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The structure of parasite communities in fish hosts: ecology meets geography and climate

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Abstract. Parasite communities in fish hosts are not uniform in space: their diversity, composition and abundance vary across the geographical range of a host species. Increasingly urgently, we need to understand the geographic component of parasite communities to better predict how they will respond to global climate change. Patterns of geographical variation in the abundance of parasite populations, and in the diversity and composition of parasite communities, are explored here, and the ways in which they may be affected by climate change are discussed. The time has come to transform fish parasite ecology from a mostly descriptive discipline into a predictive science, capable of integrating complex ecological data to generate forecasts about the future state of host-parasite systems.

Key Words: climate change, abundance, diversity, spatial variation

Introduction

The study of parasite communities in fish hosts has blossomed over the past two decades. Every month, new surveys of parasite diversity and abundance in new host species are published, and every year new checklists are compiled for different areas, adding to our growing appreciation of the richness and complexity of the parasite fauna in freshwater and marine ecosystems. Yet, despite these many new contributions, our overall understanding of the processes shaping parasite communities in fish is not improving at a similar rate. In part this is because we often can't see the forest for the trees, i.e. many investigations become so involved in the details of a particular system that they fail to see the situation as a whole, to glimpse the big picture. The large-scale approach of macroecology can be a solution to this problem, as it has proven extremely successful in tackling many of the traditional issues in community ecology (Lawton, 1999).

Another reason why our understanding of the forces controlling fish parasite communities lags behind is that most host species are either studied in a single locality, or within a very small part of their geographical range. In the few cases where several populations of the same host species have been studied, it has been painfully obvious that patterns of parasite community structure are not uniform in space. In other words, any pattern of association between parasite species in one host population are rarely observed again in a different population of the same host species (Poulin and Valtonen, 2002; Timi and Poulin, 2003; Poulin, 2007a). The substantial geographical variation that exists in the ecology of fish parasite communities presents one of the most important challenges to our understanding of parasite ecology, and overcoming it would take us one step closer to finding general laws, if any, controlling the organization of parasite systems (Poulin, 2007b). Perhaps more urgently, we need to understand the geographic component of parasite communities to better predict how they will respond to global climate change. Climate in general, and temperature in particular, affect several ecological processes, from the performance of individual organisms, to the dynamics of populations and the distribution of species. This has been clearly illustrated by a series of recent studies that have linked changes in ecosystem properties and functions with large-scale climate fluctuations (Ottersen *et al.,* 2001; Walther *et al.,* 2002; Stenseth *et al.,* 2002, 2003). Recent reports have highlighted the causal relationship between climate change and either the local prevalence or geographical distribution of parasitic diseases (e.g., Marcogliese, 2001; Harvell *et al.,* 2002; Mouritsen and Poulin, 2002; Lafferty *et al.,* 2004). The many direct and indirect effects of temperature and other climatic variables on parasite transmission are bound to affect fish parasites, and a geographical perspective is essential to predict the nature of the impact of climate change.

Here, I explore the potential links between climate change and geographical variation in the diversity and abundance of parasites in helminth communities parasitic in fish hosts. First, I discuss the large-scale variation in both the number and composition of species in fish parasite communities, and how these can be influenced by climate. Second, I turn to the abundance of common parasite species, to show that the local abundance of parasites does not always vary stochastically among their entire geographic range: latitudinal gradients exist, and they suggest that climate change could cause peaks in parasite abundance to shift northward or southward. The overall aim of this essay is to argue that parasite communities in fish hosts are not stable, but rather they are dynamic assemblages whose compo-

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sition and overall abundance change over time in large part as a response to climatic conditions.

Geography of parasite diversity

As explained above, the structure of parasite communities in different populations of the same host species is not predictable and repeatable: instead, any pattern observed in one host population tells us little about what we will observe in another population (Poulin and Valtonen, 2002; Timi and Poulin, 2003; Poulin, 2007a). One of the main reasons for this lack of repeatability is that the composition of parasite communities changes on a geographic scale. As one moves from one end of the host's geographical range to the opposite end, the similarity in the species composition of parasite communities harboured by populations of that host species decreases as an exponential function of distance (Poulin, 2003). This is well illustrated by data on the helminth communities of pike, *Esox lucius*, across North America (Fig. 1). Similar patterns have been documented among the parasite communities of other species of freshwater and marine fish (Poulin, 2003; Fellis and Esch, 2005; Oliva and González, 2005).

The relatively smooth decrease in the similarity of different parasite communities with increasing distance seen in many of these examples suggests a more-or-less gradual replacement of parasite species in one geographical area by other species in other areas within the range of the host species. Biological properties of the parasite species, such as their dispersal abilities, no doubt play a role in preventing a parasite from occupying the entire range of its host species. However, the observed patterns suggest a series of parasite species with overlapping ranges across the host's geographical range. Given that many environmental factors are spatially autocorrelated, we expect that sites in close proximity have more similar environmental conditions than distant sites. Thus, a parasite species present in one locality because suitable intermediate hosts are available and because abiotic conditions allow the survival of infective stages, becomes increasingly unlikely to occur in progressively more distant sites because the availability of intermediate hosts and the abiotic conditions become progressively further from optimal. There is no doubt that climate is the main driver of this spatial autocorrelation, as it determines to a large extent both abiotic conditions and the distribution of invertebrate intermediate host species in freshwater and marine systems. Therefore, from the available evidence, we must conclude that the distribution of parasite species, and hence the local composition of parasite communities, will be altered as climatic conditions change over the next century. Other driving forces, such as species invasions and aquatic pollution, will also come into play, but it seems inevitable that on its own climate change will leave its imprint on fish parasite communities.

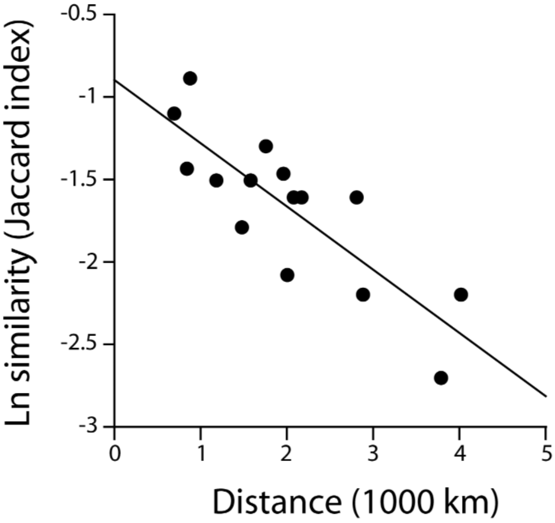

Fig. 1. Relationship between similarity in species composition and distance between component communities, for all pairwise comparisons among 6 helminth component communities of a fish host, the pike *Esox lucius* in North America. The Jaccard index corresponds to the number of parasite species shared by both component communities divided by the total number of species found in the two communities put together; it ranges from 0 (no species in common) to 1 (the two component communities have exactly the same parasite species). (from Poulin, 2003)

It is not only the composition of fish parasite communities, but perhaps more alarmingly also their diversity, that will be affected by global climate change. Indirect support for this comes from the well-documented relationship between latitude and biodiversity (Gaston and Blackburn, 2000). Latitude is a convenient surrogate measure for a range of environmental parameters, most notably temperature. As a rule, and for most plant and animal taxa, as one moves from higher latitudes towards the tropics the diversity of species increases. For fish parasites, the evidence is equivocal. Among marine fish species, the mean species richness of ectoparasites per fish population sampled increases with increasing water temperature, and thus towards lower latitudes (Poulin and Rohde, 1997; Rohde and Heap, 1998). No such pattern is detectable for endoparasitic helminths among the same fish samples (Rohde and Heap, 1998). Among freshwater fish species, the species richness of parasites seems to peak at temperate latitudes, and not in the tropics (Choudhury and Dick, 2000; Poulin, 2001). These findings are based on comparisons between tropical and temperate fish species; because they are different fish species to begin with, the comparisons cannot reliably inform us about the role of latitude, or more precisely climate, in shaping their diversity. More recently, Luque and Poulin (2007) have compared the species richness of parasites in the same fish species but from three coastal areas of the Neotropics. They found that, after correcting for unequal sampling effort and other confounding variables, fish populations from around the Caribbean Islands harbour richer parasite faunas than those of conspecifics from the coast of Brazil or Mexico (Fig. 2). Clearly, parasite diversity

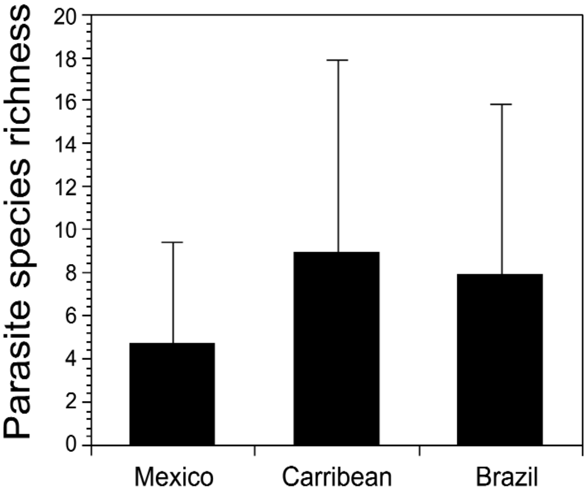

Fig. 2. Mean (± standard deviation) metazoan parasite species richness in marine fish species from the coast of Mexico, the Carribean islands, and Brazil. The data include only 57 fish species that occur in all three regions, and that were also examined for parasites in each region. (from Luque and Poulin, 2007)

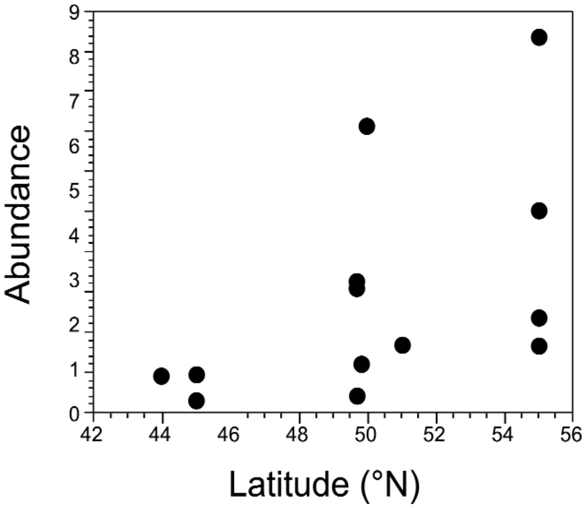

Fig. 3. Relationship between the abundance (mean number of parasites per host) of infection by the cestode *Proteocephalus pearsei* and the latitude at which populations of its host, the yellow perch *Perca flavescens*, were sampled within North America. (from Poulin and Dick, 2007)

varies on a geographic scale, and climate differences must in part be responsible for this variation. Rohde (1992) has even argued that climate, or more specifically temperature, is the key determinant of mutation and speciation rates in fish ectoparasites. Clearly, we are at a stage where we can integrate the accumulated knowledge on parasite ecology with spatial information on parasite biodiversity, and with predicted changes in climate conditions across geographical space, to try to understand how parasite diversity has evolved in the past and foresee how it will change in the near future.

Geography of parasite abundance

The interaction of climate change with parasite ecology and biogeography concerns not only parasite diversity, but also the abundance of all common species. Many parasite species infecting fish have broad geographical ranges, occurring in freshwater bodies over vast continental areas, or across large oceanic expanses. The prevalence, intensity and/or abundance of parasites of a given species vary among different populations of their hosts, but within species-specific bounds (see Poulin, 2006). However, the geographic structure of this variation has never been examined. The abundance of any given 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 (Sagarin *et al.*, 2006). Several empirical studies of free-living organisms indicate that this spatial variation often follows a regular pattern: the density of individuals tends to decrease from the centre of a species' range toward its margins. This is true for many species of plants, insects and vertebrates, but there are, however, many exceptions to this simple regular pattern (Sagarin *et al.*, 2006), and several alternative scenarios are possible. Recently, Poulin and Dick (2007) have investigated the geographical structure of abundance in different species of helminths parasitic in yellow perch, *Perca flavescens*, across North America. Each helminth species was sampled across a geographical area of at least 1500 km, and overall the data cover much of the geographical range of the host species. They found very little evidence suggesting that the abundance of any species tended to peak close to the centre of its geographic range, and to decrease toward the margins of the range (Poulin and Dick, 2007). Instead, the abundance of any given parasite species showed peaks as well as areas of low abundance spread across their range in a manner strongly suggesting that local conditions determine the transmission success and local abundance of parasites, as opposed to broader biogeographical processes. However, for species like the cestode *Proteocephalus pearsei* and the acanthocephalan *Leptorhynchoides thecatus*, local abundance was positively correlated with the latitude of the sampled population (see Fig. 3). Thus, in those species, the local density of parasites is greater in northernmost populations (Poulin and Dick, 2007). Whether directly or indirectly, climate must underpin this latitudinal gradient in abundance, by affecting the local diversity and density of host and non-host organisms and the transmission success of the parasites. The range of these two parasite species covered mainly areas around the Great Lakes, i.e. from the states of New York and Wisconsin to northern Ontario and Manitoba. Using the most reasonable scenario predicted by the coupled ocean-atmosphere climate models of the Intergovernmental Panel on Climate Change (IPCC; see http://www.ipcc.ch/), temperatures in this area are expected to rise by 4-5°C by the year 2080, while precipitation is expected to remain at current levels. What would this mean for the parasites *P. pearsei* and *L. thecatus*? It is impossible to make robust predictions based solely on temperature change, given the inherent complexities of ecological systems. Nevertheless, a simplistic scenario would see these species disappearing from the southern end of their geographical range, with the range shrinking to occupy only its current northern part. Whether or not this simple prediction comes true, there will inevitably be changes in the spatial distribution of abundance in these and many other parasites of fish. The geographic component of the host-parasite systems studied by fish parasitologists will change along with the climate, and we need now to focus on this larger-scale component to anticipate how and when it will eventually change.

Conclusions

The main purpose of this essay has been to argue that parasite communities are dynamic assemblages. They vary in space, with different populations of the same host species often harbouring very different parasite communities, and they will vary in time, as an inevitable response to changes in climate. I have tried to emphasize that (i) the diversity and abundance of fish parasites variy on a geographical scale, in large part driven by climatic factors, and (ii) the planet's climate is changing. There is a growing need for fish parasitologists to assess how parasites and diseases will respond, for both economic and conservation reasons. A good starting point would be to place more emphasis on the geographical scale in studies of parasite communities of fish, and a little less on local scales, to assess spatial variation on a level relevant for the sort of changes ahead. This is the time to transform fish parasite ecology from a mostly descriptive discipline into a predictive science, capable of integrating complex ecological data to generate forecasts about the future state of host-parasite systems.

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