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Tolerance assessment of the aquatic invasive snail *Potamopyrgus antipodarum* to different post-dispersive conditions: implications for its invasive success

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Abstract

The New Zealand mudsnail (NZMS) *Potamopyrgus antipodarum* (Gray, 1843) (Tateidae, Mollusca) is a successful invasive species able to alter the functioning of the invaded ecosystems. However, to arrive and establish in new aquatic ecosystems, this snail must survive to the overland translocation through aerial exposure and must tolerate the new physical and chemical conditions of the recipient ecosystem. In this study, we simulated different conditions for the NZMS invasion by combining two air exposure treatments (0 and 20 h) with different physical and chemical conditions of the rehydration water (low and normal water temperatures and normal and high water conductivities). Mortality, behavior and neonate production were compared across treatments. Air exposure caused a high percentage of mortality but survivors tolerated the subsequent abiotic conditions. Low temperatures and high conductivities altered the behavior of adult snails, increasing significantly their reaction time (i.e. time to start normal movement). This may have negative consequences for the survival of this species under natural conditions. Finally, these conditions did not affect significantly the production of neonates. These results supported that the surviving NZMS to a brief period of air exposure possess the ability to acclimate to contrasting abiotic conditions with a potential establishment of new populations and that survivors can reproduce in different abiotic conditions after an air exposure period.

Keywords

Air exposure, conductivity, mortality, neonate production, New Zealand mudsnail, temperature

Introduction

Biological invasions are considered one of the main forms of global change (Sala et al. 2000). Invasive exotic species can have multiple effects such as drastic changes in the structure and functioning of ecosystems (Mack and D'Antonio 1998; Strayer 1999; Riley et al. 2008). However, there are some ecosystems, such as freshwater ecosystems, that are more susceptible to biological invasions than terrestrial ones because they have been intensively used by humans (Lodge et al. 1998; Richardson 2011) and they have fewer barriers for propagation (Lodge et al. 1998).

Exotic invasive freshwater mollusks represent a threat to the functioning of the invaded ecosystems and to native species (Strayer 1999; Hall et al. 2006). For instance, they can dominate the production and the biomass in food webs and they can compete with native species affecting their distribution and abundance (Hall et al. 2006; Brenneis et al. 2011). Aquatic mollusks can be transported in ballast water (Carlton 1985; Hoy et al. 2012) and attached to fishing tools (Richards et al. 2004; Davidson et al. 2008), the body surface and the digestive tract of many species of birds and fish (Malone 1965; Haynes et al. 1985; Aarnio and Bonsdorff 1997). Moreover, the propagation between remote water bodies requires in many cases a mechanism of aerial passive translocation (Alonso and Castro-Díez 2012a). Therefore, the tolerance to air exposure is a prerequisite to the propagation of those species (Richards et al. 2004; Alonso and Castro-Díez 2012a).

The New Zealand mudsnail (NZMS), *Potamopyrgus antipodarum* (Gray, 1843), is a prosobranch native of New Zealand and an invasive species in many aquatic ecosystems around the world (Alonso and Castro-Díez 2012b). This snail has been found in a wide variety of aquatic ecosystems, both in its native and invaded range: from freshwater ecosystems to brackish and saltwaters, and from lotic to lentic habitats (Winterbourn 1970; Alonso and Castro-Díez 2012b; Hoy et al. 2012). Therefore, this species presents a wide ecological and phenotypic plasticity which might allow the NZMS to establish in a wide diversity of habitats (Richards et al. 2006). Populations of invaded regions are formed mostly by ovoviviparous clonic females that reproduce by apomictic parthenogenesis (Winterbourn 1970). Embryos develop into a female's brood pouch and emerge to the environment as fully functional neonates (Proctor et al. 2007). Moreover, females of invasive populations are able to produce nearly 230 neonates per year (Cheng and LeClair 2011). Therefore, a single female under optimal conditions could initiate a new population (Vazquez et al. 2016).

The impacts caused on invaded ecosystems by NZMS are mostly due to its elevated population density. For example, Hall et al. (2006) found populations formed by more than 700,000 individuals/m^2 in Polecat Creek River, Wyoming (USA). These population densities can account for the 80% of the secondary productivity, causing the consumption of 75% of the primary productivity in some invaded ecosystems (Hall et al. 2003, 2006). Therefore, this snail can rule carbon and nitrogen fluxes of the aquatic ecosystems that it invades (Hall et al. 2003). By contrast, there is no consensus about the impacts of NZMS on native populations as some authors report a lack of

impact (Brenneis et al. 2010; Kerans et al. 2014; Gergs and Rothhaupt 2015) while others have report negative impacts (Haynes et al. 1985; Brenneis et al. 2011; Kerans et al. 2014; Riley and Dybdahl 2015) or even positive impacts (Schreiber et al. 2002; Hellmair et al. 2011). These contrasting observations may be due to the different population densities that the NZMS can reach in colonized regions (Proctor et al. 2007).

The NZMS may tolerate a wide range of physical and chemical conditions. Some authors (Sousa et al. 2007; Lewin 2012) showed that this snail tolerates wide ranges of conductivity as it has been found in waters with conductivities from 66 µS/cm to 3240 µS/cm, or even to 7390 µS/cm (Schreiber et al. 2003). This trait is important for the survival of this species as the discharge of certain substances from anthropogenic sources, such as chloride salts, fertilizers, industrial effluents, and organic pollutants can increase the conductivity of aquatic ecosystems (Bellos and Sawidis 2005; Pal and Chakraborty 2017). Other studies have documented that the NZMS is eurythermal and, in consequence, is able to survive to a wide range of temperatures (0–29 °C) (Hylleberg and Siegismund 1987; Richards et al. 2004). Moreover, this species is able to tolerate short periods of air exposure (Haynes et al. 1985; Alonso and Castro-Díez 2008; Collas et al. 2014), which is necessary to survive an aerial translocation (i.e. attached to fish equipment, boats' hulls, etc.) (Alonso and Castro-Díez 2012a). Yet, air exposure might affect the ability of NZMS to tolerate a subsequent translocation to different water conditions. However, no information on this issue has been published. Additionally, the reproduction capacity after aerial exposure in NZMS has not been assessed, which is a key factor to the establishment of new populations.

The aim of this study was to assess the effect of a period of air desiccation (= aerial passive translocation) and two subsequent physical and chemical factors (temperature and conductivity) on the mortality, behavior and reproduction of *Potamopyrgus antipodarum*. We hypothesized that the period of air desiccation would decrease the ability of this snail to tolerate the subsequent abiotic conditions. Therefore, the mortality, behavior and reproduction of the NZMS would be affected negatively. This study can provide new data about what environmental conditions the NZMS needs to establish and multiply successfully in recipient ecosystems with different properties than those of the original ecosystem.

Methods

Experimental population

Animals for this experiment were collected from a laboratory population kept in two 60-l glass aquaria with control water (moderately hard USEPA: 96 mg $NaHCO_3$, 60 mg $CaSO_4*2H_2O$, 4 mg KCl, 122.2 mg $MgSO_4*7H_2O$/l of deionized water), enriched with calcium carbonate (10 mg de $CaCO_3$/l of deionized water) (United States Environmental Protection Agency 2002). We randomly selected 360 adults with a mean shell length (± SD) of 3.63 ± 0.24 mm. Animals were distributed randomly

in five acclimatization glass vessels (1.25 l). Individuals with similar sizes were chosen to rule out an effect of this variable, since size is known to influence the desiccation tolerance of this gastropod. In fact, larger individuals tolerate desiccation better than smaller ones (Richards et al. 2004). Individuals were subjected to an acclimatization period of 48 hours in a climatic chamber at 18 °C (ANSONIC VAC0732).

Experimental design and analyzed variables

Six treatments were established (Table 1). Three of the treatments were subjected to a desiccation process and to a subsequent rehydration. The three remaining treatments were used as controls without desiccation. Physical and chemical factors applied on each treatment (C18, D18, C10, D10, C-cond18 and D-cond18) are summarized in Table 1.

Two climatic chambers (ANSONIC®VAC0732) were used to attain the target temperatures (18 °C and 10 °C) (Table 1). These temperatures were chosen because they resembled those reached in Mediterranean aquatic habitats during spring-summer and autumn-winter respectively (Bennett et al. 2015). Normal values of conductivity (300 µS/cm; Table 1) corresponded to those of the USEPA water and high values of conductivity (3000 µS/cm; Table 1) were achieved by adding 1669.4 mg of sodium chloride NaCl (99% minimum, Lot 47H1049, Sigma, Germany) to 1.5 l of USEPA water. These physical and chemical values were chosen to simulate the values of physical and chemical conditions that occur in the aquatic environments susceptible to be invaded by the NZMS, such as endorheic basins, rivers, estuaries or inner seas (Costil et al. 2001; Dybdahl and Kane 2005; Moffitt and James 2012; Astel et al. 2016). Glass vessels (volume, 0.23 l; height, 6 cm; diameter, 8 cm; control water volume, 0.17 l) were used as experimental units. They were covered with a perforated Petri dish to reduce water evaporation. Each desiccation treatment was reproduced by slipping each snail on a filter paper until their shells lost the shine caused by water. Snails of control treatments were not slipped on a filter paper since this manipulation does not have an effect on the survival (Alonso and Castro-Díez 2012a). Then, snails were left in a climatic chamber with 18.5 ± 0.5 °C (mean ± SD; n = 37 measures) and 67.6 ± 4.5% of relative humidity (mean ± SD; n = 37 measures) during 20 hours. Each treatment was replicated seven times with eight randomly selected individuals per replicate (Fig. 1).

After the air exposure period, snails were translocated to USEPA water with the physical and chemical properties showed in Table 1. Experimental units were the same as those mentioned above. The mortality of adult snails was assessed on days 3, 4, 5 and 6 after the start of the rehydration. As few snails survived after this period (see Results), survivors to air exposure and an equal number of snails of the respective controls were individually translocated to glass vessel units (volume, 0.03 l; height, 4 cm; diameter, 4.5 cm; control water volume, 0.023 l) (Fig. 1) with the same physical and chemical conditions represented in Table 1. Glass vessels were covered with a perforated plastic lid to reduce the water evaporation.

Measures of conductivity, dissolved oxygen and temperature of water were monitored every 1–2 weeks for 50 days by randomly selecting three glass vessels of each desiccation

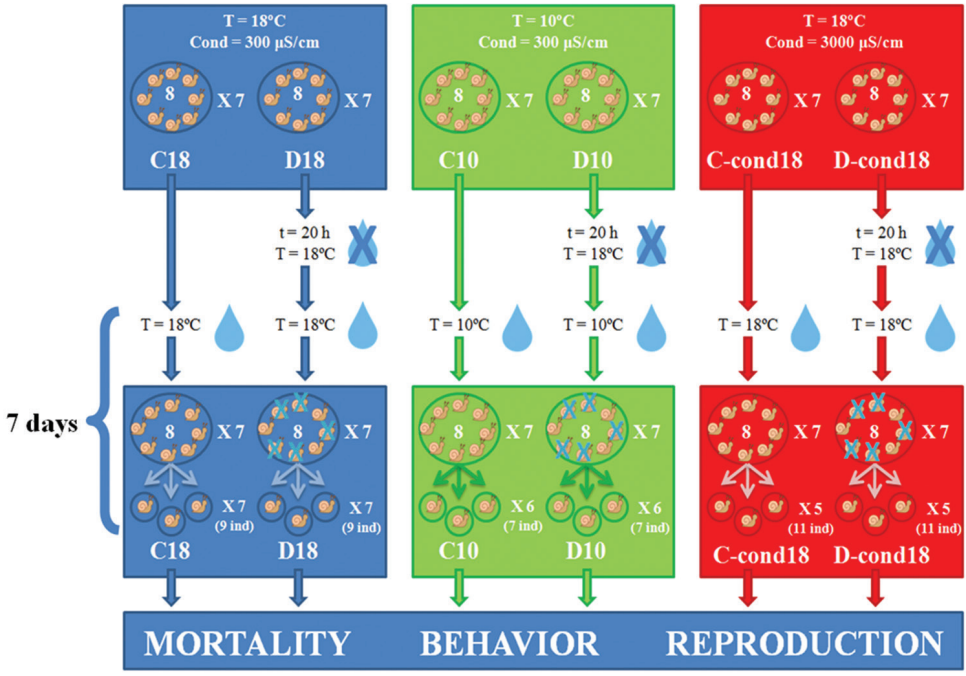

Figure 1. Diagram of the experimental design.

Table 1. Physical and chemical properties of desiccation treatments and their respective controls. In the treatment code "D" means "desiccation" and "C" means "control" (not subjected to desiccation); the number indicates target water temperature and "cond" indicates high conductivity. C18: normal temperature and normal conductivity control; D18: desiccation treatment with normal temperature and normal conductivity; C10: low temperature and normal conductivity control; D10: desiccation treatment with low temperature and normal conductivity; C-cond18: high conductivity and normal temperature control; D-cond18: desiccation treatment with high conductivity and normal temperature.

Treatment code	Desiccation period (hours)	Water temperature (°C)	Conductivity (µS/cm)
C18	0	18	300
D18	20	18	300
C10	0	10	300
D10	20	10	300
C-cond18	0	18	3000
D-cond18	20	18	3000

treatment and each control. A digital conductivimeter (TDS&EC meter, GHB) was used to measure the water temperature and conductivity and a portable oxymeter (OXI 45+, CRISON Instruments) to measure the dissolved oxygen concentration. The air temperature and the relative humidity of climatic chambers were measured every 3 hours using two climate recorders (LOG32, DOSTMANN electronic GmbH, Germany).

Selected endpoints were three parameters related with animal fitness (Table 2): 1) **Mortality** was assessed as the cumulative percentage of dead adults at day 50 after

Table 2. Summary of the analyzed parameters, the variables of each parameter and the statistical analysis applied.

Parameters	Variables	Comparisons	Statistical analysis
Mortality	Cumulative percentage of dead adults at day 50 after rehydration	Controls	Kruskal-Wallis test
		Desiccation treatments – Controls	Mann-Whitney U tests
		Desiccation treatments	One-way ANOVA
Behavior	Reaction time	–	Mixed ANOVA and post hoc test (Student t pairwise with Bonferroni correction)
	Cumulative number of immobile adults at day 50 after rehydration	Desiccation treatments – Controls	Mann-Whitney U tests
		Desiccation treatments	Kruskal-Wallis test
Reproduction	Total number of neonates per live adult at day 7 after rehydration	Desiccation treatments – Controls	Mann-Whitney U tests
		Desiccation treatments	Kruskal-Wallis test
	Cumulative number of total, dead and live neonates at day 50 after rehydration	Desiccation treatments – Controls	Mann-Whitney U tests
		Desiccation treatments	Kruskal-Wallis test

rehydration. A snail was considered to be dead if its reaction time (see below) exceeded 150 seconds and if no reaction was observed after having touched its operculum with forceps. All dead animals were removed of the experiment after monitoring. These observations were carried out 2–3 days per week until day 50 after rehydration. 2) **Behavior** was assessed by two variables: the reaction time (in seconds) employed by every live adult to start the normal movement after being disturbed and the cumulative number of immobile adults at day 50 after rehydration. Normal movement was considered when the individual pulled its soft body out of the shell and started sliding using its foot. Firstly, the retraction into the shell was stimulated by picking individuals up with a forceps by the central part of their shells. Secondly, individuals were rapidly pulled out from water and deposited at the bottom of the glass vessel with the operculum facing towards the bottom. The time employed to start the normal movement was assessed with a chronometer (Onstart 100, Geonaute) (Alonso and Camargo 2009). To study the number of snails that were immobile in each treatment, the quotient between the number of times that the individual of each replicate was immobile (= cumulative number of immobile adults at day 50 after rehydration) and the number of days when activity was measured (= number of observations between 8–50 days after rehydration) was calculated. A snail was considered immobile when its reaction time exceeded 150 seconds (a value obtained from a previous pilot study showed that most of snails started moving before that time) and movement inside the shell was detected. These observations were carried out 2–3 days per week between 8–50 days after rehydration. 3) **Reproduction** was assessed by four variables: total number of neonates per live adult at 7 days after rehydration, cumulative number of neonates in each glass vessel, cumulative number of dead neonates (i.e. animals without movement) and cumulative number of live neonates (i.e. sliding animals). The three last variables were monitored every 1–2 weeks between 8–50 days after rehydration and before every water renewal

to avoid losing neonates in the process. During the 2 hours previous to water renewal, snails of every experimental unit were fed with three or four pellets (JBL, NovoPrawn, GmbH & Co KG, Germany) provided *ad libitum*. After monitoring, neonates were removed from the experiment with a plastic pipette. The analysis of all these variables was carried out with a stereomicroscope fitted with a cold light source (Motic MLC-150C) with a 50% of light intensity.

Statistical analysis

For each variable based on the cumulative number, two comparisons were made: the three controls were compared with their respective desiccation treatments through three Mann-Whitney U tests and desiccation treatments were compared among them through a Kruskal Wallis test or through a one-way ANOVA. Table 2 summarized the statistical analysis made for each variable.

Three kinds of comparisons were performed to study the influence of treatments (desiccation treatments and controls) on the cumulative percentage of mortality of adults (Table 2). Firstly, mortality of controls (C18, C10 and C-cond18) was compared through a non-parametric Kruskal-Wallis test. Global mortality in controls was less than 10% without significant differences among them. Thereafter, the effect of desiccation on the cumulative percentage of mortality was assessed by comparing each desiccation treatment (D18, D10 and D-cond18) with its control through a Mann-Whitney U test. Eventually, desiccation treatments were compared among themselves with a one-way ANOVA, since in this case homoscedasticity assumption was met (p = 0.14; Fligner-Killeen). Effect size was also report in the ANOVA analysis as η^2.

A mixed ANOVA was performed to study the influence of time and treatments (desiccation treatments and controls) on the reaction time of the NZMS between 8–50 days after rehydration (Table 2). Reaction time was log-transformed to achieve normality. Effect size was also report as η^2. Degrees of freedom were corrected through the Greenhouse-Geisser approach as the sphericity assumption was not met (Field 2005). When significant differences were obtained, a post-hoc test (Student t pairwise with Bonferroni correction) was carried out to analyze which treatments caused the differences in reaction time (Table 2). Two comparisons were performed to assess the effects of treatments on the cumulative number of immobile adults (= 150 seconds) (Table 2): firstly, desiccation treatments were compared with their respective controls through a Mann-Whitney U test and, afterwards, desiccation treatments were compared among themselves through a Kruskal-Wallis test.

The effect of treatments (desiccation treatments and controls) on the total number of neonates at 7 days after rehydration was studied through the ratio between the total number of neonates and the number of live adults of each replicate. Differences in the total number of neonates between the desiccation treatments and their controls were studied through the Mann-Whitney U test (Table 2). The total number of neonates per live adult at 7 days after rehydration was also compared between desiccation treatments through a

Kruskal-Wallis test (Table 2). On the other hand, the influence of treatments on the number of total neonates, dead neonates and live neonates between 8–50 days after rehydration was studied by calculating the cumulative number of these variables for each replicate at day 50 after rehydration (Table 2). Differences in the number of total, dead and live neonates between controls and their desiccation treatments were analyzed through Mann-Whitney U tests. Moreover, the comparison of the effects of the desiccation treatments on total, dead and live neonates was carried out through a Kruskal-Wallis test. A descriptive analysis was made for the influence of time on the number of total, dead and live neonates.

To decrease type I errors in multiple testing, a p-value of 0.01 was chosen. Surviving individuals of the same replicates were averaged during their individualization to avoid pseudoreplication (Fig. 1). In consequence, replicates ranged from 5 to 7. All the statistical analysis were carried out with R software (R Core Team 2017).

Data resources

The data underpinning the analysis reported in this paper are deposited at Figshare, https://doi.org/10.6084/m9.figshare.7708052.v1

Results

Physical and chemical properties

Overall, values of dissolved oxygen were relatively high in all treatments (> 8.5 mg O_2/l; n = 12 measures for each treatment), air temperature (mean ± SD) in climatic chambers was 17.6 ± 2.04 °C at normal temperature and 11 ± 0.73 °C at low temperature (n = 389 measures in each climatic chamber) and the mean water conductivity (± SD) was 2811.5 ± 177.1 µS/cm in the treatments with high conductivity and 303.4 ± 43.7 µS/cm in the treatments with normal conductivity (n = 15 measures for each treatment).

Mortality and behavior of adults

Only the 16.1% of total snails of the desiccation treatments survived after the period of exposure to air at 7 days of rehydration. Cumulative percentage of mortality at day 50 after rehydration was significantly higher in the desiccation treatments than in their respective controls ($p < 0.01$; Mann-Whitney U test). By contrast, differences in the cumulative percentage of mortality were non-significant between desiccation treatments ($F_{(2,18)} = 0.68$, $p = 0.52$, $\eta^2 = 0.07$ [effect size]; ANOVA) (Fig. 2).

The influence of time and treatments on the reaction time is shown in Figure 3. Time affected significantly the reaction time in each treatment between 8–50 days after rehydration ($p = 0.01$, $\eta^2 = 0.07$ [effect size]; Table 3). This trend was similar for

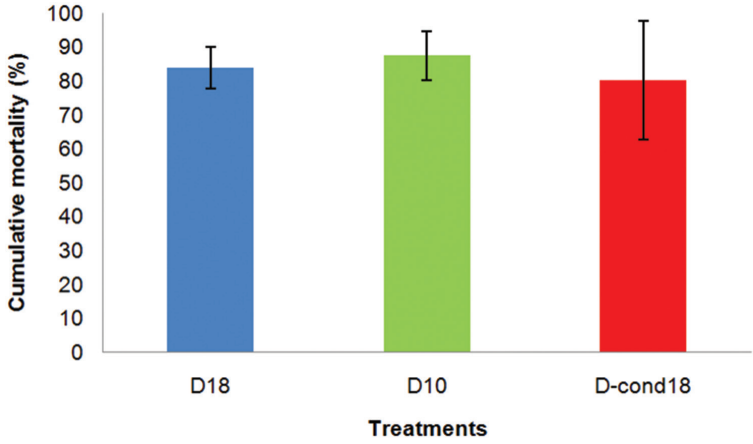

Figure 2. Mean (± SD) of the cumulative percentage of mortality in each desiccation treatment at day 50 after rehydration (n = 15 observations). No significant differences were found between the desiccation treatments (p > 0.01; ANOVA).

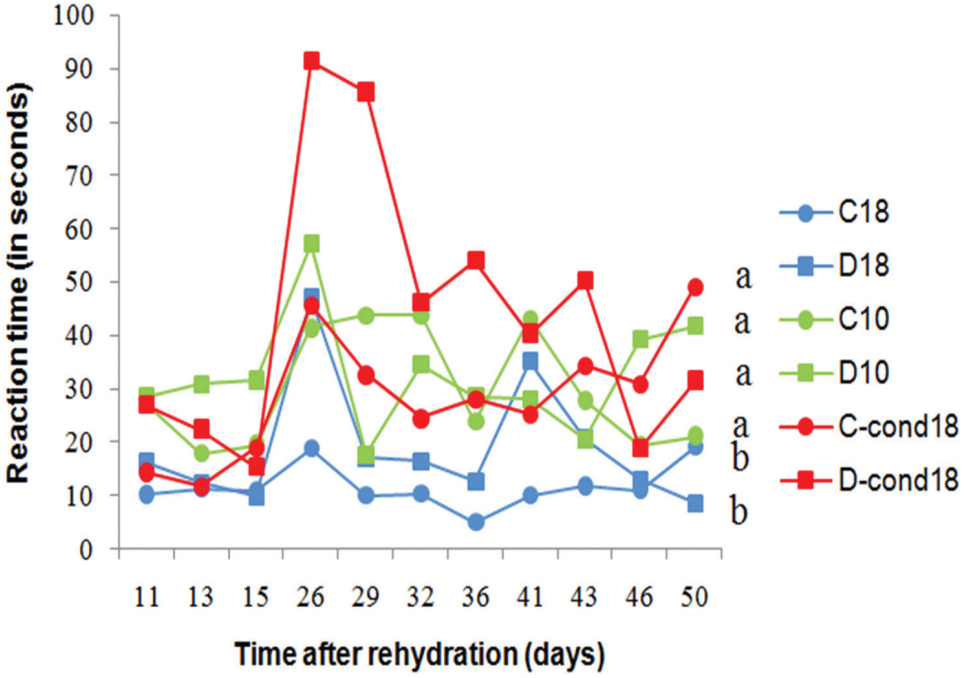

Figure 3. Mean reaction time (in seconds) of individuals of each treatment for each observation time between 8 and 50 days after rehydration (n = 11 observations). SD has been removed for clarity. Time affected significantly the reaction time (p < 0.05; mixed ANOVA). The interaction between time and treatments did not caused significant differences (p > 0.05; mixed ANOVA). Letters in right indicate significant differences in reaction time between treatments (p < 0.001; Student t pairwise with Bonferroni correction).

all treatments as interaction between treatments and time was not significant (p = 0.3, η^2 = 0.14 [effect size]) (Table 3). In contrast, the low temperature (C10 and D10) and high conductivity treatments (C-cond18 and D-cond18) affected significantly the reaction time (p < 0.001, η^2 = 0.27 [effect size]) (Table 3). In fact, C18 and D18 differed significantly with the rest of treatments (p < 0.05; Student t pairwise with Bonferroni correction). However, no significant differences were found neither between the low temperature control and its desiccation treatment (p > 0.05; Student t pairwise with Bonferroni correction) nor between the high conductivity control and its desiccation treatment (p > 0.05; Student t pairwise with Bonferroni correction).

On the other hand, no significant differences were found neither in the cumulative number of immobile individuals between controls and their respective desiccation treatments (p > 0.01 in all cases; Mann-Whitney U test) nor between desiccation treatments (χ^2 = 1.24, p = 0.54; Kruskal-Wallis) (data not shown).

Neonates production

Figure 4 shows the influence of treatments on the total number of neonates produced per live adult at 7 days after rehydration. No significant differences were found between desiccation treatments (χ^2 = 0.94, p = 0.63; Kruskal-Wallis) nor between controls and desiccation treatments (W = 42, p > 0.01 in all cases; Mann-Whitney U test). Moreover, although desiccation treatments had a lower number of adults than their respective controls, the amount of neonates per live adult was similar (Fig. 4).

Figure 5 represents the effects of treatments and time over the cumulative number of total, dead and live neonates between 8–50 days after rehydration. No significant differences in those variables between controls and their respective desiccation treatments were

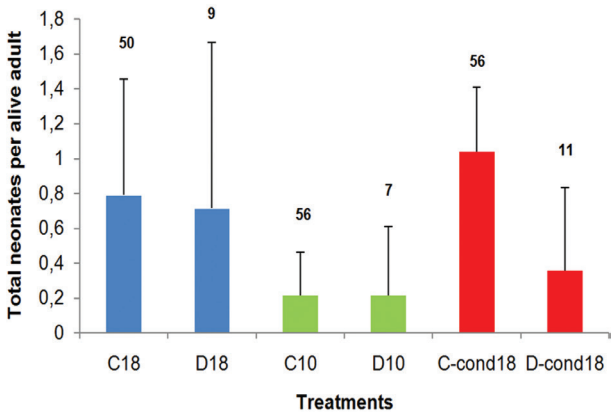

Figure 4. Mean (+ SD) of the total number of produced neonates per live adult in each treatment at 7 days after rehydration (n = 1 observation). Numbers indicate live adults of each treatment. No significant differences were found between desiccation treatments nor between controls and desiccation treatments (p > 0.01; Kruskal-Wallis and Mann-Whitney U test).

Table 3. Summary of results of mixed ANOVA assessing the influence of time and treatments on reaction time.[a]

Source of variation	Degrees of freedom[b]	F	p	Effect size
Within subject				
Time	5.8/163.4	2.82	**0.010**	0.07
Time × Treatment	29.2/163.4	1.14	0.300	0.14
Between subjects				
Treatment	5/28	9.71	**<0.001**	0.27

[a] Treatment (C18, D18, C10, D10, C-cond18 y D-cond18) was the intersubject factor, time (11 observations done between 8 and 50 days after rehydration) was the within-subject factor and reaction time (in seconds) was the dependent variable.
[b] Degrees of freedom (degrees of freedom of numerator/degrees of freedom of denominator) have been corrected for sphericity using the Greenhouse-Geisser approach (Field 2005).

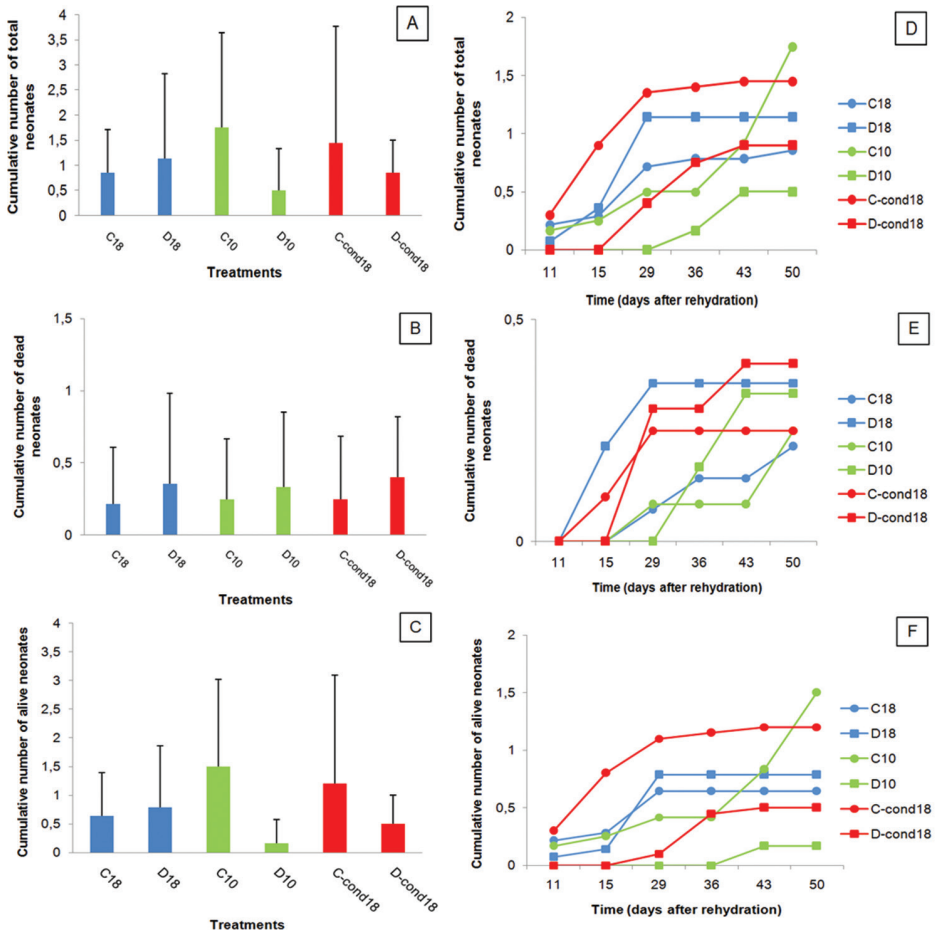

Figure 5. Mean (+ SD) of the cumulative number of total neonates (**A**), dead neonates (**B**) and live neonates (**C**) registered at day 50 after rehydration (n = 6 observations). No significant differences were found between treatments (p > 0.01; Mann-Whitney U test and Kruskal-Wallis test). Mean (SD has been removed for clarity) of the cumulative number per observation time of total neonates (**D**), dead neonates (**E**) and live neonates (**F**) registered between 8 and 50 days after rehydration (n = 6 observations).

found ($p > 0.01$ in all cases; Mann-Whitney U test) (Fig. 5A–C). In addition, a similar number of total, dead and live neonates was found in all the desiccation treatments ($p > 0.01$ in all cases; Kruskal-Wallis) (Fig. 5A–C). All treatments started producing neonates in the first day of observation (11 days after rehydration), except in the desiccation treatments with low temperature and high conductivity (D10 and D-cond18), which started producing neonates later (Fig. 5D). The conditions of the desiccation treatments D10 and D-cond18 were the ones that most delayed the production of live neonates (Fig. 5E, F). Moreover, it is worth noting that no live neonates were observed in the desiccation treatment with low temperature until almost the end of the observation period (Fig. 5F).

Discussion

This study confirmed that the NZMS is able to survive and reproduce under contrasting physical and chemical conditions after a short-term desiccation period. These conditions can be found in new regions where the NZMS can arrive after a brief period of exposure to air. We found a higher mortality than expected after a short air exposure period. For instance, Alonso and Castro-Díez (2012a) found a fewer percentage of dead snails at 24 hours. These differences may be because we established a higher temperature during the desiccation process, and higher temperatures are known to decrease the survival of this species (Richards et al. 2004). Anyway, exposure to air is a limiting factor for the aerial passive translocation of the NZMS.

A higher number of individuals died in the desiccation treatments as compared to controls. This result confirmed our initial hypothesis and it coincides with those of other studies (Alonso and Castro-Díez 2012a). However, under natural conditions, the survival of the NZMS to air exposure can be increased if the snail is carried in a moist substrate (Alonso et al. 2016). In fact, *Potamopyrgus antipodarum* is known as mudsnail because during dry periods it buries itself into the sediment (Duft et al. 2003).

Treatments affected the NZMS behavior in different ways. The high conductivity increased the reaction time. The desiccation process had little influence in this regard. Thus, high conductivity could have negative effects on the acclimatization of the mudsnail to the recipient ecosystems, because this effect may make access to resources difficult and impair the escape from potential predators. Low temperatures also caused a significant increase in the reaction time. Moreover, other authors have already confirmed that low temperatures affect negatively other life history traits, such as reproduction, in this mollusk (Gust et al. 2011). In contrast, exposure to air did not have a significant effect on the reaction time of the NZMS. Therefore, a brief exposure to air period would not impede the subsequent acclimatization of the NZMS in an aquatic habitat with a low temperature or a high conductivity.

Regarding reproduction, we found that neonates tolerated the new environmental conditions (temperature and conductivity) after rehydration. Neither high conductivities nor low temperatures reduced the number of neonates, in contrast to other authors who reported that low temperatures slow down the NZMS embryonic development and production (Gust et al. 2011). Our results also suggest that survivors to a brief

period of passive propagation by air might be able to produce neonates, even though they face unfavorable temperatures and conductivities. Besides, these results suggest that even a low number of surviving adults after an aerial translocation could generate a new population in the recipient ecosystem.

Neonates showed a wide tolerance to temperatures and conductivities. Embryos are protected against air exposure since they are housed in a brood pouch carried by adult females until they are fully formed and functional (Proctor et al. 2007). Although the growth of neonates was not monitored, our results show a likely potential for propagation in natural conditions. Besides, human disturbances can boost NZMS spread in aquatic ecosystems. For instance, the rise of the pollution in Europe has triggered an increase of the quantity of ions in great European rivers and, in consequence, the increase of the water conductivity in those aquatic ecosystems, which favors the dispersal and the establishment of exotic species resistant to high conductivities (Grabowski et al. 2009), such as the NZMS (Costil et al. 2001). However, a combination of a brief period of exposure to air and a relatively high conductivity tended to delay the production of live neonates. Therefore, an increase of the conductivity in aquatic habitats due to pollution could have negative effects in this regard. On the other hand, the desiccation treatment combined with low temperature tended to slow down the production of viable neonates. This might be a problem for the naturalization of the NZMS, as their populations with low reproductive rates are more susceptible to disturbance (Proctor et al. 2007). Therefore, low temperatures combined with a brief period of air exposure could limit the propagation of the NZMS. However, this impediment could be mitigated in the future warmer conditions predicted by climate change models.

The invasive success of the NZMS resides in various functional traits shared with other invasive species, such as fast growth rate, high fecundity rate, early sexual maturity, asexual reproduction, a tolerance to wide ranges of abiotic conditions, and a high phenotypic plasticity, among others (Alonso and Castro-Díez 2008). This study suggests that a brief period of exposure to air does not reduce the ability of this snail to tolerate subsequent low temperatures and high conductivities. Moreover, survivors to a brief period of exposure to air are able to reproduce in different abiotic conditions, which indicate a potential to colonize and to establish in the recipient ecosystems. These results suggest that management plans should take into account that an aerial translocation is a highly plausible route of introduction in aquatic habitats for this exotic species.

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References

Aarnio K, Bonsdorff E (1997) Passing the gut of juvenile flounder, *Platichthys flesus*: differential survival of zoobenthic prey species. Marine Biology 129(1): 11–14. https://doi.org/10.1007/s002270050140

Alonso A, Camargo JA (2009) Long-term effects of ammonia on the behavioral activity of the aquatic snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca). Archives of Environmental Contamination and Toxicology 56(4): 796–802. https://doi.org/10.1007/s00244-008-9266-7

Alonso A, Castro-Díez P (2008) What explains the invading success of the aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca)? Hydrobiologia 614(1): 107–116. https://doi.org/10.1007/s10750-008-9529-3

Alonso A, Castro-Díez P (2012a) Tolerance to air exposure of the New Zealand mudsnail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca) as a prerequisite to survival in overland translocations. NeoBiota 14: 67–74. https://doi.org/10.3897/neobiota.14.3140

Alonso A, Castro-Díez P (2012b) The exotic aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca): state of the art of a worldwide invasion. Aquatic Sciences 74(3): 375–383. https://doi.org/10.1007/s00027-012-0254-7

Alonso A, Valle-Torres G, Castro-Díez P (2016) Survival of an invasive aquatic snail to overland translocation in non-aquatic media: implications for spreading. Limnologica 57: 60–65. https://doi.org/10.1016/j.limno.2016.01.002

Astel AM, Bigus K, Obolewski K, Glinska-Lewczuk K (2016) Spatiotemporal assessment of water chemistry in intermittently open/closed coastal lakes of southern Baltic. Estuarine, Coastal and Shelf Science 182: 47–59. https://doi.org/10.1016/j.ecss.2016.09.010

Bellos D, Sawidis T (2005) Chemical pollution monitoring of the river Pinios (Thessalia–Greece). Journal of Environmental Management 76: 282–292. https://doi.org/10.1016/j.jenvman.2005.01.027

Bennett DM, Dudley TL, Cooper SD, Sweet SS (2015) Ecology of the invasive New Zealand mud snail, *Potamopyrgus antipodarum* (Hydrobiidae), in a Mediterranean-climate stream system. Hydrobiologia 746(1): 375–399. https://doi.org/10.1007/s10750-014-2136-6

Brenneis VEF, Sih A, De Rivera CE (2010) Coexistence in the intertidal: interactions between the nonindigenous New Zealand mud snail *Potamopyrgus antipodarum* and the native estuarine isopod *Gnorimosphaeroma insulare*. Oikos 119(11): 1755–1764. https://doi.org/10.1111/j.1600-0706.2010.18471.x

Brenneis VEF, Sih A, De Rivera CE (2011) Integration of an invasive consumer into an estuarine food web: direct and indirect effects of the New Zealand mud snail snail. Oecologia 167(1): 169–179. https://doi.org/10.1007/s00442-011-1962-88

Carlton J (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanography and Marine Biology Annual Review 23: 313–371.

Cheng YW, LeClair LL (2011) A quantitative evaluation of the effect of freezing temperatures on the survival of New Zealand mudsnails (*Potamopyrgus antipodarum* Gray, 1843), in Olympia Washington's Capitol Lake. Aquatic Invasions 6(1): 47–54. https://doi.org/10.3391/ai.2011.6.1.06

Collas FPL, Koopman KR, Hendriks AJ, Van Der Velde G, Verbrugge LNH, Leuven RSEW (2014) Effects of desiccation on native and non-native molluscs in rivers. Freshwater Biology 59(1): 41–55. https://doi.org/10.1111/fwb.12244

Costil K, Dussart G, Daguzan J (2001) Biodiversity of aquatic gastropods in the Mont St-Michel basin (France) in relation to salinity and drying of habitats. Biodiversity and Conservation 10(1): 1–18. https://doi.org/10.1023/A:1016670708413

Davidson TM, Brenneis VEF, De Rivera C, Draheim R, Gillespie GE (2008) Northern range expansion and coastal occurrences of the New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) in the northeast Pacific. Aquatic Invasions 3(3): 349–353. https://doi.org/10.3391/ai.2008.3.3.12

Duft M, Schulte-Oehlmann U, Tillmann M, Markert B, Oehlmann J (2003) Toxicity of triphenyltin and tributyltin to the freshwater mudsnail *Potamopyrgus antipodarum* in a new sediment biotest. Environmental Toxicology and Chemistry 22(1): 145–152. https://doi.org/10.1002/etc.5620220119

Dybdahl M, Kane S (2005) Adaptation vs. phenotypic plasticity in the success of a clonal invader. Ecology 86(6): 1592–1601. https://doi.org/10.1890/04-0898

Field A (2005) Discovering Statistics Using SPSS. SAGE Publications, London, 952 pp.

Gergs R, Rothhaupt K (2015) Invasive species as driving factors for the structure of benthic communities in Lake Constance, Germany. Hydrobiologia 746(1): 245–254. https://doi.org/10.1007/s10750-014-1931-4

Grabowski M, Bacela K, Konopacka A, Jazdzewski K (2009) Salinity-related distribution of alien amphipods in rivers provides refugia for native species. Biological Invasions 11(9): 2107–2117. https://doi.org/10.1007/s10530-009-9502-8

Gust M, Buronfosse T, André C, Mons R, Gagné F, Garric J (2011) Is exposure temperature a confounding factor for the assessment of reproductive parameters of New Zealand mudsnails *Potamopyrgus antipodarum* (Gray)? Aquatic Toxicology 101(2): 396–404. https://doi.org/10.1016/j.aquatox.2010.11.013

Hall RO, Dybdahl MF, VanderLoop MC (2006) Extremely high secondary production of introduced snails in rivers. Ecological Applications 16(3): 1121–1131. https://doi.org/10.1890/1051-0761(2006)016[1121:EHSPOI]2.0.CO;2

Hall RO, Tank JL, Dybdahl MF (2003) Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Frontiers in Ecology and the Environment 1(8): 407–411. https://doi.org/10.2307/3868137

Haynes A, Taylor BRJ, Varley ME (1985) The influence of the mobility of *Potamopyrgus jenkinsi* (Smith, E.A.) (Prosobranchia: Hydrobiidae) on its spread. Archiv für Hydrobiologie 103(4): 497–508.

Hellmair M, Goldsmith G, Kinziger AP (2011) Preying on invasives: the exotic New Zealand mudsnail in the diet of the endangered tidewater goby. Biological Invasions 13(10): 2197–2201. https://doi.org/10.1007/s10530-011-0054-3

Hoy M, Boese BL, Taylor L, Reusser D, Rodríguez R (2012) Salinity adaptation of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) in the Columbia River estuary (Pacific Northwest, USA): physiological and molecular studies. Aquatic Ecology 46(2): 249–260. https://doi.org/10.1007/s10452-012-9396-x

Hylleberg J, Siegismund HR (1987) Niche overlap in mud snails (Hydrobiidae): freezing tolerance. Marine Biology 94(3): 403–407. https://doi.org/10.1007/BF00428246

Kerans B, Cada CA, Zickovich J (2014) Asymmetrical behavioural interactions between the New Zealand mud snail, *Potamopyrgus antipodarum*, and scraping, collector-gathering and collector-filtering macroinvertebrates. Journal of Freshwater Ecology 25(4): 657–666. https://doi.org/10.1080/02705060.2010.9664415

Lewin I (2012) Occurrence of the invasive species *Potamopyrgus antipodarum* (Prosobranchia: Hydrobiidae) in mining subsidence reservoirs in Poland in relation to environmental factors. Malacologia 55(1): 15–31. https://doi.org/10.4002/040.055.0102

Lodge DM, Stein RA, Brown KM, Covich AP, Bronmark C, Garvey JE, Klosiewski SP (1998) Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Australian Journal of Ecology 23(1): 53–67. https://doi.org/10.1111/j.1442-9993.1998.tb00705.x

Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution 13(5): 195–198. https://doi.org/10.1016/S0169-5347(97)01286-X

Malone C (1965) Killdeer (*Charadrius vociferus* Linnaeus) as a means of dispersal for aquatic gastropods. Ecology 46(4): 551–552. https://doi.org/10.2307/1934894

Moffitt CM, James CA (2012) Dynamics of *Potamopyrgus antipodarum* infestations and seasonal water temperatures in a heavily used recreational watershed in intermountain North America. Aquatic Invasions 7(2): 193–202. https://doi.org/10.3391/ai.2012.7.2.005

Pal S, Chakraborty K (2017) Different aspects of chloride in freshwater: a review. International Journal of Current Trends in Science and Technology 7(8): 20295–20303.

Proctor T, Kerans B, Clancey P, Ryce E, Dybdahl MF, Gustafson D, Hall RO, Pickett F, Richards D, Waldeck RD, Chapman J, Wiltshire RH, Becker D, Anderson M, Pitman B, Lassuy D, Heimowitz P, Dwyer P, Levri EP (2007) National Management and Control Plan for the New Zealand mudsnail (*Potamopyrgus antipodarum*). Aquatic Nuisance Species Task Force. http://www.anstaskforce.gov/Documents/NZMS_MgmtControl_Final.pdf

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9(8): 981–993. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Richards DC, O'Connell P, Shinn D (2004) Simple control method to limit the spread of the New Zealand mudsnail *Potamopyrgus antipodarum*. North American Journal of Fisheries Management 24(1): 114–117. https://doi.org/10.1577/M02-133

Richardson DM (2011) Fifty years of invasion ecology: the legacy of Charles Elton. John Wiley and Sons, Chichester, 456 pp.

Riley LA, Dybdahl MF (2015) The roles of resource availability and competition in mediating growth rates of invasive and native freshwater snails. Freshwater Biology 60(7): 1308–1315. https://doi.org/10.1111/fwb.12566

Riley LA, Dybdahl MF, Hall RO (2008) Invasive species impact: asymmetric interactions between invasive and endemic freshwater snails. Journal of the North American Benthological Society 27(3): 509–520. https://doi.org/10.1899/07-119.1

Sala O, Chapin F, Armesto J, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke L, Jackson R, Kinzig A, Leemans R, Lodge D, Mooney H, Oesterheld M, Poff N, Sykes M, Walker B, Walker M, Wall D (2000) Biodiversity – Global biodiversity conditions for the year 2100. Science 287(5459): 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Schreiber ESG, Lake PS, Quinn GP (2002) Facilitation of native stream fauna by an invading species? Experimental investigations of the interaction of the snail, *Potamopyrgus antipodarum* (Hydrobiidae) with benthic native fauna. Biological Invasions 4: 317–325. https://doi.org/10.1023/A:1020925022843

Schreiber ESG, Quinn GP, Lake PS (2003) Distribution of an alien aquatic snail in relation to flow variability, human activities and water quality. Freshwater Biology 48: 951–961. https://doi.org/10.1046/j.1365-2427.2003.01070.x

Sousa R, Antunes C, Guilhermino L (2007) Species composition and monthly variation of the Molluscan fauna in the freshwater subtidal area of the River Minho estuary. Estuarine, Coastal and Shelf Science 75: 90–100. https://doi.org/10.1016/j.ecss.2007.02.020

Strayer D (1999) Effects of alien species on freshwater mollusks in North America. Journal of the North American Benthological Society 18(1): 74–98. https://doi.org/10.2307/1468010

United States Environmental Protection Agency (2002) Short-term methods for estimating the chronic toxicity of effluents and receiving waters to freshwater organisms. U.S. Environmental Protection Agency, Washington DC, 335 pp.

Vazquez R, Ward DM, Sepulveda A (2016) Does water chemistry limit the distribution of New Zealand mud snails in Redwood National Park? Biological Invasions 18(6): 1523–1531. https://doi.org/10.1007/s10530-016-1098-1

Winterbourn M (1970) The New Zealand species of *Potamopyrgus* (Gastropoda:Hydrobiidae). Malacologia 10(2): 283–321.