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Salinity gradient shapes distance decay of similarity among parasite communities in three marine fishes

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Published data were used to compare the distance decay of similarity in parasite communities of three marine fish hosts: Atlantic cod *Gadus morhua*, the dab *Limanda limanda* and the flounder *Platichthys flesus* in two adjacent areas that differ with respect to the strength of a salinity gradient. In the Baltic Sea, which exhibits a strong salinity gradient from its connection with the North Sea in the west to its head in the north-east, parasite communities in all three fish hosts showed a significant decline of similarity with increasing distance. In contrast, among host populations in the North Sea, which is a fully marine environment, there was no such decline or only a weak relationship. The results suggest that environmental gradients like salinity can be strong driving forces behind patterns of distance decay in parasite communities of fishes.

Key words: Baltic Sea; biogeography; North Sea; parasitism.

INTRODUCTION

Geographical variation in the composition of parasite communities in marine fishes has several useful applications, in particular with regard to their use as biological tags for stock discrimination (Mackenzie, 1983, 1987, 2002; Lester, 1990; Mackenzie & Abaunza, 2005). This variation, however, is the manifestation of broader biogeographical processes that lead to universal patterns, such as the decay of similarity in community composition with increasing geographical distance (Nekola & White, 1999; Soininen *et al*., 2007). This means that the proportion of shared species between two localities decreases exponentially with increasing distance between them. The two main underlying mechanisms are environmental gradients and the different dispersal capacities of organisms. Environmental conditions can change rapidly with increasing distance between communities, and as species differ in their environmental preferences this leads to a niche-based turnover in the community composition. Species also differ in their ability to disperse, either because of dispersal barriers in their habitats or ranges, or because of intrinsic dispersal capacities.

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Neither mechanism is mutually exclusive and they probably jointly contribute to most distance decay phenomena (Soininen *et al.*, 2007).

Distance decay in community similarity has been observed not only in free-living species but also in parasites, particularly those of fishes (Poulin, 2003; Karvonen & Valtonen, 2004; Oliva & González, 2005). Some of these studies suggest that the dispersal capacity of the parasites' hosts is an important determinant of the strength of the distance-decay relationship. For example, distance-decay relationships in parasite communities of trematodes in molluscan intermediate hosts are mediated by the dispersal capacity of their definitive hosts (which shed parasite eggs that infect the snails). In this case, the slopes of distance-decay curves are lower in parasites utilizing highly vagile bird compared with less vagile fish hosts (Thieltges *et al.*, 2009). Little is known, however, of the effects of environmental gradients on distance-decay patterns of parasite communities. Parasites can be affected by environmental factors either directly or indirectly. Direct effects often occur at the free-living stages that are an integral part of the complex life cycles of many parasites (Pietrock & Marcogliese, 2003; Thieltges *et al.*, 2008). Indirect effects occur *via* changes in the respective pools of intermediate and definitive host species resulting from differing environmental conditions. For example, eutrophication often changes the community composition of free-living species and can in turn affect the composition of the parasite communities they harbour (Kesting & Zander, 2000; Johnson & Carpenter, 2008).

The distance decays of similarity in parasite communities of three marine fish hosts were compared in two adjacent areas that differ with respect to the strength of an environmental gradient. While the North Sea is a fully marine environment, the adjacent Baltic Sea exhibits a strong salinity gradient from its connection with the North Sea in the west to its head in the north-east (Schiewer, 2008). While salinity is *c.* 30 close to the North Sea, it declines to *c.* 6–8 in the central Baltic Sea; the proximal ends of the Bothnian Bay and Gulf of Finland are fresh water. Parasites are expected to react to this salinity gradient either directly (*e.g.* sensitivity of free-living stages) or indirectly (*e.g.* composition of the intermediate and definitive host communities). Hence, it would be expected that the slope of the distance decay in parasite community similarity to be steep in communities from the Baltic Sea and gentler or absent in communities from the North Sea. Using data from the published literature, this assumption was tested for parasite communities in three fish host species that occur in both the North Sea and the Baltic Sea. The analyses attempted to provide a large-scale biogeographic study of the variation in the composition of parasite communities in marine fishes in relation to salinity gradients.

MATERIALS AND METHODS

A data set was compiled from published studies on parasite communities in the Atlantic cod *Gadus morhua* L., the dab *Limanda limanda* (L.) and the flounder *Platichthys flesus* (L.), in the North Sea and the Baltic Sea (Table I; see original publications for maps of the sampling stations). Only studies conducted by the same authors in both or one of the two regions were included to avoid artefacts arising from differences in species identification among authors. For two fish species, only trematode data were available, whereas for the other fish species data on all metazoan parasites were available. In *P. flesus*, analyses were conducted both with

Table I. Summary of data set used for the analyses. For parasite communities in *Platichthys flesus* both all metazoan parasites (ALL) and the digenean sub-set only (TREM) were analysed. Parasite groups are trematodes (Trem); cestodes (Cest), nematodes (Nem), acanthocephalans (Acanth) and copepods (Cop)

Host species	Region	Parasite groups	Number of parasite species	Number of sites	Average (minimum and maximum) inter-site distances (km)	Source
Gadus morhua	North Sea	Trem	18	9	541 (87–1176)	Køie (1984)
	Baltic Sea	Trem	18	6	274 (64–485)	Køie (1984)
Limanda limanda	North Sea	Trem	13	6	499 (72–1196)	Køie (1983)
	Baltic Sea	Trem	13	6	200 (22–350)	Køie (1983)
Platichthys flesus TREM	North Sea	Trem	6	5	56 (28–93)	Schmidt *et al*. (2003)
	Baltic Sea	Trem	5	8	462 (120–1054)	Køie (1999)
Platichthys flesus ALL	North Sea	Trem, Cest, Nem, Acanth, Cop	24	5	56 (28–93)	Schmidt *et al*. (2003)
	Baltic Sea	Trem, Cest, Nem, Acanth, Cop	27	8	462 (120–1054)	Køie (1999)

the total data set and for the trematode sub-set only, to allow for direct comparison with the other host species. For each region (North and Baltic Seas) and host species, the similarities in species composition were computed for all pairs of sites with the computer software EstimateS (Colwell, 2005). As diversity indices can give different results depending on the type of data, three widely used similarity indices were used to identify general patterns (Magurran, 2004): (1) Jaccard, (2) Morisita–Horn and (3) Bray–Curtis. While the first index is qualitative and based on the presence or absence of parasite species, the other two are quantitative as they were based on prevalence data (% infected hosts in each local population). All three indices vary from 0 (no species in common) to 1 (complete similarity). In two data sub-sets (*L. limanda* Baltic Sea; *P. flesus* North Sea), parasite richness was positively correlated with sampling effort per site, *i.e.* with the number of fishes examined for parasites. In both cases, this was based on a single locality with relatively low sample size, and excluding these sites gave similar results in subsequent analyses. Hence, the full data sets are presented.

To calculate distances among localities, the co-ordinates of the sampling stations were obtained either from the original source (Schmidt *et al.*, 2003) or from maps in the original publications. Scans of these maps were imported into a geographic information system (GIS) and georeferenced using the ESRI software ArcGIS 9.2, ArcMap (www.esri.com). While most studies gave single sampling points in the maps, Køie (1999) used several sub-sites per sampling locality, and therefore a central co-ordinate for each locality was determined. The distance among localities was calculated with ArcGIS 9.2 by determining the shortest distance between two sites on the waterway (accounting for the complex geography in the Baltic Sea). This was done using a cost–weighted-distance analysis, where water was defined as a cheap travel path and land as a very expensive travel path. A conservative calculation of the total spatial error of the georeferenced maps was *c*. 10 km, which was considered to be marginal as most sampling localities are several 100 km apart.

The rate of distance decay among parasite communities was investigated by means of linear regressions across all pair-wise comparisons between sites, using $\log_{10}$-transformed similarity index data as those gave the best fit. Due to the non-independence of the data (each parasite community is used in more than one comparison), significance levels were tested using a permutation approach. All regression probabilities were based on 10 000 permutations using the computer software Resampling (Howell, 2000). To test for homogeneity of slopes among two regions in significant regressions, an ANCOVA approach was used, testing for significance of the interaction term (region × distance) (Quinn & Keough, 2002).

RESULTS

The similarity of parasite communities strongly decreased with distance in all three fish host species in the Baltic Sea (Fig. 1). This distance decay of similarity in the Baltic Sea was significant for all but two similarity indices in *G. morhua*, for which significance was borderline (Table II). In most cases, the distance decay relationship was strong and the regressions explained large proportions of the variance in similarity as indicated by the associated r^2 values (Table II). In contrast, in the North Sea, distance decay of similarity was absent in two host species (*L. limanda* and *P. flesus*) and only detectable in parasite communities of *G. morhua* (Fig. 1 and Table II). The slope of the significant regressions (Jaccard index), however, was flatter for North Sea parasite communities than for communities from the Baltic Sea (ANCOVA, $F_{1,49} = 19{\cdot}83$, $P < 0{\cdot}001$). Similarity of parasite communities therefore decreased more strongly with increasing distance in the Baltic Sea than in the North Sea.

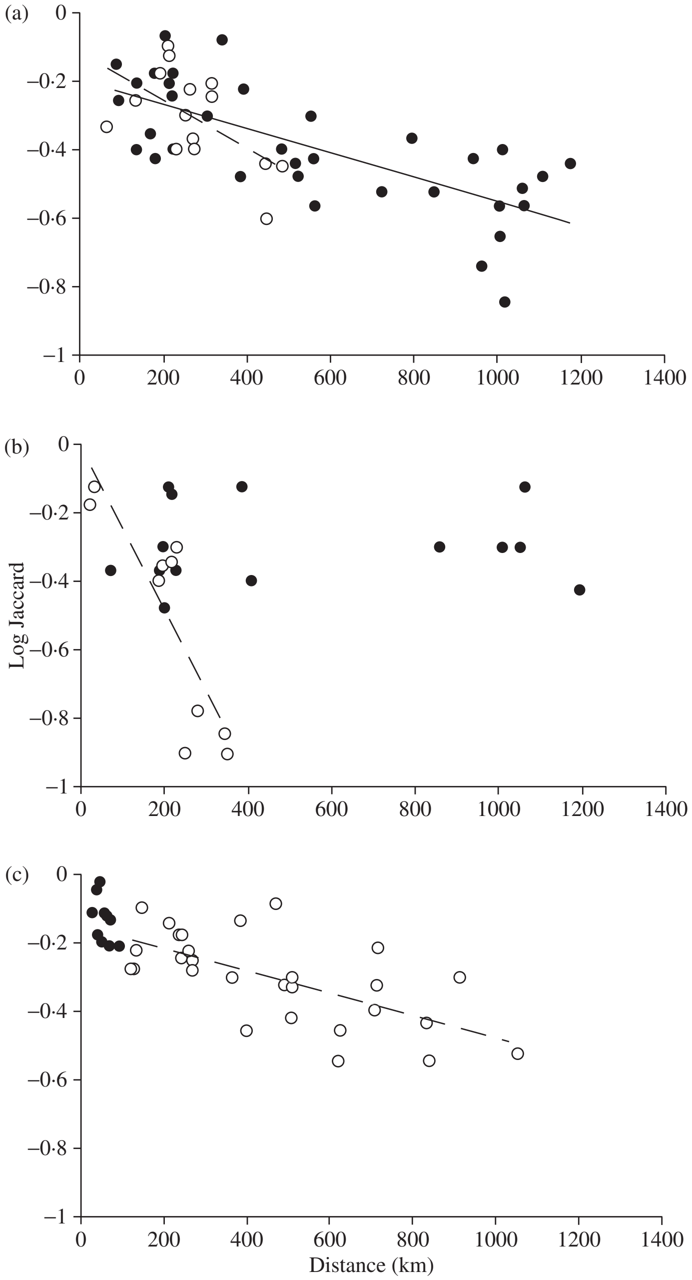

FIG. 1. Similarity ($\log_{10}$ Jaccard index) of parasite communities plotted against distance (km) for all pair-wise comparisons for (a) *Gadus morhua*, (b) *Limanda limanda* and (c) *Platichthys flesus* in the North (●) and Baltic (○) Seas. Only Jaccard index values are plotted, the other two indices tested gave similar results (see Table II). For *P. flesus*, the total data including all metazoan parasites were used in the figure, as the digenean trematode data sub-set gave similar results. Curves were fitted (see Table II) for the North (___) and Baltic (_ _ _) Seas.

TABLE II. Regression statistics for the distance decay of similarity in parasite communities of three fish host species: *Gadus morhua*, *Limanda limanda* and *Platichthys flesus* in two regions: North and Baltic Seas, using three diversity indices: Jaccard, Morisita–Horn and Bray–Curtis. For parasite communities in *P. flesus* both all metazoan parasites (ALL) and the digenean sub-set only (TREM) were analysed. Only slopes of significant regressions are given. r^2 statistics and significance tests are based on randomization procedures with all regression probabilities calculated from 10 000 permutations

		Slope	r^2	P
Gadus morhua				
Jaccard	North Sea	−0·000359	0·534	<0·001
	Baltic Sea	−0·000694	0·342	<0·05
Morisita–Horn	North Sea	−0·000167	0·186	0·01
	Baltic Sea		0·216	>0·05
Bray–Curtis	North Sea	0·000231	0·295	<0·001
	Baltic Sea		0·195	>0·05
Limanda limanda				
Jaccard	North Sea		0·013	>0·05
	Baltic Sea	−0·002350	0·723	<0·001
Morisita–Horn	North Sea		0·148	>0·05
	Baltic Sea	−0·000424	0·476	<0·05
Bray–Curtis	North Sea		0·214	>0·05
	Baltic Sea	−0·000903	0·629	<0·01
Platichthys flesus TREM				
Jaccard	North Sea		0·054	>0·05
	Baltic Sea	−0·000322	0·321	<0·01
Morisita–Horn	North Sea		0·0004	>0·05
	Baltic Sea	−0·000267	0·741	<0·001
Bray–Curtis	North Sea		0·027	>0·05
	Baltic Sea	−0·000310	0·823	<0·001
Platichthys flesus ALL				
Jaccard	North Sea		0·013	>0·05
	Baltic Sea	−0·000439	0·723	<0·001
Morisita–Horn	North Sea		0·148	>0·05
	Baltic Sea	−0·000196	0·476	<0·05
Bray–Curtis	North Sea		0·214	>0·05
	Baltic Sea	−0·000206	0·629	<0·01

DISCUSSION

In coastal marine systems, parasite communities in fish hosts exhibit the typical distance decay of similarity (Oliva & González, 2005). There has been no attempt previously, however, to investigate the role of environmental gradients as a driving force behind this pattern. In marine environments, salinity is a particularly important environmental gradient (Nybakken, 1997). Here, patterns of distance decay of similarity in the parasite communities of three fish species occurring in two very different environments with respect to salinity were contrasted: one with a strong salinity gradient impacting the community composition of free-living organisms, and the other without any pronounced salinity gradient. While parasite communities in all three fish host species showed a decline of similarity with distance among host populations in the Baltic Sea, there was no such decline or only a weak relationship in North Sea communities.

The strong west-east gradient of decreasing salinity in the Baltic Sea causes a typical structuring of free-living organisms resulting in the limited distributions of many species along the gradient (Remane, 1958; Schiewer, 2008). In the west, marine species still prevail, while the proportion of brackish and freshwater species increases towards the east. Particularly relevant for parasites are the distributional limits of gastropods which serve as first intermediate host of trematodes, the major parasitic group considered in these analyses. Many gastropod species show limited distributions determined entirely by salinity, and this indirectly imposes distributional limits on their parasites (Zander, 1998; Zander & Reimer, 2002). Salinity may also directly affect the free-living stages of parasites and lead to distributional limits. For example, cercariae of the trematode *Cryptocotyle lingua*, responsible for black spot disease in fishes, only tolerate salinities down to eight at temperatures $>10^\circ$ C (Möller, 1978). These direct and indirect distributional limits of host and parasite species result in marked turnover of the parasite community along the salinity gradient over relatively short geographical distances in the Baltic Sea as known from various fish species (Zander, 1998; Zander & Reimer, 2002). Salinity effects on parasite composition in fish hosts are known not only from within the Baltic Sea but also from other systems like the River Thames (Guillen-Hernandez & Whitfield, 2004) or from various freshwater, brackish-water and marine localities in northern Germany (Jakob *et al.*, 2009). Such parasite community changes due to salinity gradients have never been investigated in terms of their effects on distance-decay relationships. In contrast to the Baltic Sea, salinity is not a major factor structuring host communities in the North Sea. Here, the general composition of free-living species depends more on factors acting at much larger scales, such as biogeographical regions. Hence, host communities only change significantly on much larger spatial scales than in the Baltic Sea. This difference between the Baltic Sea and the North Sea is reflected in the observed patterns of distance decay in parasite communities, with distance decay being apparent in the Baltic Sea communities but absent (*L. limanda* and *P. flesus*) or weaker (*G. morhua*) in the North Sea. Salinity as an important environmental factor can thus be a strong determinant of distance decay of similarity among marine parasite communities.

Salinity is not the only determinant of distance-decay relationships. In parasite communities of *G. morhua*, there was a significant effect of distance on similarity of parasite communities in the North Sea, whereas distance decay was absent in this area for the other two host species. In *P. flesus*, this might be attributed to the relatively small distance covered by the North Sea data set (maximum distance between sites: 93 km). The data available for *L. limanda*, however, span over a similar range of geographical distances in the North Sea as those for *G. morhua*. The reason for the difference in the distance decay pattern between the two host species is unclear. It may be that some of the intermediate hosts of parasites infecting *G. morhua* are more restricted in their distribution in the North Sea than those of parasites infecting *L. limanda*, leading to a decline in similarity with distance. General information on intermediate host use and the distribution of hosts is too poor for a conclusion. It may also be that there are other unknown gradients besides salinity that affect the parasite communities of one host species more than the other. More detailed studies are needed to investigate this phenomenon.

Most patterns that were uncovered here involved trematode parasites. In the host species where data from other metazoan parasites were available (*P. flesus*), the patterns were similar irrespective of whether the full data set was used or only the trematode sub-set. This may indicate that distance-decay patterns of fish parasites in general, and not just trematodes, are sensitive to environmental gradients like salinity, although more studies are needed to confirm the generality of the observed pattern for other parasites groups. It will also be interesting to investigate whether the observed pattern also holds true for other host groups like birds and marine mammals. Overall, the results suggested that environmental gradients can be strong driving forces behind patterns of distance decay.

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