

**INVESTIGATIONS OF THE INVASIVE NEW ZEALAND MUDSNAIL
POTAMOPYRGUS ANTIPODARUM IN IDAHO: IMPLICATIONS FOR
TEMPERATURE LIMITATIONS**

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ABSTRACT

New Zealand mudsnails *Potamopyrgus antipodarum* (Gray) (family Hydrobiidae) have invaded many streams in the western United States over the past 20 years, including Idaho waterways. New Zealand mudsnails have been observed in the Silver Creek drainage, Blaine County, Idaho for at least five years, but their abundance has remained low and their range appears somewhat restricted. On the other hand, New Zealand mudsnails occur widely in Riley Creek, Gooding County, Idaho, and at high densities. This thesis provides the results of surveys for New Zealand mudsnails and monitoring of temperatures and other abiotic parameters throughout the Silver Creek drainage, and within a small reach of Riley Creek in 2004 and 2005. These studies confirmed that the distribution of New Zealand mudsnails in the Silver Creek drainage was limited and correlated with areas of the drainage where winter water temperatures remained above 0°C in Loving and Silver Creeks. In Riley Creek, the New Zealand mudsnail populations were robust and abundant, and water temperatures were nearly constant at 15°C throughout the year. Laboratory trials were conducted to assess the survival of mudsnails exposed to constant or dynamic cold water temperatures. The laboratory tests confirmed that exposure of New Zealand mudsnails to temperatures of 0°C for more than 72 h resulted in 100% mortality. The size at maturation of the two populations of New Zealand mudsnails sampled from Silver Creek and Riley Creek was different. Populations from Riley Creek were observed with developing embryos at a smaller size (≥ 2.5 mm) than snails from Loving Creek (≥ 3.0 mm). This research provides empirical evidence that winter water temperatures are likely to limit New Zealand mudsnail

invasions. Using this information, managers will be able to prioritize drainages that are at high risk of invasion by New Zealand mudsnails.

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DEDICATION

This work is dedicated to my late Grandma Gail, who provided me my fondest childhood fishing memories and who always put others first. I miss you.

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**CHAPTER I: DISTRIBUTION OF NEW ZEALAND MUDSNAILS
POTAMOPYRGUS ANTIPODARUM IN THE SILVER CREEK DRAINAGE,
BLAINE COUNTY, IDAHO**

Abstract

In 2004 and 2005, the Silver Creek drainage was sampled extensively for New Zealand mudsnails *Potamopyrgus antipodarum* (Gray) (family Hydrobiidae). Sampling sites were selected from digital maps at 1 km intervals to conduct an overall distribution survey throughout the Silver Creek drainage between June and August 2004. New Zealand mudsnails were identified at 5 of the 56 sites visited, and the relative abundance of snails from a 30 sec kick net sampling effort ranged from 2 to 2,220 snails. Water temperatures were monitored throughout the drainage with an array of temperature loggers from June 2004 to February 2006 and ranged from a high of 26.3°C in July 2005 to a low of -2.0°C in December 2005 fluctuating daily with air temperatures. Seasonal distributions of New Zealand mudsnails were constricted during the winter sampling periods (December 2004 and 2005) when compared to summer sampling events (June 2005) on Silver Creek Preserve. Winter densities throughout Butte/Loving Creek and Silver Creek were lower during winter sampling than during summer sampling and showed a strong longitudinal pattern. Densities were generally greater at upstream sites than sites located further downstream. New Zealand mudsnails appear to be limited in their distribution within the Silver Creek drainage and winter water temperatures may play a significant role in this limitation.

Introduction

New Zealand mudsnails *Potamopyrgus antipodarum* (Gray) (family Hydrobiidae) were first detected in North America in 1987 in the Middle Snake River near Hagerman, Idaho (Bowler 1991). In less than 20 years, they have spread throughout the Middle Snake River drainage and to other waterways in Idaho, Montana, Wyoming, Utah, Oregon, and California (Richards et al. 2004a) and have recently been found in the Great Lakes (Zaranko et al. 1997). During the summer of 2001, New Zealand mudsnails were detected during sampling on Silver Creek Preserve, Blaine County, Idaho, a property managed by the Nature Conservancy, hereafter referred to as Silver Creek Preserve. A more detailed survey of Silver Creek Preserve and neighboring public access sites was conducted in October of 2003 (Richards and Lester 2003). Snails were found at six sites located between Butte Creek and Loving Creek near Hayspur Hatchery operated by Idaho Department of Fish and Game, and on Silver Creek near the Silver Creek Preserve Visitor Center, hereafter referred to as Visitor Center.

Several modes of passive and active dispersal have been speculated to account for the rapid expansion of the New Zealand mudsnail. Active modes of dispersal including volitional upstream and downstream movements as well as drifting downstream (Richards et al. 2001) should limit New Zealand mudsnail expansion to within a drainage system. On the other hand, passive dispersal modes are most likely responsible for introduction into new water systems. Human activities related to aquaculture and sport-fishing are most often criticized as major vectors resulting in the spread between drainages (Bowler 1991, Frest and Bowler 1993, Richards and Lester 2003, Richards et al. 2004b). However, passive dispersal may also be mediated by more natural

mechanisms, such as waterfowl and fish migration patterns. Although none of these dispersal modes has been specifically documented, both waterfowl and fish are known to prey on New Zealand mudsnails (Graynoth et al. 1986, Sagar and Glova 1995, Levri and Lively 1996, Levri 1998, Graynoth and Taylor 2004) and tend to be abundant in areas where New Zealand mudsnails occur at in Idaho (i.e. the Hagerman Valley and the Silver Creek drainage). Researchers have shown that New Zealand mudsnails can survive the passage through the digestive system of a fish (Aarnio and Bonsdorff 1997, Bruce 2006). Also, Malone (1965) noted that birds are primary dispersal agents for fresh water molluscs and that individual snails of the species *Lymnea obrussa* (Say) were able to survive more than 14 h out of water on the amputated leg of a killdeer *Chardrius vociferous* (Linnaeus). Knowing that New Zealand mudsnails can survive desiccation for periods longer than 60 h (Richards et al. 2004b), it is easy to recognize the dispersal potential of waterfowl and other migratory birds for New Zealand mudsnails.

Because the New Zealand mudsnail is asexual and ovoviviparous, it possesses a distinct reproductive advantage over many aquatic organisms in invaded habitats in addition to predator release from the castrating parasite *Microphallus* spp present in its native range which renders the snail infertile (Jokela and Lively 1995, Levri and Lively 1996, Levri 1998, Jokela et al. 1999). A female mudsnail can brood between 20-100 embryos at a time (Winterbourn 1970b, Schreiber et al. 1998, Richards and Lester 2000, Richards 2004). The salient implication of this strategy is that only one snail would be required for reproduction and initiation of a population in a new habitat. Given the extensive spatial scale of human recreational activities (i.e. fishing, water-fowl hunting, and boating) in addition to fish and wildlife migration patterns, New Zealand mudsnails

appear highly adapted for invading naïve habitats. Indeed, Silver Creek possesses many potential invasion routes and should be a prime area for expansion of New Zealand mudsnails.

When New Zealand mudsnails reach high densities, they may affect the invaded ecosystems by altering the community structure of the primary producers and limiting the food and habitat available for aquatic insects that are important prey for fish (Hall et al. 2003, Cada and Kerans, in preparation, in Cada 2004, Hall et al. 2006). Reduced food availability for fish and altered trophic dynamics on Silver Creek may affect the resources of this important recreational area, with the potential to further disrupt the trophic level interactions beyond the aquatic environment. As of yet, little knowledge exists on the limitations for New Zealand mudsnail populations, and they appear to have the potential to expand unimpeded. The objectives of this study were to 1) better delineate the distribution of New Zealand mudsnails in the Silver Creek watershed and 2) determine if the population appears to be expanding beyond the initial reported distribution and density.

Methods

Study Area

Silver Creek is a high-desert, spring-fed stream system located in central Idaho approximately 170 km east of Boise, Idaho and 44 km south of Sun Valley, Idaho (Figure 1). Ground-water springs in the Silver Creek drainage are supplied by the Big Wood River watershed draining approximately 2,280 km² (Brown 2000). Annual discharge within Silver Creek averages 100 to 123 million m³ per year (Brown 2000) with little intra-annual variability (Francis and Bjornn 1979). Silver Creek, and its tributaries, flow

for approximately 110 km to a confluence with the Little Wood River. The uppermost tributary, Stalker Creek, is formed by the confluence of the southerly flowing Patton Creek and Buhler Drain. As Stalker Creek flows east, Cain Creek and Mud Creek contribute as tributaries from the north. Silver Creek originates when Grove Creek and Stalker Creek combine on Silver Creek Preserve. Silver Creek is fed by Loving Creek, just before it flows out of the Silver Creek Preserve. From the preserve, Silver Creek flows in an easterly direction until it turns and flows south at State Highway 20 just east of the town of Picabo, Idaho. At this junction, Silver Creek flows into a confined canyon with increased gradient and water velocity until its confluence with the Little Wood River.

Overall Distribution Survey

To determine the overall distribution of New Zealand mudsnails in the Silver Creek drainage, sites for sampling were projected from digital-orthophoto quadrangle maps (1:24,000 scale). Points were generated for sites at one km distances along the drainage and corresponding Universal Transverse Mercator (NAD-27) coordinates were extracted using ArcView/GIS v3.2 (Environmental Systems Research Institute 1999). Through this process, 117 sites were identified, but only 56 were sampled due to access restrictions on private lands.

Sites were located in the field using an e-Trex GPS unit (Garmin International, Inc., Olathe, Kansas). At each site, three separate 10-second kick-net samples were collected from the nearest gravel substrates using a D-framed kicknet with a 500 μm mesh collection net. Samples were collected by vigorously kicking the substrate to suspend the macro-invertebrates into the water column then allowing them to drift

downstream into the net. The single most dominant substrate was visually classified following the Wentworth classification scale (McMahon et al. 1996): small gravel =2-4mm, medium gravel=4-8mm, large gravel=8-16mm, small pebble=16-32mm, and large pebble=32-64mm. Each invertebrate sample was processed through a series of three sieves (4.75 mm, 2.36 mm and 1.70 mm) to remove large debris. The contents of the sieves were placed on a sorting tray and sorted to determine the presence of New Zealand mudsnails with the aid of a 10-X OptiVISOR® (Donnegan Optical Company, Lenexa, Kansas) for magnification. If New Zealand mudsnails were present, the sample was placed in a container, labeled and taken back to the field-lab for further sorting and enumeration. After final sorting, New Zealand mudsnail specimens were preserved in 10% formalin solution overnight, rinsed, and transferred to 70% ethanol for storage at the University of Idaho.

Seasonal Distribution

Samples were collected to assess the seasonal distribution of New Zealand mudsnails at the upstream and downstream boundaries of their distribution on Silver Creek Preserve. The downstream boundary, defined as Reach-1, was located at the confluence of Loving Creek and Silver Creek and extended 100 m upstream on both waterways and 100 m downstream from their confluence (Figure 2). The upstream boundary, Reach-2, was located on Silver Creek near the outflow of Sullivan Lake and extended 250 m upstream and downstream (Figure 2). Within each reach, forty points were randomly selected (Figures 3 & 4) using a Sampling Generator Extension for ArcView v.3.2 (Environmental Systems Research Institute 1999) available from the Minnesota Department of Natural Resources (<http://www.dnr.state.mn.us>). Each point

was constrained to a one meter diameter with a five meter buffer zone, ensuring that no two points were located within less than six meters of one another.

We located each point during sampling with a Garmin *e-Trex* GPS unit (Garmin International, Olathe, KS) and a hardcopy of maps from the digital projection. Invertebrate samples were collected by using the same D-framed kick-net and methods used in the overall distribution survey, except that vegetation and sediment substrates were included in this sampling regime. Following collection, the samples were processed through a series of three sieves (2 mm, 1 mm, and 500 μm) to remove larger pieces of debris and fine sediments. Samples were then be placed into a labeled container, preserved in 10% formalin solution overnight and then transferred to 70% ETOH for further processing and storage. Sampling was performed during the winter of 2004-2005, the summer of 2005, and the winter of 2005-2006 within each reach.

After collection and preservation, the samples were returned to the University of Idaho and hand sorted in the lab. The samples were sub-sampled on a sectioned sorting tray consisting of 32 equal sized cells. The sub-sampling area was contained by 4 plexiglass retaining walls ~10 cm high. Individual samples were placed into the center of the sub-sampling tray and standard tap water was added to make the sample more fluid. Samples were then swirled with a metal chemical spatula to strive for a relatively uniform distribution of all organisms. Four cells were randomly selected for removal using a random numbers generator program in SAS 9.2. Sub-samples were removed using two metal chemical spatulas for larger substances and a small pipette for smaller substances. Once collected, sub-samples were then placed into a small glass jar and filled with 70%

ETOH. Samples were then hand sorted at a later date to identify and enumerate New Zealand mudsnails.

Longitudinal Densities

From the overall distribution survey, we selected 9 sites (6 positive and 3 negative for NZMS) to assess densities of New Zealand mudsnails between winter and summer along a temperature gradient (Figure 5). The farthest upstream sites had more stable temperatures and, in general, were cooler during the summer months and warmer during the winter months in comparison to downstream sites.

At each site, a modified Hess sampler was used to collect New Zealand mudsnails. The Hess sampler (sampling area=0.086 m², 500 µm mesh) was modified with a 91.4 cm long, 35.6 cm diameter tube of sheet metal. The tube was further modified with a 35.6 cm to 30.5 cm reducer on the bottom that allowed it to be inserted into the top of the Hess sampler when water levels were higher than the Hess sampler itself. A stable fork, with its width and tongs trimmed to approximately 20 cm, was used to manipulate gravel substrate confined inside of the modified Hess sampler at each site. Gravel was selected as the sampling substrate because of the ease of processing the samples both in the field and in the lab and to reduce any variation involved with sampling multiple substrate habitats. Once collected, samples were processed and preserved in identical fashion as those previously outlined in the seasonal distribution survey.

Water Quality and Temperature Monitoring

Water quality was monitored during both the seasonal distribution survey and the longitudinal density sampling. A YSI Multi-probe 556 (Yellow Springs, OH) was used

to measure conductivity (mS/cm), total dissolved solids (TDS), dissolved oxygen (mg/L), salinity (ppt), and pH at all of the respective sampling sites when sampling was performed. Water velocities were recorded at each site during sampling, including sites sampled for the overall distribution survey. A Marsh-McBirney Flow-Mate® Model 2000 was utilized to measure velocities at 60% of depth.

Water temperatures in the drainage were recorded electronically with HOBO8 Data loggers (Onset Corporation, Pocasset, Massachusetts). For the Seasonal Distribution survey, three loggers were placed within each reach near the upper, middle, and lower bounds of each reach (Figure 2). Loggers were also placed to monitor temperatures at sampling sites for the longitudinal density experiment. Additional loggers were placed near areas of known New Zealand mudsnail locations as well as near areas where New Zealand mudsnails had not been detected (Figure 6). Water temperatures were monitored between June 2004 and February 2006, although not all sites were monitored throughout the entirety of the period. Temperature loggers were set to record temperatures at two-hour intervals and checked periodically to recover data and provide any necessary maintenance.

Data Analysis

Overall Distribution — Samples of *P. antipodarum* from the three kick net samples at each site were combined for a total count of snails in a combined 30 sec sampling effort and water velocities averaged for each site. Substrate particle sizes were converted from categorical data to numerical data with small gravel equal to one and each consecutive class increasing by an increment of one up to large pebble equal to five. Substrate data were then averaged for each site. Differences in average water velocities

and substrate particle sizes between positive and negative sites were tested using two-sample t-tests with the models $\text{water_velocity} = \text{snail_presence}$ and $\text{substrate_size} = \text{snail_presence}$.

Seasonal Distribution — Abundances at each site (snails/10 s kick-net sampling) were graphed in an x, y coordinate plane to assess any potential linear relationships. Because of the two-dimensional aspect of the sampling reach, all points were snapped to a linear line that followed the contour of the reach. The distance downstream of each site from the upper most site were plotted on the x-axis and New Zealand mudsnail abundances per 10 s kick-net sampling was plotted on the y-axis. A locally weighted regression smoother (LOESS, SigmaPlot 9.0, Systat Software, Inc.) was fit to the data to assess any linear dependencies of downstream distance and New Zealand mudsnail abundances. Because of different distance intervals between sites, a nearest neighbor distance was used for the bandwidth. Sites located within the Loving Creek portion of the Reach 1 were omitted from this assessment. Tributary inflows within each reach were also plotted on the graph to assess any potential New Zealand mudsnail sources supplied to the sampling reach.

Longitudinal Density — An analysis of variance model was used to test for differences in densities of New Zealand mudsnails between each site and season and possible interaction effects of these two sources. Prior to testing the model, density data were log transformed to meet the model assumptions of normality and equal variance. The model $\log(\text{density}) = \text{site} + \text{season} + \text{site} * \text{season}$ was fit to the data after transformation. After testing the model, differences between significant factors were tested using Fisher's protected least significant difference. Physical parameters of water

chemistry (conductivity, TDS, salinity, dissolved oxygen, and pH) were averaged for each reach between the two sampling seasons.

All statistical tests were performed using SAS v9.2 Software (SAS Institute Inc. 2003) and results with a P of ≤ 0.05 were considered significant.

Results

Overall Distribution

New Zealand mudsnails were found at five of 56 sites (Figure 7). The abundances ranged from 2 - 2,220 snails per 30 sec sampling effort (Table 1). The highest relative abundance was in Loving Creek and abundances decreased downstream to the confluence with Silver Creek (Figure 7, Table 1). The lowest abundance was just upstream of the Visitors Center at Site 5 (Figure 7, Table 1). New Zealand mudsnails were not detected upstream of Hayspur State Fish Hatchery in Butte or Loving Creek or in the old brood ponds receiving hatchery effluent (Figure 7). New Zealand mudsnails also were not detected downstream of Kilpatrick Bridge or upstream of the confluence of Stalker and Grove Creek (Figure 7). Besides Loving and Butte Creek, no other Silver Creek tributaries were positive for New Zealand mudsnails during the survey (Figure 7).

Substrate particle size and water velocities at positive sites averaged 2.60 ± 1.30 and 0.386 ± 0.154 m/s, respectively (Table 2). At negative sites, substrate particle size averaged 2.80 ± 1.23 and water velocities averaged 0.330 ± 0.178 m/s (Table 2). There was no significant difference between either substrate particle size or water velocity at positive and negative sites ($P > 0.05$, Table 3)

Seasonal Distribution

New Zealand mudsnails were detected at fewer sites during winter sampling periods compared with summer sampling in both reaches in the seasonal distribution survey (Table 4). As a result, there was a greater abundance of snails collected during the summer (Tables 5 and 6). However, Reach-2 consistently had the greatest abundance during all sampling periods (Table 6) when compared with Reach-1 (Table 5).

The distribution pattern of New Zealand mudsnails in Reach-1 was concentrated just upstream of the confluence of Loving and Silver Creek and at a few locales in Loving Creek itself (Figure 8). During the summer of 2005, New Zealand mudsnails had distributed themselves throughout the Silver Creek portion of Reach-1 with the greatest abundance occurring upstream of the Loving Creek confluence while only one positive site occurred in Loving Creek itself (Figure 8). New Zealand mudsnails were detected at two sites (Sites 30 and 31) in Reach-1 during the final sampling period of the winter of 2005-2006 (Figure 8, Table 5); an area that was consistently positive at all sampling periods. There was no consistent linear upstream to downstream trend apparent in the abundances of New Zealand mudsnails in the Silver Creek portion of Reach-1 although positive sites were generally clustered together (Figure 9).

Fewer positive sites were detected in Reach-2 during the winter sampling seasons, however positive sites were detected throughout the reach during all sampling periods (Figure 10). During the final sampling period of the winter of 2005-2006, the distribution of New Zealand mudsnails became more constricted towards the middle of the reach near the outflow of Sullivan Lake (Figure 10). There was no apparent linear trend in abundance of New Zealand mudsnails from upstream to downstream in Reach-2 during

any sampling period (Figure 11). However the greatest abundances during any given sampling period occurred in close proximity (<100 m) to the outflow of Sullivan Lake (Table 6, Figure 11), suggesting that Sullivan Lake may support an abundant population of New Zealand mudsnails throughout the year.

Except for conductivity, all other chemical water parameters measured (salinity, total dissolved solids [TDS], Dissolved Oxygen [DO], and pH) were consistent between the winter of 2004-2005 and the summer of 2005 (Table 7). Conductivity measures were greatest during the summer of 2005 sampling periods (Table 7). However, during the winter of 2005-2006 all water chemical parameters had dropped below the previous summer and winter levels (Table 7). This decrease in chemical parameters may well be attributable to an extended drop in water temperatures throughout December 2005 (Figure 12).

Longitudinal Densities

The longitudinal densities showed a similar distributional pattern as that observed in the overall distribution during the summer of 2004 (Figure 6). New Zealand mudsnails were not detected in Silver Creek from Kilpatrick Bridge downstream but were found throughout Loving Creek during both sampling periods (Summer 2005 and Winter 2005-2006; Figure 6). Densities decreased downstream from below Hayspur State Fish Hatchery to the confluence of Loving and Silver Creek (Figure 13). No snails were detected at Site 3-5 during the winter 2005-2006 sampling period.

Statistical analysis using a two-way ANOVA model resulted in no significant interaction effect of season*site on log-densities of New Zealand mudsnails (Table 8). However, both season and site had significant main effects on the resulting log-densities

($P < 0.05$; Table 8). Site 3-5 was the only site at which abundances differed significantly from all other sites (Figure 14), most likely because no snails were detected there during the winter sampling period. Sites 3-4, 3-6, 3-7, and 3-8 were statistically similar to each other while site 3-9 was similar only to sites 3-7 and 3-8 (Figure 14). *Post hoc* analysis of the season main effect showed summer densities to be significantly greater than winter (Figure 15).

Chemical water parameters (Conductivity, Total Dissolved Solids [TDS], Salinity, and pH) were greatest during the summer sampling period (Table 9). Water temperatures again appeared to play an important role in the seasonal changes to these parameters (Table 10).

Water Temperature Monitoring

Water temperature regimes in the Silver Creek drainage follow both diurnal (Figure 16) and seasonal (Table 11) temperature fluctuations. Daily temperatures in Silver Creek fluctuated nearly 10°C between 14 and 19 June 2004, and were highly correlated with ambient air temperatures (Figure 16). Similar water temperature fluctuations were observed at all monitoring sites, although the magnitude of the fluctuations varied slightly. Average monthly temperatures were lowest in the middle portions of Silver Creek Preserve and directly downstream of Hayspur Fish Hatchery on Butte/Loving Creek during the summer months of June through September while the upper and lower stretches of Silver Creek were warmer (Table 11). During the winter months of November through April, the upper and lower stretches of Silver Creek were colder while the middle portions of Silver Creek Preserve and downstream of Hayspur

State Fish Hatchery remained warmer (Table 11), possibly as a result of ground water inflow to these areas.

Mean monthly temperatures varied from a high of 20.27°C in July 2005 at the Idaho Fish and Game's Sportsmen's Access (Site 8, Figure 6) to a low of 1.0°C at Picabo Road Bridge (Site 10, Figure 6). The overall maximum temperature recorded during this research was 26.3°C recorded at Picabo Road Bridge during July 2005 (Site 10, Table 11). The lowest overall temperature of -2.4°C occurred at Picabo Road Bridge in January 2005 (Site 10, Table 11)

Discussion

New Zealand mudsnails in the Silver Creek drainage from the summer of 2004 to the winter of 2005-2006 were limited to two areas: 1) Silver Creek itself on the lower portion of Silver Creek Preserve and 2) Butte/Loving Creek downstream of Hayspur State Fish Hatchery. It is impossible to be entirely certain that this is the definitive distribution of New Zealand mudsnails in Silver Creek because all stream habitats were not sampled throughout these surveys. While it may be likely that New Zealand mudsnails were not detected in areas of low density, the current results are consistent with the distribution of New Zealand mudsnails in the Silver Creek drainage reported by Richards and Lester (2003). However, snails were observed at Site 53 on Loving Creek during the overall distribution survey approximately 500 meters upstream of a site that Richards and Lester (2003) reported as negative for New Zealand mudsnails in 2003. Abundances at Site 53 were low, both during the overall distribution survey (8 snails/ 30 sec.) and in terms of longitudinal densities (155 – 248 snails/m²). The observation of New Zealand mudsnail presence in close proximity to a site so recently reported as free

may indicate that the population is expanding its range. Results from the seasonal distribution survey and longitudinal density data, suggest that this expansion occurs on a seasonal basis during the summer and the population boundary retreats upstream during the winter in Loving Creek.

The populations of New Zealand mudsnails on Silver Creek Preserve appear independent of those below Hayspur State Fish Hatchery. The low abundances and multiple negative sites of New Zealand mudsnails in that portion of Loving Creek contained within Reach-1 of the seasonal distribution survey support this hypothesis. Also, the perpetuation of New Zealand mudsnails in Reach-1 is most likely influenced by their persistence upstream in Silver Creek. During the summer of 2005 sampling, the greatest abundance of New Zealand mudsnails in Reach-1 occurred in the uppermost portion of that reach on Silver Creek, while no mudsnails were detected during either winter sampling at those sites. These results suggest that snails further upstream in Silver Creek support summer abundances in Reach-1 of Silver Creek Preserve. In addition, given the disappearance of snails from Site 3-5 in the longitudinal distribution survey during the winter of 2005-2006, it seems likely that populations in Loving Creek and Silver Creek are disjunct during the winter.

No New Zealand mudsnails were found at Sites 36 and 52 in the overall distribution survey, but this area was reported as positive in a previous survey conducted by Dr. David Herbst, Assistant Research Biologist at the University of California Santa Barbara in 2003 (Richards et al. 2004a). Site 36 was approximately 20 meters upstream of where New Zealand mudsnails were detected. After consulting directly with Dr. Herbst and the local landowner about the location of the previous sampling, samples were

taken as near as possible to that location (Site 52). New Zealand mudsnails were not detected at this site, either. It is possible that the snails may inhabit this area at a density below detection or were present in 2003 but did not survive over the winter into 2004. Low water temperatures at this site may have been unsuitable for New Zealand mudsnails to persist. Average monthly water temperatures recorded upstream and downstream of this site between December 2004 and January 2005 were the lowest recorded averages ($<2.0^{\circ}\text{C}$) in that time period of all areas and often dropped below 0°C .

Prior to this research, little was known regarding the annual water temperature regimes in the Silver Creek drainage. Previously it was assumed to be more stable than this research indicates. Richards and Lester (2003) concluded that "...Silver Creek appears to be very good *P. antipodarum* habitat, because there are fairly stable flows and temperatures." Yet, Francis and Bjornn (1979) reported a water temperature at the Idaho Department of Fish and Game Sportsman's Access site of 1.5°C on 6 January 1976 and Riehle and Griffith (1993) reported a water temperature at an unspecified location in Silver Creek of 2.0°C on 20 January 1988. This study indicates that temperatures are not stable in the drainage and the previously reported temperatures are not representative across sites or seasons. On more than one occasion, heavy ice formation was observed in the lower portions of Silver Creek from just upstream of the IDFG Sportsmen's Access Site downstream several miles.

Aquatic primary productivity has also been noted to be a limiting factor in New Zealand mudsnail populations (Kerans et al. 2005). While conductivity and total dissolved solids (TDS) have been used as proxies for nutrient levels, and consequently productivity, this relationship does not always predict productivity (Prepas 1983). Yet in

the Silver Creek drainage, abundances of New Zealand mudsnails show a positive relationship with conductivity measures. It has been documented, though, that the conductivities of some ions are less at lower temperatures (Kalff 2002). This relationship helps explain the rise in conductivity during the summer of 2005 while measures of salinity and TDS remained nearly equivalent from the winter of 2004-2005 and any correlation between New Zealand mudsnails and conductivity may be influenced by their individual interactions with water temperatures. A greater understanding of the interactions of productivity, nutrient cycling and New Zealand mudsnails at different temperatures needs to be assessed in future research.

More comprehensive knowledge of site-specific temperature regimes may be critical to understanding New Zealand mudsnail invasion success. Hylleberg and Siegismund (1987) found that *P. jenkinsi* in Denmark survived for only a few hours at -3°C in freshwater. *Potamopyrgus jenkinsi* (E.A. Smith, 1869), which is considered to be synonymous with *P. antipodarum* (Gray, 1844), invaded Europe in the mid 1800's from New Zealand (Winterbourn 1970a, Winterbourn 1970b). Freezing is considered an effective method for killing the New Zealand mudsnails on contaminated fishing gear (Richards et al. 2004b). The present data demonstrate that temperatures in certain reaches of Silver Creek attain 0°C and can drop as low as -2°C at times. Currently, New Zealand mudsnails are present in areas of the Silver Creek drainage that do not drop below 0°C and their distributional boundaries coincide with this potential temperature threshold.

Samples were not collected downstream of the U.S. Highway 20 bridge approximately 3 km east of Picabo, Idaho, during the overall distribution survey. The

high gradient habitat within this area, as a result of the stream being confined by a narrow rock-wall, is likely unsuitable New Zealand mudsnail habitat. At 90 cm/s, 50% of New Zealand mudsnails will dislodge from cobble sized substrate (Holomuzki and Biggs 1999). The decision not to sample this portion of stream was further supported by the absence of New Zealand mudsnails in samples for the previous 13 km upstream of this bridge.

New Zealand mudsnails in Silver Creek have sufficient dispersal vectors to promote expansion of the population within the stream. Fish and waterfowl move extensively within the Silver Creek drainage and could distribute New Zealand mudsnails widely within the system, as could the anglers and hunters pursuing the fish and waterfowl. Many boater and canoers utilize Silver Creek for recreational purposes and can potentially increase the spread of the snail. Also, dense macrophyte beds annually slough off in large mats and flow downstream. There is a high likelihood that New Zealand mudsnails could be transported downstream during this annual macrophyte sloughing event. Given this level of activity, it is surprising that New Zealand mudsnails have not expanded their distribution in over five years. By comparison, in the tailwaters of Lower Salmon Falls Dam, Gooding County, ID, New Zealand mudsnails went from being common to the most dominant mollusk within two years (Bowler 1991). In Box Canyon Creek, Gooding County, ID, a tributary to the middle Snake River, New Zealand mudsnails appeared during the summer of 1989 and by fall, were nearly as common as the native snail *Fluminicola hindsi* (Langenstein and Bowler 1990). Given the current limited distribution in the Silver Creek drainage and the disappearance from previously reported sites, it may be possible that temperature regimes in the Silver Creek drainage

limit the snail's dispersal and therefore present a comparatively minimal impact to the system. Even though snails were collected near areas where temperatures dropped below freezing, given the low number of snails in these collections, they may have located micro-habitats that provided sufficient thermal refugia for their survival. Caution should still be taken, however, to ensure that New Zealand mudsnails are not dispersed to headwaters of the Silver Creek drainage, where water temperatures are most likely constant and productive for New Zealand mudsnails.

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Table 1. Location, sampling date, site number, and relative abundance (per 30 sec kick net) at sites where New Zealand mudsnails were collected in the Silver Creek drainage, 2004. Site numbers correlate to site numbers labeled in Figure 7.

Site number	Date	Stream name	Number snails/30 sec
5	4 June	Silver Cr.	2
7	4 June	Silver Cr.	10
11	8 June	Loving Cr.	2,220
53	2 July	Loving Cr.	8
54	2 July	Loving Cr.	231

Table 2. Average ± 1 -SD substrate size and water velocity at sites with and without New Zealand mudsnails from the overall distribution survey in the summer of 2004.

Site description	Substrate size	Water velocity (m/sec)
Without mudsnails (n=51)	2.80 ± 1.34	0.333 ± 0.178
With mudsnails (n=5)	2.60 ± 1.30	0.386 ± 0.154

Table 3: Results of t-test assessing differences in water velocity and substrate size between New Zealand mudsnail positive and negative sites in the overall distribution survey in the summer of 2004.

	DF	<i>t</i> -value	<i>P</i>
Water Velocity	165	-1.11	0.2684
Substrate Size	164	0.57	0.5716

Table 4. Cumulative New Zealand mudsnail positive and negative sites from monitoring sites during the Winter 2004-2005, Summer 2005, Winter 2005-2006 sampling periods.

	<i>Reach 1</i>			<i>Reach 2</i>		
	Winter 2004-2005	Summer 2005	Winter 2005-2006	Winter 2004-2005	Summer 2005	Winter 2005-2006
Present	8	21	2	17	29	12
Absent	32	19	38	23	11	28

Table 5. Total New Zealand mudsnails (# of snails/10 s sampling) collected from each site in Reach 1 during the seasonal distribution survey. Site number corresponds to site numbers from Figure 3.

Site #	Winter 2004-2005	Summer 2005	Winter 2005-2006
1	0	48	0
2	0	8	0
3	0	56	0
4	0	8	0
5	0	0	0
6	0	8	0
7	0	144	0
8	0	8	0
9	0	8	0
10	0	0	0
11	0	0	0
12	8	0	0
13	0	0	0
14	0	0	0
15	0	0	0
16	0	0	0
17	0	0	0
18	0	0	0
19	0	0	0
20	16	0	0
21	0	0	0
22	48	16	0
23	0	0	0
24	0	0	0
25	0	0	0
26	120	48	0
27	0	8	0
28	32	0	0
29	8	48	0
30	16	56	24
31	8	48	8
32	0	40	0
33	0	24	0
34	0	64	0
35	0	0	0
36	0	208	0
37	0	16	0
38	0	0	0
39	0	16	0
40	0	408	0
Total	248	1288	32

Table 6. Total New Zealand mudsnails (# of snails/10 s sampling) collected from each site during the seasonal distribution survey in Reach 2. Site number corresponds to site numbers from Figure 4.

Site #	Winter 2004-2005	Summer 2005	Winter2005-2006
41	0	32	0
42	48	24	8
43	0	2544	16
44	0	480	8
45	8	40	0
46	0	0	0
47	0	0	16
48	16	184	0
49	0	8	8
50	0	8	0
51	0	200	0
52	24	104	8
53	0	16	0
54	168	24	8
55	0	32	0
56	0	208	0
57	8	8	0
58	24	8	0
59	8	32	0
60	0	16	48
61	48	1080	32
62	0	16	0
63	8	184	168
64	168	8	0
65	0	1048	424
66	32	144	0
67	8	0	0
68	0	8	0
69	16	0	0
70	0	8	0
71	32	0	0
72	8	0	0
73	400	0	0
74	0	0	0
75	0	0	0
76	0	8	0
77	0	0	0
78	0	24	0
79	0	112	8
80	0	0	0
Total	1032	6608	752

Table 7. Mean (SE) water chemistry parameters recorded at each site (n=40) during all sampling periods for the seasonal distribution survey. NA indicates measurement was not recorded.

	<i>Winter 2004-2005</i>		<i>Summer 2005</i>		<i>Winter 2005-2006</i>	
	Reach 1	Reach 2	Reach1	Reach 2	Reach 1	Reach 2
Conductivity (mS/cm)	0.229 (0.001)	0.229 (0.002)	0.303 (0.003)	0.278 (0.001)	0.215 (0.002)	0.211 (0.002)
Total Dissolved solids (g/L)	0.240 (0.001)	0.241 (0.002)	0.243 (0.001)	0.238 (0.001)	0.226 (0.002)	0.215 (0.001)
Salinity (ppt)	0.177 (0.001)	0.177 (0.002)	0.180 (0.001)	0.177 (0.001)	0.167 (0.001)	0.159 (0.001)
Dissolved oxygen (mg/L)	12.08 (0.25)	10.01 (0.38)	11.04 (0.44)	9.41 (0.27)	10.08 (0.76)	10.63 (0.19)
pH	6.89 (0.27)	7.33 (0.35)	N/A	6.33 (0.26)	7.99 (0.01)	7.77 (0.04)

Table 8. Summary of two-way ANOVA testing the effects of Area and Season on differences in log(density) of New Zealand mudsnails from positive sites (3-4, 3-5, 3-6, 3-7, 3-8, and 3-9) in the longitudinal density survey. Sites 3-1, 3-2, and 3-3 were omitted from the analysis because New Zealand mudsnails were not detected at those sites.

Source	DF	S.S.	M.S.	<i>F</i> -value	<i>P</i>
Model	11	188.42	17.13	4.59	0.0009
<i>Area</i>	5	135.11	27.02	7.24	0.0003
<i>Season</i>	1	40.06	40.06	10.73	0.0032
<i>Area*Season</i>	5	13.25	2.65	0.71	0.6219
Error	24	89.61	3.73		

Table 9. Mean and (SE) for water chemistry parameters recorded at each sampling site (n=3) during summer and winter sampling periods for the longitudinal density objective. No data were collected for dissolved oxygen in winter due to equipment failure.

Site	Conductivity (mS/cm)		Total dissolved solids(g/L)		Salinity (ppt)		Dissolved oxygen(mg/L)	pH	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Summer	Winter
3-1	0.313 (0.001)	0.184 (<0.001)	0.230 (0.001)	0.228 (0.00)	0.170 (0.00)	0.167 (0.003)	7.81 (0.28)	7.92 (0.01)	8.01 (0.02)
3-2	0.313 (0.001)	0.184 (<0.001)	0.230 (0.001)	0.228 (0.00)	0.170 (0.00)	0.167 (0.003)	7.81 (0.28)	7.92 (0.01)	8.01 (0.02)
3-3	0.298 (0.001)	0.200 (<0.001)	0.235 (<0.001)	0.223 (<0.001)	0.170 (0.00)	0.160 (0.00)	10.06 (0.16)	8.15 (0.01)	8.11 (0.3)
3-4	0.308 (0.013)	0.186 (0.005)	0.233 (0.005)	0.229 (0.006)	0.173 (0.003)	0.167 (0.007)	13.74 (0.25)	8.52 (0.05)	7.80 (0.10)
3-5	0.336 (<0.001)	0.208 (0.00)	0.260 (<0.001)	0.245 (<0.001)	0.190 (0.00)	0.173 (0.007)	7.56 (0.24)	8.09 (0.02)	8.02 (0.02)
3-6	0.350 (<0.001)	0.214 (<0.001)	0.266 (<0.001)	0.245 (0.00)	0.200 (0.00)	0.180 (0.00)	6.74 (0.39)	7.93 (0.02)	7.98 (0.04)
3-7	0.339 (<0.001)	0.230 (<0.001)	0.259 (<0.001)	0.242 (0.00)	0.190 (0.00)	0.180 (0.00)	8.23 (0.06)	8.56 (<0.01)	8.03 (0.03)
3-8	0.326 (0.003)	0.235 (0.002)	0.270 (0.001)	0.240 (0.003)	0.200 (0.00)	0.177 (0.003)	8.38 (0.07)	7.94 (0.04)	8.04 (0.02)
3-9	0.321 (0.001)	0.247 (<0.001)	0.263 (<0.001)	0.233 (<0.001)	0.197 (0.003)	0.170 (0.00)	6.64 (0.02)	7.90 (0.02)	8.03 (0.02)

Table 10. Monthly average and (range) of water temperatures °C at longitudinal density sites between sampling periods. NA indicates data were not collected.

	July 2005	Aug. 2005	Sept. 2005	Oct. 2005	Nov. 2005	Dec. 2005	Jan. 2006
3-1	20.35 (16.3-23.2)	19.09 (14.1-24.0)	14.83 (10.6-20.2)	10.65 (6.2-14.1)	N/A	N/A	2.1 (-0.6-5.0)
3-2	17.65 (14.1-20.5)	15.90 (10.2-20.5)	11.59 (7.0-17.1)	8.02 (3.7-11.3)	3.68 (-1.0-7.4)	1.17 (-1.4-5.3)	1.5 (-1.4-4.9)
3-3	17.37 (14.1-20.5)	16.06 (10.6-20.9)	12.43 (7.8-17.8)	9.05 (4.9-12.5)	5.06 (0.2-16.3)	2.60 (-0.1-6.6)	3.0 (-0.1-6.6)
3-4	17.60 (13.7-20.9)	16.15 (7.8-21.3)	10.42 (2.4-19.4)	N/A	N/A	2.12 (-1.9-6.2)	3.7 (0.2-7.8)
3-5	17.28 (14.8-19.8)	15.96 (11.4-19.4)	12.51 (6.83-17.9)	9.35 (5.4-12.6)	6.03 (1.6-22.1)	3.90 (-0.2-8.2)	5.9 (1.6-9.4)
3-6	16.97 (14.8-18.3)	15.38 (11.4-19.0)	12.36 (8.2-16.0)	9.50 (5.8-12.9)	6.33 (2.0-9.8)	4.27 (1.2-7.8)	4.6 (1.2-7.8)
3-7	15.37 (12.2-18.3)	14.25 (9.8-18.3)	11.84 (8.2-16.4)	9.69 (6.2-12.9)	7.05 (3.7-10.6)	5.21 (2.0-8.6)	5.5 (2.5-8.6)
3-8	14.32 (11.7-20.9)	13.53 (10.2-17.4)	11.50 (7.0-16.3)	8.03 (2.8-14.4)	5.74 (1.6-21.3)	6.67 (4.5-9.0)	6.8 (4.5-9.0)
3-9	14.01 (11.7-20.2)	13.32 (10.6-16.7)	11.81 (9.4-15.6)	10.13 (7.8-12.9)	8.18 (5.8-22.4)	6.55 (4.5-9.0)	6.6 (4.5-9.0)

Table 11. Average and (range) for water temperatures (°C) recorded throughout the Silver Creek drainage at specified locations by month from June 2004 to February 2006. Site numbers are referenced in Figure 6. NA indicates sites where data were not available.

Site	June 2004	July 2004	Aug. 2004	Sept. 2004	Oct. 2004	Nov. 2004	Dec. 2004
1	NA	17.75 (13.7-22.4)	18.04 (15.9-20.5)	NA	NA	NA	NA
2		17.38 (13.7-22.4)	15.92 (10.9-20.5)	12.42 (7.4-17.4)	8.55 (3.3-14.4)	NA	1.98 (-0.1-5.8)
3	14.90 (9.4-19.8)	15.97 (11.3-21.3)	14.74 (9.4-19.4)	11.85 (7.0-17.1)	8.77 (4.1-14.1)	5.55 (1.1-9.8)	3.17 (-1.9-7.0)
4		17.27 (13.7-21.7)	15.99 (11.3-20.9)	12.62 (9.0-16.7)	9.27 (4.9-13.7)	6.04 (2.4-9.0)	4.34 (2.0-6.6)
5						3.88 (1.1-6.2)	3.59 (0.7-7.0)
6		16.73 (12.1-21.7)	15.69 (10.6-19.4)	12.65 (7.8-17.4)	9.27 (3.7-14.1)	5.35 (0.7-9.4)	2.88 (-1.9-7.0)
7	16.11 (10.6-20.5)	17.51 (12.9-22.8)	15.80 (10.9-20.9)	12.61 (7.8-17.4)	9.10 (4.1-14.1)	5.51 (0.7-9.8)	3.10 (-1.0-7.0)
8		18.83 (14.1-24.8)	17.32 (11.3-21.7)	13.22 (7.8-19.0)	9.07 (3.3-15.2)	4.74 (-0.1-9.4)	2.07 (-0.1-5.80)
9		18.98 (13.7-25.2)	17.40 (11.7-22.1)	13.28 (7.8-19.8)	9.04 (2.8-15.6)	4.39 (-0.1-9.0)	1.61 (-0.1-5.3)
10		19.72 (14.4-25.6)	18.16 (12.1-22.4)	13.70 (8.2-20.5)	8.99 (1.1-20.9)	4.21 (-0.6-13.7)	1.39 (-1.0-5.8)
12	16.15 (11.7-20.5)	17.49 (13.7-22.4)	15.98 (11.7-20.5)	12.40 (5.3-19.4)	NA	7.13 (5.8-8.6)	5.40 (3.3-7.4)
13	14.40 (9.8-19.0)	14.72 (10.9-19.4)	13.73 (9.8-18.2)	12.15 (7.0-17.4)	NA	6.47 (4.5-8.6)	6.15 (3.3-9.8)

Table 11. (Cont.)

Site	Jan. 2005	Feb. 2005	Mar. 2005	Apr. 2005	May 2005	Jun. 2005
1	1.72 (-0.6-6.6)	2.67 (-0.2-7.0)	NA	NA	13.45 (7.0-20.2)	14.84 (7.8-21.7)
2	1.84 (-0.1-7.0)	2.78 (-0.1-7.8)	4.92 (2.0-9.4)	9.90 (4.9-17.1)	13.87 (8.6-19.8)	15.18 (9.0-21.7)
3	3.26 (-1.9-8.6)	4.27 (0.2-9.4)	6.01 (2.0-11.3)	9.42 (3.7-17.4)	12.30 (6.6-19.8)	13.49 (7.4-19.8)
4	4.50 (1.6-7.4)	5.30 (2.4-8.2)	7.92 (4.5-11.3)	10.21 (6.2-15.2)	12.96 (8.2-19.4)	13.71 (9.0-19.4)
5	3.61 (0.2-8.2)	4.43 (0.2-9.4)	6.55 (2.8-11.3)	10.37 (4.9-17.8)	13.39 (8.2-20.5)	14.30 (8.2-20.5)
6	3.58 (0.2-8.2)	3.48 (-0.6-7.8)	5.86 (0.7-11.7)	10.73 (4.9-18.2)	13.74 (8.6-20.9)	14.51 (8.6-20.2)
7	3.30 (-0.1-8.2)	4.70 (0.2-9.8)	7.29 (3.3-12.9)	10.28 (3.7-17.4)	13.24 (7.8-20.2)	14.40 (8.2-19.8)
8	2.31 (-0.1-7.4)	4.59 (0.7-10.2)	7.86 (3.7-12.9)	11.37 (4.9-17.4)	15.07 (9.4-21.7)	16.62 (10.2-25.9)
9	1.86 (-0.1-7.0)	3.19 (-0.1-7.4)	6.64 (2.4-11.3)	10.14 (4.5-17.1)	13.95 (8.2-20.9)	15.50 (8.6-22.8)
10	1.00 (-2.4-5.8)	1.71 (-1.9-6.2)	6.06 (-1.9-10.6)	11.08 (5.8-19.0)	16.02 (10.6-23.2)	18.04 (11.7-24.0)
11	N/A	N/A	10.20 (8.6-13.3)	10.94 (8.6-15.2)	11.85 (9.4-15.9)	12.34 (9.4-15.9)
12	4.58 (2.0-7.8)	5.33 (2.4-8.6)	7.77 (4.1-10.6)	NA	NA	NA
13	NA	NA	NA	10.41 (7.0-16.7)	12.28 (8.6-17.8)	13.21 (9.0-19.4)
14	4.38 (0.2-9.0)	5.14 (0.7-8.6)	NA	NA	NA	NA

Table 11. (Cont.)

Site	July 2005	Aug. 2005	Sept. 2005	Oct. 2005	Nov. 2005	Dec. 2005	Jan. 2006	Feb. 2006
3	16.27 (10.9-21.3)	14.80 (9.0-20.2)	11.61 (7.4-17.1)	8.71 (3.7-14.1)	5.12 (1.1-9.0)	2.67 (-0.1-6.2)	2.95 (0.2-7.0)	3.08 (-0.1-8.6)
4	16.46 (11.7-20.9)	15.33 (10.2-20.9)	12.20 (8.6-17.8)	9.52 (7.0-11.7)	6.20 (1.6-9.0)	4.81 (2.0-7.0)	4.66 (2.4-7.0)	4.67 (2.0-7.8)
5	17.44 (12.1-22.4)	15.42 (9.4-20.5)	12.11 (7.4-17.4)	9.05 (4.9-12.1)	5.27 (1.1-9.0)	3.31 (0.2-7.0)	3.72 (0.7-7.4)	3.78 (0.2-8.6)
6	17.42 (11.7-22.8)	16.16 (10.6-21.0)	12.55 (8.2-18.7)	9.41 (5.4-12.2)	5.73 (1.2-9.4)	3.36 (-0.2-7.4)	3.80 (0.3-7.0)	4.00 (-0.2-9.0)
7	17.65 (12.5-22.1)	16.06 (10.6-20.9)	12.43 (7.8-17.8)	9.05 (4.9-12.5)	5.03 (0.2-8.6)	2.60 (-0.1-6.6)	3.04 (-0.1-6.6)	2.99 (0.7-6.6)
8	20.27 (13.7-25.2)	NA	NA	NA	NA	2.61 (0.73-4.6)	2.07 (-0.6-5.0)	2.24 (-0.6-7.4)
9	20.01 (14.8-25.6)	19.09 (14.1-24.0)	14.82 (10.6-20.2)	10.65 (6.2-14.1)	6.34 (3.3-9.4)	NA	4.18 (2.4-6.6)	4.29 (2.4-9.4)
10	21.31 (15.9-26.3)	18.06 (12.5-23.6)	13.12 (9.4-17.8)	9.95 (6.6-12.5)	6.71 (4.1-9.4)	4.76 (3.7-8.6)	NA	NA
11	13.14 (10.2-16.3)	11.90 (10.2-15.2)	11.55 (9.4-15.2)	10.38 (8.2-12.1)	8.53 (6.2-10.6)	NA	NA	NA
12	12.74 (11.0-15.2)	12.26 (10.2-15.2)	11.45 (9.8-14.1)	9.98 (5.8-13.3)	7.80 (3.3-11.8)	NA	NA	NA
13	14.65 (10.6-19.8)	13.48 (9.8-17.8)	11.61 (8.6-16.3)	9.53 (7.0-12.5)	7.70 (5.3-10.2)	NA	NA	NA
14	17.84 (14.8-21.3)	15.96 (11.4-19.4)	12.51 (8.6-17.9)	9.35 (5.4-12.6)	5.87 (1.6-9.4)	3.90 (-0.2-8.2)	5.95 (1.6-9.4)	6.98 (3.31-11.8)

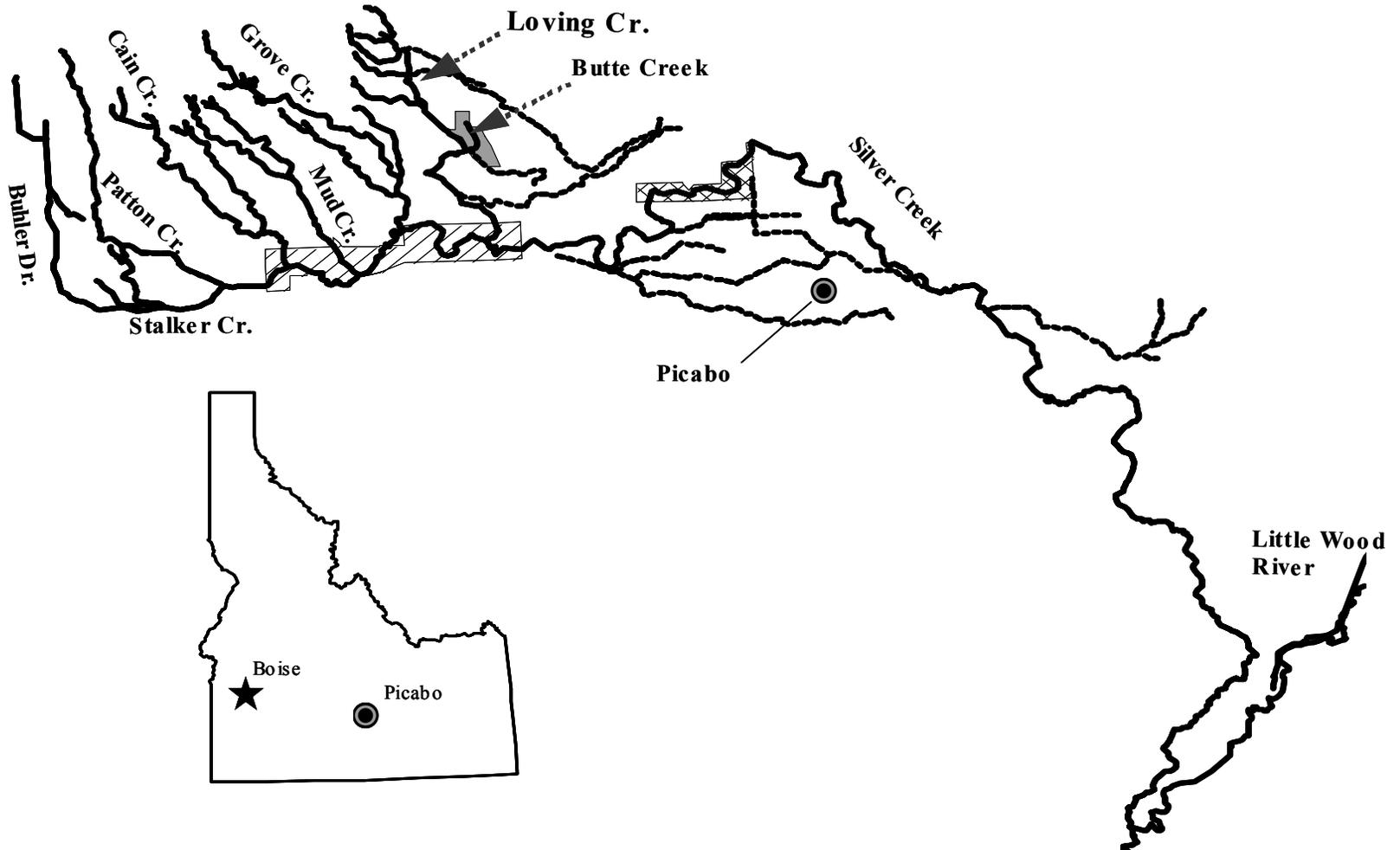


Figure 1. Map of the Silver Creek drainage from its headwaters to its confluence with the Little Wood River. Dotted lines depict irrigation diversions from the drainage. The location of Silver Creek Preserve, the Nature Conservancy is indicated by a diagonal striped polygon. A cross-hatched polygon represents Idaho Department of Fish and Game's Sportsmen's Access and the location of the Idaho Department of Fish and Game's Hayspur State Fish Hatchery is shown by a gray polygon.

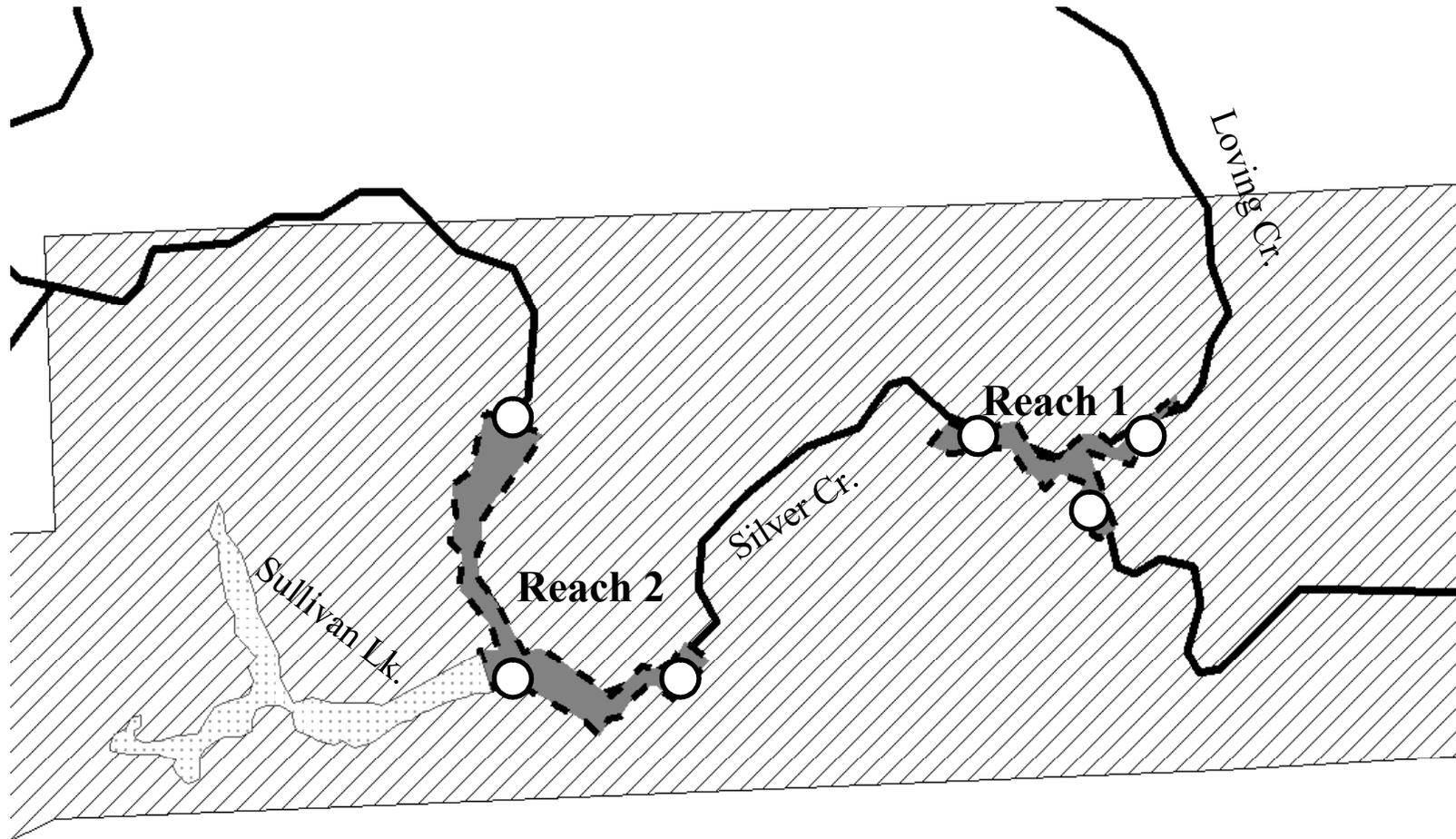


Figure 2 Locations of Reach-1 and Reach-2 sampling areas on Silver Creek Preserve (diagonally striped polygon) for the seasonal distribution survey. Open circles denote approximate locations of thermograph recorders.

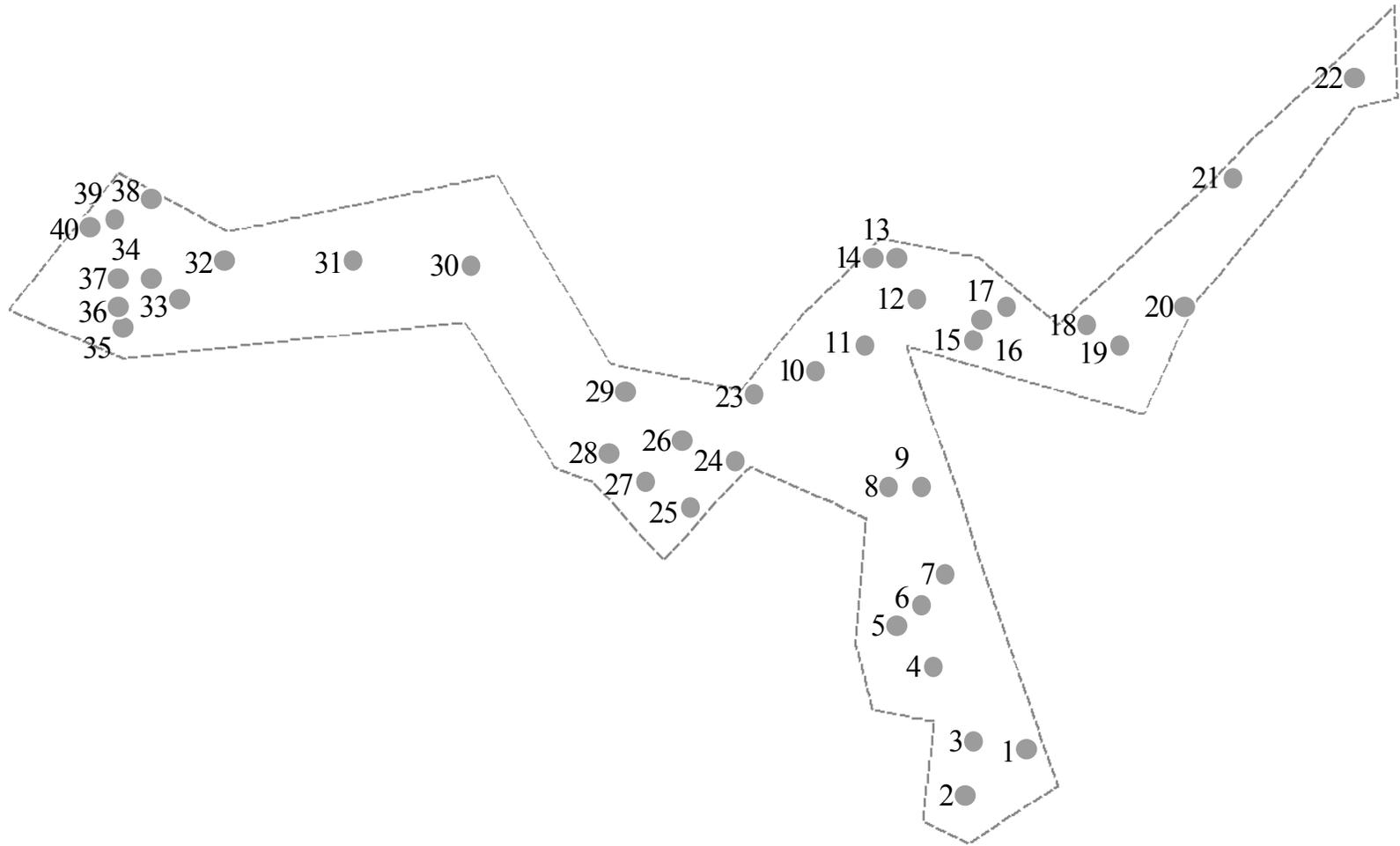


Figure 3. Location of 40-randomly selected sample sites in Reach-1 for the seasonal distribution survey. Site numbers correspond to site numbers listed in Table 5.

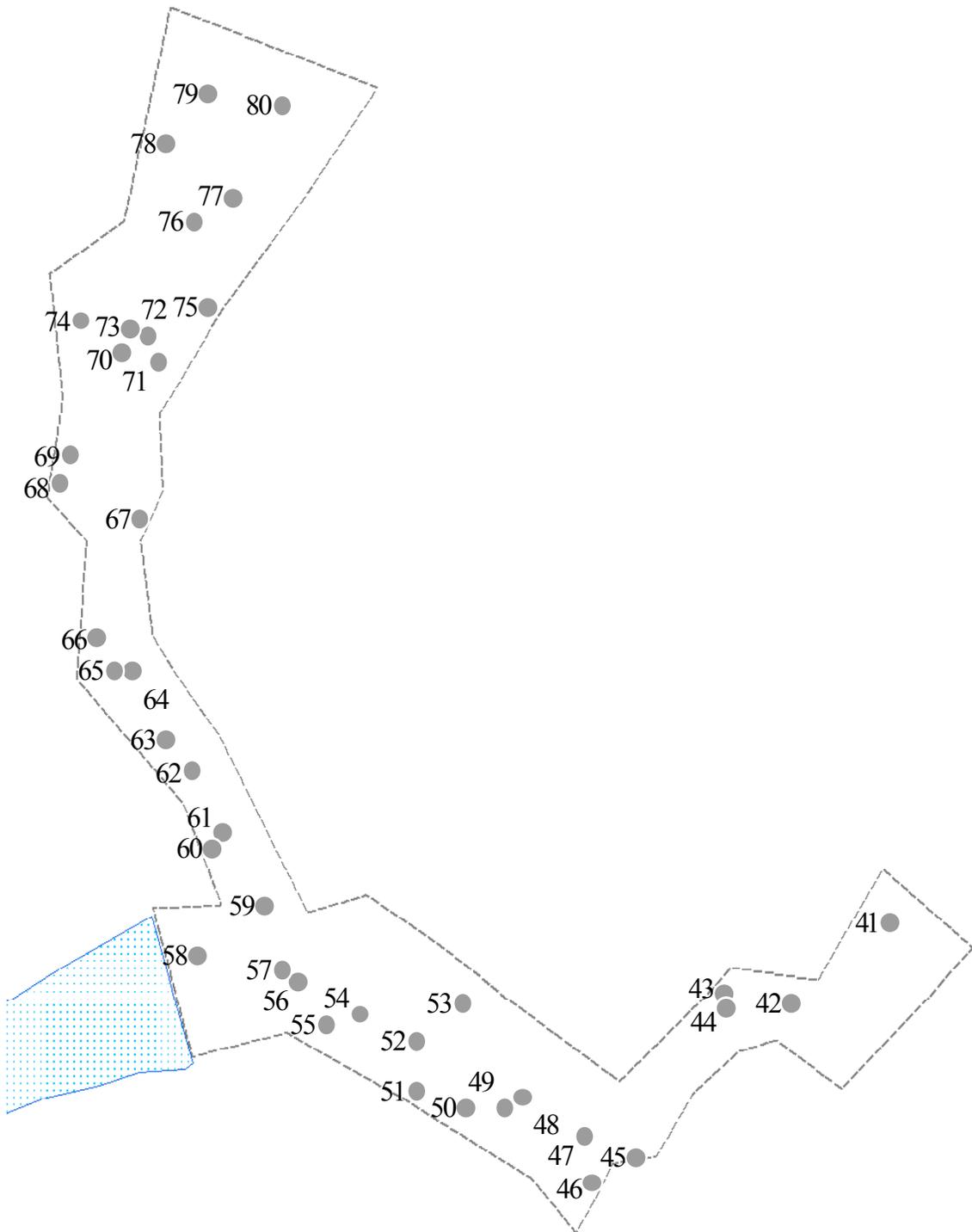


Figure 4. Location of 40-randomly selected sample sites in Reach-2 for the seasonal distribution survey. Site numbers correspond to site numbers listed in Table 6.

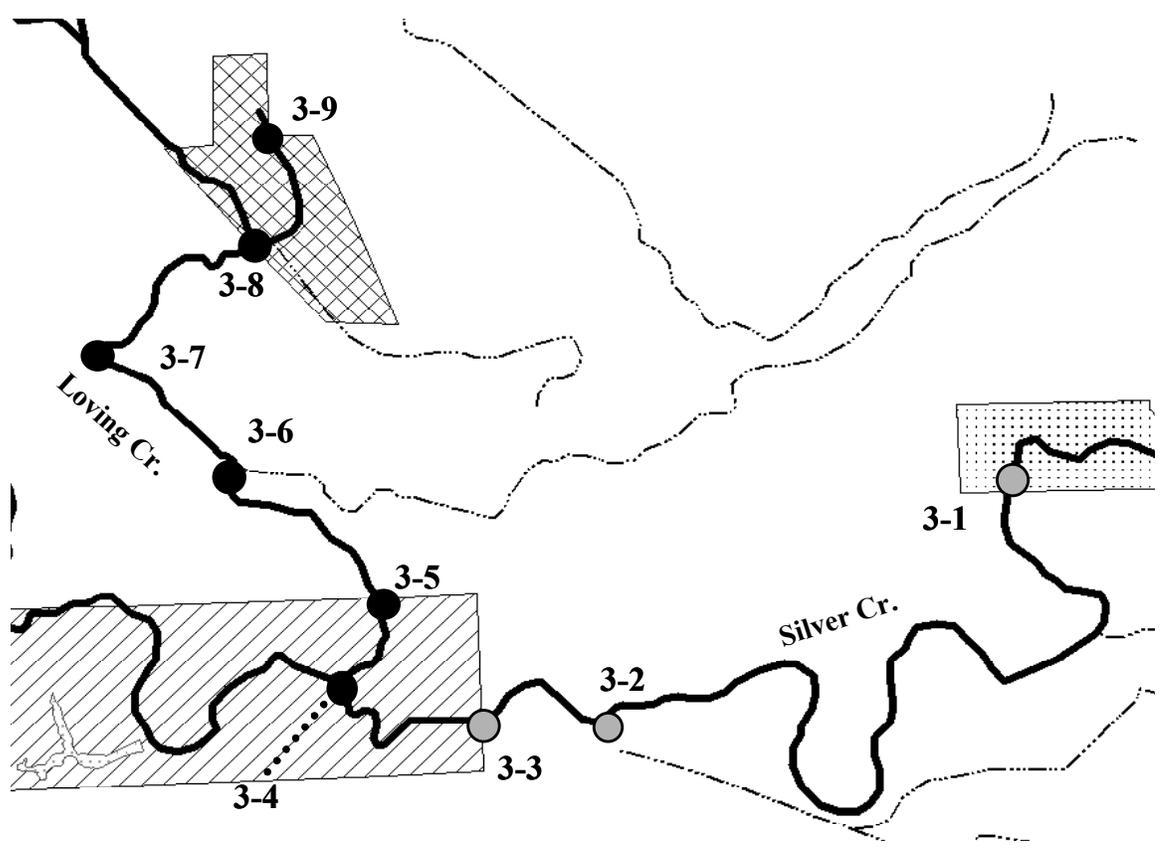


Figure 5. Sampling site locations selected for inclusion in the longitudinal density survey. Gray circles depict sites negative for New Zealand mudsnails while black circles depict sites positive for New Zealand mudsnails. Silver Creek Preserve is depicted with a diagonally striped polygon. Idaho Fish and Game's Sportsmen's Access is depicted by the stippled polygon. Hayspur State Fish Hatchery (IDFG) is depicted by the cross-hatched polygon.

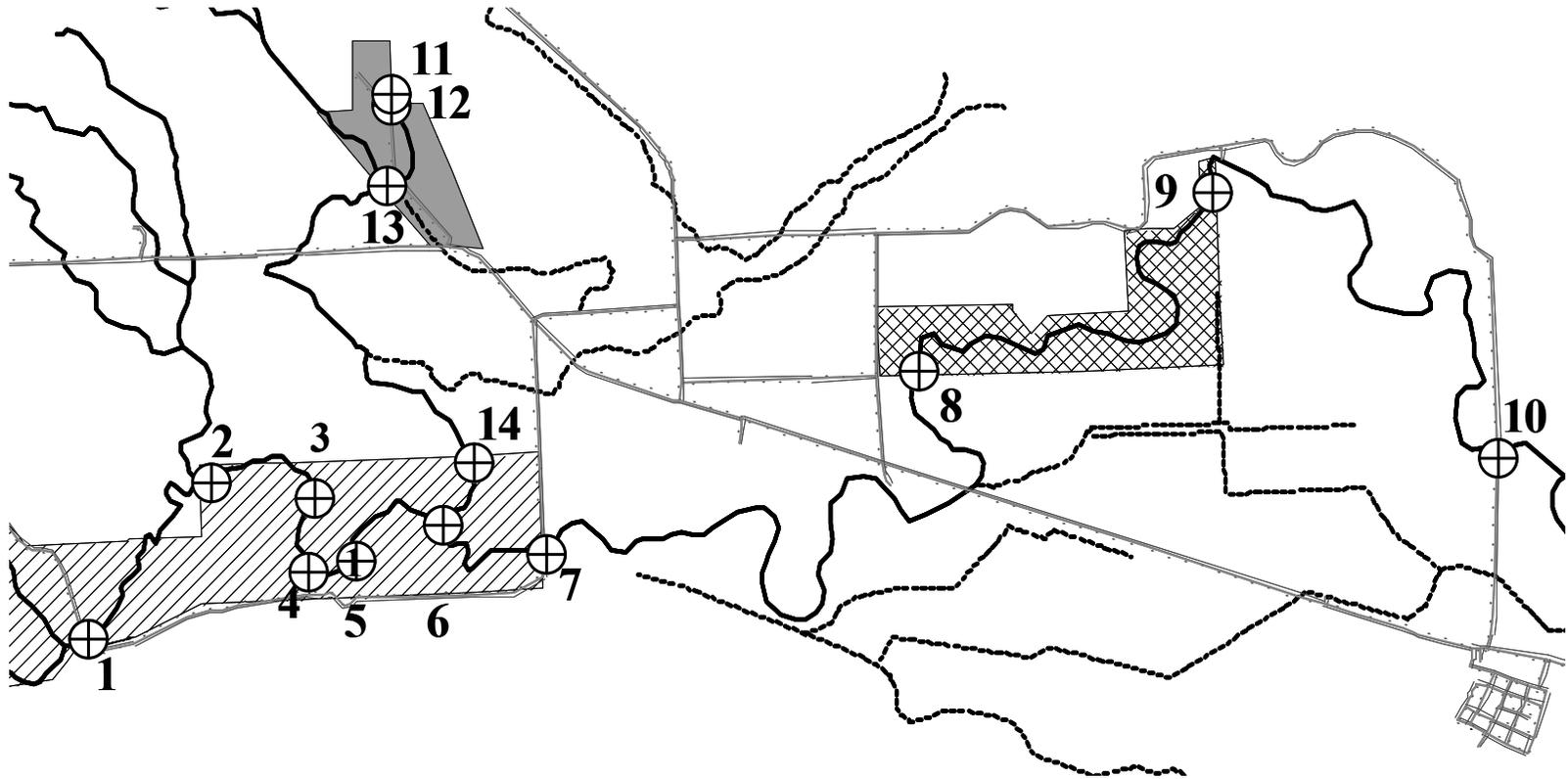


Figure 6. Location of temperature recorders deployed in the Silver Creek drainage. Numbered locations correspond to site numbers listed in Table 4. The diagonally striped polygon represents Silver Creek Preserve, the Nature Conservancy, and the cross-hatched polygon represents the Sportsmen's Access, Idaho Department of Fish and Game. The gray polygon represents Hayspur Hatchery, Idaho Department of Fish and Game.

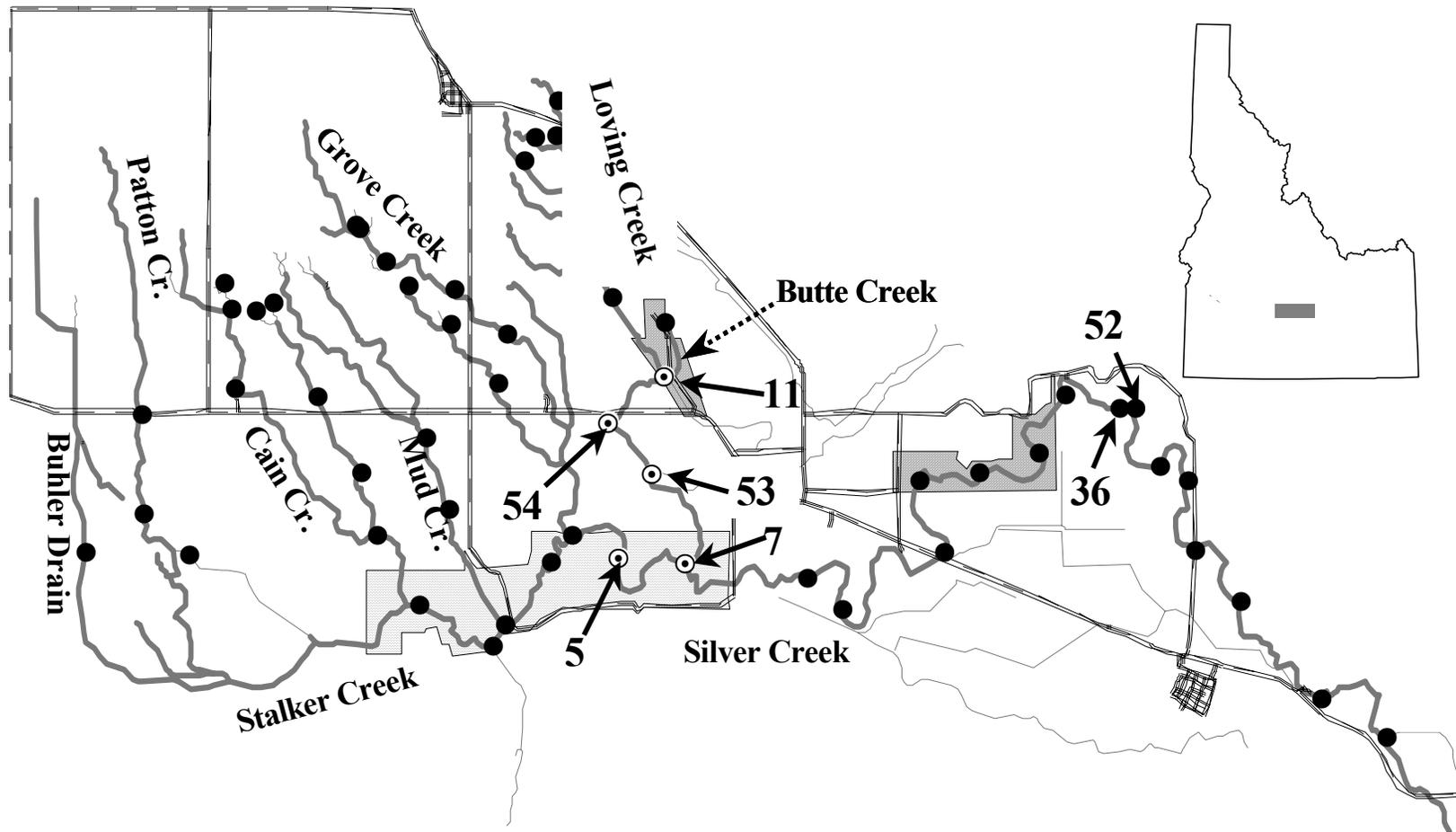


Figure 7. Map of sites sampled in the Silver Creek Drainage, June - August 2004. Dotted open-circles represent locations with New Zealand mudsnails and site numbers are detailed in Table 1. Closed circles indicate sites with no New Zealand mudsnails detected. Sites 36 and 52 were in the vicinity of previous detections of New Zealand mudsnails but none were found in 2004. The boundary of Silver Creek Preserve, The Nature Conservancy is indicated by a stippled polygon and Hayspur Hatchery (on Butte Creek) and Silver Creek Sportsman's Access (on Silver Creek), Idaho Department of Fish and Game, are shown with diagonally striped polygons.

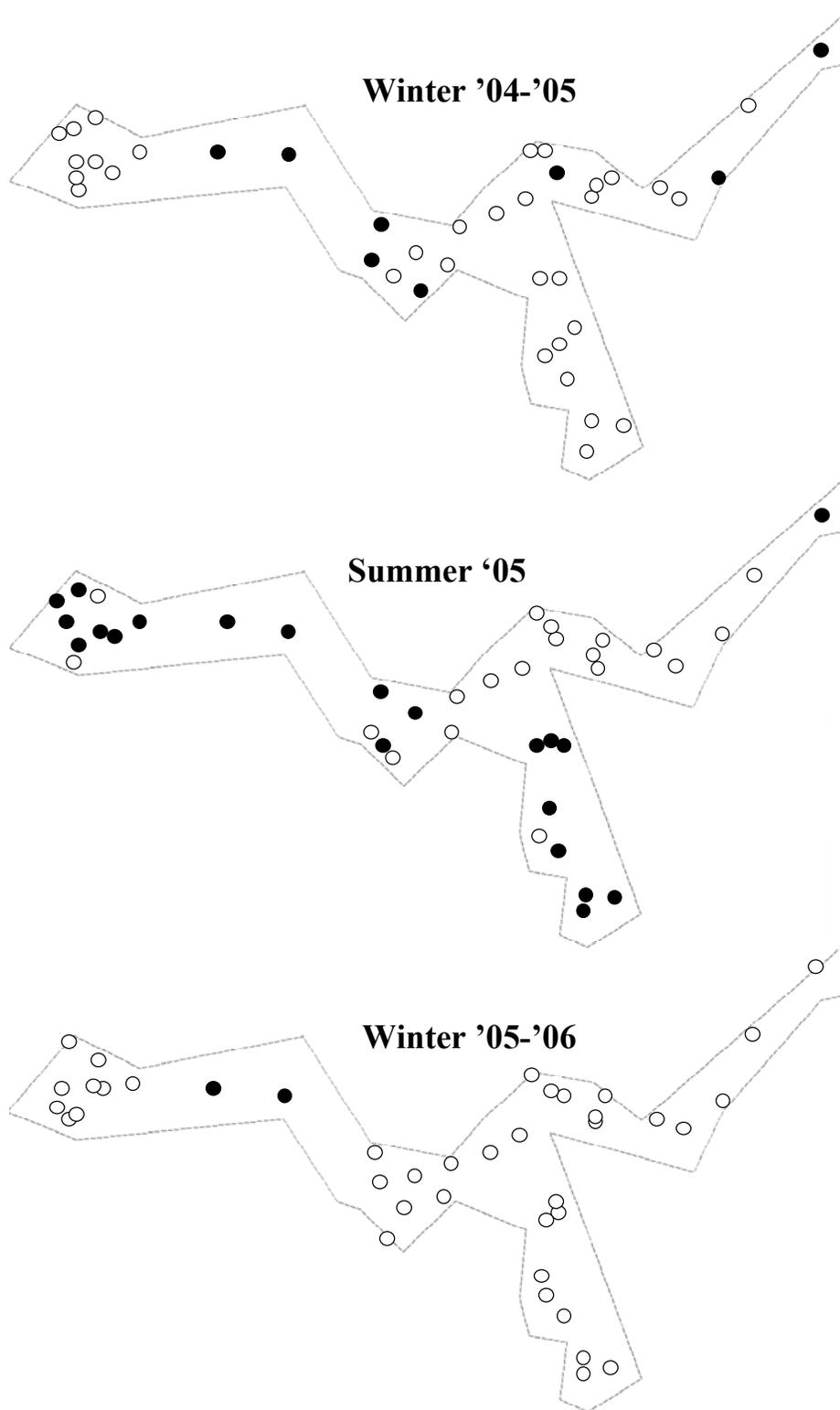


Figure 8. Spatial distribution of New Zealand mudsnail positive (closed circles) and negative (open circles) sites in Reach-1 collected during the seasonal distribution survey.

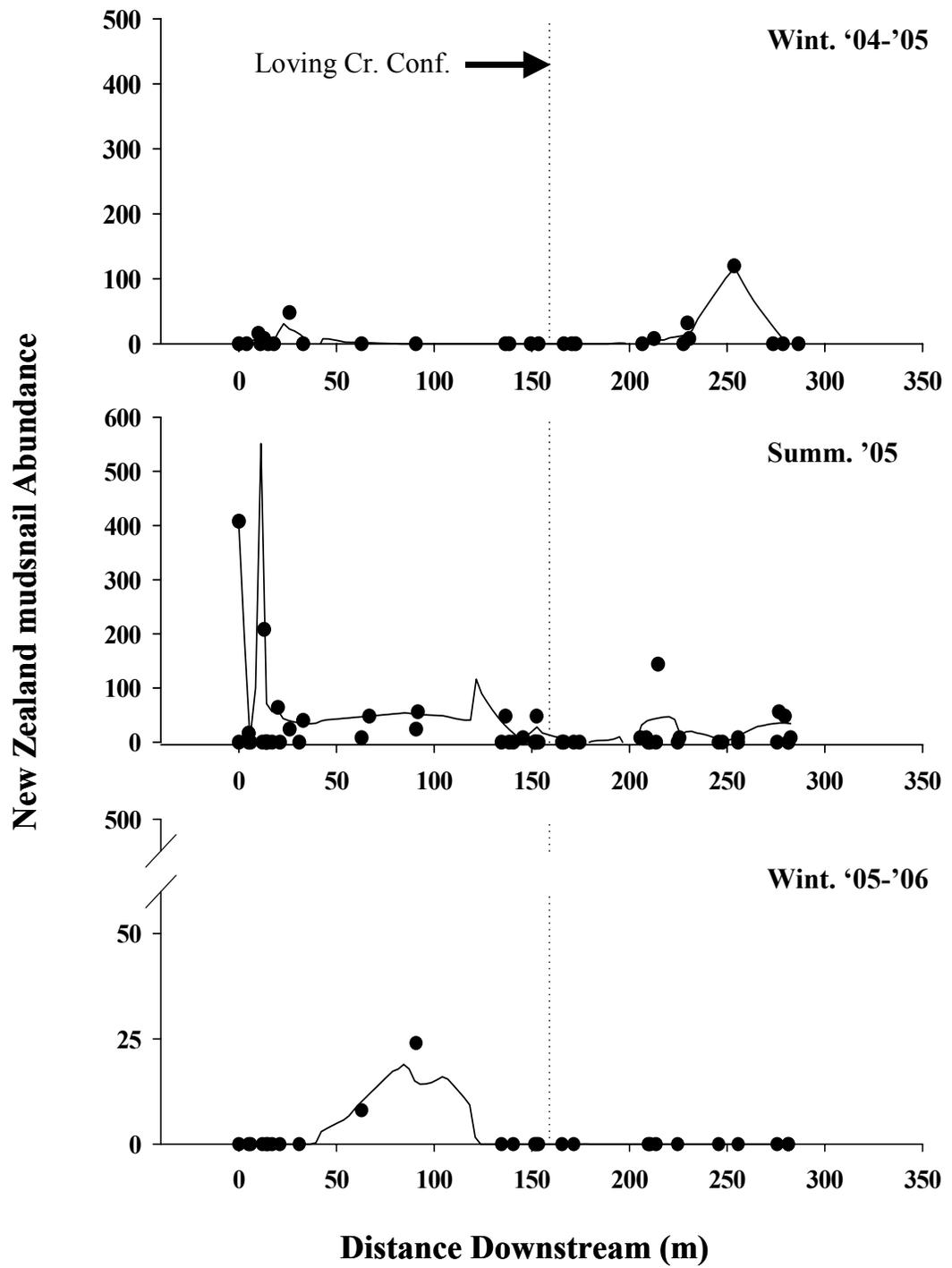


Figure 9. Abundance of New Zealand mudsnails along the stream gradient, upstream to downstream, for the Silver Creek portion of Reach-1. Stippled vertical line represents the confluence with Loving Creek.

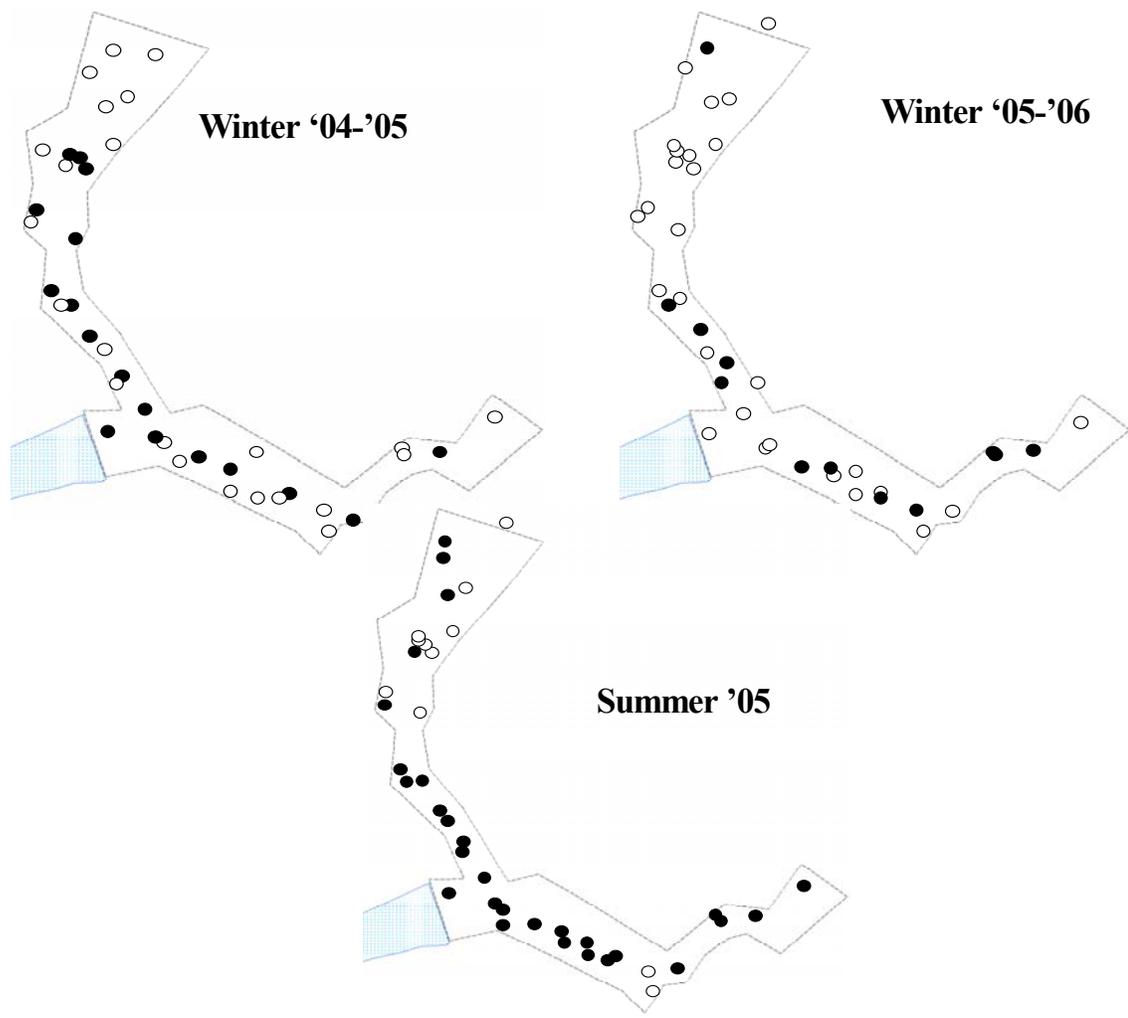


Figure 10. Spatial distribution of New Zealand mudsnail positive (closed circles) and negative (open circles) sites in Reach-2 collected during the seasonal distribution survey.

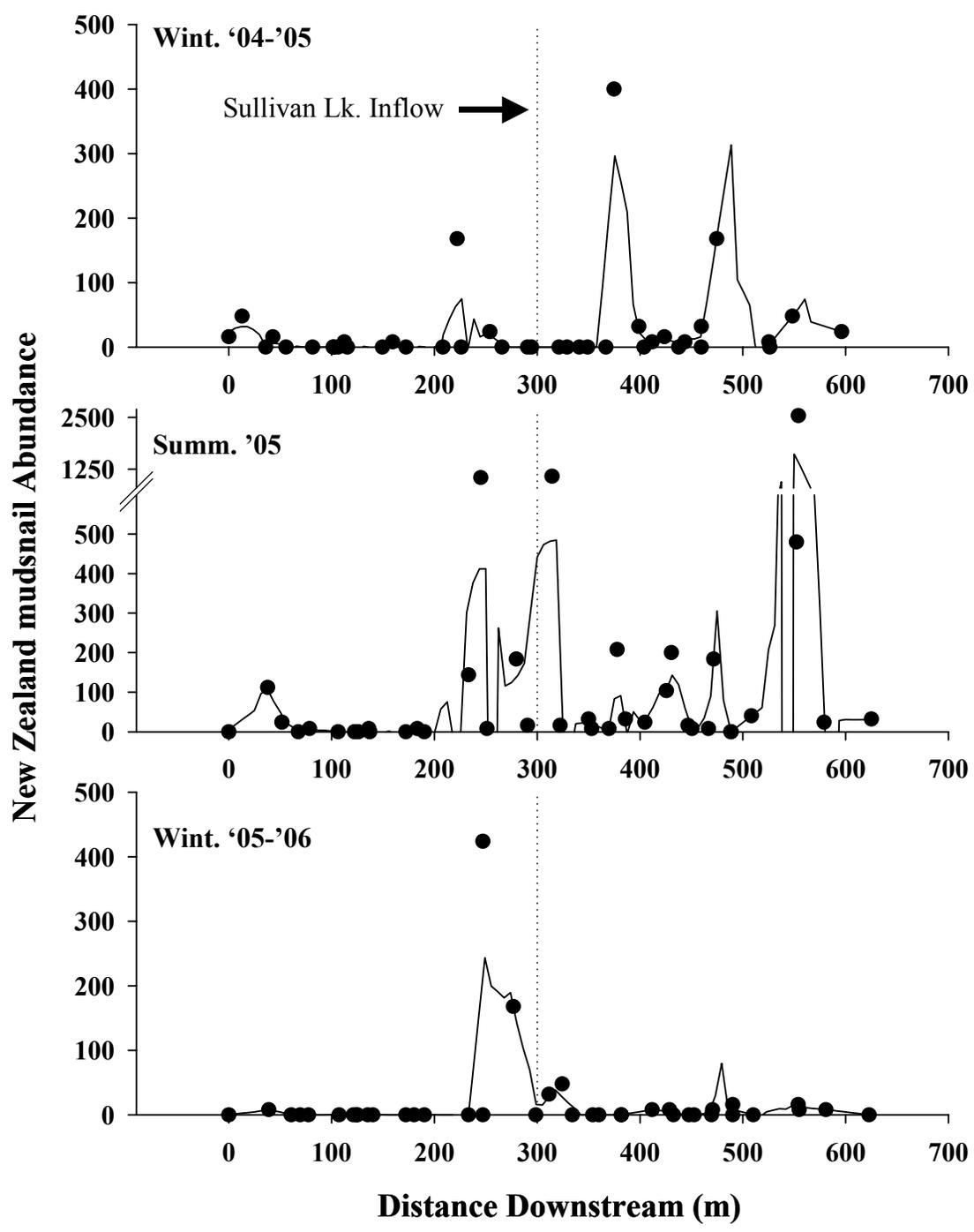


Figure 11. Abundance of New Zealand mudsnails along the upstream to downstream gradient of Reach-2. Stippled vertical line represents the inflow of Sullivan Lake.

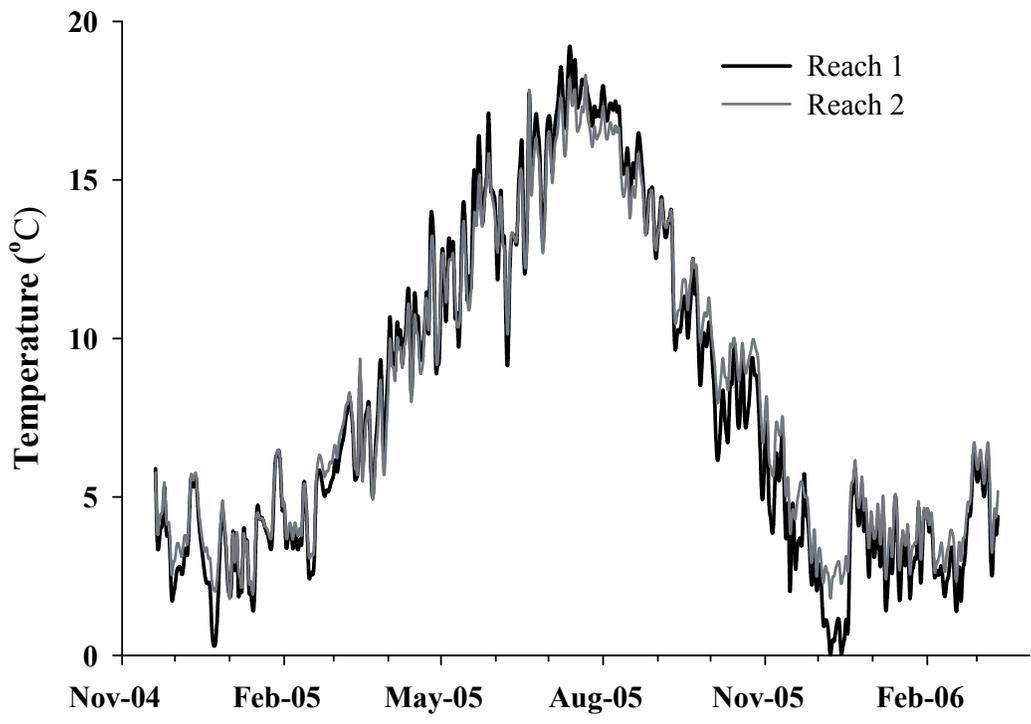


Figure 12. Thermal regimes observed in Reach-1 and Reach-2 during sampling events for the Seasonal Distribution Survey. Three thermograph data loggers were deployed in each reach and temperatures were recorded every 2 hours.

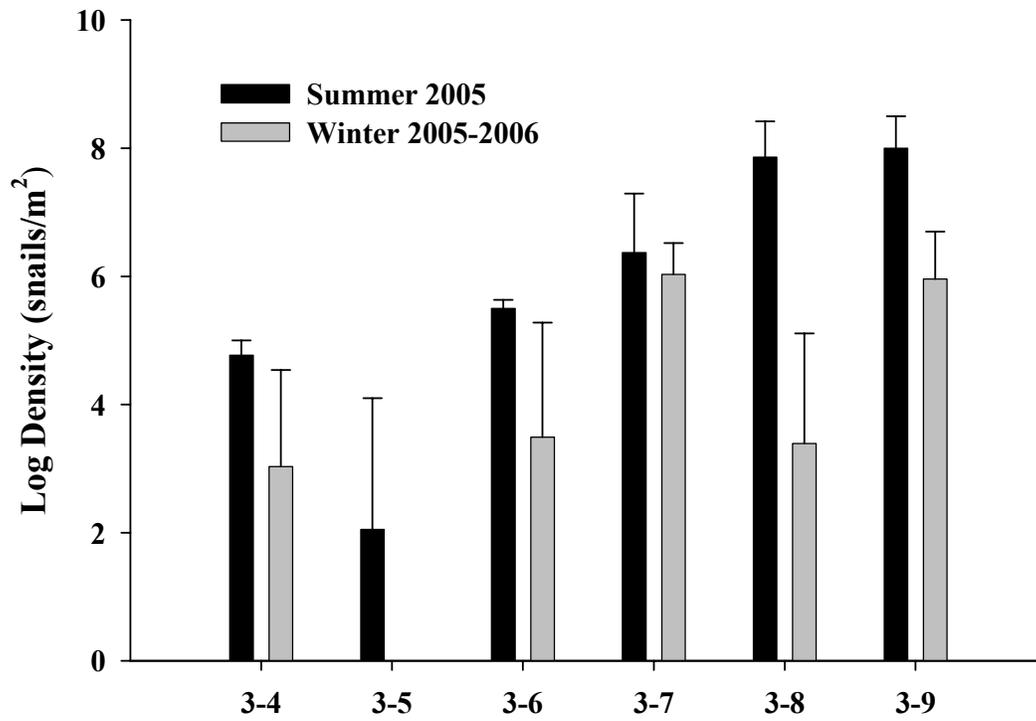


Figure 13. Mean log(density) of New Zealand mudsnails from positive sites in the large-scale density survey. Error bars represent 1-S.E.

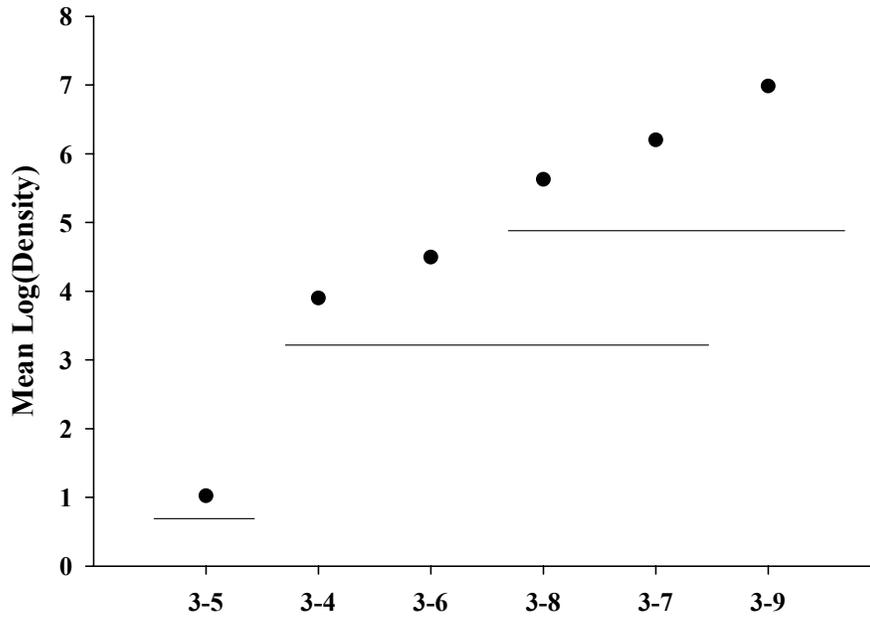


Figure 14. Multiple comparison of mean log(density) results for each site in the large-scale density survey using Fisher's protected least significant differences. Sites with common horizontal lines are not statistically significant ($P>0.05$).

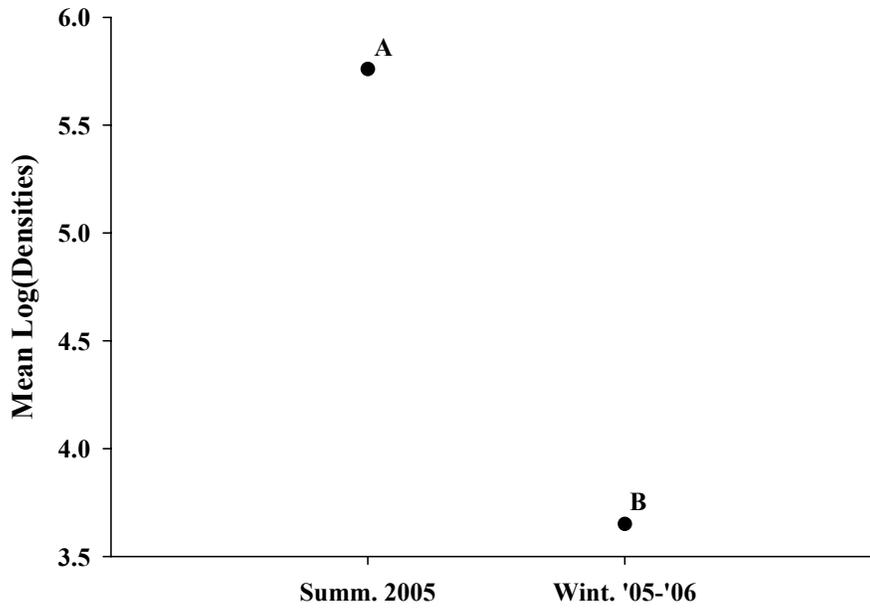


Figure 15. Multiple comparison results using Fisher's protected least significant differences of season effect on mean log(density) for the large-scale density survey. Points with different letters are significantly different from each other ($P \leq 0.05$).

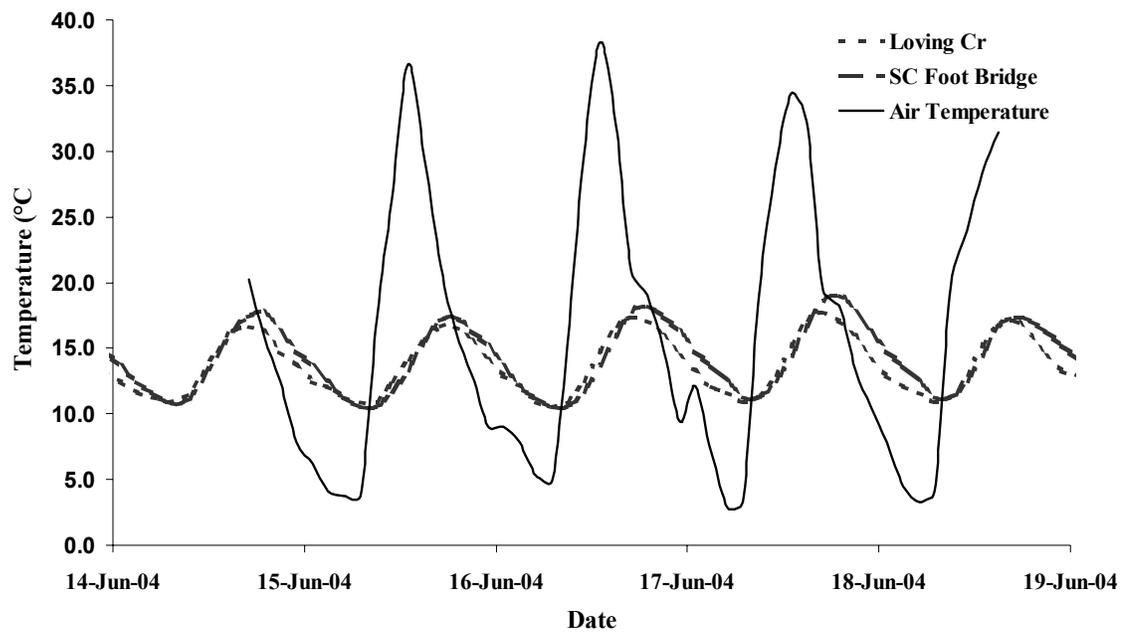


Figure 16. Water temperatures recorded on Loving Creek and Silver Creek (Silver Creek Foot Bridge) and air temperatures on Silver Creek, between 14 June and 19 June, 2004.

**CHAPTER II: RELATIONSHIP OF LOWER LETHAL TEMPERATURES AND
DURATION OF EXPOSURES ON MORTALITY OF NEW ZEALAND**

MUDSNAILS *POTAMOPYRGUS ANTIPODARUM*

Abstract

The lower thermal tolerance of New Zealand mudsnails *Potamopyrgus antipodarum* (Gray) (family Hydrobiidae) was estimated in laboratory experiments, to evaluate the response of mudsnails to field observed winter water temperatures in a controlled setting. Snail mortality over time of exposure to constant and dynamic temperatures was evaluated. Mortality of New Zealand mudsnails occurred only in treatments where temperatures were maintained at or below 0°C. The estimated median lethal time of exposure (LT₅₀) was lower for snails exposed to dynamic temperature regimes (33-42 h) than for snails exposed to a more constant temperature regime (72 h). These results suggest that New Zealand mudsnails may be limited in their ability to disperse into areas where seasonal temperatures drop below 0°C for longer than 3 to 4 days and that dynamic temperature regimes can cause earlier mortalities.

Introduction

Water temperature is an important habitat quality determinant for many aquatic invertebrates (Saunders 1980, Quinn et al. 1994, Cox and Rutherford 2000, Johnstone and Rahel 2003). Since temperature can affect all physiological processes growth, survival, and the distribution of aquatic invertebrates are directly related to water temperature (Laudien 1973) and are maximized at optimal temperatures (Cheper 1979). The low body weight and the large ratio of surface area to volume of most invertebrates allows heat exchange with the environment to occur very rapidly (Jankowsky 1973) and affect physiological processes. Unless such animals possess behavioral, structural, and/or physiological adaptations that allow them to withstand such stressors (Irons et al. 1993), temperatures can be lethal and possibly exclude them from certain reaches of aquatic habitat. Therefore, identifying these temperature limits is important for managing the flora and fauna of specific water bodies.

Many researchers have worked to define the temperature limitations of a variety of aquatic invertebrates (Sweeney 1976, Sweeney and Schnack 1977, Sweeney and Vannote 1978, Sweeney 1978, Sweeney and Vannote 1986, Quinn et al. 1994, Johnstone and Rahel 2003). However, data on the thermal tolerances of the invasive New Zealand mudsnail *Potamopyrgus antipodarum* (Gray) (family Hydrobiidae) are limited. Quinn et al. (1994) identified the upper thermal limit for New Zealand mudsnails as $\sim 30^{\circ}\text{C}$ in a laboratory experiment in which the snails were held at constant temperatures. Cox and Rutherford (2000) observed that diurnally fluctuating temperatures ($\pm 5^{\circ}\text{C}$) could lower the mean upper lethal temperature of the New Zealand mudsnail from a constant temperature of 30°C to a mean of 28.5°C . In New Zealand, *P. antipodarum* are not

observed at temperatures above 28°C (Winterbourn 1969). *Potamopyrgus jenkinsi* (E.A. Smith), agreed to be synonymous with *P. antipodarum*, collected from the river Mattrup in Denmark, were observed to survive just a few hours at -3°C in freshwater, and low survival at -2°C in 15 ppt seawater after 7 days (Hylleberg and Siegismund 1987). Richards et al. (2004) documented total mortality of *P. antipodarum* within 1 h at -3°C on dry substrate under laboratory conditions, identifying the method as a form of disinfection for wading gear.

The distribution of New Zealand mudsnails *P. antipodarum* in the Silver Creek drainage appears limited to ~5 km reach of stream on Loving/Butte Creek and ~2 km on Silver Creek (Richards and Lester 2003, James and Moffitt 2004). Fluctuating temperature regimes and lower winter water temperatures in some reaches of this system (James and Moffitt 2004) may limit the snail's dispersal and survival. Temperatures below freezing are lethal to New Zealand mudsnails, but temperatures in the laboratory or cursory field observations may not be representative of temperatures or conditions experienced by New Zealand mudsnails in aquatic habitats in the western U.S. Many streams within the expanding range of New Zealand mudsnails in the western U.S. have fluctuating temperatures (Johnstone and Rahel 2003) and invertebrates in dynamic temperature regimes may experience different physiological effects than those held in constant temperatures (Precht 1973, Sweeney 1976). Consequently, extrapolation of results from constant lethal temperature trials to organisms occupying streams with temporally and spatially dynamic temperatures must be interpreted with caution (Sweeney and Schnack 1977).

The cause of mortality of organisms exposed to lower lethal temperatures is generally a result of cellular damage due to ice formation either intracellularly or extracellularly (Storey and Storey 1988). Damage can occur as either chill injury or freeze injury. Chill injury occurs prior to ice nucleation and affects the physical properties of molecules and the rate of physiological processes, and when severe or prolonged, lead to irreversible and lethal metabolic imbalances (Storey and Storey 1988). Freeze injuries occur as a result of physical damage by ice crystals and structural/metabolic consequences of freeze concentration. Damage can distort or deform cellular membranes and disrupt cellular osmoregulation capacities (Storey and Storey 1988). In aquatic environments, freezing is a major concern for invertebrates as ice nucleation in the aquatic habitat can promote internal ice crystal formation of the organism (Frisbie and Lee 1997). In dynamic temperature regimes, the accrual of cellular damage is dependent on the length of time an organism is exposed to temperatures extreme enough to cause damage (Laudien 1973) and the effect of subsequent freeze-thaw events does more damage than constant low temperatures (Voelkel 1925 in Laudien 1973).

The objectives of this study were to use laboratory experimentation with field collected *P. antipodarum* from Idaho to determine 1) the lower lethal temperature and corresponding duration of exposure at constant temperatures; and 2) the influence of fluctuating temperatures on survival of *P. antipodarum*.

Methods

Snail Collections

New Zealand mudsnails were collected from established populations in Riley Creek, Gooding County, Idaho (October 2005 and January 2006) and from Loving Creek, Blaine County, Idaho (January 2006). Both locations are characterized as spring fed systems and collection sites were downstream of the water discharge from fish hatcheries. Hayspur State Fish Hatchery on Loving Creek is operated by the Idaho Department of Fish and Game. The U.S. Fish and Wildlife Service operates Hagerman National Fish Hatchery on Riley Creek. Loving Creek has pronounced diel ($\sim 10^{\circ}\text{C}$) and annual ($\sim 15^{\circ}\text{C}$) temperature fluctuations while Riley Creek maintains fairly constant temperature of 15°C .

We collected snails using a D-framed kick-net with a 500-micron mesh net, by placing the net at the streambed surface and kicking the upstream substrate to drift snails into the net. The samples were transferred into plastic bags and placed in a cooler for transport to the University of Idaho. Aquatic vegetation (*Characaceae* spp. and *Ranunculaceae* spp.) was collected along with the snails and transported to the University of Idaho in a separate container to provide periphyton as a food source for snails prior to initiation of the experiments. Snails and vegetation were delivered to the University of Idaho's wet lab within 24 hrs of collection. Snails collected in October 2005 from Riley Creek were acclimated in the laboratory in water containers (2 L) filled with dechlorinated and aerated municipal water for five days at a constant 15°C . Snails collected in January 2006 from both Riley Creek and Loving Creek were tested in trials within 24 h upon arrival at the University of Idaho.

Constant Temperature Trials

Replicated groups of snails were monitored at one of four constant water temperatures: 0, 2, 4, or 15°C to determine survival over time. To conduct a trial, polypropylene specimen cups (120 mL, n=64) were filled with 100 ml of 15°C dechlorinated aerated municipal water and 10 New Zealand mudsnails ≥ 2 mm were placed into a “holding” cup approximately 2 h before the trial started, and maintained at 15°C. Similar cups were filled with 100 mL from the same water source and were placed into incubators set at each of the test temperatures 1 d prior to the trial. At the start of the trial, the holding cup with snails was inverted over a 100 μ m mesh stainless steel screen, and the snails transferred to their respective test container. Cups with snails were then returned to individual incubators held at 0°C, 2°C, 4°C, and 15°C. The incubators were maintained on a continual dark cycle while those snails in the 15°C control incubator, which doubled as the recovery room, were held on a 10-hr dark, 14-hr light cycle.

At each specified time interval (1, 2, 4, 8, 24, 48, 72, and 96 h), two cups were removed from each incubator (temperature treatment) and placed into the 15°C recovery room. Mortalities were assessed immediately, at 24 h and 48 h after removal. Snails that had retreated into their shells and did not show activity when prodded with a dissecting needle were considered dead. At 48 h after removing from test temperature a final evaluation of survival was made under a dissecting microscope for quality assurance of the survival estimate.

Dynamic Temperature Trials

Replicate snails from two separate New Zealand mudsnail populations were exposed to dynamic temperature regimes to assess their differences in ability to withstand

fluctuating lower temperatures. Three dynamic temperature regimes were designed to mimic those observed in Loving Creek during the winter: 1) -2 to 2 °C, 2) 0 to 4 °C, and 3) 2 to 6 °C. Temperatures fluctuated on a 24-hour cycle with 10 hours warm and 14 hours cold. As a control, snails from Riley Creek were held at a constant 15 °C and snails from Loving Creek were held at a constant 8 °C. Control incubators were also used as recovery incubators for the respective snail source. All incubators were maintained on a 24 h dark cycle. Snails exposed to dynamic temperature trials were not acclimated in the lab prior to the start of the trial. All temperature ($n=4$) by time ($n=8$) by source ($n=2$) were replicated for a total of 164 treatment combinations.

Polypropylene cups (120 mL, $n=164$) were filled with 100 mL of 15 °C or 8 °C dechlorinated aerated municipal water, and ten New Zealand mudsnails (≥ 2 mm) were placed into each cup 2 hrs before the trial started. Snails from Riley Creek were maintained at 15 °C and snails from Loving Creek were maintained at 8 °C. Identical cups were filled with 100 mL of dechlorinated municipal water that had been chilled to the designated experimental temperature.

At each specified time interval (1, 2, 4, 8, 24, 48, 72, and 96 h), two cups in each temperature treatment for each snail source were removed and placed into respective recovery incubators. Mortality assessments were conducted in the same manner as previously outlined for constant temperature trials.

Temperature Monitoring

Temperatures were monitored throughout both experiments using HOBO 08 temperature loggers (Onset Corp., Pocasset, Massachusetts) to record temperatures of exposure. Loggers were deployed to record temperatures at 10-minute intervals

throughout the duration of the constant temperature trial. Temperatures were not recorded during the dynamic temperature trials in the -2 to 2°C incubator, and instead a mock trial was conducted with similar methods but without any snails. Temperatures for the dynamic temperature trials were recorded at 2 h intervals.

Data Analysis

All statistical analyses were conducted with data collected at 48 h assessments, since earlier mortality assessments were not always accurate because of snails retreating behavior during the trials. Observations from the immediate and 24 h assessments are used in interpretation of these results. Median lethal time (h) of exposure at 0°C was calculated using a probit model (SAS Institute Inc. 2003). Using the equation $\Phi^{-1}(\chi) = \alpha + \beta\chi$, where $\Phi^{-1}(\chi)$ is the cumulative distribution of mortality for the standard normal distribution, α is the estimated parameter for the intercept, β is the estimated parameter for the slope, and χ is the $\log_{10}(\text{Time})$, the normal maximum likelihood estimates of a median lethal time (LT_{50}) were generated with corresponding 95% CI. Differences in the slopes and intercepts, when slopes were similar, were tested for the probit models between Riley Creek and Loving Creek snails exposed to the dynamic temperature regime using Wald's Chi-square analysis.

Results

Constant Temperature Trials

New Zealand mudsnails from Riley Creek exposed to constant temperatures greater than 0°C showed zero to five percent mortality throughout the duration of the experiment (Table 12). However, snails exposed to temperatures of 0°C experienced high mortality over the course of the experiment (Table 12). After 72 h, 50% of snails

held at 0°C were dead and 100% were dead at 96 h (Table 12, Figure 17). The probit model estimated the LT_{50} at 72 hours (Figure 18). However, the estimated model parameters were not statistically robust ($P=0.9999$; Table 13). Intermediate mortalities were not observed frequently enough throughout the experiment at 0°C in order to calculate 95% CI for this data set.

Temperatures recorded in the incubation chambers were within ~1°C of target temperatures throughout the experiment (Table 14; Figure 19).

Dynamic Temperature Trials

Mortality in Riley Creek snails held in treatment temperatures maintained at or above 0°C experienced zero to five percent mortality while five to 20% mortality was observed in the snails held at the control temperature of 15°C (Table 15). Snails held at -2 to 2°C showed 66.7% mortality at 48 h and 100% mortality at 72 h and 96 h (Table 15; Figure 20). The LT_{50} estimated by the probit model for Riley Creek snails held at -2 to 2°C was 33h (95%C.I. = 24.5-41.5 h; Figure 21).

Loving Creek snails exposed to temperatures at or above 0°C, showed zero to five percent mortality during the 96 h experiment (Table 15). Snails in the 0 to 4°C treatment group experienced one mortality (5%) at 8h of exposure (Table 15). No mortalities were observed for snails held at 2 to 6°C or 8°C_{Constant} treatment groups (Table 15). Snails held at -2 to 2°C began dying at 24h and all were dead at 72 h (Table 15; Figure 20). The calculated LT_{50} for Loving Creek snails was 42h (95%C.I. = 35-49 h; Figure 21). The slope estimates for the Loving Creek and Riley Creek snail data (Table 16) were significantly different (Walds $\chi^2 = 5.8821$, $P = 0.0153$; Table 17) indicating that snails

from Loving Creek showed more rapid and higher mortalities than did snails from Riley Creek at -2 to 2°C .

Target and observed temperatures during this study were not equivalent for all treatments. Mean temperatures in the -2 to 2°C , 2 to 6°C , and the constant 8°C treatments were similar to target temperatures (Table 14). Temperatures observed in the constant 15°C treatment were about 2.5°C lower than anticipated (Figure 22) and averaged 12.4°C (Table 14). Although temperature profiles in the 0 to 4°C had an average close to the target temperature (1.36°C vs. 2.00°C , respectively; Table 14), the magnitude and amplitude of the cycle did not mimic the anticipated regime (Figure 23).

Discussion

New Zealand mudsnails were able to survive temperatures less than 2°C for up to 96 h, but temperatures at or below 0°C were lethal. These results are consistent with the work of Hylleberg and Siegismund (1987), and also suggest that the rate of the lethal response is dependent on the degree and duration of the exposure temperatures. Hylleberg and Siegismund (1987) reported 100% mortality after a few hours at -3°C in their study. During the present study at a constant 0°C , greater than 72 h were needed for complete mortality of New Zealand mudsnails and greater than 48h were required in dynamic temperatures of -2 to 2°C .

No mortalities were observed in snails that were exposed to dynamic temperatures of 0 to 4°C . Temperatures in this treatment never reached 0°C , and were generally closer to 1°C , only slightly lower than the average 1.6°C temperature observed in the constant

temperature trial (Table 2). The lack of mortality in this treatment group may be attributable to the failure in reaching the desired target temperatures.

The estimated LT_{50s} for dynamic temperatures were lower than the estimated LT_{50} for snails held at constant temperatures, although the inability to calculate confidence intervals prevents statistical comparison. Under fluctuating temperature regimes, 50% mortality of New Zealand mudsnails was reached in less than 48-h with snails from both Riley Creek and Loving Creek when temperatures fluctuated between 2°C and -2°C under 24 hour cycles. Fifty percent mortality was not achieved in the constant temperature trial until samples were removed at 72-h.

Size, as well as age and development, can influence the thermal resistance of animals, both positively and negatively (Precht 1973). This study used snails larger than 2 mm; smaller snails may be less tolerant to cold temperatures. Richards et al. (2004) determined that New Zealand mudsnails <2 mm held in a dry environment were more susceptible to freezing when compared to larger snails (>2 mm). Further research on mortality levels of small snails in an aqueous environment needs to be conducted.

Throughout this experiment snails exposed to both constant and dynamic temperature regimes $\leq 2^{\circ}\text{C}$ for more than 4 h retreated into their shells. After a 24 h recovery period, most snails were active and moving around the cups. This behavioral trait may be an adaptive response for survival at lower lethal temperatures. It has been reported that external coverings including chitin exoskeletons, wax coatings, and egg casings can endure freezing while still protecting interior organs unless the barrier is weakened by tears or lesions (Precht 1973). In addition to the possible thermal protection provided by the shell and operculum, retreating into the shell may allow the snail to drift

downstream and escape the cold temperature. Richards et al. (2001) noted that New Zealand mudsnails were the second most abundant macroinvertebrate in 24-hr drift samples in Banbury Springs, Gooding County, Idaho, indicating that New Zealand mudsnails may utilize stream currents to aid in dispersal. Furthermore, water temperatures tend to be more stable in higher ($\geq 4^{\text{th}}$) order streams (Vannote and Sweeney 1980) and drifting downstream would likely provide a greater chance of encountering suitable thermal habitat. However, the majority of the Silver Creek drainage is only a 3rd order stream and winter temperatures in the lower reaches fluctuate daily from 4-5°C, frequently dropping below 0°C during the winter (Chapter I, this thesis). Unless the snail can locate sufficient thermal refugia in the hyporheic zone, it must travel several stream kilometers (possibly up to 100 rkm to the confluence with the Little Wood River) to reach an area where temperatures may allow survival. This potential movement is impeded by several irrigation impoundments throughout the drainage.

Although New Zealand mudsnails may volitionally travel at relatively high rates of speeds up to one m/h (Richards et al. 2001, Richards and Lester 2003), there must exist some limit to the distance they could travel in order to locate optimal thermal refugia, especially at lower environmental temperatures. During this experiment, activity levels of New Zealand mudsnails were impeded at lower treatment temperatures, especially those below 4°C. Snails from constant temperature regimes of 2°C and 4°C as well as snails in the dynamic temperature regime $2\pm 2^{\circ}\text{C}$ often appeared lethargic with slow retreating responses when prodded with the dissecting needle, even at 48h of recovery. Such slow movements at colder laboratory temperatures imply that colder

temperatures in the field may increase the amount of time it takes a snail to travel to locate thermal refugia.

Because Riley Creek snails were removed from constant, warmer ($\sim 14^{\circ}\text{C}$) temperatures, they should have experienced the greatest stress when tested at temperatures below acclimation. However, snails from Loving Creek showed more rapid mortality when tested. It is likely that snails from Loving Creek may have been more stressed in their natural environment where daily average temperatures in December 2005 had decreased to $\sim 6.5^{\circ}\text{C}$. Thus when challenged at average temperatures $\sim 0^{\circ}\text{C}$, already stressed snails were unable to compensate for increased stress when compared with snails from Riley Creek that had been acclimatized at temperatures of $\sim 14^{\circ}\text{C}$. In general, experiments assessing thermal tolerances of organisms are conducted by gradually decreasing the temperature of the organism from holding temperature to treatment temperatures in order to minimize the thermal shock experienced (Precht 1973). However, by immediately exposing New Zealand mudsnails to treatment temperatures, an assessment of the time to lethal response was not confounded by different acclimation times. This rapid temperature change may have been a factor in these results, but is unlikely since significant mortalities were only observed in temperatures less than 0°C .

A large number of embryos were released from the snails in both temperature experiments. This response may be an evolutionary reproductive strategy for New Zealand mudsnails during environmental stressors. Mature snails may retain embryos during stressful events (i.e. low temperature), however, if the environmental stressor is severe, New Zealand mudsnails may be “programmed” to release their remaining embryos as a strategy that some may survive long enough after the stress is reduced to

locate a more suitable habitat. In addition, New Zealand mudsnail embryos may also drift well in a streams current increasing the likelihood of escaping the unfavorable condition. Laboratory trials of mature New Zealand mudsnails force-fed to rainbow trout *Oncorhynchus mykiss* observed that embryos were released from the snails removed from the intestinal tract of the fish (Bruce 2006). Determining what effect severe stress actually has on New Zealand mudsnail reproduction and eventual survival of offspring could be an important aspect for potential management options for this invasive species.

The studies reported here support the hypothesis that temperatures may influence the distribution of New Zealand mudsnails in the Silver Creek drainage. In areas where New Zealand mudsnails have been identified in the Silver Creek drainage winter water temperatures are maintained between 4 and 6°C whereas areas where New Zealand mudsnails have not been detected drop below 0°C often throughout the winter. In the Riley Creek drainage water temperatures rarely drop below 13.5°C in the wintertime and New Zealand mudsnails are most likely not limited by colder water temperatures. Although temperatures are playing an important role in New Zealand mudsnail dynamics in Silver Creek, nutrition and the chemical composition of the aquatic environment including pH, salinity, and dissolved oxygen may also affect the thermal resistance (Precht 1973) of New Zealand mudsnails.

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Table 12. Percent mortality observed in New Zealand mudsnails held in constant temperature trials during October 2005. Snails (N=640) >2.0mm from Riley Creek were evenly distributed into 64 replicate incubation cups and 16 cups placed into individual temperature treatments (0°C, 2°C, and 4°C). At the specified time intervals (1, 2, 4, 8, 24, 48, 72, and 96h) 2 cups were removed from each temperature to assess mortalities. As a control, snails were maintained at maintained at 15°C, comparable Riley Creek temperatures.

Time (h)	0°C	2°C	4°C	15°C
1	0.0	0.0	5.0	0.0
2	0.0	0.0	0.0	0.0
4	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	0.0
24	0.0	0.0	0.0	0.0
48	0.0	0.0	0.0	0.0
72	50.0	5.0	0.0	0.0
96	100.0	5.0	0.0	0.0

Table 13. Parameter estimates for the probit model of New Zealand mudsnails from Riley Creek tested in constant temperature trials during October 2005. No confidence intervals were estimated because of the large standard error (SE).

Parameter	Estimate	SE (10^4)	χ^2	<i>P</i>
Intercept	-104.82	63.2678	0.00	0.9999
Log ₁₀ (Time)	56.47	34.0638	0.00	0.9999

Table 14. Mean and (range) of target and observed temperatures ($^{\circ}\text{C}$) during constant and dynamic temperature trials of New Zealand mudsnails. $\Delta_{(\text{Target-Observed})}$ is the difference between the target and observed temperature mean for constant and dynamic trials and minimum and maximum for dynamic trials only. Constant trials were conducted during October 2005 and dynamic trials during January 2006.

Target Mean Temperature (Min.-Max)	Observed Mean Temperature (Min.-Max.)	$\Delta_{(\text{Target-Observed})}$
<i>Constant</i>		
0 $^{\circ}\text{C}$	-0.42 (-0.61 — -0.16)	-0.42
2 $^{\circ}\text{C}$	1.63 (1.60 — 2.03)	-0.37
4 $^{\circ}\text{C}$	2.47 (2.46 — 2.89)	-1.53
15 $^{\circ}\text{C}$	16.35 (14.47 — 17.14)	1.35
<i>Dynamic</i>		
0 $^{\circ}\text{C}$ (-2 — 2)	-0.27 (-1.51 — 0.73)	-0.27 (0.49 — -1.27)
2 $^{\circ}\text{C}$ (0 — 4)	1.36 (0.30 — 3.47)	-0.64 (0.30 — -.53)
4 $^{\circ}\text{C}$ (2 — 6)	3.38 (2.46 — 4.99)	-0.62 (0.46 — -1.01)
8 $^{\circ}\text{C}$	6.40 (6.22 — 8.63)	-1.60
15 $^{\circ}\text{C}$	12.43 (12.16 — 15.62)	-2.57

Table 15. Percent mortality observed in New Zealand mudsnails collected from Riley Creek (Riley) and Loving Creek (Loving) during January 2006 held in dynamic temperature trials. Snails (N=640 from each source population) were evenly distributed between 128 and cups and 16 cups from each population were placed into all temperature treatments ($0\pm 2^{\circ}\text{C}$, $2\pm 2^{\circ}\text{C}$, $4\pm 2^{\circ}\text{C}$, 8°C for Riley control, and 15°C for Loving). At each time intervals (1, 2, 4, 8, 24, 48, 72, and 96h) four cups (2 from each source population) were removed to assess mortality. For controls, only snails from the respective streams were placed into those control temperatures. Loving Creek snails were maintained at 8°C and Riley Creek snails were maintained at 15°C as controls.

Time (h)	$0\pm 2^{\circ}\text{C}$		$2\pm 2^{\circ}\text{C}$		$4\pm 2^{\circ}\text{C}$		Controls	
	Riley	Loving	Riley	Loving	Riley	Loving	Riley (8°C)	Loving (15°C)
1	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0
4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	5.0	5.0	0.0	0.0	0.0
24	0.0	20.0	0.0	0.0	0.0	0.0	0.0	15.0
48	66.7	30.0	0.0	0.0	0.0	0.0	0.0	0.0
72	100.0	100.0	0.0	0.0	0.0	0.0	0.0	5.0
96	100.0	100.0	5.0	0.0	0.0	0.0	0.0	20.0

Table 16. Parameter estimates for probit models for New Zealand mudsnails collected from Riley Creek and Loving Creek for dynamic temperature trials conducted during January 2006.

Parameter	Estimate	SE	χ^2	<i>P</i>
<u>Riley Creek</u>				
Intercept	-4.2463	0.6100	48.45	<0.0001
Log ₁₀ (Time)	2.8016	0.3787	54.73	<0.0001
<u>Loving Creek</u>				
Intercept	-8.5380	1.5526	30.24	<0.0001
Log ₁₀ (Time)	5.2420	0.9248	32.13	<0.0001

Table 17. Wald's Chi-square analysis for testing differences between parameter estimates for Riley and Loving Creek snail survival in dynamic temperature regimes during January 2006. Intercept estimates were not testable because of significant differences in the slope estimates.

Parameter	χ^2	<i>P</i>
Slope	5.8821	0.0153
Intercept	—	—

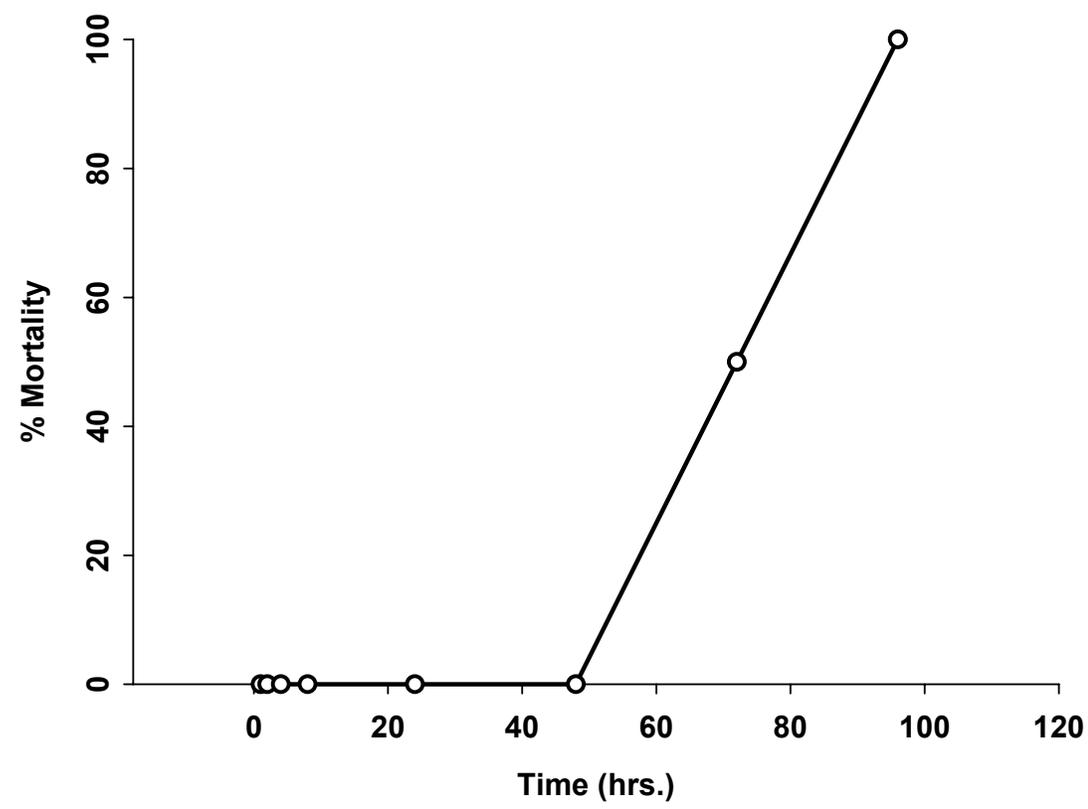


Figure 17. Percent mortality of New Zealand mudsnails exposed to constant 0°C at different time intervals during October 2005.

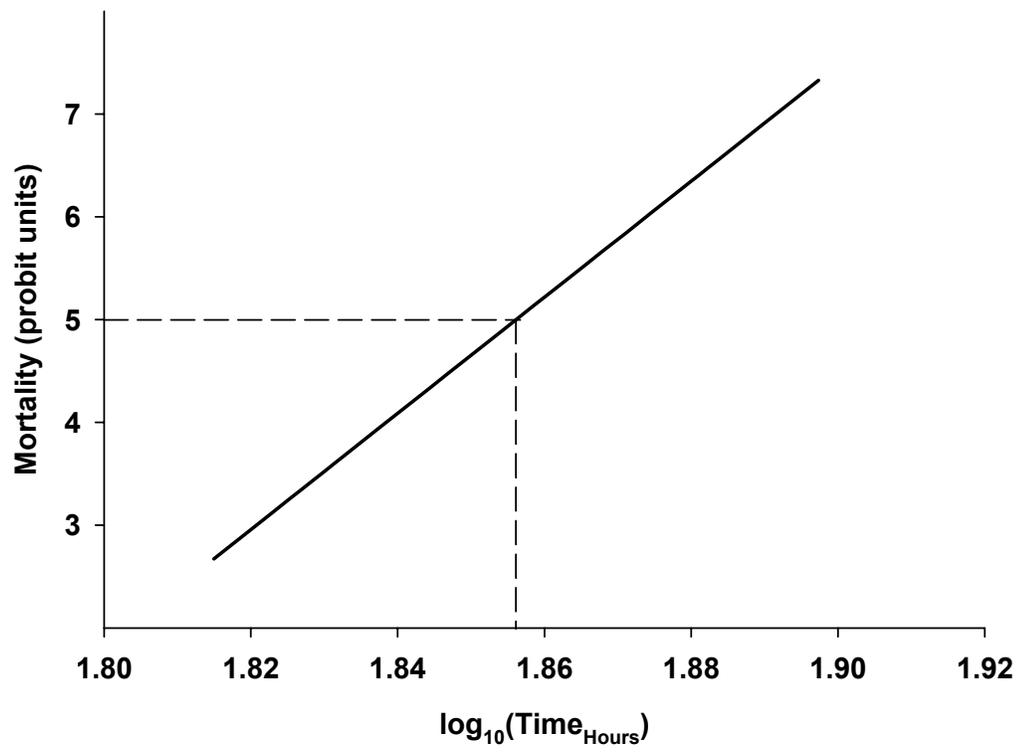


Figure 18. Probit model plots for mortality response of New Zealand mudsnails from Riley Creek exposed to constant 0°C in October 2005. Dashed lines represent calculated LT₅₀.

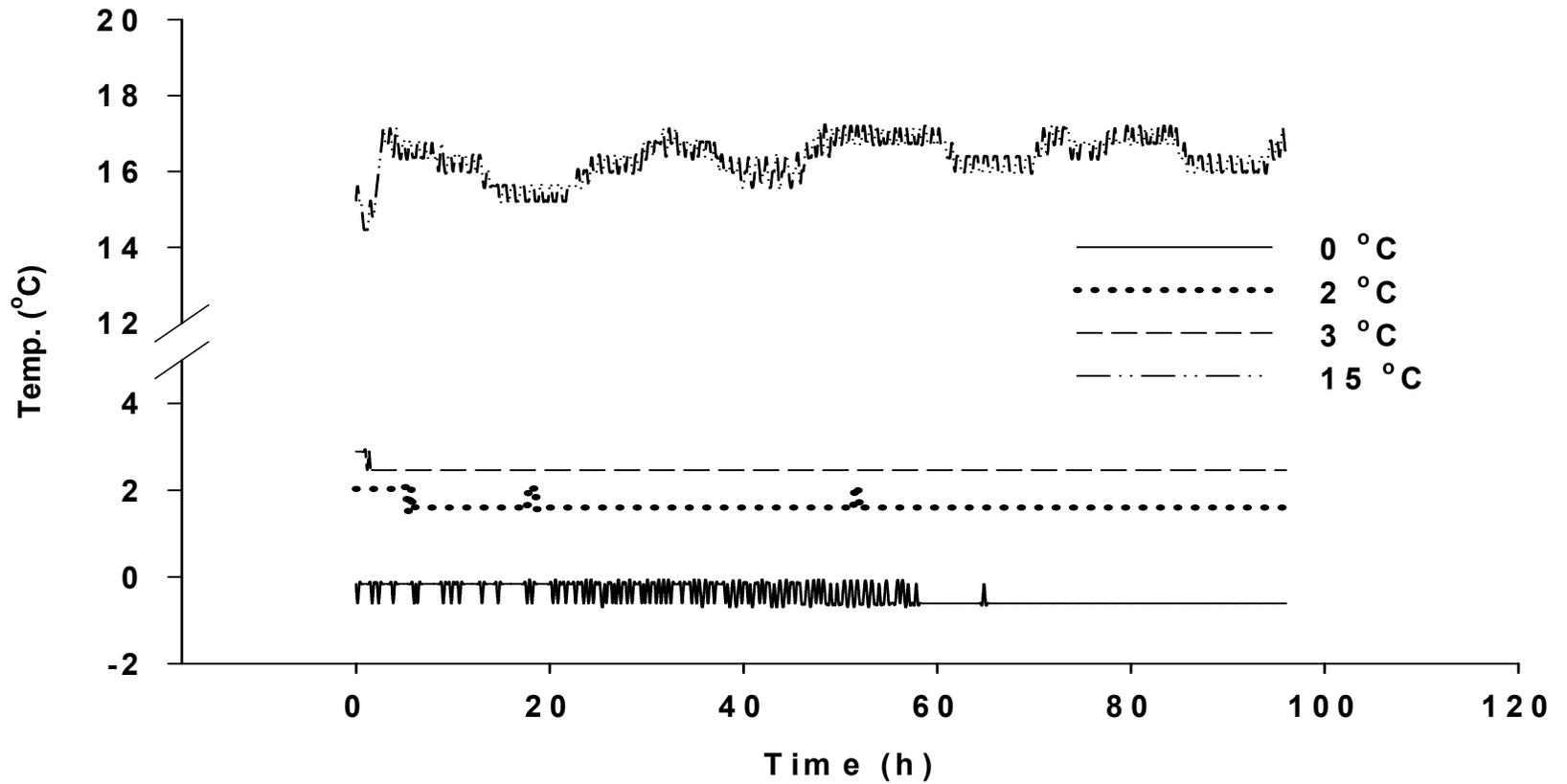


Figure 19. Temperatures in incubation chambers during constant temperature trials of New Zealand mudsnails in October 2005.

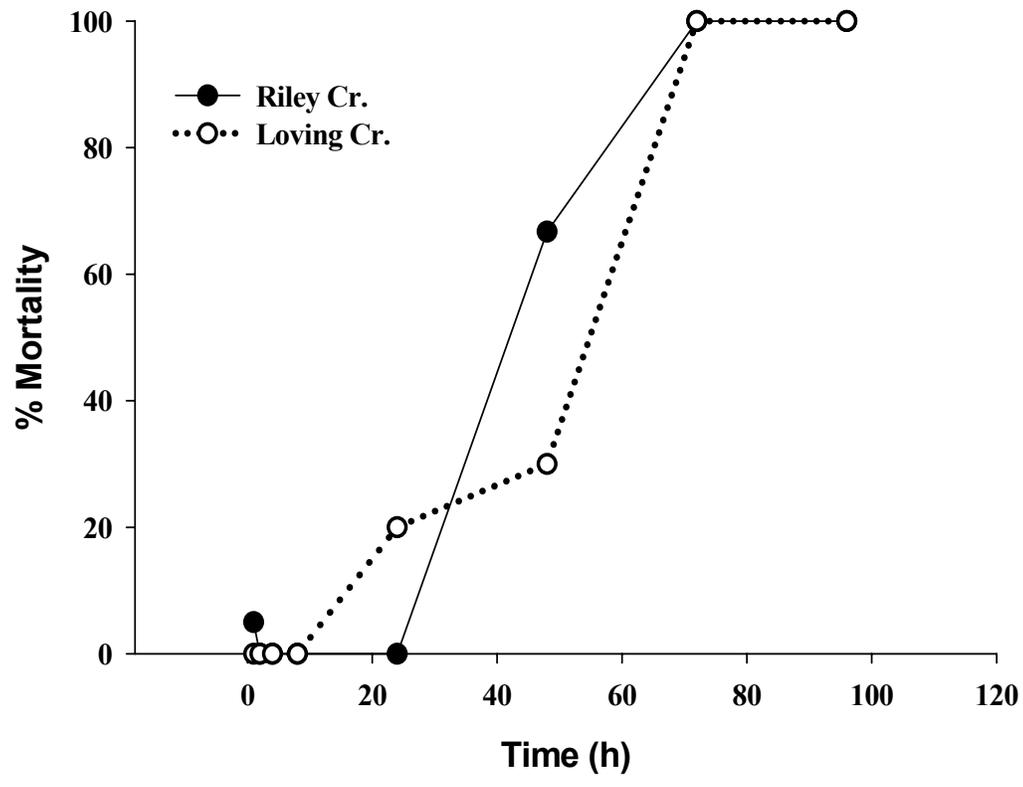


Figure 20. Percent mortality of New Zealand mudsnails from Riley Creek (closed circles) and Loving Creek (open circles) exposed to -2 to 2 °C in temperature trials during January 2006.

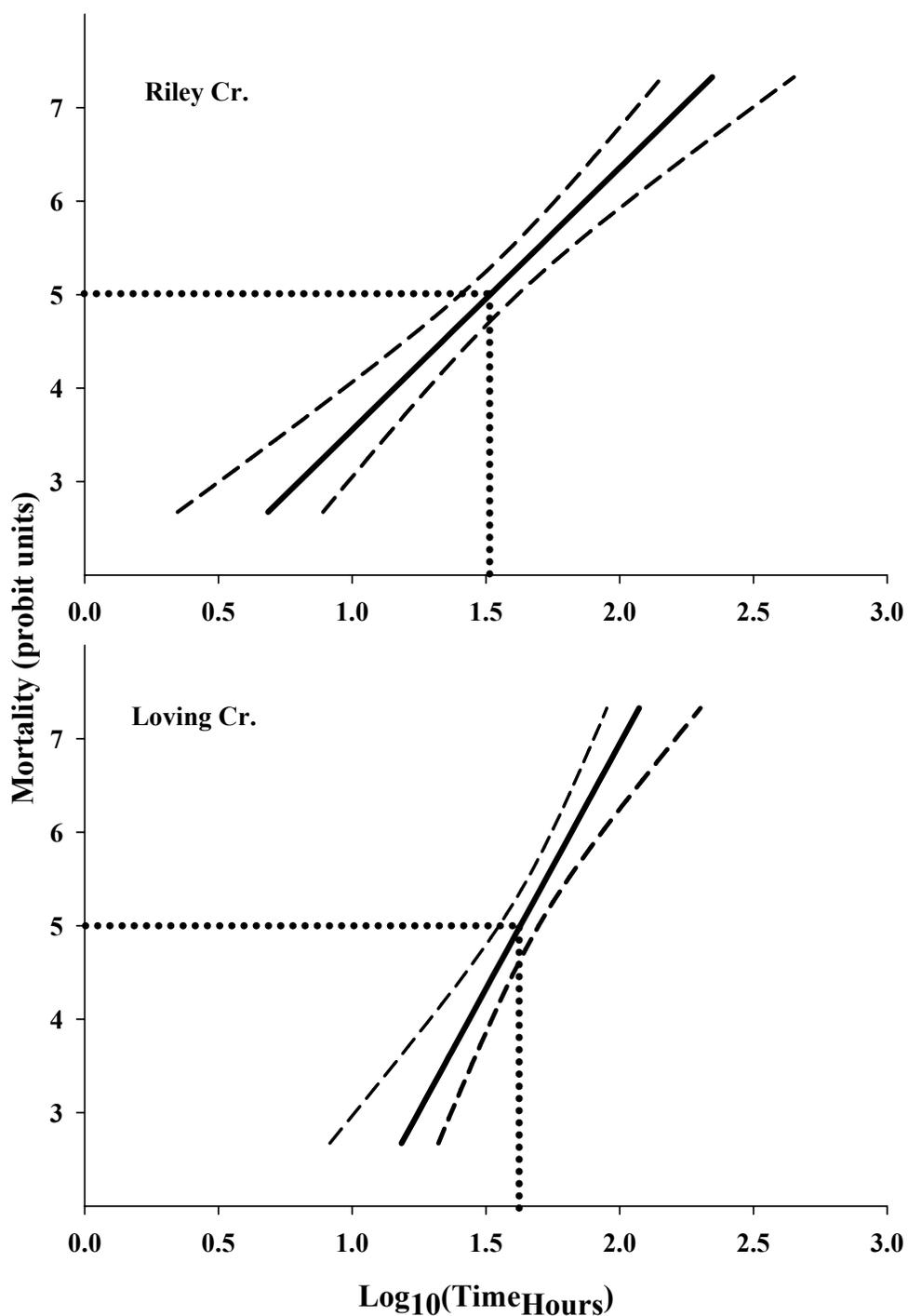


Figure 21. Probit model plots for mean (solid line) \pm 95% CI (dashed line) mortality response of New Zealand mudsnails from Riley Cr. and Loving Cr. exposed to fluctuating temperature of $0\pm 2^{\circ}\text{C}$ in January 2006. The slopes of the two lines are significantly different (Wald's $\chi^2 = 5.8821$, $P = 0.0153$). Dotted lines represent the calculated LT_{50} .

Control Temperatures

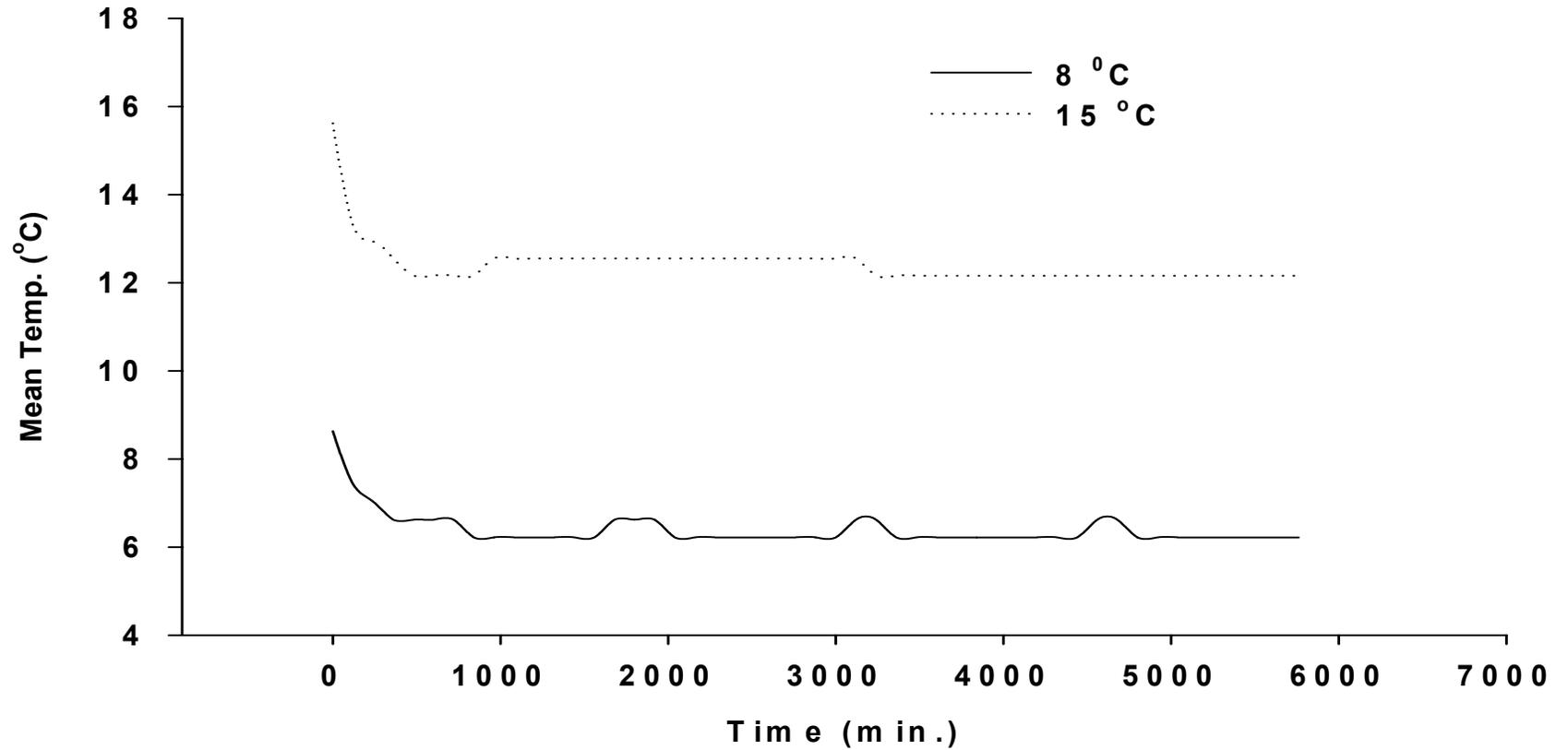


Figure 22. Temperature profiles for recovery/control treatments experienced by New Zealand mudsnails during January 2006, dynamic temperature tests.

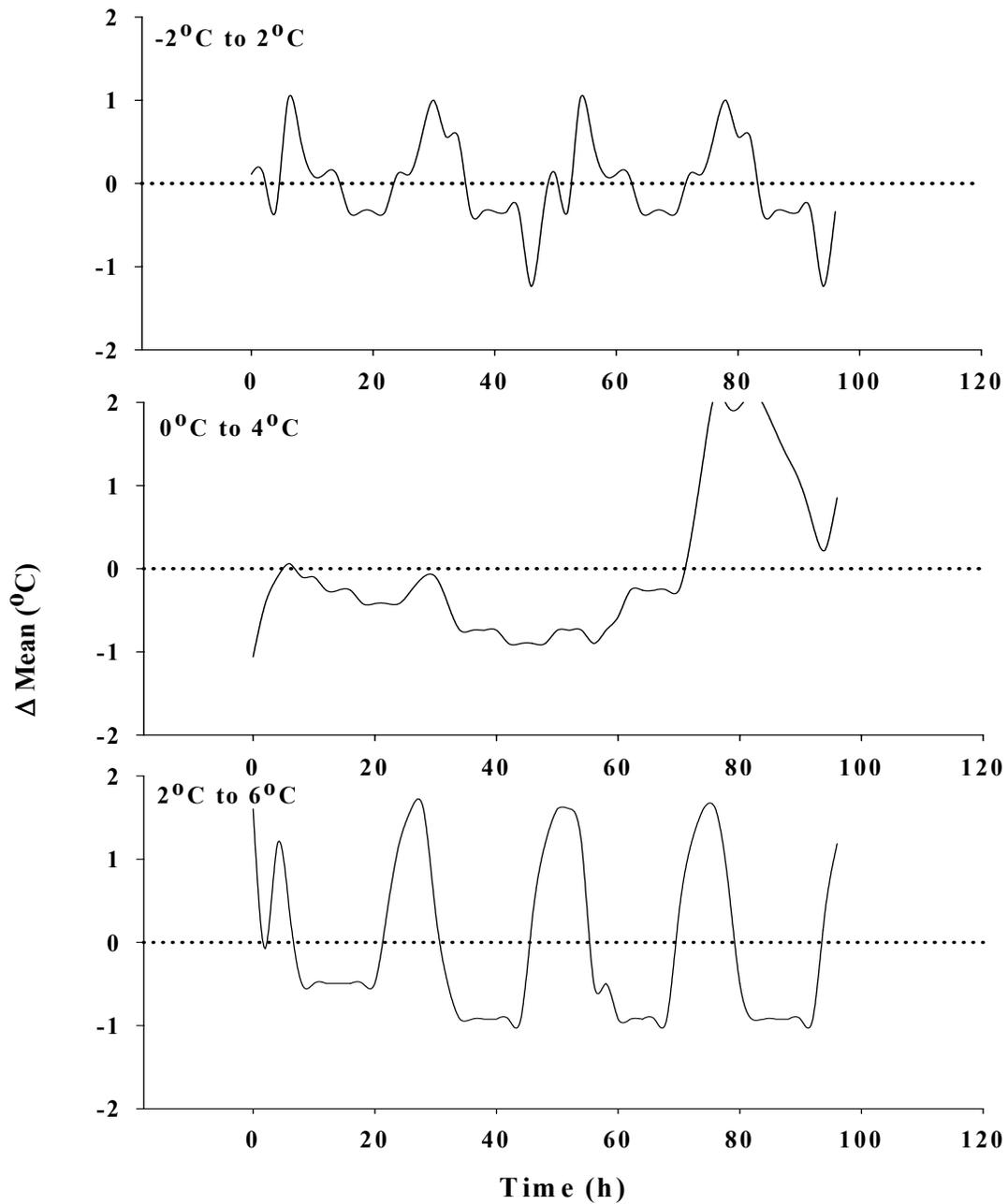


Figure 23. Temperature deviations from the mean temperature experienced by New Zealand mudsnails in three different treatment regime.

**CHAPTER III: POPULATION DYNAMICS OF NEW ZEALAND MUDSNAILS
POTAMOPYRGUS ANTIPODARUM IN SPRING FED STREAMS BELOW TWO
FISH HATCHERIES**

Abstract

Differences in densities, population dynamics, and brood sizes of New Zealand mudsnails *Potamopyrgus antipodarum* (Gray) (family Hydrobiidae) were examined in two spring fed streams in southern Idaho. Both study locations were downstream of fish hatcheries and had similar water quality parameters. However, one site, Riley Creek, had year round constant temperature and one, Loving Creek, had fluctuating temperatures. The environment with more stable temperature, Riley Creek, supported significantly higher densities of New Zealand mudsnails, but brood sizes relative to shell length in Loving Creek appear to be significantly greater than that of Riley Creek. Snails in Riley Creek matured at a smaller size (<3.00 mm) than snails from Loving Creek. Despite the large brood sizes in Loving Creek, the population does not appear to be expanding and future effects of trophic disruption from invasive New Zealand mudsnails will most likely not occur. These conclusions are consistent with laboratory findings that New Zealand mudsnails are limited by fluctuating cold water temperatures.

Introduction

Since their introduction in 1987, New Zealand mudsnails *Potamopyrgus antipodarum* (Gray) (family Hydrobiidae) have spread throughout the western United States and are found in waterways in nearly every western state (Bowler 1991, Cada 2004, Richards and Shinn 2004, Richards 2004, Richards et al. 2004a, Kerans et al. 2005). Populations of *P. antipodarum* can reach densities of 750,000/m² in streams and dominate carbon and nitrogen cycling (Hall et al. 2003) as well as secondary production (Hall et al. 2006). It is hypothesized that at these densities, populations of New Zealand mudsnails will disrupt ecosystem dynamics (Richards et al. 2001, Richards and Lester 2003, Cada 2004, Richards and Shinn 2004, Richards 2004, Richards et al. 2004b, Kerans et al. 2005). New Zealand mudsnails dominated the secondary production of invaded streams within the Greater Yellowstone Area (Hall et al. 2006); however, no significant effects on the individual or pooled family density or biomass of co-occurring Baetidae mayflies (*Baetis tricaudatus*, *Dipheter hageni*, and *Acerpenna pygmaea*) were detected in Darlinton Spring Ditch, Montana (Cada 2004).

Several factors can influence the density and dynamics of invertebrate populations including predator abundance (Lafontaine and McQueen 1991, Osman and Whitlatch 1996, Hamels et al. 2001, Bohn et al. 2004, Purcell and Decker 2005), food resources (Crenshaw et al. 2002), and habitat quality (Death 1989). In aquatic environments, food quality/quantity and water temperature are of primary importance (Precht 1973, Death 1989, Irons et al. 1993, Kerans et al. 2005). Many aquatic organisms lack the physiological capabilities to thermoregulate and must therefore use behavioral adaptations to ensure survival in suboptimal conditions (Precht 1973, Jankowsky 1973,

Irons et al. 1993). Behavioral thermoregulation is easily accomplished for motile aquatic organisms such as fish, which can readily migrate many kilometers in search of thermally optimal environments. However, for obligate aquatic invertebrates, migration may not be the most efficient behavioral response to thermal stressors especially during winter. Aquatic invertebrates that are not oviparous and that are not able to locate thermal refugia may be affected by extreme temperature regimes (Irons et al. 1993).

Since its initial observation in Silver Creek, Blaine County, Idaho in 2001, concerns have been raised about the impact that New Zealand mudsnails could have on the food web and how local hatchery management practices might promote its expansion (Richards and Lester 2003). In the intervening time, little to no expansion of the *P. antipodarum* populations have occurred within Silver Creek even in areas receiving hatchery effluents (James and Moffitt 2004). Hatchery wastewater often includes increased nitrogen and phosphorous, in addition to other suspended solids, that can influence the production of aquatic systems (Michael 2003). These added nutrients can increase the primary productivity of the receiving system, resulting in additional food resources for primary consumers like the New Zealand mudsnail, which tend to thrive in streams with high productivity (Kerans et al. 2005). Although New Zealand mudsnails appear well established within the Silver Creek drainage (Richards and Lester 2003, James and Moffitt 2004), they have not reached high densities, or expanded throughout the drainage to the extent that is typical for this invasive species (Bowler 1991, Richards et al. 2004b).

Research on the life history and population dynamics of New Zealand mudsnails is increasing our ability to understand mudsnail invasions and ecological impacts

(Richards and Lester 2000, Richards et al. 2001, Cada 2004, Richards and Shinn 2004, Richards 2004, Kerans et al. 2005). Conflicting conclusions have arisen, though, as to the potential factors limiting New Zealand mudsnail distribution in these streams. Most notably, the debate centers around two main factors: temperature and food resources. The focus of the present research was a comparative examination of New Zealand mudsnail population dynamics in two springs-fed stream systems receiving effluent from fish hatchery facilities. The objectives were 1) to determine whether densities of New Zealand mudsnails differed between sites during winter and summer and 2) to assess how the size-class distribution and brood sizes of these two sites may influence any detectable differences in densities.

Methods

Field Sites

The areas below both Hagerman National Fish Hatchery on Riley Creek, Gooding County (Figure 24) and Hayspur State Fish Hatchery on Loving/Butte Creek, Blaine County, Idaho (Figure 25) receive hatchery wastewater effluents. In addition, hatchery production water sources are ground water springs or wells, which maintain fairly constant temperatures. However, the temperature regimes downstream of Hayspur State Fish Hatchery are more variable (James and Moffitt 2004) than below Hagerman National Fish Hatchery (HNFH 2004) and may affect populations of New Zealand mudsnails differently.

The United States Fish and Wildlife Service operates Hagerman National Fish Hatchery (HNFH). Water is supplied to HNFH by several springs surfacing near the hatchery, which then eventually flow into Riley Creek. The water source maintains a

fairly constant temperature of ~15°C year round at 1,892 L/s. As part of the Lower Snake River Compensation Plan, HNFH rears ~1.2 million spring run steelhead trout *Oncorhynchus mykiss* as mitigation for the four lower Snake River Hydro-electric facilities. In addition to rearing steelhead smolts, HNFH also rears catchable rainbow trout *O. mykiss* (~130,000 annually) for Dworshak Reservoir mitigation program.

Of the ~1,892 L/s supplied from the surrounding springs, the hatchery's water needs for steelhead production vary from about 566 L/s during the summer to 1,892 L/s during the winter. Before entering Riley Creek, hatchery production waste water passes through two concrete settling ponds (1,900 m³ each) before being discharged into Riley Creek.

Hayspur State Fish Hatchery (Loving/Butte Creek) — Hayspur State Fish Hatchery (HSFH) is operated by the Idaho Department of Fish and Game as a broodstock facility supplying Hayspur strain and Kamloops strain rainbow trout, along with westslope cutthroat trout *O. clarki* broodstocks. As a broodstock facility, fish are kept year round on station with little annual fluctuation in the 9,000 kg of brood fish present. During the summer months, HSFH has higher production levels, as it holds catchable rainbow trout from other hatcheries for redistribution into the Little Wood and Big Wood River drainages. Approximately 20,500 kg of catchable rainbow trout are distributed from HSFS between April and September.

Water is supplied to HSFH via two sources: three artesian pumped wells and one covered spring. Ground water from these sources maintains temperatures of approximately 10-12°C in the hatchery and together supply 226 L/s of water for

production purposes. Abandoned brood ponds, located in the Butte Creek channel are utilized as settling ponds for wastewater.

Field Collections

Three 100 m sampling areas were established downstream from the outflows of both HSFH and HNFH. The area closest to each hatchery outflow was located approximately 80 m downstream of the outflow and each of the areas was spatially separated from the next by 100 m. Nine sites within each area were randomly selected using a random points generator (Minnesota Department of Natural Resources Sampling Generator Extension) and corresponding Universal Transverse Mercator (NAD-27) coordinates identified within each area in ArcView 3.2. Each sampling point was constrained with a 1 m diameter sampling area and a 5 m buffer zone, ensuring that no two points were located within less than 6 m of each other in order to minimize the potential for disturbing one site while sampling at another. Each point was located in the field using both a Garmin *eTrex* GPS unit and a hardcopy of maps from the digital projections in ArcView.

A modified Hess sampler was used to collect New Zealand mudsnails at each site. The Hess sampler (sampling area=0.086 m², 500 µm mesh) was modified with a 91.4 cm long, 35.6 cm diameter tube of sheet metal. The tube was further modified with a 35.6 cm to 30.5 cm reducer on the bottom that allowed it to be inserted into the top of the Hess sampler when water levels were higher than the Hess sampler itself. A stable fork, with its width and tongs trimmed to approximately 20 cm, was used to manipulate the substrate confined inside of the modified Hess sampler at each site. Substrates were manipulated to a depth of 8-10 cm by vigorously raking them in a crosshatched pattern.

Vegetation was collected in the net and shaken vigorously to remove as many invertebrates as possible. The samples were then passed through a series of three sieves (2 mm, 1 mm, and 500 μm) to remove larger debris. After sieving, the residue on both the 1 mm and 500 μm sieve were retained and transferred to a labeled plastic jar and preserved in 10% formalin solution.

Directly after sampling, water temperature ($^{\circ}\text{C}$), dissolved oxygen (mg/L), conductivity (mS/s), total dissolved solids (TDS), and pH were measured using a YSI Multi-probe meter. Water velocity was also determined using a Marsh-McBirney Flow-Mate® Model 2000 at each site. Water temperature was monitored within each sampling area with HOBO8 Data loggers.

Lab Processing

Field samples were sub-sampled in the lab on a sectioned sorting tray with 32 numbered and equally sized 4 x 5 cm cells. The 32-cells were contained by 4 plexiglass retaining walls ~ 10 cm high. Individual samples were placed into the center of the sub-sampling tray and standard tap water was added to make the sample more fluid. The samples were then swirled with a metal spatula to achieve a heterogeneous distribution of all organisms and then four of the 32 cells were selected randomly for removal. The selected portions of each sub-sample were removed and placed into a small glass jar and filled with 70% ETOH until they were finally processed.

These selected sub-samples were examined and New Zealand mudsnails were removed and counted. One-third of the sub-samples from each stream was recounted for quality assurance. If the difference between the counts was greater than 10%, the sample was resorted.

Size-Class Distribution

Snails were separated into size categories large (≥ 2.5 mm), medium (> 1.5 mm and < 2.5 mm), and small (≤ 1.5 mm) based on shell lengths, using a series of three sieves: 16 ASTM (large), 35 ASTM (medium), and 270 ASTM (small). After placing snails on the sieves, the sieves were moved into a bucket with enough water to come within 5 cm of the lip of the top sieve. The sieves were then rapidly pulled out of the water and shaken vigorously to allow the snails to be sorted out on the sieve screens. This process was repeated 15-20 times to ensure that snails separated out adequately.

The contents of each sieve were placed on a paper-towel and allowed to air dry for ~5 minutes. Snails were then placed in a weighing boat and weighed (0.001g; or 0.0001g if the sample weight was less than 0.01g). After the preserved wet weight was recorded, approximately 10% of the snails were counted and the proportion of snails in each size class estimated based on sample weights.

Brood Sizes

At least 30 snails ≥ 2.5 mm from each sample were dissected to determine the number of embryos per snail. Snails ≥ 2.0 mm were examined, but only snails ≥ 2.5 mm were sexually mature and contained embryos. Dissections were done by slicing the snail in half directly behind the second whirl from the aperture. The remaining portion containing the head and operculum was further dissected from the shell until all that remained was the periostracum. Once isolated, the brood pouch was easily accessible and embryos removed and enumerated.

Data Analysis

Because the density data were not normal the data were ranked and analyzed using a mixed-effects general linear model: $y = \text{stream} + \text{season} + \text{substrate} + \text{error}$. Substrate was considered a random effect because sampling sites were selected randomly within each polygon and because the habitat structure of Loving Creek changes between winter and summer. When samples were obtained from the same locations over the seasons, it was unlikely to be the same habitat type (i.e. gravel, sediment, or vegetation) that was present during sampling events. All two and three-way interactions were included in the model. A post-hoc multiple comparisons test was performed after model fitting on the highest order effects that were significant. Tukey's pairwise comparison adjustment was utilized for these multiple comparisons in order to protect against Type I error.

The potential differences between size-classes were analyzed using a categorical data modeling procedure. The modeling procedure used a maximum-likelihood analysis represented with a two-dimensional contingency table. A log-linear model analysis was used to test for differences in the proportion of snails within each size class between streams, season, and substrate. In the event that a higher order interaction was non-significant at $\alpha = 0.05$, a reduced model was fit that did not include the non-significant interaction. The process was repeated until no further interaction terms were non-significant.

Simple linear regression was used to model the response of brood sizes. The model, $y = \text{shell-length} + \text{error}$, where y is the number of embryos in the brood, was fit to the data for each season and stream. To test for differences in slopes of these models, we

modeled the data by hatchery using the analysis of covariance model $y = \text{season} + \text{shell_length} + \text{error}$, where y is the number of embryos in a brood and shell size was considered the covariate factor. The slopes were considered significantly different if the interaction ($\text{season} * \text{shell_length}$) was significant ($P \leq 0.05$). Tukey's multiple comparison test was used after fitting the model to assess which slopes were significantly different from each other. All data analyses were conducted using the SAS software (SAS Institute Inc. 2003)

Results

New Zealand Mudsnaill Densities

Mixed model analysis of ranked mudsnail densities identified the substrate main effect and the interaction of $\text{stream} * \text{season}$ as significant ($P < 0.05$; Table 18). Ranked densities of mudsnails were higher in the Riley Creek drainage compared to Loving Creek across all sampling periods ($P < 0.05$; Table 19; Figures 26 and 27). Both gravel and vegetation had significantly greater ranked densities of New Zealand mudsnails than sediment ($P < 0.05$; Table 20; Figure 28).

During the winter 2004-2005 sampling period, the mean rank score of New Zealand mudsnails was higher for Riley Creek than for Loving Creek ($P < 0.01$; Table 19; Figure 27). Snails were most likely to be found in vegetation in both systems while presence on gravel was also high relative to sediment substrates during this sampling period (Figure 26). Average ranks for Riley Creek were 133.8 (110,207 snails/m²) and 128.5 (54,271 snails/m²) in vegetation and gravel, respectively (Figure 26). In Loving Creek the average ranks were 69.7 (5,281 snails/m²) and 57.3 (1,600 snails/m²) in

vegetation and gravel, respectively (Figure 26). Sediment substrate had the fewest New Zealand mudsnails in both Loving Creek and Riley Creek (Figure 26).

During the summer of 2005, New Zealand mudsnail densities were significantly higher in Riley Creek than in Loving Creek, ($P < 0.05$; Table 19; Figure 27). However, summer densities in Riley Creek were lower than those observed in winter 2004-2005 in the same stream ($P = 0.0314$; Table 19). Densities of snails in Loving Creek were comparable between summer 2005 and winter 2004-2005 ($P = 0.8596$; Table 19). In Riley Creek, New Zealand mudsnails achieved similar densities on all three substrate types (Figure 26). In Loving Creek, New Zealand mudsnails were most abundant on gravel substrates with vegetation and sediment having lower, although similar abundances (Figure 26).

During the final sampling period (Winter 2005-2006), New Zealand mudsnail densities were higher in Riley Creek and increased from levels observed during the summer of 2005 ($P = 0.0496$; Table 19). Mudsnails were most abundant on vegetation and gravel substrates during this sampling period in Riley Creek (Figure 26). Densities in Loving Creek during the winter 2005-2006 sampling period were the lowest of all observed (Figure 27), however they were not significantly different from either the winter 2004-2005 ($P = 0.8596$) or the summer 2005 ($P = 0.4727$) samplings events in Loving Creek (Table 19). Density of snails in Loving Creek sampled in sediments during the winter 2005-2006 were similar to densities observed during other collection times at that location (Figure 26). Densities in vegetation were comparable to levels observed during

the previous summer, but winter samples in gravel substrate taken in the winter 2005-2006 season were almost 50% lower (Figure 26).

Water physico-chemical parameters varied between streams, with Loving Creek generally having higher levels of conductivity (mS/s), total dissolved solids (TDS; g/L) and salinity (ppt; Table 21). These same parameters also varied across seasons with summer levels generally greater than winter levels (Table 21). Dissolved oxygen (mg/L) and pH were fairly consistent between streams and across seasons (Table 21). Water temperatures measured during sampling events varied between streams during all sampling periods and temperatures in Loving Creek also varied across seasons (Table 21). However, year round temperature monitoring showed even greater variation in Loving Creek both diurnally and seasonally (Figure 29) than was evident from temperatures recorded during sampling.

Size-Class Distribution

Log-linear categorical modeling of the size class distribution resulted in a significant three-way interaction of Sample_Period*Substrate*Size_Class for both Loving and Riley Creek data sets ($P < 0.05$; Table 22). Because of the low densities of New Zealand mudsnails in Loving Creek, some data points were highly influential on the results and *a priori* hypothesis were not tested with these data. For instance, during the winter 2004-2005 sampling period, ~80% of the population were small (<1.5 mm) snails (Figure 30). This variation was from one sample with over 300 small snails while the next highest count in any size class was only 35 snails. Therefore, only general

observations of the Loving Creek data will be made here, while linear contrasts of the Riley Creek data will be used to test *a priori* hypotheses.

Nearly all snails from the winter 2004-2005 sampling in Loving Creek were small snails while medium and large snails constituted 4.5% and 7.3%, respectively (Figure 30). Small snails were most abundant in vegetative substrates, followed by gravel and sediment (Figure 30). Although snails were found on all substrate types, no large (>2.5 mm) snails were collected from the soft sedimentary substrate during this sampling period. There were nearly equal proportions of large and small snails from Loving Creek during the summer 2005 while medium snails composed 20% of the population (Figure 30). Of all available substrates, snails were most prevalent on gravel substrates during the summer 2005 sampling season (Figure 30). During the winter 2005-2006 sampling period, the size class distribution was the inverse of that observed for Loving Creek during the winter 2004-2005 sampling. Large snails comprised the majority of the samples while small snails were least abundant.

During the initial sampling period of the winter 2004-2005 in Riley Creek, a significantly large proportion of the snails collected were small snails across all substrate types ($P < 0.05$; Table 23). Vegetative substrates had the largest proportion of snails in all size classes during this sampling period (Figure 31). Approximately 30% of snails collected were from gravel substrate with the majority being small snails (Figure 31). Sediment appeared to be the least inhabited substrate sampled with ~20% of the population occurring within that substrate (Figure 31).

Large snails were the dominant size class (50%) of snails sampled from Riley Creek during the summer of 2005 with 38% medium and 12% small snails (Figure 31).

Snails from all size classes were most prevalent on vegetative substrate in Riley Creek followed by gravel and sediment substrates, respectively (Figure 31). Large snails made up a significantly larger portion of the samples in vegetation (Table 23). In gravel substrates there were no detectable differences between the proportion of medium and small snails. Small snails were the most abundant size class found on sediment substrates (Table 23).

In the winter 2005-2006 samples from Riley Creek, small snails constituted more than half of the snails collected (Figure 31). Almost 40% of all small snails were observed in vegetative substrate, which was significantly greater than the proportions of medium and large snails within that substrate ($P < 0.001$; Table 23). Within the sediment substrate, small snails again made up the largest portion of snails in this substrate (Table 23). Approximately 40% of the snails collected were observed on gravel substrate with small snails constituting the greatest portion and large snails the smallest portion (Figure 31).

A distinct seasonal pattern appears evident in the population dynamics of New Zealand mudsnails in Riley Creek. During the summer 2005 sampling, small snails were the least abundant size class followed by medium and large snails, which were most prolific. This size-class structure, however, is influenced extensively by the proportion of snails detected on vegetative substrates (~90%; Figure 31). During both winter sampling periods, there was a complete reversal of this structure. Small snails were most prevalent in winter while large snails were least abundant. The only detectable difference between large snails collected in either winter sampling period was in snails collected from vegetation (Table 23).

Snail and Brood Size Relationship

Regression modeling to determine the number of embryos brooded by snail shell length produced variable results between streams and season. All models had positive slopes, but regression coefficients were not consistent across all models. This model fit snails from Loving Creek better than Riley Creek. The model explained between 12-52% of the variation in Loving Creek but only 5-18% of the variability in Riley Creek (Table 24).

During the winter of 2004-2005 sampling period, the parameter estimate for the slopes of the regression models for Loving and Riley Creek were not significantly different ($P=0.1776$; Table 25; Figure 32). In the summer of 2005 and winter of 2005-2006, mature snails from Loving Creek had significantly more embryos per millimeter shell length than Riley Creek snails ($P<0.0001$, Table 25; Figures 33 and 34). Embryos were found in snails from Riley Creek as small as 2.5 mm, while no snails less than 3.0 mm in Loving Creek had embryos during all three sampling periods. During the summer 2005 sampling period, snails from Loving Creek had the greatest number of embryos per shell length of all streams in any given sampling period with a slope of 3.19 (Table 24). This response was significantly greater than the estimate for Riley Creek snails during the same sampling period ($P<0.0001$; Table 25) or for Loving Creek in either of the winter sampling periods ($P<0.0001$; Table 26). In the winter 2005-2006 sampling period, reproductive potential fell from the levels observed during summer 2005. Loving Creek again had a greater parameter estimate compared with Riley Creek and this difference was significant ($P=0.0006$; Table 25). Although reproductive levels had fallen during this winter sampling, the estimate for Riley Creek was the only one that had dropped to

levels observed during the winter of 2004-2005 (Table 24). The estimate for Loving Creek during the winter 2005-2006 was significantly greater than the estimate for Winter 2004-2005.

Discussion

New Zealand mudsnail densities were strikingly different between Riley Creek and Loving Creek. Densities of New Zealand mudsnails in Riley Creek were similar to most other densities reported at locations in the western United States (Richards et al. 2001, Richards 2004, Richards and Shinn 2004, Kerans et al. 2005) while only Cada (2004) reported densities that were similar to those observed in Loving Creek. Cada (2004) reported densities of New Zealand mudsnails from Darlinton Spring Ditch, Montana ranging from zero snails/m² in a low density reach during November 2002 to 24,750 snails/m² in a high density reach during July 2002. Densities of New Zealand mudsnails in Loving Creek were also similar to those reported for locations in their native range by Scott et al. (1994) and lower than densities in Pupa Springs, New Zealand (Michaelis 1977).

In the time since New Zealand mudsnails were first detected in the Silver Creek drainage, there has been relatively little expansion or growth of the population (Richards and Lester 2003, James and Moffitt 2004, Chapter I, this thesis), which seems surprising for a species that generally expands rapidly in waterways after introduction (Bowler 1991). Some factor, or a suite of factors, is likely limiting the population. Several factors have been described that affect population abundance, distribution, and dynamics. These factors include hydrological processes (Death 2002), predator abundance (Lodge et al. 1987, Lafontaine and McQueen 1991), habitat stability (Death 1996a), water chemistry

(Russel-Hunter 1978; Lodge et al. 1987), and macrophyte presence (Lodge et al. 1987). Two other common limiting factors for aquatic invertebrates are temperature (Precht 1973, Vannote and Sweeney 1980, Saunders 1980, Sweeney and Vannote 1986) and food resources (Sweeney and Vannote 1986, Crenshaw et al. 2002) especially for New Zealand mudsnails (Richards et al. 2001, Cada 2004, Cada 2004, Kerans et al. 2005).

While New Zealand mudsnail densities generally peak during summer months (Cada 2004, Richards 2004, Hall et al. 2006), the maximum density of New Zealand mudsnails in Riley Creek occurred during the winter, coinciding with peak fish production at Hagerman National Fish Hatchery. Although Hagerman National Fish Hatchery has off-line settling ponds to reduce nutrient inputs into Riley Creek, effluents from fish production facilities can provide additional nutrients for primary production (Selong and Helfrich 1998) which likely helps support high densities of New Zealand mudsnails. Production at HNFH ranged from 1,944 kg of fish/cms in May 2005 to 131,577 kg of fish/cms in March 2005. This same trend in New Zealand mudsnail densities was not observed in Loving Creek, below Hayspur State Fish Hatchery when fish production doubled from a base level of 9,000kg to ~18,000kg of fish (39,729 kg of fish/cms of flow to 79,458 kg of fish/ cms of flow) between April and September (B. Dredge, HSFH Manager, personal communication). Hayspur State Fish Hatchery effluents are also diverted into Loving Creek where vacant brood ponds act as settling ponds, and a greater proportion of the resulting nutrient-enriched effluents are probably entering directly into Loving Creek and into the food-web.

In addition to increased fish production at Hayspur State Fish Hatchery during the summer, there is an increase in water temperatures that should provide an even more

suitable environment for New Zealand mudsnail growth. Growth rates of New Zealand mudsnails were maximized at temperatures of 20°C to 22°C in a laboratory with a significant increase in growth rates of snails reared at 15°C (~0.0090mm/day) compared with snails reared at 6°C (0.0035mm/day) (Richards 2004). Average monthly temperatures in Loving Creek were 13.1°C, 14.6°C, and 13.7°C in June, July and August 2005, respectively, with daily highs reaching 16°C. These temperatures are much higher than winter averages of 6 to 8°C (December 2005 and January 2006, respectively) in the same reach (Figure 34).

Taken together, both nutrient and temperature increases should promote NZMS population growth during the summer months, however such increases were not observed during this research. Brood sizes in Loving Creek, as measured by embryo counts per mm of shell length, are higher compared those observed in Riley Creek, but this difference does not appear to result in increased population abundance in Loving Creek. It is possible that our sampling intervals were too broad (December 2004, 2005, and July 2005) to detect differences in densities of New Zealand mudsnails in Loving and therefore future efforts should incorporate more temporal sampling intensity.

Physicochemical parameters have been used as surrogates for stream nutrient and productivity levels (Prepas 1983), including conductivity and total dissolved solids (TDS). At all sampling times, Loving Creek had greater responses for both conductivity and TDS. Nitrogen and phosphorous, known to be limiting factors in primary production of lentic and lotic systems (Kalff 2002), have been collected in these streams by various agencies and were also collected during both winter sampling periods of the present work (Appendix A). Phosphorous appears to have the greatest seasonal variation in both

stream systems while nitrogen is fairly consistent, although it was quite high in Loving Creek when assessed during this project (1.4 mg/L). Differences in these nutrient levels could be related to differences in fish production cycles at each hatchery, but also to differences in nutrient cycling by primary producers in each stream. If phosphorous is the major limiting factor for primary production in Loving and Riley Creek, it could explain the difference between population dynamics of New Zealand mudsnails.

However, New Zealand mudsnails are known to limit periphyton accrual even in nutrient enriched streams (Hill et al. 1992). The samples collected in this study were grab samples, and perhaps a flow integrated diel sample would have provided better validation of these trends. Further understanding on the dynamics of primary production in each stream and nutrient cycling within the stream will be useful in discerning its affect on New Zealand mudsnail populations.

During this study, mats of vegetation were observed sloughing off and drifting downstream in the Silver Creek drainage. Other researchers have noted this event occurring (Francis and Bjornn 1979). Disturbance regimes have been recognized as influencing the structure and distribution of invertebrates in aquatic systems (White and Pickett 1985, Death and Winterbourn 1995, Death 1996b, Holomuzki and Biggs 2000, Death 2002) and losses of submerged macrophytes can reduce the local densities of various pulmonate and prosobranch snails inhabiting them (Lodge et al. 1987).

Macrophyte beds are known to maintain temperatures 2-5°C warmer than the open flowing channel (Saunders 1980) and their reduction would decrease the available thermal refugia for New Zealand mudsnails in Loving Creek. During the winter in Loving Creek a larger proportion of New Zealand mudsnails were detected on the

remaining vegetative substrates, while during the summer the greatest proportion of New Zealand mudsnails were detected on gravel substrate. The combined effect of the loss of macrophyte beds and decreased temperatures together during the winter can result in multiple disturbance events which may overall impact New Zealand mudsnail populations. Diel fluctuation in oxygen that likely occurs in the macrophyte beds during summer conditions could also affect the survival of snails.

Kerans et al. (2005) proposed that chemical water parameters and algal production, rather than temperature, are more important factors limiting New Zealand mudsnails, especially in the Madison River. The results of my study suggest that water temperature plays a significant role in limiting the explosive nature of New Zealand mudsnails as well. Recent studies by Hall et al. (2006) support a temperature association with and density. They observed lower and less seasonal variability in the abundance of New Zealand mudsnails in the colder Gibbon River, Greater Yellowstone Area, when compared with warmer streams in the same area. In Darlinton Spring Ditch, Montana, Cada (2004) reported New Zealand mudsnail densities similar to those of Loving Creek and similar annual temperature regimes (range = 4°C in February to 23°C in August). The multiple effects of variable and seasonally cooler temperatures, along with macrophyte sloughing, has probably limited the ability of New Zealand mudsnails to become extremely dense and prolific in the Silver Creek drainage.

Most authors concludes that 3.00 mm is the minimum size that New Zealand mudsnails begin sexual maturation (Winterbourn 1970a, Winterbourn 1970b, Richards and Lester 2000, Richards 2004). However, in my study embryos were common in snails less than 3.0 mm shell length from Riley Creek and maximum shell length rarely

exceeded 4.0mm. Within the invertebrate community, early maturation is often observed in populations that are at extremely high densities (Van Buskirk 1993, Lee and Ban 1999). The results for the Riley Creek population may indicate that those snails are responding to density dependent factors as a result of high densities. While it has been noted that New Zealand mudsnails reared at higher densities had a lower growth rates (Richards 2004), it has not been determined what effect this may have on overall maximum size or early maturation. In Loving Creek, embryos were only observed in a single snail smaller than 3.0 mm in shell length during the summer of 2005, and maximum shell length consistently approached 5.00 mm. It was suspected that warm, constant water temperatures and high densities were major factors in the early maturation of New Zealand mudsnails in Riley Creek. However, (Cada 2004) reported the presence of embryos in snails less than 3.0 mm from Darlinton Spring Ditch, Montana where maximum densities of New Zealand mudsnails averaged $24,750 \text{ m}^{-2}$ during July, while stream temperatures ranged from a high of 21°C August to a low of 4°C in February . Intraspecific competition may be a plausible explanation for early maturation of New Zealand mudsnails in Riley Creek, yet it does not appear to explain the presence of early maturation in Darlinton Spring Ditch. However, other factors could be driving early maturation in a select few areas including genetic differences. Recently, a second clonal variation has been documented to occur in the Hagerman Valley, Idaho near the Riley Creek population. The ability of this snail to reach maturation at a smaller size in two streams with strikingly different physical characteristics begs further investigation.

While hatchery management practices can influence downstream food-web dynamics (Michael 2003), anthropogenic inputs into Loving Creek, mostly from Hayspur

State Fish hatchery, do not appear to be enhancing New Zealand populations. In fact, density independent factors such as temperature regimes and habitat loss through macrophyte bed die-offs are likely affecting the abundance and dynamics of New Zealand mudsnails in Loving Creek. The decreased maximum size of New Zealand mudsnails in Riley Creek may be a result of density dependent factors and the resulting intraspecific competition and inputs from Hagerman National Fish Hatchery effluents may be promoting New Zealand mudsnail production especially during the wintertime.

Other factors that were not considered during this research could be influencing these two populations. While conductivity was utilized as a proxy for stream productivity, it does not necessarily give an accurate representation for true primary production and therefore differences may actually exist between both streams in primary production. Considerations must be made, though, to determine what factors may affect primary production in these streams including nutrient loads, abundance and diversity of primary consumers, as well as the effects of temperature and light on periphyton growth. Likewise, differences in predator abundance may influence differences in population dynamics. Both fish and waterfowl are known to prey on New Zealand mudsnails and are common in both streams, but to what extent they utilize New Zealand mudsnails in either stream is unknown. Leaches are also prevalent in Riley and Loving Creek and could be predated on New Zealand mudsnails.

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Table 18. Summary of mixed model analysis of variance (ANOVA) testing the differences between mean ranked density (snail·m⁻²) of NZMS between streams (Riley Creek or Loving Creek), among seasons (winter 2004-2005, summer 2005, or winter 2005-2006), substrates (gravel, vegetation, or sediment), and all main effect interactions.

Source	DF	SS	MSE	<i>F</i> -value	<i>P</i>
Stream	1	172937.34	172937.34	209.29	<0.0001
Season	2	5497.34	2748.67	3.33	0.0387
Substrate	2	10938.61	5469.30	6.62	0.0018
Stream*Season	2	24602.00	12301.00	14.89	<0.0001
Stream*Substrate	2	4048.97	2024.49	2.45	0.0899
Season*Substrate	4	6965.36	1741.34	2.11	0.0829
Stream*Season*Substrate	4	5634.52	1408.63	1.70	0.1521

Table 19. Summary of *P* values from multiple comparisons using Tukey's LS means of the mean ranked density Hatchery*Season interactions from the mixed model ANOVA.

	Riley Cr. Winter 2004-2005	Riley Cr. Summer 2005	Riley Cr. Winter 2005-2006	Loving Cr. Winter 2004-2005	Loving Cr. Summer 2005
Riley Cr. Summer 2005	0.0314				
Riley Cr. Winter 2005-2006	0.9966	0.0496			
Loving Cr. Winter 2004-2005	<0.0001	0.0006	<0.0001		
Loving Cr. Summer 2005	<0.0001	0.0043	<0.0001	0.9885	
Loving Cr. Winter 2005-2006	<0.0001	<0.0001	<0.0001	0.8596	0.4727

Table 20. Summary of P values from Tukey's LS means multiple comparisons test for differences in mean ranked density scores between the substrate main effects.

	Gravel	Sediment
Sediment	<0.0001	
Vegetation	0.4432	0.0003

Table 21. Mean and (SE) for chemical and physical water parameters recorded during sampling events in Riley Creek and Loving Creek during winter 2004-2005, summer 2005, and winter 2005-2006.

	Winter 2004-2005		Summer 2005		Winter 2005-2006	
	Riley	Loving	Riley	Loving	Riley	Loving
Conductivity (mS/s)	0.259 (0.001)	0.281 (0.001)	0.275 (0.001)	0.321 (0.001)	0.226 (0.002)	0.250 (0.001)
Total dissolved solids (g/L)	0.211 (0.001)	0.273 (0.001)	0.212 (0.000)	0.269 (0.001)	0.183 (0.001)	0.239 (0.001)
Salinity (ppt)	0.158 (0.001)	0.202 (0.001)	0.160 (0.000)	0.201 (0.001)	0.136 (0.001)	0.176 (0.001)
Dissolved oxygen (mg/L)	N/A	N/A	9.78 (0.15)	9.75 (0.30)	10.12 (0.14)	10.68 (0.10)
pH	7.78 (0.13)	7.22 (0.12)	8.31 (0.04)	7.97 (0.03)	7.92 (0.01)	7.76 (0.02)
Temperature (°C)	14.44 (0.04)	7.69 (0.20)	16.81 (0.08)	13.22 (0.15)	14.57 (0.01)	8.20 (0.07)
Velocity (m/s)	0.424 (0.05)	0.107 (0.02)	0.139 (0.03)	0.090 (0.01)	0.394 (0.04)	0.138 (0.02)

Table 22. Summary of maximum likelihood analysis for size class distribution using categorical data modeling among seasons (winter 2004-2005, summer 2005, or winter 2005-2006), substrate (gravel, vegetation, or sediment), size (small, medium, and large) and all main effect interactions.

Source	DF	χ^2	<i>P</i>
<i>Riley Creek</i>			
Season	2	1144.02	<0.0001
Substrate	2	1741.65	<0.0001
Size	2	1038.29	<0.0001
Season*Substrate	4	895.79	<0.0001
Season*Size	4	1192.29	<0.0001
Substrate*Size	4	173.82	<0.0001
Season*Substrate*Size	8	460.68	<0.0001
<i>Loving Creek</i>			
Season	2	36.97	<0.0001
Substrate	2	0.45	0.7969
Size	2	3.77	0.1519
Season*Substrate	4	208.57	<0.0001
Season*Size	4	35.80	<0.0001
Substrate*Size	4	14.79	0.0052
Season*Substrate*Size	8	47.93	<0.0001

Table 23. Results of individual contrasts of select three-way interactions from categorical data modeling in Riley Creek between season, substrate, and size.

Season	Substrate	Size Class	DF	χ^2	<i>P</i>
Winter 2004-2005	Gravel	Large	1	0.42	0.5166
		Medium vs. Small	1	33.69	<.0001
vs.	Sediment	Large	1	0.55	0.4571
		Medium vs. Small	1	15.12	0.0001
Winter 2005-2006	Vegetation	Large	1	3.96	0.0467
		Medium	1	8.04	0.0046
		Small	1	17.21	<0.0001
	Gravel	Large	1	1.15	0.2846
		Medium	1	1.45	0.2283
		Small	1	0.14	0.7111
	Sediment	Large	1	26.00	<0.0001
		Medium	1	0.20	0.6510
		Small	1	0.59	0.4424
Winter 2004-2005	Gravel	Large vs. Medium	1	0.20	0.6510
		Medium vs. Small	1	33.69	<.0001
		Large vs. Small	1	6.08	0.0137
	Vegetation	Large vs. Medium	1	5.89	0.0152
		Medium vs. Small	1	15.12	0.0001
		Large vs. Small	1	15.12	0.2646
	Sediment	Medium vs. Small	1	75.34	<0.0001
		Large vs. Small	1	0.59	0.4424
		Large vs. Small	1	0.59	0.4424
Summer 2005	Gravel	Large vs. Medium	1	5.74	0.0166
		Medium vs. Small	1	0.51	0.4732
		Large vs. Small	1	26.74	<0.0001
	Vegetation	Large vs. Medium	1	26.74	<0.0001
		Medium vs. Small	1	122.22	<0.0001
		Large vs. Small	1	122.22	<0.0001
	Sediment	Large vs. Medium	1	1.85	0.1733
		Medium vs. Small	1	73.44	<0.0001
		Large vs. Small	1	14.36	0.0002
Winter 2005-2006	Gravel	Large vs. Medium	1	4.28	0.0386
		Medium vs. Small	1	17.73	<0.0001
		Large vs. Small	1	0.19	0.6635
	Vegetation	Large vs. Medium	1	2.93	0.0872
		Medium vs. Small	1	209.83	<0.0001
		Large vs. Small	1	209.83	<0.0001
	Sediment	Large vs. Medium	1	0.10	0.7552
		Medium vs. Small	1	37.44	<0.0001
		Large vs. Small	1	37.44	<0.0001

Table 24. Parameter estimates and (SE) of simple linear regression analysis for brood sizes based on shell length from Riley Creek and Loving Creek during all three sampling periods.

Source	Intercept	Slope	R ²
<i>Riley Creek</i>			
Winter 2004-2005	0.62 (0.355)	0.66 (0.112)	0.043
Summer 2005	-1.89 (0.401)	1.56 (0.127)	0.187
Winter 2005-2006	0.71 (0.639)	0.71 (0.204)	0.038
<i>Loving Creek</i>			
Winter 2004-2005	0.77 (0.602)	0.900 (0.142)	0.118
Summer 2005	-7.87 (1.05)	3.19 (0.256)	0.546
Winter 2005-2006	-3.20 (1.09)	1.78 (0.257)	0.357

Table 25. Summary of analysis of covariance (ANCOVA) testing differences in slope for the number of embryos per shell length unit (mm) by season, using shell length as a covariate.

Source	DF	SS	MSE	F-value	P
<i>Winter 2004-2005</i>					
Stream	1	0.051	0.051	0.04	0.8338
Length	1	85.779	85.779	73.65	<0.0001
Stream*Length	1	2.120	2.120	1.82	0.1776
<i>Summer 2005</i>					
Stream	1	48.912	48.913	43.70	<0.0001
Length	1	447.158	447.158	399.46	<0.0001
Stream*Length	1	52.209	52.209	46.64	<0.0001
<i>Winter 2005-2006</i>					
Stream	1	13.520	13.520	11.92	0.0006
Length	1	71.944	71.944	63.42	<0.0001
Stream*Length	1	13.418	13.418	11.83	0.0006

Table 26. Summary of analysis of covariance (ANCOVA) testing differences in slope for the number of embryos per shell length unit (mm) by Stream, using shell length as a covariate.

Source	DF	SS	MSE	F-value	P
<i>Riley Creek</i>					
Season	2	917.72	458.86	11.72	<0.0001
Length	1	5591.63	5591.63	142.77	<0.0001
Length*Season	2	1136.76	568.38	14.51	<0.0001
<i>Loving Creek</i>					
Season	2	9059.99	4529.99	38.64	<0.0001
Length	1	28780.61	28780.61	245.51	<0.0001
Length*Season	2	11514.10	5757.06	49.11	<0.0001

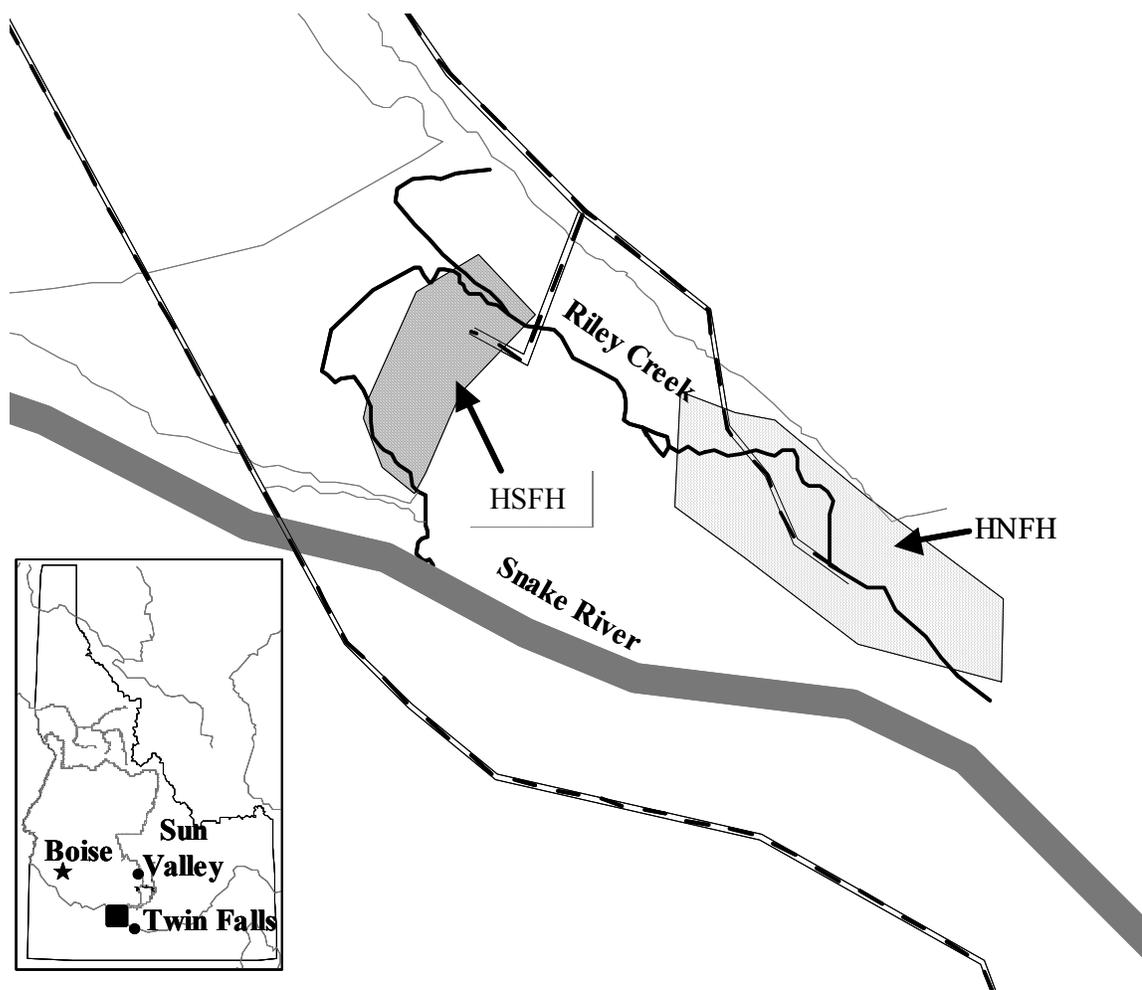


Figure 24. Map of the Riley Creek drainage in the Hagerman valley from its headwaters to its confluence with the Snake River. HSFH is the Idaho Department of Fish and Game's Hagerman State Fish Hatchery. HNFH is the U.S. Fish and Wildlife Service's Hagerman National Fish Hatchery

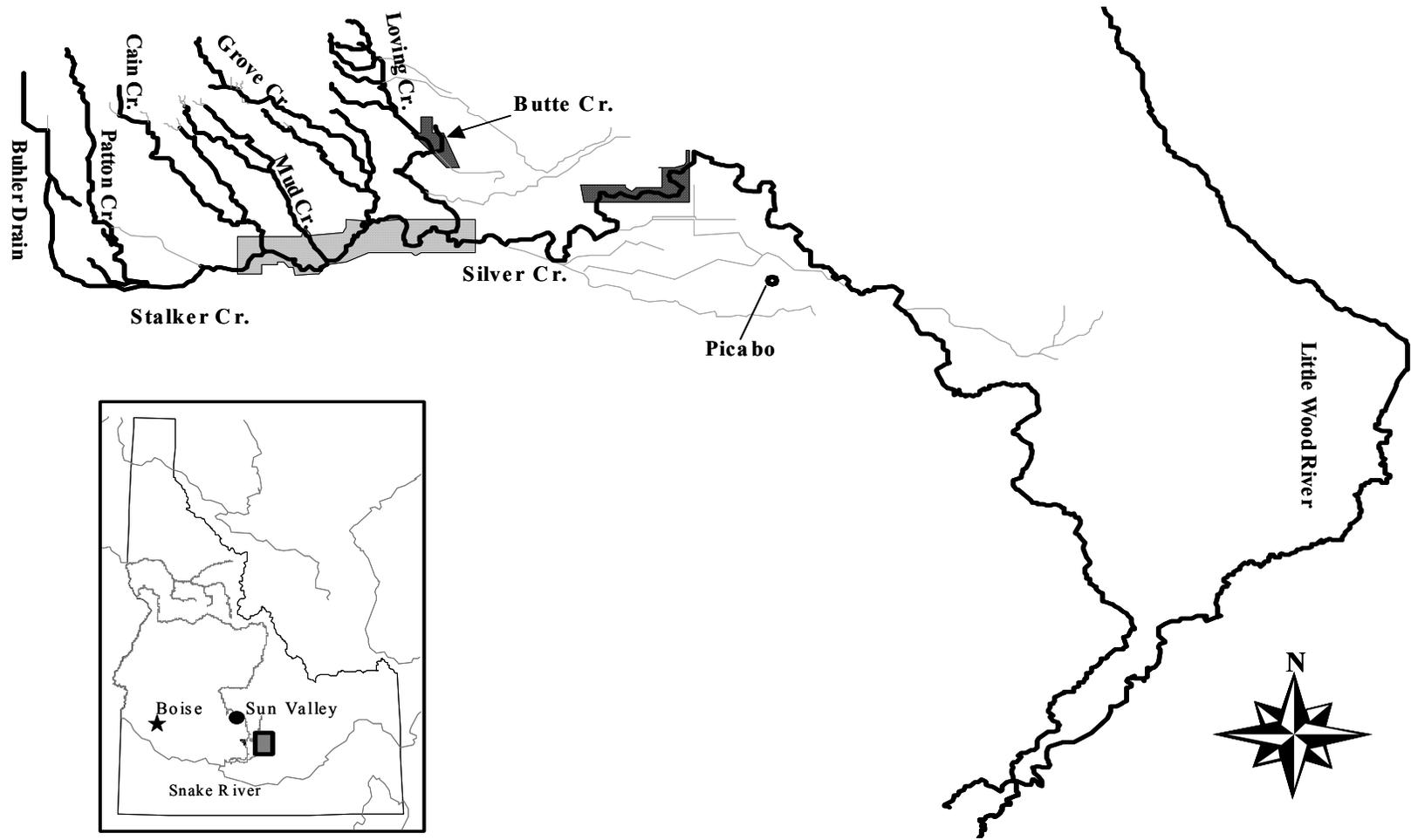


Figure 25. Map of the entire Silver Creek drainage from its headwaters to its confluence with the Little Wood River. Irrigation diversions are noted by grey lines. Silver Creek Preserve, the Nature Conservancy, is indicated by the gray polygon. The black polygons represent Idaho Department of Fish and Game properties: Hayspur Fish Hatchery on Butte/Loving Creek and the Silver Creek Sportsman's Access Site on Silver Creek.

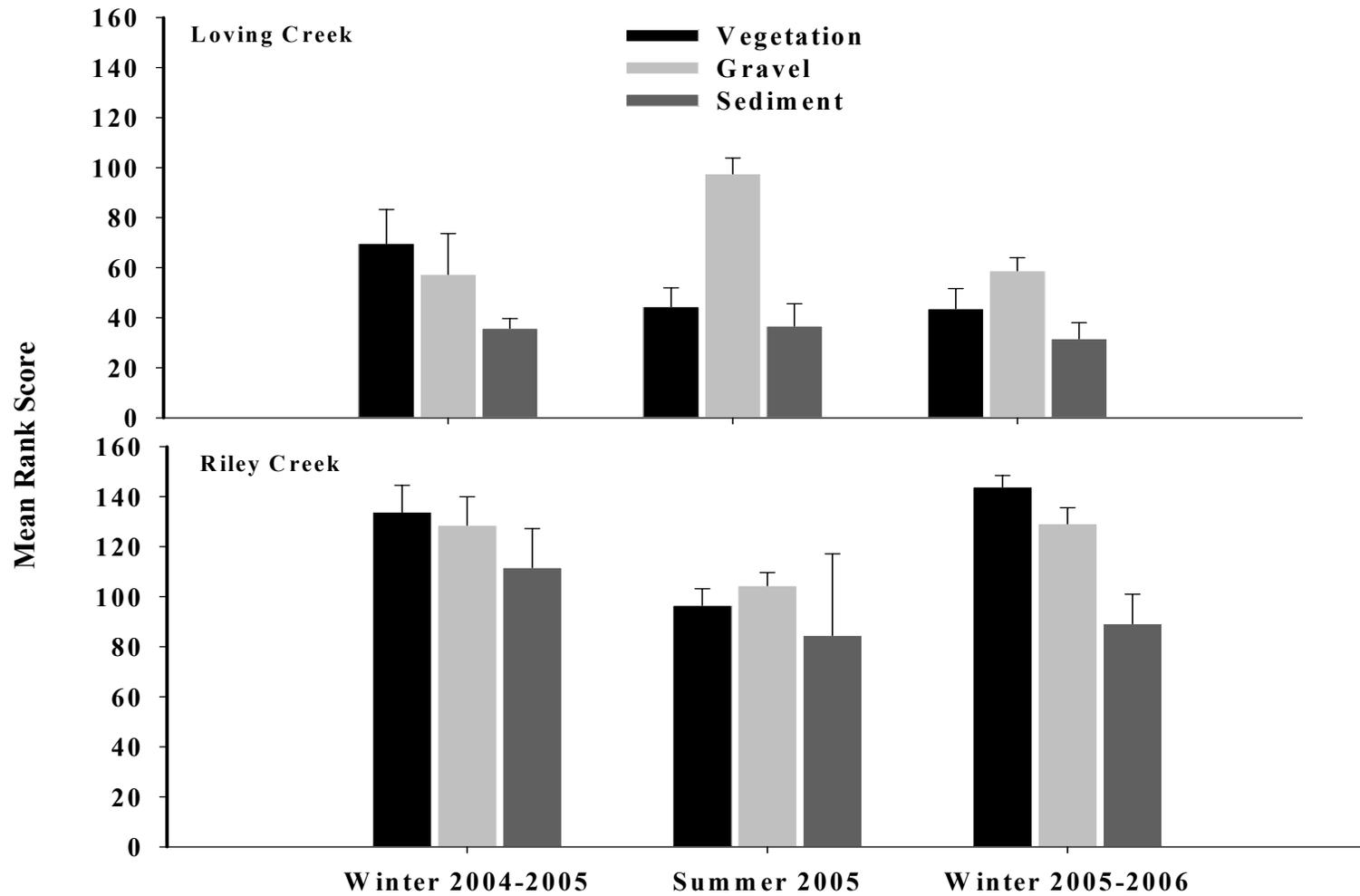


Figure 26. Mean ranked density scores of NZMS observed in Loving Creek and Riley Creek from winter 2004-2005 to winter 2005-2006 in different substrate types. Error bars represent 1-Standard Error.

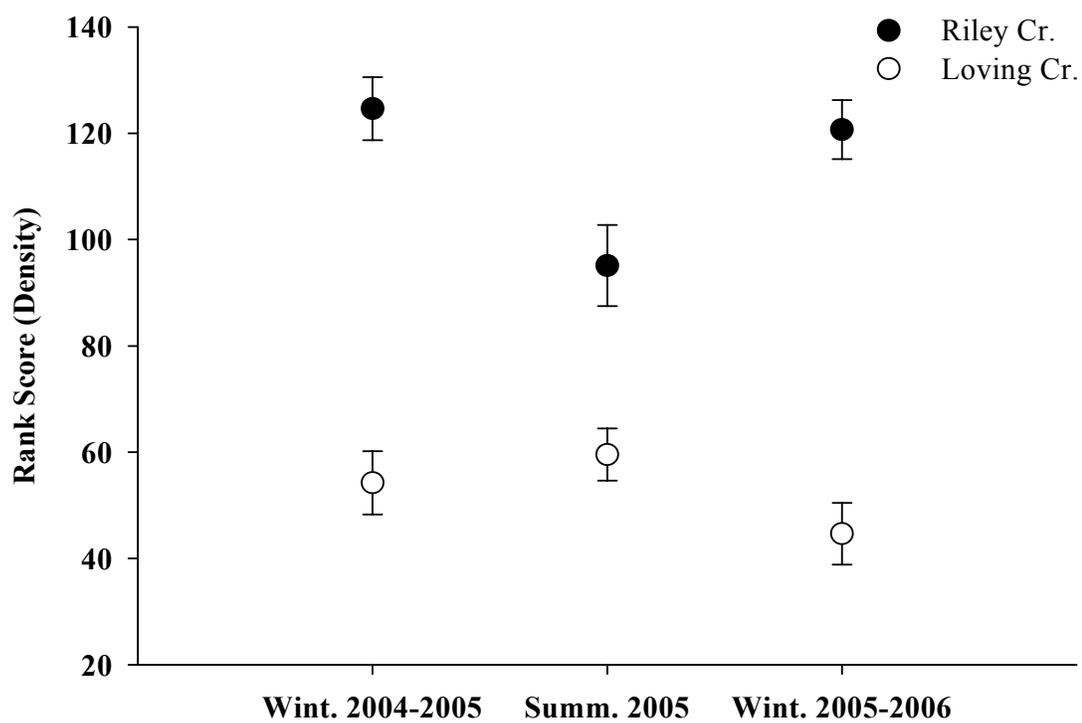


Figure 27. Least square means comparison of mean ranked density scores of New Zealand mudsnails between Riley Creek and Loving creek across three different seasons. Error bars depict ± 1 SE.

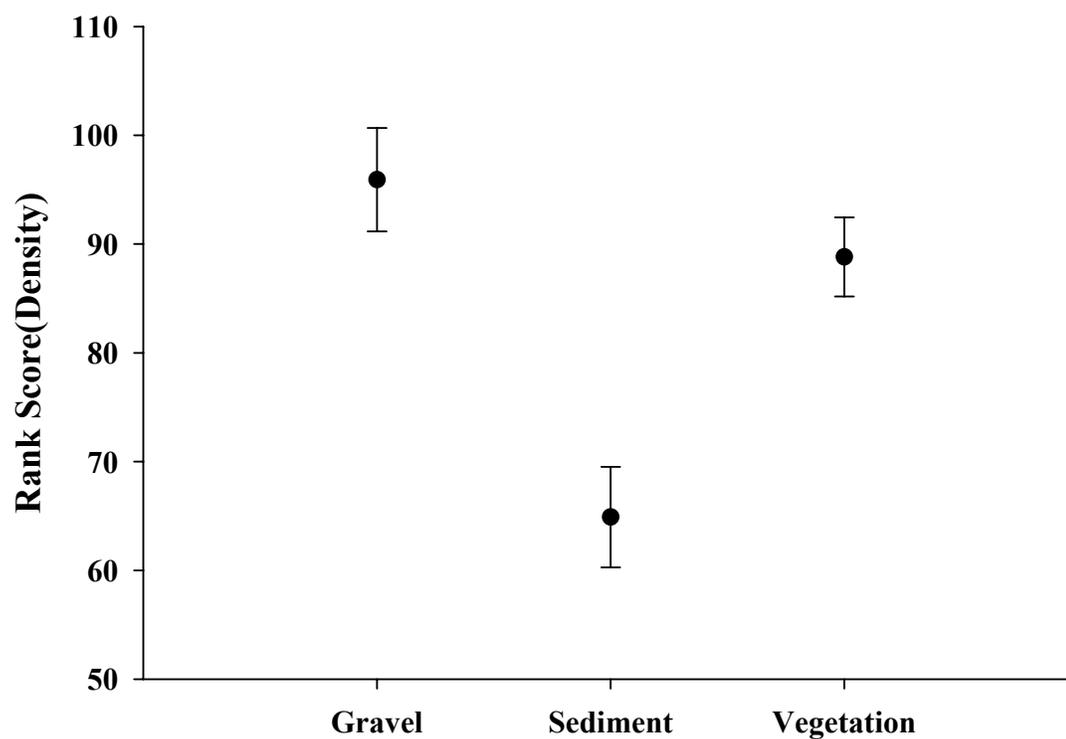


Figure 28. Least square means comparison of mean ranked density scores for New Zealand mudsnails from both Riley Creek and Loving Creek, combined, across three different substrates. Error bars depict ± 1 SE.

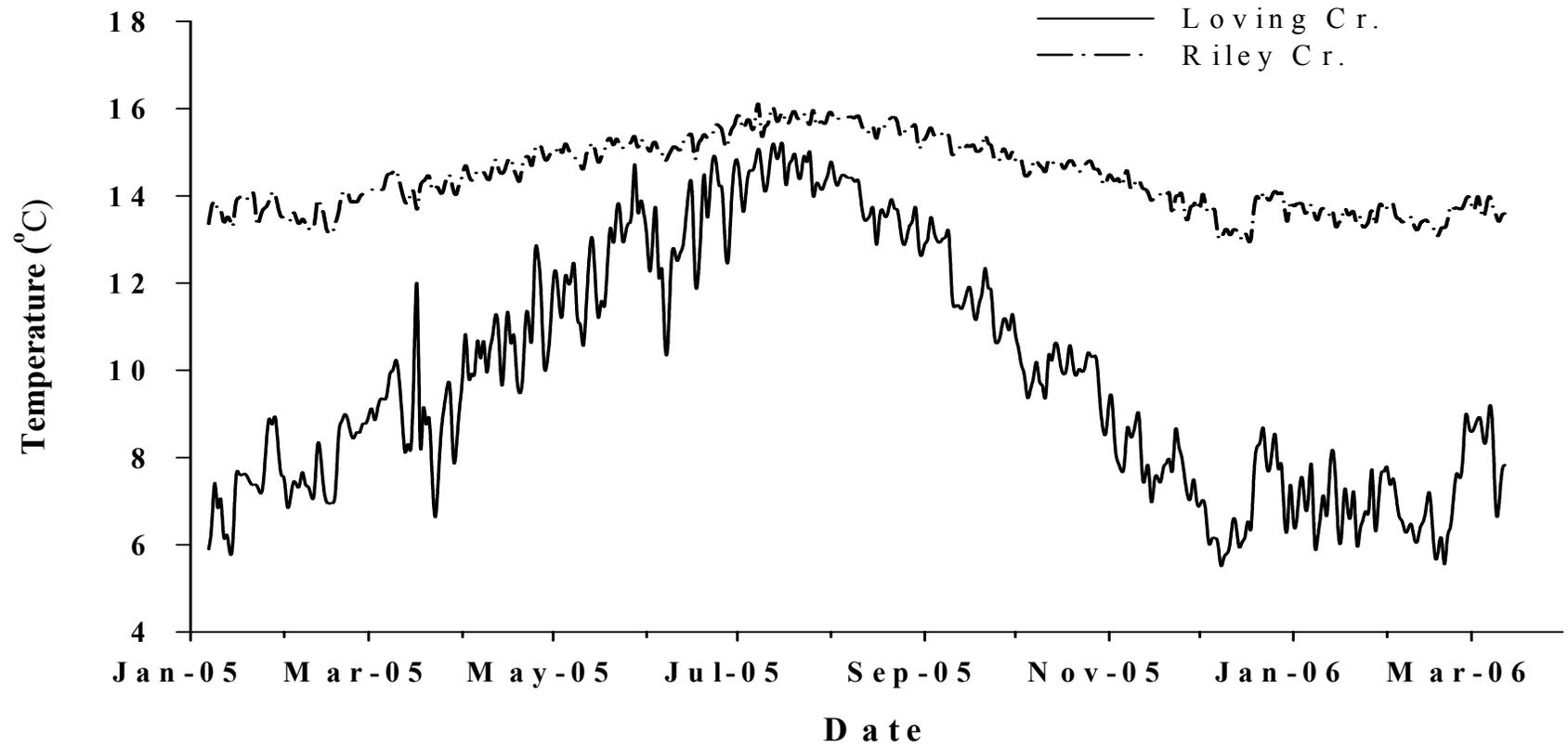


Figure 29. Average daily temperatures recorded every two hours areas of where New Zealand mudsnails were collected from Riley Creek (dash dotted line) and Loving Creek (solid line) between January 2005 to March 2006.

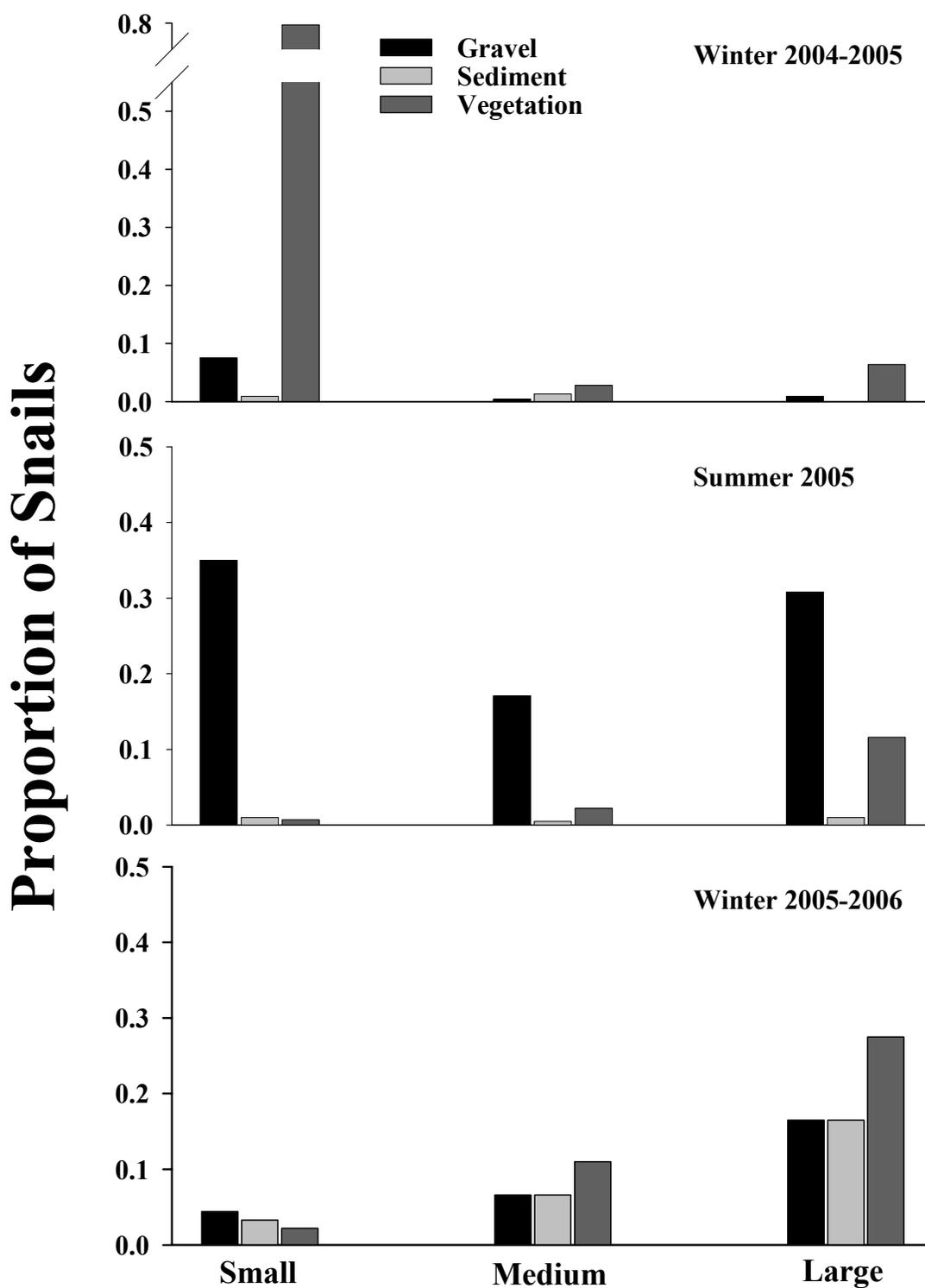


Figure 30. Distribution of the proportion of snails in individual size classes from Loving Creek during three sampling periods from winter 2004-2005 to winter 2005-2006 in different substrates.

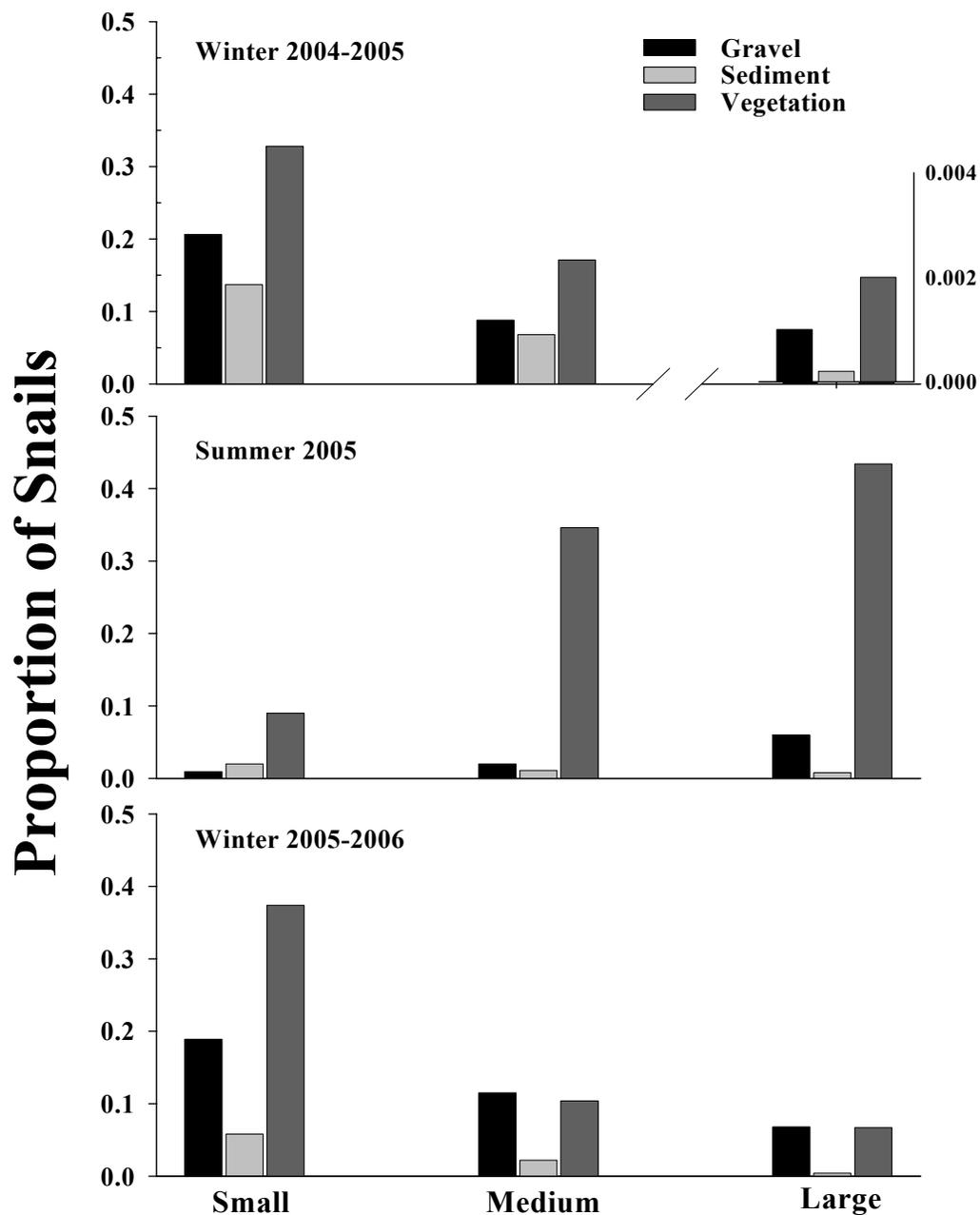


Figure 31. Distribution of the proportion of snails in individual size classes from Riley Creek during three sampling periods from winter 2004-2005 to winter 2005-2006 in different substrates. The right y-axis in the winter 2004-2005 pane is scaled for large snails only.

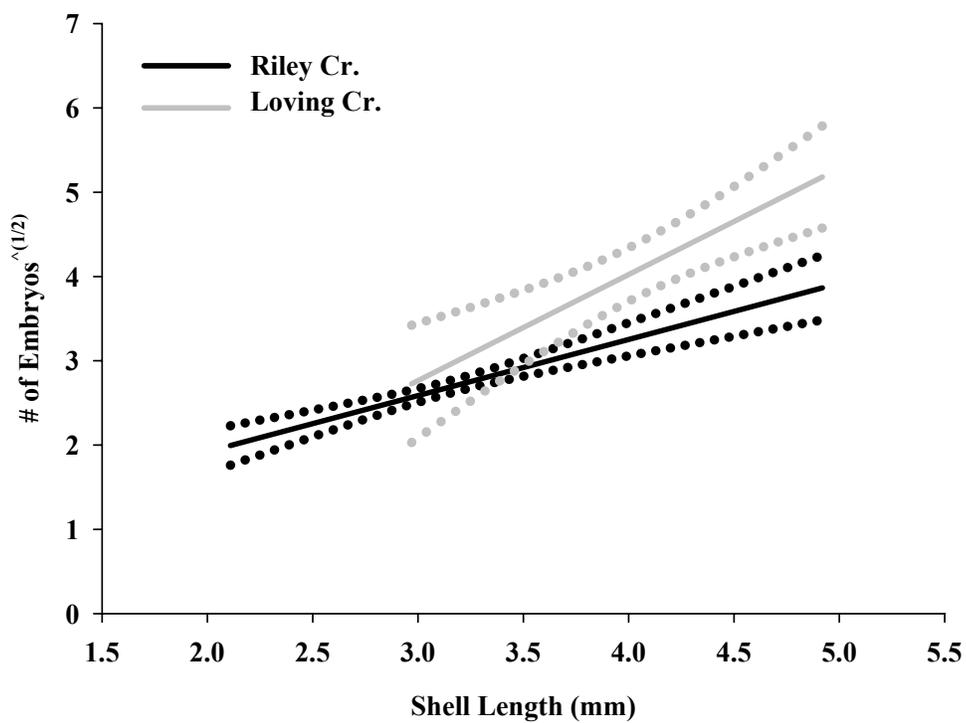


Figure 32. Simple linear regression and 95% C.I. of the number of embryos per brood vs. shell length for snails from Riley and Loving Creek during the winter of 2004-2005.

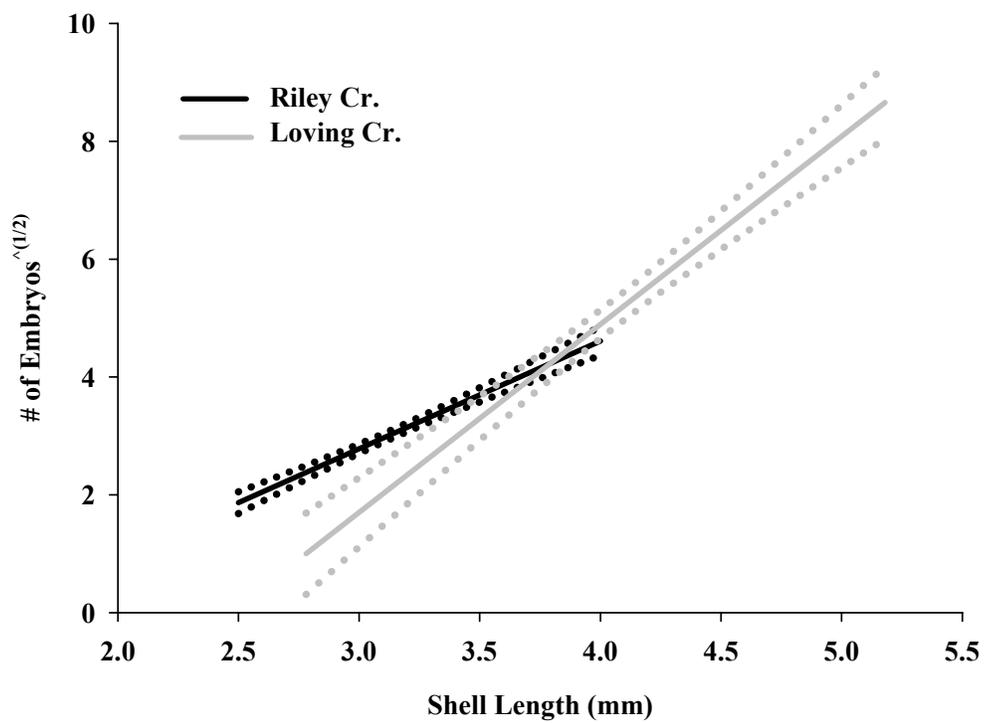


Figure 33. Simple linear regression and 95% C.I. of the number of embryos per brood vs. shell length for snails from Riley and Loving Creek during the summer of 2005.

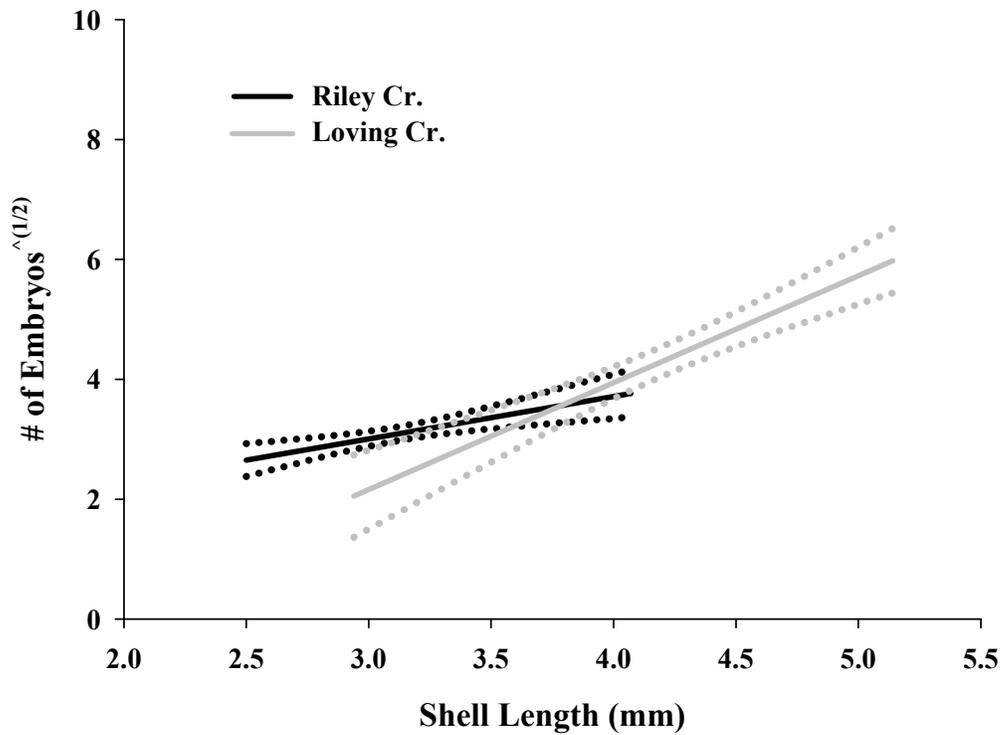


Figure 34. Simple linear regression and 95% C.I. of the number of embryos per brood vs. shell length for snails from Riley and Loving Creek during the winter of 2005-2006.

Appendix A. Nutrient levels recorded in Riley Creek below Hagerman National Fish Hatchery (HNFH) and throughout the Silver Creek drainage by various resource agencies. Nr denotes measurements not recorded.

Location	Date	Collector	Total Phosphate (mg/L)	Ortho-phosphate (mg/L)	Nitrate (mg/L)
Riley Cr. (HNFH)	Sep-1975	IDEQ	0.06	0.00326	0.77
	Dec-1975	IDEQ	0.18	0.04238	0.69
	Mar-1976	IDEQ	0.14	0.0163	0.60
	Jun-1976	IDEQ	0.11	0.02282	0.65
	May-1991	HNFH	0.11	Nr	0.63
	Sep-1991	HNFH	0.08	Nr	0.68
	Dec-1991	HNFH	0.24	Nr	0.92
	Mar-1992	HNFH	0.45	Nr	0.83
	Jan-2005	UofI	Nr	0.025	0.83
	Jan-2006	UofI	Nr	0.0345	0.945
Thomson Cr. (Silver Cr. tributary)	May-1975	IDEQ	0.02	0.02282	0.66
	Oct-1975	IDEQ	0.14	0.00652	0.76
Silver Creek Sportsmen's Access	Jan-1976	IDHW	0.17	Nr	0.90
	May-1976	IDHW	0.03	Nr	Nr
	Oct-1976	IDHW	0.00	Nr	0.55
	May-1977	IDHW	0.02	Nr	0.36
Loving Creek (HSFH)	Jan-2005	UofI	Nr	0.018	1.4
	Jan-2006	UofI	Nr	0.016	1.4