Spatial variation in population density across the geographical range in helminth parasites of yellow perch *Perca flavescens*

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The abundance of a species is not constant across its geographical range; it has often been assumed to decrease from the centre of a species' range toward its margins. The central assumption of this "favourable centre" model is tested for the first time with parasites, using different species of helminth parasites exploiting fish as definitive hosts. Data on prevalence (percentage of hosts that are infected) and abundance (mean no. parasites per host) were compiled for 8 helminth species occurring in 23 populations of yellow perch *Perca flavescens*, from continental North America. For each parasite species, correlations were computed between latitude and both local prevalence and abundance values. In addition, the relationships between the relative prevalence or abundance in one locality and the distance between that locality and the one where the maximum value was reported, were assessed separately for each species to determine whether abundance tends to decrease away from the presumed centre of the range, where it peaks. For both the cestode *Proteocephalus pearsei* and the acanthocephalan *Leptorhynchoides thecatus*, there was a positive relationship between prevalence or abundance and the latitude of the sampled population. There was also a significant negative relationship between relative prevalence and the distance from the locality showing the maximum value in *P. pearsei*, but no such pattern was observed for the other 7 parasite species. Since this single significant decrease in prevalence with increasing distance from the peak value may be confounded by a latitudinal gradient, it appears that the distribution of abundance in parasites of perch does not follow the favourable centre model. This means that the environmental variables affecting the density of parasites (host availability, abiotic conditions) do not show pronounced spatial autocorrelation, with nearby sites not necessarily providing more similar conditions for the growth of parasite populations than distant sites.

The abundance of any given plant or animal species is not constant across its entire geographical range; typically, individuals of one species occur at high densities in some areas, but are only sparsely dispersed in other parts of their range (Rapoport 1982, Hengeveld 1990, Sagarin et al. 2006). Several empirical studies indicate that this spatial variation can follow a regular pattern: the density of individuals may decrease from the centre of a species' range toward its margins. This is true for at least some species of plants, insects and vertebrates (Whittaker and Niering 1965, Whittaker 1967, Hengeveld and Haeck 1982, Brown 1984, Root 1988, Telleria and Santos 1993). There are, however, many exceptions to this simple regular pattern (Sagarin and Gaines 2002, Gaston 2003, McGeoch and

Price 2004, Murphy et al. 2006), and several alternative scenarios are possible.

In simple terms, a decrease in density from the centre toward the margins can be explained by a relationship between environmental conditions and location within the geographic range of a species. Conditions for survival and reproduction may be most favourable at the centre of the range, and become progressively worse as one proceeds toward the margins (Hengeveld 1990). This does not hold in many cases (Sagarin and Somero 2006), and remains mostly an untested assumption. It would require that local populations respond to local conditions, and that the density achieved locally reflects the extent to which local environments meet the niche requirements of a species

(Brown 1984, 1995). This niche-based explanation also assumes that the environmental variables affecting the density of a species tend to be autocorrelated over space, such that sites in close proximity have more similar environmental conditions than distant sites (Brown 1984, 1995). Since environmental conditions are likely to change more-or-less continuously across the landscape, the "favourable centre" model predicts a unimodal distribution of density in space, peaking near the centre of the range and dropping off along a gradient toward the margins. In contrast, if environmental factors, especially those that are important niche parameters, do not change gradually but instead irregularly over space, or periodically over time, then the density of a species is likely to show multimodal variation across its geographical range (Brown 1995). Spatial variation in density in this "local oasis" model would resemble an irregular series of peaks and valleys. With data on density of a species from many sites within its range, there is a simple empirical test to distinguish between these two models. Under the "favourable centre" scenario, the site of maximum observed density should be at, or very near, the centre of the species' distributional range; thus, when local density is plotted against distance from the site with maximum density, one would expect a significant negative relationship for the "favourable centre" model. In contrast, no relationship at all is expected between local density and distance from the site of maximum observed density for the "local oasis" model.

In the present study, we test the central assumption of spatial autocorrelation underpinning the "favourable centre" model, with data on populations of parasites in freshwater fish hosts. For parasites, local density in a host population is best measured as either prevalence (the proportion of hosts that are infected) or intensity of infection (the mean number of parasites per infected host), or, even better, their product which is referred to as abundance (the mean number of parasites per host, including uninfected ones). The prevalence, intensity and/or abundance of parasites of a given species vary among different populations of their hosts, but within species-specific bounds (Arneberg et al. 1997, Poulin 2006, Krasnov et al. 2006). However, the geographic structure of this variation has never been examined. In the case of parasites of freshwater fishes, the parasites' distributions will be just as discontinuous as those of their hosts, which only occur in lakes and rivers; on a large geographical scale, however, patterns across the whole distributional range should still be detectable, if they exist. The local abundance of a parasite species will not only depend on the local availability of its fish hosts, but also on the local availability of intermediate hosts necessary for the completion of the parasite's life cycle, and on the abiotic conditions to which the parasite's infective

stages are exposed. These variables will need to be tightly autocorrelated over space for the "favourable centre" model to apply to parasites (Brown 1984, 1995).

Here, the relationship between both local prevalence, intensity and abundance of infection and the distance from the site where these values peak, is quantified for several helminth parasites of yellow perch *Perca flavesvcens*, a widespread North American freshwater fish. The present study provides the first analysis of the spatial distribution of abundance across the geographical range of parasite species, and points toward local factors as important determinants of population abundance within different parasite species.

Methods

Of the many helminth parasites of yellow perch (Carney and Dick 1999), we selected the 8 species that were reported from at least 6 localities where sufficient host individuals have been examined (Table 1). All are intestinal helminths occurring in perch as adults and thus using this fish as definitive host. Data on prevalence, intensity and/or abundance of infection were obtained from published surveys (Table 1). Because estimates of these infection parameters are influenced by host sample size (Gregory and Blackburn 1991, Poulin 2007), data from any given locality were only included if at least 35 individual hosts per population have been examined in a survey. On a map showing all perch populations sampled, localities where a given parasite species is present tend to be clustered in part of the host range, with absences only recorded on the margins of this cluster or well outside. The cluster of non-zero values is our best estimate of the range of the parasite. Since the margins of the range are likely to be "jagged" and not smooth, any zero along the margins most probably falls outside the range. All localities from which a given parasite species was absent were excluded from the analysis of geographical variation in prevalence or abundance for that species, since including zero values from outside a species' range would invariably generate negative relationships between local prevalence/abundance and distance from the maximum recorded value.

We performed separate analyses for prevalence, intensity and abundance (the product of prevalence and intensity). Prevalence data were available from all localities, whereas intensity data were only available from some of the surveys. Intensity data were only available from sufficient localities for 4 of the parasite species, and thus whereas prevalence data are analysed for all 8 species, analyses of intensity and abundance data were only possible for 4 species. For basic descriptive analyses, data were log-transformed to fit

Table 1. Summary data on the 8 helminth species included in the analyses.

Helminth species	Measure of density	Min. extent of range (km)	Number of populations	Sources*
Trematoda				
Bunodera luciopercae	prevalence	2800	6	1,2,3,4,5,6
Bunodera sacculata	prevalence	1508	13	1,3,7,8,9,10,11,12,
	abundance		8	13,14,15,16,17
Crepidostomum cooperi	prevalence	2170	16	1,3,4,7,9,10,11,13,
	abundance		9	14,15,16,17,18,19,
				20,21
Cestoda				
Bothriocephalus cuspidatus	prevalence	2170	12	4,5,7,8,9,10,11,12,
	abundance		8	16,18,19,21
Proteocephalus pearsei	prevalence	2150	22	1,2,3,4,5,7,8,9,10,
	abundance		14	11,12,13,14,15,16,
				17,18,19,20,21,22,
				23
Nematoda				
Camallanus oxycephalus	prevalence	1567	6	1,4,8,18,19,23
Dichelyne cotylophora	prevalence	1567	8	1,3,4,8,13,18,20,23
Acanthocephala				
Leptorhynchoides thecatus	prevalence	1567	6	3,4,7,8,13,18

* Sources, with number of fish examined (n): 1, van Cleave and Mueller 1934, Oneida Lake, NY, n =273 (43°N, 76°W); 2, Tedla and Fernando 1969, Lake Ontario, n =634 (44°N, 77°W); 3, Cannon 1973, Lake Opeongo, ON, n =1310 (45°N, 78°W); 4, Bangham and Hunter 1939, West Lake Erie, n =49 (42°N,83°W); 5, Carney and Dick 1999, Beaufort Lake, MB, n =99 (50°N, 100°W); 6, Zelmer and Arai 1998, Garner Lake, AB, n =60 (54°N, 111°W); 7, Noble 1970, Oneida Lake, NY, n =54 (43°N, 76°W); 8, Dechtiar 1972, Lake of the Woods, ON, n =67 (49°N, 95°W); 9, Poole 1985, Heming Lake, MB, n =201 (55°N, 101°W); 10, Poole 1985, Wapun Lake, MB, n =63 (55°N, 101°W); 11, Poole 1985, Home Lake, MB, n =78 (55°N, 101°W); 12, Poole 1985, Demarch Lake, MB, n =40 (55°N, 101°W); 13, Bangham 1955, Lake Huron, n =201 (46°N, 82°W); 14, Johnson 2001, experimental lake 239, ON, n =476 (49°N, 93°W); 15, Johnson 2001, experimental lake 240, ON, n =504 (49°N, 93°W); 16, Johnson 2001, experimental lake 377, ON, n =369 (50°N, 93°W); 17, Johnson 2001, Triangle Lake, ON, n =402 (49°N, 93°W); 18, Bangham 1972, Lake Erie, n =93 (42°N, 83°W); 19, Carney and Dick 1999, Lake Winnebago, WI, n =95 (45°N, 87°W); 20, Bangham 1944, Madeline Lake, WI, n = 41 (45°N, 89°W); 21, Carney and Dick 1999, Dauphin Lake, MB, n =265 (51°N, 99°W); 22, Carney and Dick 1999, Lake Michigan, n =38 (44°N, 87°W); 23, Carney and Dick 1999, Green Bay, WI, n =107 (45°N, 87°W).

the assumptions of parametric tests. This applies to prevalence, too, even if this measure is a percentage often best accommodated by an arcsine transformation; the fact that we excluded all zero values and the absence of 100% values meant that a logarithmic transformation was the best procedure. These descriptive analyses included searching for correlations between either local prevalence, intensity or abundance of infection, and the latitude of the sampled locality, within each parasite species, to account for possible latitudinal gradient.

For each measure of population density (prevalence, intensity and abundance), and for each parasite species, the locality with highest value was used as a reference point for other localities. All other values were expressed as proportions of the maximum value, to obtain relative measures on the same scale that could be compared across species. The geographical distance between each locality and the site of maximum prevalence, intensity or abundance was calculated as the linear distance between the localities, obtained from a map. The scale of the map was 1 cm =52.5 km, and the precision of each measurement of distance was to within 1 mm, or 5 km. Given that typical distances between localities are

in the order of 10^2 and 10^3 km, this imprecision is probably insignificant.

In the main analyses, values from the site with maximum prevalence, intensity or abundance were excluded; these only serve as a reference point, and including them would artificially generate a negative relationship between relative values and distance by placing the highest recorded value at a zero distance from itself. For each species, and for each of the three measures (relative prevalence, relative intensity and relative abundance) in the 4 species for which this was possible, Pearson correlation coefficients were computed between the relative values and the log-transformed distance to the site of maximum prevalence, intensity or abundance.

Results

The 8 parasite species each occurred in 6 to 22 of the 23 lakes included in our dataset (Table 1). They included 3 trematode species, 2 cestodes, 2 nematodes and 1 acanthocephalan. The minimum extent of their

geographical ranges, based on the maximum distance between any two lakes in which they occurred, ranged from 1508 to 2800 km (Table 1).

Among localities, there were no significant relationships between host sample size and either local prevalence, intensity or abundance for any of the 8 parasite species (Pearson correlation coefficients on log-transformed data, all $p > 0.22$). There is thus no reason to believe that inadequate sampling effort resulted in a systematic error in the estimates of prevalence, intensity or abundance. In the 4 species for which sufficient intensity data were available, there were no significant correlations between prevalence and intensity across populations (all $p > 0.07$). However, as one would expect since they are not independent of each other, values of intensity and abundance of infection were strongly correlated across different parasite populations (*Bunodera sacculata*: $r = 0.936$, $n = 8$, $p = 0.001$; *Crepidostomum cooperi*: $r = 0.914$, $n = 9$, $p = 0.001$; *Bothriocephalus cuspidatus*: $r = 0.896$, $n = 8$, $p = 0.003$; and *Proteocephalus pearsei*: $r = 0.650$, $n = 13$, $p = 0.012$). In the analyses that follow, results obtained using intensity data were practically identical to those obtained with abundance data, and thus we only report the ones based on the latter. Values of prevalence and abundance of infection were also generally positively correlated across parasite populations, but not as strongly (*B. sacculata*: $r = 0.818$, $n = 8$, $p = 0.013$; *C. cooperi*: $r = 0.667$, $n = 9$, $p = 0.050$; *B. cuspidatus*: $r = 0.119$, $n = 8$, $p = 0.780$; and *P. pearsei*: $r = 0.643$, $n = 13$, $p = 0.018$); the relationship was not significant in one case, most likely because data were only available for a few localities. Still, this means that the analyses that follow, whether based on prevalence or on abundance (the product of prevalence and intensity), all capture the same essential features of the geographical distribution of local density in parasites.

There was only a 13° range in latitude between the northernmost and southernmost lake sampled. For 6 of the 8 parasite species, there was no correlation between latitude of the locality and either local prevalence or abundance (Pearson correlation coefficients on log-transformed data, all $p > 0.12$). However, for both *Proteocephalus pearsei* (prevalence: $r = 0.686$, $n = 22$, $p = 0.001$; abundance: $r = 0.750$, $n = 14$, $p = 0.003$) (Fig. 1) and *Leptorhynchoides thecatus* (prevalence: $r = 0.929$, $n = 6$, $p = 0.007$), there was a positive relationship between prevalence or abundance and the latitude of the sampled population. Thus, in those species, the local density of parasites is greater in northernmost populations.

In most cases, there was no relationship between either relative prevalence or relative abundance and the distance from the locality showing the maximum value (Table 2). Although there was a very weak tendency for relative values of prevalence and abundance to decrease
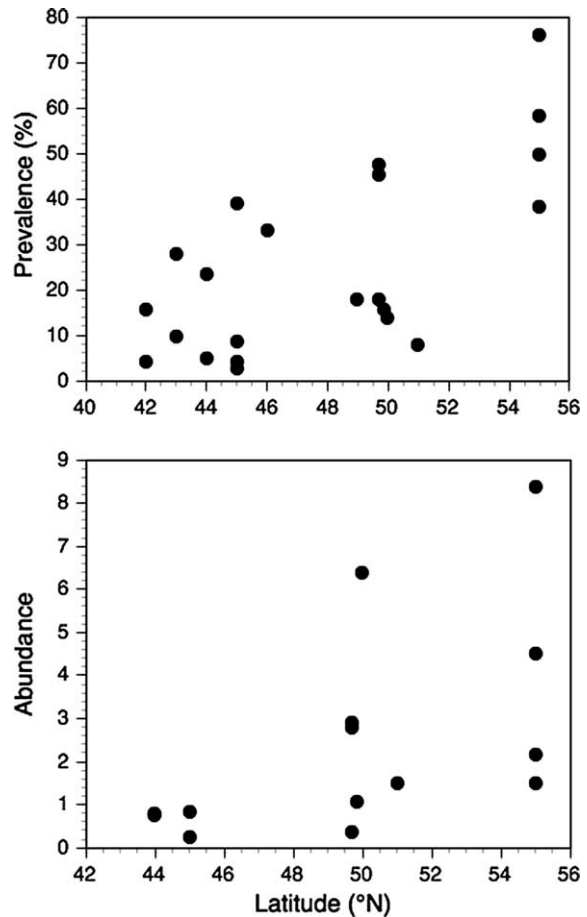

Fig. 1. Relationship between both prevalence and abundance (mean number of parasites per host) of infection by the cestode *Proteocephalus pearsei* and the latitude at which populations of its host, the yellow perch *Perca flavescens*, were sampled.

with increasing distance from the site where they peak in the cestode *Bothriocephalus cuspidatus*, it is only in the cestode *Proteocephalus pearsei* that the trend was significant (Fig. 2). This was true only of prevalence, however, not abundance. Interestingly, the only significant relationship also corresponds to the analysis that included the most populations (Table 2).

Discussion

The assumption that species are most abundant in the centre of their range and decline in abundance toward its edges is one of the most widespread in biogeography and ecology (Sagarin et al. 2006). It has become the cornerstone of numerous ecological and evolutionary hypotheses, touching on metapopulation dynamics,

Table 2. Relationships between relative prevalence or relative abundance and distance from the maximum recorded value, for the 8 helminth species included in the analyses.

Helminth species	Measure of density	Correlation coefficient	Number of populations*	p-value
Trematoda				
Bunodera luciopercae	prevalence	0.093	5	0.882
Bunodera sacculata	prevalence	−0.035	12	0.914
	abundance	−0.143	7	0.760
Crepidostomum cooperi	prevalence	0.076	15	0.786
	abundance	−0.351	8	0.394
Cestoda				
Bothriocephalus cuspidatus	prevalence	−0.540	11	0.086
	abundance	−0.685	7	0.090
Proteocephalus pearsei	prevalence	−0.609	21	0.003
	abundance	−0.344	13	0.250
Nematoda				
Camallanus oxycephalus	prevalence	−0.136	5	0.828
Dichelyne cotylophora	prevalence	−0.419	7	0.350
Acanthocephala				
Leptorhynchoides thecatus	prevalence	−0.416	5	0.486

*The population where the maximum value of prevalence or abundance was recorded is not included.

gene flow, competitive interactions, and speciation and extinction processes (reviews in Sagarin and Gaines 2002, Sagarin et al. 2006). These hypotheses serve as predictive tools for conservation policies and the potential impact of climate change on the distribution of plants and animals. Yet, in their review of 145 separate empirical tests of the favourable centre model, Sagarin and Gaines (2002) found that it was only supported by 56 (39%) of them.
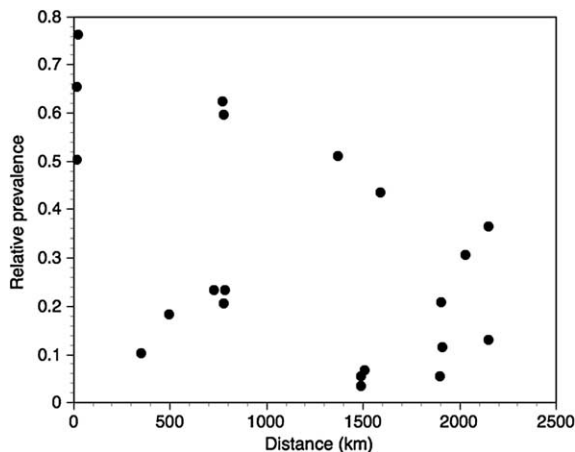

Fig. 2. Relationship between local prevalence of infection by the cestode *Proteocephalus pearsei* and the distance to the site where maximum prevalence was recorded; each point represents a different yellow perch *Perca flavescens* population, and thus a different lake. Prevalence in each locality is expressed as a proportion of the maximum value observed, with the latter not shown here.

The studies reviewed did not include any tests on parasitic species, but our results point in the same direction: we found no general support for the favourable centre distributional model. Helminth parasites of yellow perch show peaks in local density that are more or less independent from the values recorded in nearby populations. Our study measured density differently than all previous studies of abundance distribution, all of which focused on free-living organisms where population density is expressed as number of individuals per unit area. For parasites, host individuals represent discrete habitat patches, and density is best expressed as abundance, i.e. the mean number of individual parasites per host. This is the most relevant measure of density for parasites, since host individuals represent "units" of available habitat, and it is equivalent to traditional measures of population density. Therefore, despite these slight differences in the measurement of abundance, our results are comparable to those obtained earlier for free-living plants and animals.

The cestode *Proteocephalus pearsei* was the exception to the rule. In this species, the relative prevalence of parasites in one locality decreased with increasing distance from the site where its prevalence was maximum. Still, there are two reasons why this single result fitting the expectation of the favourable centre model fails to be convincing. First, it applies only to prevalence, and not to abundance. Because the latter includes estimates of the number of parasite individuals per host as well as the percentage of hosts that are infected in a population, it captures population density much better than prevalence on its own. Second, the pattern of variation in prevalence as a function from the

presumed centre of distribution (Fig. 2) may be a mere by-product of a latitudinal gradient in prevalence (Fig. 1). The cestode *P. pearsei* achieves high prevalence in the northernmost locations among the ones surveyed, and these also happen to be distant from many southern localities where prevalence is lower. The existence of a latitudinal effect on prevalence is enough to generate the appearance of a geographical distribution with a centre of high abundance in analyses such as ours. At present, the reasons for the latitudinal gradient are unclear, though they may involve the geographical distribution of the cestode's intermediate hosts (*P. pearsei* requires at least one of a few related species of copepods as intermediate hosts in addition to a fish definitive host to complete its life cycle; Scholz 1999).

Potential sources of error can influence the outcome of analyses of this nature, and at least three of them deserve attention. First, the accuracy of taxonomic identification of parasites must vary to some extent among the surveys included in this study, although it is impossible to determine whether this was a potential problem in this case. Incorrect identification, or the existence of cryptic parasite species lumped under one name, would make it difficult to find patterns in the geographic distribution of abundance within species.

Second, it is likely that only a portion of the parasites' geographical range was sampled by the surveys we compiled. The true range of these 8 species is not known in detail, and it is possible that partial coverage of a species' range would not allow detection of existing spatial variation in density. Still, the surveys we used covered at least 1500 km across the range of each species (Table 1). Also, our coverage reached well over half of the geographical range of the host fish, *Perca flavescens*, with only eastern and southeastern parts of the range not included (Scott and Crossman 1973). The localities where a particular parasite species was recorded tended to cluster within the larger range of perch, suggesting that most if not all of the parasite's range was included. There are also no major physical barriers within the part of the geographical range of perch covered in the present analysis, or within the range as a whole. Thus an insufficient coverage is unlikely to be the reason why the favourable centre model is not supported. Similarly, although only a fraction of the localities where a parasite actually occurs have been sampled, these do not represent a mere linear cross-section through the range, but are instead scattered throughout two-dimensional space.

Third, in addition to geographical variation in parasite prevalence or abundance, the dataset may also have included a temporal element of variability, as the surveys were carried out over several decades (see Table 1 for sources). If local parasite populations go through cycles of low and high abundance, sampling different parts of the geographical range at different times could create apparent spatial patterns of abundance that are merely artefacts. This is unlikely to have been the case in this study, however, as there was no relationship between the geographical distance between all pairs of localities and the temporal difference, in years, between the times at which they were sampled ($r = 0.056$, $n = 276$ pairwise contrasts between all 23 localities, $p = 0.354$). Thus, distant sites, for example, were not consistently sampled years before or after lakes situated closer to the presumed centre of the geographical range. There were also no significant correlations between year of sampling and abundance for any of the 8 parasite species studied (all $p > 0.16$), making it unlikely that long-term climate trends might have affected local estimates of abundance. The possibility that some surveys were carried out in favourable years and that others were done in less favourable years remains, but it cannot be tested. The results of our analyses are therefore unlikely to be artefacts of the noise generated by potential influences of taxonomic errors, incomplete coverage of the geographical range, and temporal changes in abundance.

The most parsimonious interpretation of our results is that the local abundance of a parasite species, although in some cases influenced by factors associated with latitude, is generally independent of where the locality happens to be situated within the parasite's geographic range. Instead, it must be determined mainly by local factors. In addition to the density of suitable intermediate hosts, the presence of alternative definitive hosts can be a key element contributing to local abundance of a parasite species. Like most other helminth parasites of fish, the 8 species studied here are not strictly specific to yellow perch: they all can infect and develop in several other fish species (Margolis and Arthur 1979, McDonald and Margolis 1995). The presence of these generalist parasites in a host population is not strictly the outcome of association by descent. Instead, not only the presence, but also the abundance of a generalist parasite in a host population depends on several local factors, including the complexity of the fish community (Nelson and Dick 2002). Furthermore, the survival and infectivity of the free-living infective stages (i.e. cercariae for trematodes) or eggs of these helminths are highly susceptible to local abiotic conditions (Pietrock and Marcogliese 2003). Superimposing the distributions of these other host species and of abiotic water conditions may create a patchy geographic mosaic in which foci of high parasite abundance appear wherever conditions are optimal. These foci are not necessarily contiguous, but may be separated by areas of low abundance, as in the local oasis model described in the Introduction. Thus, environmental variables affecting the density of parasite

species (host availability, abiotic conditions) do not show pronounced spatial autocorrelation, with nearby sites not necessarily providing more similar conditions for the growth of parasite populations than distant sites (Brown 1984, 1995).

At the parasite community level, there are smooth geographical gradients in species composition. For instance, among lake populations of the yellow perch *Perca flavescens*, the similarity between any pair of parasite communities decreases exponentially with the geographical distance between them (Poulin 2003). This pattern also applies to parasite communities in other fish or mammal host species (Poulin 2003, Fellis and Esch 2005, Oliva and González 2005, Krasnov et al. 2005). In contrast, at the population level, abundance does not show smooth gradients over space in the species studied here, except in a couple of cases where it roughly increases with latitude. As emphasized by Sagarin et al. (2006), the geographical distribution of species abundance is much more complicated, and at the same time more interesting, than assumed previously.

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