Life-history Trait Variation in Native vs. Invasive Asexual New Zealand Mud Snails

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Abstract

Potamopyrgus antipodarum is a New Zealand freshwater snail that is invasive worldwide. While native *P. antipodarum* populations are characterized by frequent coexistence between obligately sexual and obligately asexual individuals, only the asexual snails are known to invade other ecosystems. Despite low genetic diversity and the absence of sex, invasive asexual *P. antipodarum* are highly successful. Here, we quantified variation in three key life-history traits across invasive *P. antipodarum* lineages and compared this variation to already documented variation in these same traits in asexual native lineages to provide a deeper understanding of why some lineages become invasive. In particular, we evaluated 1) if invasive lineages of *P. antipodarum* could be successful because they represent life-history variation from native ancestors that could facilitate invasion, and 2) if invasive populations with higher genetic variation would display relatively high phenotypic variation. We found that invasive snails displayed a non-representative sample of native diversity, with invasive snails growing more slowly and maturing more rapidly than their native counterparts. These results are consistent with expectations of a scenario where invasive lineages represent a subset of native variation that is beneficial in the setting of invasion. Nevertheless, there was no evidence for a relationship between genetic and phenotypic variation, indicating that increased genetic variation does not necessarily translate into greater phenotypic variation, and consistent with earlier studies suggesting an important role for phenotypic plasticity in the *P. antipodarum* invasion. Together, these results help illuminate the mechanisms driving the worldwide expansion of invasive populations of these snails.

Introduction

Biological invasions have become a worldwide problem as a consequence of the increased spread of non-native species via anthropogenic activities (Mallez and McCartney 2018). Some non-native species will be able to establish in the novel environment, becoming invasive species that can pose serious problems such as decreasing native biodiversity and altering ecosystem function, and with the potential for severe economic impacts (Sakai et al. 2001).

Species that are able to adapt more quickly to novel environments are more likely to become successful invaders (Colautti and Barrett 2013; Gozlan et al. 2020), with life-history trait (LHT) variation of particular potential relevance to invasion success (Dlugosch and Parker 2008a; Dlugosch and Parker 2008b; Li et al. 2015). In particular, high growth rate, rapid reproduction, and short life span - so-called R-selected traits (MacArthur and Wilson 1967; Bengtsson and Baur 1993) - tend to characterize invasive taxa (Sakai et al. 2001; Kimberling 2004), to the extent that Sakai et al. (2001) proposed that LHT variation across taxa could directly explain why some species become successful invaders while others do not.

While it seems clear that taxa with R-selected LHT are often more likely to be invasive, we know comparatively little about why some lineages *within* species become invasive while others do not (Sakai et al. 2001; Neiman and Krist 2016). Under the logic that the same principle of characterizing LHT variation can be applied within taxa to understand invasiveness (Hierro et al. 2006; Eriksen et al. 2012),

we evaluated intraspecific variation in LHT with respect to invasive status in a globally invasive New Zealand snail, *Potamopyrgus antipodarum*. These snails are destructive invaders, exemplified in the categorization of *P. antipodarum* as one of the “one-hundred worst” invasive species in Europe (Nentwig et al. 2018). Invasion success of *P. antipodarum* has been attributed to factors including high population growth rate and tolerance to a wide range of environmental conditions (Møller et al. 1994; Alonso and Castro-Diez 2008; Verhaegen et al. 2018a) and adaptive phenotypic plasticity (Kistner and Dybdahl 2013, 2014; Verhaegen et al. 2018a; Verhaegen et al. 2018b).

Invasive *P. antipodarum* populations can achieve densities up to 800,000 individuals/m² (Dorgelo 1987; Møller et al. 1994; McKenzie et al. 2013), which might help explain why and how *P. antipodarum* can alter invaded ecosystems. This effect has been especially well documented in Polecat Creek, Wyoming, USA, where invasive *P. antipodarum* are found at densities as high as 500,000/m² (Hall et al. 2006), consume 75% of primary production, and alter nutrient cycles (Hall et al. 2003). Invasive *P. antipodarum* also have the potential to disrupt native food webs, with evidence from California and Utah that native fish – including the endangered tidewater goby (*Eucyclogobius newberryi*) (Hellmair et al. 2011) and the rainbow trout (*Oncorhynchus mykiss*) (Vinson and Baker 2008) – are losing weight as a consequence of consumption of consuming *P. antipodarum*, which have low nutritional value.

Larkin et al. (2016) demonstrated substantial genetic variation for LHT phenotypes across native *Potamopyrgus antipodarum* asexual lineages (defined as all snails descended from a single asexual female), making this system a powerful candidate for assessing how intraspecific LHT variation might drive invasion success. These tiny New Zealand freshwater snails have invaded every continent except Antarctica and Africa in the last 200 years (Alonso and Castro-Diez 2012; Collado 2014). Although native-range *P. antipodarum* populations harbor sexual and asexual individuals, invasive *P. antipodarum* are exclusively asexual (Lively 1987; Alonso and Castro-Diez 2012). Similar to other invasive species, invasive *P. antipodarum* populations harbor low genetic diversity relative to the native range (Dybdahl and Drown 2011; Estoup et al. 2016; Verhaegen et al. 2018a; Donne et al. 2020). High genetic diversity has been thought to be associated with successful invasion, but the likelihood that genetic variation will often be lost via founder effects during colonization leads to a potential “genetic paradox”: successful invasion despite low genetic variation (Dlugosch and Parker 2008; Dybdahl and Drown 2011; Estoup et al. 2016). While phenotypic plasticity likely plays some role in invasion success for *P. antipodarum* (Kistner and Dybdahl 2013, 2014; Verhaegen et al. 2018a; Verhaegen et al. 2018b), the very low genetic diversity characterizing invasive populations of these snails makes *P. antipodarum* a powerful system to apply to the still-unresolved question of how species become successful invaders in the absence of genetic diversity (Dybdahl and Drown 2011; Estoup et al. 2016).

Here, we used a common-garden approach to quantify variation in LHT of individual growth rate, age at maturity, and size at maturity across invasive lineages in *P. antipodarum*. We compared the means and variances of these LHT to the data from the same traits characterized by Larkin et al. (2016) in a large set of asexual *P. antipodarum* from the native range in New Zealand. These comparisons allow us to assess whether and to what extent the trait values and variation in the invasive lineages reflects that of the

native snails. An outcome where the invasive snails consistently have LHT values that both reflect only a small fraction of the native range and are as expected under selection in a new habitat (e.g., for relatively rapid reproduction, early growth) is consistent with a scenario where selection favoring these phenotypes in the invaded range has played a major role. By contrast, if variation in invasive snails is similar to that of native snails and/or does not reflect expectations for selection in the invaded range, drift (including but not limited to founder effects) might be more likely than selection to be a primary evolutionary force in the invaded range (Keller and Taylor 2008). We also investigated whether genetic and phenotypic variation were associated across invasive *P. antipodarum* populations by using previously available SNP genotyping information for the invasive populations. A positive relationship between genetic and phenotypic variation would indicate that genetic variation could be relevant to invasive success. Regardless of particular outcomes, these comparisons between invasive and native ranges will provide insight into the mechanisms underlying invasion success of a destructive global invader.

Methods

We started by haphazardly selecting 40 asexual adult *P. antipodarum* females from each of seven laboratory cultures that were originally founded by single female *P. antipodarum* sampled from seven invasive populations in the United States and Belgium (Table 1). These “founding females” were isolated in individual one-liter cups filled with ~ 200 ml carbon-filtered tap water housed in a room held at 16°C. All snails were fed dried *Spirulina ad libitum*, which is standard for laboratory-cultured *P. antipodarum* (e.g., Zachar and Neiman, 2013). The three founding females from Lake Ontario (On) did not survive the initial experiment setup. We checked each of the remaining 37 founding female cups three times a week for newly born offspring (“G1”).

Table 1

Characteristics of founding females. These eight 36-locus SNP genotypes represent results from the same collections reported in Donne et al. (2020), which are also used in the present study.

Sampling Location	Sample ID	# Founding Females	# Founders that Reproduced	SNP Genotypes
Geraardsbergen, Belgium	Gb	8	2	328
Madison River, MO, USA	Md	8	6	327
Gunpowder Falls, MD, USA	Mr	5	5	327;333
Spring Creek, PA, USA	PA	5	4	327
Polecat Creek, WY, USA	Pc	6	4	327;332;338
Snake River, ID, USA	Sn	5	4	327;332;333; 338;339;341
Lake Ontario, NY, USA	On	3	0	328;336

For the first five G1s produced by each founding female, we recorded the date that each G1 was found and then isolated each G1 in an individual one-liter cup filled with ~ 200ml carbon-filtered water. We checked these G1 cups once a week until we observed calcification of the G1 shell, typically about a month after birth. We then measured the G1 to the nearest hundredth of a millimeter by placing the snail next to a ruler and taking a photo of the snail and ruler under a dissecting microscope. We then used ImageJ software to measure the length of each shell from the aperture to apex. We continued to check the G1 cups weekly, recording the date when a G1 reached 3 mm, which is considered the lower threshold of size for potential reproductive maturity for *P. antipodarum* females (McKenzie et al. 2013). We then continued to check G1 cups once a week for offspring (G2), and we recorded the date upon which the first G2 produced by each G1 was observed ("age at maturity"). On the day of first observation of G2 production, we again measured snail length as previously described ("final length"; *P. antipodarum* growth ends at or shortly prior to reproduction) (Winterbourn 1970; McKenzie et al. 2013).

Statistical analyses of life-history trait values

We used these newly collected data as well as data collected in an identical manner from the same experimental setup in native asexual *P. antipodarum* (Larkin et al. 2016) to evaluate whether native vs. invasive status affected growth rate (growth per day of each G1 until 3 mm), age at maturity (age in number of days between G1 birth and G2 production), and final length (shell length at first reproduction for each G1). We started by using a Kolmogorov-Smirnov (K-S) test with the combined data from the invasive and native snails in order to evaluate whether the three dependent variables followed the normal distribution required for parametric analyses. While final length was normally distributed (K-S statistic =

0.030, $df = 301$, $p = 0.200$), age at maturity (K-S statistic = 0.111, $df = 301$, $p < 0.001$) and growth rate (K-S statistic = 0.080, $df = 301$, $p < 0.001$) were not. We then used an inverse square-root transformation to achieve normality for age at maturity (K-S statistic = 0.043, $df = 301$, $p = 0.200$), and we used an inverse log transformation to achieve normality for growth rate (K-S statistic = 0.045, $df = 301$, $p = 0.200$).

Because Larkin et al. (2016) showed that growth rate is negatively correlated with age at maturity and positively correlated with final length in native-range asexual *P. antipodarum*, we used Kendall rank correlation to evaluate the relationship between growth rate and age at maturity and final length in the invasive snails. We used Kendall rank correlation because this analytical approach is not restricted to only linear relationships as are other correlation analyses. Similar to Larkin et al. (2016), age at maturity was negatively associated with growth rate and final length was positively associated with growth rate (age at maturity: $\tau = -0.516$, $p < 0.001$; final length: $\tau = 0.163$, $p = 0.047$). To analyze whether these LHT (growth rate, age at maturity and final length) differed between the native and invasive lineages, we used a three-level nested ANOVA model ($\alpha = 0.05$) to analyze growth rate and a three-level nested ANCOVA model ($\alpha = 0.05$), including growth rate as a covariate to analyze age at maturity and final length. Status (invasive vs. native) was a fixed main factor while population and family were random factors. Family (defined as all G1 produced by the same founding female) was nested within population (lake or stream of origin), allowing us to control for descent from the same founding female. Nesting population within status allowed us to account for variation contributed by the source of the population.

Does genetic variation predict phenotypic variation?

The invasive snails that we used for this experiment were sampled from populations that had been previously genotyped in Verhaegen et al. (2018a, b) and Donne et al. (2020) (Table 1). We used these data to make an initial attempt to address whether genetic and phenotypic variation were associated across invasive populations. Under the presumption that phenotypic variation is at least partially linked to genetic variation, we expected that invasive populations with relatively low genetic variation should harbor less phenotypic variation than invasive populations with relatively high genetic variation. With specific respect to the populations that we used, we predicted that snails from populations Gb, Md and PA - each with only one genotype detected in Donne et al. (2020) - should exhibit low phenotypic variation relative to populations Sn and Pc, which harbored 6 and 5 SNP genotypes, respectively. We also predicted that populations Md and PA should display similar phenotypes because they share a SNP genotype. Finally, we evaluated whether there was a relationship between the extent to which there was significant among-family differences in LHT within invasive populations and population genetic variation, predicting a greater magnitude of among-family differentiation for populations with higher SNP genotype diversity. We addressed this possibility by using two-level nested ANOVA models ($\alpha = 0.05$) for each of the eight invasive populations to determine whether the random factor of family differed in growth rate. We used the same approach but with a two-level nested ANCOVA model ($\alpha = 0.05$), including growth rate as a covariate, to evaluate across-family variation in age at maturity and final length for each of the eight populations. We then used Kendall rank sum correlation analyses to determine whether the F statistic for the family factor for each invasive population from the one ANOVA and two ANCOVA analyses were

associated with the number of SNP genotypes per population. We predicted that a situation where genotypic diversity reflected phenotypic diversity should manifest in a positive relationship between F statistics and population genotype number.

Results

Effect of status and population on life-history traits

There was a significant effect of invasive status on growth rate, with invasive snails growing more slowly than native counterparts (Fig 1; $p = 0.016$). Invasive status also influenced age at maturity, with invasive snails maturing earlier than native snails (Fig 2; $p < 0.001$). The nested factor of population also affected growth rate (Fig. 4; $p < 0.001$) but did not influence age to maturity (Figure 5; $p = 0.111$). While invasive status did not affect final length (Fig. 3; $p = 0.337$), final length did differ across populations (Fig. 6; $p < 0.001$).

We then used the R package *ggplot2* v.3.2.1 to visually compare the distributions of the LHT between the native and invasive lineages, asking whether these distributions suggested that the invasive lineages reflected a non-representative sample of the variation found in the native lineages. These visual comparisons of the distribution of the growth rate and age and maturity data across native and invasive lineages were consistent with a situation where the invasive snails do not representatively feature native variation. In particular, the invasive snails exhibit the part of the native distribution associated with lower growth rate (Fig. 7) and earlier age of maturity (Fig. 8). By contrast, there was no evidence for non-representative sampling of final length between native and invasive lineages (Fig. 9).

Genetic variation vs phenotypic variation

Counter to predictions if genetic variation drives phenotypic variation, our comparisons of SNP genotype diversity against phenotypic variation or trait standard deviation (e.g., growth rate SD) did not reveal any obvious relationships (Figs. S1-3; Kendall's rank sum correlations: growth rate: tau: -0.149, $p = 0.687$; age at maturity: tau = -0.149, $p = 0.687$; final length: tau = 0.00, $p = 1.00$). Our analysis of whether there existed relationships between the extent of within-population family-level variation for LHT in the invasive populations vs. population SNP genotypic diversity did not reveal evidence for such relationships (Figs. S4-6, Tables 2 and 3; Kendall's rank sum correlations: growth rate: tau: -0.447, $p = 0.227$; age at maturity: tau = 0.00, $p = 1.00$; final length: tau = 0.00, $p = 1.00$).

Table 2 Summary of outcomes of ANOVA/ANCOVA models evaluating the effect of family within invasive populations on life-history traits.

Trait	Population	Effect	<i>F</i> (df)	<i>p</i>
Growth rate	Gb	Family(Population)	0.803(1,8)	0.4
	Md		8.184(2,5)	0.026
	Mr		1.347(4,14)	0.301
	PA		2.712(3,12)	0.092
	Pc		0.741(3,7)	0.56
	Sn		0.963(3,10)	0.45
Age at maturity	Gb	Family(Population)	4.678(1,6)	0.074
		Growth rate	0.166(1,6)	0.7
	Md		1.703(2,3)	0.32
			28.501(1,3)	0.013
	Mr		2.584(4,11)	0.096
			2.202(1,11)	0.17
	PA		0.922(3,11)	0.46
			5.486(1,11)	
	Pc		5.733(3,6)	0.039
			19.446(1,6)	
	Sn		0.630(3,8)	0.034
			10.487(1,8)	
				0.005
				0.62
				0.012
Final length	Gb	Family(Population)	0.951(1,6)	0.37
		Growth rate	0.563(1,6)	0.48
	Md		67.452(2,3)	0.003
			58.307(1,3)	0.005
	Mr		7.125(4,11)	0.004

	21.102(1,11)	0.001
PA	0.419(3,11)	0.74
	6.942(1,11)	0.023
Pc	0.780(3,5)	0.55
	7.314(1,5)	0.043
Sn	1.922(2,6)	0.23
	0.109(1,6)	0.75

Table 3 Summary of Kendall rank sum correlation analysis evaluating the relationship between F -statistics and number of SNP genotypes for invasive populations.

Trait	Kendall's tau	p
Growth rate	-0.447	0.23
Age at maturity	0.000	1
Final length	0.000	1

Discussion

Our goal was to provide a deeper understanding of why some lineages within species become invasive, and in particular, if variation in life-history traits may help promote invasive success in *P. antipodarum*. This experiment revealed significant differences in growth rate and age at maturity between native and invasive snails, suggesting that invasive and native *P. antipodarum* differ with respect to important life-history traits. As expected, invasive lineages matured earlier than native lineages. This result is consistent with study outcomes in other invasive species (Chucholl 2012; Hôrková and Kováč 2014). By contrast, the lower growth rate in invasive vs native lineages departed both from our predictions and from studies in other invasive taxa (Chucholl 2012; Hôrková and Kováč 2014). Together, these data suggest that invasive *P. antipodarum* display some distinct life-history variation from native counterparts but do not wholly exhibit the suite of life-history trait variation commonly associated with invasion success.

Invasive lineages almost exclusively reflect the relatively slow component of native variation in growth rate (Fig. 7). While this result also suggests that invasive lineages are capturing only a small fraction of the phenotypic distribution from native lineages, at face value, relatively low growth rate in invasive lineages differs from expectations for invasive populations. The *lower* growth rate that we observed in invasive *P. antipodarum* relative to native counterparts is particularly puzzling in light of the general

expectation that early maturation is associated with rapid growth rate (Stearns and Koella 1986). One possible explanation for this result could lie in the distribution of phenotypic variation in native *P. antipodarum*. In particular, there is marked phylogeographic structure dividing North and South Island New Zealand *P. antipodarum* (Neiman and Lively 2004; Paczesniak et al. 2013). Because invasive *P. antipodarum* primarily originate directly or indirectly from the North Island (Städler et al. 2005; Donne et al. 2020), we considered whether the phenotype we observed - relatively low growth rate and early maturation - is a common feature of North Island *P. antipodarum*.

We addressed this question by visually comparing life-history phenotypes across invasive *P. antipodarum* versus North Island and South Island-origin snails. This comparison revealed that while there do exist asexual lineages that harbor the combination of high growth rate and early maturation that we expected, these lineages are almost exclusively from South Island populations (Fig. 10). The implications are that the invasive *P. antipodarum* might tend to grow slowly because they did not sample genotypes associated with high growth rate. Because these invasive snails are asexual, there is no way - barring the generation of new phenotypes via mutation - for the rapid evolution of a combined high growth rate/early maturation phenotype. Because current sampling of North Island lineages is quite sparse (Fig. 10), additional wider characterization of phenotypic variation in North Island *P. antipodarum* will be needed to provide a more definitive test of this hypothesis.

Relatively small size at maturity is commonly reported among invasive taxa (Sakai et al. 2001). Counter to this expectation, we did not observe a difference in final length between native and invasive *P. antipodarum*. It is important to note that these life-history generalizations may not apply to all invasive taxa. Indeed, Bengtsson and Baur (1993) found that size at maturity did not differ between invasive and native terrestrial gastropod species (primarily slugs and snails). Bengtsson and Baur (1993) went on to suggest that invasive species could exhibit a combination of r and k-selected traits rather than strictly r-selected traits. More recent studies do report that invasive species often differ in the traits associated with successful invasion (van Kleunen et al. 2015; Hodgins et al. 2018). Indeed, van Kleunen et al. (2015) suggests that invasive species do not have a “one size fits all” combination of traits that explains success.

Population of origin affects life-history traits in *P. antipodarum*

Growth rate and final length differed across invasive *P. antipodarum* populations (Figs. 4 and 6). Evidence for population-level differences in growth rate in invasive *P. antipodarum* has also demonstrated by Dybdahl and Kane (2005), who showed that populations from Snake River, ID grew at higher rates at 24°C than populations from Columbia River, OR and Madison River, MO. We found that snails from Snake River, ID grew more slowly than Madison River, MO in a common environment at 16°C. Because our experiment was conducted in a common-garden condition, it is tempting to conclude these differing responses are due to genetic adaptation to local habitat or nonadaptive population structure that translate into different responses to the laboratory conditions in which the experiment took place. A non-mutually exclusive explanation for these results is an adaptive plastic response to temperature. In

particular, the Snake River population could fit a Master-of-some situation (Richards et al. 2006) where plasticity in LHT allows invasive snails to increase their fitness under favorable conditions.

The across-population variation in final length is in agreement with previous studies in *P. antipodarum*, where shell height (similar measurement to present study: length of shell from the aperture to apex) in invasive European populations varied as a function of local habitat conditions. Thus, one possibility is that some of the across-population variation that we observed in final length could also be due to genetic adaptation to local habitat as well as nonadaptive heritable differences in size across invasive populations. Previous studies of *P. antipodarum* shell morphology have concluded that shell size is predominantly driven by phenotypic plasticity (Kistner and Dybdahl 2013; Verhaegen et al. 2018a). In particular, Kistner and Dybdahl (2013) found significant differences in shell size between asexual founder females sampled from natural populations and their offspring produced in a lab setting. These phenotypic differences between mothers and their asexually produced offspring is expected if phenotypic plasticity plays an important role in determining shell size in invasive *P. antipodarum*. Determination of the extent to which these results regarding plasticity in shell size extend across *P. antipodarum* will require inclusion of a wide range of invasive populations and careful quantification of maternal vs. offspring shell size in controlled environmental conditions.

Is there a relationship between genotypic and phenotypic variation?

Invasive *P. antipodarum* populations may have non-representatively sampled native genetic variation that is beneficial for invasion. This possibility is consistent with the fact that invasive lineages of *P. antipodarum* display specific and narrow fractions of the life-history variation expressed in native *P. antipodarum*. In particular, the invasive lineages express primarily the early-maturation fraction of variation in this trait found in native *P. antipodarum*, suggesting that invasive lineages reflect a non-representative sample of native distribution (Fig. 8).

Whether those observed phenotypic changes in invasive *P. antipodarum* are primarily due to natural selection versus genetic drift (e.g., founder effect) is a harder question to tackle. Keller and Taylor (2008) suggested that this question could be answered by using molecular markers to pair the invasive lineages (descendants) to the ancestral lineages found in the native range. With this information in hand, researchers can then use a common garden experiment to quantify and compare the phenotypic divergence between individuals sampled from the two ranges. Next, comparison of the genotypic diversity of the ancestor and descendants across neutral markers (e.g. microsatellites, SNPs) can allow the researchers to establish a neutral expectation of founder effect consequences for genetic diversity in the invasive population. If LHT are subject to selection, and if observed phenotypic change in these traits exceed the expectation of divergence at neutral loci between the native and invasive populations, it is reasonable to interpret this outcome as evidence for selection as a driver of the change in the invasive range. This conclusion is especially well supported if the direction of selection favors LHT that promote invasiveness (Keller and Taylor 2008).

We do not have available the genetic data that we would need to differentiate between selection and genetic drift as the main mechanism for the different values and distributions of important LHT between native and invasive *P. antipodarum* populations. We did take initial steps towards this goal by using previously available SNP genotyping information for the invasive populations to evaluate whether genetic variation might be relevant to invasive success (Table 1). We predicted that populations with relatively high genotypic variation (e.g., Pc, Sn) would display more phenotypic variation than populations with lower genotypic variation (e.g., Gb, Md, PA). These comparisons of SNP genotype diversity against trait standard deviation (e.g., growth rate SD) did not reveal obvious relationships, counter to our prediction that greater genotypic variation would lead to greater phenotypic variation. It was especially striking that snails from Sn, which harbors six SNP genotypes, did not exhibit more phenotypic variation than any of the other invasive populations (Figs. S1-3). We similarly found no evidence for a relationship between the extent of across-family phenotypic variation and genotypic variation (Figs. S4-6). Although these results suggest that increased genetic variation does not necessarily translate into greater phenotypic variation in invasive *P. antipodarum*, a greater number of invasive populations sampled from a wider geographic range need to be genotyped and phenotyped to provide a rigorous test of this possibility.

Summary & Conclusions

We detected significant differences in growth rate and age at maturity between native and invasive *P. antipodarum*. These results - and especially the notably short time to maturity of invasive vs. native snails - suggest that these LHT could be important for invasion success. The invasive *P. antipodarum* exhibited lower growth rate than their native counterparts, counter to general assumptions that high growth rate is beneficial for invasive success. We did not detect a significant difference in final length between the native and invasive snails, which differs from predictions of life-history models that higher growth rate is associated with early maturation at a small body size (Stearns and Koella 1986). Our results also indicate that invasive *P. antipodarum* are non-representatively reflecting certain parts of the native-range variation, also consistent with the possibility that selection may favor those traits in the invasive range. Finally, we found no evidence for a strong relationship between genotypic diversity and phenotypic diversity in invasive populations, providing an indirect line of evidence in support of the idea that phenotypic plasticity is an important source of adaptive variation for these asexual snails.

Altogether, our study helped illuminate connections between LHT variation and invasive success while also raising future questions about the invasive success of *P. antipodarum*. Future studies should aim to directly compare phenotypes and genotypes of ancestral lineages to descendent lineages to provide more insight into the role of genetic and phenotypic variation in invasion success.

Declarations

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Figures

Figure 1

There was a significant effect of invasive status on growth rate, with invasive snails growing more slowly than native counterparts (Fig 1; $p = 0.016$).

Figure 2

Invasive status also influenced age at maturity, with invasive snails maturing earlier than native snails (Fig 2; $p < 0.001$).

Figure 3

While invasive status did not affect final length (Fig. 3; $p = 0.337$), final length did differ across populations (Fig. 6; $p < 0.001$).

Figure 4

Invasive status also influenced age at maturity, with invasive snails maturing earlier than native snails (Fig 2; $p < 0.001$). The nested factor of population also affected growth rate (Fig. 4; $p < 0.001$)

Figure 5

Invasive status also influenced age at maturity, with invasive snails maturing earlier than native snails (Fig 2; $p < 0.001$). The nested factor of population also affected growth rate (Fig. 4; $p < 0.001$) but did not influence age to maturity (Figure 5; $p = 0.111$). While invasive status did not affect final length (Fig. 3; $p = 0.337$), final length did differ across populations (Fig. 6; $p < 0.001$).

Figure 6

Invasive status also influenced age at maturity, with invasive snails maturing earlier than native snails (Fig 2; $p < 0.001$). The nested factor of population also affected growth rate (Fig. 4; $p < 0.001$) but did not influence age to maturity (Figure 5; $p = 0.111$). While invasive status did not affect final length (Fig. 3; $p = 0.337$), final length did differ across populations (Fig. 6; $p < 0.001$).

Figure 7

In particular, the invasive snails exhibit the part of the native distribution associated with lower growth rate (Fig. 7)

Figure 8

In particular, the invasive snails exhibit the part of the native distribution associated with lower growth rate (Fig. 7) and earlier age of maturity (Fig. 8).

Figure 9

By contrast, there was no evidence for non-representative sampling of final length between native and invasive lineages (Fig. 9).

Figure 10

We addressed this question by visually comparing life-history phenotypes across invasive *P. antipodarum* versus North Island and South Island-origin snails. This comparison revealed that while there do exist asexual lineages that harbor the combination of high growth rate and early maturation that we expected, these lineages are almost exclusively from South Island populations (Fig. 10).

Supplementary Files

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