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Local adaptation in a crustacean parasite–molluscan host interaction: a field experiment

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ABSTRACT

Hypothesis: The Red Queen hypothesis predicts that parasites are locally adapted to their most common host genotypes.

Organisms: The parasitic copepod *Paraergasilus rylovi* and its host, the freshwater clam *Anodonta piscinalis*.

Sites of research: Lake Saravesi and River Kuusaankoski, which are 4 km apart.

Methods: We expelled parasites from wild hosts. Then we performed a reciprocal transplant experiment: we returned hosts to their natural environment at two transplant sites, and allowed clams to become infected naturally.

Results: At both sites, local hosts, the home-clams, harboured more *P. rylovi* than the away-clams. In addition, at both transplant sites the reproductive performance of the parasite (proportion of females carrying egg sacs) was higher in the home-clams. The results indicate that *P. rylovi* is both genetically specialized and locally adapted to its host population.

Keywords: *Anodonta piscinalis*, Ergasilidae, freshwater, host–parasite interactions, local adaptation, *Paraergasilus rylovi*, Unionidae.

INTRODUCTION

The Red Queen hypothesis states that between-species interactions, such as those between hosts and parasites, lead to natural selection for adaptations and counter-adaptations. According to the Red Queen hypothesis, parasites are expected to be locally adapted to the most common host genotypes. This is partly because of the higher evolutionary potential of parasites, due to their larger population sizes and higher mutation rates (e.g. Hamilton *et al.*, 1990; Ebert, 1994; Lively, 1999; Krist *et al.*, 2000; Dybdahl and Storfer, 2003). Locally adapted parasites should have, on average, higher infectivity and/or greater reproductive success in the local (sympatric) host population than in a non-local (allopatric) host population (Ebert, 1994; Ebert and Hamilton, 1996; Gandon and Van Zandt, 1998; Kaltz *et al.*, 1999). Within a population, parasite adaptation to the most common host genotypes is expected to drive down the frequency of corresponding

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host genotypes and to give an advantage to rare host genotypes, thus allowing counter-adaptation by the host (Hamilton, 1980; Bell and Maynard Smith, 1987; Lively and Dybdahl, 2000). Frequency-dependent and time-lagged, parasite-mediated selection against common host genotypes is expected to lead to oscillations in genotype frequencies in both the host and the parasite with particular resistance and infectivity, respectively, and hence to the maintenance of genetic variation in both host and parasite traits (Bell and Maynard Smith, 1987; Hamilton *et al.*, 1990). Frequency-dependent selection is commonly explored by reciprocal transplant experimentation between host populations, where infectivity is used as a measure of adaptation to local and non-local hosts (Lively, 1989; Gandon and Van Zandt, 1998; Roy, 1998; see review in Dybdahl and Storfer, 2003).

Adaptation of parasites to their local hosts has been observed in several host–parasite systems, including plant–herbivore, plant–pathogen, crustacean–microsporidian and snail–trematode (see review by Kaltz and Shykoff, 1998). To date, most local adaptation experiments have been conducted in the laboratory, and only rarely under field conditions (but see Davelos *et al.*, 1996; Roy, 1998). In the present experiment, local adaptation was studied using previously infected, wild host individuals from which the parasites were expelled prior to the experiment. In addition, the experiment used natural infection under field conditions.

Anodonta piscinalis (Mollusca, Bivalvia) is a widespread and abundant clam inhabiting slowly running waters and littoral zones of temperate lakes in northern Europe (Bauer *et al.*, 1991). It is widely used in environmental (e.g. Pellinen *et al.*, 1994), ecological (e.g. Jokela and Palokangas, 1993) and parasitological (e.g. Taskinen and Valtonen, 1995) research.

Adult females of the ergasilid copepod *Paraergasilus rylovi* (Copepoda, Ergasilidae) inhabit the gills of *A. piscinalis* (Chernysheva and Purasjoki, 1991; Saarinen and Taskinen, 2004). Ergasilids of fishes feed on gill tissues and blood, and may cause deformation or necrosis of the gill filaments (Bauer *et al.*, 1973). Thus, *P. rylovi* is potentially harmful to *A. piscinalis*. Taskinen and Saarinen (1999) found reproductive, glochidia-bearing female *A. piscinalis* to be more abundantly parasitized by *P. rylovi* than the non-reproducing females, which may indicate a reduction in host defence ability due to reproductive effort. In addition, Saarinen and Taskinen (2005) observed that susceptibility to *P. rylovi* infection increased in experimentally stressed clams.

The aim of this study was to examine local adaptation of the copepod parasite *P. rylovi* in the freshwater clam host, *A. piscinalis*. To do this, we performed a reciprocal transplant experiment between two locations. Before the experiment, we expelled parasites from wild hosts in the laboratory using the method described by Saarinen and Taskinen (2003a). During the experiment, clams were kept in their natural environment and allowed to become infected naturally. In addition, we transplanted the clams to three different depths in one of the sites. We used both infectivity (parasite abundance) and reproduction (proportion of parasites carrying egg sacs) as measures of parasite adaptation.

MATERIALS AND METHODS

Using scuba, 213 clams were collected from the littoral zone of Lake Saravesi (depth 2.0 m, 150 m offshore), southern Finland (62°25′N, 26°00′E) and 134 clams from River Kuusaankoski, which flows to Lake Saravesi, on 16 May 2003. The populations are 4 km apart. Clams were transported to the laboratory in their original water, which was 10°C. On the day of collection, 20 clams from each population were randomly chosen as reference samples and were dissected. Clam length was measured and the number of *P. rylovi* was

determined by pressing clam gills between two large glass plates and examining microscopically using transmitted light. The number of (female) *P. rylovi* carrying egg sacs was counted. The remaining clams were marked on the shell using a boring tool, mixed and transferred to two 500-litre containers of aged tap water, at 15°C with aeration, 154 and 153 clams per container.

The clams, including *P. rylovi*, were allowed to adjust to the laboratory conditions for 3 days. Then the parasites were expelled from the clams by increasing water temperature to 26°C for 3 weeks (see Saarinen and Taskinen, 2003a). The water was changed completely on days 7 and 14. During each water renewal, clams were re-mixed and randomly divided into the two containers. Temperature and oxygen concentration ($mg \cdot l^{-1}$) were measured using a YSI 55/12 FT (Yellow Springs Instrument Co., Inc., Ohio, USA) and any dead clams were removed daily. A total of 15 clams from Lake Saravesi were dissected on days 7, 14 and 21 to confirm the disappearance of *P. rylovi* from the host clams.

On 11 June, the surviving clams, 153 specimens originally from Lake Saravesi and 92 individuals originally from River Kuusaankoski, were returned to the field for a reciprocal transplant experiment. Clams were placed in plastic 12-litre basins (diameter 34 cm) filled one-third with sand. In Lake Saravesi, seven basins, each containing six clams originally from Lake Saravesi and four clams originally from River Kuusaankoski, were placed 300 m offshore, where the water was 4.0 m deep. Another seven basins, each containing six clams from Lake Saravesi and four clams from River Kuusaankoski, were placed 150 m offshore, where the water was 2.0 m deep. Finally, seven basins, each containing six clams from Lake Saravesi and three clams from River Kuusaankoski, were placed 20 m offshore, where the water was 0.8 m deep. Thus, a total of 117 clams from Lake Saravesi and 72 clams from River Kuusaankoski were placed in Lake Saravesi. In River Kuusaankoski, five basins, each containing six clams from Lake Saravesi and four clams from River Kuusaankoski, were placed at a depth of 1.5 m, 10 m from the bank. Thus, a total of 36 clams from Lake Saravesi and 20 clams from River Kuusaankoski were placed in River Kuusaankoski.

The normal reproductive period of the parasite is between June and August (Saarinen and Taskinen, 2004). Therefore, the clams were kept in the field from June to August 2003, to allow exposure to parasites. On 11 August 2003, after 2 months in the field, the clams were returned to the laboratory, measured and dissected. Two basins were lost at the depth of 4.0 m in Lake Saravesi. On 14 August 2003, 20 clams from each population were collected in the field for use as reference samples. These were later dissected in the laboratory.

The effect of place of origin, water depth and basin on the mean abundance of *P. rylovi* and on the mean proportion of *P. rylovi* females carrying egg sacs in those clams placed in Lake Saravesi was analysed using univariate ANOVA (a randomized complete block design with two main factors), using place of origin (Lake Saravesi, River Kuusaankoski) and water depth (0.8, 2.0 and 4.0 m) as factors of the main effect of interest, and basin as a blocking factor. We included length in models at first by using ANCOVA, but later dropped it, as its effect was not statistically significant. Normally distributed and homoscedastic residuals were achieved for both parasite numbers and proportion of females with egg sacs by using a $\ln(x + 10)$ transformation.

Differences in the mean abundance of *P. rylovi* between the field reference samples collected before and after the experiment from Lake Saravesi were analysed using one-way ANOVA. Differences in the mean abundance of parasitism and the mean proportion of female *P. rylovi* carrying egg sacs between the reference sample collected from Lake Saravesi after the experiment from a depth of 2.0 m, and the experimental clams originating from

Lake Saravesi at a depth of 2.0 m (and kept at a depth of 2.0 m in Lake Saravesi) were analysed using one-way ANOVA.

The effect of place of origin on the abundance of *P. rylovi* and on the proportion of *P. rylovi* females carrying egg sacs among the clams placed in River Kuusaankoski was analysed using the non-parametric Mann-Whitney *U*-test, because of many zero observations. The effect of basin on the mean abundance of *P. rylovi* and on the proportion of *P. rylovi* females with egg sacs was analysed using the non-parametric Kruskall-Wallis test. Differences in the mean abundance of *P. rylovi* between the field reference samples collected before and after the experiment from River Kuusaankoski were analysed with the non-parametric Mann-Whitney *U*-test. Differences in the mean abundance of parasitism and in the mean proportion of female *P. rylovi* carrying egg sacs between the reference sample collected from River Kuusaankoski after the experiment, and the experimental clams originating from River Kuusaankoski (and kept in River Kuusaankoski) were analysed using the non-parametric Mann-Whitney *U*-test.

RESULTS

The mean abundance of *P. rylovi* was 15.1 ± 1.4 in Lake Saravesi and 0.6 ± 0.3 in River Kuusaankoski in the reference samples collected before the experiment on 16 May 2003. The mean abundance of *P. rylovi* was 32.9 ± 3.4 in Lake Saravesi and 0.8 ± 0.2 in River Kuusaankoski in reference samples collected after the experiment on 14 August 2003. Reference samples collected from Lake Saravesi before and after the experiment differed from each other ($F_{1,39} = 25.807$, $P < 0.001$) in *P. rylovi* numbers, but the reference samples from River Kuusaankoski did not (Mann-Whitney $U = 166.000$, $P > 0.1$).

The mean (± standard error) water temperature and oxygen concentration in the two temperature treatment containers were 25.9 ± 0.3°C, 6.58 ± 0.31 mg·l^{-1} and 26.1 ± 0.3°C, 6.58 ± 0.16 mg·l^{-1} during the 3 week temperature treatment to expel the parasites before the experiment. During the temperature treatment, 25 of 154 clams (16.2%) died in container 1, and 22 of 153 clams (14.4%) died in container 2. All dead clams were infected by the trematodes *Rhipidocotyle fennica* or *R. campanula*, or both. These are common digenean parasites of *A. piscinalis* in the study area (Taskinen and Valtonen, 1995). Clams dissected on days 7, 14 and 21 during the course of the temperature treatment revealed that the 3 week treatment had successfully freed the clams from the copepod parasites. During the 2 month field period, 22 of 189 clams (11.6%) died in Lake Saravesi and 4 of 56 clams (7.1%) died in River Kuusaankoski.

The effect of place of origin on the abundance of *P. rylovi* among the clams placed in Lake Saravesi was statistically significant (univariate ANOVA: $F_{1,137} = 13.768$, $P < 0.001$). Clams originally from Lake Saravesi, the home-clams, harboured more *P. rylovi* than clams originally from River Kuusaankoski, the away-clams (Fig. 1a). The effect of water depth was also significant ($F_{2,137} = 84.436$, $P < 0.001$), with the mean abundance of the parasite being highest at the depth of 2.0 m (Fig. 1a). The effect of origin was similar at all depths as indicated by the statistically non-significant interaction between place of origin and water depth ($F_{2,137} = 2.094$, $P > 0.1$). The effect of the blocking factor, basin, was also not significant ($F_{6,37} = 1.522$, $P > 0.1$). The difference in the mean abundance of *P. rylovi* between the field reference sample collected after the experiment from Lake Saravesi from the depth of 2.0 m, and the experimental clams originating from Lake Saravesi at a depth of 2.0 m (and kept at a depth of 2.0 m in Lake Saravesi), was not significant ($F_{1,56} = 1.110$, $P > 0.1$).

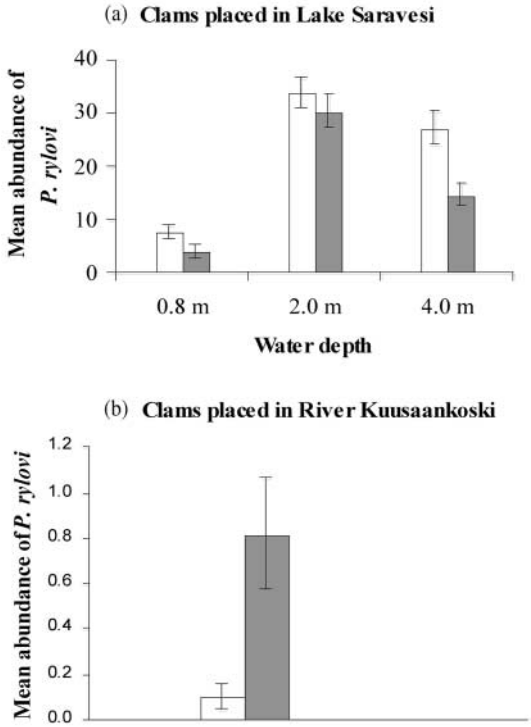

Fig. 1. Mean (± standard error) abundance of *Paraergasilus rylovi* in relation to (a) the place of origin and water depth in Lake Saravesi (open bars) and (b) the place of origin in River Kuusaankoski (grey bars). Error bars can be asymmetrical due to back-transformation from logarithmic values.

Among clams placed in River Kuusaankoski, the effect of place of origin on the abundance of *P. rylovi* was also statistically significant (Mann-Whitney $U = 148.500$, $P = 0.003$). Clams originally from River Kuusaankoski were parasitized by more *P. rylovi* than clams originally from Lake Saravesi (Fig. 1b). The effect of the blocking factor, basin, was not significant (Kruskal-Wallis, $\chi^2_4 = 7.880$, $P = 0.096$). The difference in the mean abundance of *P. rylovi* between reference samples collected after the experiment from River Kuusaankoski, and the experimental clams originating from and kept in River Kuusaankoski, was not significant (Mann-Whitney $U = 166.000$, $P > 0.1$).

The effect of place of origin on the proportion of *P. rylovi* females carrying egg sacs among the clams placed in Lake Saravesi was statistically significant (univariate ANOVA: $F_{1,137} = 14.888$, $P < 0.001$). The mean proportion (means calculated over each clam) of female *P. rylovi* carrying egg sacs was higher in clams originally from Lake Saravesi than clams originally from River Kuusaankoski (Fig. 2a). The effect of water depth was also significant ($F_{2,137} = 27.780$, $P < 0.001$), so that the mean proportion of female *P. rylovi* carrying egg sacs decreased with water depth (Fig. 2a). The effect of origin was similar at all depths, as indicated by the non-significant interaction between place of origin and water depth ($F_{2,137} = 1.296$, $P > 0.1$). However, the effect of the blocking factor, basin, on the mean proportion of *P. rylovi* females carrying egg sacs was significant ($F_{6,137} = 4.661$, $P < 0.001$). The difference in the mean proportion of *P. rylovi* females with egg sacs between the

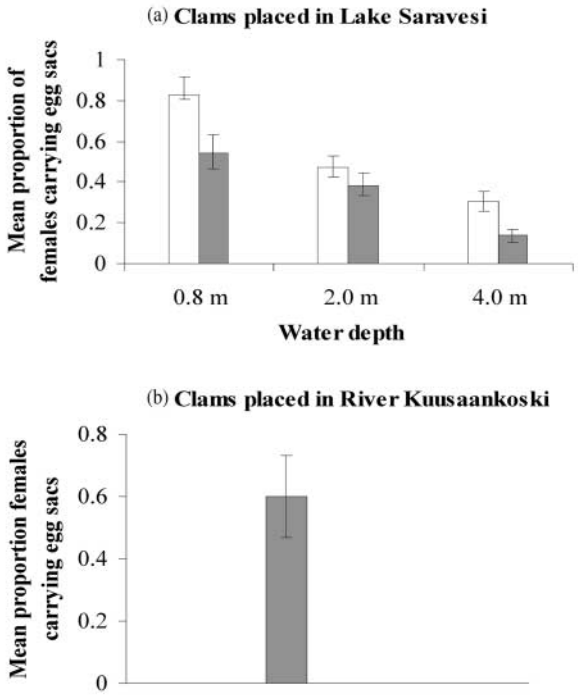

Fig. 2. Mean (± standard error) proportion of *Paraergasilus rylovi* females carrying egg sacs in relation to (a) the place of origin and water depth in Lake Saravesi (open bars) and (b) the place of origin in River Kuusaankoski (grey bars). In River Kuusaankoski, *P. rylovi* females did not produce egg sacs in clams originally from Lake Saravesi. Error bars can be asymmetrical due to back-transformation from logarithmic values.

reference sample collected after the experiment from Lake Saravesi from the depth of 2.0 m, and the experimental clams originating from Lake Saravesi at a depth of 2.0 m (and kept at a depth of 2.0 m in Lake Saravesi), was not significant ($F_{1,55} = 1.694$, $P > 0.1$)

Among clams placed in River Kuusaankoski, the effect of place of origin on the proportion of female *P. rylovi* carrying egg sacs was statistically significant (Mann-Whitney $U = 145.000$, $P < 0.001$). The mean proportion of female *P. rylovi* carrying egg sacs was higher in clams originally from River Kuusaankoski than clams originally from Lake Saravesi (Fig. 2b). The effect of the blocking factor, basin, on the proportion of *P. rylovi* females carrying egg sacs was not significant (Kruskal-Wallis, $\chi^2_3 = 2.162$, $P > 0.1$). The difference in the mean proportion of *P. rylovi* females with egg sacs between the field reference sample collected after the experiment from River Kuusaankoski, and the experimental clams originating from and kept in River Kuusaankoski, was not significant (Mann-Whitney $U = 78.000$, $P > 0.1$).

DISCUSSION

If parasites are locally adapted to their host, they should have, on average, higher infectivity and/or performance in the local host population than in a non-local host population

(Ebert, 1994; Ebert and Hamilton, 1996; Gandon and Van Zandt, 1998; Kaltz *et al.*, 1999). In the present reciprocal transplant experiment, both parasite infectivity and reproductive performance were higher among home-clams than among away-clams at both transplant sites. Thus, our results indicate that the crustacean parasite, *P. rylovi*, may be genetically specialized to the sympatric host populations – that is, locally adapted to its bivalve host, *A. piscinalis*. In addition, in Lake Saravesi, the infectivity and reproduction of the parasite were higher in home-clams regardless of the transplant habitat (depth), as indicated by the non-significant interactions between host origin and transplant depth. It is worth noting that *A. piscinalis* occurs densely in all three habitats used in the present study. The most significant difference between the habitats is that the shallowest one (0.8 m) is protected from wave action by macrophytes. This assumedly limits water currents that carry the infective stages of *P. rylovi*. That we did not find any interaction between host origin and habitat, even though the parasite abundances differed between the habitats, suggests that local adaptation may not be affected by the exposure rate, or dose of the parasite, in the present system. In addition, the non-significant interaction, in spite of the clear differences in egg production of the parasite between the habitats, indicates that local adaptation for infectivity may not be affected by the habitat-related differences in the performance of the parasite.

During the experiment, the clams were kept in the field in their natural habitats. A plastic basin filled one-third with sand provides an environment in which clams perform their natural crawling and burrowing behaviours, including variations in burrowing depth and angle (see Saarinen and Taskinen, 2003b). The density of clams in the present experiment, 100 and 111 individuals per square metre, is high but less than the maximal densities in the study areas. Even though natural conditions were the aim, the clams were probably disturbed by handling and temperature treatments. However, the results of a growth experiment on *A. piscinalis* using similar methods to the present study indicate that the growth of clams does not differ markedly from undisturbed control clams in the current experimental set-up (Taskinen, 1998). In addition, reference samples collected after the experiment did not differ from the experimental clams in the mean abundance of parasitism or in the mean proportion of female parasites carrying egg sacs. Therefore, we believe that the conditions experienced by the clams and the parasites in the present experiment were close to those they experience in their natural environment.

The results of the present experiment suggest that a new host–parasite combination – bivalve mollusc–ergasilid crustacean – can be added to the list of host–parasite associations in which local adaptation has been observed. However, our experimental design consisted of a reciprocal transplant between two populations, and therefore the results should be verified in the future by using more replicates.

According to simulation models, local adaptation is more likely in highly virulent parasites or when moderate virulence is combined with low migration by the parasite (Gandon *et al.*, 1996; Lively, 1999; Gandon, 2002; Gandon and Michalakis, 2002). The virulence of the parasite *P. rylovi* is unknown, but probably is not high at least when compared with castrating digeneans of the present host, *A. piscinalis* (see Taskinen and Valtonen, 1995). The parasite has a planctic larva, the nauplius, the migration of which relies on water currents. The host has a larval phase, the glochidium, which attaches to fish, such as roach, *Rutilus rutilus* (Negus, 1966). Roach perform spawning migrations in spring (Mills, 1991) during the period when glochidia attach to fish (Jokela *et al.*, 1991). Thus, the migration rate of the present parasite probably is not high when compared with that of the host. In some studies demonstrating parasite adaptation to local host populations, the parasite has been highly virulent (Ebert, 1994; Lively, 1989; Lively and

Dybdahl, 2000). It is possible that the local adaptation by the parasite observed in the present study was contributed to by a relatively low migration rate of the parasite, rather than a high virulence.

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