ADAPTATION VS. PHENOTYPIC PLASTICITY IN THE SUCCESS OF A CLONAL INVADER

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Abstract. The relative importance of plasticity vs. adaptation for the spread of invasive species has rarely been studied. We examined this question in a clonal population of invasive freshwater snails (*Potamopyrgus antipodarum*) from the western United States by testing whether observed plasticity in life history traits conferred higher fitness across a range of temperatures. We raised isofemale lines from three populations from different climate regimes (high- and low-elevation rivers and an estuary) in a split-brood, common-garden design in three temperatures. We measured life history and growth traits and calculated population growth rate (as a measure of fitness) using an age-structured projection matrix model. We found a strong effect of temperature on all traits, but no evidence for divergence in the average level of traits among populations. Levels of genetic variation and significant reaction norm divergence for life history traits suggested some role for adaptation. Plasticity varied among traits and was lowest for size and reproductive traits compared to age-related traits and fitness. Plasticity in fitness was intermediate, suggesting that invasive populations are not general-purpose genotypes with respect to the range of temperatures studied. Thus, by considering plasticity in fitness and its component traits, we have shown that trait plasticity alone does not yield the same fitness across a relevant set of temperature conditions.

Key words: adaptation; clonal reproduction; general-purpose genotypes; invasiveness; phenotypic plasticity; Potamopyrgus antipodarum; *reaction norm.*

INTRODUCTION

The success and rate of spread of an invasive species sometimes depends largely on ability to tolerate abiotic conditions (Kareiva el al. 1996, Moyle and Light 1996). The ability to survive and reproduce under a broad spectrum of environmental conditions through phenotypic plasticity should lead to a high probability of successful invasion in species with general-purpose genotypes (Baker 1965). Recent studies (Williamson 1996, Huey et al. 2000, Grosholz 2001, Garcia-Ramos and Rodriguez 2002, Lee 2002; reviewed in Stockwell et al. 2003) have also suggested that the spread of a successful invader might be due to adaptation to new environments given sufficient evolutionary potential. Plasticity is sometimes considered more important to invasiveness than adaptation (Barrett and Richardson 1986), but their relative importance in the history and process of colonization and spread has been studied rarely (Rice and Mack 1991*a, b,* Parker et al. 2003). Such knowledge could be useful in predicting and managing the invasion process. For example, a slow rate of adaptation may provide an opportunity for management intervention during the lag phase (Sakai et al. 2001, Stockwell et al. 2003).

Descriptive studies of the plasticity of a specific trait in manipulated environmental conditions, which are numerous, can reveal the reaction norm, or the level of environmental influence over the trait. However, such a study does not necessarily demonstrate that plasticity vs. adaptation facilitates invasions (Parker et al. 2003). The importance of adaptation could be examined using invasive populations originating across environmental gradients in common-garden environments, testing for divergence in average values and reaction norms for ecologically important traits. The adaptive nature of plasticity itself for invasiveness requires that trait plasticity is associated with low variance (a flat reaction norm) in fitness over a relevant range of environments, as expected for a general-purpose genotype to thrive in a range of conditions (Baker 1965). To our knowledge, this test has not been done for invasive species.

In this paper, we examine the relative importance of adaptation and phenotypic plasticity in the invasion dynamics of the freshwater snail *Potamopyrgus antipodarum*, an invader in Europe, Australia, and North America. The spread of this snail should be hindered by a lack of both genetic variation and generalist traits. Introduced populations of this species are composed of females and hence reproduce clonally by apomictic parthenogenesis (Wallace 1992). In North America and Europe, widespread *Potamopyrgus* populations are

PLATE 1. The snail *Potamopyrgus antipodarum* on a rock taken from the bottom of the Firehole River in the Madison River watershed of Yellowstone National Park, Wyoming (USA). Photo credit: M. Dybdahl.

composed of a single clone as determined by allozyme genetic markers (M. Dybdahl and A. Emblidge, *unpublished data*). The ability of a single clonal female to begin a new population is an important colonization advantage (Barrett and Richardson 1986). However, an individual clone might possess limited genetic variation and evolutionary potential unless mutational variance has accumulated (Lynch and Gabriel 1983, Lynch 1985; reviewed in Lynch and Walsh 1998). In addition, there is little evidence in *Potamopyrgus* for the existence of general-purpose genotypes (sensu, Lynch 1984) among individual clones from native populations in New Zealand (Dybdahl and Lively 1995, Fox et al. 1996, Jokela et al. 1997, Jokela et al. 1999, Negovetic and Jokela 2001, Jokela et al. 2003).

Here, we use a laboratory common-garden study of clonal sublines from three western U.S. populations of *Potamopyrgus* that differ in exposure to average temperatures and seasonal temperature fluctuations. We examine (1) adaptation to each site in terms of life history traits and their reaction norms, (2) evolutionary potential as genetic variation among clonal sublines, and (3) the extent of plasticity in life history traits and whether this plasticity confers high fitness across three temperatures. We found that there was a small amount of genetic variation for growth and life history traits, but no evidence for divergence in the average value of these traits among the three populations, and little evidence for reaction norm divergence. However, we found significant plasticity in some fitness components and in fitness itself. These results are inconsistent with the

model of invasive spread by general-purpose genotypes, whereby high fitness would be expected across environmental conditions in the new range.

METHODS

Study system

Potamopyrgus antipodarum is a prosobranch snail native to lakes and rivers of New Zealand. This species is dioecious and females produce crawl-away juveniles from a brood chamber. In New Zealand, female snails are either obligately sexual (diploid) or apomictic parthenogens (triploid clones; Wallace 1992, Dybdahl and Lively 1995). Introduced populations are entirely clonal, and few males are known from European (Wallace 1992) and North American populations (M. Dybdahl, *unpublished data*). Females reach maturity in about six to nine months (see Fig. 2).

Potamopyrgus is locally abundant in western U.S. rivers from six disparate invasion foci ranging from Oregon to Montana to Arizona (see Plate 1). These six locations include national parks (Yellowstone, Grand Canyon), rivers with economically important trout fisheries, and the range of five threatened or endangered snails and other narrow endemic snails in the intermountain west (Federal Register 1992, Hershler 1998). *Potamopyrgus* first appeared in North America in the Snake River in central Idaho in 1985, a second population was discovered in 1994 in the Madison River in Yellowstone National Park, Wyoming, and a third population was discovered in 1996 in the estuary of

the Columbia River in Oregon (Zaranko et al. 1997). All populations share an identical six-locus allozyme genotype, and are noncontiguous. This same six-locus genotype is found in Victoria, Australia, which along with DNA sequence similarity suggests that Australia is the source of this invasion (M. Dybdahl and A. Emblidge, *unpublished data*). Since the Australian populations are about 100 years old (at least 200 generations), this clone likely accumulated genetic diversity through mutation accumulation, some of which might have been introduced to the U.S. populations.

Study populations and collections

We collected snails in September 1999 from sites that differ in environmental conditions including temperature (Appendix A): the Snake River near Grandview, Idaho; the Madison River near West Yellowstone, Wyoming; and the Columbia River estuary near Hammond, Oregon. The Snake River site water temperatures vary from a mean of 22.6°C in August to 5.0°C in January. In contrast, Madison River water temperatures averaged 20.9°C in August and 8.4°C in January, due to geothermal input (see also Goldstein 1999). The Columbia River estuary site has cool year-round temperatures due to ocean influence (means of 13.3°C in August and 7.8°C in January), and salinities fluctuate widely (0–32‰).

Common-garden experiment

We conducted a common-garden experiment in the laboratory at three temperatures (12°C, 18°C, and 24°C). We varied the temperature for the following reasons. Climatic conditions are comparatively stable in the source range of the western U.S. clone in southern Australia (Quinn et al. 1996, Schreiber et al. 1998). Since temperature typically influences reproduction and population dynamics in poikilotherms, and specifically in *Potamopyrgus* (Winterbourn 1970, Okland 1979, 1983, Hylleberg and Siegismund 1987, Quinn et al. 1994), we reasoned that invasion dynamics might depend on the range of thermal performance.

To initiate clonal sublines, thirty snails from each population were collected and maintained in the laboratory individually in 5-oz clear plastic cups (maternal generation). Cups were housed in an environmental chamber at a constant temperature of 18°C for at least one month. Water in the cups was changed from an artificial pond system in our laboratory and 0.0166 mg of *Spirulina* in solution was added three times per week. Cups were checked each week for the presence of offspring (first laboratory generation, F_1), and all embryos would have developed during the laboratory holding period. Offspring were placed in a new cup, and all offspring from the same female were housed together for the first month. In a split-brood design, offspring of each female were individually housed in separate cups and randomly assigned to one of three temperatures (12°C, 18°C, and 24°C). Snails in the 12°C

and 18°C treatments were placed in environmental chambers; those in the 24°C treatment were placed in the 18°C chamber on heated pads. The photoperiod for all snails was 12L:12D.

The shell length of F_1 snails was measured monthly (to nearest 0.1 mm) until they reached a size of 3.0 mm. At this point, snails were measured weekly and examined for the presence of brooding offspring (visible through the shell) and the number of crawl-away offspring within the cup (which were removed). Therefore, each snail was assessed for weekly growth increments, age and size at first offspring, and the rate of offspring produced (offspring per week), and the total number of offspring produced. After at least two months of reproduction, observations of individuals from the F_1 generation were terminated.

Statistical analyses

In order to examine differences in the growth traits, we employed a curve-fitting analysis (Khattre and Naik 1999, Juliano 2001) that uses a nonlinear least-squares regression to estimate the parameters for individual growth curves (Proc NLIN, Gauss-Newton method, SAS Version 8.1, SAS Institute, Cary, North Carolina, USA). *Potamopyrgus* shell length follows a logistic pattern of growth, reaching an asymptotic size near the age at which they start producing offspring (Winterbourn 1970, Jokela et al. 1999). Therefore, we fitted curves to the equation $Y = \alpha/(1 + \exp[-\beta \cdot (X - \delta)])$, where Y is the length of the snail at a given age, X is the age of the snail, α is the asymptotic size, β is the growth rate of the snail, and δ is the age at which the snail had achieved 50% of its asymptotic size (the inflection point of the curve). The parameter estimates (α, β, δ) were obtained for each individual in our population and analyzed using MANOVA (Proc GLM, Type III Sums of Squares, SAS Version 8.1) to test for the effect of population, temperature (fixed effects) and their interaction, maternal line (random effect nested within population) and its interaction with temperature.

Nested mixed-model ANOVA and ANCOVA were used to analyze life history traits (age and size at first reproduction, total offspring production, and reproduction rate; Proc GLM, Type III Sums of Squares, SAS Version 8.1). Population and temperature were fixed main effects and maternal line was a random effect. For total offspring production, the interval in weeks over which reproduction was recorded was used as a covariate. For reproduction rate (number of offspring per week), age at death was used as a covariate to account for variation in fertility across age classes. Snails reared at 24°C were not included in the analysis of life history traits because few individuals reproduced at that temperature. A significant effect of temperature would demonstrate a plastic response. A significant effect of population would indicate divergence in the average traits among populations, whereas a significant

population × temperature interaction would indicate divergence among populations in the norms of reaction.

Genetic variation

To complement the ANOVA for maternal line effects, we also estimated variance components and heritabilities for the four life history traits as an estimate of evolutionary potential. The variance among clonal maternal lines estimates the genetic variance within a population, V_G, whereas the variance among offspring within a maternal line estimates random environmental variance, V_E. Variance components and their 95% confidence intervals were obtained through restricted maximum-likelihood (REML) using Proc MIXED (SAS Version 8.1). Population was included as a fixed main effect, and analyses were performed separately for each temperature. REML does not include information about fixed effects in its estimation of variance components (population, in this data set), and wide confidence intervals using REML are not uncommon for unbalanced designs (such as ours). Nevertheless, estimates tend to be accurate (Shaw 1987). From these values, the broad-sense heritability, H^2, was calculated using the formula $H^2 = V_G/(V_G + V_E)$ (Lynch and Walsh 1998).

Fitness variation

We estimated fitness as the growth rates (λ) for each population at each temperature using age-specific projection matrices (Caswell 2001). We used age-specific mortality and fecundity from our lab-reared snails at each temperature with month as the unit of time. Our estimate of λ is intended to illustrate relative thermal performance, rather than expected fitness in nature. Because few snails in this experiment survived past age 10 months (snails were terminated after two months of reproduction), we set the age-specific survival at month 11 to zero. In order to test the hypothesis that traits related to fitness are more variable than population growth rate, we calculated the unbiased coefficient of variations (CV) for each population across temperatures for the life history traits and growth parameters and their associated standard errors as $CV_{ADJ} = (1 + [1/4n])(100\sigma/\bar{x})$, $SE = [1 + (1/4n)][CV/(2n)^{-1/2}]$ (Sokal and Rohlf 1995). We then compared the average across populations of these coefficients of variation to the average CV for λ from the three populations using a one-sample t test against the expected mean (Sokal and Rohlf 1995). We predicted that the CV for λ of a widely successful invader would be smaller than the CV for life history traits, leading to a one-tailed test.

RESULTS

Growth parameters

Temperature had a large and significant effect on growth parameter estimates (Pillai's Trace = 0.592, F = 22.17, P = 0.0001; Appendix B). As temperature increased, snails reached a smaller maximum size, had

a faster rate of growth, and reached 50% of asymptotic size at a younger age (Appendix C). In general, growth curves for all three populations clustered within temperature, but Columbia River snails raised at 24°C were one notable exception. Consequently, we detected significant differences in the responses of the three populations to temperature (MANOVA population × temperature interaction, Pillai's Trace = 0.154, F = 2.15, P = 0.0131). Population effects were also significant for growth traits (Pillai's Trace = 0.079, F = 2.16, P = 0.0463); however by dropping the 24°C treatment and including maternal line in the model, only the population × temperature interaction remained significant (Pillai's Trace = 0.57, F = 2.93, P = 0.0172).

In order to explore the significant population × temperature interaction further, we conducted univariate contrasts of the individual parameter estimates among populations within temperatures. For asymptotic size, Madison River snails reached a significantly larger size than Snake River snails at 18°C (P = 0.0111; Fig. 1A). For the growth rate parameter, Columbia River estuary snails grew significantly slower than Snake River snails at 24°C (P = 0.0214) as did the Madison River snails (P = 0.0441; Fig. 1B). Finally, age at 50% asymptotic size was significantly later for Columbia River snails at 24°C than for Snake River snails (P = 0.0070), and was marginally, but not significantly, later than Madison River snails (P = 0.0585; Fig. 1C).

To examine the potential for a response to selection in the traits or their norms of reaction, we examined the maternal line effects for growth parameters. For this analysis we used the 12°C and 18°C treatments due to limited replication of maternal lines at 24°C. Neither maternal line nor the maternal line × temperature interaction had a significant effect on growth parameters (Appendix C).

Life history traits

Temperature treatment had a significant effect on three of the four life history traits. The majority of snails did not reproduce at 24°C (this treatment was dropped from this statistical analysis). Snails reproduced earlier and at smaller size, and produced more offspring at 18°C than at 12°C (Fig. 2A–C). Temperature had a significant effect on size at first reproduction (P = 0.0007) and total offspring production (P = 0.0007), but had a highly significant effect on age of first offspring (P < 0.0001, Appendix D). Snails from all populations delayed reproduction at the cooler temperature by about fifty days (Fig. 2B).

The main effect of population was not significant for any life history traits, but the response to temperature of three of the life history traits differed among the three populations, indicating differentiation of reaction norms (Appendix D). For size at first reproduction, there was a significant population × temperature interaction (P = 0.0053, Fig. 2A); univariate contrasts revealed that the Snake River population reproduced
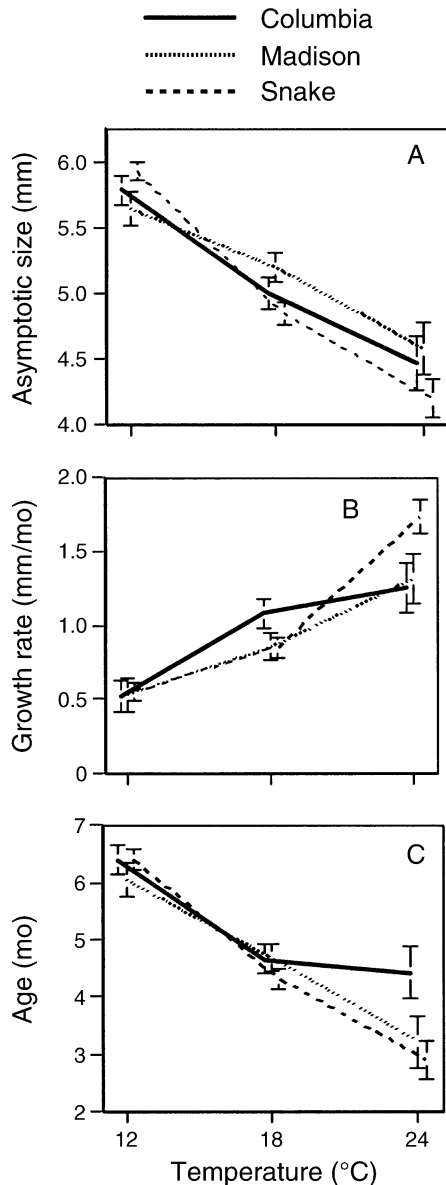
FIG. 1. Comparison of growth parameters for all three river populations at 12°C, 18°C, and 24°C showing least-square means (±SE): (A) asymptotic size; (B) growth rate; (C) age at 50% of asymptotic size.

at a significantly smaller size at 18°C than Columbia River estuary ($P = 0.0317$) and Madison River ($P = 0.0055$) populations. For total offspring production (population × temperature effect, $P = 0.014$), the Columbia River population produced significantly more offspring at 18°C than 12°C but the opposite was true for the other populations ($P = 0.0002$; Fig. 2C). For reproduction rate, we detected a significant population × temperature effect ($P = 0.0269$). Snake River had a significantly lower reproduction rate at 18°C ($P = 0.0133$) than at 12°C. Madison River also had a lower reproduction rate at 18°C, though it was nonsignificant.

Columbia River showed the opposite trend, and at 18°C had a significantly higher reproduction rate than Madison River ($P = 0.0254$), and a marginally nonsignificant higher reproduction rate than Snake River ($P = 0.0794$, Fig. 2D).

A maternal line effect, suggestive of selectable among-line genetic variation, was detected for two of the four traits (Fig. 3; see also Appendix D). For size at first reproduction, there was a significant ($P = 0.0493$) effect of maternal line. For age at first reproduction, we detected a significant maternal line × temperature interaction ($P = 0.0007$), indicating maternal lines varied according to the temperature treatment.

Genetic variation

Variance component estimations varied widely, but yielded low estimates of heritability (<0.30) for all traits (Table 1). There was no detectable genetic variation, V_G, present for age at first reproduction, and H^2 estimates were also low for size at first reproduction. Genetic variation, V_G, for total offspring production varied between temperatures, such that heritability was quite low at 18°C but quite high at 12°C. Reproduction rate had the highest levels of genetic variance, with H^2 estimates at 0.21 and 0.12 for 12°C and 18°C, respectively.

Fitness variation

Population growth rates (λ) varied among temperatures but varied little among populations within temperatures (Fig. 4). The highest estimates of population growth rate for all populations were measured in the 18°C treatment (range of λ 1.51–1.59), followed by 12°C (range 1.29–1.38) and 24°C (range 0.93–1.28). It is likely that there was greater variance for 24°C because calculations were based on relatively few reproducing individuals.

We compared the coefficient of variation for population growth rate with that of other growth and life history traits to examine the relative level of plastic variation in total fitness across temperature environments. Of the seven traits, four were less variable than population growth rate, one significantly so (Table 2). These traits were related to size and fecundity (size at asymptotic size, first reproduction, total offspring production, and reproduction rate). Three age-related traits were more variable, one of which significantly so (growth rate, age at 50% maximum size, and age at first reproduction).

DISCUSSION

Plasticity is widely cited as a cause of invasion success, but its role relative to adaptation in determining invasion dynamics is known for few invasive species. We studied this issue in the clonal freshwater snail *Potamopyrgus* in western North America. We found that heritabilities for several traits were nonzero, but there was no evidence for local adaptation in the av-
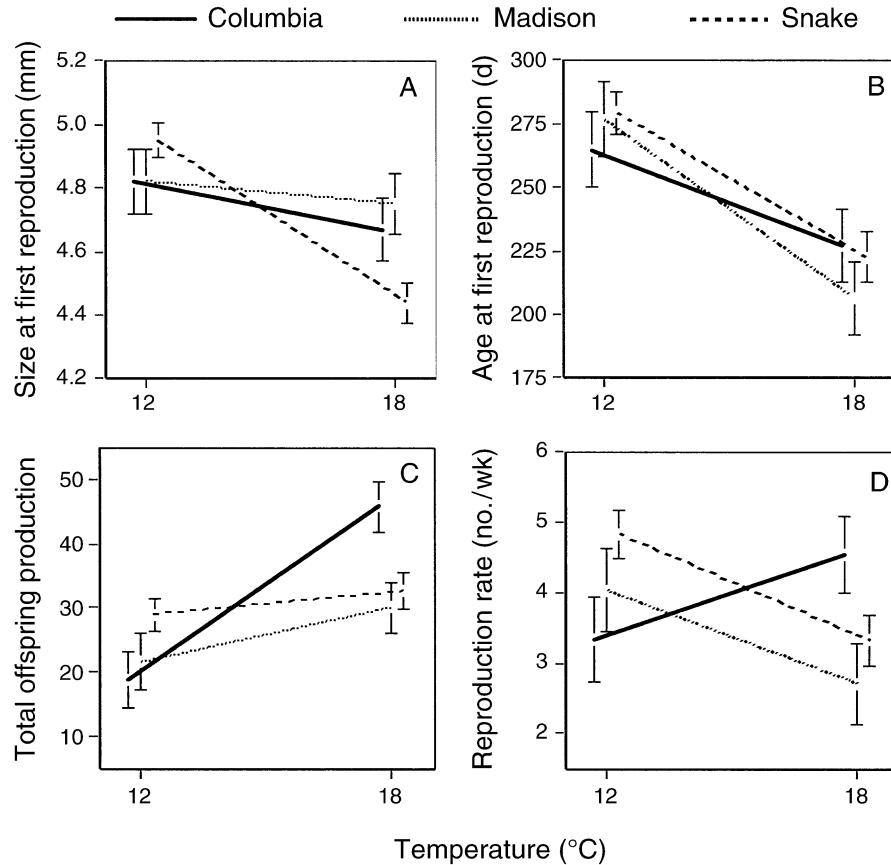
FIG. 2. Life history traits of Columbia River estuary, Madison River, and Snake River snails. Values presented are least-square means ($\pm$SE). (A) Snail length at first reproduction; (B) snail age at first reproduction; (C) total number of offspring produced; (D) rate of reproduction (number of offspring per week).

erage value of life history traits. Evolutionary change in reaction norms might have played a role in invasion success, based on the divergence in reaction norms for several traits. The observed phenotypic plasticity in fitness was higher than plasticity for size-related life history traits, but lower than plasticity for age-related traits. This result suggests that plasticity in life history and growth traits facilitates invasiveness but is inconsistent with a general-purpose genotype model that predicts high fitness (and low fitness variation) across environments.

Evolutionary potential in a clonal population is possible if it is composed of numerous lineages of distinct origins, or possesses quantitative genetic variation owing to the accumulation of mutations (Lynch 1985; reviewed in Lynch and Walsh 1998). Equilibrium levels of mutational variance can accumulate in as few as 60 generations (Lynch and Gabriel 1983). Populations of the clone of *Potamopyrgus* studied here are likely to have descended from Australian populations (M. Dybdahl and A. Emblidge, *unpublished data*) that were founded before 1895 (Ponder 1988, Zaranko et al. 1997), making this clone at least 100 years old. The amount of genetic variation captured from the ancestral population by the colonist group that established the western U.S. population is unknown. Nevertheless, there have been at least 15 years (at least 30 generations) since the founding of the U.S. population for further variance accumulation. Furthermore, population sizes as high as 750 000/m² in the western United States (Hall et al. 2003) increase the likelihood of the accumulation of mutational variance. Consistent with this context, we found significant maternal line effects for life history traits and nonzero heritabilities. The potential for evolution of the reaction norm for age at first reproduction was indicated by the significant maternal line × temperature interaction. Finally, a clone identified by slowly evolving allozyme characters is likely to accumulate mutational variation at polygenic life history traits. This evolutionary potential of an invading population may provide for continual adaptation during spread (Sakai et al. 2001, Garcia-Ramos and Rodriguez 2002).

Although we found evidence for low levels of genetic variation for life history traits in a clone, we found little evidence for a response in life history trait means among populations inhabiting distinct environments. In other aquatic species introductions, evolutionary di-
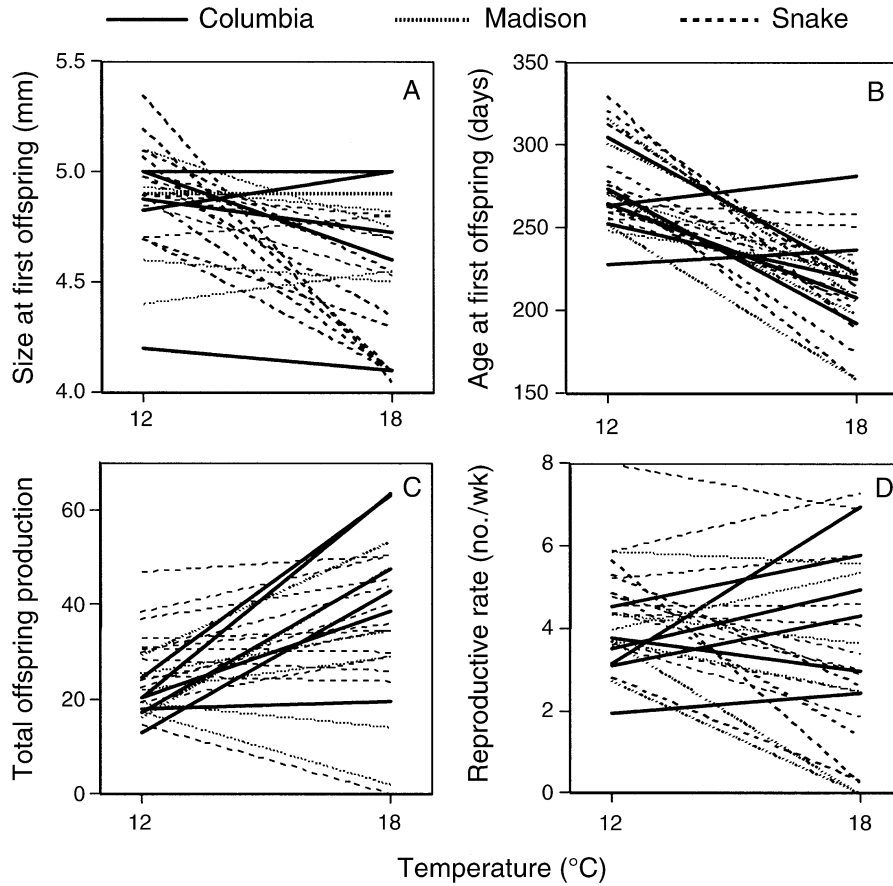
FIG. 3. Life history traits for each maternal line from the Columbia River estuary, Madison River, and Snake River populations. Values are least-square means.

vergence among populations in reaction norms has been observed across heterogeneous environments (e.g., Hendry et al. 1998, Haugen and Vollestad 2000). Consistent with this expectation, we found significant population × temperature interactions for some traits, suggesting that these snail populations responded differently to changes in temperature. These differences could be due to residual maternal environmental effects, and comparisons of individuals after several generations in a common environment would be required

to resolve this question. Nevertheless, the observed reaction norms for growth parameters are reasonable because Columbia River estuary snails, which experience cooler summer temperatures than the other populations, showed much slower growth at 24°C than other populations.

Plasticity of life history phenotypes can be adaptive if it allows organisms to inhabit a wider range of environmental conditions than those with nonplastic phenotypes (Schlichting 1986, Scheiner 1993), yet our re-

TABLE 1. Restricted maximum-likelihood (REML) point estimates of variance component (V_G and V_E) and heritability (H^2) estimates for life history traits, by temperature, for *Potamopyrgus antipodarum*.

Trait	Temperature (°C)	V_G	V_E	H^2
Size at first reproduction	12	0.04667	7.79	0.01
	18	1.435	7.70	0.16
Age at first reproduction	12	77.97	747.23	0.09
	18	39.21	757.01	0.05
Total offspring	12	30.89	68.92	0.31
	18	64.62	637.44	0.09
Reproduction rate	12	0.3453	1.25	0.22
	18	0.1024	11.96	0.01

Note: V_G, genetic variance; V_E, environmental variance.
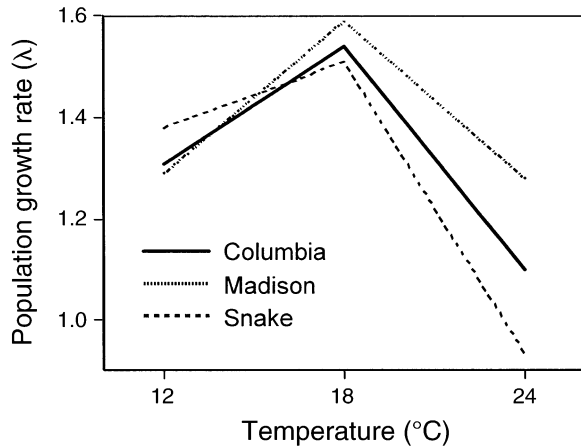
FIG. 4. Estimates of population growth rates (λ) for the three populations, indicating that the fitness peaks at 18°C.

sults suggest that growth and life history plasticity does not preserve high fitness across the full range of temperature conditions studied. As a species, *Potamopyrgus* seems to have wide temperature tolerances (from 0°C to 32°C) measured in terms of LD_{50} (Hylleberg and Siegismund 1987, Quinn et al. 1994, Cox 2000). Our results suggest that the suitable temperature range for successful invasion of the western U.S. clone is much narrower. Lower temperatures caused slower rates of development and lower fecundity than higher temperatures, but had a weaker effect on size at maturity (Figs. 1 and 2). Hence, overall fitness showed a peak at 18°C and declined at cooler and warmer temperatures. Consistent with our results, a reciprocal transplant experiment suggested that the survival and reproduction rates of clones can be quite plastic with respect to habitat use and thereby limit invasiveness across habitats (Negovetic and Jokela 2001).

It is not surprising that the range of environmental conditions suitable for a population comprising a single clone would be narrower than the range for its sexual ancestors (Vrijenhoek 1979, Case and Taper 1986; reviewed in Vrijenhoek 1998). Most individual clones of *Potamopyrgus* seem to have narrow distributions, being restricted to single lakes (Dybdahl and Lively 1995) and habitat conditions (Fox et al. 1996, Jokela et al. 1999). Hence, in New Zealand, clonal populations are able to occupy a range of habitats because of high clonal diversity. These patterns are inconsistent with the general-purpose genotype model (Dybdahl and Lively 1995, Jokela et al. 1997, 2003). On the other hand, colonization of continental Europe by one of three clones identified by morphological and molecular markers (Ponder 1988, Hauser et al. 1992, Jacobson et al. 1996; M. Dybdahl, *unpublished data*) suggests that general-purpose genotypes may exist (Jacobson and Forbes 1997) or have evolved in the process of colonization (Jokela et al. 2003). The wide distribution of

the western U.S. *Potamopyrgus* clone also might be explained by plasticity if it is adaptive for invasiveness.

Some forms of plasticity can be explained under a model of physical and chemical constraints (Gotthard and Nylin 1995), but plasticity would be considered adaptive for invasion if it increases the demographic success of an invader across environmental gradients (Parker et al. 2003). A general-purpose genotype invader would be expected to have high fitness and minimal fitness plasticity (flat reaction norms) over a range of environmental conditions, which translates into a lower variance in fitness. For the western U.S. clone of *Potamopyrgus*, plasticity was higher for age traits than for size and reproductive traits, indicating that this clone delayed maturity to begin reproduction at a larger size rather than at a given age. Plasticity for fitness (as indicated by the CV for λ) was intermediate; it was lower than age-related traits, but higher than size and fecundity traits (Table 2). The nonflat reaction norm for fitness is inconsistent with the general-purpose genotype model, such that invasion dynamics would vary across the set of temperatures tested here.

In conclusion, a single clonal lineage should possess limited capacity for invasive spread across heterogeneous environmental conditions, a proposition that is supported by studies of a clonal invader *Potamopyrgus* in its native range. For widespread monoclonal invasive populations of this species, we compared genetically based variation and plasticity in fitness and its component traits to examine the role of plasticity and adaptation in invasion success. We found that genetic variation for life history traits and divergence in their reaction norms could contribute to adaptation during invasion. More importantly, several fitness components exhibited weaker plastic responses across temperature conditions compared to the plastic responses in overall fitness. The observed fitness plasticity is inconsistent with the model of invasive spread by general-purpose

TABLE 2. Coefficients of variation (CV) across temperature treatments for population growth rate (λ), three individual growth parameters, and four fitness components.

Parameter	CV	t	P
Population growth rate (λ)	17.44		
Growth parameters			
Asymptotic size	15.91	0.274	0.3988
Growth rate	53.61	2.722	**0.0264**
Age at 50% maximum size	33.89	1.832	0.0705
Fitness components			
Age at first reproduction	26.98	1.076	0.1804
Size at first reproduction	5.27	2.219	0.0566
Total offspring production	0.63	3.166	**0.0253**
Reproduction rate	12.73	0.750	0.2539

Note: Coefficients of variation for growth parameters (N_2 = 3) and fitness components (N_2 = 2) were compared to that for population growth rate (N_1 = 3) using a t distribution (df = N_1 + N_2 − 2). Boldface type indicates statistical significance ($P < 0.05$).

genotypes, whereby high fitness would be expected across environmental conditions in the new range. Hence, trait plasticity alone does not yield the same fitness and invasiveness across a relevant set of temperature conditions.

LITERATURE CITED

Baker, H. G. 1965. Characteristics and modes of origin of weeds. Pages 147–168 in H. G. Baker and G. L. Stebbins, editors. The genetics of colonizing species. Academic Press, New York, New York, USA.

Barrett, S. C. H., and B. J. Richardson. 1986. Genetic attributes of invading species. Pages 21–33 in R. H. Groves and J. J. Burdon, editors. Ecology of biological invasions, an Australian perspective. Australian Academy of Science, Canberra, Australia.

Case, T. J., and M. L. Taper. 1986. On the coexistence and coevolution of asexual and sexual competitors. Evolution 40:366–387.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. Sinauer, Sunderland, Massachusetts, USA.

Cox, T. J. 2000. Thermal tolerances of two stream invertebrates exposed to diurnally varying temperature. New Zealand Journal of Marine and Freshwater Research 34(2): 203–208.

Dybdahl, M. F., and C. M. Lively. 1995. Diverse, endemic and polyphyletic clones in mixed populations of a freshwater snail (Potamopyrgus antipodarum). Journal of Evolutionary Biology 8:385–398.

Federal Register. 1992. Endangered and threatened wildlife and plants: determination of endangered or threatened status for five aquatic snails in south central Idaho. Volume 57. Number 240.

Fox, J. A., M. F. Dybdahl, J. Jokela, and C. M. Lively. 1996. Genetic structure of coexisting sexual and clonal subpopulations in a freshwater snail (Potamopyrgus antipodarum). Evolution 50:1541–1548.

Garcia-Ramos, G., and D. Rodriguez. 2002. Evolutionary speed of species invasions. Evolution 56:661–668.

Goldstein, J. N. 1999. Effects of geothermal effluents on rainbow trout and brown trout in the Firehole River, Yellowstone National Park, Wyoming. Thesis. University of Wyoming, Laramie, Wyoming, USA.

Gotthard, K., and S. Nylin. 1995. Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. Oikos 74:3–17.

Grosholz, E. 2001. Small spatial-scale differentiation among populations of an introduced colonial invertebrate. Oecologia 129:58–64.

Hall, R. O., J. Tank, and M. F. Dybdahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Frontiers in Ecology and the Environment 1: 407–411.

Haugen, T. O., and L. A. Vollestad. 2000. Population differences in early life history traits in grayling. Journal of Evolutionary Biology 13:897–905.

Hauser, L., G. R. Carvalho, R. N. Hughes, and R. E. Carter. 1992. Clonal structure of the introduced freshwater snail Potamopyrgus antipodarum (Prosobranchia: Hydrobiidae),

as revealed by DNA fingerprinting. Proceedings of the Royal Society of London 249:19–25.

Hendry, A. P., J. E. Hensleigh, and R. R. Reisenbichler. 1998. Incubation temperature, developmental biology, and the divergence of sockeye salmon. Canadian Journal of Fisheries and Aquatic Science 55:1387–1394.

Hershler, R. 1998. A systematic review of the hydrobiid snails (Gastropoda: Rissooidea) of the Great Basin, western United States. Part I. Genus Pyrgulopsis. Veliger 41:1–132.

Huey, R. B., G. W. Gilchrist, M. L. Carlson, D. Berrigan, and L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science 287:308–309.

Hylleberg, J., and H. R. Siegismund. 1987. Niche overlap in mud snails (Hydrobiidae): freezing tolerance. Marine Biology 94:403–407.

Jacobsen, R., and V. E. Forbes. 1997. Clonal variation in life history traits and feeding rates in the gastropod, Potamopyrgus antipodarum: performance across a salinity gradient. Functional Ecology 11:260–267.

Jacobsen, R., V. E. Forbes, and O. Skovgaard. 1996. Genetic population structure of the prosobranch snail Potamopyrgus antipodarum (Gray) in Denmark using PCR-RAPD fingerprints. Proceedings of the Royal Society of London B 264: 1065.

Jokela, J., M. F. Dybdahl, and C. M. Lively. 1999. Habitat-specific variation in life history traits, clonal population structure, and parasitism in a freshwater snail (Potamopyrgus antipodarum). Journal of Evolutionary Biology 12: 350–360.

Jokela, J. C., M. Lively, M. F. Dybdahl, and J. A. Fox. 2003. Genetic variation in sexual and clonal lineages of a freshwater snail. Biological Journal of the Linnean Society 79: 165–181.

Jokela, J., C. M. Lively, J. A. Fox, and M. F. Dybdahl. 1997. Flat reaction norms and ''frozen'' phenotypic variation in clonal snails (Potamopyrgus antipodarum). Evolution 51: 1120–1129.

Juliano, S. A. 2001. Non-linear curve fitting: predation and functional response curves. Pages 178–196 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Oxford University Press, New York, New York, USA.

Kareiva, P., I. M. Parker, and M. Pascual. 1996. Can we use experiments and models in predicting the invasiveness of genetically engineered organisms? Ecology 77:1670–1675.

Khattre, R., and D. N. Naik. 1999. Applied multivariate statistics with SAS software. Second edition. SAS Institute, Cary, North Carolina, USA.

Lee, C. E. 2002. Evolutionary genetics of invasive species. Trends in Ecology and Evolution 17(8):386–391.

Lynch, M. 1984. Destabilizing hybridization, general purpose genotypes and geographic parthenogenesis. Quarterly Review of Biology 59:257–290.

Lynch, M. 1985. Spontaneous mutations for life history characters in an obligate parthenogen. Evolution 39:804–818.

Lynch, M., and W. Gabriel. 1983. Phenotypic evolution and parthenogenesis. American Naturalist 122:745–764.

Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer, Sunderland, Massachusetts, USA.

Moyle, P. B., and T. Light. 1996. Fish invasions in California: do abiotic factors determine success? Ecology 77:1666–1670.

Negovetic, S., and J. Jokela. 2001. Life history variation, phenotypic plasticity, and subpopulaiton structure in a freshwater snail. Ecology 82:2805–2815.

Okland, J. 1979. Distribution of environmental factors and fresh-water snails (Gastropoda) in Norway: use of European invertebrate survey principles. Malacologia 18:211–222.

Okland, J. 1983. Factors regulating the distribution of freshwater snails (Gastropoda) in Norway. Malacologia **24**:277–288.

Parker, I. M., J. Rodriguez, and M. E. Loik. 2003. An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. Conservation Biology **17**:59–72.

Ponder, W. F. 1988. *Potamopyrgus antipodarum*, a molluscan colonizer of Europe and Australia. Journal of Molluscan Studies **54**:271–286.

Quinn, G. P., P. S. Lake, and E. S. B. Schreiber. 1996. Littoral benthos of a Victorian lake and its outlet stream: spatial and temporal variation. Australian Journal of Ecology **21**:292–301.

Quinn, J. M., G. L. Steele, C. W. Hickey, and M. L. Vickers. 1994. Upper thermal tolerances of twelve New Zealand stream invertebrate species. New Zealand Journal of Marine and Freshwater Research **28**:391–397.

Rice, K. J., and R. N. Mack. 1991*a*. Ecological genetics of *Bromus tectorum*. II. Intraspecific variation in phenotypic plasticity. Oecologia **88**:84–90.

Rice, K. J., and R. N. Mack. 1991*b*. Ecological genetics of *Bromus tectorum*. III. The demography of reciprocally sown populations. Oecologia **88**:91–101.

Sakai, A. K., et al. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics **32**:305–332.

Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. Annual Review of Ecology and Systematics **24**:35–68.

Schlichting, C. 1986. The evolution of phenotypic plasticity in plants. Annual Review of Ecology and Systematics **17**:667–693.

Schreiber, E. S. G., A. Glaister, G. P. Quinn, and P. S. Lake. 1998. Life history and population dynamics of the exotic snail *Potamopyrgus antipodarum* (Prosobranchia; Hydrobiidae) in Lake Purrumbete, Victoria, Australia. Australian Journal of Marine and Freshwater Research **49**:73–78.

Shaw, R. G. 1987. Maximum-likelihood approaches applied to quantitative genetics of natural populations. Evolution **41**:812–826.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. W. H. Freeman, New York, New York, USA.

Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation biology. Trends in Ecology and Evolution **18**:94–101.

Vrijenhoek, R. C. 1979. Factors affecting clonal diversity and coexistence. American Zoologist **19**:787–797.

Vrijenhoek, R. C. 1998. Animal clones and diversity. BioScience **48**:617–628.

Wallace, C. 1992. Parthenogenesis, sex and chromosomes in *Potamopyrgus*. Journal of Molluscan Studies **58**:93–107.

Williamson, M. 1996. Biological invasions. Chapman and Hall, London, UK.

Winterbourn, M. J. 1970. Population studies on the New Zealand freshwater Gastropod, *Potamopyrgus antipodarum* (Gray). Proceedings of the Malacological Society of London **39**:139–149.

Zaranko, D. T., D. G. Farara, and F. G. Thompson. 1997. Another exotic mollusk in the Laurentian Great Lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae). Canadian Journal of Fisheries and Aquatic Sciences **54**:809–814.

APPENDIX A

A table of mean monthly temperatures (mean, minimum, and maximum) for the warmest and coldest months of the year for three sites, and salinity (mean, minimum, and maximum) for the Columbia River estuary is available in ESA's Electronic Data Archive: *Ecological Archives* E086-087-A1.

APPENDIX B

A table of MANOVA results for the growth parameters from the nonlinear curve-fitting model for snails from three populations is available in ESA's Electronic Data Archive: *Ecological Archives* E086-087-A2.

APPENDIX C

A figure of the fitted growth curves for all populations at 12°C, 18°C, and 24°C is available in ESA's Electronic Data Archive: *Ecological Archives* E086-087-A3.

APPENDIX D

Results of analyses of life history traits of three populations raised at two temperatures (12°C and 18°C) are available in ESA's Electronic Data Archive: *Ecological Archives* E086-087-A4.