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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 to examine the effect of increasing the lake's salinity on NZMS survival. We present pre- and postbackflush survival rates from 26 sample stations, 8 of which were supplemented with the topical application of salt. Increasing 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 postbackflush NZMSs to laboratory saltwater trials and used the data to construct a generalized linear model to predict survival rates under various salinity exposure regimes. More NZMSs were killed in response to the backflush than was predicted by the generalized linear model. Water temperatures in the lake were lower than those used in the laboratory and this may have decreased NZMS resistance to increased salinities in the lake.

KEY WORDS: salinity tolerance, New Zealand mudsnail, *Potamopyrgus*, survival rate, generalized linear model

INTRODUCTION

The New Zealand mudsnail (NZMS) is a hydrobiid mollusc that is native to New Zealand. Its impact on native fauna and ecological processes outside its native range is not well understood (but see Schreiber et al. (2002), Hall et al. 2003, Kerans et al. (2005), Strzelec (2005), Strzelec et al. (2006), Hall et al. (2006)); however, its expansion during the past century to estuarine and freshwater environments around the world, and its ability to reach very high densities rapidly when 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 United States 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 nonnative 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 & Finlayson 2005, Schisler et al. 2008). Large-scale *in situ* eradication has not been attempted (but see McMillin & Trumbo (2009)). In this study, we (1) examined the effect on NZMS survival of backflushing a freshwater lake (Capitol Lake in Olympia, WA) with saltwater introduced through an existing engineered tide gate dam that connects the lake to the sea (Puget Sound), (2) subjected prebackflush and surviving postbackflush NZMSs to a laboratory-conducted saltwater trial to evaluate the population's posttreatment 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 nonnative NZMS infestations.

LITERATURE SYNOPSIS: SALINITY TOLERANCES FOR THE NZMS

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. In the source documents, salinities are expressed in parts per thousand using the per mille symbol (‰). We have adopted the modern convention of reporting salinities as numbers without unit, thus dispensing with the per mille symbol. 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 (1970b) found NZMSs in salinities as high as 26 in the species' native New Zealand. Under laboratory conditions, the same author noted that after 24 h, snails acquired from both freshwater and brackish water sources remained active at a salinity of 17.5, exhibited reduced movement at a salinity of 21, and withdrew completely into their shells and were inactive in higher salinities.[1] All the snails resumed normal activity within 24 h of being returned to low-salinity water (3.5). Johnsen (1946) reported finding a single NZMS on the northeast shore of Bornholm, Denmark, near the mouth of the Baltic Sea in a tide pool with a salinity of 33. The pool was described as having been part of a once larger pool that had been

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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)	21		X
Winterbourn (1970b)	26	X	

reduced in size through evaporation. Because 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, although 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 increasing 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 NZMSs 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 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 mollusc encountered in the basin's polyhalinic (salinity, 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 6 sites in Denmark to salinities of 0 and 10 (all 6 sites) and 5 and 15 (2 of the 6 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, whereas 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 7 traits (probability of survival, probability of reproducing, growth rate, time to asymptotic shell size, time of first reproduction, shell size of first reproduction, and individual fitness) from ancestral- and invasive-range lineages of NZMSs across a salinity gradient (0, 5, 10, and 15). Snails held at nonzero salinities were acclimated by increasing the salinity by 5 every 6 h 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 a salinity of 30 resulted in high mortalities for some lineages and precluded their use for comparative analyses over all 7 examined traits, although they observed that only the invasive strains were successful at reproduction in salinities of 15 and 30. They concluded that invasive NZMS lineages are adapted to a higher salinity compared with ancestral lineages.

Consistent with Jacobsen and Forbes (1997), Muss (1963) listed 0–15 as being a rough estimate of the salinity 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 3 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 3 strains maintained hyperosmotic 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 there was an observed decrease in activity (e.g., motility, feeding, and so forth) at higher salinities. Similarly, Duncan (1967) tested the salinity tolerance of NZMS acquired from freshwater 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 h 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 2 days at a salinity of 18 before transferring them to higher salinities nearly doubled the survival rate. Furthermore, they found that NZMSs acquired from both sources maintained hyperosmotic hemolymph 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 1-mo intervals, the surviving snails from each batch were moved to a slightly higher salinity. Snails that were placed directly in salinities of 22 or higher at the beginning of the experiment failed to survive the first month. Of the snails that were initially introduced to a salinity of 20, only 9 survived the first month; however, those 9 survived the

next 7 monthly transfers up to a salinity of 34, after which they all died. Offspring were produced in salinity as high as 28, although 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 NZMSs acquired from a small (11-ha) freshwater lake near Aberdeen, Scotland, and respiration and heart rate from juvenile NZMSs collected from a brackish water marsh near Plymouth, England (Duncan & Klekowski 1967). Some of the freshwater-derived snails survived in salinity as high as 64 when acclimated every 2 days by an increase in salinity of 2–3, and the authors noted that even at a salinity of 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 (the salinity was increased by 8 every 24 h) and did not survive beyond a salinity of 58. The authors speculated that observed increases in respiratory rate with increased salinity may be the result of increased osmoregulatory demands. Boycott (1936, p. 141) 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 9 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, pers. comm..). 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. NZMSs are now well established at many freshwater 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, pers. comm.). However, salinity in the lower Columbia River fluctuates widely from 0–30, and it is likely that NZMSs in the lowermost 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, pers. comms.), and densities of up to 20,000/m^2 have since been detected (A. Pleus, Aquatic Invasive Species Unit, WDFW, pers. comm..). 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 during the past 8 y.

The published accounts of NZMS salinity tolerances and occurrences suggest the species is generally restricted to salinities ranging from freshwater to brackish water in the wild. Results from laboratory manipulations, however, indicate they may be acclimated to withstand hypersaline water, likely as a result of 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 h, 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 ha. 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 2 adjoining streams (Deschutes River and Percival Creek) to inundate the tidal flats permanently (Fig. 1). Puget Sound is a saltwater estuary fjord of mixed semidiurnal 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 (Washington State Department of Ecology 2010). A salinity measurement taken from just seaward of the dam on the afternoon of March 1, 2010 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 U.S. 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 as a result of meteorological effects (Moffatt & Nichol 2008). Air temperatures remained above freezing (minimum, 3°C; maximum, 12°C) during all phases of the experiment. Thus, exposure to subfreezing temperatures during the drawdown phases of the experiment was not a factor affecting survival (Cheng & 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 restratification 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 prebackflush drawdown on NZMS survival was assumed to be insignificant as a result of the known ability of NZMSs to survive unsubmerged in

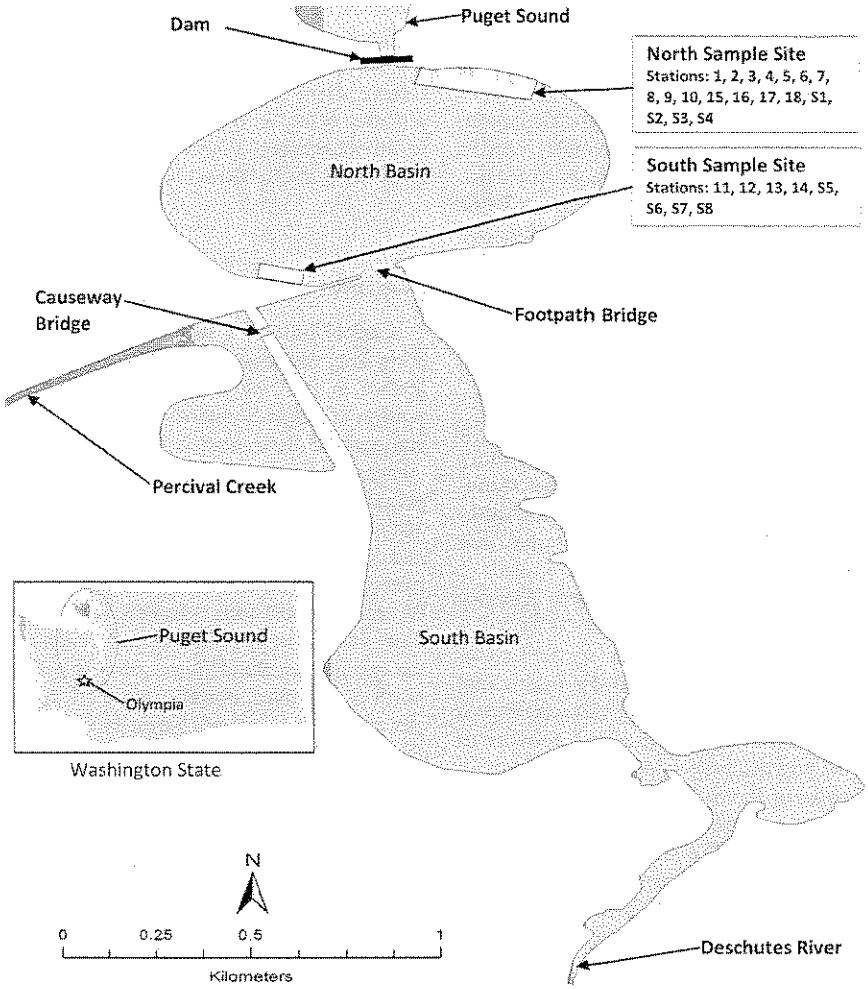

Figure 1. Map of Washington state showing the location of Puget Sound and Olympia (Capitol Lake), and of Capitol Lake showing the 2 sample sites used to evaluate the effect of a saltwater backflush on New Zealand mudsnail survival.

damp environments for long periods of time (Winterbourn 1970b). Cloud cover, high humidity (maximum, 100%; minimum, 61%), low winds, and moderate temperatures prevented the exposed lakebed 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 was 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 prebackflush level (Fig. 2).

During the time the lake level was lowered but prior to the backflush, 14 stations were selected along the north shore near the dam where we judged maximum salinity would be achieved during the backflush, resulting from close proximity to the saltwater source and maximum distance from freshwater flowing into the lake from the two adjoining streams. Half 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 8 stations, 4 each at the north and south sample sites, were treated with a topical application of rock salt (Morton White Crystal® Rock Salt, Morton, Inc., Chicago, IL) applied at the rate of 1 kg/m^2 over an area of approximately 1 m^2. Each of the 26 stations (Fig. 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 min 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 4 h 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 the surface and one near the bottom, were taken at each of 10 locations in the northern basin of the lake on March 2, shortly after the initial saltwater backflush phase of the experiment began. 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 2 NZMS sample sites (≈60 m distant) registered 10.5 and 12.4 (near surface),

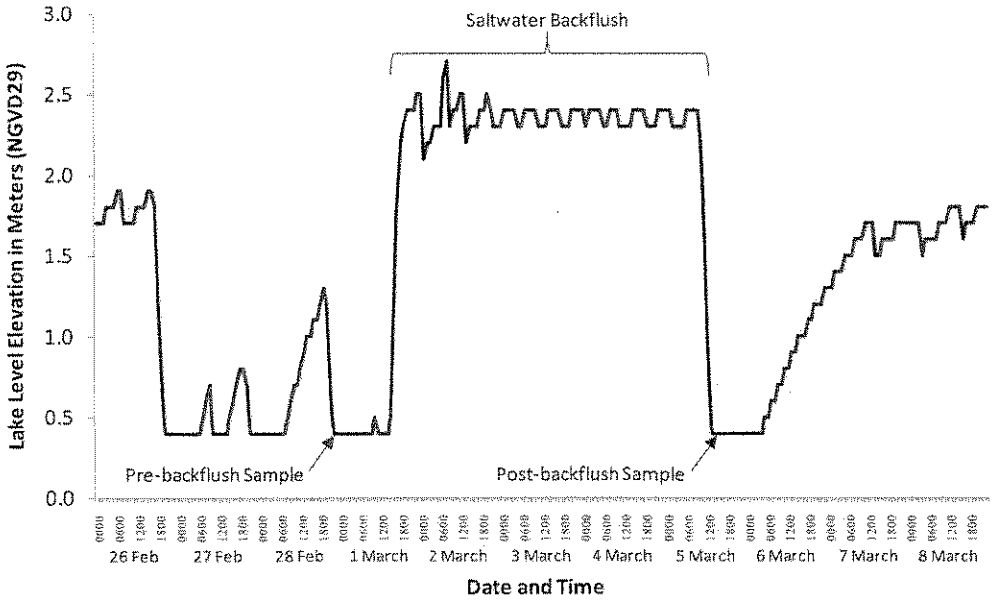

Figure 2. Lake-level elevations before, during, and after the saltwater backflush, and before and after backflush sample dates and times. NGDV29, National Geodetic Vertical Datum of 1929.

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

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 3 days prior to and 5 days after the backflush in each of 5 separate, covered 15-L containers. The containers were filled respectively with (1) freshwater from Capitol Lake; (2) brackish water (salinity, 21) from Budd Inlet approximately 200 m north of the dam; (3) brackish water (salinity, 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 (salinity, 27) from the entrance to Budd Inlet, and (5) saltwater (salinity, 35) produced by mixing Instant Ocean with freshwater from Capitol Lake. All 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 h. 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 4 h in freshwater were judged dead. All live snails were returned to their respective source containers after the number of dead snails had been determined.

Statistical Analysis

We used a generalized linear model (GLM) (McCullagh & Nelder 1989, Cheng & 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 (before vs. after the backflush). For the laboratory saltwater trial, the predictor variables were time (measured in hours), salinity, and the status of the experiment (before vs. after the backflush). The response variable for both the field and laboratory experiments was the proportion of dead NZMSs. The chosen GLM submodels for the field and laboratory experiments, using all the respective predictor variables, were selected by both Akaike information criteria (AIC) (Akaike 1974) and Bayesian information criteria (Schwarz, 1978). Student's *t*-test was used to test the significance of each predictor variable. Fitted values were plotted against observed values 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 (SD, 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, whereas the larger sample size decreased the proportion by 7.5% and 3.8%, respectively. 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

TABLE 2.

Sample size (n) and pre- and postbackflush percent survival at each of 26 sample stations.

Station no.	Prebackflush n	Prebackflush % Live	Postbackflush n	Postbackflush % Live	Elevation (NGVD29*)
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

* National Geodetic Vertical Datum of 1929.
Stations S1 through S8 were supplemented with topically applied rock salt.

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 nonlinear and thus likely to be a function of other factors, as well.

The chosen submodel for the field observations includes 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 is not included ($P > 0.2$). The fitted GLM results and the observed laboratory data are plotted in Figure 3. Although 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 submodel for the laboratory saltwater trial uses all three predictor variables (time, salinity, and status of the experiment), each of which is highly significant ($P < 0.001$), to predict the proportion of dead NZMSs (Fig. 4). When standardized to a sample size of 100, the model indicates that prior to the backflush, a salinity of at least 27 maintained over a period of 5 days would be necessary to achieve complete eradication.

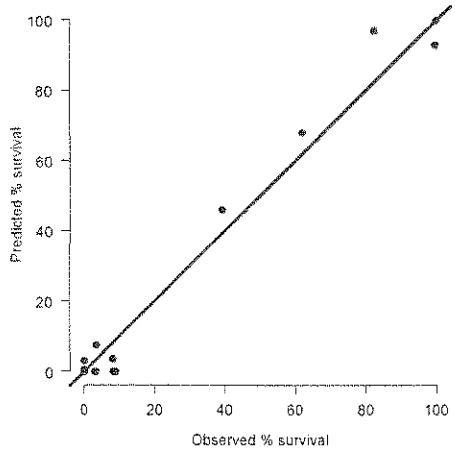

Figure 3. Fitted generalized linear model predicted and laboratory observed results.

Substantial impacts to survival could be realized at salinities of 24 or less; however, the exposure time necessary to effect complete eradication at any practically achievable concentration by backflush alone may be beyond reach in Capitol Lake as a result of constraints imposed by the lake system's local hydrology.

Results from the laboratory saltwater trial conducted with NZMSs sampled 5 days after the backflush showed a remarkable difference in salinity tolerance when compared with those NZMSs sampled prior to the backflush. After 120 h in a salinity of 27, 83% of the NZMSs sampled postbackflush were still alive compared with just 7% of the snails sampled prebackflush. Although nearly all snails (pre- and postbackflush) were able to survive for 120 h in a salinity of 24, neither the pre- nor postbackflush NZMSs survived the 120-h immersion in 35 salinity.

DISCUSSION

Temporarily increasing 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 h, as predicted. Maintaining the lake-level elevation below flood level during the backflush required that the dam be opened periodically to release excess water entering the lake via the two adjoining streams. Because 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, might 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 the result of lower temperatures in the lake (≈9°C throughout the course of the backflush) that decreased NZMS resistance to increased salinities,

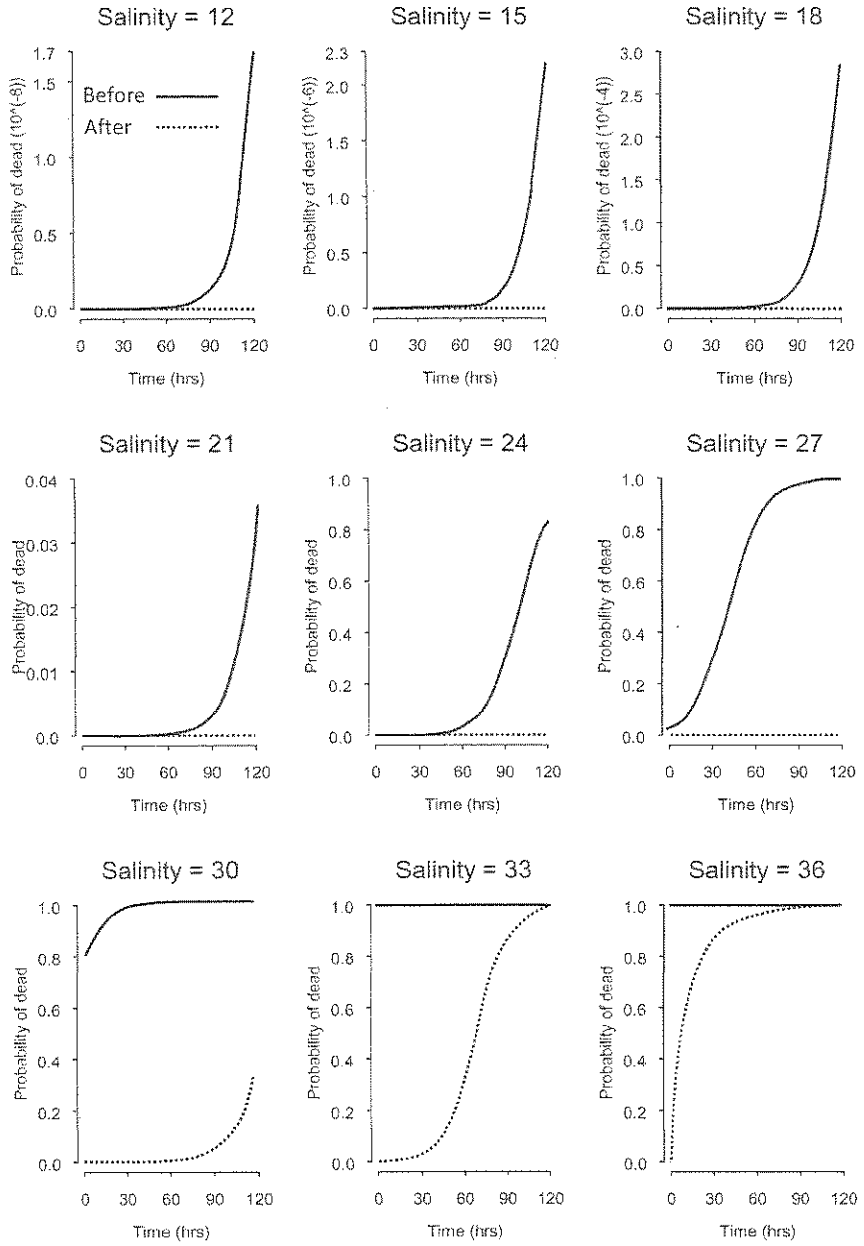

Figure 4. Generalized linear model predicted mortality curves constructed from pre- and postbackflush laboratory saltwater trials. Note that the y-axis scales may differ among salinities.

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 pretreatment mortality predicted by GLM (≈0.5%) could have been the result of natural mortality, induced handling effects or some other factors.

The increased salinity tolerance of NZMSs collected from Capitol Lake after the backflush was likely the result of acclimatization, and it is noteworthy that several live and actively crawling juvenile snails were observed in the postbackflush sample at a salinity of 27 after 216 h (all other trials were terminated at 120 h). This anecdotal observation agrees well with the findings of Adam (1942) and Drown et al. (2011) (see Literature Synopsis). Given that the pre- and postbackflush 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 acclimated successfully.

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 primarily the result of 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 epigenetically transmitted, the effect would likely be lost throughout 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 nonanthropogenic 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 *Platichthys 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 (Herrera Environmental Consultants 2004). Dean (1904) noted that NZMS can pass through perch (species not indicated) as intact shells, although the author did not indicate whether 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 may 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 postbackflush showed that although 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 5 dominant species. As was NZMSs, the other benthic macroinvertebrates appeared to have sustained a greater impact at those sample stations that received a topical application of rock salt. Because of the high reproductive potential of NZMSs, a reduction in numbers of resident competitors or predators could result in an increase in NZMS abundance if their ability to repopulate and exploit habitat and food resources outpaces that of other inhabitants (Adams 2010). The rate of NZMS recolonization after the backflush warrants further investigation, as does the extent and magnitude of collateral ecological 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. Sea gates 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.

NOTES

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 (1970a), rather than Winterbourn (1970b).

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