

CONTROLS OF SPATIAL VARIATION IN THE PREVALENCE OF TREMATODE PARASITES INFECTING A MARINE SNAIL

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Abstract. Geographic variability in abundance can be driven by multiple physical and biological factors operating at multiple scales. To understand the determinants of larval trematode prevalence within populations of the marine snail host *Littorina littorea*, we quantified many physical and biological variables at 28 New England intertidal sites. A hierarchical, mixed-effects model identified the abundance of gulls (the final hosts and dispersive agents of infective trematode stages) and snail size (a proxy for time of exposure) as the primary factors associated with trematode prevalence. The predominant influence of these variables coupled with routinely low infection rates (21 of the 28 populations exhibited prevalence <12%) suggest broad-scale recruitment limitation of trematodes. Although infection rates were spatially variable, formal analyses detected no regional spatial gradients in either trematode prevalence or independent environmental variables. Trematode prevalence appears to be predominantly determined by local site characteristics favoring high gull abundance.

Key words: Bayesian statistics; *Cryptocotyle lingua*; dispersal; environmental forcing; hierarchical models; *Larus argentatus*; *Littorina littorea*; macroecology; nested spatially explicit analyses; reversible-jump Markov chain Monte Carlo; rocky intertidal zone; species abundance.

INTRODUCTION

Determinants of parasite prevalence in host communities influence important ecological and evolutionary processes. For example, the drivers of variability of host infection underlie the strength and variability in host life-history evolution (Tscharren and Richner 2006, Crossan et al. 2007), host population regulation (Hatcher et al. 1999, Sasal et al. 2001), and even community-level ecological consequences of host infection (Wood et al. 2007). Furthermore, understanding which factors determine a host's risk to parasitic infection is of increasing interest given the rising incidence of many infectious diseases.

In general, ecological factors that determine infection risk and parasite prevalence include interactions of the host with the physical environment, biological interactions among resident species, and the supply (vectors) of the infectious agent. The strength of these three infection factors can be scale dependent (Aukema 2004), and epidemiological studies have increasingly stressed the insight to be gained from large-scale analyses (e.g., Srividya et al. 2002, Jackson et al. 2006, Werneck et al. 2007). Analyses conducted at large, nested spatial scales may be particularly informative because, although infection processes are proximately driven by local

environmental conditions, resources, or biotic interactions, ultimately those factors may be correlated over a large regional scale by, e.g., temperature or differential dispersal patterns of vectors and predators (e.g., Brown et al. 1995, Holdenrieder et al. 2004, Farnsworth et al. 2006). By ensuring a wider breadth of environmental variables and their interactions, experiments and observations over a hierarchy of scales may help to detect the influence of drivers that are correlated at different scales. Furthermore, due to increased spatial heterogeneity, environmental factors in large-scale studies typically encompass a broad range of variability, which increases the probability of detecting significant associations. Such associations can be more difficult to detect in small-scale studies because they are likely to examine more restricted ranges of each variable (Jackson et al. 2001).

A system in which associations between physical and biological factors may be influenced by nested processes across local and large scales is host parasitism by digenetic trematodes. On the coast of northeastern North America, the highly abundant intertidal snail *Littorina littorea* serves as a first intermediate host to at least five parasitic trematode species, all with obligate, multi-host life cycles (Pohley and Brown 1975, Pohley 1976, Stunkard 1983). *Littorina littorea* can live 5–10 years (Hughes and Answer 1982), and once a snail becomes infected it typically remains infected for life (Rothschild 1942, Robson and Williams 1970). Infective stages of the trematodes are periodically shed from the

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snails as short-lived, free-swimming cercariae, which locate, penetrate, and encyst as metacercariae in the tissues of a second intermediate host. *Littorina littorea* hosts are primarily dominated by one particular trematode species, *Cryptocotyle lingua*, which uses fish as second intermediate hosts (Stunkard 1930). Second intermediate hosts transmit infection when they are eaten by the definitive (final) host, typically a shorebird (e.g., gulls, cormorants, eiders), in which the adult worms live for several weeks (Stunkard 1930, Lauckner 1985). The life cycle is completed when snails contract infections by ingesting parasite eggs, which are spread in the feces of infected birds.

We sought to determine the relative importance of trematode egg supply and various environmental attributes as drivers of trematode prevalence, as well as the spatial scale over which these factors operate. We focused on the determinants of trematode infection in the first intermediate snail hosts, which represent the most tractable stage of the life cycle because at this stage the trematodes occur in discrete, easily sampled "habitat parcels," i.e., individual snail hosts. Also, due to their obligate multi-host life cycle, trematodes do not transmit from snail to snail; thus, snails are independent replicates of habitat, nested within sites that vary in environmental conditions along the coast.

The marine trematode system we studied has the advantage of a trematode supply that can be indexed with an easily observable proxy, the abundance of shorebirds, which are the sole definitive hosts in this system. Although trematode prevalence in snails has been shown to be high in places where the densities of bird definitive hosts are high (Matthews et al. 1985, Smith 2001, Hechinger and Lafferty 2005, Fredensborg et al. 2006), the role of bird density relative to other controlling influences and its influence across large scales is largely unknown. To examine environmental drivers, variables were chosen that could be recorded over relevant temporal and spatial scales and were likely to influence parasite biology (i.e., host diversity, densities, and demography; rugosity; temperature; salinity; wave energy). Such habitat characteristics and environmental variables have been shown to influence the prevalence of parasites, particularly by increasing transmission between hosts (reviewed by Sousa and Grosholz 1991, Lafferty and Kuris 1999, Bush et al. 2001, Pietrock and Marcogliese 2003). Finally, due to different movement scales of the trematodes' three host levels (snail, fish, bird) and potential regional autocorrelation in environmental variables, an analysis at various spatial scales is especially valuable. Using multilevel logistic regression analyses we analyzed the effects of the physical and biological environmental variables to reveal which were most influential on trematode prevalence at a large regional scale. We also employed spatial statistics to examine the presence of spatial autocorrelation in trematode prevalence as well as in influential independent variables.

METHODS

Snail host collection and trematode examination

To measure trematode abundance across a wide range of environmental and habitat attributes, we chose 28 intertidal sampling sites along the New England coast to obtain a systematic spread across the entire region while sampling more intensely (with higher spatial resolution) in the local area surrounding our base of operation (University of New Hampshire, Durham, New Hampshire, USA; Fig. 1). Our sites included estuarine ($n = 8$), coastal ($n = 10$), and island ($n = 10$) sites. Eight of the 10 island sites we sampled were systematically spread around the Isles of Shoals archipelago, 10 km offshore of Portsmouth, New Hampshire. Because of the configuration of the islands in the archipelago, these Shoals sites were relatively close to one another (Fig. 2).

During late May–September 2002, we collected a mean of 184 (range, 148–279) *Littorina littorea* snails from each site. This summer sampling period for parasite prevalence is the most relevant because it is when the trematode hosts are active and accessible and the trematode transmission cycle is most active (Sindermann and Farrin 1962, Robson and Williams 1970, Pohley 1976). Because trematodes typically infect the gonad of their snail hosts, only nearly or fully mature snails (≥ 8 mm) were collected. To test for differences in trematode prevalence as a function of tidal height, we collected snails by stratifying half the collection from the high intertidal and half from the low. The high-tide contour was based on the onset of the fucoid layer in the intertidal zone (~ 1.5 m above mean lower low water [MLLW]), and the low-tide region was at ~ 0.5 m above MLLW. Snails are found abundantly within this intertidal range, yet physical and biological factors can vary greatly across this range. Within each tidal height, we collected snails haphazardly over a linear distance of ~ 40 m.

In the laboratory, we measured snail lengths from the apex to the anterior tip of the aperture with vernier calipers. Because size and age are well correlated in *L. littorea* (Robson and Williams 1970), size serves as a useful proxy for the time a snail has been exposed to trematodes in the environment. Larger snail size is not a consequence of infection in this snail species, i.e., the snails do not grow faster upon infection (gigantism). Most published accounts show that *Littorina littorea* infected with *Cryptocotyle lingua* (the predominant infecting trematode) do not grow at a different rate from their uninfected counterparts (Hughes and Answer 1982, Mouritsen et al. 1999; J. E. Byers, unpublished data). One study has shown that *L. littorea* infected with *C. lingua* grow more slowly (Huxham et al. 1993). We dissected snails to examine the gonad and digestive tissues under a stereomicroscope (40 \times) to determine the occurrence of trematode parasites. We identified trematode species under a compound microscope using

published keys (James 1968a, b, Werding 1969, Stunkard 1983).

Field measurements of environmental variables

To determine which environmental factors were most influential in governing trematode prevalence, we quantified several physical and biological variables multiple times over the summer at each of the sites. Physical factors included temperature, salinity, wave energy, and rugosity, which we selected to broadly capture important habitat attributes. Temperature and salinity are known in general to affect trematodes, especially the free-living, host-finding life stages (e.g., Pietrock and Marcogliese 2003). Higher temperatures and salinity have been shown to be preferable for *L. littorea*'s predominant trematode, *Cryptocotyle lingua* (Sindermann and Farrin 1962, Möller 1978, Frimeth 1987). Decreased wave energy has been associated with higher prevalence (James 1968b, Galaktionov and Bustnes 1995). Finally, we hypothesized rugosity might be an important variable because it can influence host mobility and usage of a site and thus transmission.

Biological factors included the abundance and diversity of birds (the dispersive vector for the trematode eggs), crab, fish, and snail species. Positive associations have been suggested and sometimes shown between trematode prevalence in snails and the density of (1) definitive hosts (Smith 2001, Hechinger and Lafferty 2005, Fredensborg et al. 2006), (2) intermediate hosts (Kristoffersen 1991, Hechinger et al. 2007), and (3) the snail hosts themselves (Ewers 1964, Wilson and Taylor 1978). For certain snail and crab species, we also recorded size and biomass measurements. Sampled species were chosen based on their role as trematode hosts and as predators or prey of hosts based on literature accounts and personal observations.

Five of the environmental measurements (rugosity and quadrat estimates of snail and crab densities and sizes) were tidal-height specific, i.e., measured at low and high tidal heights. The other quantified environmental variables had a single value that characterized each site as a whole. We computed means of all environmental variables across their spatial replicates (for fish, crab, snails, and rugosity) or temporal replicates (for birds, temperature, and salinity) to use in the subsequent modeling. We obtained geographical positioning system (GPS) coordinates to construct a spatially explicit, geo-referenced database. We measured all environmental variables at low tide, except water temperature. Detailed methodologies for measurement of these physical and biological variables are presented in Appendix A.

Because of fundamental differences in the sites that were not apparent in the measured variables, we experimented with various geographic stratification and grouping of the sites based on biological and oceanographic issues. These stratifications included island vs. mainland, estuarine vs. coastal, Isles of Shoals vs. non-Isles of Shoals, and north vs. south of Cape

Cod, Massachusetts (a zoogeographic boundary; Parr 1933, Ayzvazian et al. 1992).

Hierarchical statistical modeling and analysis

For the statistical modeling we included linear terms and two-factor interaction terms in the physical and biological variables as well as indicators of geographic stratification and their interactions with the other variables. To reduce the influence of extreme variables of skewed distributions, we transformed most of the biological abundance variables to the natural logarithmic scale [$\ln(x + 1)$ transformation was used for gull abundance, which contained some zero values].

Our sampling design produced three levels of nesting of the measured variables: snail within tidal height within site. Therefore, to fully utilize all data and to objectively account for the statistical error structure imposed by the nested data, we assumed a three-level hierarchical (or multilevel) statistical model (McMahon and Diez 2007). Two estimation methods for hierarchical models with a binary response (i.e., presence or absence of trematode at the snail level) are prevalent in the literature: frequentist methods based on penalized likelihood calculations (see e.g., Demidenko 2004) and Bayesian estimation. We found that the Bayesian estimation was more completely developed for non-Gaussian data, while several issues, such as model selection criteria, have not been fully solved in the frequentist approach to hierarchical modeling.

In the Bayesian framework (see, e.g., Banerjee et al. 2004, Gelman et al. 2004), external information is described using probability distributions in each level of the hierarchy and unknown parameters are modeled using prior distributions. In the absence of strong external information about the parameters it is customary to assume noninformative prior distributions. The disadvantage of the Bayesian method is that estimation is computationally more intensive, requiring a Markov chain Monte Carlo (MCMC) algorithm, such as the Gibbs sampler or the more general Metropolis–Hastings algorithm or a combination of the two (see Gelman et al. 2004).

At the first level of the hierarchy, we modeled the prevalence of trematode infection at the snail level as a logistic function of snail length for a snail at a tidal height at a particular site:

$$\Pr(I_{Sn}) = p = \frac{1}{1 + \exp[-\beta_0 - \beta_1(L_{Sn} - 19.76)]}$$

where I is the infection of an individual snail and L is the length of an individual snail. We centered the predictor variable L_{Sn} by subtracting the mean length of snails sampled across all sites, 19.76 mm, which resulted in the site-specific intercept (β_0) being more stable and easier to interpret as the logit [$=\ln(p/1 - p)$] of the trematode infection rate of an average-sized snail. Comparison of logit scale mean posterior infection thus helps to standardize comparisons of trematode prevalence

TABLE 1. Bayesian hierarchical model of trematode infection.

Level and model	Specifications
1) Snail-level logistic model	$Y_{i,k} = \begin{cases} 1 & \text{with prob } p_{i,k} \\ 0 & \text{with prob } 1 - p_{i,k} \end{cases}$ $\text{logit}(p_{i,k}) = \log\left(\frac{p_{i,k}}{1 - p_{i,k}}\right) = \beta_{0,i} + \beta_{1,i}(\text{Length}_{i,k} - 19.76)$
2) Site-level regression model for the intercept	$\beta_{0,i} = \begin{cases} \alpha_{0:\text{NS}} + \alpha_1 \ln(\text{gulls}_i) + \varepsilon_{i:\text{NS}} & \text{if } i \text{ is not a Shoals site} \\ \alpha_{0:\text{S}} + \alpha_1 \ln(\text{gulls}_i) + \varepsilon_{i:\text{S}} & \text{if } i \text{ is a Shoals site} \end{cases}$
3) Prior distributions	$\beta_{1,i} \sim \begin{cases} \mathcal{N}(\mu_{\beta_{1:\text{NS}}}, \sigma_{\beta_{1:\text{NS}}}^2) & \text{if } i \text{ is not a Shoals site} \\ \mathcal{N}(\mu_{\beta_{1:\text{S}}}, \sigma_{\beta_{1:\text{S}}}^2) & \text{if } i \text{ is a Shoals site} \end{cases}$ $\varepsilon_{i:\text{NS}} \sim \mathcal{N}(0, \sigma_{\beta_{0:\text{NS}}}^2); \quad \varepsilon_{i:\text{S}} \sim \mathcal{N}(0, \sigma_{\beta_{0:\text{S}}}^2)$
4) Hyperprior distributions	noninformative normal hyperpriors for the regression coefficients $\alpha_{0:\text{NS}}, \alpha_{0:\text{S}}, \alpha_1, \mu_{\beta_{1:\text{S}}}, \mu_{\beta_{1:\text{NS}}}$; noninformative inverse gamma hyperpriors for the variance parameters $\sigma_{\beta_{0:\text{NS}}}^2, \sigma_{\beta_{0:\text{S}}}^2, \sigma_{\beta_{1:\text{NS}}}^2, \sigma_{\beta_{1:\text{S}}}^2$

Note: $\text{Length}_{i,k}$ values are centered on the mean of all snail lengths (19.76 mm). Hence $\beta_{0,i}$ represents the expected probability of infection of this average-sized snail at a site.

among sites where natural sizes of snails may vary. Because snails rarely lose infections or die from infections (Rothschild 1942, Robson and Williams 1970), trematode prevalence increases in older (and correspondingly larger) snails.

At the second level of the hierarchy we modeled the logistic function parameter β_0 as a linear regression of tidal height specific covariates. An example is

$$\beta_0 = \gamma_0 + (\gamma_1 \times \text{rugosity}) + (\gamma_2 \times \text{crab density}).$$

Finally at the site level, we posed a regression model for γ_0 with site-specific variables as predictors. A typical example is

$$\gamma_0 = \alpha_0 + [\alpha_1 \times \ln(\text{gulls})] + [\alpha_2 \times \ln(\text{total crab biomass})] + (\alpha_3 \times \text{salinity}).$$

For Bayesian estimation, we also need to provide prior distributions for the parameters at previous levels, which results in an additional fourth level consisting of only prior distributions.

Extensive data exploration and model fitting with different sets of predictor variables resulted in no significant variables at the second (i.e., tidal height) level of our hierarchical model. Although several of the physical and biological tidal-height-specific variables differed considerably between tidal heights, for most sites infection rates did not differ much between high and low tidal heights. As a result, we were not able to find a meaningful model for tidal-height-specific effects. We therefore eliminated this middle level in the conceptual hierarchical model. For the remaining two levels, snail level and site level, we applied the method of reversible-jump MCMC (Lunn et al. 2005) for variable selection at the site level nested within the logistic model at the snail level. We averaged measurements of tidal-height-specific covariates over the entirety of each site to

include at the site level of the analysis. The resulting simplified model is described in detail in Table 1. To express the goodness of fit we calculated the level-specific R^2 measures and λ measures proposed by Gelman and Pardoe (2006) for hierarchical models.

Lengths of dissected snails varied from 8.0 to 33.7 mm with a mean of 19.76 mm. The site-specific coefficients for length (β_1 of the snail-level logistic regressions) varied greatly and even resulted in nonsensical negative values for some sites. These estimates had very large variances, particularly for the sites with low infection rates, which made them unsuitable for prevalence prediction. We therefore modeled the length coefficient as a simple random effect. Within the Bayesian paradigm a random effect is equivalent to a hierarchical structure with a prior distribution without including additional explanatory variables. The effect of the prior is a pooling of the individual slope estimates toward a more stable overall mean value (Gelman et al. 2004), which is reasonable for our situation. It allows us to control for the high influence of sites with small infection rates and to weigh relative importance of other drivers.

Parameter estimation for a Bayesian model requires calculation of the posterior distributions of all parameters using Bayes' theorem. For hierarchical models this calculation is nontrivial and requires iterative numerical methods. For most nontrivial models sequential draws from the posterior distributions of all model parameters can be obtained by the method of Markov chain Monte Carlo. We used the popular software WinBUGS (version 1.4.1) to perform these analyses (Spiegelhalter et al. 2003); our code is presented in the Supplement. In MCMC the sequence of draws represents a Markov chain that eventually, after a so-called burn-in period, becomes stationary, with the posterior distribution of all parameters as the stationary distribution. We tested convergence to the stationary distribution using the

TABLE 1. Extended.

Indices/notes
Y = incidence of trematode infection, where 1 = infected, 0 = uninfected; $i = 1, \dots, 28$ denotes sites; k denotes the k th snail: $k = 1, \dots, 5139$.
$\ln(\text{gulls})$ denotes $\ln(\text{average number of gulls} + 1)$; S = Shoals, NS = non-Shoals; Shoals and non-Shoals sites have different regression constants (α_0) but a common regression coefficient (α_1).
$\mathcal{N}(\mu, \sigma^2)$ denotes a normal distribution with mean μ and variance σ^2 .

See Gelman et al. (2004) for details about using the inverse gamma distribution as a prior for the variance parameter.

standard diagnostics, such as running multiple chains and calculating the Gelman-Rubin criterion (Gilks et al. 1996). Finally, we tested the relative influences of the most significant variables on trematode prevalence among sites (sensitivity analysis).

Many environmental variables quantified in the field vary at a larger spatial scale than a single sampled site. That is, several variables may have high regional-level spatial correlation, e.g., temperature or birds. Thus, first, as described above (*Methods: Field measurements of environmental variables*), we explored spatial relationships through the categorization of sites into different geographic groupings. We also examined spatial variograms of the influential independent variables to informally analyze their spatial correlation. Then, more formal statistical approaches were used to examine additional variation due to the spatial arrangements of sites. Specifically, our final model selection exercises concerned geographical effects in two ways. First, we assumed a residual spatial random field (Diggle et al. 1998) that attempts to capture part of the unexplained variation via a spatially correlated function. Second, as an alternative we modeled the coefficient of $\ln(\text{gull abundance})$ (the most spatially patterned variable in our informal analyses) as a site-specific effect with a spatial random field prior (Banerjee et al. 2004) with an exponential autocorrelation function. Such models can be fit using the WinBUGS add-on module GeoBUGS (Thomas et al. 2002).

RESULTS

We examined 5139 *Littorina littorea* of which 605 were infected, for an overall infection rate of 11.8%. However, prevalence of trematodes varied significantly by site, ranging from 0.7% to 47% (Fig. 1, Appendix B). With a median prevalence of 6%, the distribution of trematode infection rates was heavily skewed toward low prevalence. At the Shoals archipelago where we had high spatial resolution, *L. littorea* populations had high infection, including the five highest prevalences in our

New England survey (Fig. 2). We found a total of five trematode species. However, one of these species, *Cryptocotyle lingua*, dominated our surveys, accounting for >90% of all observed infections (Table 2). As such, our statistical models are, in effect, largely explaining the prevalence of this single predominant trematode species.

Gull abundance (combined *Larus argentatus* and *L. marinus*) and snail size significantly influenced infection rates of snails, with higher values of both associated with higher trematode prevalence (Table 3). At the site level of analyses, the natural log of gull abundance explained 68% of the variation in trematode prevalence ($R^2 = 0.68$). The λ measures at the site level, which quantify the amount (or fraction) of pooling that occurs for these parameters by fitting the hierarchical model, were $\lambda = 0.367$ for β_0 and $\lambda = 0.406$ for β_1 . Although Common Eiders (*Somateria mollissima*) and Double-crested Cormorants (*Phalacrocorax auritus*) can serve as definitive hosts for these trematode species, the abundance of these species did not emerge as significant during model selection when gull abundance was already in the model. Furthermore, total bird abundance, which included these species, did not perform better in the model than the abundance of only gulls.

The classification of sites into Shoals and non-Shoals also significantly improved the fit of the model of trematode prevalence (Table 4, Fig. 3). Specifically, Shoals sites had higher trematode prevalence even after standardizing for snail size and gull abundance. The logit scale mean posterior infection rates (α_0) for average-sized snails (19.76 mm) as a function of gull abundance at Shoals and non-Shoals sites were, respectively, -3.323 and -4.459 , which correspond to infection rates of 0.035 and 0.011 (the intercepts in Fig. 3). Table 3 gives these and additional summaries of the posterior distributions of the parameters. Reversible-jump MCMC overwhelmingly supports gull abundance and Shoals/non-Shoals as the most parsimonious influential explanatory model of site-level variables (Table 4). Specifically, posterior probabilities indicated this model fit better by at least a factor of two over any other model.

Based on the deviance information criterion (DIC) and the estimates of standard error, models that included spatial autocorrelation did not fit the data well. Most notably, adding spatially correlated error terms (model 2 in Appendix C) and spatially correlated random effects (model 3 in Appendix C) increased the DIC by ~ 20 and produced unrealistically high values in the posterior distributions of the standard deviations of the error term, in particular for the Shoals sites. Further, in model 2 the correlation range is near zero for non-Shoals sites and has an unstable (highly skewed) distribution for Shoals sites. Given the concern regarding overfitting the data, the most parsimonious model (model 1) had separate priors for the coefficients of snail length for Shoals and non-Shoals sites and the logarithm of gull abundance as the only site-specific variable.

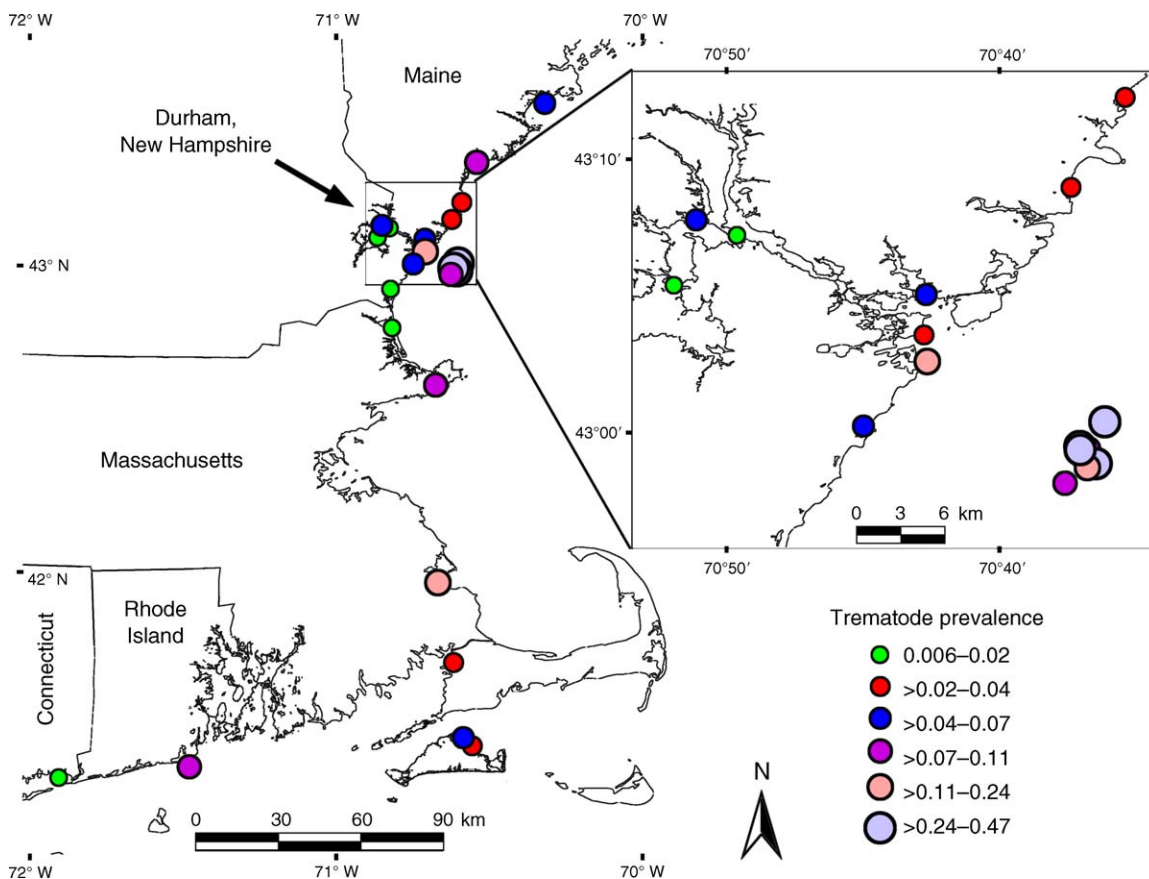


FIG. 1. Trematode prevalence in *Littorina littorea* at the 28 sampled intertidal sites in New England, USA. The inset shows higher resolution of the area sampled most intensively around the base of operation in Durham, New Hampshire. The cluster of overlapping points offshore at the border of New Hampshire and Maine is on the Isles of Shoals, depicted in higher resolution in Fig. 2.

Thus, neither of the spatially explicit analyses of the model improved the fit over the nonspatial model. However, the spatial configuration of the sites may not have lent itself well to spatial statistical modeling due to insufficient spatial coverage. To attempt to improve our spatial resolution to enhance the power of the regional effects modeling, we parceled out the northern, more densely sampled area around our Durham, New Hampshire, base of operation, which provides denser spatial coverage, and attempted to fit the above spatial hierarchical models. Specifically, the sites used included all but the six southernmost sites, which were the most highly separated. Here again, there was no improvement in the fit over the model with no spatial component. Thus the model identified by reversible-jump MCMC without any spatial effects is the most parsimonious and upon which our figures and tables are based.

One fish genus (*Fundulus* sp. [mummichugs]), two crabs species (*Carcinus maenas* and *Hemigrapsus sanguineus*), and three snails (*Littorina littorea*, *L. obtusata*, and *L. saxatilis*) dominated our biological sampling. Although these species represent known predators or competitors of *Littorina littorea* and known hosts of *L.*

littorea's trematode parasites, none significantly influenced trematode prevalence in our final model.

Physical variables, such as temperature and salinity, varied among the sites but none of these variables appeared as strong drivers of trematode infection. Rugosity was a moderately good predictor variable in full model runs, but did not emerge as a significant variable in final variable and model selection.

Our sensitivity analysis tested the relative effects of the two most significant variables on site-level infection (gull abundance and snail size) for Shoals and non-Shoals sites separately. Using the overall model describing the effect of snail length on infection, we doubled and halved the number of gulls to quantify their influence on infection probability. Doubling and halving gulls brackets realistic densities and also provides useful numerical points for comparison. Thus, for each suite of sites (i.e., Shoals or non-Shoals) we could compare, for example, how much a snail would have to grow (age) to equal the increase in the probability of infection caused by doubling gulls. This analysis demonstrated differences in the relative importance of gulls vs. snail size (length of exposure) (Fig. 4). For an average-sized snail (20

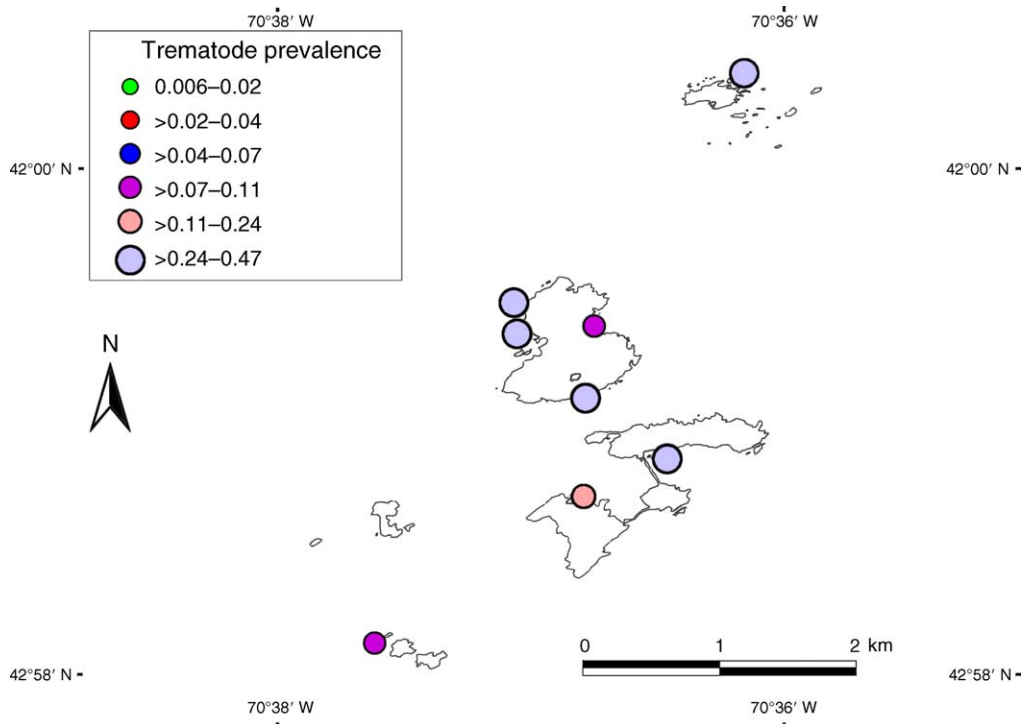


FIG. 2. Trematode prevalence in *Littorina littorea* at the Isles of Shoals archipelago.

mm), a doubling of gull abundance increases trematode infection prevalence equivalently to an increase of 6.1 mm length (non-Shoals sites) or an increase of 3.2 mm length (Shoals sites). Similarly, a halving of gull abundance corresponds to a decrease in trematode infection probability equivalent to a decrease of 6.3 mm length (non-Shoals sites) or a decrease of 3.3 mm length (Shoals sites). Based on field measurements conducted over five weeks and extrapolated (J. E. Byers, unpublished data), a *L. littorea* individual of 20 mm should grow ~ 2 mm/yr. Thus, doubling gulls on Shoals advances infection the same amount as would holding gulls at the current level and waiting ~ 1.5 yr. In contrast, doubling gulls on the mainland advances infection the same as would waiting ~ 3 yr (Fig. 4).

DISCUSSION

Trematode prevalence in the host *Littorina littorea* varied significantly among sites over a large geographic scale. Spatial heterogeneity in parasite prevalence has been previously noted (e.g., Robson and Williams 1970, Kuris 1990, Sousa 1990, Kuris and Lafferty 1994, Galaktionov 1996, Granovitch and Johannesson 2000, Smith 2007); however, until recently drivers of this variation have been unclear. Several authors have indicated that differential habitat use by definitive hosts should naturally lead to uneven deposition of their parasites (Kuris 1990, Sousa 1990, Sousa and Grosholz 1991). Some earlier research on littorinids, including *L. littorea*, suggested that at a small (1–3 km) scale,

shorebird (mostly gull) abundance correlates with prevalence of trematodes (Hoff 1941, Robson and Williams 1970, Bustnes and Galaktionov 1999, Skirnisson et al. 2004). However, few studies have quantified bird abundance explicitly, and those that have, have done so within only one or a few distinct sites. Still, the results have been somewhat mixed. In two studies the relationship between bird abundance and infection levels in first intermediate hosts was weak (Latham and Poulin 2003) or not found (Kube et al. 2002). However, Hechinger and Lafferty (2005) show that within a single marsh, fine-scale bird abundance is positively correlated with trematode abundance in snails. Also within a single marsh, Smith (2001) found positive correlations of definitive bird host densities and trematode prevalence in a salt marsh snail, *Cerithidea scalariformis*. Similarly,

TABLE 2. Trematode species richness and frequency of occurrence in 605 infected hosts.

Trematode species	Occurrence among infected snails (%)
<i>Cryptocotyle lingua</i>	90.91
<i>Cercaria parvicaudata</i>	7.76
<i>Renicola roscovita</i>	0.66
<i>Microphallus pygmaeus</i>	0.17
<i>Microphallus similis</i>	0.17
Double infection†	0.33

Note: Sampling was conducted at 28 intertidal sites along the New England coast.

† *Cryptocotyle lingua* and *Cercaria parvicaudata*.

TABLE 3. Posterior summaries of model parameters based on 20 000 Markov chain Monte Carlo iterations after the burn-in period.

Parameter	Mean	SD	5th percentile	Median	95th percentile
Common					
α_1	0.661	0.171	0.386	0.658	0.947
Non-Shoals sites					
α_0	-4.459	0.366	-5.077	-4.448	-3.877
$\mu_{\beta 1}$	0.0758	0.0534	-0.0108	0.0754	0.164
$\sigma_{\beta 0}$	0.662	0.204	0.367	0.641	1.026
$\sigma_{\beta 1}$	0.187	0.0462	0.122	0.182	0.270
Shoals sites					
α_0	-3.323	0.628	-4.393	-3.296	-2.353
$\mu_{\beta 1}$	0.143	0.0467	0.0682	0.143	0.219
$\sigma_{\beta 0}$	0.994	0.376	0.555	0.918	1.689
$\sigma_{\beta 1}$	0.112	0.0416	0.0632	0.104	0.189

Notes: Definitions of parameters: α_0 is the logit scale posterior mean infection rate for an average-sized snail on Shoals and non-Shoals (intercept); α_1 is the slope with respect to $\ln(\text{gulls} + 1)$ [with each increase of 1 in the natural log of gulls, the logit scale posterior mean infection rate for an average-sized snail increases by 0.661 for both Shoals and non-Shoals sites]; $\mu_{\beta 1}$ is the average slope (across all Shoals sites and across all non-Shoals sites, separately) with respect to snail length [as such, for a constant number of gulls, the logit scale posterior mean infection rate increases by 0.143 for each 1-mm increase in length on Shoals and by 0.0758 for each 1-mm increase in length on non-Shoals sites]. The 5th and 95th percentiles denote the confidence intervals for the mean estimates of each regression coefficient and thus whether each is significantly different from 0. The σ 's are the standard deviations of the parameters denoted by their subscripts.

Fredensborg et al. (2006), working within a single bay, show that at 12 sites over the scale of 10–15 km, birds, in particular gulls, highly influenced trematode prevalence in snails. Finally, Smith (2007) showed that at eight sites over 800 km, shorebird abundance was positively correlated with the prevalence of an acanthocephalan and a trematode in its intermediate crab host. Our study quantitatively demonstrates that over a scale of hundreds of kilometers, heterogeneity of trematode prevalence stems largely from gull abundance, implicating variation in the delivery of trematode eggs as a primary factor limiting trematode prevalence in snail hosts at a large spatial scale.

Trematode prevalence was especially low at the non-Shoals (mostly mainland) sites where birds were sparse (Fig. 3). Successful recruitment of trematodes to their snail host “habitat” is dependent upon a two-stage delivery process. Infected bird feces must first land in the intertidal, and trematode eggs in the feces must then be ingested by a grazing snail. Gulls are a proxy for the former event and snail size (age) is an integrated probability of the two. That is, snail size indexes the duration of a snail’s exposure to deposited trematode eggs, reflecting the cumulative time the snail has had over its life to encounter eggs. Growing bigger (and thus spending more time) at a mainland site does little to increase the probability of trematode infection compared to the effect of changes in gull abundance (Table 3, Fig. 4). Essentially, the delivery of eggs in gull feces is so occasional that there is limited infection risk to which to be exposed naturally over time. In contrast, at Shoals sites, time (as indexed by snail growth) is very influential on infection relative to changes in gulls, which were typically in higher abundance (Fig. 3). That is, high

baseline infection rates are integrated over time into high infection probability. Thus, while delivery of recruits from bird hosts is the limiting factor for trematodes across a regional scale, the relative importance of the two stages of the snail infection process varies between Shoals and non-Shoals sites.

TABLE 4. Reversible jump variable selection for the site-level prior regression model for the intercept term of the logistic snail infection model.

Variable	Marginal probability
Shoals	0.579
$\ln(\text{gulls})$	0.923
$\ln(\text{crab biomass})$	0.289
Rugosity	0.201
$\ln(\text{all snails density})$	0.155
$\ln(\text{littorinid species density})$	0.168
$\ln(\text{gulls} \times \text{Shoals})$	0.0767
$\ln(\text{crab biomass} \times \text{Shoals})$	0.295
Rugosity \times Shoals	0.291
$\ln(\text{all snails density} \times \text{Shoals})$	0.230
$\ln(\text{littorinid species density} \times \text{Shoals})$	0.291

Notes: Because the number of models increases exponentially with each variable included, for ease of interpretation and presentation we present a reduced model run with the five best variables plus their interactions with Shoals. Littorinid species density is the mean density of all three *Littorina* species combined (*L. littorea*, *L. obtusata*, and *L. saxatilis*). Values in boldface type indicate gull abundance and Shoals/non-Shoals as the most parsimonious influential explanatory model of site-level variables. The posterior probabilities for the model selections are as follows: for $\ln(\text{gulls})$, both the posterior probability and the cumulative probability are 0.109; for Shoals + $\ln(\text{gulls})$, the posterior probability is 0.0763, and the cumulative probability is 0.186. Because the first model is a nested subset of the second, we selected the latter as the best (most powerful and parsimonious) model. The next best model has a posterior probability that drops to less than half of the value of the second model.

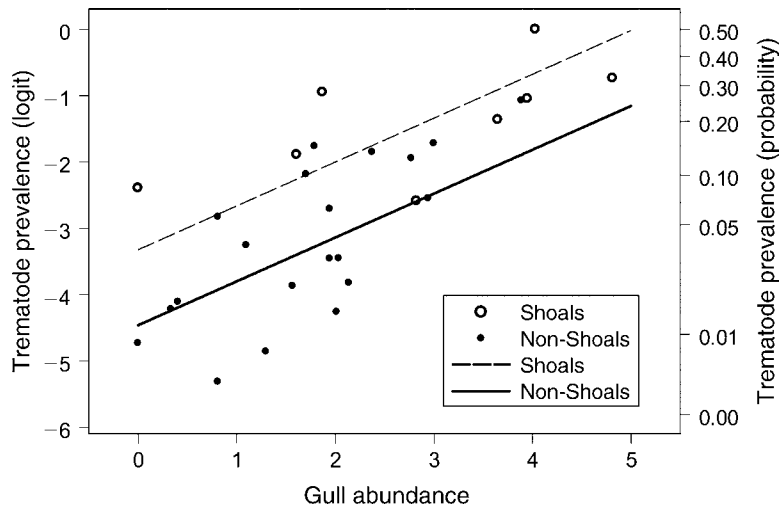


FIG. 3. The posterior mean fitted effect of gull abundance [$\ln(x + 1)$ transformed] on trematode prevalence in *Littorina littorea* populations across all 28 intertidal sites. Data shown are “length-adjusted” observed logits (for standardized snails of mean length [19.76]; left axis) and corresponding prevalence scale (right axis).

The importance of snail size and consequent exposure time could be slightly overestimated at Shoals sites. Because snails may not grow at equal rates among all sites, size may not be universally calibrated to index exposure time. *Littorina littorea* could grow slower at sites with high wave exposure (Boulding and Van Alstyne 1993). Values of $\mu_{\beta 1}$ (Table 3) suggest that at our sites on Shoals, which on average are more exposed to waves, the relationship of trematode prevalence to

snail length is roughly two times (0.143/0.076) more sensitive to snail growth than at our non-Shoals sites. This sensitivity may simply reflect that snails grow more slowly at Shoals and thus have been exposed to trematodes longer for a given size. If a 1-mm increase in size takes $\sim 90\%$ longer at Shoals than at a mainland site, this would equalize the heightened sensitivity of Shoals snails to snail growth. Spatial variability in growth has been observed in *L. littorea* and

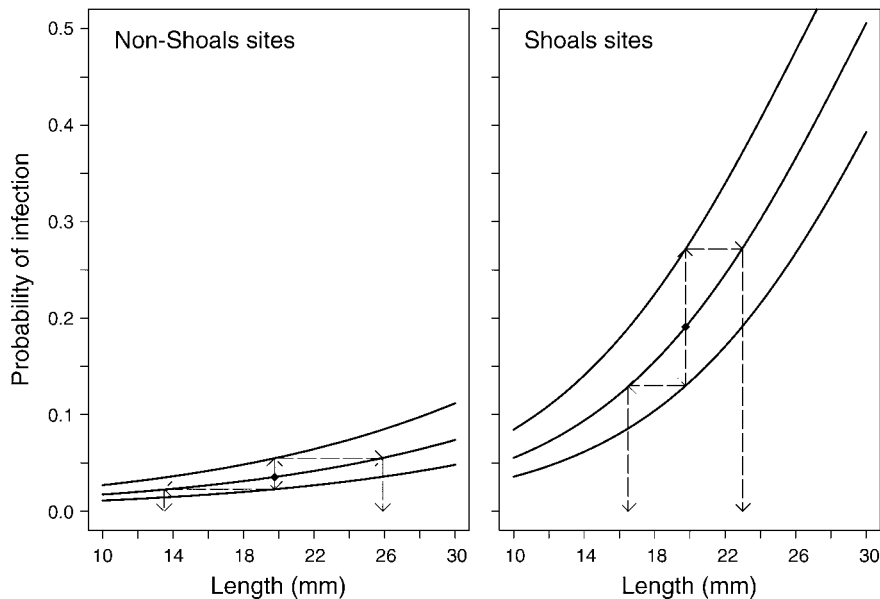


FIG. 4. The effects of halving and doubling the gull population on trematode prevalence in *Littorina littorea* for Shoals and non-Shoals sites. Curves depict the estimated trematode prevalence for mean gull abundance (middle curve), i.e., as the model fit the observed data; estimated prevalence if gull abundance were one-half of the mean (lower curve); and if gull abundance were twice the mean (upper curve). The central dot and points where the vertical and horizontal dashed arrows intersect the solid curves provide reference points depicting the relative sensitivity of infection probabilities to changes in gulls and snail size (as discussed in Results).

may be large enough to equalize at least some of this difference. For example, Fish (1972) showed *L. littorea* in an open coast population in Wales grew ~20% slower than a nearby estuarine population.

Slower growth on Shoals would also equalize some of the difference in gull effects (on size-standardized snails) between Shoals and non-Shoals (Fig. 3) since an averaged standardized snail at Shoals would have an inflated prevalence due to differentially longer exposure. However, there are a couple of additional factors that likely also contribute to the heightened effect of gulls on infection at Shoals sites (Fig. 3). First, each individual gull probably carries more trematodes (and therefore delivers more eggs in its feces) at the Shoals than at non-Shoals sites because gulls at Shoals prey more heavily on appropriate hosts. All seabirds examined in this study breed during summer on offshore islands such as Shoals (e.g., Pierotti and Good 1994, Good 1998). Chick hatching often induces gulls on islands to switch to a diet heavy in fish (Annett and Pierotti 1989, Goodale 2000), the second intermediate host for *L. littorea*'s most prevalent trematode, *Cryptocotyle lingua*. Fledglings also forage heavily on *C. lingua* host fish and are the most heavily infected year class of gulls (Threlfall 1967). At Shoals, a huge proportion of the nearshore forage fish (e.g., herring, rock gunnel) are heavily infected (J. E. Byers, A. M. H. Blakeslee, and T. J. Maguire, *personal observations*). In contrast, gulls found on the mainland during the breeding season (especially at sites far from colonies) are less likely to be breeding. They are thus less likely to consume fish and become infected (Wells 1994). Therefore, even when gull abundance was relatively equal, Shoals sites had higher trematode prevalence than mainland sites (Fig. 3).

Another contributing factor may explain some of the Shoals/non-Shoals difference. Compared to mainland sites, gulls remain in residence at Shoals sites for a longer period of time because that is where they are nesting and raising young (Pierotti and Good 1994, Good 1998; J. C. Ellis, *unpublished data*). Our bird measurements were only performed in the summer. If gulls simply remain in residence longer at Shoals than at mainland sites, a similar number of birds could transmit more infection by supplying feces over a longer time period.

Although birds other than gulls may serve as definitive hosts (e.g., cormorants, eiders), gull abundance was the significant bird metric identified by the model; even aggregate bird counts did not perform as well. Lauckner (1985) identifies larids as the main definitive host for *C. lingua*. In addition to the supposed physiological proclivity of *C. lingua* for gulls, ecologically, gulls are likely to be better vectors of *C. lingua* because gulls spend more time in the intertidal zone where their feces have immediate contact with the snails. In contrast, cormorants were more frequently seen upshore above the intertidal zone or offshore, and eiders were almost always swimming offshore.

With the exception of the Shoals/non-Shoals dichotomy, we found no spatial correlations in either trematode infections or gull abundance, suggesting the importance of local conditions driving trematode prevalence. Given the high dispersal capability of avian definitive hosts, trematode recruitment could seemingly correlate over large spatial scales. We were therefore surprised to detect no evidence of systematic variation or regional spatial correlation of either gull abundance or trematode prevalence at a large scale. Although we lacked strong statistical power, the absence of large-scale spatial patterns suggests gull effects are predominantly localized, a finding confirmed for shorebirds in general wherein fine-scale bird abundance and associated trematode prevalence in snails were correlated among closely spaced sites within the same wetland (Smith 2001, Hechinger and Lafferty 2005). Poulin and Mouritsen (2003), using a meta-analysis across 255 studies of 54 species of marine gastropods, examined the effects of host life-history characteristics, latitude, substrate type, and tidal height on trematode prevalence. They failed to detect large-scale determinants of prevalence, similarly concluding that local factors played bigger roles in determining prevalence rates.

Tidal height has been found in some studies to be a significant factor in snail infection prevalence, but across many sites as we examined here, its influence is not consistent. In two site-specific studies of *L. littorea*, slight differences in prevalence rates were found between high and low tidal heights (Sindermann and Farrin 1962, James 1968b). Sindermann and Farrin (1962) found higher rates in the high intertidal and suggested this was because the high intertidal zone had higher gull abundance because less inundation in the high zone provided longer exposure time for birds to feed. Furthermore, deposited trematode eggs may be less likely to be dislodged if they are in the high intertidal zone. In our study, the probability of infection differed substantially between tidal heights at only a few sites (and in such cases was usually higher in the high intertidal zone). We may have had limited resolution to detect tidal-height differences across our sites given low trematode prevalence, especially at mainland sites. Also, because of differences in beach slope or fucoid distribution (which defined our high-tide zone), the distance between high- and low-intertidal collection areas varied across sites. Due to the overwhelming influence of gulls driving infection, we believe it is logical that any tidal height at which gulls spend more time would be likely to exhibit higher infection.

Although we found snail size to be influential in determining trematode prevalence, snail density was not a significant factor. The fact that snail density was not a significant factor is not surprising given that these trematodes have obligate, multi-host life cycles and trematodes in one snail are not directly contagious to another snail. However, at least one study has shown decreased trematode prevalence with higher snail

density, suggesting a dilution of infective trematode stages as they are “used up” by an increasing number of snail hosts (Ewers 1964). In the present system a dilution effect likely does not occur because each infected bird dropping contains hundreds of infected eggs (Lauckner 1985; J. E. Byers, *personal observation*), and this clumped egg delivery makes it unlikely that the density of snails in the immediate vicinity of a dropping is high enough to exhaust the eggs. Over the range of snail densities tracked here (16–640 snails/m²), the density of gulls (and their feces) remains the most important factor in determining trematode prevalence. Low prevalence of infection in snails at a site is more likely driven by lower numbers of infected bird droppings, a factor that can limit site-level snail infection prevalence, but is independent of snail density.

Because parasitic species do not just live at a locality per se, but also must reside within a host species, a further factor that may be important to consider in studies that examine the spatial variability of parasite prevalence is host genotype. For example, Lively (1989) and Grosholz (1994) demonstrated the role of genetics of molluscan hosts in influencing infection rates of trematodes. However, because *L. littorea* is a broadcast spawner with open populations and wide gene flow (Johannesson 1992), variation in genetic resistance is likely to be minimal for this snail host.

In summary, spatial variation in parasite prevalence can be driven by environmental variables acting over a hierarchy of scales. However, our comprehensive large-scale investigation of trematode prevalence found evidence only of local site-level processes, particularly those that favor high gull abundance. The strong dependence of trematode prevalence on the abundance of its dispersal agent, coupled with the typically low trematode infection prevalence in the snail host populations, indicates that trematodes in this system are often limited by delivery of their definitive host.

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APPENDIX A

Methodologies for field measurements of physical and biological variables (*Ecological Archives* E089-025-A1).

APPENDIX B

Sampled intertidal sites: locations, sample sizes, and trematode prevalences (*Ecological Archives* E089-025-A2).

APPENDIX C

Summary of model fits of several competing models (*Ecological Archives* E089-025-A3).

SUPPLEMENT

WinBUGS model code (*Ecological Archives* E089-025-S1).