

Behavior in invasive New Zealand mud snails (*Potamopyrgus antipodarum*) is related to source population

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Abstract Behavior can be an important determinant of invasion success. In the New Zealand mud snail (*Potamopyrgus antipodarum*), behavior is influential in predator avoidance and probably plays a role in dispersal. The present study investigated differences in behavior among populations of different asexual clones of this species and compared introduced populations characterized by various levels of invasiveness and New Zealand native clonal populations with respect to rheotactic, geotactic, photokinetic, and dispersal behaviors. There was a significant difference in behavior among populations in all behaviors evaluated. A population of a widespread clone (US1) behaved most differently from the other populations exhibiting differences in all behaviors including a greater propensity to disperse. These results indicate that there is a population and possibly a genotypic effect on behaviors in this freshwater snail, and this variation may help to explain why some clones are more invasive than others.

Keywords Snail · *Potamopyrgus antipodarum* · Clone · Behavior

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Introduction

The reason why some introduced species are successful invaders while others are not has been the subject a great amount of research (Sakai et al. 2001). Many traits have been associated with invasion success at the species level, but these traits have been less consistently correlated with invasion success across taxa (Kolar and Lodge 2001; Hayes and Barry 2008). It appears that at least in some taxa, behavior of the invader plays an important role in successful invasions (Holway and Suarez 1999; Pavlov et al. 2006; Dick 2008; Phillips and Suarez 2012). However, information on behavior is often lacking in studies of invasion, and behavior has received less attention than other characteristics that may explain invasion success (Holway and Suarez 1999; Lester 2005).

Typically, invasive species are compared to native species that they compete with or to similar species that are not invasive to determine what traits of the introduced species make it invasive. One of the difficulties in these approaches is the fact that different species are likely to have numerous trait differences aside from those suspected of influencing invasion, making it difficult to determine exactly what trait or traits result in greater invasive ability. Clonal species present an opportunity to study invasion by comparing clonal genotypes that vary in invasion success. Clones of the same species are more genetically similar to each other than different species are to each other, and thus, any trait differences between invasive and non-

invasive clones are more likely to be related to invasion success.

The invasive New Zealand mud snail is a small freshwater hydrobiid snail endemic to New Zealand, which has spread rapidly to Europe, Australia, Japan, west Asia, and North America (Proctor et al. 2007; Alonso and Castro-Díez 2012). It possesses several traits that appear to make it a successful invader including a wide tolerance of physico-chemical variation, release from biological enemies, and clonal reproduction (Alonso and Castro-Díez 2008). It lives in mixed populations of sexuals and asexual clones in its native New Zealand (Lively 1987). However, in its invaded range, it appears to be entirely clonal (Alonso and Castro-Díez 2012). At least three populations of invasive, asexual clones have proliferated in freshwater ecosystems in North America. These populations originated in the western US rivers and streams (US1 and US3 clones) (Proctor et al. 2007) and in the Laurentian Great Lakes [Ontario clone (=US2)] (Zaranko et al. 1997; Levri et al. 2007a). Some of these clones are more invasive than others. In the western US, the snail was first documented in 1987 (Bowler 1991) and the majority of western US snails have been identified as the US1 clone since the early 2000's (Fromme and Dybdahl 2006). The US3 clone was first identified in 2005 (Proctor et al. 2007) but it is not clear how long it has been in North America. Since the US3 clone was found in the same location as where the US1 clone was first discovered, it is a strong possibility that they were introduced together (Dybdahl and Drown 2011). It is also possible that the US3 clones were introduced some time after the US1 clone and the differences in their distribution may be in part due to time. The US1 clone has expanded its range to most of the western US while the US3 clone lives in a small portion of the Snake River and has not expanded its range appreciably in, at least, the last decade (Proctor et al. 2007; Dybdahl and Drown 2011). The invasiveness of the Ontario clone (US2) is difficult to compare to the others since it occurs largely in lake habitats. It has spread to four of the five Laurentian Great Lakes since its discovery in Lake Ontario in the early 1990's (Zaranko et al. 1997; Levri et al. 2007a, 2008, 2013) and has recently been discovered in some streams emptying into Lake Ontario (Levri and Jacoby 2008; Levri et al. 2012a). Thus, within this species there is variation in invasion success that may be related to

genotype. Efforts to determine why the US1 clone is invasive and others are less so have focused on the phenotypic plasticity of the clones with respect to tolerance of various environmental variables. These experiments have demonstrated little difference among these introduced clones with respect to tolerance to variation in salinity (Drown et al. 2011), conductivity and temperature (Levri et al. 2014). However the clones introduced to North America appear more salt tolerant than New Zealand native clones (Drown et al. 2011).

Another possible explanation for the variation in invasion success among clones is differences in behavior. Behavior varies among populations of this species in New Zealand (Levri et al. 2012b), and these behaviors influence nutrient acquisition (Levri and Lively 1996; Levri 1999) and predator avoidance (Levri 1998). Populations from different lakes differ in their speed in response to light (photokinesis) and their light-dependent response to gravity (geotaxis), and the populations respond to predator odors differently (Levri et al. 2012b). The purpose of these experiments was to determine if there are source population differences in various behaviors that could potentially influence the invasiveness of the snail. We examined rheotaxis, geotaxis, photokinesis, and dispersal. Rheotaxis, the movement of individuals into or with a current, commonly influences dispersal rates in gastropods in general (Kappes and Haase 2012) and in this species (Sepulveda and Marczak 2012). Geotaxis and photokinesis in this species have been associated with predator avoidance (Levri and Fisher 2000; Levri et al. 2007b, 2012b). *Potamopyrgus antipodarum* also attach themselves to the water surface using surface tension, which may allow them to float substantial distances (Levri 1998). The role of variation in dispersal and exploratory behaviors may be especially important in influencing invasion success (Holway and Suarez 1999; Rehage and Sih 2004; Leibl and Martin 2012). Behavioral differences between introduced genotypes and New Zealand natives have not been noted before. If behavior is important to invasion success in this species we expected that the more invasive clones (US1 and US2) would show a greater propensity to disperse than the less invasive clone (US3) and New Zealand endemic clones and show more pronounced predator avoidance than the less invasive clone (US3).

Methods

Endemic non-invasive snail samples were obtained from multiple lakes in New Zealand. Invasive asexual snail samples were collected from rivers in Idaho and Wyoming and streams near Lake Ontario. The invasive clones used in these experiments were US1, US3, Ontario 1 and Ontario 2 [Ontario 1 and Ontario 2 are the same genotypic clone (i.e. US2) collected from two locations in streams in New York state (Levri et al. 2012a)]. The native New Zealand clones were Mapourika75 (Lake Mapourika), Kn4 (Lake Kaniere), Clearwater1 (Lake Clearwater), Peorua4, Peorua72, and Peorua74 (Lake Peorua), Gunn2 (Lake Gunn), and AC51 and B52 (Lake Alexandrina), all from the South Island, and Wak1 (Lake Waikaremoana), from the North Island). All New Zealand clones were started from an isolated female. Most were genotyped using mitochondrial haplotype data (Neiman et al. 2010, 2011; Neiman unpublished data). The only New Zealand clone used here that was not genotyped was Gunn2, although clones from different lakes have separate origins (Pacziesniak et al. 2013). All New Zealand clones used in the experiments have spent multiple generations in a lab environment. The introduced clones (US1, Ontario, and US3) have also been reared in the lab for multiple generations. The snails were originally taken from the field. The US1 and US3 clones were originally genotyped using allozyme, microsatellite DNA, and mitochondrial DNA genetic markers (Dybdahl and Drown 2011). The size of the snail can vary in nature (Winterbourn 1970) but there is little variation in maximum length among these clones in a lab environment (Levri unpublished data), and snail shell size and shape is phenotypically plastic (Kistner and Dybdahl 2013). The introduced clones exhibit similar growth rates in the lab (Drown et al. 2011). All clones were maintained prior to the experiments in one-liter plastic bins in water containing 3ppt seawater, in which they grow faster than in freshwater (Drown et al. 2011). Snails were fed *Spirulina* powder and their water was changed three times per week. The US1, US3, and at least one Ontario clone (Ontario1) were used in each of the experiments. Various New Zealand native clones were used in the experiments as availability and abundances of each clone varied over the year during which the experiments were conducted.

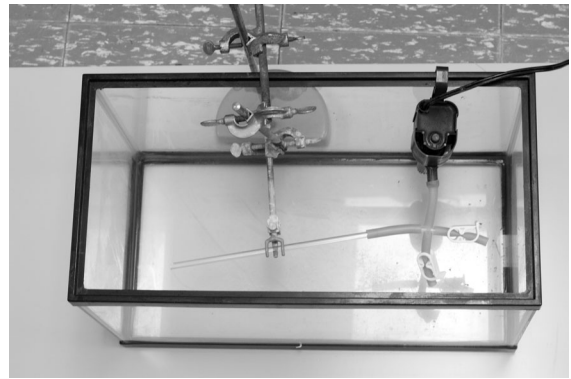


Fig. 1 A top-down view of the set-up for the rheotaxis experiment. The flow rate was controlled through the glass tube by adjusting the clamps on the rubber tubing

Two weeks before the experiments started, snails were placed in ambient sunlight on a windowsill to acclimate them to a natural light–dark cycle. Immediately prior to the experiments, the length (shell apex to aperture lip) of the snails was measured, and only snails 4.0–5.0 mm were used in the experiments to control for any effect of size on behavior, which has been found previously (Levri and Lively 1996). Four behaviors were assessed.

Rheotaxis was measured by placing 25 snails individually from each population used in a glass tube and exposing them to a water current. In a 37.85 L aquarium filled with aged tap water, a current was generated by using a Cobalt International MJ-400 Multi-Purpose Powerhead Pump. The pump was connected to a 3 cm rubber tube connected to an X-splitter with 5 cm of rubber tubing attached to each split resulting in water exiting three tubes (Fig. 1). The rate of flow in one tube could be adjusted by clamping off the two other tubes to various degrees. In the open rubber tube, a 20 cm long, 10 mm diameter glass tube was attached and held with a clamp so that it was in a horizontal position. The rate of flow was adjusted to 0.18 m/s because preliminary trials demonstrated it to be the greatest flow rate that did not result in snails consistently becoming unattached from the glass tube. Individual snails were placed in the tube and moved to the center using a glass rod. Once the snail emerged from its shell the pump was turned on and the trial began. The direction and distance travelled in 5 min was noted for each. The entire apparatus was rotated

90° after each trial to control for orientation to sources other than the water current.

Dispersal was assessed by placing snails of the same clone 20 at a time in a square plastic container measuring 12 cm by 12 cm by 6 cm (length \times width \times height) filled with aged tap water and noting how many snails were on the floor and walls of the container as well as attached to the surface of the water after 10 min. The clonal populations used and their sample sizes in the experiment were US1 (80), US3 (40), Ontario1 (80), Ontario2 (60), AC51 (20), Peorua4 (80), B52 (80), and Gunn2 (80).

Geotaxis and photokinesis were measured as by Levri and Fisher (2000) by placing snails from each population in a 20 cm long and 10 mm in diameter glass tube within a 37.85 L aquarium filled with water from a local stream. Once the snail emerged from the shell, the tube was oriented vertically in the geotaxis trials and horizontally in the photokinesis trials in ambient light for 2 min. Trials were also performed in the dark for 2 min in both experiments. Previous work determined that the geotactic response is light-dependent (Levri and Fisher 2000; Levri et al. 2007a, b). The sequence of light and dark trials was alternated. The distance travelled (up or down in the case of phototaxis) was noted. The clonal populations used and their sample sizes in this experiment were US1 (25), US3 (11), Ontario1 (25), Gunn2 (15), Peorua72 (15), Peorua74 (15), Clearwater1 (15), and Map75 (15).

Statistical analyses

All statistical analyses were performed using IBM SPSS Statistics statistical software v. 20. For the rheotaxis experiment, a univariate analysis of variance was used to compare distance travelled among clones and a post hoc Tukey's Honest Significant Difference test was performed to compare the US1 clone to each of the others. To determine if snails within a clone moved significantly toward or away from the current a one-sample *t* test was used. In the dispersal experiment, the data were analyzed using a hierarchical log linear analysis with a backward elimination procedure to compare the proportions of each snail clone found in each location to each other. We then performed post hoc tests by comparing the proportion of US1 clone that attached to the water's surface to the proportion of each other clone, adjusting the critical *P* value using a Bonferroni correction. In the geotaxis and photokinesis

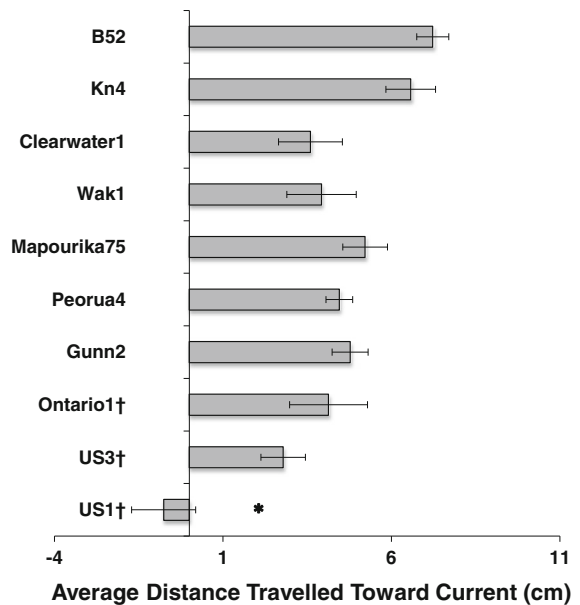


Fig. 2 Results of the rheotaxis experiment. Positive values indicate movement toward the current. Introduced populations are indicated with “†.” Statistically significant differences from other populations are indicated with “*.” Error bars are standard errors

experiments, data were analyzed using univariate ANOVAs to determine differences in distance travelled (up or down in the case of geotaxis) and the influence of light on distance travelled on the different populations. Post-hoc Tukey's Honest Significant Difference tests were performed to compare the US1 clone to each of the other clones and to compare the two clones from Lake Peorua to each other.

Results

Rheotaxis

Snails showed significant variation in their rheotactic response ($F_{1,9} = 7.64$, $P < 0.001$). All snails moved significantly toward the direction of the current ($P < 0.003$ in all cases) except for the US1 clone ($t_{24} = -0.79$, $P = 0.432$) (Fig. 2). The US1 population was significantly different in its rheotactic response when compared individually to every other population ($P < 0.006$ in all cases), except for the US3 clone from which the difference was not quite significant ($P = 0.055$).

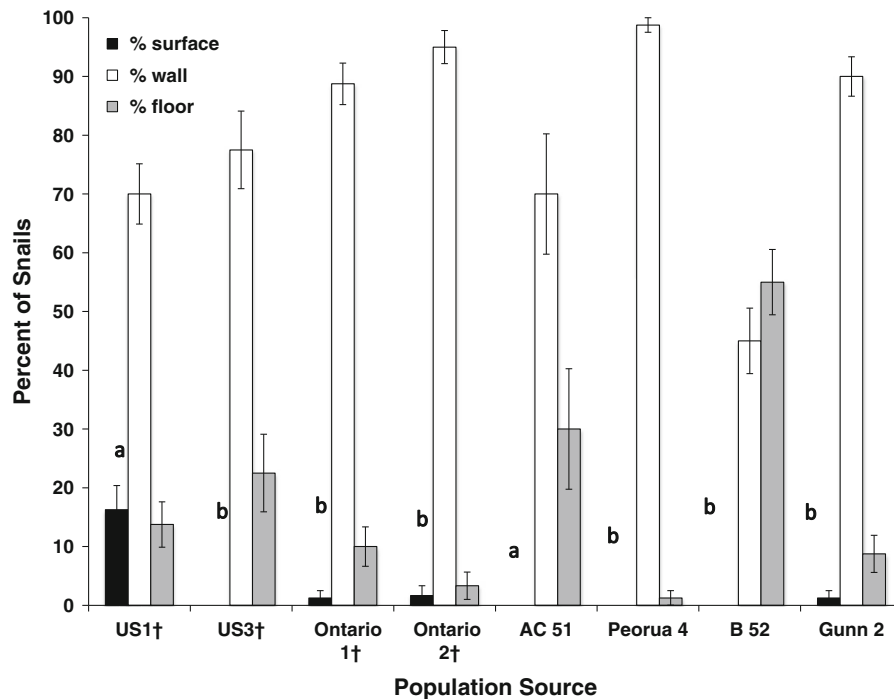


Fig. 3 Results of the dispersal experiment. Introduced populations are indicated with “†.” Different letters above the surface bar (a, b) indicate significant differences in pairwise comparisons. Error bars are 95 % confidence intervals

Dispersal

There was significant variation among clones in use of the different areas in the container [$\chi^2_{(14, N=520)} = 142.7, P < 0.0005$]. The US1 population was more likely to be attached to the water surface than any of the other populations ($P < 0.003$ in all cases; $P_{\text{crit}} = 0.0071$ —Bonferroni correction) except the AC51 population ($P = 0.012$), although only 20 AC51 individuals were used compared to at least 40 for all other populations (Fig. 3).

Geotaxis

We found a significant overall effect of source population on geotactic behavior ($F_{1,7} = 22.5, P < 0.0005$), as well as significant variation among populations depending on light or dark conditions (clone \times light interaction) ($F_{1,7} = 9.48, P < 0.0005$) (Fig. 3). The Tukey HSD post hoc comparison showed that the US1 population behaved significantly differently from all other populations ($P < 0.001$ in all cases) (Fig. 4). In a planned comparison the Peorua 72 and Peorua 74 populations differed in the variation in

distance travelled between light and dark conditions (population \times light interaction) ($F_{1,1} = 11.85, P = 0.001$), demonstrating variation between similar populations from the same lake.

Photokinesis

The snails moved faster in the light than in the dark ($F_{1,1} = 80.9, P < 0.0005$) and all populations showed at least some positive photokinesis (Fig. 5). However, some populations moved significantly faster than others ($F_{1,7} = 28.05, P < 0.0005$; Fig. 5), and some responded to light more than others (population \times light interaction) ($F_{1,7} = 3.37, P = 0.002$). Post hoc comparisons showed that the US1 population behaved differently from the US3 population ($P < 0.005$) and the Ontario population ($P < 0.005$). The US1 population did not differ significantly from the Gunn2, Peorua74, and the Clearwater1 populations ($P > 0.6$ in all cases). As in the geotaxis experiments, in a planned comparison, the two populations from the same lake (Peorua 72 and 74) differed in their response to light ($F_{1,1} = 10.58, P = 0.002$), further demonstrating variation between populations from the same lake.

Fig. 4 Results of the geotaxis experiments. Introduced populations are indicated with “†.” Error bars are standard errors

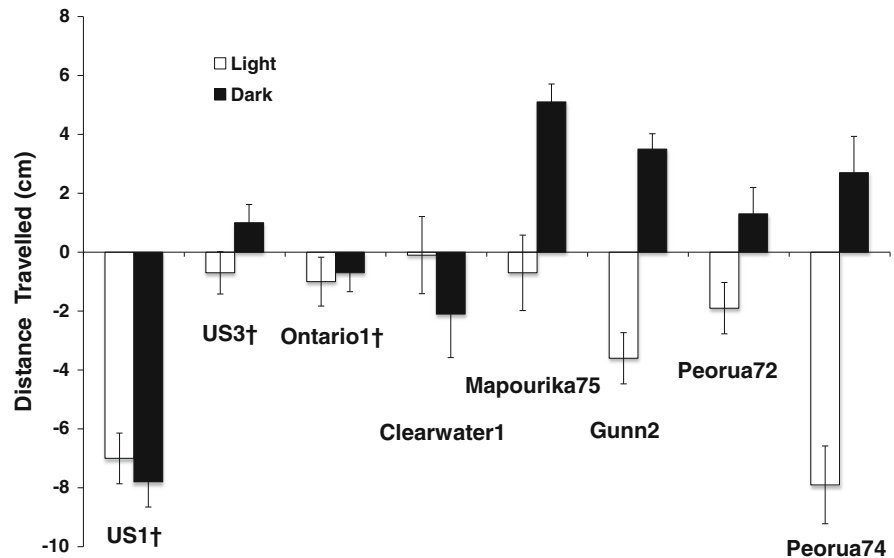
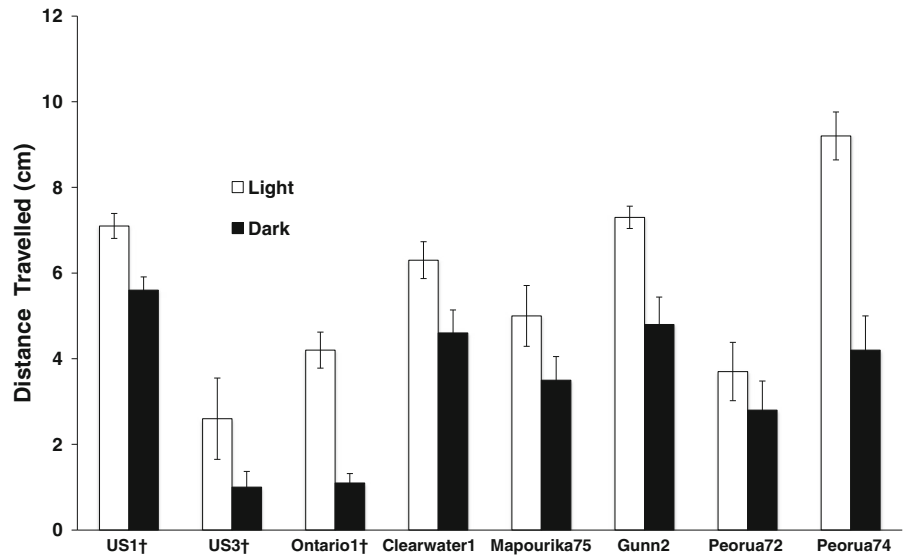


Fig. 5 Results of the photokinesis experiments. Introduced populations are indicated with “†.” Error bars are standard errors



Discussion

This is the first demonstration that variation in behavior among populations of the same species may influence invasion success. It is also the first evidence that behavior may vary among clonal genotypes of *P. antipodarum*, even between two endemic clones from the same lake in New Zealand (Peorua72 vs. Peorua74). Since only single lineages of each clone were used, the differences cannot definitively be attributed to clonal genotype, only to population. However, the results are suggestive that there could be clone-dependent variation in behavior.

The populations from clones that have been introduced into the United States (US1, US3 and Ontario [US2]) showed differences in rheotactic, geotactic, photokinetic and dispersal behaviors. The most widespread population (US1) exhibited behaviors that deviated from the norm more than any other population across experiments. This suggests the possibility that behavioral differences among clones influence invasion success.

The three introduced populations were collected from streams but the New Zealand native populations were originally taken from lakes. Thus it is possible that differences between introduced and native

populations could be due to their habitat of origin. However, the Ontario clone population is found extensively in the Laurentian Great Lakes (Zaranko et al. 1997; Levri et al. 2008), and the US1 clone has also been found in multiple lentic habitats in the western United States (USGS 2013). Water chemistry could potentially influence behavior, for example due to the presence of kairamones (Levri 1998; Levri et al. 2012b). The physical and chemical properties of the water at the locations of the source populations are not known, so behavior in the lab may not have completely reflected behavior in nature.

Foraging behaviors of an invasive may differ between the native and invaded ranges, increasing invasion success (Pintor and Sih 2009), and invasives may forage more efficiently than natives (Rehage et al. 2005a, b). Photokinesis and geotaxis are related to foraging behavior (Levri et al. 2007b) and the foraging patterns in the native range of the snail in New Zealand appear important in predator avoidance (Levri 1998). Thus, these different clones may have different vulnerabilities to aquatic predators, and predator avoidance behaviors may contribute to invasion success (Hazlett et al. 2003; Pennuto and Keppler 2008). Individuals from the US1 population seem to move down more than individuals from other populations and move faster than other introduced populations. Moving down will result in the snails spending less time in areas exposed to predators. This species responds to chemical cues from fish predators (Levri 1998) by adjusting its geotactic and photokinetic response so as to reduce foraging and increase predator avoidance (Levri 1998; Levri et al. 2007b). The water used in the photokinesis and geotaxis experiments was taken from a stream, so it is possible that behavior-influencing kairomones from fish were present, which are known to influence the behavior of this species (Levri 1998; Levri et al. 2012b). Invasives may use plastic behavioral responses to kairomones to avoid predation by unfamiliar predators (Hazlett et al. 2003; Naddafi and Rudstam 2013). Other studies have found that behavioral responses to kairomones may differ between invasives and natives and may contribute to invasion success (Hazlett et al. 2003).

In previous experiments, snails moved substantially faster in the light than the dark. Positive photokinesis was also found in this experiment. Positive photokinesis would probably result in individuals spending

more time in dark than light conditions and less exposure to predators. However, there was little difference in speed in light and dark of individuals from the US1 population. Several other populations, including the two other introduced populations, moved much faster in the light than the dark. It is possible that the strong geotactic response of the US1 population is sufficient to reduce exposure of these individuals, as these two behaviors seem to work in concert (Levri et al. 2007b), making a strong photokinetic response less important. Regardless, the US1 population did differ significantly from some other populations in its photokinetic response, further demonstrating variation in behavior.

Of the behaviors examined in these experiments, the difference in dispersal behavior between the US1 population and the other populations may be the most likely behavior to influence invasion success. By attaching to the surface of the water, the snails could very quickly disperse, especially in flowing waters. The greater frequency of the US1 population attaching to the surface may in part explain why this particular clone is spreading so rapidly in western North America. The high rate of dispersal of this species has been primarily attributed to human-associated transmission via attachment to clothing, fishing gear, etc. (Proctor et al. 2007), and human-aided dispersal appears to be common with other invasive gastropods as well (Aubry et al. 2006). In addition to using humans as a vector, the snail's clonal nature and ability to survive out of the water for extended periods may also increase its invasiveness (Proctor et al. 2007). Downstream dispersal via attachment to the water's surface would increase the snail's distribution within a water body thus increasing the encounter rate with humans and further facilitate its dispersal to other water bodies via human vectors. An understanding of dispersal in flowing waters is of increased importance as the Ontario clone, previously only found in the lotic waters of the Laurentian Great Lakes, has recently colonized streams that empty into Lake Ontario (Levri and Jacoby 2008; Levri et al. 2012a).

Positive rheotaxis is common in aquatic invertebrates and the behavior has been used to explain why populations of organisms are not depleted because of drift downstream (Hughes 1970). *P. antipodarum* is positively rheotactic (Haynes et al. 1985; Sepulveda and Marczak 2012). The US1 population in this experiment was the only population that did not exhibit positive

rheotaxis. This at first appears inconsistent with the results of Sepulveda and Marczak (2012), who found positive rheotaxis under most conditions in a genotype that was probably the US1 clone (since it is the only clone known from the area in which their snails were collected). However, Sepulveda and Marczak (2012) found that their snails did not move toward the current, and actually trended away from the current, when the flow rate was high (0.48–0.53 m/s) and food resources were low. The conditions in our experiment were similar as no food for the snails was present in the tube and the flow rate was just below the threshold of dislodging the snails. The flow rate of Sepulveda and Marczak (2012) was greater than that we used. However, the flow rate in their experiment was determined in the center of an artificial stream at a height 3–6 cm above the substrate (Sepulveda pers. comm.). The current velocity in a stream decreases as the distance to the bottom decreases to the point of near 0 flow rate extremely close to the bottom (Wetzel 2001). *P. antipodarum* is small with a height of at most 3 mm when upright. Thus, it is likely that the flow rate experienced by the snails in Sepulveda and Marczak's (2012) experiment was somewhat less than they measured. It is not clear how the lack of a rheotactic response in the US1 population may influence their invasive potential except for the possibility that they may be less likely to move upstream and more likely to drift downstream than individuals from other populations. Sepulveda and Marczak (2012) demonstrated a propensity of the species (probably the US1 clone) to disperse upstream especially when flow rates are low. However, if the primary introduction method is through human vectors, such a pattern may be difficult to observe in the field.

The origin of the behavioral variation in non-native clones could have arisen by at least two mechanisms. First, there may have been variation in behavior in clones that were introduced and those clones with favorable behavioral traits were more likely to establish and/or spread. Behavioral traits improve predictions of establishment success in other species (Suarez et al. 2005, Sol et al. 2002, 2008; Blackburn et al. 2009). Another possibility is that originally there was little behavioral variation among the introduced clones, and, once introduced, selection on behavior varied depending on the environment the clone found itself in. Thus evolution of the behavioral differences occurred following introduction (Phillips and Suarez

2012). It is also possible that both mechanisms could work in concert. These results provide some evidence of there being substantial variation in behavior among the clones prior to introduction as there is variation in most of the behaviors examined in the native range and even within snails from the same habitat of the same lake (Peorua). This points to, albeit not conclusively, the idea that the different clones that were introduced already possessed variation in behavior, and behavioral traits of particular clones may have influenced which clones established and spread.

The results reported here provide evidence that there is variation due to source population in behaviors that may influence invasion success, and that a highly invasive clone exhibits some behavioral phenotypes that would seem to enhance its ability to survive, reproduce and spread. However, there is no direct evidence that these behavioral differences actually result in increased invasion success. Future studies of this system should determine if the variation is in fact due to clonal genotype and look for variation within genotypes (sub-clonal variation). Research suggests that behaviors such as propensity to disperse should be selected for differently at the invasion front of the introduced species range than in the interior of the range (Phillips et al. 2008). The range of at least two clones of the New Zealand mud snail (US1 and Ontario) are still expanding in North America, so this species could be an ideal system in which to look for such an effect.

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