

Research Article

A quantitative evaluation of the effect of freezing temperatures on the survival of New Zealand mudsnails (*Potamopyrgus antipodarum* Gray, 1843), in Olympia Washington's Capitol Lake

Yuk W. Cheng and Larry L. LeClair*

Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, WA 98501, USA

E-mail: Yuk.Cheng@dfw.wa.gov (YWC), Larry.Leclair@dfw.wa.gov (LLC)

*Corresponding author

Received: 1 October 2010 / Accepted: 17 December 2010 / Published online: 6 January 2011

Abstract

First detected in the United States in Idaho's Snake River in 1987, the New Zealand mud snail (NZMS), *Potamopyrgus antipodarum*, was discovered in Olympia Washington's Capitol Lake in 2009. The snail is not native to North America and may be capable of adversely impacting native species diversity and food web dynamics in aquatic ecosystems. In this study, we evaluated the effect of lowering the lake level during freezing weather on the survival of NZMSs. Both generalized linear models with link function logit and nonlinear mixed effects models were used to investigate the rates of detection and survival with four temporal and environmental predictor variables. The rate of detection of NZMSs was affected by substrate depth and proximity to shore. The location of sample stations (upshore versus offshore), substrate depth, and elapsed time between collection from the field and laboratory processing did not affect survival rates. The survival rate of NZMSs decreased rapidly with time and the predicted survival rate at the conclusion of the freezing episode was 1.8%. The results indicate that lowering the water level during freezing weather can be a highly effective means for controlling the distribution and abundance of NZMSs and reducing the risk of their spread to other water bodies.

Key words: freezing weather, survival rate, generalized linear models

Introduction

The New Zealand mudsnail (NZMS) (*Potamopyrgus antipodarum* Gray, 1843) is a hydrobiid mollusk that is native to New Zealand, but occurs throughout eastern Australia and Europe where it was formerly known as *Potamopyrgus jenkinsi* Smith, 1889 (Ponder 1988). The first recorded discovery of the species in North America occurred in 1987 in Idaho's Snake River (Bowler 1991). Subsequently, five species of mollusks native to the Snake River drainage were listed under the U.S. Endangered Species Act as either "threatened" or "endangered", in part due to the proliferation of NZMSs (Richards 2002). Since then, the NZMS has been found in nine additional western states (Gustafson et al. 2002), and one western Canadian province (British Columbia) (Davidson et al. 2008), and five Great Lakes states and one eastern Canadian province (Ontario) (Benson 2010). In the absence of co-evolved predators and parasites, NZMSs can

multiply to astounding numbers under favorable conditions. For instance, in less than a decade, snail densities have gone from undetectable levels to 229,000 snails per square meter of streambed in some rivers of Yellowstone National Park (Kerans et al. 2005).

Any new biotic component to an aquatic ecosystem, including non-native species such as the NZMS, must necessarily carve an ecological niche in order to survive. In doing so, the structure (i.e., species diversity) and function (i.e., energy flow) of the native food web may be disrupted. The non-native NZMS competes with native invertebrates, including native mollusks, for space and food resources. Because of their high reproductive potential, NZMSs can constitute up to 80% of the invertebrate biomass and consume more than 75% of the gross primary production (Hall et al. 2003). Thus, they have the potential to control the energy dynamics and nutrient cycling in an aquatic ecosystem. Adverse impacts to lower levels of the food web may have implications for organisms at higher

trophic levels, such as fish, which rely on lower-level organisms as a food source. The presence of NZMSs may reduce the availability of native invertebrate prey for fish such as salmonids and sculpins and at the same time, do not constitute a viable food source themselves. Their hard shell and resistance to digestion allow them to pass through fish without lending any nutritional value or caloric input to the consumer (Ryan 1982; Haynes et al. 1985; Aarnio and Bonsdorff 1997; Vinson and Baker 2008; Bruce et al. 2009). Bersine et al. (2008) documented the first occurrence of NZMSs in the diet of juvenile Chinook salmon (*Oncorhynchus tshawytscha* Walbaum, 1792). Seasonal migrations of both juvenile and adult Chinook salmon occur in Capitol Lake. The presence of NZMSs in the guts of fish, including salmon, may be an early indicator that an aquatic food web's dynamics are undergoing change due to the presence of NZMSs. Interestingly, few studies have investigated the negative impacts on entire fish populations in areas of high NZMS densities. While fish can still swim to un-invaded reaches to seek food, many biologists feel that it is only a matter of time until the NZMS spreads far enough within invaded streams to begin having a negative impact on fish growth. In general, it often takes decades for the impacts of a non-native species on native biota to fully manifest. Both positive and negative relationships between densities of native benthic invertebrates and NZMS have been observed (Cada 2004; Kerans et al. 2005; Schreiber et al. 2002).

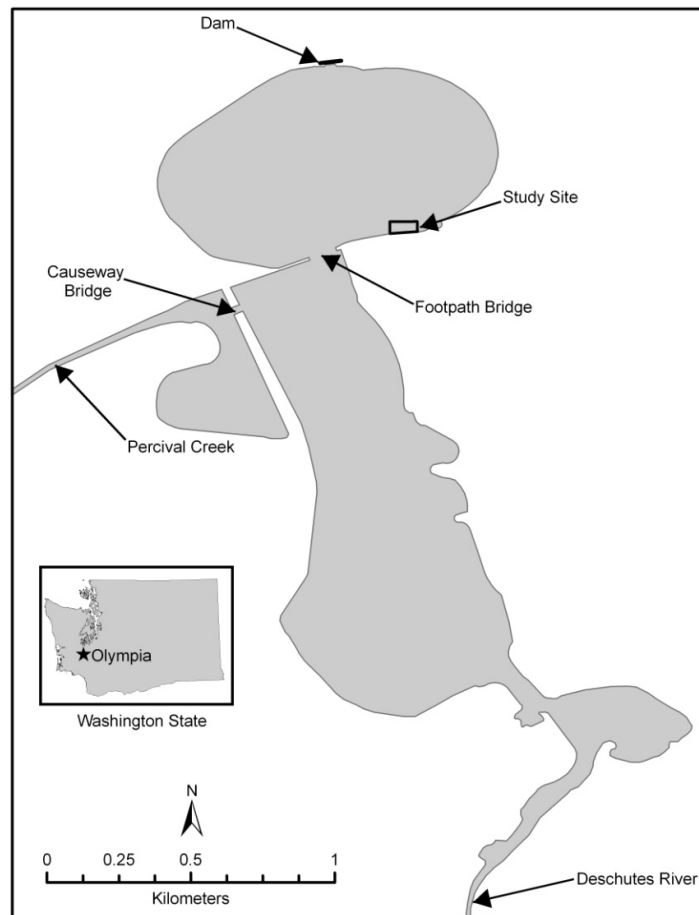
The biology of the NZMS has been described in detail elsewhere (see Zaranko et al. 1997 and references therein) and only those attributes that are particularly relevant to the design and outcome of this study will be summarized here. In brief, they are tiny aquatic snails that reach a maximum length of about 6mm in their non-native range, but may attain twice that length in New Zealand. They have an annual life cycle and, age at maturity ranges from about three to nine months (Anonymous 2007). In New Zealand, females may reproduce either sexually or parthenogenically; however, in North America, known populations of NZMSs are composed almost entirely of parthenogenic females, therefore, colonization may occur from the introduction of a single female. In the western U.S., reproduction occurs in the spring and summer. Females brood embryos in a specialized brood pouch and release from 20 to

120 free crawling juveniles and may produce up to 230 offspring per year. Though optimal salinity for growth and reproduction is between 0 and 5 psu, they are considered euryhaline and are capable of withstanding salinities up to 35 psu for short periods of time, and may thrive and reproduce at salinities as high as 15 psu (Jacobsen and Forbes 1997; Alonso and Camargo 2004). They tolerate a broad range of temperatures above freezing up to 34°C, but are not capable of surviving in temperatures at or below freezing (Zaranko et al. 1997; Cox and Rutherford 2000). Although they are resistant to desiccation and can survive up to 24 hours without water, and for weeks on damp surfaces, they are not tolerant of high temperatures.

The NZMS was first reported from Washington's Capitol Lake in October, 2009 (B. Bartleson and E. Johannes, personal communication). Shortly afterward, a rapid qualitative synoptic survey of the lake's nearshore environment and adjoining streams was conducted. The survey indicated a patchy distribution of snails throughout the lake with some areas of very high density, and, that the adjoining waterways were not infested. Capitol Lake is a shallow manmade lake that is 3 km long, and covers an area of approximately 105 hectares (Figure 1). It was formed in 1951 when a constructed berm and dam enclosed the southernmost tidal basin of Puget Sound and enabled the retention of outflow from two adjoining streams (Deschutes River and Percival Creek) to permanently inundate the tidal flats. The lake was originally conceived as an aesthetic accompaniment to the landscape and architecture of the State Capitol building. In recent years, the disposition of the lake has fallen under intense public scrutiny and debate, hinging on whether or not to return the lake, either partially or entirely, to a tidal estuary. The lake is managed by the Washington State Department of General Administration, which controls the water level by opening or closing spillways at the foot of the lake. As a first measure to stem the threat of transfer of the NZMS to other nearby water bodies, the lake was closed to public access in November, 2009.

The objectives of this study were to investigate the effect of freezing temperature on the mortality of NZMSs in situ and identify variation in the change of the density of NZMSs with substrate depth. During a seven day period beginning December 7, 2009, daily low

Figure 1. Map of Washington State showing the location of Olympia and Capitol Lake, and map of Capitol Lake.



temperatures in Olympia ranged from -8°C to -14°C and did not exceed 2°C . A rapid partial lowering of the lake level during this period enabled us to test the effect of freezing temperatures on nearshore NZMS survival and to evaluate the potential use of full lake draw-downs to control NZMSs in Capitol Lake. Specifically, we tested the following four hypotheses:

H₁: The rate of detection of NZMSs varies with substrate depth from the surface to 70 cm;

H₂: The survival rate of NZMSs decreases with time under freezing temperatures;

H₃: The survival rate of NZMSs varies within sites and by proximity to shore; and

H₄: The survival rate of NZMSs varies among sample stations.

Methods

Field and laboratory

Lake draw-down commenced at 1500 on December 9. The lake level was lowered by 0.75 m below its normal winter level at a rate of 0.5 m per hour. At the time of the draw-down, the lake surface was frozen to a depth of approximately 7 cm, leaving the newly exposed shore blanketed in a layer of slab ice. Four transects running perpendicular to shore and spaced 10 m apart were established in an area known to harbor high densities of NZMSs. Two sample stations were positioned along each transect, one upshore at the pre draw-down water's edge, and one offshore located 1.5 m shoreward of the post draw-down water's edge. Approximately 4 sq. m of slab ice was cleared

from each sample station in order to fully expose the substrate and eliminate any possible insulating effect the ice may have provided against freezing temperatures. Field sampling commenced 18 hours after the completion of the draw-down. At each station, approximately 250 cm³ of substrate was sampled from each of three substrate depth strata (surface, 30cm, and 70 cm) on three separate occasions (December 10, 11, and 14), except that a 70 cm sample was not taken on December 14. The temporal replicates from each station were excavated from immediately adjacent, but non-overlapping holes. The substrate samples were placed in plastic bags and transported to a laboratory for processing.

In the laboratory, each substrate sample was worked through a 0.425 mm stainless steel sieve in order to facilitate visual detection of the snails. Using forceps, each snail was carefully removed from the remaining substrate and placed in a petri dish filled with lake water, which was at room temperature. The snails were allowed to sit undisturbed in the petri dish for approximately 5 minutes before being examined under a dissecting microscope to determine if they were alive or dead. Snails were considered live if they emerged from their shells or if the operculum of non-emergent snails showed signs of movement when disturbed. Dead snails were further subcategorized as “recent dead” if one or more of the following conditions were met:

- 1) The periostracum appeared to be intact;
- 2) The operculum was present; or,
- 3) The body was present.

They were considered “long dead” if the periostracum, operculum, and body were all absent. Snails that were considered long dead were not included in the statistical analysis. All laboratory processing took place within 24-32 hours after collection from the field. Snail counts ranged from 0-55 individuals per substrate sample core.

Determining the minimum number of replicates

We used 5% and 20% probabilities for Type I (α) and Type II (β) errors, respectively, where $1 - \beta$ is the power of the test. We assumed, conservatively, that the mean survival rate at days 0 and 4 were 0.5 (μ_{max}) and 0.05 (μ_{min}), respectively. Judging from a cursory visual exam of snail abundance at the study site, we deduced that at least 15 (m) NZMSs would be attainable from the surface at each sampling station. The minimum effective number of replicates (n) was

determined by α , β , d , and k , where $d = (\mu_{max} - \mu_{min})/\sigma$, k is the number of treatments, and σ is the common population standard deviation estimated from a subsample of 15 (m) (Searcy-Bernal 1994). Each temporal sample (days 0, 1, and 4) is expected to affect the survival rate; therefore the number of treatments (k) is equal to 3. An estimation of the population standard deviation ($\hat{\sigma}$) can be produced by $\sqrt{2\bar{p}\bar{q}/m}$, where $\bar{p} = \frac{\mu_{max} + \mu_{min}}{2}$, and $\bar{q} = 1 - \bar{p}$ (Fleiss et al. 2003: pp 69-70). The effective size index (f) is equal to $d\sqrt{0.5/k} = 1.13$. With known values of f , k , α , and $1 - \beta$, we determine from Table A.2 of Searcy-Bernal (1994) that $n = 4$.

Statistical analysis

Analysis of variance of arcsine transformed data is a commonly used approach when the response variable from a Bernoulli trial and the number of trials are equal among treatments and replicates; however, the number of trials among treatments and replicates are often not equal. If there is a difference among the various levels of the predictor variables (treatments), additional tests are needed. A generalized linear model (GLM) (McCullagh and Nelder 1989; Cheng and Gallinat 2004) using the canonical link function for the binomial distribution (logit) can be used to overcome problems associated with different sample sizes among the various levels of predictors. The differences among all treatment levels when the response variable is from a Bernoulli trial can be tested with systematic changes of the control treatment in GLM. In addition, GLM can overcome the possible prediction of negative values produced by multiple regression tests.

The response variables are rate of detection and rate of survival for NZMSs. They are both Bernoullian with outcomes of either live or dead. The predictor variables are substrate depth (0 to 70 cm), station location (upshore and offshore), days (0, 1, and 4), and, elapsed time between field collection and laboratory processing (24 - 32 hrs). There are four replicates in the experiment.

The chosen GLM submodel was selected by both Akaike Information Criteria (AIC) (Akaike 1974) and Bayesian Information Criteria (BIC) (Schwarz, 1978), and was investigated with nonlinear mixed effects models (NLME) (Pinheiro 1994; Pinheiro and Bates 2000). NLME models compare individual curves and

group survival curves rather than group observations, as occurs with repeated measures analysis of variance (ANOVA) (Cheng and Kuk 2002; Purcell and Cheng 2010). The model accounts for the nonlinear survival rates, fixed effects from experimental factors and, random effects (Laird and Ware 1982) due to natural variation among sites. The likelihood ratio test was used to assess the significance of natural variation among sites. The *glm()* and *nlme()* functions in SPlus 2000 (Insightful Corporation) were used for the analyses.

Results

Rate of detection

The final submodel selected by both AIC (154.17) and BIC (161.66) was with the predictor variables substrate depth (estimated coefficient = 2.23, $P < 0.001$, Student's t-test), station location (upshore versus offshore) (estimated coefficient = -0.89, $P < 0.01$, Student's t-test) and intercept (estimated coefficient = 2.23, $P < 0.001$, Student's t-test) from the GLM fitted results (residual deviance = 41.23485, $df = 45$). The predicted mean rates of detection for upshore and offshore stations by substrate depth (0 to 70 cm) are plotted in Figure 2. The rate of detection was not affected by time or station location ($P > 0.5$, Student's t-test). The estimated rates of detection of NZMS in upshore and offshore surface samples were 75% and 94%, respectively. The difference between upshore (67%) and offshore (27%) detection rates increased at a substrate depth of 30 cm. At 70 cm substrate depth, the estimated rates of detection up- and offshore were 5% and 21%, respectively.

Survival rate

The final GLM fitted submodel selected by both AIC (92.18) and BIC (95.23) is with the predictor variable day (estimated coefficient = -0.95, $P < 0.01$, Student's t-test) without intercept. The location of the sample stations (upshore and offshore), substrate depth, and elapsed time between collection from the field and laboratory processing did not affect the survival rates. Both the observed and predicted survival rates were plotted against time in Figure 3. On day 0, the predicted survival rate was 50% (s.e. = 0.08). On day 4 the survival dropped to 1.8% (s.e. = 0.01). By day 4, the variation in survival rate was minimal.

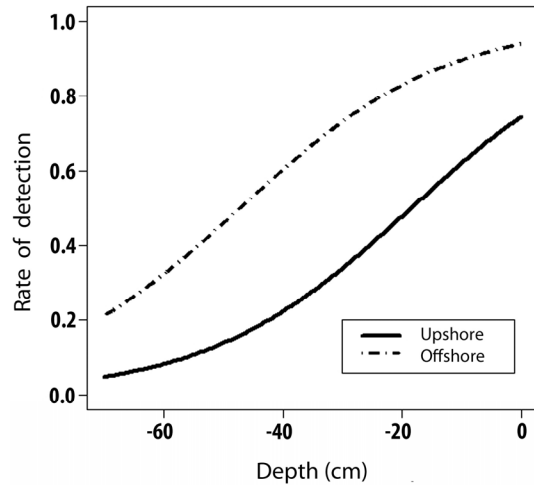


Figure 2. Plot of the expected rate of detection of New Zealand mudsnails against substrate depth at up- and offshore sample stations.

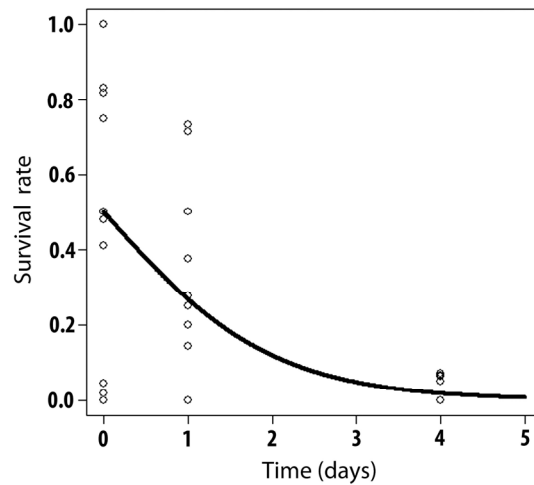


Figure 3. Plot of the expected survival rate of New Zealand mudsnails against time. The dots are raw data.

We modeled individual sample station variation with NLME on the selected submodel. We refitted the final submodel with non-linear regression (NLR) and NLME with the response variables equal to $1/(1+\exp(-b \cdot \text{time}))$, where b is the unknown to be determined in NLR and random effects to be determined in NLME. The estimated coefficient of time from GLM, NLR, and NLME were -0.95 (s.e. = 0.42), -1.00 (s.e. = 0.38) and -1.00 (s.e. = 0.38), respectively. The

difference in results between GLM and the other two models may be due to the estimation methods used (e.g. fisher scoring, least square method), and the assumption of errors (e.g. non-normal distribution, normal distribution). In general, all three of them are very close. The estimated standard deviation of random effects was 0.00083. The random effects were not significant ($P = 0.92$, likelihood ratio test). The NLR fit was the preferred model by both AIC and BIC. Since all of the sample stations were located in close proximity to one another, we conclude that the variation within each sample station did not affect the survival rate over time.

Discussion

There were notable spatial differences in detection rate between the upshore and offshore stations. The detection rate decreased consistently with increased substrate depth both upshore and offshore; however, detection rates differed less consistently between upshore and offshore at the various substrate depths. At the surface and at 70 cm, the rate of detection was considerably higher offshore, near the water's edge, while at 30cm, the detection rate was much higher upshore. The higher offshore detection rate at the surface might be due to a hydrotactic response in order to escape the freezing temperature, differences between the upshore and offshore environments, or sampling error. Similarly, environmental factors (e.g. substrate type, wind exposure, shade, etc.) may account for the high variability in survival between day 0 and day 4, though efforts were made to ensure that the sample stations were similar in substrate type and atmospheric exposure.

NZMS density in one nearshore area of Capitol Lake was estimated to be 20,000 per square meter, and may be higher in other areas (A. Pleus, personal communication). This suggests that NZMSs have been living in Capitol Lake for several years and that conditions are favorable for their proliferation. Judging from colonization events elsewhere, and, given their capacity for active and passive dispersal, their rate of reproduction, and the lack of predators and parasites in introduced populations relative to those found in New Zealand (Anonymous 2007), it seems likely that NZMSs will continue to spread throughout the lake and that their densities will increase if no action is taken to control them. Further, the likelihood that they

will be transported to neighboring lakes and streams will also increase.

In Olympia, it is common to have 3 to 7 consecutive days with daily high temperatures of about 0°C between the months of December and February. In this study, we demonstrated that lowering the water level during a prolonged freeze can kill as many as 98% of the snails exposed to freezing temperatures. Assuming that each NZMS needs about 6 months to reach maturity and bears about 70 live offspring every three months, lowering the water level during freezing temperatures once per year would result in a substantial drop in productivity that would eventually reach a condition of equilibrium. This lower density equilibrium condition would lower the likelihood of transport through human or other animal contact, particularly in the nearshore environment where contact is most likely to occur. In Olympia, during the summer, there are occasionally days that exceed 34°C, and temperatures may reach as high as 39°C in some years. Given that NZMSs are not tolerant of extremely high temperatures, lowering the water level once during a summer heat wave may add an additional control measure by inducing further mortality during peak spawning season, though this treatment was not investigated here.

Owing to high labor costs, equipment purchases, and other project management expenses, controlling the population of any nonnative species is usually very expensive and time consuming. Controlling NZMSs in Capitol Lake through water level changes affords a rare opportunity to significantly reduce or eradicate the presence of an invasive species of high concern and decrease the likelihood of its spread to other water bodies at a very low cost. The impact of water level draw-downs on the lake's existing ecology, other aquatic species, and aesthetics would be dependent on the extent and duration of the treatment. The impact of partial draw-downs for short durations may be minimal, while complete draw-downs over protracted periods of time would probably result in more substantial impacts. In the case of Capitol Lake, balancing the risks posed by NZMSs and the means available to eradicate or stem their spread against other lake management concerns will likely present a challenge to managers. Although this study was geographically limited, it is highly doubtful that NZMS populations elsewhere would exhibit substantially different responses to freezing temperatures, and there are many places

that are at risk of invasion that could be subjected to this kind of control measure. Indeed, dozens of dammed lakes and reservoirs exist in Washington State and throughout the country where water levels can be manipulated and that experience periods of sub-freezing temperatures. Drawdowns are routinely used in Washington, Oregon, and Idaho to accommodate passage of migrating anadromous fish, thus the idea of using water-level manipulation as a biological management tool is one with which resource managers in the Pacific Northwest are well acquainted. Locks and reservoirs used to facilitate waterborne commerce exist across the country in climates subject to freezing temperatures and water level manipulations at these facilities could be used to control the spread of NZMSs should they become invaded.

This study did not address the rate at which the NZMS may recolonize the lakeshore subsequent to freezing. Given the NZMS's life history, and the physical and biotic complexity of the lakeshore environment, it is doubtful that a full eradication could be achieved at Capitol Lake. Knowing how quickly NZMSs can become reestablished in an area after a freeze treatment would help managers plan the frequency of drawdowns and should be examined in future studies.

Acknowledgements

The authors wish to thank Jesse Schultz, Will Morris, Allen Pleus, and Susie Reszczyński for their assistance in the lab and in the field. Edward Johannes provided expert species identification and assisted with the laboratory evaluation of snail survival. Ocean Eveningsong prepared the map of Capitol Lake. Portions of this project were produced with support from the Puget Sound Partnership. Theresa Tsou, Dayv Lowry, Kurt Reidinger, Allen Pleus and two anonymous reviewers provided helpful comments on an earlier draft.

References

- Anonymous (2007) National Management and Control Plan for New Zealand Mudsnail (*Potamopyrgus antipodarum*), the New Zealand Mudsnail Management and Control Plan Working Group, 52 pp
- Aarnio K, Bonsdorff E (1997) Passing the gut of juvenile flounder, *Platichthys flesus*: differential survival of zoobenthic prey species. *Marine Biology* 129: 11–14, doi:10.1007/s002270050140
- Akaike H (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723, doi:10.1109/TAC.1974.1100705
- Alonso A, Camargo JA (2004) Sub-lethal responses of the aquatic snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca) to unionized ammonia: A tolerant invading species. *Fresenius Environmental Bulletin* 13: 607–615
- Benson AJ (2010) New Zealand Mudsnail Sightings Distribution. <http://www.newzealandmudsnaildistribution.aspx> (Accessed December 8, 2010)
- Bersine K, Brenneis VEF, Draheim RC, Michelle Wargo Rub A, Zamon JE, Litton RK, Hinton SA, Sytsma MD, Cordell JR, Chapman JW (2008) Distribution of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) in the Columbia River Estuary and its first recorded occurrence in the diet of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Biological Invasions* 10: 1381–1388, doi:10.1007/s10530-007-9213-y
- Bowler P (1991) The rapid spread of the freshwater Hydrobiid snail *Potamopyrgus antipodarum* (Gray) in the Middle Snake River, Southern Idaho. *Proceedings of the Desert Fishes Council* 21: 173–182
- Bruce RL, Moffitt CM, Dennis B (2009) Survival and passage of ingested New Zealand mudsnails through the intestinal tract of rainbow trout. *North American Journal of Aquaculture* 71: 287–301, doi:10.1577/A08-033.1
- Cada CA (2004) Interactions between the invasive New Zealand Mud Snail, *Potamopyrgus antipodarum*, baetid mayflies, and fish predators. M.S. thesis. Montana State University, 136 pp
- Cheng YW, Gallinat M (2004) Statistical analysis of the relationship among environmental variables, inter-annual variability and smolt trap efficiency of salmonids in the Tucannon River. *Fisheries Research* 70: 229–238, doi:10.1016/j.fishres.2004.08.005
- Cheng YW, Kuk AYC (2002) Determination of the unknown age at first capture of western rock lobsters (*Panulirus cygnus*) by random effects model. *Biometrics* 58: 459–462, doi:10.1111/j.0006-341X.2002.00459.x
- Cox TJ, Rutherford JC (2000) Thermal tolerances of two stream invertebrates exposed to diurnally varying temperature. *New Zealand Journal of Marine and Freshwater Research* 34: 203–208, doi:10.1080/00288330.2000.9516926
- Davidson TM, Brenneis VEF, de Rivera C, Draheim R, Gillespie GE (2008) Northern range expansion and coastal occurrences of the New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) in the northeast Pacific. *Aquatic Invasions* 3: 349–353, doi:10.3391/ai.2008.3.3.12
- Fleiss J, Levin B, Paik MC (2003) Statistical methods for rates and proportions (3rd ed.). John Wiley & Sons, New Jersey 704 pp, doi:10.1002/0471445428
- Gustafson D (2002) New Zealand mudsnail in the western USA. Montana State University. Available from <http://www.esg.montana.edu/aim/mollusca/nzms/status.html> (Accessed December, 2009)
- Hall RO, Tank JL, Dybdahl MF (2003) Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Frontiers in Ecology and the Environment* 1: 408–411, doi:10.1890/1540-9295(2003)001[0407:ESDNAC]2.0.CO;2
- Haynes A, Taylor BJR, Varley ME (1985) The influence of the mobility of *Potamopyrgus jenkinsi* (Smith, E. A.) (Prosobranchia: Hydrobiidae) on its spread. *Archives of Hydrobiologie* 103:497–508
- Jacobsen R, Forbes VE (1997) Clonal variation in life-history traits and feeding rates in the gastropod, *Potamopyrgus antipodarum*: Performance across a salinity gradient. *Functional Ecology* 11: 260–267, doi:10.1046/j.1365-2435.1997.00082.x
- Kerans BL, Dybdahl MF, Gangloff MM, Jannot JE (2005) *Potamopyrgus antipodarum*: distribution, density, and effects on native macroinvertebrate assemblages in the Greater Yellowstone Ecosystem. *Journal of the North American Benthological Society* 24: 123–138, doi:10.1899/08-87-3593(2005)024<0123:PADDAE>2.0.CO;2
- Laird NM, Ware JH (1982) Random-effects models for longitudinal data. *Biometrics* 38: 963–974, doi:10.2307/2529876

- McCullagh P, Nelder J (1989) Generalized Linear Models (2nd ed.). Chapman and Hall, New York, 532 pp
- Pinheiro JC (1994) Topics in mixed effects models. PhD thesis, University of Wisconsin, Madison, 261pp
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-Plus. Springer-Verlag, New York, 528 pp, doi:10.1007/978-1-4419-0318-1
- Ponder WF (1988) *Potamopyrgus antipodarum* - a molluscan colonizer of Europe and Australia. *Journal of Molluscan Studies* 54: 271–285, doi:10.1093/mollus/54.3.271
- Purcell SW, Cheng YW (2010) Stock enhancement and seasonal visibility of a coral reef gastropod assessed by temporal modeling. *Aquatic Biology* 9: 227–238, doi:10.33 54/ab00253
- Richards DC (2002) The New Zealand mudsnail invades the Western United States. *Aquatic Nuisance Species Digest* 4: 42–44
- Ryan P (1982) Energy contents of some New Zealand freshwater animals. *New Zealand Journal of Marine and Freshwater Research* 16: 283–287, doi:10.1080/00288330.1982.9515971
- Schreiber ESG, Lake PS, Quinn GP (2002) Facilitation of native stream fauna by an invading species? Experimental investigations of the interaction of the snail, *Potamopyrgus antipodarum* (Hydrobiidae) with native benthic fauna. *Biological Invasions* 4: 317–325, doi:10.1023/A:1020925022843
- Schwarz G (1978) Estimating the dimension of a model. *Annals of Statistics* 6: 461–464, doi:10.1214/aos/11176344136
- Searcy-Bernal R (1994) Statistical power and aquaculture research. *Aquaculture* 127: 371–388, doi:10.1016/0044-8486(94)90239-9
- Vinson MR, Baker MA (2008) Poor growth of North American rainbow trout (*Oncorhynchus mykiss*) fed New Zealand mud snail (*Potamopyrgus antipodarum*). *North American Journal of Fisheries Management* 28: 701–709, doi:10.1577/M06-039.1
- Zaranko DT, Farara DG, Thompson FG (1997) Another exotic mollusk in the Laurentian Great Lakes: the New Zealand native *Potamopyrgus antipodarum* (Gray 1843) (Gastropoda, Hydrobiidae). *Canadian Journal of Fisheries and Aquatic Sciences* 54: 809–814, doi:10.1139/cjfas-54-4-809