A review of salinity tolerances for the New Zealand mudsnail (*Potamopyrgus antipodarum*, Gray 1843) and the effect of a controlled saltwater backflush on their survival in an impounded freshwater lake

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Abstract

The New Zealand mudsnail (NZMS) is an invasive first discovered in Olympia, Washington's Capitol Lake in 2009 and has since been detected in the lake at high densities. In this study, we review salinity tolerances from NZMS investigations conducted in the wild and in the laboratory. Based on the review, we backflushed Capitol Lake with saltwater introduced through a dam that connects the lake to the sea in order to examine the effect of raising the lake's salinity on NZMS survival. We present pre- and post-backflush survival rates from 26 sample stations, eight of which were supplemented with the topical application of salt. Raising the lake's salinity decreased survival and the topical application of salt increased the effect. Sample size and location had a significant effect on survival. We subjected pre- and post-backflush NZMSs to laboratory saltwater trials and used the data to construct a generalized linear model (GLM) to predict survival rates under various salinity exposure regimes. More NZMSs were killed in response to the backflush than was predicted by GLM. Water temperatures in the lake were lower than those used in the laboratory and this may have decreased the NZMS's resistance to increased salinities in the lake.

Keywords*: salinity tolerance · New Zealand mudsnail · survival rate · generalized linear model.*

Introduction

The New Zealand mudsnail (NZMS) is a hydrobiid mollusk that is native to New Zealand. Its impact to native fauna and ecological processes outside its native range is not well understood (but see Schreiber et al., 2002; Kerans, 2005; Strzelec, 2005; Strzelec et al., 2006; Hall et al., 2006, 2003); however, its expansion over the last century to estuarine and freshwater environments around the world, and its ability to rapidly reach very high densities once established, has led to concerns of disruption to local food web and trophic dynamics, ecosystem functions, and native community structures (Hall et al., 2003). Developing strategies and methods to control and manage NZMS populations in the U.S. is listed as one of the objectives of the National Management and Control Plan for the New Zealand mudsnail (New Zealand Mudsnail Management and Control Plan Working Group, 2007) that was developed under the auspices of the intergovernmental national Aquatic Nuisance Species Task Force to address these and other concerns.

Thus far, NZMS management efforts in their non-native range have focused primarily on controlling their spread by limiting public access to infested water bodies, educating citizens through public awareness campaigns, and developing decontamination methods and protocols for recreationists and natural resource field workers (Richards et al., 2004; Hosea and Finlayson, 2005; Schisler et al., 2008). Large-scale *in situ* eradication has not been attempted (but see McMillin and Trumbo, 2009). In this study, we: 1) examined the effect on NZMS survival of backflushing a freshwater lake (Capitol Lake in Olympia, Washington) with saltwater introduced through an existing engineered tide gate dam that connects the lake to the sea (Puget Sound); 2) subjected pre-backflush and surviving post-backflush NZMSs to a laboratory conducted saltwater trial in order to evaluate the population's post-treatment response to increased salinity; 3) tested the effect of augmenting the saltwater backflush with topically applied rock salt, and; 4) used the data to construct a predictive model for determining the probability of NZMS survival under various salinity exposure regimes that can be used to inform managers who are considering saltwater treatments as an eradication or control measure against non-native NZMS infestations.

Literature Synopsis – Salinity Tolerances for NZMSs

Potamopyrgus antipodarum is variously referred to as *Hydrobia jenkinsi*, *Paludestrina jenkinsi*, and *Potamopyrgus jenkinsi* in the historical literature. All are synonymous and in the interest of clarity, the widely accepted vernacular NZMS will be used throughout this review. A summary of the salinity tolerances reported in this review is presented in Table 1.

The first recorded occurrences of the NZMS outside its native range were from estuarine environments in Western Europe, and only later were they noted from inland freshwater locations (reviewed by Bondesen and Kaiser, 1949; Lassen, 1978; and Hughes, 1996). Nicol (1936) reported finding NZMSs in salinity as high as 23‰ in the brackish-water marshes of

North Uist in Scotland's Outer Hebrides. Winterbourn (1970a) found NZMSs in salinities as high as 26‰ in the species' native New Zealand. Under laboratory conditions, the same author noted that after 24 hours, snails acquired from both fresh- and brackish water sources remained active in 17.5‰, exhibited reduced movement in 21‰, and withdrew completely into their shells and were inactive in higher salinities[1]. All of the snails resumed normal activity within 24 hours of being returned to low salinity water (3.5‰). Johnsen (1946) reported finding a single NZMS on the NE shore of Bornholm, Denmark near the mouth of the Baltic Sea in a 33‰ tide pool. The pool was described as having been part of a once larger pool that had been reduced in size through evaporation. Since the surface-water salinity of the Baltic Sea in the Bornholm Basin rarely exceeds 15‰, it would seem likely that the snail had arrived in the pool at a time when the water was less saline - prior to evaporation. The disposition of the snail at the time of discovery was not noted, though it is presumed to have been living. Thus, it may have been active, having acclimated to higher salinity over the time it took the pool to evaporate, or it may have retracted into its shell and become quiescent in response to rising salinity. Costil et al. (2001) examined the biodiversity of aquatic gastropods across several biotopes in the Mont St-Michel basin of northern France. They encountered NZMS over a wide range of salinities up to 28‰ and, of 59 stations sampled, those stations where NZMSs were found had the highest salinities; however, the authors did not indicate whether or not the snails were active at higher salinities. Gérard et al. (2003) studied the rate of trematode parasitism in relation to salinity and gastropod community structure in the same basin. The NZMS was the only hydrobiid mollusk encountered in the basin's polyhalinic (18-30‰) waters. The rate of infection by trematode parasites decreased with increasing salinity over all species examined and NZMSs were not infected at the highest salinities.

Jacobsen and Forbes (1997) subjected NZMSs sampled from six sites in Denmark to salinities of 0‰ and 10‰ (all six sites) and 5‰ and 15‰ (two of the six sites). The sites represented a mixture of the two most common morphologically distinguishable genetic strains (A and B) occurring in Britain and continental Europe (Hauser et al., 1992; Jacobsen et al., 1996). The A strain is most often associated with inland freshwater lakes and streams, while B is found in coastal estuarine environments. They tested the effect of salinity on four fitness-related traits (reproductive output, feeding rate, growth rate, and size at birth) and compared results between strains. All four traits were influenced by salinity in both strains; however, the authors concluded that NZMSs are able to feed, grow, and reproduce over a salinity range of 0-15‰ and that the general response to salinity of both strains suggested a salinity optimum of ≈5‰. Drown et al. (2011) compared six fitness-related traits (survival probability, probability of reproducing, growth rate, time to asymptotic shell size, time of first reproduction, shell size of first

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[1] The New Zealand Mudsnail Management and Control Plan Working Group (2007) appears to have incorrectly ascribed Winterbourn's observation of complete withdrawal in salinities greater than 21 ‰ to Winterbourn (1970b), rather than Winterbourn (1970a).

reproduction, and individual fitness) from ancestral- and invasive-range lineages of NZMSs across a salinity gradient (0, 5, 10, and 15‰). Snails held at non-zero salinities were acclimated by increasing the salinity 5‰ every six hours until the desired treatment salinity was achieved. Snails were held at their respective treatment salinities for up to 230 days. The authors noted that attempts to acclimate snails to 30‰ resulted in high mortalities for some lineages and precluded their use for comparative analyses over all six examined traits, though they observed that only the invasive strains were successful at reproduction in 15‰ and 30‰. They concluded that invasive NZMS lineages are adapted to a higher salinity compared to ancestral lineages.

Consistent with Jacobsen and Forbes (1997), Muss (1963) listed 0-15‰ as being a rough estimate of the range over which NZMSs may be considered common in Denmark. In a later study, the same author noted that NZMSs were common in Kysing (Norsminde) Fjord, Denmark in salinities up to ≈22‰, and occurred sporadically in salinities as high as 24‰ near the seaward entrance to the fjord (Muss, 1967). This is similar to the findings of Siegismund and Hylleberg (1987), who described the distribution of the three most abundant hydrobiids (including NZMS) in the same fjord and assessed the factors leading to their coexistence. They found NZMSs at times and locations when, according to the hydrographic data they present, salinities would have been on the order of 20-22‰. In a different study, the same authors tested the effect of salinity in combination with temperature (Hylleberg and Siegismund, 1987). They reared NZMSs in salinities as high as 30‰ and concluded that NZMS tolerance to near-freezing temperatures decreased rapidly with increased salinity, and that the observation seemed to agree well with the temporal and spatial distribution of NZMSs in Kysing Fjord.

Todd (1964) tested the osmotic balance of strains A and B, and a less common European strain known as type C. Changes in internal osmotic concentration occurred rapidly as the snails were transferred from lower to higher salinities and all three strains maintained hyper-osmotic urine relative to the rearing medium over a range of salinities up to 32‰, the maximum salinity tested. The author also reported that NZMSs survived indefinitely in salinities up to 32‰ if conditioned first to lower salinities, but did not describe how the conditioning was achieved or if the snails were active at higher salinities. Similarly, Duncan (1967) tested the salinity tolerance of NZMS acquired from fresh- and brackish water sources in Poland over salinities ranging from freshwater to full seawater. They found that 100% of the snails tested from both sources survived for at least 24 hours after direct immersion in salinities up to 18‰, but, that the survival rate decreased rapidly with increased salinity above 18‰ to just 10% in full seawater. However, acclimatizing snails for up to two days in 18‰ before transferring them to higher salinities nearly doubled the survival rate. Further, they found that NZMSs acquired from both sources maintained hyper-osmotic haemolymph in the highest salinities tested.

Adam (1942) acclimated NZMSs obtained from a freshwater creek in Belgium by placing batches of 20 snails each in 14 ordinal salinities ranging from 0-24‰. At approximately one month intervals, the surviving snails from each batch were moved to a slightly higher salinity. Snails that were placed directly in 22‰ or higher at the beginning of the experiment failed to survive the first month. Of the snails that were initially introduced to 20‰, only nine survived the first month; however, those nine survived the next seven monthly transfers up to a salinity of 34‰, after which they all died. Offspring were produced in salinities as high as 28‰, though the number of offspring was notably lower in higher salinities and, consistent with Jacobsen and Forbes (1997), was greatest in salinities less than 16‰. In similarly devised experiments Klekowski and Duncan (1966) measured respiration in juvenile NZMS acquired from a small (11-hectare) freshwater lake near Aberdeen, Scotland, and respiration and heart rate from juvenile NZMSs collected from a brackish-water marsh near Plymouth, England (Duncan and Klekowski, 1967). Some of the freshwater-derived snails survived in salinity as high as 64‰ when acclimated every two days by an increase of 2-3‰, and the authors noted that even at 58‰, a few snails were still capable of searching for food. The snails derived from brackish water were subjected to a more aggressive acclimatization process (8‰ increase every 24 hours) and did not survive beyond 58‰. The authors speculated that observed increases in respiratory rate with increased salinity may be the result of increased osmoregulatory demands. Boycott (1936) stated that, "…freshwater strains may easily be got to live and breed in sea water…", but did not provide any details.

The first recorded discovery of NZMS in North America occurred in 1987 in Idaho's Snake River (Bowler, 1991). Since then, NZMSs have been found in nine additional western states (Gustafson, 2002) and Dybdahl and Kane (2005) suggest that the western North American lineages may be genetically linked to Australia. The western North American and Australian lineages both appear to be genetically dissimilar to the European strains (M. Dybdahl, School of Biological Sciences, Washington State University, personal communication). Davidson et al. (2008) reported occurrences of NZMSs from several low-salinity estuarine locations along the Oregon coast, and from one estuarine location on the west coast of Vancouver Island, British Columbia. New Zealand mudsnails are now well established at many fresh- and brackish water sites throughout the lower Columbia River estuary (reviewed by Bersine et al., 2008). The highest salinity in which NZMSs have been documented in the lower Columbia River (Baker Bay) is 11‰ (Sytsma et al., 2004), and this is the highest salinity from which the NZMS has been recorded along the west coast of North America (T. Davidson, Aquatic Bioinvasion Research and Policy Institute, Portland State University, personal communication). However, salinity in the lower Columbia River fluctuates widely from 0-30‰, and it is likely that NZMSs in the lower-most reaches of the river experience at least intermittent exposures to higher salinities. The NZMS was first reported from Washington State's Capitol Lake in October, 2009 (B. Bartleson, Pacific Northwest Shell Club; E. Johannes, Deixis Consultants, personal communications) and densities of up to 20,000 per m^2 have since been detected (A. Pleus, Aquatic Invasive Species Unit, WDFW, personal communication). Invertebrate surveys of the lake conducted as recently as 2003 (reviewed by Hayes et al., 2008) did not detect the presence of NZMS. The current infestation, therefore, is likely a recent phenomenon, having reached detectable levels sometime in the last eight years.

The published accounts of NZMS salinity tolerances and occurrences suggest the species is generally restricted to salinities ranging from fresh- to brackish water in the wild. Results from laboratory manipulations, however, indicate they may be acclimated to withstand hyper-saline water, likely due to their ability to osmoregulate over a broad range of environmental conditions, and that their maximum salinity tolerance is limited primarily by temperature and the rate of acclimatization. Based on Capitol Lake's freshwater hydrology and the predicted rate of seawater inflow from Puget Sound, we anticipated that we could rapidly achieve, and maintain for at least 48 hours, lake-water salinities of up to 24‰ in the lake's northern basin. This is close to the maximum salinities reported for most NZMSs collected from the wild elsewhere (Table 1).

Methods

Study area

Capitol Lake is a shallow manmade freshwater lake that is 3 km long, and covers an area of approximately 105 hectares. It was formed in 1951 when a constructed berm and dam enclosed a portion of Puget Sound's southernmost tidal basin (Budd Inlet) and enabled the retention of outflow from two adjoining streams (Deschutes River and Percival Creek) to permanently inundate the tidal flats (Figure 1). Puget Sound is a saltwater estuary fjord of mixed semi-diurnal tides. Salinity in Budd Inlet varies seasonally and is largely dependent on rainfall and input from adjoining rivers and streams, and storm water runoff from the city of Olympia (population ≈46,000). During the course of the backflush, surface salinity measurements taken at a station located near the entrance to Budd Inlet, approximately 14.5 watercourse km north of the dam, ranged from 27.3-28.3‰ (mean 27.8‰) and are typical for the months of February and March (Anonymous 2010). A salinity measurement taken from just seaward of the dam on the afternoon of March 1 during the initial phase of the backflush registered 28.7‰ (Hallock, 2010).

Unless otherwise noted, all depths and elevations in this study are reported relative to the National Geodetic Vertical Datum of 1929 (NGVD29). This datum is the benchmark elevation used by the City of Olympia and forms the basis for US Geodetic Survey quadrangle maps of the area. The mean winter elevation of Capitol Lake is 1.5 m. Mean sea level on the seaward side of the dam is approximately 0.3 m. This experiment took advantage of a spring tidal series that resulted in higher than usual tides in Puget Sound and enabled large volumes of saltwater to be backflushed into Capitol Lake through the dam. During the backflush, astronomically predicted high tides ranged from 2.38-2.74 m. Actual tide heights were not measured and may have differed somewhat from predicted heights due to meteorological effects (Anonymous, 2008). Air temperatures remained above freezing (3°C min., 12°C max.) during all phases of the experiment. Thus, exposure to sub-freezing temperatures during the drawdown phases of the experiment was not a factor affecting survival (Cheng and LeClair, 2011).

Field sampling

The dam is fitted with two steel radial arm gates that open upward so that the exchange or discharge of lake water occurs from beneath them. Freshwater was allowed to drain from the lake during low tides and the lake level elevation was kept lowered for a period of approximately 3 days prior to the backflush. This allowed some time for density re-stratification of the water on the seaward side of the dam to occur and reduced the potential for less dense freshwater to be refluxed into the lake during the backflush. The effect of the pre-backflush drawdown on NZMS survival was assumed to be insignificant due to the NZMS's known ability to survive unsubmerged in damp environments for long periods of time (Winterbourne, 1970a). Cloud cover, high humidity (100% max., 61% min.), low winds, and moderate temperatures prevented the exposed lake bed from drying out and all sampling occurred at locations that remained thoroughly moistened during the drawdown. The first lowering of the lake level commenced on February 26, 2010. The lake was rapidly refilled with saltwater during high tide on March 1 and lowered at the conclusion of the backflush on March 5. On March 6, the gates at the dam were closed and the lake was permitted to refill to the pre-backflush level (Figure 2).

During the time the lake level was lowered but prior to the backflush, fourteen stations were selected along the north shore near the dam where we judged maximum salinity would be achieved during the backflush, due to close proximity to the saltwater source and maximum distance from freshwater flowing into the lake from the two adjoining streams. Half of the stations were located upshore away from the water's edge (elevation > 0.5 m), and half were located near the water's edge (elevation < 0.5 m). Four more stations were selected along the south shore near the 1.5 m mean winter lake level isobath. An additional eight stations, four each at the north and south sample sites, were treated with a topical application of rock salt (Morton® White Crystal Rock Salt) applied at the rate of 1 kg/m^2 over an area of approximately 1 m^2. Each of the 26 stations (Figure 1) was marked with a numbered steel stake and NZMSs were sorted in the field from random substrate samples taken within 1 m of the stake. We aimed for a minimum sample size of 50 NZMSs from each station. At low density stations where it became apparent that the desired minimum sample size could not be achieved, we collected as many NZMSs as could be found in approximately 20 minutes of searching. All snails were immediately transported to a laboratory and examined microscopically. Any shells that did not contain a body were discarded. The remaining snails were examined for signs of movement and, arbitrarily, any snail that could not be induced to move after four hours was deemed dead. The same sampling procedure was repeated at each station immediately after the backflush during the second drawdown.

Salinity measurements, including one near-surface and one near-bottom, were taken at each of ten locations in the northern basin of the lake on March 2, shortly after the initial saltwater backflush phase of the experiment was begun. Near-surface salinities ranged from 7.5-14.2‰, and near-bottom salinities ranged from 12.7-24.9‰. The salinity measurements taken nearest the two NZMS sample sites (≈60 m distant) registered 10.5‰ and 12.4‰ (near-surface), and

24.8‰ and 22.8‰ (near-bottom), at the north and south sample sites, respectively. A weak halocline was evident at a depth below the surface of ≈1.5 m (not corrected to NGVD29) (Hallock, 2010).

Laboratory saltwater trial

In order to construct a predictive model for estimating the probability of NZMS survival under various salinity exposure regimes before and after the backflush, we placed 200 live adult snails collected from near the north sample site three days prior to, and five days after the backflush in each of five separate 15 L containers. The containers were filled respectively with: 1) fresh water from Capitol Lake; 2) brackish water (21‰) from Budd Inlet approximately 200 m north of the dam; 3) brackish water (24‰) produced by blending saltwater from the more saline entrance to Budd Inlet, approximately 11 km north of the dam, with freshwater from Capitol Lake; 4) brackish water (27‰) from the entrance to Budd Inlet, and; 5) saltwater (35‰) produced by mixing Instant Ocean® with fresh water from Capitol Lake. All of the containers were held at room temperature (≈ 25°C) to increase activity and expedite the identification of live snails.

We monitored survival of the snails from each container at timed intervals of 1, 24, 48, and 120 hours. At the prescribed times, all snails were removed from their containers and placed in fresh lake water. Snails that failed to show any signs of movement after four hours in freshwater were judged dead. All live snails were returned to their respective source containers once the number of dead snails had been determined.

Statistical analysis

We used a generalized linear model (GLM) (McCullagh and Nelder, 1989; Cheng and Gallinat, 2004) using the canonical link function for the binomial distribution (logit) to overcome problems associated with different sample sizes among various levels of predictors. For field observations, predictor variables were the sample site location (north vs. south), sample station elevation, sample size, presence or absence of topically applied rock salt, and the status of the experiment (i.e., before vs. after the backflush). For the laboratory saltwater trial, the predictor variables were time (hours), salinity (‰), and the status of the experiment (i.e., before vs. after the backflush). The response variable for both the field and laboratory experiments was the proportion of dead NZMSs. The chosen GLM sub-models for the field and laboratory experiments, using all of the respective predictor variables, were selected by both Akaike Information Criteria (AIC) (Akaike, 1974) and Bayesian Information Criteria (BIC) (Schwarz, 1978). The Student's t-test was used to test the significance of each predictor variable. Fitted values were plotted against observed values in order to compare how well the predictions compared with laboratory observations.

Results

Sample sizes, percent survival, and station elevations from field observations are presented in Table 2. The mean sample size averaged over all 26 stations was 107 (standard deviation = 69). The density of NZMS varied widely among stations, and higher density stations yielded greater sample sizes. We examined the effect of sample size on the modeled proportion of dead NZMSs by adding assumed sample sizes of 50 and 150. The smaller sample size resulted in a 9.9% and 5.7% increase in the proportion of dead NZMS at the north and south sites, respectively; while the larger sample size decreased the proportion by 7.5% and 3.8%, respectively. In order to standardize the effect of sample size, we modeled survival using a sample size of 100. With an assumed sample size of 100, the predicted proportion of dead NZMSs prior to the backflush was ≈0.5% at both sites. After the backflush, the predicted average proportion of dead NZMSs was 22.1% at the north sample site, and 10.2% at the south sample site. The application of topically applied rock salt added 4.3% and 2.4% to the predicted values for the north and south sites, respectively. This implies that topically added rock salt can increase the mortality of NZMSs; however, the relationship between added salt and mortality is non-linear and thus likely to be a function of other factors, as well.

The chosen sub-model for the field observations included the predictor variables sample site location ($P < 0.001$), sample size ($P < 0.0001$), presence or absence of topically applied rock salt ($P = 0.07$), and the status of the experiment ($P < 0.001$); sample station elevation was not included ($P > 0.2$). The fitted GLM results and the observed laboratory data are plotted in Figure 3. While the fitted GLM predicted values agreed well with the observed laboratory saltwater trial data; the predicted proportion of dead NZMSs under various salinity exposure regimes, based on the laboratory data, are slightly out of agreement with the mortality rate observed in the field.

The chosen sub-model for the laboratory saltwater trial used all three predictor variables (time, salinity, and status of the experiment), each of which was highly significant ($P < 0.001$), to predict the proportion of dead NZMSs (Figure 4). When standardized to a sample size of 100, the model indicates that prior to the backflush, at least 27‰ maintained over a period of five days would be necessary to achieve complete eradication. Substantial impacts to survival could be realized at 24‰ or less; however, the exposure time necessary to effect a complete eradication at any practically achievable concentration by backflush alone may be beyond reach in Capitol Lake due to constraints imposed by the lake system's local hydrology.

Results from the laboratory saltwater trial conducted with NZMSs sampled five days after the backflush showed a remarkable difference in salinity tolerance when compared with those NZMSs sampled prior to the backflush. After 120 hours in 27‰, 83% of the NZMSs sampled post-backflush were still alive, compared with just 7% of the snails sampled pre-backflush. While nearly all snails (pre- and post-backflush) were able to survive for 120 hours in 24‰, neither the pre- or post-backflush NZMSs survived the 120 hour immersion in 35‰.

Discussion

Temporarily raising the salinity of Capitol Lake impacted NZMS survival. Although we succeeded in achieving the maximum predicted salinity in the deeper water of the lake's north basin, freshwater input and the concomitant drop in lake-water salinity occurred more rapidly than anticipated. Measured surface salinities did not exceed 15‰ and the maximum achieved salinities recorded in deeper water were not sustained for 48 hours, as predicted. Maintaining the lake-level elevation below flood level during the backflush required that the dam be opened periodically in order to release excess water entering the lake via the two adjoining streams. Since the dam opens upward from the bottom, flood control releases would have consisted of denser (more saline) near-bottom water, and effectively increased the depth of the overriding mass of less saline water. Our study sites were located in the nearshore environment (i.e., shallower water), and probably were not exposed for appreciable lengths of time to the maximum salinities that were recorded at depth. Pumping surface water over the top of the dam, rather than releasing it from beneath, may have reduced the depth extent of the freshwater layer.

More NZMSs were killed in response to the backflush than was predicted by GLM. This may be due to lower temperatures in the lake (≈9°C throughout the course of the backflush) that decreased the NZMS's resistance to increased salinities as noted by Hylleberg and Siegismund (1987) (see Literature Synopsis). The water used for the laboratory saltwater trials was not chilled to the same temperature as the lake. The GLM predicted estimates of survival could therefore be viewed as conservative with saltwater treatments using cooler water. The pre-treatment mortality predicted by GLM (≈0.5%) could have been the result of natural mortality, induced handling effects, or some other factor(s).

The increased salinity tolerance of NZMSs collected from Capitol Lake after the backflush is likely due to acclimatization, and it is noteworthy that several live and actively crawling juvenile snails were observed in the post-backflush, 27‰ laboratory-reared sample after 216 hours (all other trials were terminated at 120 hours). This anecdotal observation agrees well with the findings of Adam (1942) and Drown et al. (2011) (see Literature Synopsis). Given that the pre- and post-backflush samples were taken less than a week apart, we assume that multiple cohorts were not sampled and that adaptability over multiple generations could not have occurred during the sampling period. During the backflush, the lake's salinity was increased gradually and, in light of the circumstances under which snails were able to survive in high salinities according to previous accounts, probably over a sufficient period of time for some snails to have successfully acclimated.

Determining to what extent the surviving NZMS population response was functionally adaptive would require further study. If it was largely adaptive we would expect the resiliency to be persistent with little or no impact to overall fitness. If, on the other hand, it was due primarily to acclimatization mediated by non- or maladaptive phenotypic plasticity, we might predict that some cost to overall fitness would be incurred, and that the response would be ephemeral. Even if the tolerance were epigentically transmitted, the effect would likely be lost over the course of several generations. Among the concerns to managers responding to the Capitol Lake NZMS infestation is the potential for spread into the low salinity waters of adjacent southern Puget Sound and the threat that NZMSs may pose to the marine ecosystem there, including effects on the distribution and abundance of native littorinid snails. An adaptive NZMS population response to salinity, mediated by genetic variability, would increase the threat.

There are numerous potential transport vectors from Capitol Lake into Puget Sound. In addition to the direct outflow of water from Capitol Lake into Puget Sound through the dam, potential non-anthropogenic transport vectors include fecal deposits left by invertebrate-feeding fishes that pass through the dam. Aarnio and Bonsdorff (1997) studied the resistance to digestion of benthic prey organisms, including snails belonging to the same family as the NZMS, consumed by juvenile flounder (*Platichthys flesus*) in the Baltic Sea. They found that the snails could pass through the gut of juvenile flounder alive. *Platichthys flesus* is closely related to *P. stellatus* (Borsa et al., 1997), which is a common inhabitant of the waters just seaward of the dam and has been found in ichthyofauna surveys of Capitol Lake (Anonymous, 2004). Dean (1904) noted that NZMS can pass through perch (species not indicated) as intact shells, though the author did not indicate whether or not the snails were alive. Yellow perch (*Perca flavescens*) are known to be present in Capitol Lake (Hayes et al., 2008) and other species of perch occur in abundance on the seaward side of the dam. Bersine et al. (2008) documented the occurrence of NZMSs in the diet of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and determined that they could pass through the alimentary canal alive. Capitol Lake is a seasonal migration corridor for both juvenile and adult Chinook salmon on their way to and from Puget Sound. Lassen (1978) speculated that waterfowl may have been an important means of local, if not long range, dispersal of NZMSs in Europe. The snails may get caught in plumage, or adhere to feet and bills (Coates, 1922). There are several species of wading and diving birds that use the nearshore environment of both Capitol Lake and Puget Sound. Mammals, including pets, also pose a transfer risk. Potential human transport vectors include unintentional distribution through the movement of contaminated recreational, construction, and natural resource field sampling equipment.

Also of concern to lake managers is the impact that the backflush may have had on other resident benthic macroinvertebrate fauna. A pilot-scale study conducted by the Washington Department of Ecology using benthic samples acquired pre- and post-backflush showed that while the overall abundance of macroinvertebrates (including NZMSs), and the species diversity decreased after the backflush, the proportion of live NZMSs to the overall benthic macroinvertebrate community increased, and NZMS remained among the top five dominant species. As with NZMSs, the other benthic macroinvertebrates appeared to have sustained a greater impact at those sample stations that received a topical application of rock salt. Owing to the NZMS's high reproductive potential, a reduction in numbers of resident competitors or predators could result in an increase in NZMS abundance if their ability to re-populate and exploit habitat and food resources outpaces that of other inhabitants (Adams, 2010). The rate of NZMS re-colonization following the backflush warrants further investigation, as does the extent and magnitude of collateral ecologic impacts to other species.

There are many water bodies that are at least partially amenable to controlled saltwater backflushes. For instance, navigation locks that connect inland freshwater lakes and canals to the sea are common and are often equipped with controllable saltwater barrier features designed to prevent excessive intrusion of seawater into freshwater ecosystems. Seagates are sometimes positioned along the perimeters of diked freshwater impoundments and may, under some circumstances, be used to alter the salinity of the contained water. The efficacy of saltwater treatments for controlling NZMS infestations at any location would depend on each system's unique hydrology and the ability of managers to control it. It is clear from the results of this study and previous accounts, that temperature and the rate at which maximum salinities are achieved are important factors in determining the outcome of a saltwater treatment. By incorporating predictions of maximum achievable salinities and durations, our GLM results can be used by managers to make informed decisions about the potential efficacy of eradicating or controlling localized infestations of NZMSs.

Table 1 References to salinity tolerances reported for the New Zealand mudsnail (*Potamopyrgus antipodarum).*

Reference	Salinity (‰)	Wild	Laboratory
Adam (1942)	34		X
Costil et al. (2001)	28	X	
Drown et al. (2011)	30		X
Duncan (1967)	34		X
Duncan and Klekowski (1967)	58		X
Hylleberg and Siegismund (1987)	30		X
Jacobsen and Forbes (1997)	15		X
Johnsen (1946)	33	X	
Klekowski and Duncan (1966)	64		X
Muss (1963)	15	X	
Muss (1967)	24	X	
Nicol (1936)	23	X	
Siegismund and Hylleberg (1987)	22	X	
Todd (1964)	32		X
Winterbourn (1970a)	26	X	
Winterbourn (1970a)	21		X

Table 2 Sample size (*N*) and pre- and post-backflush percent survival at each of 26 sample stations. Stations S1 – S8 were supplemented with topically applied rock salt.

	Pre-backflush		Post-backflush		Elevation
Station #	*N*	% Live	*N*	% Live	(NGVD29[a])
1	141	100.00	55	69.09	0.74
2	200	100.00	237	89.03	0.79
3	146	100.00	130	45.38	0.79
4	200	100.00	122	72.13	0.28
5	28	100.00	73	90.41	0.91
6	200	100.00	184	97.83	0.91
7	48	100.00	37	48.65	0.36
8	79	100.00	116	69.83	0.36
9	244	98.36	207	96.14	0.89
10	119	100.00	73	79.45	0.74
11	100	100.00	258	99.22	1.47
12	40	97.50	114	88.60	1.75
13	127	100.00	100	100.00	1.75
14	92	97.83	23	78.26	1.17
15	119	100.00	105	94.29	0.23
16	207	99.52	125	92.80	0.23
17	100	100.00	71	76.06	0.28
18	169	100.00	61	70.49	0.38
S1	55	96.36	124	91.94	0.84
S2	72	100.00	133	78.95	0.66
S3	166	98.80	106	67.92	0.64
S4	30	100.00	3	66.67	0.81
S5	45	100.00	74	70.27	0.38
S6	2	100.00	5	80.00	0.41
S7	61	96.72	38	84.21	0.13
S8	2	100.00	17	76.47	0.46

[a] National Geodetic Vertical Datum of 1929.

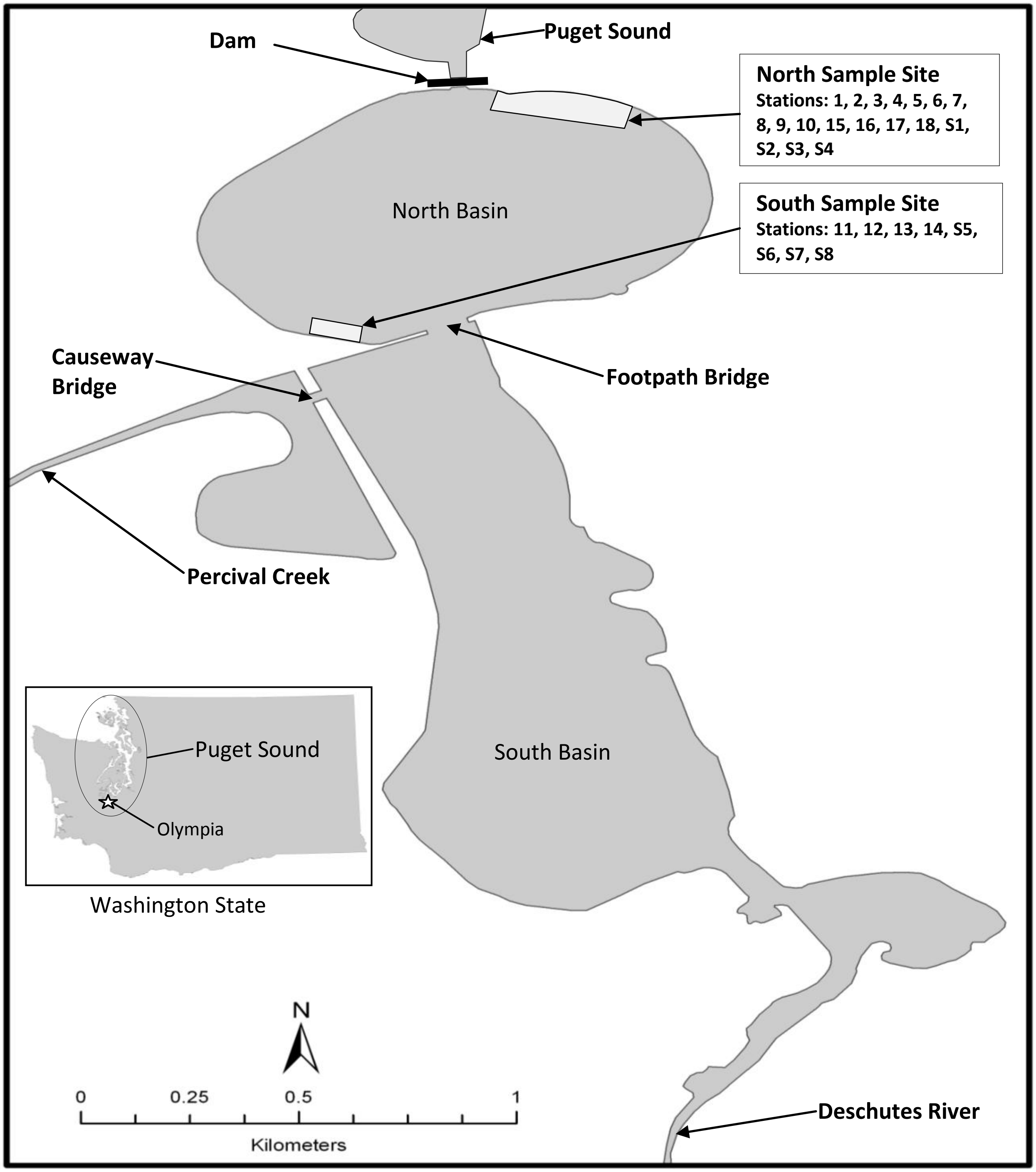

Fig. 1 Map of Washington State showing the location of Puget Sound and Olympia (Capitol Lake), and of Capitol Lake showing the two sample sites used to evaluate the effect of a saltwater backflush on New Zealand mudsnail survival.

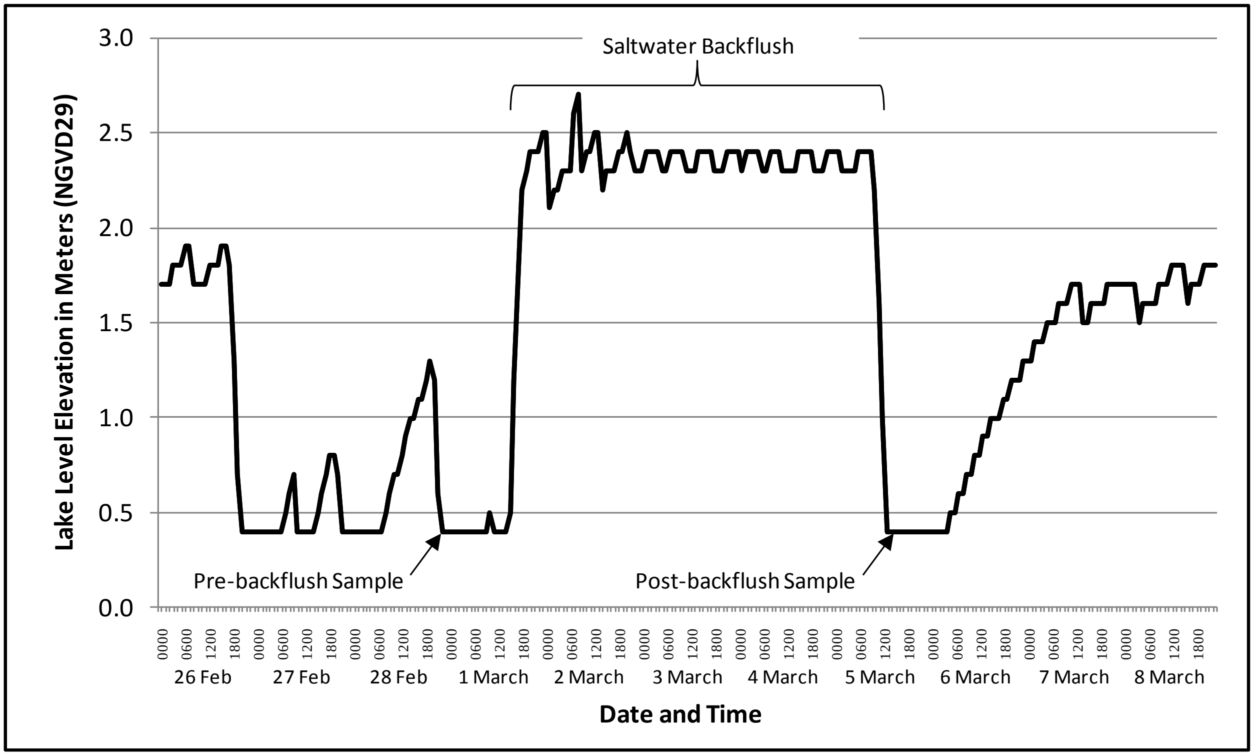

Fig. 2 Lake level elevations before, during, and after the saltwater backflush, and, pre- and post-backflush sample dates and times.

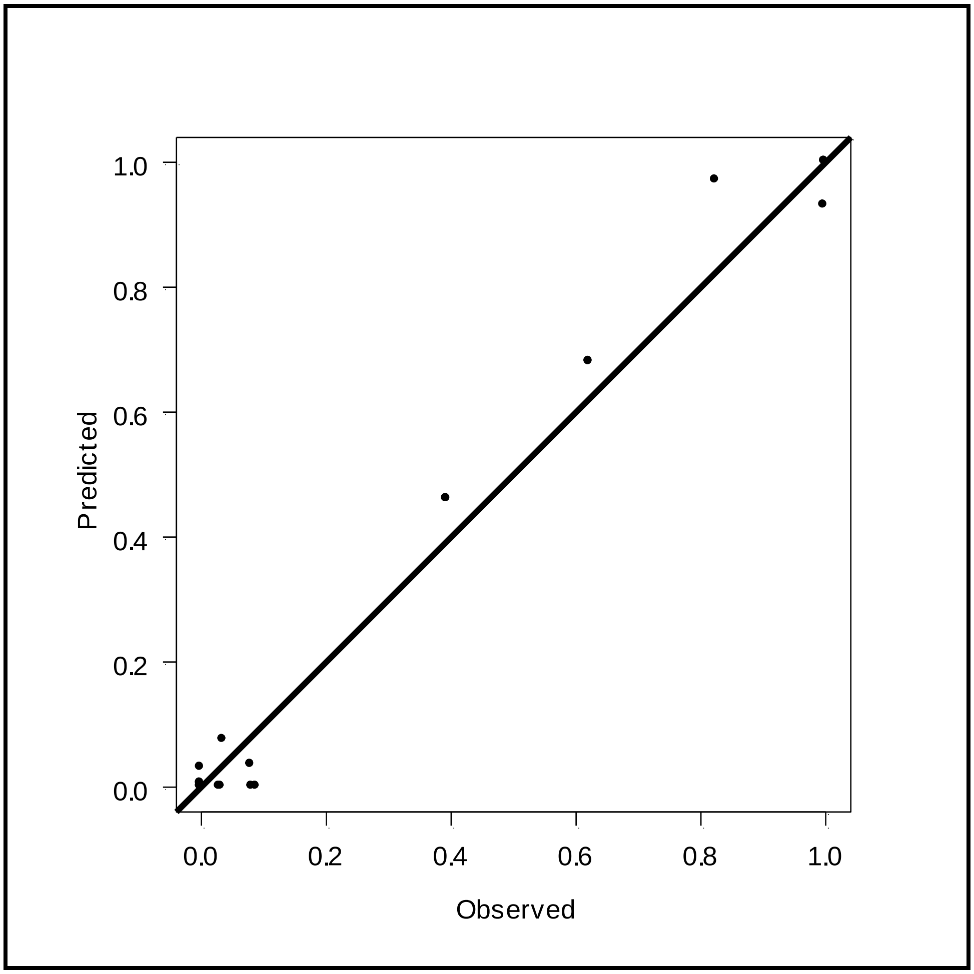

Fig. 3 Fitted GLM predicted and laboratory observed results. Axes represent percent survival.

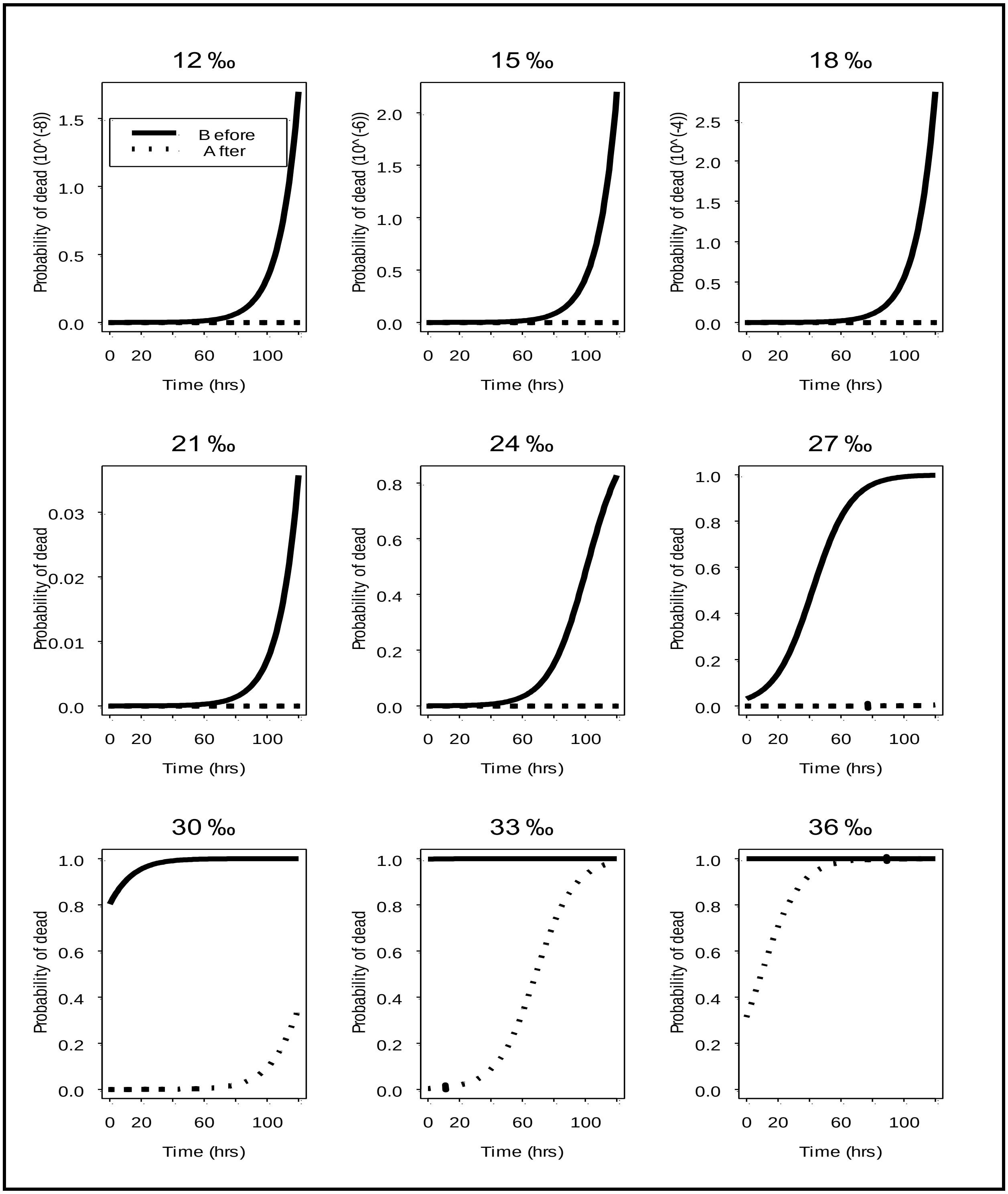

Fig. 4 GLM predicted mortality curves constructed from pre- and post-backflush laboratory saltwater trials. Note that the y-axis scales may differ among salinities.

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