Range limits and parasite prevalence in a freshwater snail

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Geographical range limits are thought to be set by species' physiological or ecological adaptation to abiotic factors, but the importance of biotic factors such as parasitism in determining range limits has not been well explored. In this study the prevalence of trematode parasitism in populations of a freshwater gastropod snail, *Lymnaea stagnalis*, increased sharply as this species approached its western UK range limit. The likelihood of trematode infection increased with snail size, but high prevalence at the range edge was not a result of interpopulation variation in snail size. Changes in population growth rates resulting from high rates of parasitism at the range edge could contribute to range limitation. The mechanism driving high rates of parasitism at the range edge is not clear, but changes in abiotic factors towards the range limit may influence snail life history and immune response to trematode infection, indirectly altering the prevalence of parasites in marginal host populations.

Keywords: geographical range; life history; Lymnaeidae; parasitism; range edge; trematode

1. INTRODUCTION

All species have a limited distribution in space and determining the processes that limit a species distribution is an important issue in ecology (Hoffman & Blows 1994; Brown 1995). Distributions are commonly seen to be restricted by limits to species' physiological or ecological adaptation to abiotic factors (Chown & Gaston 1999). However, Spicer & Gaston (1999) have pointed out that abiotic gradients towards range limits may change the relative importance of biotic interactions in limiting distribution. Theoretical studies (Hochberg & Ives 1999; Holt & Keitt 2000) have demonstrated that biotic interactions such as predation and parasitism can contribute to range limitation, but there is almost no empirical information on spatial variation in the extent of parasitism across the geographical range of a host species.

Freshwater gastropods of the genus *Lymnaea* are obligate primary intermediate hosts for many species of trematode parasite. Trematodes have a complex life cycle involving one or two (rarely three) intermediate hosts prior to infection of the definitive host (Esch & Fernandez 1994). Infection occurs through ingestion of the eggs or penetration of the snail by free-swimming miracidia (Esch & Fernandez 1994). One or more intramolluscan developmental stages may then be involved before the

production of motile cercariae that leave the snail to infect the second intermediate or definitive host.

Trematode infection usually results in parasitic castration of the snail host (Esch & Fernandez 1994), which may have important effects on gastropod population biology and life history (Brown *et al.* 1988; Sorensen & Minchella 2001) and could contribute to the regulation of host populations at high prevalence (Lie & Ow-Yang 1973; Brown *et al.* 1988). Prevalence of trematode infection generally increases with snail size (and age). Several different factors, such as parasitic alteration of growth rates, changes in survivorship and increased exposure to infection with age may contribute to this pattern (Brown *et al.* 1988; Sorensen & Minchella 2001). There is considerable intraspecific variation in parasite prevalence in snail hosts (Kuris & Lafferty 1994). However, geographical patterns of variation in trematode prevalence, and how these relate to variation in snail growth rates and life history, remain unknown.

Here I establish whether there is any systematic change in parasite prevalence in populations of *L. stagnalis* L. (Gastropoda: Pulmonata) as this species approaches its western UK range limit. The aim of this study was to determine if there was any evidence that parasitism could contribute to range limitation in this species. *Lymnaea stagnalis* is a Holarctic freshwater snail (Kerney 1999) and a common host for many trematode parasite species (Loy & Haas 2001).

2. MATERIAL AND METHODS

Snails were sampled in July 2002 along an east-west transect of 12 sites (canals or lakes) which varied in distance from the western UK range limit of *L. stagnalis*, and which were approximately in the centre of the north-south UK distribution (figure 1). Here the range limit was defined as the edge of the most western 10 km square occupied on the transect. Other more western sites (see figure 1) are isolated populations, some of which result from deliberate introductions (Kerney 1999). Snails were collected with a hand-net (mesh size of 500 µm) from a 100 m stretch of bank to minimize the influence of local variation in parasite prevalence on the results. The number of snails collected at each site varied between 56 and 121. Water pH and conductivity (µS cm⁻¹) were recorded at each site using portable meters (WTW model pH 320 and LF 325, respectively). Five measurements were taken at approximately equal intervals along the stretch of bank sampled and means calculated.

Within 48 h of collection, snails were screened for mature cercarial infections in the laboratory by isolating them individually in 50 ml glass vials containing filtered water from the site where the snails were obtained. The snails were held under *ca.* 7000 lx illumination at 20 °C for 12 h to stimulate the production of cercariae (Brown *et al.* 1988). Shed cercariae were identified using Nasir & Erasmus (1964). The percentage of snails shedding cercariae (total trematode prevalence) was then calculated for each site. Following determination of cercarial infections, snail size (measured from the tip of the spire to the base of the body whorl) was recorded to the nearest 0.1 mm by using Vernier calipers in order to assess whether variation in parasite prevalence was due to differences in snail population size structure.

3. RESULTS

Five species of trematode were recorded from *L. stagnalis* at the sites sampled: two furcocercariae, *Diplostomum spathecum* Rudolphi and *Cotylurus brevis* Dubois and Roach; two echinostome cercaria, *Echinostoma revolutum* Fröelich and *Echinoparyphium recurvatum* von Linstow; and a xiphidocercaria, *Cercaria edgbastonensis* Nasir. Data on the distribution and prevalence of individual species are available from the author on request.

The total percentage prevalence was high towards the western range limit and lower, but variable, with increasing

Figure 1. Distribution of *Lymnaea stagnalis* in the UK. Filled circles are 10 km grid squares in which populations have been recorded and open circles are grid squares from which populations were sampled in the present study. Based on data in Kerney (1999) and records generated by the present study. The map is truncated to the north for clarity; a few scattered populations in Scotland are consequently not shown.

Figure 2. Total prevalence of trematode parasites in populations of *Lymnaea stagnalis* in relation to distance from the western UK range limit. The fitted line is an inverse power function (see § 3 for details).

distance from the range edge (figure 2). The decline in prevalence with distance from the range limit was well described by an inverse power function (fitted to ln-transformed data: $F_{1,11} = 15.48$, $p = 0.003$; adjusted $r^2 = 0.57$; figure 2). Total parasite prevalence did not vary consistently between the two habitat types sampled (Mann-Whitney U -test: $U_{7,5} = 22.5$, $p = 0.461$). Up to three species were recorded at each site, but no mixed species infections (more than one species of trematode per snail) were recorded. Parasite species richness and prevalence of individual trematode species did not vary systematically

Table 1. Results of logistic regression of trematode infection in relation to size of *Lymnaea stagnalis* and distance from the western range edge. (See § 3 for details of logistic regression model.)

variable	coefficient	s.d.	Z	p
constant	-14.01	2.09	6.67	< 0.001
log snail size	13.73	1.95	7.06	< 0.001
log distance	-3.41	1.29	2.63	0.008
log snail size $\times$ log distance	0.33	1.11	0.30	0.765

with distance from the range limit or with the number of snails sampled. There was a weak correlation between total prevalence and pH (Spearman's rank correlation: $r_{11} = -0.560$, $p = 0.058$), but conductivity was not related to prevalence.

The likelihood of trematode infection increased with snail size and decreased with distance (logistic regression model: $G^2_3 = 588.62$, $p < 0.001$; table 1). There was no significant interaction between snail size and distance from the range edge, indicating that the observed changes in prevalence were not due to a gradient in the size of snails.

4. DISCUSSION

There is clear evidence of a systematic change in the prevalence of trematode infection in *L. stagnalis* as this species approaches its western UK range limit. Prevalence was significantly higher close to the range limit than in more central parts of its UK geographical range. Prevalence was not related to habitat type, suggesting that a habitat-specific risk of parasitism did not contribute to the observed pattern (see also Wulschleger & Jokela 1999). Prevalence data were based on determination of mature cercarial infections and hence do not include snails that are infected, but not yet shedding cercariae. The true rate of infection may therefore be higher than that recorded (Loy & Haas 2001). Differences between recorded and true rates of infection are unlikely to significantly alter the observed pattern of parasite prevalence, and the proportion of immature infections is unlikely to show strong geographical variation.

Prevalence was not uniformly low away from the range limit; there was evidence of other local peaks in parasite prevalence (figure 2). Prevalence values from greater than 80% to less than 1% have been reported elsewhere (Adam & Lewis 1993; Loy & Haas 2001) suggesting that geographical patterns of variation in parasite prevalence across a host species range may be complex. The marked increase in the prevalence of parasites at the range edge suggests that parasitism could contribute to the range limitation of this species by influencing local population growth. In a study of *Lymnaea elodes*, Brown *et al.* (1988) found that average parasite prevalences of between 9% and 24% resulted in a 10–20% reduction in snail population growth. At the higher prevalences recorded here in marginal populations, parasitism may have an accordingly greater impact and reduce population growth rates to an extent that limits the further expansion of the species into adjacent habitats.

Species approaching their range limits may experience increasing abiotic stress due to changes in environmental conditions. Abiotic stress may influence the interactions between host and parasite, potentially increasing or decreasing the effects of parasites on hosts depending on the context (Lafferty & Kuris 1999; Kiesecker & Skelly 2001). In common with all shell-bearing molluscs, *L. stagnalis* has a fundamental requirement for environmental calcium, and its UK distribution is linked to the distribution of calcium-rich waters (Kerney 1999; Briers 2003). The continual uptake and deposition of calcium in the shell involves considerable metabolic expenditure (McMahon 1983). There is evidence of a trade-off between energy diverted to immune function and other activities (Langland *et al.* 1998; Rigby & Jokela 2000). If populations in marginal habitats have to expend more energy to enable them to successfully complete development, they may be less able to resist infection by trematodes, resulting in higher prevalence.

Alternatively, high trematode prevalence in marginal populations could be due to changes in snail life history towards range limits. There was no evidence of a gradient in snail size, but growth rates and life histories of freshwater molluscs vary in response to environmental conditions (McMahon 1983). Slower growth in marginal populations may therefore result in snails of a given size having a higher risk of infection due to their greater age (Brown *et al.* 1988). The distribution and abundance of definitive hosts also influences the prevalence of trematode infection (e.g. Smith 2001). There is no evidence of a large-scale gradient in definitive host species richness or abundance in the study area to support this hypothesis (Gibbons *et al.* 1993), but as data on the abundance of definitive hosts were not collected, it cannot be entirely ruled out.

In conclusion, this study suggests that gradients in abiotic factors may interact with biotic interactions such as parasitism to limit species' distributions. While the mechanism behind the peak in parasitism at the range edge of this species is presently unclear, the observed pattern of variation in parasite prevalence strongly suggests that parasitism of freshwater snail populations could contribute to the limitation of geographical ranges.

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