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ORIGINAL ARTICLE

Biogeographical patterns of marine larval trematode parasites in two intermediate snail hosts in Europe

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ABSTRACT

Aim We used published inventories of trematodes in *Littorina littorea* (L.) and *Hydrobia ulvae* (Pennant) in European seas to search for two basic biogeographical patterns in the spatial occurrence of various trematode species: (1) do parasite distribution and richness patterns in the two host snails overlap with known ecoregions of free-living organisms; and (2) does trematode species richness in the snails follow latitudinal or longitudinal gradients?

Location North East Atlantic.

Methods We used multidimensional scaling (MDS), analysis of similarity (ANOSIM) and analysis of variance (ANOVA) to test whether there were overlaps of parasite distribution and richness with known ecoregions of free-living organisms. In addition, we used linear regression analyses to test whether trematode richness in snails (corrected for sampling effort) was correlated with the latitude or longitude of the sampling sites.

Results When corrected for sampling effort, mean trematode species richness per site did not differ among the different ecoregions in *L. littorea*. In contrast, in *H. ulvae*, mean species richness was much lower for sites from the Celtic Sea compared with sites from the Baltic Sea and the North Sea. Based on the results of MDS analyses, trematode species composition was distinct among ecoregions; in particular, communities from the Baltic Sea differed markedly from communities in the Celtic Sea, for both snail species. Latitude and longitude were not significantly correlated with parasite species richness in either snail species. Most trematode species had restricted distributions, and only three species in *L. littorea* and five species in *H. ulvae* occurred at more than 50% of the sites.

Main conclusions There is more structure in the large-scale distribution of trematodes in gastropods than one would expect from the large-scale dispersal capabilities of their bird and fish final hosts. We propose mechanisms based both on limited dispersal via fish and bird final hosts and on gradients in environmental factors to explain the observed patterns.

Keywords

Dispersal, distribution, gastropod hosts, *Hydrobia ulvae*, intermediate hosts, *Littorina littorea*, North East Atlantic, parasites, trematodes.

INTRODUCTION

Species generally show recognizable large-scale biogeographical patterns in distribution and abundance (Cox & Moore, 2005; Lomolino *et al.*, 2006). Many species exhibit similar distributions depending on similar regional conditions, a phenomenon allowing the detection of distinct faunal provinces and regions (Briggs, 1995; Cox & Moore, 2005; Lomolino *et al.*, 2006). Whereas free-living species have received much attention in this respect, much less is known about biogeographical

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patterns in parasites (Kennedy & Bush, 1994; Rohde, 2002). One might expect that the geographical distribution of a parasite would match closely that of its host; however, especially in parasite species with complex life cycles requiring a series of different host species, several factors can create mismatches between the spatial occurrences of host and parasite species.

Almost all we know about the biogeographical patterns of parasites is derived from studies on fish parasites, particularly in the marine realm (Rohde, 1993, 2002). Early studies suggested a decrease in the similarity of parasite communities in marine fish with increasing distance between them (Manter, 1940, 1955, 1963), as well as the existence of distinct zoogeographical regions (Lebedev, 1969). Such distributional patterns of parasites are not always consistent with the biogeographical regions characterizing free-living species (González & Moreno, 2005). There might thus be ecological processes affecting the distributions of marine parasites that do not influence the distribution of free-living marine organisms. In addition, the existence of latitudinal gradients in parasite species richness remains controversial (Rohde, 2002). In general, the diversity of ectoparasites increases with decreasing latitude (or increasing water temperature) (Rohde, 1993, 2002; Poulin & Rohde, 1997; Rohde & Heap, 1998). In contrast, no such pattern seems to exist for endoparasites of fish (Rohde & Heap, 1998; Choudhury & Dick, 2000; Poulin, 2001; Rohde, 2002). In addition to latitude, other environmental gradients such as depth or longitudinal gradients may affect diversity patterns of marine parasites (Rohde, 1993). In all earlier studies, the fish in question serve as final hosts for a variety of parasite groups. These groups have either direct life cycles or more complex indirect life cycles that involve one or two intermediate hosts. To date, the biogeographical patterns of parasitism in intermediate hosts remain largely unknown.

Gastropods are important intermediate hosts of parasites in marine systems (Mouritsen & Poulin, 2002). They serve as first intermediate hosts for digenean trematodes. In the snails, these parasites usually produce a free-living infective stage, the cercaria, which is shed in large numbers into the environment before it goes on to infect a second intermediate host (invertebrate and/or vertebrate, depending on the parasite species). When the second host is consumed by a final host (fish, bird or mammal, again depending on the species), the life cycle is completed; it starts again with eggs being produced by adult worms inside the final host. In coastal ecosystems, the majority of trematodes use birds as final hosts and to a lesser extent fish (Mouritsen & Poulin, 2002). There is good evidence that the final host diversity and abundance in an area determine the diversity and abundance of parasites in snail hosts on small to medium spatial scales (Smith, 2001; Hechinger & Lafferty, 2005; Fredensborg *et al.*, 2006; Byers *et al.*, 2008). In addition, local parasite diversity in snails is also positively correlated with the diversity of free-living benthic species (Hechinger *et al.*, 2007). Hence, one would expect that biogeographical patterns of parasites in snails should follow closely those of their hosts; that is, they should reflect the biogeographical regions that characterize marine free-living species. However, host groups serving as final hosts for trematodes (birds and fish) are highly mobile and can show regular large-scale migrations, so that we might instead expect a mixing of the parasite species pool on larger scales (10–1000 km).

Snails provide an excellent way to assess trematode diversity and distribution because their limited movements do not matter on biogeographical scales. Even in species with planktonic dispersal stages, the large-scale movements of larvae are irrelevant, as trematode infections occur only in post-juvenile stages settled permanently in one locality. A local snail population can thus capture local trematode diversity by archiving any past visits to the locality by bird or fish final hosts. Early reviews suggested a more or less homogenous distribution of parasites in marine molluscs over large spatial scales (Cheng, 1967; Lauckner, 1980), but this has never been properly tested. Alternatively, the large-scale distribution patterns of parasites in snail intermediate hosts might be driven by environmental factors associated with latitude or longitude (Poulin & Mouritsen, 2003); it is thus important to distinguish between latitudinal or longitudinal gradients and other biogeographical patterns.

Here, we focus on two marine gastropods with a rich parasite fauna and relatively wide distributions along European coastlines: *Littorina littorea* (L.) and *Hydrobia ulvae* (Pennant). Both have been extensively studied with respect to parasites, and inventories of their trematodes are available from a variety of sites across the hosts' range in Europe. We did not include data on *L. littorea* from North America because of the invasive status of the species on that continent. There, factors such as enemy release during invasion and the subsequent acquisition of local parasites have resulted in very different, and generally depauperate, trematode communities (Blakeslee & Byers, 2008). We compiled a database on parasite distributions from European studies to investigate biogeographical patterns of larval trematodes in these two prominent host species. First, we investigated whether parasite communities in the two snails are homogeneous over large geographical scales, or whether they show distinct large-scale distributional patterns. We also compared observed biogeographical patterns of trematodes with the known biogeographical regions defining the distributions of European marine organisms. Second, we determined whether there is a statistical effect of latitude (as a proxy for temperature) or longitude (as a proxy for salinity decreasing eastwards in the Baltic Sea) on parasite species richness across populations of these snails.

MATERIALS AND METHODS

Database

We searched bibliographical databases and our own reprint collections for inventories of trematode parasites in *L. littorea* and *H. ulvae* in European seas. We included in our database only studies that (1) investigated the entire trematode community, (2) identified parasites to species level, (3) recorded the sampling effort (i.e. the numbers of snails dissected), and (4) examined at least 80 individual snails from one locality. A minimum of 80 individuals was chosen as a trade-off between minimizing any effects of sampling effort on trematode richness and retaining enough samples for the analyses. For each sampling site, we recorded the presence or absence of parasite species in our database. We refrained from using prevalence (percentage of population infected) to avoid a bias from potential differences in host sizes investigated at the different sites (prevalence usually increases with host size). The mean shell size sampled at a locality might also affect richness patterns, as larger snails accumulate more parasites. However, preliminary analyses indicated that there was no consistent bias in the data sets that could influence the analyses.

All parasite species names were carefully matched with their known synonyms (e.g. James, 1968; Deblock, 1980; Lauckner, 1980, 1983), to allow faunal comparisons between sites unmarred by differences in nomenclature. In addition to the presence/absence of parasite species, we recorded the sampling effort for each site. If the same site was sampled at different times, we used the total parasite inventory obtained and the total number of snails dissected. For each sampling site, we also obtained the coordinates either from the literature or using site descriptions from the original study and Google Earth (http://earth.google.com). In cases for which the mean of several sub-sites within a range of a few kilometres was reported in the literature, we used coordinates from the centre of the range. We also assigned each site to one of four ecoregions based on a recent classification: Baltic Sea, North Sea, Celtic Sea, South European Atlantic Shelf (Spalding *et al.*, 2007). The type of final host (bird, fish or mammal) used by each parasite species was obtained from previously published information on life cycles.

Statistical analyses

We calculated the total number of trematode species per ecoregion by summing all species occurrences in our database. To test for effects of sampling effort on species richness, we used linear regressions of the number of species vs. sampling effort (both ln-transformed) across all sites, separately for each snail species. As there was a slight positive correlation in both host species, we compared the mean number of species per site among ecoregions using residuals from the regression in order to correct for potential influences from unequal sampling effort. To test for differences in species richness among ecoregions we used one-way ANOVA designs with the number of species (corrected for sampling effort) as the dependent variable. Relationships between species richness (corrected for sampling effort) and latitude or longitude were tested with linear regressions. To investigate patterns in parasite community composition among the four ecoregions, we used multidimensional scaling (MDS) techniques based on Bray–Curtis similarity matrices using presence/absence data (PRIMER 5, version 5.2.9). We first analysed the total data set, and then repeated the analysis using only species occurring at more than 10% of the sites. To test for differences in parasite community composition among the four ecoregions, we used analysis of similarity (ANOSIM) procedures (PRIMER 5, version 5.2.9), again using first the total and then a reduced data set.

RESULTS

We obtained parasite inventories for *L. littorea* from 35 sites, and for *H. ulvae* from 36 sites (Table 1; see Appendix S1 and S2 in Supporting Information). In total, 10 trematode species have been reported from *L. littorea* and 44 from *H. ulvae* (Tables 2 and 3). The total numbers of parasite species recorded within an ecoregion followed roughly similar trends in the two snail host species, being higher in the North Sea and Celtic Sea than in the Baltic Sea (Table 1). In the Southern European Shelf Region, the total species number was similar to that in the Celtic Sea in *H. ulvae* but extremely low in *L. littorea* (Table 1). However, the latter value is based on a single locality with relatively low sample size (120 snails), and may only poorly reflect the actual parasite fauna in the ecoregion.

The number of species recorded (ln-transformed) at each site was positively correlated with sampling effort (*L. littorea*: $R^2 = 0.13$, $P = 0.03$; *H. ulvae*: $R^2 = 0.4$, $P = 0.02$). Mean species richness (corrected for sampling effort) per site was not different among the ecoregions in *H. ulvae* (ANOVA, $F_{3,32} = 12$, $P = 0.94$) [Baltic Sea: 0.75 ± 2.63; North Sea: −0.51 ± 0.81; Celtic Sea: 0.25 ± 2.71; South European Atlantic Shelf (South EAS): 0.07 ± 0.76]. In contrast, mean species richness (corrected for sampling effort) per site differed among ecoregions in *L. littorea* (ANOVA, excluding South EAS owing to single data point only: $F_{2,\ 31} = 3.7$, $P = 0.035$), with lower species richness in sites from the Celtic Sea (−0.68 ± 0.35) than in sites from the Baltic Sea (0.11 ± 0.31) and the North Sea (0.44 ± 0.25).

Latitude was not significantly correlated with parasite species richness (corrected for sampling effort) in *H. ulvae* ($P = 0.96$) and showed only a weak positive correlation in *L. littorea* ($R^2 = 0.2$; $P = 0.008$) (Fig. 1). However, when the southernmost data point with its relatively low sample size (120 snails) was excluded, this relationship was no longer significant ($R^2 = 0.09$, $P = 0.08$). No effect of longitude was found in *L. littorea* ($P = 0.06$) nor in *H. ulvae* ($P = 0.72$).

The composition of the parasite communities differed among the four ecoregions, as indicated by the significant ANOSIM *R* statistics (Global *R*) (Table 4, Fig. 2). This test is the rough equivalent of an ANOVA and tests whether there are compositional differences between groups of samples. In the subsequent pair-wise comparisons (*R*) (equivalent to ANOVA *post-hoc* tests), parasite communities from the Baltic Sea differed from communities in the Celtic Sea for both snail hosts. The associated *R*-values suggest overlapping but clearly different species compositions between the two regions ($R > 0.5$) (Table 4). Whereas this was the only significant difference among ecoregions in *H. ulvae* using the reduced data set, parasite species composition in *L. littorea* was also

Table 1 Summary statistics of data used for the analyses (for details see Appendix S1 and S2) of parasite assemblages in (a) *Littorina littorea* and (b) *Hydrobia ulvae* for the four biogeographical regions: Baltic Sea (Baltic), North Sea (North), Celtic Sea (Celtic) and South European Atlantic Shelf (South). Note that the mean richness per site gives mean values uncorrected for sampling effort.

	Baltic	North	Celtic	South
(a) *Littorina littora*				
Mean no. of snails dissected per site (± SD)	5700 ± 12173	5892 ± 20331	1159 ± 1960	120
Median no. of snails investigated	1291	575	300	120
Total no. of snails dissected	45,597	100,170	10,430	120
Total no. of sites	8	17	9	1
Total richness	5	7	7	1
Mean richness per site (± SD)	4.1 ± 1	4.2 ± 0.9	3 ± 1.3	1
(b) *Hydrobia ulvae*				
Mean no. of snails dissected per site (±SD)	1526 ± 2072	2247 ± 3617	1267 ± 1359	1833 ± 1893
Median no. of snails investigated	540	1000	1000	1000
Total no. of snails dissected	4578	47,183	11,400	5500
Total no. of sites	3	21	9	3
Total richness	16	29	22	23
Mean richness per site (± SD)	8.3 ± 5.7	9.6 ± 4.3	8 ± 2.8	9.7 ± 7.6

Table 2 Parasite species found in *Littorina littorea* for the four ecoregions [Baltic Sea (Baltic), North Sea (North), Celtic Sea (Celtic) and South European Atlantic Shelf (South)] and the type of final host used by each parasite species.

Family	Species	Baltic	North	Celtic	South	Final host
Echinostomatidae	*Himasthla elongata*	×	×	×	×	Birds
Renicolidae	*Renicola roscovita*	×	×	×		Birds
	Cercaria emasculans			×		Birds
	Cercaria A		×			Birds
Notocotylidae	*Paramonostomum chabaudi*		×	×		Birds
Heterophyidae	*Cryptocotyle lingua*	×	×	×		Birds/Seals
Microphallidae	*Microphallus similis*			×		Birds
	Microphallus pygmaeus	×	×			Birds
Opecoelidae	*Podocotyle atomon*	×	×			Fish
	Cercaria littorinae			×		Fish

different in North Sea sites compared with sites in the Celtic and Baltic seas (Table 4). However, the associated *R*-values suggest a weaker separation of the faunas compared with the difference between the Celtic Sea and the Baltic Sea.

The observed difference in parasite species composition among the four ecoregions obviously results from differences in the occurrence of certain parasites among the regions (Tables 2 and 3). Clearly, many parasites seem to have restricted ranges and do not occur in all four ecoregions. For example, the Baltic Sea seems to be a centre for species with restricted ranges in *H. ulvae*. There are also substantial differences in the frequency of occurrence of single parasite species. Only three species in *L. littorea* and five species in *H. ulvae* occur in more than 50% of the sites investigated (Fig. 3). Most parasite species occur in fewer than 20% of the sites (Fig. 3).

DISCUSSION

Trematode parasites in gastropods are not as evenly distributed over the study area as one would assume from the large-scale dispersal capabilities of their bird and fish final hosts. Our analyses revealed differences in trematode species richness among some ecoregions, and indicated restricted distributions of many parasite species. Latitude (as a proxy for temperature) and longitude (as a proxy for salinity decreasing eastwards in the Baltic Sea) had no effect on species richness in both host snails. All this suggests that there are dispersal limits for many parasite species even though the dispersal potential of parasite propagules (eggs in the final hosts' faeces) must be high considering the general vagility of birds and fish and their regular large-scale migrations. Several mechanisms may act as dispersal barriers for trematode parasites in snails, ranging from constraints on host dispersal to environmental effects. Although many birds generally use the East Atlantic Flyway along the coast of Europe, this flyway is not a fixed corridor but instead integrates several species-specific migration routes that vary considerably in spatial scale (Smit & Piersma, 1989). Hence, the extent to which the four ecoregions are used by migrating birds differs, as does the local composition of the migrating bird fauna within each region. This may impose dispersal limits for the parasites carried in the birds' intestines.

Table 3 Parasite species found in *Hydrobia ulvae* in the four ecoregions [Baltic Sea (Baltic), North Sea (North), Celtic Sea (Celtic) and South European Atlantic Shelf (South)] and the type of final host used by each parasite species.

Family	Species	Baltic	North	Celtic	South	Final host
Monorchiidae	*Asymphylodora demeli*	×				Fish/Polychaete
Cryptogonimidae	*Cryptogonomidae* sp.		×			Fish
	Aphalloides timmi	×				Fish
Hemiuridae	*Cercaria sinitzini*	×			×	Fish
	Bunocotyle progenetica		×	×	×	Fish/Gastropod
	Bunocotyle cingulata	×				Fish/Gastropod
Haploporidae	Sp. no. 3		×	×	×	Fish
	Sp. no. 4		×	×	×	Fish
	Sp. no. 6				×	Fish
	Haploporus benedeni				×	Fish
	Sp. no. 7		×	×	×	Fish
Acanthocolpidae	*Deropristis inflata*		×			Fish
Echinostomatidae	*Himsthla continua*	×	×	×		Birds
	Himasthla interrupta	×	×	×	×	Birds
	Sp. no. 8		×			Birds
	Sp. no. 9				×	Birds
Psilostomatidae	*Psilochasmus aglyptorchis*		×			Birds
	Psilochasmus oxyurus	×				Birds
	Psilostomum brevicolle		×	×	×	Birds
Heterophyidae	*Cryptocotyle jejuna*		×	×	×	Birds/Seals
	Cryptocotyle lingua	×				Birds/Seals
	Cryptocotyle concavum	×	×	×	×	Birds/Seals
	Pygidiopsus ardae		×	×	×	Birds
Notocotylidae	*Paramonostomum alveatum*	×				Birds
	Sp. no. 10		×	×	×	Birds
	Sp. no. 11		×	×		Birds
	Sp. no. 12		×	×		Birds
Microphallidae	*Cercaria microphallidarum*	×				Birds
	Microphallus claviformis	×	×	×	×	Birds
	Maritrema subdolum	×	×	×	×	Birds
	Sp. no. 15		×	×	×	Birds
	Sp. no. 16				×	Birds
	Maritrema oocysta		×	×		Birds
	Microphallus pirum		×		×	Birds
	Microphallus abortivus		×	×	×	Birds
	Levinseniella sp. no. 17		×	×	×	Birds
	Microphallus primas		×	×		Birds
	Microphallus scolectroma		×			Birds
	Microphallus papillorobustus	×				Birds
	Levinseniella brachysoma		×	×		Birds
	Cercaria camarguensis		×		×	Birds
	Levinseniella sp.	×				Birds
Acanthostomatidae	*Timoniella praeteritum*		×	×	×	Fish
	Acanthostomum balthicum	×				Fish

Similarly, fish also often use corridors for migrations that differ in location and extent among species (Harden Jones, 1981). In addition, many fish species utilizing intertidal systems are residents with limited large-scale dispersal (Horn *et al.*, 1999). Again, this restricted dispersal of final hosts should result in limits to parasite dispersal. Parasite communities in final hosts also differ among species as a result of restricted host specificity (Poulin, 2007), and parasite species may thus never make it into certain regions where their final hosts do not occur.

Environmental factors may also act to constrain the distribution of trematodes among snail populations. The composition of the free-living fauna of coastal waters differs among regions, thus supplying different potential second intermediate hosts for trematodes. Although parasites show little specificity towards second intermediate hosts, these may differ in their susceptibility to infective stages. The local composition of intermediate hosts can thus be a crucial determinant of richness patterns as parasite richness is positively correlated with the diversity of benthic free-living

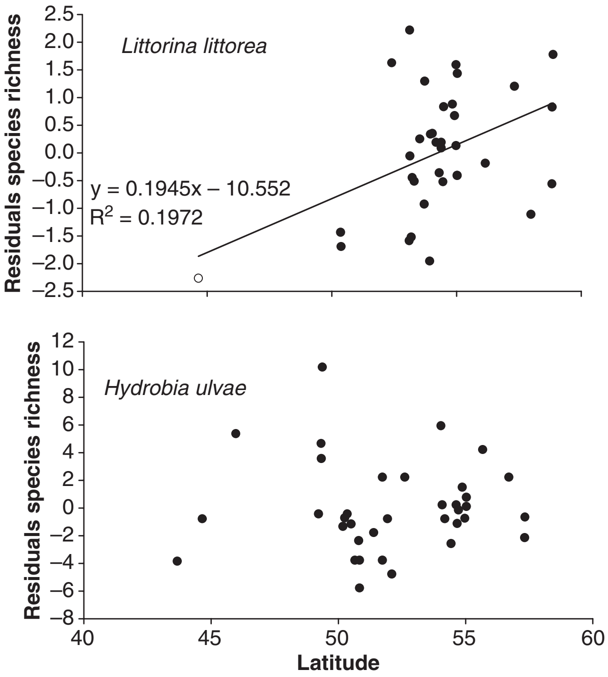

Figure 1 Relationship between latitude and parasite species richness (corrected for sampling effort) in the two host snails, *Littorina littorea* and *Hydrobia ulvae*. For *L. littorea*, the single point from the Southern European Shelf Region is indicated by a different symbol (open circle).

Table 4 Results of ANOSIM procedures on the full data set (top) and on only parasites occurring at more than 10% of the sites (bottom). Total data set: *Littorina littorea*: Global $R = 0.416$, $P = 0.001$; *Hydrobia ulvae:* Global $R = 0.239$, $P = 0.01$. Species > 10% sites: *Littorina littorea*: Global $R = 0.441$, $P = 0.001$; *Hydrobia ulvae:* Global $R = 0.164$, $P = 0.045$. The ecoregions are the Baltic Sea (Baltic), North Sea (North), Celtic Sea (Celtic) and South European Atlantic Shelf (South). Entries in bold denote significant differences.

	Littorina littorea		*Hydrobia ulvae*	
	R	*P*	*R*	*P*
Total data set				
North, Celtic	0.345	**0.001**	0.017	0.386
North, Baltic	0.251	**0.008**	0.537	**0.011**
North, South	0.974	0.056	0.345	0.071
Celtic, Baltic	0.556	**0.002**	0.740	**0.005**
Celtic, South	0.568	0.100	0.451	**0.027**
Baltic, South	1000	0.110	0.093	0.600
Species > 10% sites				
North, Celtic	0.330	**0.001**	0.028	0.336
North, Baltic	0.270	**0.004**	0.273	0.112
North, South	0.984	0.056	0.256	0.118
Celtic, Baltic	0.690	**0.001**	0.525	**0.005**
Celtic, South	0.685	0.100	0.373	0.055
Baltic, South	1.000	0.111	0.185	0.300

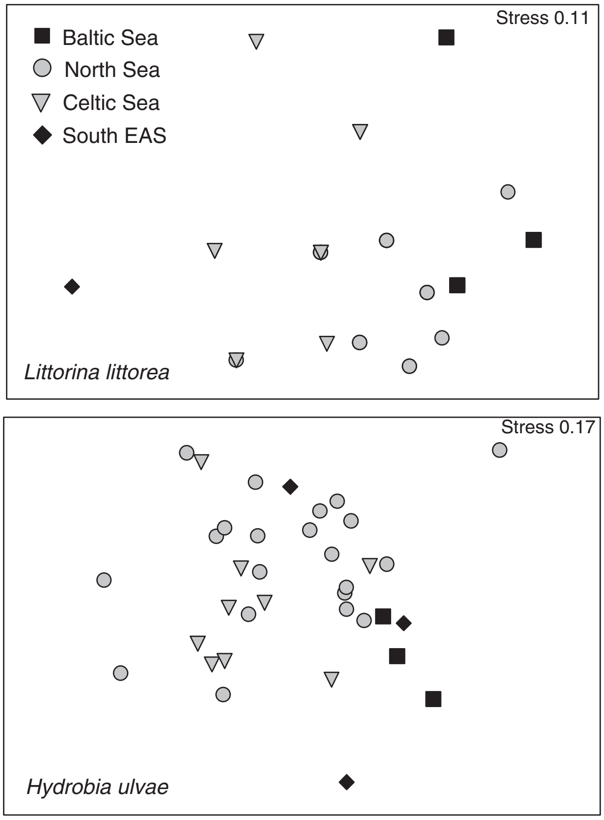

Figure 2 Multi-dimensional scaling (MDS) plots comparing the parasite species composition in the two host snails *Littorina littorea* and *Hydrobia ulvae* among the four ecoregions: Baltic Sea, North Sea, Celtic Sea and South European Atlantic Shelf (South EAS). Plots are based on Bray–Curtis similarities and presence/absence data.

species (Hechinger *et al.*, 2007). In addition, there are known links between parasite richness in bird final hosts and the composition of intermediate host communities (Simkova *et al.*, 2003). Although dispersed by final hosts, many parasites may not have a chance to establish locally because suitable second intermediate hosts are lacking. This may explain the large proportion of rare trematode species in our database that occur at only a few sites. These parasites might be either local 'endemics' or species not able to find suitable hosts elsewhere.

Besides faunal composition, differences in abiotic factors may also set dispersal limits for parasites. The Baltic Sea, with its brackish waters, stands out in several respects. It has a lower species richness compared with the other regions, the composition of its parasite communities shows the most significant differences from other regions, and the region has a high number of species that have only been recorded there. The lower parasite species richness reflects a lower richness of free-living species owing to the brackish character of the enclosed sea basin (Zander & Reimer, 2002). However, we could not detect a longitudinal gradient in trematode species richness (as a proxy for salinity decreasing eastwards in the Baltic Sea), probably because the water is fully saline for most of the western part of the gradient and only becomes increasingly

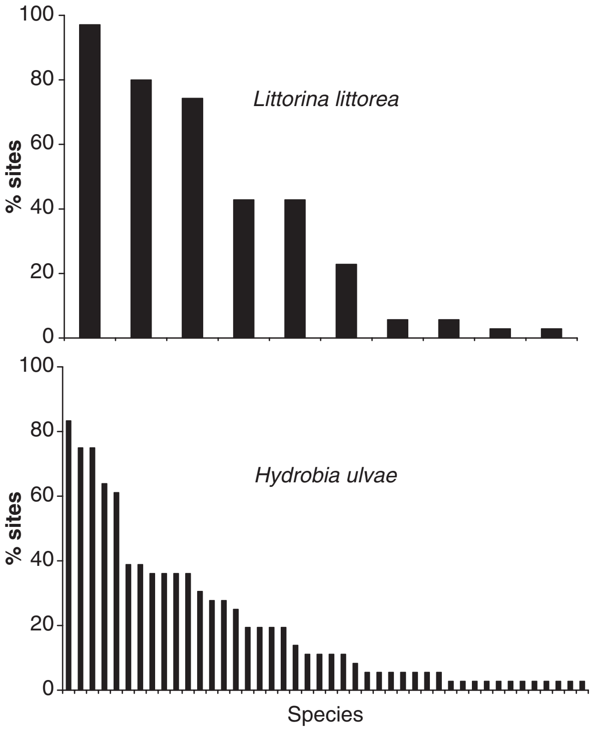

Figure 3 Proportion of sites (%) in which a parasite species has been recorded in the host snails *Littorina littorea* and *Hydrobia ulvae* in European seas; parasite species are ordered from most to least common.

brackish in its eastern part. Reduced salinity makes the Baltic Sea a peculiar environment for marine parasites, with some endemic free-living and parasite species shared with the Mediterranean and the Black Sea (Zander & Reimer, 2002). This peculiar environment sets dispersal limits for many parasite species and causes some of the patterns in distribution we observed. A similar effect of abiotic factors has been reported from the Barents Sea, where the increasingly harsh conditions to the east cause changes in the parasite fauna (Galaktionov & Bustnes, 1999). Concerning the Baltic parasites, it remains possible that some typical Baltic parasite species occurring in *H. ulvae* (Table 4) are actually synonyms of species occurring elsewhere. All Baltic species were described or re-described by researchers in the Baltic (e.g. Reimer, 1963, 1970), and Deblock (1980) discusses the possibility of synonyms in some cases. It is likely that local forms have evolved in the Baltic Sea; however, morphological studies paired with molecular analyses are needed to validate their status.

Our failure to detect any effect of latitude might simply reflect the lack of such a relationship in final hosts. Data for birds are not available, but endoparasites in marine fish do not seem to show a latitudinal trend in species richness per host (Rohde & Heap, 1998; Rohde, 2002). However, a meta-analysis of trematode richness in marine gastropods found an increase in richness (corrected for sampling effort) with increasing latitude using a database including many different host species (Poulin & Mouritsen, 2003), suggesting that latitudinal gradients in trematode species richness may occur in gastropods. Trematodes in *L. littorea* followed that pattern in our data set, but the significance of the regression was based on a single data point with a relatively small sample size. It may be that the latitudinal extent from which data were available was too narrow to detect any effect of latitude. More data from low latitudes are needed to investigate gradients in latitudinal trematode richness in *L. littorea* further. In contrast, there was no latitudinal trend in trematode richness at all in the data available from *H. ulvae*. For this species, data were available for lower latitudes, suggesting that the observed pattern is real. However, on a smaller spatial scale (Great Britain), a strong positive correlation between species richness and latitude has been recorded (Ferguson, 2008). This apparently contradictory pattern may have an explanation in factors other than temperature that override any latitudinal effect on large spatial scales. Although the sampling sites in the British Isles are relatively similar with respect to bird distribution and environmental conditions, these conditions may be very different on larger spatial scales. This may result in a confounding effect that obscures the latitudinal trends observable on smaller spatial scales. Again, more data, especially from low and high latitudes, may be helpful in validating the findings.

Although we observed patterns in the distribution of parasites over the study area, the separation of the parasite communities into the four ecoregions was not particularly strong, as indicated by the relatively low *R*-values and considerable stress in the MDS plots. This may be a result of biological and/or methodological reasons. Although dispersal limitations exist for parasites as discussed above, we can still expect broad dispersal for many parasite species on the scale of the study area. In addition, although the ecoregions differ in the composition of their free-living fauna, their borders are of course not sharp and may be different for different taxa (Spalding *et al.*, 2007). Hence, the ecoregions are only a rough proxy for differences among areas in terms of species composition, and much overlap can be expected. This might be reflected in the parasite fauna and might therefore blur any regional patterns. Spatial segregation would probably be stronger at higher-level biogeographical categories such as provinces. For example, the endoparasite fauna of a marine fish clearly reflects the biogeographical provinces of free-living species on large spatial scales (González *et al.*, 2006). However, we had only limited data to compare the southern Lusitanian province with the northern province of Northern European Seas (Spalding *et al.*, 2007). Again, more data from southern locations are needed to investigate the pattern further.

The relatively weak regional structure in parasite communities might also result from the usually high spatial heterogeneity in parasitism of gastropods on small to medium spatial scales, mainly caused by heterogeneity in final host distribution and abundance (Hechinger & Lafferty, 2005; Fredensborg *et al.*, 2006; Byers *et al.*, 2008). This heterogeneity on small spatial scales may result in much scatter in the data, making it difficult to identify regional patterns on larger scales. Methodological factors may add to this scatter. We corrected for sampling effort in our analyses, and the

ANOSIM that excluded rare species yielded similar results. Seasonal or annual effects might also generate some noise in the data, as samples were taken in different seasons and years. However, there is no reason to believe that there is a regional or latitudinal bias in sampling seasons, and many data points were based on repeated sampling over several seasons and/or years. And again, analyses excluding rare parasites that might be missed at some sites as a result of seasonal or annual variation gave similar results. Hence, we think that the structure and the scatter in the data do reflect the situation in the field.

Whatever the exact mechanisms, there is obviously more structure in the large-scale distribution of trematodes in gastropods than one would expect from the large-scale dispersal capabilities of their bird and fish final hosts. There seem to be many factors limiting parasite dispersal, resulting in many rare and few widespread trematode species. Future studies should attempt to validate the special situation in the Baltic Sea, and to investigate the influence of lower latitudes on the parasite communities in the two snail species. They should also attempt to identify the underlying mechanism(s) of limited dispersal in order to gain an understanding of distributional patterns of trematodes in invertebrate hosts. Gastropods are ideal candidates for biogeographical analysis because their limited movements do not matter on biogeographical scales, and because they capture local trematode diversity by archiving any past visits to the locality by bird or fish final hosts. This also makes them suitable model systems with which to study the effects of climate change on future parasite distributions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 & S2 Sources and additional information of the databases used for the analyses.

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