

Trematode prevalence–occupancy relationships on regional and continental spatial scales in marine gastropod hosts

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ABSTRACT: The positive inter-specific relationship between local abundance and large-scale spatial occupancy is one of the most universal patterns in the distribution of species. However, evidence for the validity of this relationship in the marine realm is still scarce, especially for parasites. Using data from published studies, we investigated this relationship in trematode parasites infecting several marine gastropod species. On a regional spatial scale (<100 km between any pair of sites), we found a positive relationship between mean local prevalence (percentage of infected individuals in a population) and large-scale site occupancy among trematode species in all 4 gastropod host species investigated (*Littorina obtusata*, *L. saxatilis*, *Hydrobia ventrosa*, *Ilyanassa obsoleta*), although this was not significant in the case of *L. saxatilis*. Similar positive relationships were observed on a continental scale (>1000 km between the most distant sites) in 2 host species (*L. littorea*, *H. ulvae*). Further analyses pointed to the role of dispersal by the definitive hosts in shaping these prevalence–occupancy relationships as we found a significant interaction between definitive host type and mean local prevalence affecting the spatial occupancy of the trematodes infecting *H. ulvae*. While trematode species that use highly dispersive birds as definitive hosts exhibited a significant positive relationship, the ones that use less dispersive fish did not. Our results indicate that a positive relationship between local abundance and large-scale distribution also holds true for marine parasites, and they suggest a strong role of definitive host dispersal in linking local epidemiological infection patterns of parasites with their large-scale biogeographic distributions.

KEY WORDS: Parasitism · Macroecology · Biogeography · Species distributions

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INTRODUCTION

One of the most universal patterns in the distribution of species is the so-called abundance–occupancy relationship. Whereas species with a high local abundance tend to be widely distributed, locally rare spe-

cies tend to occur only at a few sites, resulting in a positive inter-specific relationship among species between local abundance and large-scale site occupancy (Brown 1984, Gaston 1996, Gaston et al. 2000). Although this universal pattern has mainly been described for terrestrial ecosystems (Blackburn et al.

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2006), several studies suggest it to be also valid in the marine realm. For example, estuarine and subtidal macroinvertebrates exhibit positive abundance–occupancy relationships (Foggo et al. 2003, 2007, Webb et al. 2009a,b), and similar relationships have been observed among offshore fishes (Fisher & Frank 2004, Frisk et al. 2011). The positive relationship between local abundance and spatial distribution has been linked to life-history traits. For instance, in subtidal macroinvertebrates the developmental mode is a strong driver of the abundance–occupancy relationship, with species having planktonic larval stages showing elevated relationships (i.e. a larger number of sites occupied for a given abundance) compared to non-planktonic species (Foggo et al. 2007). This suggests an important role of dispersal in shaping abundance–occupancy relationships (Foggo et al. 2007). However, there are also several other, not mutually exclusive, mechanisms that may underlie abundance–occupancy relationships (Gaston & Blackburn 2000).

In contrast to free-living species, we know very little about the relationship between the local abundance and the spatial distribution of parasites. Parasites may be subjected to similar patterns and processes as free-living species, but they may alternatively just follow their hosts' distributions, given the strong link between host and parasite diversity (Hechinger & Lafferty 2005, Poulin et al. 2011a, Thieltges et al. 2011). The latter would indirectly result in a positive relationship between abundance and site occupancy and thus obscure any direct patterns and processes acting on the parasites themselves. Hence, abundance–occupancy relationships for parasites are best studied by focussing on parasite communities of single host species. In one of the few studies including marine habitats to date, Poulin et al. (2012) identified a positive inter-specific relationship between local abundance and occupancy in parasite communities from sticklebacks *Gasterosteus aculeatus*. In addition, the coefficient of variation (CV, ratio of the standard deviation to the mean) in abundance among sites co-varied positively with parasite site occupancy, suggesting that parasite species with a high variability in abundance among localities may be able to sustain viable populations under a large range of environmental conditions. A high tolerance to environmental conditions is likely to enhance the colonisation ability of parasites, thus leading to a higher number of occupied sites compared to parasites with a lower tolerance. Apart from this study, abundance–occupancy relationships in parasites have only been studied in another marine

fish host, the sparid *Boops boops* (Pérez-del-Olmo et al. 2009, 2011). Hence, our knowledge of abundance–occupancy relationships of marine parasites is still very limited, which clearly hampers our understanding of both the universality of the pattern and, more generally, the processes underlying it.

Here, we study the inter-specific relationship between local abundance and spatial distribution of trematode parasites in several marine gastropod hosts. Trematodes are ubiquitous in coastal ecosystems, with wide-reaching effects on their host populations and local communities (Mouritsen & Poulin 2002). Trematodes have complex life cycles, including several sequential hosts (Galaktionov & Dobrovolskij 2003). Gastropods primarily serve as first intermediate hosts. At this stage, host specificity is usually very high, i.e. a parasite species only infects a single host species or closely related sister species (Galaktionov & Dobrovolskij 2003). In infected snails, a free-living larval stage is produced, the cercaria, which is released into the water and infects a second intermediate host (invertebrates or small fish, depending on the species), becoming the metacercarial stage. When the second intermediate host is preyed upon by the definitive host, the life cycle is completed and starts again by reproduction and egg release into the environment. As the infection of gastropod first intermediate hosts results in the constant production of a large but varying number of clonal cercarial stages, studies usually refrain from noting the abundance of these stages. Instead, they record local infection levels as prevalence, which is the proportion of individuals in a local host population infected by a given parasite species. However, from other studies on parasites it is known that prevalence and abundance are usually highly correlated (e.g. Morand & Guégan 2000, Thieltges et al. 2009a). Hence, prevalence can be used as a measure of the local abundance of a parasite species to test whether there is a positive relationship between local abundance and the proportion of sites occupied across a broader area. For some examples using fish in freshwater habitats see Barker et al. (1996) and Cone et al. (2004).

The relationship between abundance and site occupancy may differ among spatial scales as differences in environmental conditions among locations are likely to increase with the distance among them, leading to increasingly different parasite communities in hosts (Poulin 2003, Thieltges et al. 2009b, Poulin et al. 2011b, Locke et al. 2012). On smaller spatial scales, parasites are more likely to encounter similar conditions (in particular in highly connected

marine systems) so that their individual epidemiological potential will determine their spatial distribution, i.e. parasites which can attain large local abundance will also have greater chances of occupying a larger number of sites. In contrast, over larger spatial scales, parasites are likely to encounter very different environmental conditions; these may override any species-specific epidemiological potential of parasites, leading to an uncoupling between local success and regional dispersal, i.e. independent distributions of abundance and site-occupancy values. However, parasites may have varying tolerance to cope with differences in environmental conditions, with a higher tolerance enabling them to occupy a higher number of sites. This could be indicated by positive covariation of the CV in abundance with parasite site occupancy (Poulin et al. 2012). Independent of spatial scale and environmental tolerance, dispersal, just as in free-living species, is likely to have a strong effect on abundance–occupancy relationships. Since the mobility of their intermediate hosts is usually very limited, the dispersal of trematodes should be mainly driven by the mobility of their definitive hosts. In freshwater systems, it is generally assumed that parasites using birds as definitive hosts (*allogenic* parasites) have a higher dispersal capacity than parasites using fish as definitive hosts (*autogenic* parasites; Esch et al. 1988). Similarly, in coastal environments, birds generally show a high dispersal capacity, for example due to their large-scale seasonal migrations, using tidal flats as stop-over or wintering grounds. In contrast, many coastal fish species have a restricted dispersal ability (Horn et al. 1998). Hence, one would expect that, regardless of abundance and all else being equal, parasites using bird definitive hosts should occupy a larger number of sites than parasites using fish as definitive hosts.

Using published data from the literature on trematode infections in several marine gastropod species, we pursued the following questions: (1) Is there a

positive interspecific relationship between local prevalence and the proportion of sites occupied by a parasite species? (2) Do prevalence–occupancy relationships differ between spatial scales (regional vs. continental)? (3) Is there a link between the environmental tolerance of parasites (CV in abundance) and site occupancy? (4) What is the effect of the dispersal capacity of the definitive hosts on the prevalence–abundance relationships of their parasites (allogenic vs. autogenic parasites)? Our study is the first to investigate these questions in invertebrate intermediate hosts with the aim of linking local epidemiological infection patterns with large-scale biogeographic distributions.

MATERIALS AND METHODS

We used 6 different data sets (see Table 1 and the Supplement at www.int-res.com/articles/suppl/m490p147_supp.xls) on trematode infections in marine gastropod hosts, covering 2 types of spatial scales, regional (<100 km between any pair of sites) and continental (>1000 km between the most distant sites). First, on a continental scale, we used data on trematode infections in *Hydrobia ulvae* and *Littorina littorea* from localities stretching over the European coast (43° to 57° N and 44° to 59° N, respectively), compiled in an earlier study (Thieltges et al. 2009c). Second, we searched online databases and our own reprint collections for studies that reported on quantitative surveys of trematodes infecting marine gastropod hosts on smaller regional spatial scales. In both types of data sets, only studies which fulfilled the following criteria were used for the analyses: (1) studies had to provide complete inventories of all trematode species found at a locality to avoid any bias in the sampling effort of individual hosts dissected per parasite species (Poulin et al. 2012), and (2) studies had to include at least 7 locations and 7

Table 1. Data sets and their sources used for analyses on a regional (<100 km between any pair of sites; *Littorina obtusata*, *L. saxatilis*, *Hydrobia ventrosa*, *Ilyanassa obsoleta*) and a continental (>1000 km between the most distant sites; *L. littorea*, *H. ulvae*) spatial scale

No. of sites	No. of snails dissected	No. of parasite species	Location	Spatial scale	Source
27	4032	8	Kandalasksha Bay, White Sea	Regional	Granovitch et al. (2000)
27	2658	7	Kandalasksha Bay, White Sea	Regional	Granovitch et al. (2000)
12	4539	8	Melabakkar peninsula, Iceland	Regional	Skirnisson et al. (2004)
9	11774	9	Delaware estuary, USA	Regional	Curtis (1997)
28	153919	8	Europe	Continental	Thieltges et al. (2009c)
36	65037	31	Europe	Continental	Thieltges et al. (2009c)

trematode species to allow for a reasonable level of power in the analysis of prevalence–occupancy relationships.

In total, we used 6 data sets, all involving different gastropod species. Each of the 4 regional and 2 continental data sets were analysed separately. For each spatial scale, only parasites that occurred in at least 2 sites per host species were included in the analysis. If data were given for several years or seasons, we pooled those data and used mean prevalence per location. For each parasite species, we calculated the proportion of sites occupied within the study area (occupancy) and the mean prevalence (proportion of individual hosts per site infected by a given trematode species) in infected host populations. Due to their bounded nature, both prevalence and occupancy data were arcsine-transformed prior to any analysis. To test for an interspecific relationship between prevalence and occupancy we used separate linear regressions for each gastropod host species (i.e. each data set), with each trematode species contributing 1 data point. In addition, we investigated the effect of the type of definitive host used by trematodes and their tolerance to environmental conditions on prevalence–occupancy relationships in one of the two continental studies (host *Hydrobia ulvae*), where enough data were available. To test for an effect of the definitive host type (fish vs. birds) and tolerance to varying environmental conditions (using the CV in prevalence calculated across all localities where the parasite occurred) on the prevalence–occupancy relationship, we used a general linear model (GLM) approach, with host type, mean prevalence (arcsine-transformed) and CV in prevalence as predictors and occupancy as the response variable. The models used a normal error structure with an identity link function after investigating the data for heteroscedasticity and normality. We also added second-order interaction terms to test for potential interactions among the 3 predictor variables. In addition to the GLM, we also used linear regression to investigate the relationship between prevalence and occupancy separately for bird and fish parasites.

RESULTS

The final data sets consisted of studies from 4 host species on a regional scale, and 2 host species on a continental scale (Table 1). In both cases, all data sets were based on a large total number of dissected snails (2658 to 153 919) and localities (9 to 36) and contained data on 7 to 31 trematode species (Table 1).

The main trematode families represented in the data sets differed among the host species but generally consisted of a wide range of families. More details about the taxonomic composition of the data sets and general information on the life cycles of the respective trematode species, as well as on the locations, can be found in the original sources (see Table 1) and in the Supplement.

On a regional scale, there was a positive relationship between mean prevalence and site occupancy among trematode species in all 4 gastropod host species, although this was not significant in 1 case (*Littorina saxatilis*, $p = 0.131$) (Fig. 1a–d, Table 2). In all significant cases, this relationship explained between 60 and 66% of the variance in site occupancy. The positive relationship between mean prevalence and occupancy was reflected on a continental scale, too, where it was significant in both host species (Fig. 1e,f, Table 2). However, the variance explained by this relationship was higher in *Littorina littorea* (71%) than in *Hydrobia ulvae* (30%). When only bird

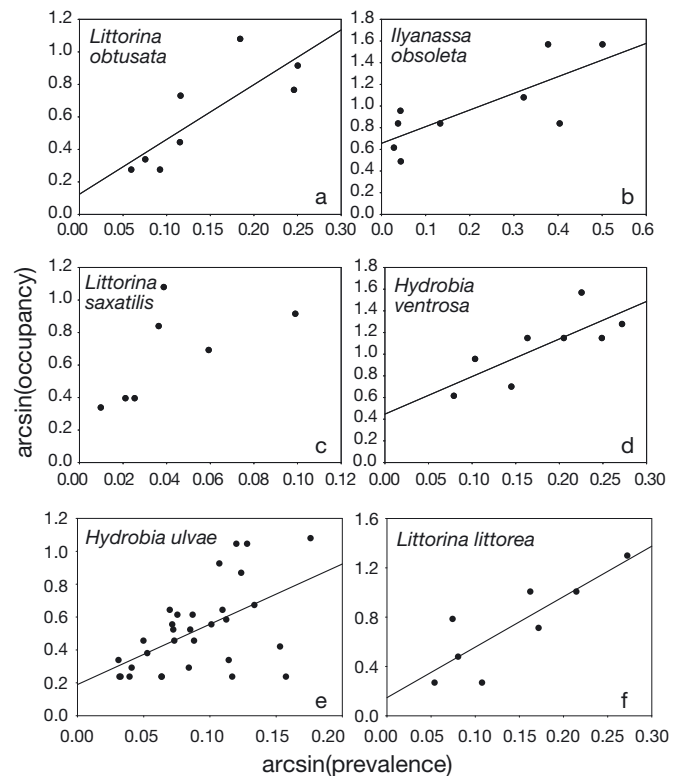


Fig. 1. Relationship between mean prevalence and spatial occupancy (both arcsine-transformed) of trematode species in different species of marine gastropod first intermediate hosts on a (a–d) regional spatial scale (<100 km for any pair of sites) and (e,f) continental spatial scale (>1000 km between the most distant sites). Note the different scales on axes

Table 2. Results of separate linear regressions of the relationship between mean prevalence and occupancy (both arcsine-transformed) of trematode species for each gastropod host species. ns: not significant

Host species	r^2	p	Regression
Regional			
<i>Littorina obtusata</i>	0.661	0.014	$y = 0.124 + 3.370x$
<i>Littorina saxatilis</i>	0.395	0.131	ns
<i>Hydrobia ventrosa</i>	0.596	0.015	$y = 0.656 + 1.538x$
<i>Ilyanassa obsoleta</i>	0.599	0.024	$y = 0.447 + 3.465x$
Continental			
<i>Littorina littorea</i>	0.710	0.009	$y = 0.147 + 4.097x$
<i>Hydrobia ulvae</i>	0.303	0.001	$y = 0.189 + 3.668x$

Table 3. Results of a general linear model testing for the main effects of definitive host type (bird vs. fish), mean prevalence (arcsine-transformed) and coefficient of variation (CV), as well as for second-order interactions among these factors on the spatial occupancy of trematode species infecting the gastropod *Hydrobia ulvae*. **Bold**: statistically significant ($p < 0.05$)

Factor	df	MS	F	p
Host type	1	0.051	1.387	0.251
Prevalence	1	0.004	0.105	0.749
CV	1	0.004	0.108	0.745
Host type × Prevalence	1	0.164	4.477	0.045
Host type × CV	1	0.006	0.158	0.695
Prevalence × CV	1	0.029	0.789	0.383
Error	24	0.037		

parasites were considered in the latter, the variance explained increased to 50 % (see next paragraph).

When investigating this relationship further in *H. ulvae*, we found significant interaction between the definitive host type and the prevalence affecting the spatial occupancy of the trematode species infecting it (Table 3). Although a significant interaction term makes the testing of the main effects (definitive host type and prevalence) inappropriate, there was a clear effect of definitive host type on site occupancy. Trematode species using birds as definitive hosts showed a clear positive relationship between mean prevalence and occupancy, whereas there was no such relationship among parasites using fish (Fig. 2). This was also indicated by separate linear regressions where only the relationship between prevalence and occupancy for parasites using birds as definitive hosts was significant, and not that for parasites using fish ($r^2 = 0.502$, $p < 0.001$ and $r^2 = 0.041$, $p = 0.603$, respectively). The other 2 interaction terms in the GLM ('Host type × CV' and 'Prevalence × CV')

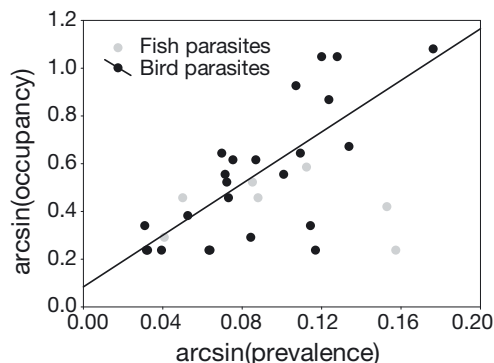


Fig. 2. Effect of different types of definitive hosts (fish vs. birds) on the relationship between mean prevalence and spatial occupancy (both arcsine-transformed) in trematode species using the gastropod *Hydrobia ulvae* as first intermediate host. The line indicates the best fit of a linear regression for parasites using birds as definitive hosts ($y = 0.084 + 5.405x$); $n = 9$ for trematodes using fishes and $n = 22$ for trematodes using birds as definitive hosts

were not significant; there was no significant main effect of the overall variation in prevalence among sites either (CV; Table 3).

DISCUSSION

This study found a strong positive relationship between mean local prevalence and the geographical distribution of trematodes in 6 gastropod first intermediate hosts belonging to the genera *Ilyanassa*, *Littorina* and *Hydrobia*, both on regional and continental spatial scales. In addition, we identified the type of definitive host as a strong driver of prevalence–occupancy relationships, with parasites using birds as definitive hosts exhibiting this relationship, while it was absent in those using fish.

The positive relationship found between prevalence and occupancy echoes the results from earlier studies on parasites in marine and freshwater fish (Barker et al. 1996, Cone et al. 2004, Pérez-del-Olmo et al. 2009, 2011, Poulin et al. 2012) and suggests that it is a universal pattern in parasites just as it is in free-living species (Brown 1984, Gaston et al. 1997, Gaston & Blackburn 2000). In general, the prevalence–occupancy relationships observed in our study were quite strong, explaining 50 to 70 % of the variance. The non-significance of one of the relationships on a regional scale (*Littorina saxatilis*) was probably due to a small sample size (fewest number of snails dissected and fewest number of parasite species found); and the low proportion of variance (30 %) explained by one of the two relationships on a continental scale

(*Hydrobia ulvae*) can be ascribed to the different effects of the type of definitive host as the explained variance increased to about 50% when only bird parasites were considered. In general, prevalence–occupancy relationships were similarly strong and showed comparable slopes on both regional and continental scales (Table 2, Fig. 1), indicating that different magnitudes of variation in environmental conditions have little effect on the relationship.

Overall, these strong prevalence–occupancy relationships at both spatial scales suggest that local epidemiological infection patterns in trematode snail hosts have a strong effect on their large-scale distributional patterns. Previous studies on trematodes have shown that the more first intermediate hosts are infected at a site, the higher the chances are that the down-stream second intermediate hosts of the parasites (invertebrates or fish, depending on the species) become infected (Thieltges & Reise 2007). In turn, higher infection levels in second intermediate hosts increase the chances for definitive hosts to become infected and then disperse the parasites to other sites. Hence, locally common parasite species will have a greater chance of becoming distributed over more sites than locally rare species by increased chances for dispersal via their definitive hosts (the dispersal capacity of their intermediate hosts—invertebrates or small fish—is usually very limited). In other words, sites of high prevalence act as sources of colonisers for other sites, linking local abundance with spatial occupancy.

The importance of dispersal by definitive hosts for the large-scale distribution of the parasites is highlighted by the different patterns observed in trematodes using birds or fish as definitive hosts. For the large majority of trematode species in our data set, birds serve as definitive hosts (see the Supplement). However, the mudsnails *Hydrobia ulvae* are also infected by 9 trematode species that use fish as definitive hosts, which allowed us to test for the effect of the type of definitive host on prevalence–occupancy relationships. While bird parasites showed a strong positive prevalence–occupancy relationship, it was absent in fish parasites. This reflects the general assumption that parasites using birds as definitive hosts have a higher dispersal capacity than parasites using fish, which has been supported by molecular (Criscione & Blouin 2004) and macroecological studies (Thieltges et al. 2009b). It is also generally in line with the documented importance of dispersal capacity for shaping abundance–occupancy relationships in free-living species like birds (Gaston & Blackburn 2003) and marine macroinvertebrates (Foggo et al. 2007).

However, although the general pattern seems to hold, it may be possible that some fish parasites also achieve high dispersal capacities, e.g. via infecting migratory fish species or by having a very large host range. For example, the fish trematode *Derogenes varicus* is one of the most widely distributed fish parasites and infects a large range of hosts (Manter 1955, 1966). However, for most fish trematodes in coastal waters, the limited dispersal capacity observed in the *Hydrobia ulvae* parasites investigated here may be the more common scenario. Although these patterns seem to be universal, all these studies are effectively correlative, thus restricting any inference on the actual direction of causality. Hence, it may actually be the large-scale distributional patterns of free-living species and parasites which drive local abundance of these 2 groups. However, an extensive review of the literature suggests that the predominant direction of causality seems likely to run from local abundance to large-scale distributional patterns like occupancy (Gaston & Blackburn 2000).

Although the dispersal capacity of the definitive hosts and local prevalence were identified to have a strong effect on the large-scale distributions of trematodes infecting gastropods, there remains a considerable proportion of variance not explained by these factors in all analyses. It is well documented that myriad abiotic and biotic environmental factors can affect local parasite infection levels directly by influencing the success of infective stages (Pietrock & Marcogliese 2003, Thieltges et al. 2008). Hence, local variations in these factors may add considerable noise to the observed prevalence–occupancy relationship. Based on an earlier study on stickleback parasites (Poulin et al. 2012), we expected some parasites to better cope with such varying environmental conditions due to a higher tolerance toward external factors (indicated by a higher CV in prevalence) and thus to exhibit positive covariation of the CV with site occupancy. However, such a relationship was absent in trematodes infecting gastropods, suggesting a lesser importance of tolerance to environmental conditions in this case.

We can only speculate about the underlying mechanisms responsible for this difference between the 2 studies. It is possible that our sample sizes (numbers of sites or trematode species) were simply too low to detect an effect, in particular given the strong interaction between prevalence and type of definitive host. However, there might also be an ecological explanation. The stickleback study

(Poulin et al. 2012) contained metazoan parasites from numerous different phylogenetic lineages (helminths and arthropods), with relatively low host specificity in many cases. In contrast, our study was limited to trematodes, which are known to exhibit an extremely high host specificity in their first intermediate gastropod hosts (Galaktionov & Dobrovolskij 2003). This may point to a much stronger role of first intermediate host distribution and definitive host dispersal than of tolerance to environmental conditions in shaping large-scale distributions of trematodes in gastropod hosts. As long as parasites are transported by their definitive hosts to new sites where their appropriate first intermediate host snails are present, parasites may simply colonise any new site, regardless of small to moderate variation in environmental conditions. For example, salinity ranges widely among the localities in the *Hydrobia ulvae* data set, from fully marine sites along the Atlantic coast and in the North Sea to brackish sites along the coast of the Baltic Sea (Thieltges et al. 2009c). Also, mean environmental temperatures vary among localities, for example along a latitudinal gradient. However, as long as the respective host species, and thus their respective parasites, do not reach their distributional limits due to salinity or temperature levels (see Zander & Reimer 2002 for examples from the Baltic Sea), environmental differences do not seem to matter much for the distribution of the parasites. In other words, host specificity, and the environmental tolerances of those hosts, probably override other sources of environmental flexibility of the parasites.

Although host specificity of trematodes towards their first intermediate snail hosts is generally high, some trematode species are also able to infect closely related sister species. For example, several trematode species infect both *Littorina saxatilis* and *L. obtusata* and thus may utilise several host species at the same locality (Granovitch et al. 2000). Thus our analyses may be confounded by the presence of multiple hosts. However, the overlapping trematode species usually show strong covariation in prevalence of the different snail hosts within the sites investigated (Granovitch et al. 2000). Therefore, the prevalence in one host well reflects the relative prevalence of these trematodes in other host species. Hence, some potential overlap in host use does not prevent us from gaining insights into the relationship between local prevalence and large-scale occupancy. Besides differing in the degree of first intermediate host specificity, trematodes also differ in their second intermediate host use. Several variations exist on the general

trematode life cycle theme described above, for example cercariae can, in some cases, develop into metacercariae in their first intermediate hosts, or encyst without the need for a host by attaching themselves to structures in the environment (Galaktionov & Dobrovolskij 2003; see our Supplement for the respective life cycles). In these cases, dispersal can be assumed to be very limited. In other cases, small fish are used as second intermediate hosts, which may allow for some—if still restricted dispersal—in this life-cycle stage. These life-cycle variations may underlie some of the residual noise in the observed prevalence–occupancy relationships, but our data are too limited to investigate this further.

In conclusion, our study shows that there is a strong link between local epidemiological infection patterns of trematodes infecting marine gastropods and their large-scale biogeographic distributions. This link seems to be strongly driven by the dispersal capacity of the definitive hosts. These results add to our still limited knowledge on the relationship between local abundance and geographic distributions of marine organisms. More studies on other marine parasite–host groups and free-living taxa would be valuable to evaluate the generality of the observed patterns in the marine realm.

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