite abundance matrices, we used the Bray–Curtis similarity index, which is related to the Sorensen index and which assesses similarity between two localities based on differences in abundance of parasites, and not merely on presence/absence. It also ranges from 0 (no similarity) to 1 (same species in both localities all occurring at the same abundance in both sites). Because this index can only be computed with integers, abundance data were first multiplied by 1000 and rounded up prior to calculations; this has no effect on the resulting index values since the index is not sensitive to scale. The choice of similarity indices has been much debated lately (Soininen and Hillebrand 2007). Here, we used the Jaccard and Bray–Curtis indices to allow comparisons with previous studies of distance decay relationships. However, we repeated our analyses with the Morisita-Horn index instead, since it has long been recognised as robust to inter-site variation in species richness (Wolda 1981). These additional analyses yielded the same results as those obtained with the Jaccard and Bray–Curtis indices, and we only report here the findings based on the latter two indices.

Similarity in the abundance of selected parasite species between pairs of sites within a geographical region was calculated only for species occurring in at least 8 localities in a region. Similarity in abundance is expressed as the difference in abundance values between two sites divided by the maximum difference observed for a given parasite species. This procedure allowed similarity values to be standardized to a scale ranging from 0 (no difference in abundance between two localities) to 1 (maximum observed difference), facilitating contrasts between different parasite species that naturally occur at very different mean abundances.

Statistical analyses

Prior to analysis, all similarity measures (Jaccard, Bray–Curtis, and abundance differences) were $\log10(x+1)$-transformed, since transformed similarity values versus untransformed distance values generally provide the best fit to the data, and because a linear relationship in semi-log space between similarity and distance would indicate the expected exponential decay. Pairwise values of similarity and distances are not truly independent in a statistical sense, since each locality is used in more than one pairwise comparison. For this reason, and to account for some deviations from normality in certain variables, the significance of each regression model (see below) was tested using a randomization approach implemented with the software RT 2.1 (Manly 1997). Significance was based on 10 000 permutations, and in all cases it confirmed that obtained from standard parametric tests; therefore, only the latter probabilities are presented here.

For each geographic region, similarity in community composition (Jaccard and Bray–Curtis indices) or difference in relative abundance of given parasite species was regressed (ordinary least-squares regression) against geographical distance between pairs of localities. In addition, this relationship was evaluated within an ANCOVA framework, with the main factor being the contrast in habitat type (the same, moderately different, very different) based on salinity for each pairwise comparison. Finally, for similarity in community composition (both Jaccard and Bray–Curtis indices), slopes were compared between geographic regions using the F-test recommended by Sokal and Rohlf (1995, pp. 493–499).

Results

General patterns

In total, we obtained data for 126 parasite communities in different threespine stickleback populations (Fig. 1, Table 1). Although the three geographic regions are distinct and separated by huge distances, they nevertheless shared many parasite species (see lists of species in Supplementary material Appendix 1, 2). Of the parasite species found in either Eurasia or NE North America, 30.6% were common to both regions; the overlap in species composition was 18.8% between Eurasia and NW North America, and 31.1% between NE and NW North America. However, Eurasia was characterised by a greater parasite species pool, greater maximum local species richness, and on average greater distances between localities (Table 1).

At a local scale, however, most parasite assemblages in local stickleback populations in Eurasia harboured very few species, and modal values were slightly higher in both North American regions (Fig. 2). Based on the presence/absence datasets, most parasite taxa occurred in fewer than

Table 1. Summary of parasite community data in threespine stickleback populations from three geographical regions.

Geographical region	No. of localities	Total parasite species richness	Parasite richness per locality (range)	Average (SD) distance between localities (km)
Presence/absence matrices				
Eurasia	67	86	1–25	1059 (729)
NE North America	44	44	1–13	631 (335)
NW North America	15	30	3–13	352 (628)
Parasite abundance matrices				
Eurasia	38	61	1–19	1277 (813)
NE North America	28	41	1–12	439 (273)

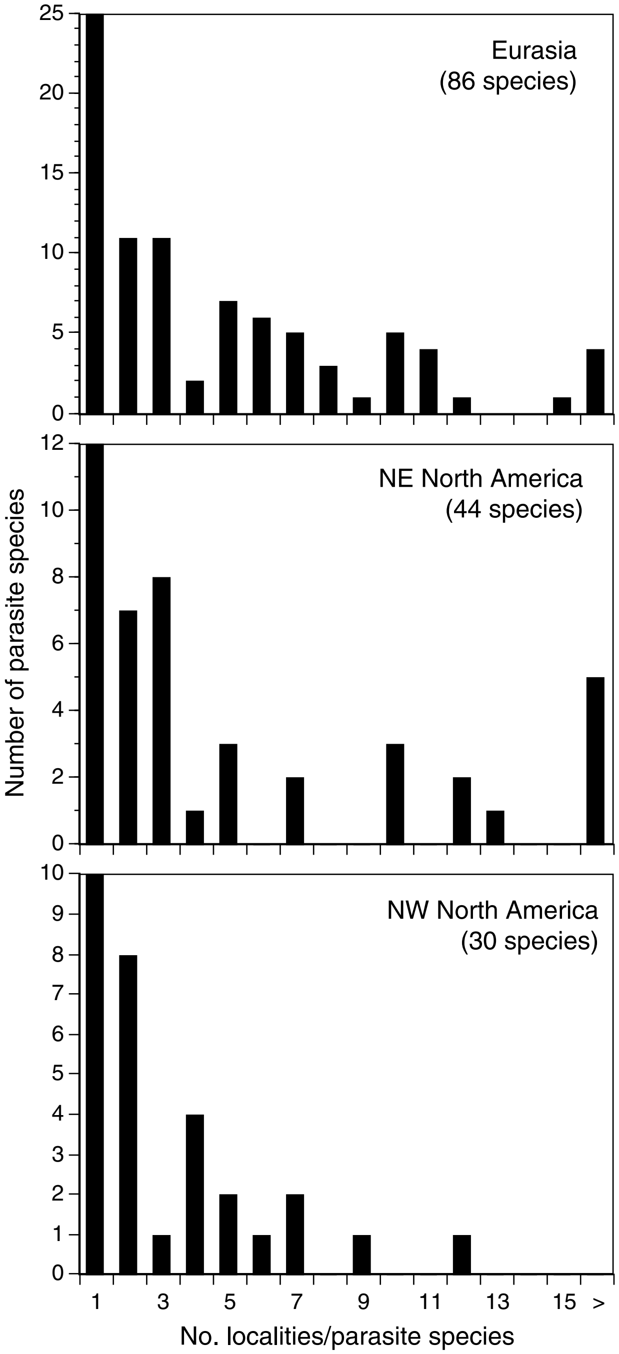

Figure 2. Frequency distributions of parasite species richness values observed in threespine stickleback populations from different localities in three distinct geographical regions.

5 localities within a region, whatever the geographic region they inhabit (Fig. 3).

Sample size, or the number of fish examined, was not available from all surveys included in our datasets. Among those available, median sample size was 24 fish (interquartile range 10–68), with only 13% being above 100 fish examined. Using the presence/absence datasets for which more localities were available, we found no significant correlation between local stickleback sample size and local parasite species richness across localities in Eurasia ($r = -0.188$, $n = 28$, $p = 0.337$) and NW North America ($r = 0.247$, $n = 15$, $p = 0.374$). Surveys that did not specify host sample size only came from Eurasia; we found no difference in parasite species richness between surveys with known and unknown sample sizes (Wilcoxon two-sample test, $Z = 1.53$, $p = 0.126$). There was a significant correlation between host sample size and parasite species richness among NE North American localities ($r = 0.448$, $n = 41$, $p = 0.0033$). However, this was due to only two localities: the one with the fewest fish examined for parasites, i.e. only 5 sticklebacks, and the only locality where more than 50 fish were examined, i.e. 153 sticklebacks. When these two localities are excluded from the correlation, it is no longer significant ($r = 0.278$, $n = 39$, $p = 0.0904$). Removing these two localities from subsequent analyses does not affect their results, therefore we retained data from these two sites.

Decay in community similarity

Based on the presence/absence matrices, similarity in parasite community composition decreased with increasing distance between localities in all three geographic regions (Table 2, Fig. 4). This was true when all comparisons were treated together, and also when they were treated as subsets based on whether or not they involved similar habitat types (Table 2). The patterns remained practically unchanged when the analyses for Eurasia were repeated after excluding data from surveys in which the number of fish examined for parasites was not available (results not shown). The data for NW North America showed a clear discontinuity, with most pairs of localities being < 500 km apart except a few that were separated by > 1500 km; this was due to a single marine location in Alaska, with all other freshwater and marine sites being in the southern part of British Columbia (there were no brackish water sites in that region). Excluding that one isolated locality resulted in the only non-significant relationship between similarity and distance, for comparisons between marine versus freshwater

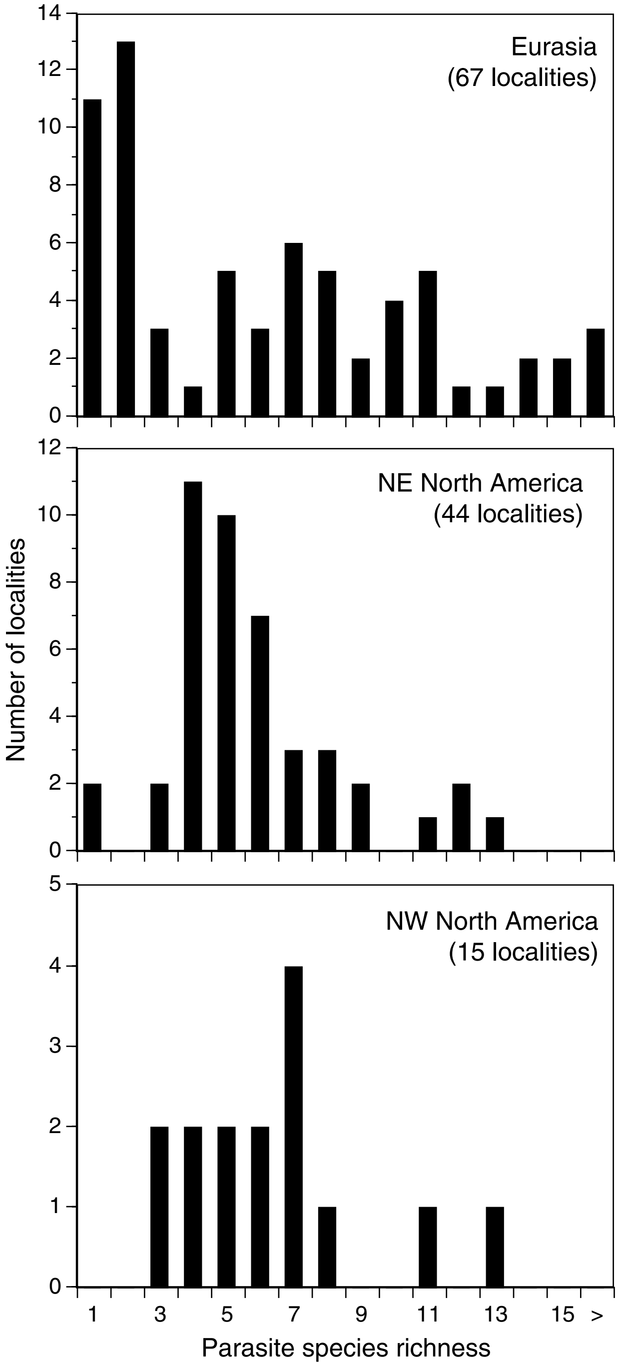

Figure 3. Frequency distributions of the number of localities (i.e. the number of threespine stickleback populations) in which a parasite species occurred, among all parasites from three distinct geographical regions.

localities (Table 2; though note the very small number of comparisons in this case).

In ANCOVAs testing for an effect of differences in habitat type between pairs of localities on the similarity of their parasite communities, a significant effect was found in all three geographical regions (Eurasia: $F_{2,2207} = 13.36$, $p < 0.0001$; NE North America: $F_{2,942} = 26.46$, $p < 0.0001$; NW North America, including only distances < 500 km: $F_{1,88} = 4.02$, $p = 0.0478$). For any given distance between two sites, their parasite communities were more similar if they were of the same habitat type than of different habitat types. This is reflected in the generally higher intercepts for regressions among same-habitat comparisons than among different-habitat comparisons (Table 2), and in the higher placement of points for same-habitat comparisons than for different-habitat comparisons in the scatter plots (Fig. 4). It is also apparent from the raw numbers of species shared between localities, which are clearly higher for same-habitat comparisons, especially those among marine localities, than for different-habitat comparisons (Fig. 5).

Based on the parasite abundance matrices (available for two of the three geographical regions), similarity in parasite community composition again generally decreased with increasing distance between localities (Table 3, Fig. 6). The similarity-versus-distance slope was positive, though not quite statistically significant, in one case, and the only truly non-significant negative relationship again involved very few comparisons (Table 3). ANCOVAs revealed a significant effect of differences in habitat type between pairs of localities on the similarity of their parasite communities in both regions (Eurasia: $F_{2,699} = 67.53$, $p < 0.0001$; NE North America: $F_{2,374} = 64.83$, $p < 0.0001$). Again, independent of the distance between them, parasite communities were more similar if they were of the same habitat type than of different habitat types, as seen from intercept values in the regressions (Table 3) and the placement of points in the scatter plots (Fig. 6).

Comparisons of slope values were made between Eurasia and NE North America only. These comparisons were made for each regression (i.e. across all pairwise locality comparisons or for different habitat type combinations; Table 2, 3) and for the presence/absence (Jaccard index) and abundance (Bray–Curtis index) data matrices separately, resulting in 12 comparisons. In 10 of the 12 tests, slopes were significantly ($p < 0.05$) steeper in NE North America than in Eurasia. In one test (abundance data, freshwater–only comparisons), there was no difference between the slopes in Eurasia and NE North America, and in the remaining one (abundance data, brackish vs other comparisons) the slope in NE North America was significantly higher than in Eurasia.

Intraspecific differences in abundance

The relationship between differences in the abundance of given parasite species and the distance between pairs of sites within a geographical region could be assessed for 8 species from Eurasia and 4 from NE North America (Table 4). In 4 of these 12 species, we observed the expected positive relationship between differences in abundance and distance between localities, i.e. the greater the geographical separation between host populations, the greater the difference in the abundance achieved by the parasite (Table 4). The pattern was sometimes clear (see Fig. 7 for an example), but not always striking. In addition, in one species, we found a negative relationship between differences in abundance and inter-locality distance (Table 4). ANCOVAs revealed a significant (or near significant) effect of differences in habitat type between pairs of localities on differences in the abundance achieved by parasites for 3 species, the cestode

Table 2. Regression statistics for the decay in similarity (Jaccard index based on presence/absence data) with increasing distance in parasite communities of threespine sticklebacks from three distinct geographical regions. Separate regressions were run for pairs of localities from the same habitat type based on salinity, from moderately different habitat types (one locality is brackish and the other is either marine or freshwater), or from very different habitats (one is freshwater and the other is marine). Slope values are in units of log(similarity) per 1000 km distance. For northwestern North America, results are shown both for all pariwise comparisons and for only those from localities within 500 km of each other.

Geographical region	No. comparisons	intercept	slope	r^2	p
Eurasia					
all comparisons	2211	0.048	−0.019	0.091	<0.0001
marine only	55	0.106	−0.042	0.358	<0.0001
brackish only	171	0.061	−0.028	0.180	<0.0001
freshwater only	666	0.060	−0.026	0.107	<0.0001
brackish vs other	912	0.041	−0.015	0.075	<0.0001
marine vs freshwater	407	0.033	−0.011	0.063	<0.0001
NE North America					
all comparisons	946	0.121	−0.083	0.211	<0.0001
marine only	136	0.184	−0.127	0.476	<0.0001
brackish only	66	0.098	−0.072	0.231	<0.0001
freshwater only	105	0.102	−0.055	0.079	0.0037
brackish vs other	384	0.073	−0.031	0.043	<0.0001
marine vs freshwater	255	0.124	−0.088	0.215	<0.0001
NW North America					
all comparisons	105	0.093	−0.050	0.212	<0.0001
all comparisons (<500 km only)	91	0.119	−0.306	0.174	<0.0001
freshwater only	78	0.130	−0.357	0.218	<0.0001
marine vs freshwater	26	0.069	−0.033	0.654	<0.0001
marine vs freshwater (<500 km only)	13	0.071	−0.061	0.021	0.6391

Proteocephalus filicollis in Eurasia ($F_{2,149} = 15.69$, $p < 0.0001$) and the trematode *Podocotyle atomon* ($F_{2,101} = 6.91$, $p = 0.0015$) and the monogenean *Gyrodactylus* sp. ($F_{2,149} = 2.52$, $p = 0.0837$) in NE North America. In all three cases, the largest differences in abundance were observed in comparisons between brackish water habitats and other habitat types.

Discussion

Our analysis shows that: 1) the similarity in species composition of parasite communities between populations of the threespine stickleback *Gasterosteus aculeatus* decays significantly with increasing geographical distance; 2) their similarity is also greater, independently of distance, when the populations compared inhabit similar types of habitats with respect to salinity; 3) similarity decay rates are generally steeper among stickleback populations in NE North America than in Eurasia; and 4) the differences in local abundance of specific parasite species between host populations are not consistently affected by distance or habitat types. These results suggest that the presence of a parasite species in a locality depends both on the probability of colonization from nearby localities and on the habitat's general suitability for parasite establishment, whereas the abundance subsequently achieved by the parasite is more dependent on local factors.

There have been earlier studies showing that the similarity in parasite communities of fish hosts decays with distance (Poulin 2003, Oliva and Gonzalez 2005, Seifertova et al. 2008, Pérez-del-Olmo et al. 2009, Thieltges et al. 2010). The present study supports the conclusion of these earlier ones that distance is the main barrier to parasite dispersal, as it is with other organisms, with homogeneity among distinct communities only possible on very small spatial scales (Soininen et al. 2007, Morlon et al. 2008). Other studies of distance decay of similarity in parasite communities of fish have emphasized the role of dispersal abilities in parasites, by contrasting decay patterns of species constrained to complete their life cycle in a water body (autogenic species) with those of species using birds as definitive hosts and thus benefiting from greater passive dispersal among water bodies (allogenic species) (Karvonen and Valtonen 2004, Fellis and Esch 2005). Our study goes one step further, and demonstrates that beyond the effects of distance and dispersal, habitat characteristics can play a significant role in determining whether two localities share parasite species. Taking advantage of the fact that threespine sticklebacks can inhabit both freshwater and marine, as well as brackish water, habitats, we revealed two patterns. First, we show that species sharing is greatest among marine localities. This is most probably explained by the continuous nature of marine systems and the greater homogeneity of their environmental conditions compared to the more physically isolated freshwater sites. It is also worth noting that parasite communities in freshwater stickleback populations consist of a greater proportion (mean ± SD across localities: 33.6 ± 24.3%) of allogenic species than those in brackish (26.1 ± 27.0%) or marine (13.5 ± 14.5%) habitats. Thus, allogenic species, which benefit from greater dispersal in their definitive host, are more common among the fragmented freshwater habitats than among marine localities, despite the latter sharing a greater proportion of species. This may reflect the importance of birds in transmitting fish parasites in freshwater and inshore ecosystems, that are generally shallower than pure marine sites. Second, we also showed that independently of the spatial distance between any two sites, they are more likely to share many parasite species if their salinities are similar. The establishment of a parasite in a particular location depends on the local presence of suitable hosts for

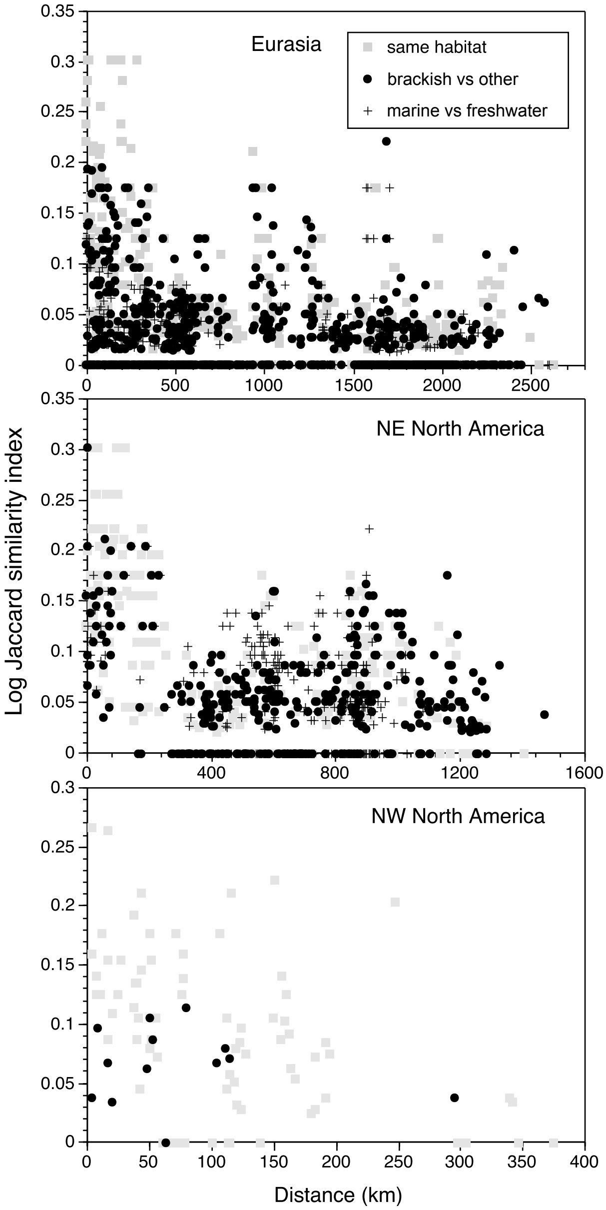

Figure 4. Similarity between parasite communities plotted against the geographical distance between them, for all pairwise comparisons of communities found in threespine stickleback populations from different localities in three distinct geographical regions. Regression lines not shown but statistics are given in Table 2. Similarity values are based on species presence/absence data, and different symbols show values for pairs of localities from the same habitat type based on salinity, from moderately different habitat types (one locality is brackish and the other is either marine or freshwater), or from very different habitats (one is freshwater and the other is marine). There were no localities sampled from brackish habitats in northwestern North America, and only those separated by <500 km are shown for this region.

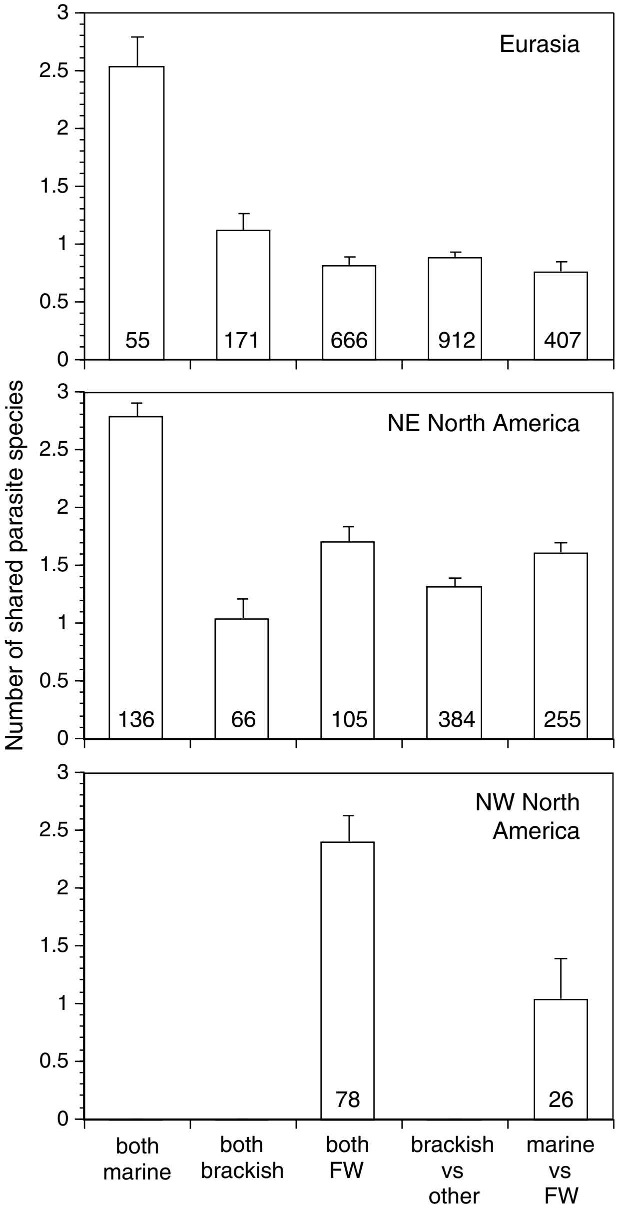

Figure 5. Mean (±SE) number of shared parasite species across all pairwise comparisons of parasite communities found in threespine stickleback populations from different localities in three distinct geographical regions. Results are shown separately for pairs of localities from the same habitat type based on salinity, from moderately different habitat types (one locality is brackish and the other is either marine or freshwater, FW), or from very different habitats (one is freshwater and the other is marine). There were no localities sampled from brackish habitats, and only two from marine habitats, in northwestern North America. Numbers on the bars indicate the number of pairwise comparisons in each category.

all stages of its life cycle, as well as on other local biotic and abiotic conditions that can both impact the success of its transmission stages (Pietrock and Marcogliese 2003, Thieltges et al. 2008). These conclusions echo those of studies on ectoparasitic arthropods in terrestrial systems (Krasnov et al. 2005, Vinarski et al. 2007). Our results are the first demonstration for aquatic systems that proximity in environmental conditions between two localities is as important as proximity in space for the similarity of their parasite faunas.

The above interpretations apply to community composition, based on presence/absence data and to some extent also to community similarity incorporating abundance data (Bray–Curtis index). When comparing the abundance

Table 3. Regression statistics for the decay in similarity (Bray–Curtis index based on abundance data) with increasing distance in parasite communities of threespine sticklebacks from two distinct geographical regions. Separate regressions were run for pairs of localities from the same habitat type based on salinity, from moderately different habitat types (one locality is brackish and the other is either marine or freshwater), or from very different habitats (one is freshwater and the other is marine). Slope values are in units of log(similarity) per 1000 km distance.

Geographical region	No. comparisons	intercept	slope	r^2	p
Eurasia					
all comparisons	703	0.041	−0.018	0.104	<0.0001
marine only	55	0.132	−0.027	0.092	0.0244
brackish only	15	0.014	−0.006	0.286	0.0398
freshwater only	210	0.069	−0.035	0.298	<0.0001
brackish vs other	192	0.018	−0.007	0.082	<0.0001
marine vs freshwater	231	0.002	−0.001	0.038	0.0030
NE North America					
all comparisons	378	0.114	−0.148	0.275	<0.0001
marine only	91	0.194	−0.219	0.368	<0.0001
brackish only	28	0.113	−0.145	0.454	<0.0001
freshwater only	15	0.037	−0.013	0.009	0.7319
brackish vs other	160	0.009	0.017	0.019	0.0758
marine vs freshwater	84	0.022	−0.017	0.045	0.0535

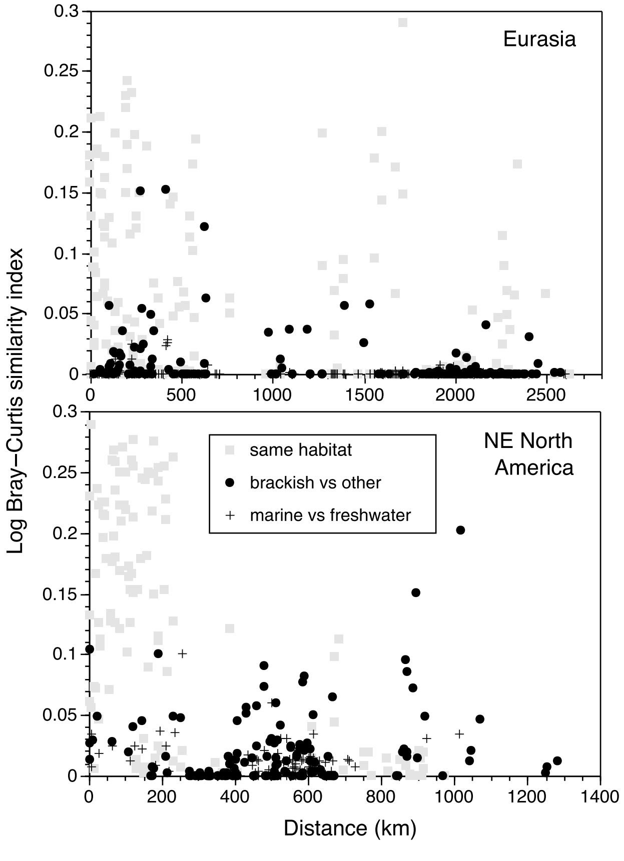

Figure 6. Similarity between parasite communities plotted against the geographical distance between them, for all pairwise comparisons of communities found in threespine stickleback populations from different localities in two distinct geographical regions. Regression lines not shown but statistics are given in Table 3. Similarity values are based on relative abundance data, and different symbols show values for pairs of localities from the same habitat type based on salinity, from moderately different habitat types (one locality is brackish and the other is either marine or freshwater), or from very different habitats (one is freshwater and the other is marine).

achieved by a particular parasite species among localities where it occurs, however, the influences of geographical distance and of habitat similarity based on salinity disappear, or at least become inconsistent. The presence of a given parasite in one locality may be determined by that locality's distance, both in terms of space and environmental conditions, to potential sources of colonizers, but the abundance that the parasite can subsequently achieve in that locality might depend on totally different factors. For instance, local food web characteristics may differ substantially from those of nearby localities. For trophically-transmitted parasites (8 of the 12 species for which abundance analyses were possible) food web structure can be a key determinant of transmission success and thus abundance (Lafferty et al. 2008). Foci of high parasite abundance may thus be dispersed across a parasite's geographical range, without necessarily clustering within a few nearby localities (Poulin and Dick 2007). At the parasite community level, spatial distances and related habitat features seem to provide a robust framework to explain patterns of similarity, but at the parasite population level their influence may be overshadowed by the effect of local factors controlling parasite transmission.

Our results also allowed a comparison of rates of decay in the similarity of parasite communities between two distinct geographical areas that fall within the distributional range of threespine sticklebacks. Overall, decay rates were steeper among localities in NE North America than among localities in Eurasia, whatever the habitat type concerned. There are certainly no obvious biogeographical barriers within the areas covered by the localities in our analyses that could explain this consistent difference. This pattern might therefore indicate greater levels of endemism in North American parasite taxa, with a greater species turnover per unit distance than in Eurasia. On the other hand, the spatial scale and total species pool involved in these analyses also differ between the two regions (Table 1), and caution is required when comparing slopes in such circumstances (Soininen et al. 2007).

Table 4. Regression statistics for the relationship between difference in abundance and distance between localities for parasites of threespine sticklebacks from two distinct geographical regions. Slope values are in units of log(similarity) per 1000 km distance.

Parasite species	Taxon	Abundance (range)	No. comparisons	intercept	slope	r^2	p
Eurasia							
Proteocephalus filicollis	Cestoda	0.01–3.84	153	0.047	0.005	0.002	0.5470
Schistocephalus solidus	Cestoda	0.01–1.21	28	0.084	0.015	0.007	0.6716
Schistocephalus pungitii	Cestoda	0.03–1.39	36	0.045	0.468	0.364	<0.0001
Diplostomum spathaceum	Trematoda	0.01–7.71	28	0.091	0.185	0.248	0.0069
Gyrodactylus rarus	Monogenea	0.01–8.30	55	0.042	0.095	0.366	<0.0001
Thersitina gasterostei	Copepoda	0.10–22.31	55	0.099	−0.004	0.001	0.8543
Contracaecum sp.	Nematoda	0.02–0.42	45	0.072	0.411	0.125	0.0170
Glochidia	Mollusca	0.01–11.92	28	0.109	−0.010	0.001	0.9299
NE North America							
Brachyphallus crenatus	Trematoda	0.02–149.50	231	0.094	−0.042	0.022	0.0246
Podocotyle atomon	Trematoda	0.13–2.60	105	0.137	−0.009	0.001	0.7669
Gyrodactylus sp.	Monogenea	0.10–23.85	153	0.076	0.011	0.001	0.6461
Contracaecum sp.	Nematoda	0.03–0.60	105	0.089	−0.023	0.004	0.5132

Analyses like those conducted in this study rely on the validity of data collected by several different researchers, and in particular on consistent taxonomic identification of parasite species among different workers. In most surveys, several parasites are identified only to genus level, sometimes only to family level (Poulin and Leung 2010). Here, we only included taxa identified at least to genus, though these may nevertheless comprise more than one undistinguishable species. It is unlikely that these few taxa have influenced the results of our analyses because they are limited in their occurrence to few localities. Indeed, the most widely occurring parasite species included in our study (those on the right-hand side in Fig. 3) are fully-named species: the cestodes *Proteocephalus filicollis* (found in 25 localities) and *Schistocephalus solidus* (17 localities), and the copepod *Thersitina gasterostei* (27 localities) in Eurasia, and the trematodes *Brachyphallus crenatus* (22 localities) and *Podocotyle atomon* (15 localities) in northeastern North America. The only commonly occurring taxa where cryptic species could possibly influence our analyses are the trematode *Diplostomum spathaceum* (8 localities in Eurasia), the monogenean *Gyrodactylus* spp. (18 localities in northeastern North America) and the nematode *Contracaecum* sp. (10 localities in Eurasia, 15 in northeastern North America). For instance, a molecular investigation of *Diplostomum* larval stages from fishes in eastern Canada revealed a rich complex of cryptic species (Locke et al. 2010), just the sort of scenario that can invalidate community similarity analyses based on published identifications. However, deleting these species from the datasets and repeating the analyses yielded essentially the same patterns and conclusions.

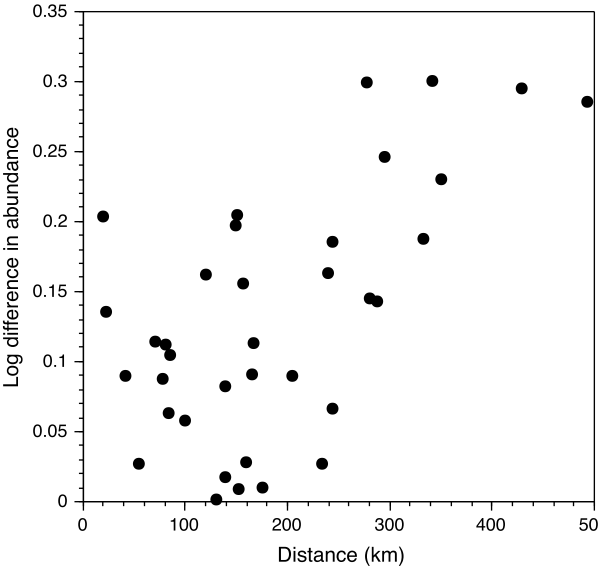

Figure 7. Difference in abundance of the cestode *Schistocephalus pungitii* as a function of distance between localities, for all pairwise comparisons among 9 Eurasian populations of threespine sticklebacks. Abundance is measured as the mean number of parasites per individual host, and differences in abundance are expressed as proportions of the maximum observed difference between any two host populations.

Another potential source of noise comes from the fact that the data were collected over a period spanning several decades, from the late 1950s to the present. Temporal changes in both the occurrences and particularly in the abundances of parasites from various localities might have resulted from environmental or climatic changes in aquatic habitats (Kesting and Zander 2000, Morley and Lewis 2007), potentially obscuring spatial patterns. Temporal turnover of species affects similarity among communities in many cases (Korhonen et al. 2010), but not in the present study. Indeed, a preliminary analysis in which pairwise distances in time (i.e. the difference in years between two samples) were included along with spatial distances in multiple regressions, indicated that temporal patterns do not exist in our data, ruling out this factor as a source of error.

Overall, our findings indicate that parasite communities of sticklebacks are structured on geographical scales by both a pure distance effect and a marked influence of local salinity conditions, with populations close to each other in space and in local conditions harbouring similar parasite assemblages. Our results also indicate that these strong effects at the community level do not translate into correspondingly strong effects at the parasite population level: the abundance levels achieved by a given parasite in different host populations are not consistently more similar among localities close to each other or with similar salinities. These patterns suggest that parasite dispersal and population dynamics are controlled by different processes, and that geographic patterns are only likely to emerge for parasite community composition, not for parasite population parameters.

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Supplementary material (Appendix E6826 at <www.oikos.ekol.lu.se/appendix>). Appendix 1–3.