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LOW SPECIFIC CONDUCTIVITY LIMITS GROWTH AND SURVIVAL OF THE NEW ZEALAND MUD SNAIL FROM THE UPPER OWENS RIVER, CALIFORNIA

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ABSTRACT.—The New Zealand mud snail (NZMS), *Potamopyrgus antipodarum* (Gray), is an invasive species of aquatic snail that is becoming widespread in inland and coastal waters of the western United States. The New Zealand mud snail can have significant impacts on stream ecosystems, as they may consume a large fraction of available algae production and compete with and displace native invertebrates. Even though the distribution of this species is expanding, the habitat conditions conducive to invasion are incompletely understood. Surveys following the NZMS invasion in the Upper Owens River, California, indicated that the snail may be excluded from waters where dissolved solute content is low, so experimental studies were undertaken to evaluate survival and growth as a function of varied specific conductivity (SC) and calcium availability. Juvenile snails were collected from the Upper Owens River and reared in dilutions of natural river water adjusted to 10, 50, 100, 200 and 300 $\mu S \cdot cm^{-1}$ SC. Experiments were also conducted with newborn clones raised in river water dilutions ranging from 25 to 200 $\mu S \cdot cm^{-1}$ to examine mortality and growth at this sensitive stage of development. In addition, calcium-free artificial river water was prepared at 200 $\mu S \cdot cm^{-1}$ to test for the independent effect of limitation of this mineral ion required for shell-building. Significant reductions in survival and growth occurred among treatments diluting river water from 300 to 50 $\mu S \cdot cm^{-1}$. No growth was found at or below 25 $\mu S \cdot cm^{-1}$. Growth was also inhibited in calcium-free artificial water compared to natural river water with the same SC, showing that lack of this mineral impedes development. These results suggest that many streams in the range of 25–200 $\mu S \cdot cm^{-1}$ cannot support productive NZMS populations and that nuisance invasions may be most prevalent in waters above 200 $\mu S \cdot cm^{-1}$ where sufficient dissolved mineral content is present for growth.

Key words: New Zealand mud snail, Potamopyrgus antipodarum, *specific conductivity, invasive species, physiological stress, Hydrobiidae, Upper Owens River.*

Since the introduction of the New Zealand Mud Snail (NZMS), *Potamopyrgus antipodarum* (Gray), into streams of the western United States in the mid-1980s, there has been growing concern over how this exotic species might alter freshwater ecosystems. As the range and incidence of the NZMS invasion has expanded, biologists have conducted toxicological studies on how to decontaminate fishing gear, which is thought to be a primary vector for dissemination (Richards et al. 2004, Hosea and Finlayson 2005), initiated public education campaigns (e.g., www.protectyourwaters.net), and conducted basic research on how the snails affect aquatic ecosystems (Hall et al. 2006). Studies in New Zealand (Winterbourn 1970, Broekhuizen et al. 2001, Suren 2005) have shown that this snail has an affinity for streams in disturbed agricultural landscapes and in association with sediment deposits (presumably the derivation of the common name), but there is little information on physicochemical requirements that might permit an understanding of where snails may invade and multiply. Mapping the spread of the New Zealand mud snail in western North America has enabled tracking (www.esg.montana.edu/aim/mollusca/nzms/status.html), but the absence of water quality data from these location records limits insight in to the habitat conditions promoting invasion.

The potential for the New Zealand mud snail to displace native stream invertebrates (Kerans et al. 2005), alter ecosystem structure and function (Hall et al. 2003), and threaten recreational fisheries and native fish through a loss of food resources (Vinson and Baker 2008) is a widely recognized problem. The conventional wisdom is that the snail can occur in many kinds of habitat, from inland freshwater streams and lakes to coastal estuaries, but again, data on water chemistry in relation to

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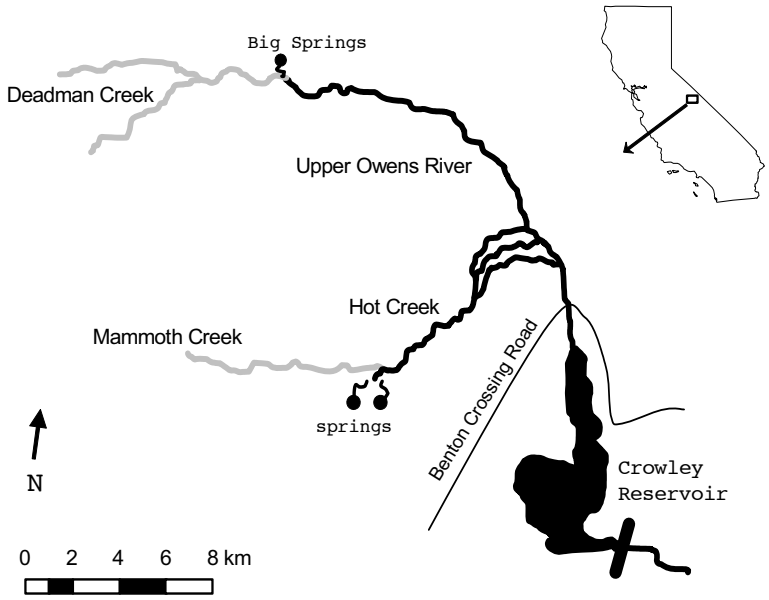

Fig. 1. Map of Upper Owens River and tributaries showing the varied specific conductivities in the mainstem of the river and tributaries. Waters with low specific conductivities (<100 μS · cm^{-1}) are shown in gray and those with higher conductivities (>200 to 500 μS · cm^{-1}) are shown in black. Note that the New Zealand mud snail occurs in the mainstem river and in the Hot Creek tributary, but not in Deadman Creek or Mammoth Creek.

snail density are seldom available. Areas of concentration in the western United States include the Snake River system (ID), the Greater Yellowstone area (MT, WY), the Wasatch Mountains (UT), coastal estuaries (CA, OR), the lower Colorado River (AZ), and the Owens River (CA). Traits which make the New Zealand mud snail an especially problematic invasive species include reproduction that is typically through asexual cloning with birth to live young from an internal brood chamber, resistance to desiccation via a closeable operculum, and tolerance of physical habitat disturbance and pollution (Haynes et al. 1985, Dybdahl and Lively 1995, Schreiber et al. 2003, Suren 2005). Although salinity tolerance of the New Zealand mud snail has been examined (Jacobsen and Forbes 1997), its capacity to live in waters of dilute mineral content has been overlooked in previous studies and observations. Freshwater gastropods are known to maintain osmotic content of body fluids and tissues above that of the environment and so incur an expense both in ionic solute balance and excretion of excess water as hyperosmotic regulators (McMahon 1983). In addition, calcium uptake from dilute waters and deposition into shells comes at considerable metabolic cost. Although most freshwater mollusk diversity tends to be found in hard waters, many species can survive in low-calcium habitats (Russell-Hunter et al. 1981, Pip 1986), and there is often a lack of correlation between shell calcium, growth, and dissolved calcium concentrations (Hunter and Lull 1977). The absence of a general pattern justifies the need to conduct specific studies of NZMS tolerance to dilute water chemistry conditions.

Introduction of the New Zealand mud snail into the Upper Owens River, Mono County, California, likely occurred just prior to 1999 when the snail was first found in low numbers at several localities in the river (D.B. Herbst unpublished data). The snail has since expanded throughout the river (specific conductivities ranging from 200 to 500 μS · cm^{-1}), and upstream to Big Springs and Hot Creek (areas of groundwater-dominated inflow), but has not been found above these points in the snowmelt-dominated (usually in the range of 50–100 μS · cm^{-1}) Deadman Creek or Mammoth Creek tributaries (Fig. 1). The only other mollusks found in the Upper Owens River are fingernail clams (*Pisidium;* also found in Deadman Creek) and the snail *Physa*, neither of which are abundant. Though habitat disturbance from

livestock grazing, bank erosion, sedimentation, and stream channel modification likely play a role in NZMS abundance in the Upper Owens River, the continued absence of snails in the more dilute tributary waters suggested that the New Zealand mud snail might not survive in waters of low specific conductivity (SC). The objective of this research was to test the hypothesis that environments of reduced dissolved solute content and calcium availability restrict the growth and survival of the New Zealand mud snail. If confirmed, this hypothesis could provide an explanation quantifying the apparent limitations on NZMS distribution in waters of low ionic concentration. The experiments presented here provide an explicit test of how SC from 10 to 300 $\mu S \cdot cm^{-1}$ and absence of calcium affects the survival and growth rates of the New Zealand mud snail. We also outline how these results may be used to interpret known distribution and anticipate future invasions in a predictive framework, as has been proposed for other freshwater snails (Lodge et al. 1987) and biological invasions (Lodge 1993, Moyle and Light 1996).

METHODS

Specific Conductivity Range-finding Experiment

New Zealand mud snails were collected from the Upper Owens River above Benton Crossing Road (37°41′51.22″N, 118°45′50.17″W; 2080 m elevation) using a D-frame sampling net (500-micron mesh) in late March 2006. Sediment and macrophytes were removed in the field and mud snails were then sorted in the laboratory to obtain a size cohort of approximately 1-mm spire height (range 0.75–1.5 mm). Fifty New Zealand mud snails were randomly selected from the 1-mm size cohort for measurement of initial length (aperture base to spire tip) and weight distributions. Length measurements to ±0.01 mm were made with an eyepiece micrometer under a stereoscope at 10X magnification. After drying at 70°C for 36 hours, individual snails were weighed with a Cahn electrobalance after drying.

Water collected from the Upper Owens River at Benton Crossing (SC = 365 $\mu S \cdot cm^{-1}$, alkalinity 180 $mg \cdot L^{-1}$) was used to prepare all experimental treatment solutions. After being filtered through 0.45-micron GF/B filters, the river water was diluted with deionized water to create treatment solutions of 5 conductivity levels: 300, 200, 100, 50 and 10 $\mu S \cdot cm^{-1}$. To test the separate role of Ca^{+2} in altering growth and survival of snails, an artificial 200 $\mu S \cdot cm^{-1}$ calcium-free solution was also prepared using a combination of the following salts: 65.9 $mg \cdot L^{-1}$ $NaHCO_3$, 15.5 $mg \cdot L^{-1}$ KCl, 38.6 $mg \cdot L^{-1}$ $MgCl_2$–$7H_2O$ and 46.5 $mg \cdot L^{-1}$ $MgSO_4$–7 H_2O (final concentrations after adjusting to 200 $\mu S \cdot cm^{-1}$). Specific conductivity ($\mu S \cdot cm^{-1}$) was measured throughout the entire experiment with a portable Oakton 35630-00 pH/conductivity meter (temperature compensating readings to 25°C).

Benthic algae were collected from shallow river margin substrates at Benton Crossing on the Upper Owens River to serve as a food source during the experiment. Algae and fine particles passing through a 2-mm sieve were placed in a volume of 2 L natural river water and 10 $mL \cdot L^{-1}$ $NaNO_3$ was added to stimulate algal growth. Eight clear plastic culture containers were then filled with 250 mL of this algae and nutrient solution and placed in direct sunlight. Any snails found were picked out of the culture containers until none remained. After 10 days, algal cultures were combined and allowed to settle, the supernatant was poured off, and the remaining algae was centrifuged for 5 minutes. Pelleted algae were combined and resuspended in deionized water to form an algal "paste" for immediate use as an initial food source in each treatment dish.

Eight replicate plastic petri dishes were prepared for each of the 6 treatments (300, 200, artificial 200 Ca^{+2}-free, 100, 50, and 10 $\mu S \cdot cm^{-1}$). Each replicate dish was prepared by combining 30 mL of treatment solution with 1 mL of algal paste. Twenty-five randomly selected mud snails (of the 1-mm cohort) were then added to each replicate dish. All replicate dishes were examined for mud snail mortality at intervals of 3–7 days, and mortalities were removed. Mortality was judged as an absence of response to repeated light tactile stimulation (touching soft tissue with a probe). One replicate dish from each treatment was sacrificed at about weekly intervals to create length and weight growth curves over the course of the experiment. To ensure that water quality did not degrade over the course of the experiment, 15 mL of water was removed from each dish and replaced with fresh treatment solution

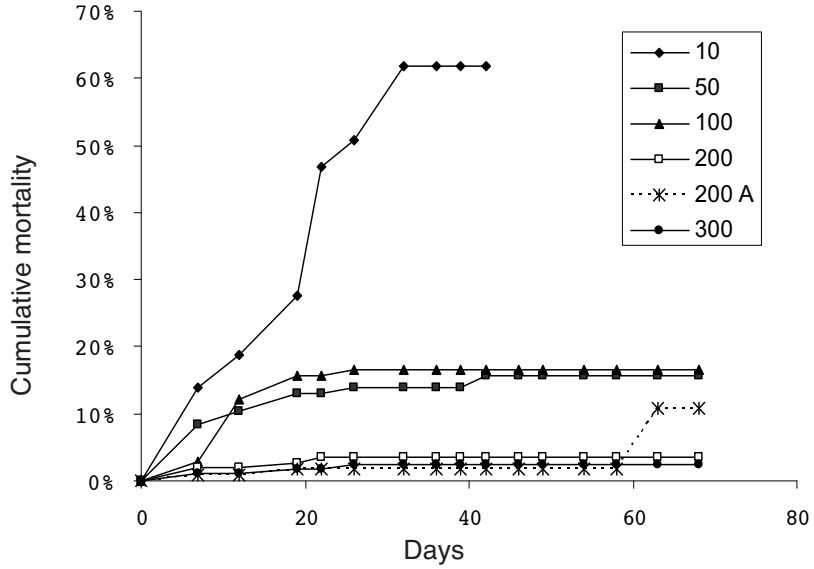

Fig. 2. Cumulative mortality of New Zealand mud snail among different specific conductivity treatments of diluted water from the Upper Owens River, except 200A, which refers to calcium-free artificial river water adjusted to 200 μS · cm^{-1}. Mortality accounted for removals for growth harvests, and 50 μS · cm^{-1} treatment was discontinued as snails were depleted.

every 3–4 days. Water temperature was held at 15–20°C (within the range of summer river temperatures) in both this and the newborn clone experiment described below. This experiment was carried out over a period of just over 2 months.

Newborn Clone–initiated Experiment

After establishing a response range in the 1st experiment, a narrower range of SCs were tested using clonal newborn mud snails, which are expected to be more sensitive to varied environmental conditions and so should provide a more realistic assessment of ecological limits in nature. Mature adult New Zealand mud snails were collected from the Owens River at Benton Crossing in October 2006 as a brood source for newborn clones. These snails were monitored regularly and new clonal progeny were collected within a 24-hour period for use in experimental treatments.

Six treatment solutions were prepared for the juvenile experiment. Five were created by diluting filtered Owens River water as previously described to obtain a SC series (200, 100, 75, 50, and 25 μS · cm^{-1}), while the 6th was the 200 μS · cm^{-1} Ca^{+2}-free solution described above. One petri dish was prepared for each of the 6 treatments with 30 mL of treatment solution and 1 mL of algal paste (prepared from fresh algal cultures as described above). Twenty-five new (24-hour cohort) clonal progeny were then added to each petri dish (using lightweight broad-tipped forceps) and checked twice to ensure that all juvenile mud snails survived the transfer. In each petri dish, 15 mL of treatment solution was refreshed regularly, as described above. Solution removal was monitored under a microscope to ensure that juveniles were not accidentally removed from the dishes during solution replacement. All treatments were monitored daily for mortality, and dead snails were removed. After 1 month, all snails were harvested and lengths were measured as described above.

Data Analysis

Differences in survival between treatment groups were evaluated with cumulative mortality curves over the duration of the experiment (accounting for snails removed for growth measures). Growth was measured in the range-finding experiments as the slope of the linear regression of dry weights of individuals removed from each treatment cohort at intervals

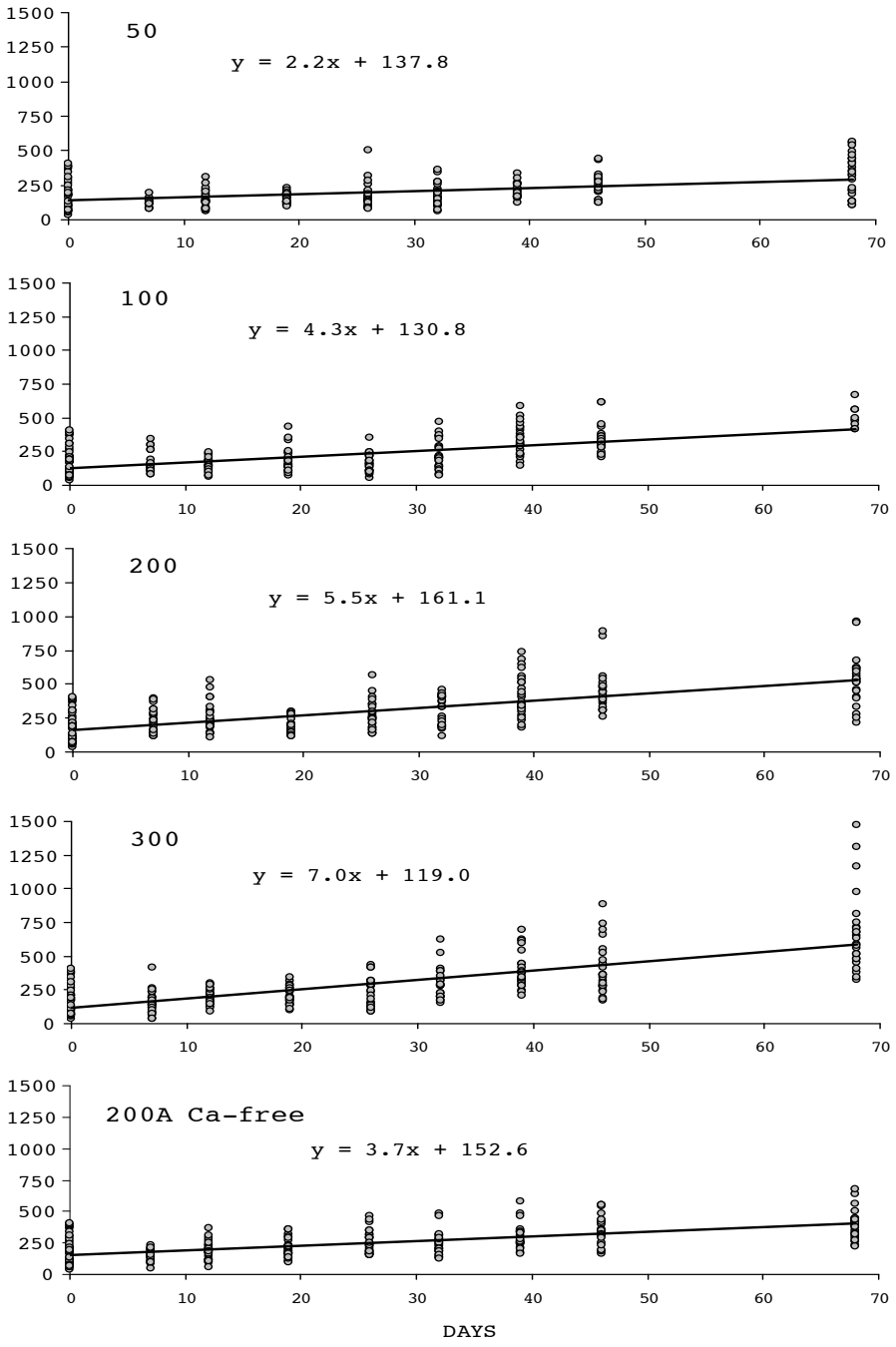

Fig. 3. Growth regressions of NZMS dry weight (μg) over 60+ days at varied specific conductivities (μS · cm^{-1}) of Upper Owens River water and in comparison to calcium-free artificial river water at 200 μS · cm^{-1} (200A).

over the course of the experiment. In the newborn clone experiment, however, extremely low weights and difficulty in transferring individuals to the Cahn electrobalance without damaging them made weight an unreliable measure of growth. As a proxy for weight, we used aperture-to-shell-spire length to quantify growth in the newborn clone experiment.

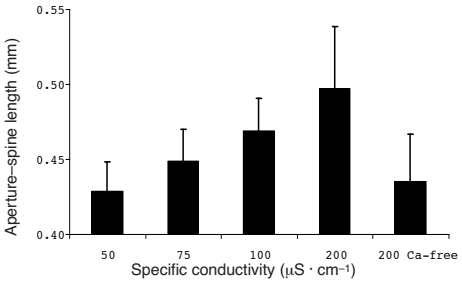

Fig. 4. Growth of clonal newborn New Zealand mud snails at varied specific conductivities of Upper Owens River water after 1 month. The y-axis is scaled based on an initial average size of 0.40 mm. Sample sizes (in order left to right) were 16, 20, 21, 21, and 19 snails. Error bars represent 1 standard deviation.

Overall differences in the slope of growth-rate regressions among treatments in the range-finding experiment were tested using analysis of covariance (the y-intercept was not tested, as this was derived from a random sample of the same initial cohort for each treatment) followed by Tukey's HSD multiple comparisons to test for differences between treatments. Shell spire lengths after 1 month's growth in the newborn clone experiment were compared by a Kruskal-Wallis test followed by paired treatment comparisons using Dunn's procedure (Zar 1999). More conservative nonparametric tests were used in this case because of unequal sample size and variance among treatments.

RESULTS

In the initial range-finding experiment, NZMS cohorts were either moribund and without any sign of growth or they perished in the most dilute water of 10 μS · cm^{-1}. NZMS cohorts exhibited increased mortalities at 50 and 100 μS · cm^{-1}, but all higher SC treatments (200 and 300 μS · cm^{-1}) had low mortality (Fig. 2). Shells were observed to be fragile (i.e., thin and breakable), with whitening at the mantle growth margin in many mortalities seen at 10 and 50 μS · cm^{-1}. Invasive growth of fungus on soft tissue or shells, along with general morbidity (slow or inactive, with no feeding), was also observed in dying snails.

Growth rates of the NZMS cohorts over the 2-month experimental period also showed significant declines with diminishing SCs of treatments from 300 to 50 μS · cm^{-1} (Fig. 3). In addition to low SC limits on survival and growth, snails in Ca^{+2}-free culture media also showed reduced growth relative to natural Ca^{+2}-containing water of equal conductivity (Fig. 3, panel 200A). Growth rates varied significantly among treatments, with ANCOVA showing differences in regression slopes ($F_{5,1156}$ = 56.205, $P < 0.0001$). Using Tukey's HSD multiple comparisons test, growth rates over the series of SC treatments were ordered [300 = 200] > [100 = 200 Ca^{+2}-free] > [50] ($P < 0.0001$). Regression slopes decreased in rank order: 300 > 200 > 100 > 50 μS · cm^{-1}. The 200 Ca^{+2}-free regression slope was intermediate between the 100 and 50 μS · cm^{-1} regression slopes.

In the experiment using newborn clone cohorts, only a few snails survived the treatment at 25 μS · cm^{-1}, and those snails were moribund and exhibited no growth. Growth measured as shell length in the remaining treatments was also curtailed under more dilute conditions (Kruskal-Wallis: $K = 51.38$, $P < 0.0001$). Paired comparisons showed growth at [200 = 100] > [75 = 50 = 200 Ca^{+2}-free] ($P < 0.0001$). Shell length increased with SC, again with shell lengths in the Ca^{+2}-free 200 μS · cm^{-1} treatment intermediate between shell lengths in the 50 and 75 μS · cm^{-1} treatments (Fig. 4).

DISCUSSION

The range of SCs tested in this study was representative of a wide variety of streams found in mountainous areas with snowmelt-dominated hydrology or where groundwater sources can dominate at least during base-flow conditions. The results indicate that NZMS survival would not be expected at SCs <25 μS · cm^{-1}. Additionally, growth was inhibited over the range of 25–200 μS · cm^{-1}, while above 200 μS · cm^{-1} we observed less limitation of SC on growth or survival. We suspect that both calcium limitations on shell-building and ionic and osmotic imbalances account for the growth inhibition and mortality of snails. Slower growth in 50 μS · cm^{-1} river water compared with 200 μS · cm^{-1} Ca^{+2}-free water suggests that, even with calcium present, dilute conditions may result in solute losses from cells or extracellular fluids and may carry osmoregulatory costs. Upper Owens River water at 50 μS · cm^{-1} contains about 0.25 mM Ca^{+2}, and below about 100 μS · cm^{-1} (~0.5 mM Ca^{+2}), a small electrochemical gradient may exist for Ca^{+2} that requires active transport from

external fluids into internal fluids, as shown in the freshwater snail *Limnaea stagnalis* (L.) (Greenaway 1971). Notably, the uptake kinetics for calcium in *L. stagnalis* saturated at >1.0 mM Ca^{+2}, equivlalent to about 200 $\mu S \cdot cm^{-1}$ river water. The gradient for acquiring ions such as sodium and potassium from 50 $\mu S \cdot cm^{-1}$ will require still greater energy costs, since these are essential internal solutes, but these ions occur in much lower concentration in river water. Poorer growth in 50 $\mu S \cdot cm^{-1}$ river water compared with the artifical 200 $\mu S \cdot cm^{-1}$ water may therefore reflect the consequence of deficient Na^{+}, K^{+}, and Mg^{+2} for ionic and osmotic regulation, while limited growth may still proceed in calcium-free artifical river water because of the availability of calcium stored in the shell/mantle or small amounts present in the algal food. Prosobranch gastropods, which include New Zealand mud snails, have been reported to have body fluid osmotic concentrations of 74–113 $mOsm \cdot kg^{-1}$, while stream water is usually less than 10 $mOsm \cdot kg^{-1}$ (McMahon 1983).

Other laboratory studies of the effects of low dissolved calcium on freshwater snails are consistent with our results. Growth rates of *Biomphalaria glabrata* increase over the calcium concentration range of 0.06–2.0 mM Ca^{+2} (Thomas et al. 1974), and rearing in 0.05 mM Ca^{+2} solution inhibits growth, development, survival, and reproduction in *Planorbella trivolvis* compared with snails reared in a 1.5 mM Ca^{+2} solution (Hunter 1990).

That the alkalinity component ($CaCO_3$ content) of dissolved solutes can play an important ecological role has been shown in studies of freshwater gastropod distribution in Tennessee, one of the richest regions in the world for molluscan diversity (Shoup 1943). Surveys showed that only 10% of streams below an alkalinity of 20 $mg \cdot L^{-1}$ held any snails, while at least 40%–75% of streams with alkalinities above 20 $mg \cdot L^{-1}$ held a diverse snail fauna. Similarly, lake surveys in England, Scotland, and the northeastern United States demonstrated limited occurrence of snails in lakes with low calcium content (Macan 1950, Russell-Hunter 1978, Jokinen 1987). Even so, other studies have shown that some freshwater mollusks, including both gastropods and bivalves, can inhabit water with low ranges of dissolved solute and calcium content (Rooke and Mackie 1984, Pip 1986).

Although there is little information available from field studies to evaluate the relationship of dissolved solute content to NZMS distribution, some research has provided pertinent data. In certain streams of the Greater Yellowstone Area, where several published studies of abundant NZMS populations have been conducted (Hall et al. 2003, 2006, Kerans et al. 2005), SCs are high—typically in the range of 300-600 $\mu S \cdot cm^{-1}$—except during spring runoff when levels may fall to 150–200 $\mu S \cdot cm^{-1}$ for several weeks (Sean Eagan personal communication). New Zealand mud snail populations in these areas can reach densities of hundreds of thousands of individuals per square meter in local patches, similar to densities in the Upper Owens River. In a detailed distributional study along a series of stream sites in Yellowstone National Park (Kerans et al. 2005), New Zealand mud snails were present at all locations below inflows from thermal groundwater sources but were completely absent above these inflows where SCs were much lower and in the range of potential growth inhibition (60–120 $\mu S \cdot cm^{-1}$ in the Firehole River, WY; 50–200 $\mu S \cdot cm^{-1}$ in the Gibbon River, WY). The authors suggest that physicochemical factors may restrict occurrence, and our results indicate that absence of New Zealand mud snails in this setting could be due to the debilitating effects of reduced solute content on growth and survival.

The effect of dissolved solute concentration on NZMS development has been examined in relation to the relatively high concentrations of brackish seawater (Jacobsen and Forbes 1997). In seawater salinity of 5–15 ppt (about 10,000–25,000 $\mu S \cdot cm^{-1}$), tested in relation to an artificial freshwater solution (estimated SC 500–1000 $\mu S \cdot cm^{-1}$), all treatments were found to support survival and growth to maturity with an optimum at 5 ppt. Although this shows that *P. antipodarum* can live within a range of brackish estuarine habitat conditions, these results have little relevance to understanding NZMS distribution in most freshwater streams, where SCs are typically much lower.

The distribution of freshwater snails within and among habitats is likely due to a combination of water quality and ecological factors. In a conceptual model of these interactions, the influence of calcium limitation has been suggested to occur only below 5 $mg \cdot L^{-1}$, with control of snail distribution above this level

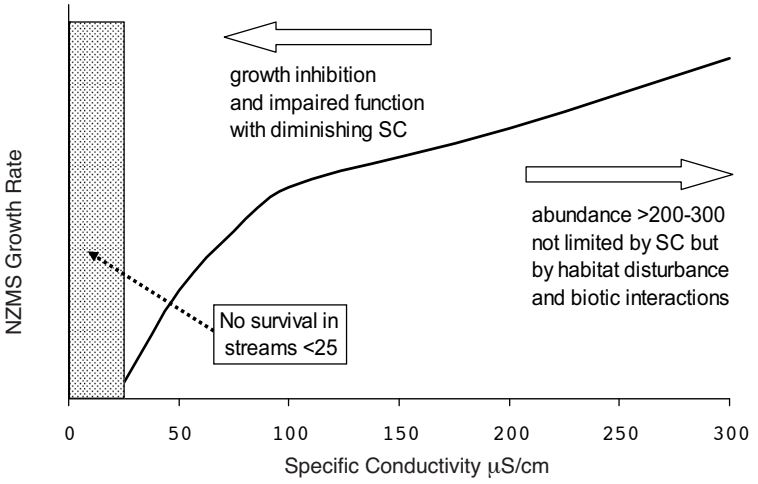

Fig. 5. Model of ecophysiological constraints on distribution and abundance of New Zealand mud snails. Shape of curve is based on growth rate regression slopes (Fig. 4). Physiological debilitation over the range of growth inhibition is predicted to reduce the competitive dominance that the New Zealand mud snails can exert under higher levels of dissolved solute content.

exerted by predation and disturbance regimes (Lodge et al. 1987). Our data suggest that not only can the range of calcium influence extend up to 200 $\mu S \cdot cm^{-1}$ of Upper Owens River water (30–40 $mg \cdot L^{-1}$ calcium) but that, in addition to simple exclusion from low-calcium waters, growth inhibition in waters of dilute ionic composition could place sublethal constraints on snail production and distribution, independent of ecological factors.

The New Zealand mud snail has been associated with agricultural land-use disturbance (livestock grazing/pasture), where streams can be degraded by bank erosion, fine sediment, and elevated levels of nutrients and where streams often have higher SC (Harding and Winterbourne 1995, Schreiber et al. 2003). In experimental trials, the New Zealand mud snail has been shown to display a preference for sediment-contaminated cobbles and the presence of filamentous green algae (Suren 2005). Productive NZMS populations are therefore likely those that inhabit water not only of high conductivity and alkalinity but where habitat disturbance has also undermined the viability of native benthic invertebrates. The long-term success of invasive species in freshwater communities is usually promoted where there is a close physiological match between the invader and the habitat and in systems that have been extensively altered by human disturbance (Moyle and Light 1996).

Invasive species are often thought to have wide environmental tolerances (Lodge 1993), but phenotypic plasticity permitting adaptation to low SC was not evident in our experiments. Though our studies were restricted to New Zealand mud snails from the Upper Owens River, most introductions in western North America are thought to be derived from a single clone, so our results should be applicable elsewhere in this region. Further evidence of the limited adaptability of this NZMS strain comes from studies of life history traits and fitness performance in relation to temperature. For populations derived from an Oregon estuary and from rivers in Idaho and Wyoming, NZMS reproduction failed almost entirely at 24°C; and reproduction was delayed and fecundity was reduced at cooler temperatures of 12°C relative to the optimum at 18°C (Dybdahl and Kane 2005). Physiological and developmental studies of environmental reaction norms to other physicochemical factors could provide a more complete basis for predicting the range of habitat conditions where the New Zealand mud snail would be most successful.

We propose that the distribution and productivity of the New Zealand mud snail are restricted by ecophysiological limitations of water chemistry (Fig. 5). Invasion by the New Zealand mud snail may be excluded from streams and rivers with SCs below 25 $\mu S \cdot cm^{-1}$, and physiological debilitation over the

range 25–200 $\mu S \cdot cm^{-1}$ may place snails at an energetic disadvantage in competition with native benthic organisms for food or space. The impeded growth and poor survival are likely to result in slower population production, maturation at smaller body size and suboptimal nutritional status, delay of reproduction, and/or reduced brood size (Stearns 1992, Jokela et al. 1997). Above 200 $\mu S \cdot cm^{-1}$ there may be little growth limitation with respect to calcium requirements for shell growth and minimal cost related to osmotic and ionic regulation.

This paradigm provides a framework for predictive modeling of the potential vulnerability of streams and rivers to NZMS invasion and for understanding the conditions that have been conducive to the colonization and expansion of NZMS populations. Using data on the distribution of specific conductivity in surface waters, it should be possible to develop GIS-based predictive models and maps showing where new invasions of snails are most likely to occur and proliferate. A similar analysis was recently performed for invasion risk of the zebra and quagga mussels based on maps of calcium concentrations in waters of the conterminous United States (Whittier et al. 2008). Our results may provide further insight into the role of spatial and temporal variations in specific conductivity on population fluctuations and presence/absence of the New Zealand mud snail where seasonal snowmelt and low summer flows can markedly alter dissolved solute concentrations.

Acknowledgments

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