

# A race against time: Establishing baseline data on redwood ecosystem food webs before New Zealand mud snails invade



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Cover photo: New Zealand mud snails on emergent vegetation in Maple Creek/Big Lagoon, Humboldt County, California. July 2012. Photo by Darren Ward.

## Abstract

Invasive New Zealand mud snails have recently become established in multiple streams along the Redwood Coast in Northern California- including Redwood Creek in Redwood National and State Parks. New Zealand mud snails are very prolific and they have the capacity to spread rapidly and reach very high biomass and abundance at invaded sites. The purpose of this project was to (1) document the current distribution of New Zealand mud snails in streams in and around Redwood National and State Parks at this early stage of invasion, (2) identify habitat characteristics associated with the presence of New Zealand mud snails, and (3) characterize food web linkages within stream ecosystems and between streams and adjacent riparian areas at invaded sites as well as sites with no New Zealand mud snails to provide a baseline for comparison if mud snails do become established at additional sites. In surveys conducted in 2011 and 2012, we found that the range of New Zealand mud snails in Redwood Creek does not appear to have expanded beyond the area in the lower main stem and estuarine lagoon where they were first documented in 2009. A similar pattern of restricted distribution holds in nearby Maple Creek, other tributaries of Big Lagoon, and other coastal streams in Northern California. The physical and chemical habitat in these estuarine sites is generally distinct from conditions in upstream sites, making it difficult to narrow down the key factors that constrain the distribution of New Zealand mud snails. However, based on work completed elsewhere, we suspect that lower water conductivity and lower calcium concentrations outside of estuarine areas play a role in limiting New Zealand mud snail distribution; this hypothesis is supported by preliminary results of laboratory assays evaluating New Zealand mud snail survival and reproduction in waters varying in conductivity and calcium content. In our surveys of the estuarine areas where New Zealand mud snails are established, we found densities up to 10,000 per m<sup>2</sup> and particularly high abundance in areas with organic substrate (emergent vegetation, filamentous algae, or large woody debris) and on boulder-size rocks used to stabilize banks along the Redwood Creek levee. New Zealand mud snails were found in the stomachs of steelhead and cutthroat trout in the Redwood Creek estuary. However, as in other reported instances of mud snail ingestion by salmonids, most snails recovered from fish stomachs were undigested and still alive. Diet analysis and stable isotope characterization food webs at sites upstream of the estuary indicate strong terrestrial-aquatic linkages in which stream-dwelling invertebrates make both terrestrial and aquatic primary production available for consumers in the stream (fish, salamanders) and in adjacent riparian areas (spiders). This integrated food web would be vulnerable to disruption if mud snails eventually expand their distribution beyond the estuary and lower main stem.

## Introduction

New Zealand mud snails (NZMS) were first documented in Northern California in 2008 and they were found in Redwood Creek in Redwood National and State Parks in 2009 (Hellmair et al. 2011) Keith Benson, Redwood National Park, personal communication). A widespread and prolific invasive species, the presence of NZMS in Northern California is a potential threat to stream ecosystems. Invasive populations of NZMS are composed of females that can reproduce asexually, so introduction of just a single individual can establish a new population. Under ideal conditions, each female can produce broods of up to 80 daughters every 2-3 months, allowing populations to rapidly reach densities  $>100,000$  per  $m^2$  (Hall et al. 2006). In other invaded regions, NZMS are known to sequester 65-92% of stream primary production and competitively exclude native primary consumers, particularly aquatic insects (Hall et al. 2006, Moore et al. 2012). Unlike the native aquatic insects they displace, NZMS are effectively a trophic dead-end. Some fish do eat NZMS, but most species assimilate very little energy from them and suffer reduced growth rates (Vinson and Baker 2008). Further, NZMS are not available to terrestrial consumers that rely on emerging aquatic insects.

Potential effects of NZMS invasion on threatened salmon and trout (salmonid) populations are a particular concern. Juvenile anadromous salmonids that grow rapidly generally have higher survival through migration and at sea (Zabel and Achord 2004), but rapid juvenile growth depends on a healthy stream insect community. Thus, NZMS invasion could further suppress already declining salmon populations in Redwood Creek and other Northern California streams and rivers. The importance of productive and abundant salmon populations to coastal ecosystems has been well documented. Annual return of adult salmon to freshwaters results in the transfer of marine-derived nutrients and biomass to nutrient-limited streams and terrestrial ecosystems. Such inputs can cascade through aquatic and terrestrial food webs, stimulating autotrophic and heterotrophic production within streams and the riparian corridor (Bilby et al. 1996). As much as 30% of the foliar nitrogen in terrestrial plants growing adjacent to salmon streams is of marine origin (Ben-David et al. 1998) and significantly enhances growth of riparian trees (Drake et al. 2006). Nitrogen availability, in particular, is a growth-limiting factor in temperate forests and marine-derived nitrogen may be critical to the maintenance of riparian forest productivity.

In addition to affecting fish, NZMS may disrupt the connections between aquatic and terrestrial food webs. Emerging aquatic insects are a substantial resource subsidy for terrestrial food webs. They are captured by birds, bats, spiders, and amphibians, which are then eaten by terrestrial predators from higher trophic levels. Some riparian spiders obtain 100% of their diet from emerging aquatic invertebrates while songbird nestlings obtain  $> 80\%$  of their diet from riparian spiders (Baxter et al. 2005). Because of these aquatic-terrestrial linkages, reductions in stream invertebrate abundance or biomass associated with NZMS invasion may drive population declines in riparian spider and bird abundance (Sanzone et al. 2003). Therefore, the effects of NZMS invasion may extend beyond the stream ecosystems that they inhabit.

The purpose of this project was to (1) document the current distribution of New Zealand mud snails in streams in and around Redwood National and State Parks at this early stage of invasion, (2) identify

habitat characteristics associated with the presence of New Zealand mud snails, and (3) characterize food web linkages within stream ecosystems and between streams and adjacent riparian areas at invaded sites as well as sites with no New Zealand mud snails to provide a baseline for comparison if mud snails do become established.

## Methods

In order to ensure that our research did not facilitate the spread of NZMS, we followed a strict decontamination protocol in all field work. All field gear was cleaned of visible debris and decontaminated by one of the following techniques between uses at different sites: (1) freezing for 12 hours and drying completely, (2) immersion in a >7% chlorine bleach solution for 10 minutes.

**Objective 1:** Document the current distribution of New Zealand mud snails in streams in and around Redwood National and State Parks.

We used field surveys to monitor the occurrence of NZMS in streams in the summers of 2011 and 2012. We conducted surveys at sites in the lower main stem and estuarine lagoon of Redwood Creek (2011 and 2012) and Maple Creek (2012) where NZMS populations were first documented and at upstream sites in Redwood Creek, Maple Creek, and other tributaries in the respective basins (including Prairie Creek, Lost Man Creek, and Little Lost Man Creek in the Redwood Creek basin; see Figure 1). Survey sites in the Redwood Creek basin were 500 m long; sites in the Maple Creek/Big Lagoon basin were 200 m long. Sites were adjacent, so that upon completion we had contiguous survey data for each stream. To avoid confounding spatial variation and potential temporal trends in NZMS presence or other measures, all sites were mapped prior to the start of surveys and surveys were completed in a random sequence. Snail sampling was conducted in conjunction with habitat measurements at each site (see objective 2). We used 3 snail sampling techniques: (1) 1-minute kick samples collected from shallow (<20 cm deep) riffles (>20 cm/s velocity) at sample locations evenly distributed along each site (10 per site, 2011 only). All kick samples at each site were combined and placed in 5-gallon buckets, transported to the laboratory, and snails sorted from substrate, identified, and counted within 48 hours. (2) Visual inspection of 100 rocks along transects across the stream (5 transects, 500 rocks total per site), in conjunction with substrate measurements. (3) Controlled-effort searches consisting of a 10-minute focused search of likely NZMS habitat by two people (2012 only). Controlled-effort searches replaced kick samples in 2012 to increase the likelihood of detecting low-density, newly-established NZMS populations.

In late summer 2012, as there were no NZMS detections at any locations outside of the lagoons or estuarine stream reaches, we incorporated an additional sampling technique to gain more information about the fine-scale patterns of abundance of mud snails within the Redwood Creek lagoon. We deployed 20 passive samplers (Hester-Dendy, 14 plates, 7.5 cm x 7.5 cm) along the bank of Redwood Creek along a 500 m reach that encompassed the entire area where we visually detected snails during surveys. Samplers were deployed at 10 locations spaced approximately 50 m apart, with a replicate pair of samplers attached to an anchor at each location. Samplers were left in place from 13 September through 18 October 2012.

**Objective 2:** Identify habitat characteristics associated with the presence of New Zealand mud snails.

We conducted a standard set of habitat measurements at all survey sites. On five transects at each site, we measured width, maximum depth, canopy cover, and substrate composition (100 point samples per transect, substrate at each point classified according to the Wentworth scale). In addition, we measured water quality parameters (pH, specific conductivity, temperature) at each site. These habitat measurements were intended to serve as predictors in a generalized linear model of NZMS presence and abundance. However, this analysis was not conducted as planned because NZMS were detected at very few sites. Based on research at other locations (Herbst et al. 2008) and the restricted distribution we observed, we developed a hypothesis that the spread of NZMS in Redwood Creek and the other study streams is limited by low conductivity and low calcium concentrations in the water. We have started a set of laboratory experiments to fully evaluate this hypothesis. For completeness, a poster presentation with a preliminary report of the results of these experiments is included here as Appendix 1.

**Objective 3:** Characterize food web linkages within stream ecosystems and between streams and adjacent riparian areas at invaded sites as well as sites with no New Zealand mud snails to provide a baseline for comparison if mud snails do become established.

Our approach to characterizing food web linkages had two complementary components: stomach contents analysis for fish and amphibian secondary consumers and stable isotope analysis of fish, their primary prey items, and potential sources of primary production from the stream or estuary and nearby terrestrial areas. The ratio of stable isotopes of atoms of different elements in consumers is derived from their food. So, if basal resources vary in their stable isotope composition, then differential consumption can be identified in consumers at higher trophic levels (Peterson and Fry 1987). We measured stable isotopes of carbon and nitrogen in tissues of organisms from our sites and nearby terrestrial areas in order to evaluate transfer of biomass between aquatic and terrestrial food webs.

Fish and salamanders were collected by electrofishing (un-pulsed DC <300 V, upper basin stream sites) or seining (lower main stem and estuary/lagoon, seining was conducted by Redwood National Park personnel as part of ongoing monitoring efforts) for non-lethal diet and stable isotope sampling. Electrofishing was conducted in 20-minute bouts of standardized effort so that catch would provide an index of relative abundance across sites (7 sites sampled in Little Lost Man, Lost Man, and Prairie Creeks). Up to 15 individuals of each taxa per sample event were retained for sampling (juvenile trout < 60 mm fork length were not distinguishable to species). Individuals sampled were sedated with Finquel (< 100 mg/L), measured (nearest mm, fork length for fish, snout to vent length for salamanders), stomach contents removed via gastric lavage, and a small tissue sample (ca. 1 mm x 2 mm) was collected from the caudal fin (fish) or tail (salamander) for stable isotope analysis (Sanderson et al. 2009). Fish and salamanders were allowed to recover in buckets before release at the site of capture. Partially digested stomach contents were preserved in 70% ethanol prior to sorting to the lowest feasible taxonomic grouping (usually order, NZMS were easily identified to species) under a dissecting scope.

Besides fish and salamanders, we targeted a standardized set of taxa for additional stable isotope sampling to characterize the food web at all sites. These included: Heptageniidae (mayflies), *Juga* spp. (snails), alder leaves, and Tetragnathidae (riparian spiders that specialize on emerging aquatic invertebrates). We sampled NZMS at all sites where they were present. Additional samples, including other families of mayflies, other types of riparian vegetation, non-tetragnathid spiders found in riparian vegetation, and aquatic algae were collected opportunistically at sites where they were abundant. This sample strategy was intended to characterize the aquatic (snails and grazing mayflies) and terrestrial (riparian vegetation) stable isotope signatures at each site (Moore et al. 2012) in order to characterize the basal resources contributing to the production of consumer species. All isotope samples were kept on ice for transport, and then frozen until processing. Analysis preparation consisted of thawing the sample, drying to constant mass at 60°C, homogenizing (if necessary for subsampling large samples), and loading ca. 1 mg of sample into a pre-weighed tin capsule. Isotope analysis was conducted at the UC Davis Stable Isotope facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Isotope ratios are expressed in parts per thousand units as the deviation ( $\delta$ ) between the ratio in the measured sample and the ratio in a reference material (Pee Dee Belemnite for C, air for N). Every tenth sample was prepared in duplicate for assessment of repeatability of analysis. All duplicate runs were within 8% of the average value.

## Results

**Objective 1:** Document the current distribution of New Zealand mud snails in streams in and around Redwood National and State Parks.

We only detected NZMS at the downstream-most sample sites in Redwood Creek (Figure 1). These locations overlap with those where NZMS were first detected in Redwood Creek in 2009, suggesting that there has been minimal spread of the population over at least 3 years. Similar to the restricted distribution in Redwood Creek, we detected NZMS at the downstream-most site in Maple Creek and at the downstream boundaries of other tributaries of Big Lagoon. NZMS are widespread in Big Lagoon itself, but their abundance apparently fluctuates considerably over time associated with the opening and closing of the sand bar (Hellmair et al. 2011). All NZMS detections during surveys were by visual inspection of the substrate. No NZMS were found in kick net samples, although native snails (particularly *Juga* spp.) were often found in kick net samples at high abundance. This may be because NZMS were generally associated with organic substrates (emergent vegetation, filamentous algae, or large woody debris) or boulder rip-rap along the Redwood Creek levee, while we took kick net samples in shallow mid-stream riffle habitats where the substrate was dominated by cobble and gravel.

The passive samplers placed within the lagoon or Redwood Creek to characterize patterns in abundance at a small spatial scale revealed a unimodal abundance pattern along the 500-m stream reach, with peak abundance near the flow-control grate that feeds the side-channel slough near the Thomas H. Kuchel Visitor Center and decreasing abundance both upstream and downstream from there (Figure 3). No NZMS were captured in the upstream-most and downstream-most traps. During most of the year,

NZMS are abundant throughout the side-channel slough on Redwood Creek. However, during the low late-summer flows when we deployed the passive samplers, much of the slough was dry.

In our surveys of stream sites in the upper basin, we found that a native snail species (*Juga* spp.) was often very abundant and dominated the biomass of the invertebrate community at some sites (up to 137 individuals in a single kick-net sample). *Juga* are morphologically similar to NZMS, with similar shell shape, coloration, and an operculum over the aperture (Figure 4). While *Juga* reach much larger size than NZMS (maximum shell length >20 mm), juvenile *Juga* that are similar-size to NZMS were very common through the survey season. *Juga* snails were present at all study sites, including the Redwood Creek lagoon, but they were particularly abundant in Little Lost Man Creek and Prairie Creek (average±standard error snails per kick net sample: Little Lost Man Creek: 69±38, Prairie Creek: 41±15, Redwood Creek: 18±9, Lost Man Creek: 5±3).

**Objective 2:** Identify habitat characteristics associated with the presence of New Zealand mud snails.

Our sample sites encompassed a wide range of habitat characteristics ranging from small tributaries with heavy canopy shading from riparian trees and mostly gravel and cobble substrate to large main stem and estuary sites with very little shading and generally smaller substrate. NZMS were typically found at wider, deeper sites with little canopy cover, but they were not consistently associated with a particular substrate size at the study site scale (Figures 5 and 6). Sites where NZMS were present also had higher specific conductivity than sites without NZMS (Table 1). Statistical modeling of habitat conditions associated with NZMS presence was not conducted due to the small number of sites where we detected NZMS.

Table 1 Water quality characteristics at study sites (average and range of data). Measurements were conducted near mid-day during surveys in June and July 2012.

| Stream                              | Temperature (°C)        | Specific conductivity (µS/cm) | pH            |
|-------------------------------------|-------------------------|-------------------------------|---------------|
| Little Lost Man Creek               | 11.1 (9.5-11.8)         | 58 (57-58)                    | 7.5           |
| Lost Man Creek                      | 10.8 (9.5-11.7)         | 41 (37-45)                    | 7.4 (7.3-7.6) |
| Prairie Creek                       | 11.2 (10.0-12.1)        | 71 (66-74)                    | 7.5 (7.4-7.5) |
| Redwood Creek                       | 20.9 (20.5-21.2)        | 114 (111-117)                 | 7.5           |
| <i>Redwood Estuary- NZMS</i>        | <i>16.8 (15.9-18.0)</i> | <i>113 (105-121)</i>          | <i>7</i>      |
| Maple Creek                         | 12.9 (12.0-14.2)        | 66 (63-69)                    | 7.3           |
| <i>Maple Creek- NZMS</i>            | <i>13</i>               | <i>85</i>                     | <i>7.5</i>    |
| Big Lagoon tributary                | 18.8                    | >10,000                       | 7.4           |
| <i>Big Lagoon tributaries- NZMS</i> | <i>15 (14.4-16.4)</i>   | <i>5165 (4430, 5900)</i>      | <i>7.9</i>    |

**Objective 3:** Characterize food web linkages within stream ecosystems and between streams and adjacent riparian areas at invaded sites as well as sites with no New Zealand mud snails to provide a baseline for comparison if mud snails do become established.



## Diet samples

We sampled salmon and trout stomach contents in and near the area where NZMS occur in the Redwood Creek lagoon and salmon, trout, and salamander stomach contents at upper-basin sites outside the documented range of NZMS. Within the lagoon, we collected samples from a total of 277 individual fish (54 Chinook salmon, 32 coho salmon, 41 cutthroat trout, and 150 steelhead trout) during monthly sampling from June-August in 2011 and June-September 2012 (lagoon fish were sampled by Redwood National Park personnel as part of ongoing population monitoring efforts). Diets of lagoon-dwelling fish were dominated by amphipods (45% of all prey items). Only 1.2% of the prey items recovered from estuary fish were of terrestrial origin (mostly spiders and winged insects).

Of the lagoon fish sampled, 24 had NZMS in their stomachs (1 cutthroat trout, 23 steelhead trout). Stomach samples that contained NZMS had from 1-21 NZMS (average $\pm$ SE: 7.9 $\pm$ 1.5). Nearly all (95%) of the NZMS recovered from fish stomachs had shells intact. Most NZMS recovered from fish stomachs were preserved immediately in ethanol, but 70% of individuals in a subsample of 57 snails placed in water for observation were still alive (snails retained from 10 different fish on 3 sample dates). Consistent with previous studies (Vinson and Baker 2008), these observations suggest that steelhead that were consuming NZMS were not gaining an energetic benefit and they may suffer reduced growth if NZMS consistently replace more-digestible prey items in their diets. Individuals that consumed NZMS did tend to have fewer non-NZMS items in their stomachs (Figure 7). However, individuals that had NZMS in their diet samples were not consistently smaller than individuals that did not have NZMS in their diet samples (Figure 8). At present, it is not clear if individuals that consume NZMS persist in eating them over time long enough to have an effect on growth.

Within the upper basin tributary streams, we collected stomach samples from a total of 188 individual fish (69 coho salmon, 19 cutthroat trout, 21 steelhead trout, and 79 unidentified juvenile trout) and 59 coastal giant salamanders. Fish diets were dominated by Diptera (21% of all prey items), Trichoptera (21% of all prey items), and Ephemeroptera (15% of all prey items). Terrestrial prey was a substantial component of the diet of stream fish (28% of all prey items, mostly ants, spiders, winged insects, and caterpillars). The terrestrial proportion of the diet was likely much higher on a biomass basis because the terrestrial prey items were generally larger than aquatic prey items, but we could not directly measure mass because most samples were partially digested and very fragmented. The small sample size (5-15 of each taxa per site) and high individual and spatial variability preclude evaluating differences in diet among the fish species. Coastal giant salamander diets were dominated by Trichoptera (32% of prey items), Diptera (22% of prey items) and *Juga* (20% of prey items). One individual had 8 *Juga* ranging from 6-12 mm long sampled from its stomach. Others have previously documented the prevalence of *Juga* in coastal giant salamander diet samples in streams where they co-occur (Esselstyn and Wildman 1997), but it remains unclear if this is due to heavy predation pressure or long retention times of shells in salamander stomachs. Terrestrial prey items made up 10% of the salamander diet (mostly caterpillars).

## Stable isotope samples

Stable isotopes ratios of N and C differed substantially among sites and species (Figures 9 and 10). Typically, C isotopes ratios are expected to be similar in a consumer and its primary food, while N

isotope ratios are expected to increase by about 3.4‰ from food to consumers due to differential uptake and elimination during digestion and metabolism (Post 2002). Given these expected relationships, on a scatterplot of  $\delta^{13}\text{C}$  (horizontal axis) against  $\delta^{15}\text{N}$  (vertical axis), top predators should be at the top (relatively high  $\delta^{15}\text{N}$ ) high and basal resources at the bottom (relatively low  $\delta^{15}\text{N}$ ), with intermediate consumers in between. Consumers should be directly above their primary food, or if they eat a combination of foods with different  $\delta^{13}\text{C}$  ratios they should be between their primary foods on the horizontal axis and above them on the vertical axis. Our isotope measurements are consistent with these patterns for N, with basal resources (terrestrial vegetation) lowest, primary consumers (aquatic herbivores) intermediate, and predators (fish and salamanders) highest (Figure 9). However, the C isotope data suggests that we did not sufficiently characterize aquatic-derived resources by sampling snails and aquatic insects (groups nominally grouped as grazers on algae). Instead, these aquatic taxa had  $\delta^{13}\text{C}$  ratios close terrestrial vegetation, while consumers and predators had higher  $\delta^{13}\text{C}$  (Figure 9). We did not sample any prey species or basal resources with high  $\delta^{13}\text{C}$  ratios that could explain the consistent increase in  $\delta^{13}\text{C}$  with trophic position. We hypothesize that there is a seasonal influx of high- $\delta^{13}\text{C}$  resources into these streams (e.g. salmon carcasses, autumn leaf fall from other terrestrial plant species, or seasonal algae production) that elevates the  $\delta^{13}\text{C}$  of large, long-lived consumers but is not reflected in the consumers and basal resources we collected in our late-summer sampling.

Isotope results from lower Redwood Creek and Maple Creek/Big Lagoon sites with NZMS place them as likely omnivores that consume both aquatic and terrestrial production ( $\delta^{13}\text{C}$  intermediate between algae and terrestrial vegetation) at these sites (Figure 10). NZMS  $\delta^{13}\text{C}$  was highly variable among samples, suggesting a high degree of individual variation in diet across sample locations within sites. This broad dietary niche of NZMS, combined with their high production potential and maximum abundance, suggests that they could have effects on a broad range of species in these food webs.

## Discussion

We found that NZMS have not as of yet expanded their distribution upstream in the Redwood Creek or Maple Creek basins. Further, the NZMS populations in Redwood Creek have not reached population densities comparable to those observed at other sites in western North America where NZMS invaded and came to dominate aquatic consumer biomass. Based on results of our field surveys, work in other locations with similar water chemistry (Herbst et al. 2008), and our laboratory experiments (Appendix A), we suggest that NZMS populations are constrained by low ion concentrations in the study streams—particularly low calcium availability. In our laboratory experiments, NZMS reproduction increased up to 5-fold in treatments with added calcium compared to natural water from the study sites. We note that this does not mean that upstream, low-conductivity sites are not susceptible to future NZMS invasion. NZMS populations in the Columbia River have shown rapid adaptation to local variation in water chemistry (Hoy et al. 2012), such changes may eventually allow the Redwood Creek and other Northern California populations to expand their distribution upstream.

Given their restricted distribution, current impacts of NZMS on native organisms are likely limited to the estuary and lagoon sites. We found that juvenile steelhead in the Redwood Creek lagoon do consume NZMS at a relatively high rate compared to other species in the lagoon and other estuarine systems

where predation on NZMS by salmonids (Bersine et al. 2008) and other fish species (Brenneis et al. 2011) has been documented. Rapid growth of juvenile steelhead in productive lagoon habitats can substantially increase their survival rates at sea (Bond et al. 2008). Consumption of NZMS in the estuary could threaten this life history strategy if the steelhead that eat NZMS suffer reduced growth. Reduced growth on a diet of NZMS has been observed in experiments (Vinson and Baker 2008), but it remains unclear if the fish in our study lagoons consistently eat enough NZMS over time to have an effect on growth. NZMS could also suppress the growth of estuarine fish if they outcompete other prey items. Much work remains to be done on competitive effects of NZMS on other species in estuaries, but recent work in other streams suggests that competition between NZMS and estuarine isopods is weak (Brenneis et al. 2010).

Our stable isotope and diet data from the stream and riparian food webs in upstream and tributary sites where NZMS do not yet occur provides a valuable baseline for comparison in the event that NZMS do expand their distribution to these sites. These data also show that terrestrial production is an important component of the energy budget for stream fish in late summer in these systems and suggest a complementary relationship in which riparian spiders have similar diets of combined aquatic and terrestrial insects (based on similar isotope ratios of spiders and fish). This integrated aquatic-terrestrial food web would be vulnerable to disruption if NZMS become abundant in stream habitats in the Redwood ecosystem.

## References

- Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* **50**:201-220.
- Ben-David, M., T. A. Hanley, and D. M. Schell. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: The role of flooding and predator activity. *Oikos* **83**:47-55.
- Bersine, K., V. E. F. Brenneis, R. C. Draheim, A. M. W. Rub, J. E. Zamon, R. K. Litton, S. A. Hinton, M. D. Sytsma, J. R. Cordell, and J. W. Chapman. 2008. Distribution of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) in the Columbia River Estuary and its first recorded occurrence in the diet of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Biological Invasions* **10**:1381-1388.
- Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: Evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* **53**:164-173.
- Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. *Canadian Journal of Fisheries and Aquatic Sciences* **65**:2242-2252.
- Brenneis, V. E. F., A. Sih, and C. E. de Rivera. 2010. Coexistence in the intertidal: interactions between the nonindigenous New Zealand mud snail *Potamopyrgus antipodarum* and the native estuarine isopod *Gnorimosphaeroma insulare*. *Oikos* **119**:1755-1764.
- Brenneis, V. E. F., A. Sih, and C. E. de Rivera. 2011. Integration of an invasive consumer into an estuarine food web: direct and indirect effects of the New Zealand mud snail. *Oecologia (Berlin)* **167**:169-179.
- Drake, D. C., R. J. Naiman, and J. S. Bechtold. 2006. Fate of nitrogen in riparian forest soils and trees: An N-15 tracer study simulating salmon decay. *Ecology (Washington D C)* **87**:1256-1266.

- Esselstyn, J. A. and R. C. Wildman. 1997. Observations of Juga in the diet of larval Pacific giant salamanders (*Dicamptodon tenebrosus*). *Northwestern Naturalist* **78**:70-73.
- Hall, R. O., Jr., M. F. Dybdahl, and M. C. VanderLoop. 2006. Extremely high secondary production of introduced snails in rivers. *Ecological Applications* **16**:1121-1131.
- Hellmair, M., G. Goldsmith, and A. P. Kinziger. 2011. Preying on invasives: the exotic New Zealand mudsnail in the diet of the endangered tidewater goby. *Biological Invasions* **13**:2197-2201.
- Herbst, D. B., M. T. Bogan, and R. A. Lusardi. 2008. LOW SPECIFIC CONDUCTIVITY LIMITS GROWTH AND SURVIVAL OF THE NEW ZEALAND MUD SNAIL FROM THE UPPER OWENS RIVER, CALIFORNIA. *Western North American Naturalist* **68**:324-333.
- Hoy, M., B. L. Boese, L. Taylor, D. Reusser, and R. Rodriguez. 2012. Salinity adaptation of the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) in the Columbia River estuary (Pacific Northwest, USA): physiological and molecular studies. *Aquatic Ecology* **46**:249-260.
- Moore, J. W., D. B. Herbst, W. N. Heady, and S. M. Carlson. 2012. Stream community and ecosystem responses to the boom and bust of an invading snail. *Biological Invasions* **14**:2435-2446.
- Peterson, B. J. and B. Fry. 1987. Stable Isotopes in Ecosystem Studies. *Annual Review of Ecology and Systematics* **18**:293-320.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* **83**:703-718.
- Sanderson, B. L., C. D. Tran, H. J. Coe, V. Pelekis, E. A. Steel, and W. L. Reichert. 2009. Nonlethal Sampling of Fish Caudal Fins Yields Valuable Stable Isotope Data for Threatened and Endangered Fishes. *Transactions of the American Fisheries Society* **138**:1166-1177.
- Sanzone, D. M., J. L. Meyer, E. Marti, E. P. Gardiner, J. L. Tank, and N. B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. *Oecologia* **134**:238-250.
- Vinson, M. R. and M. A. Baker. 2008. Poor growth of rainbow trout fed New Zealand mud snails *Potamopyrgus antipodarum*. *North American Journal of Fisheries Management* **28**:701-709.
- Zabel, R. W. and S. Achord. 2004. Relating size of juveniles to survival within and among populations of chinook salmon. *Ecology* **85**:795-806.

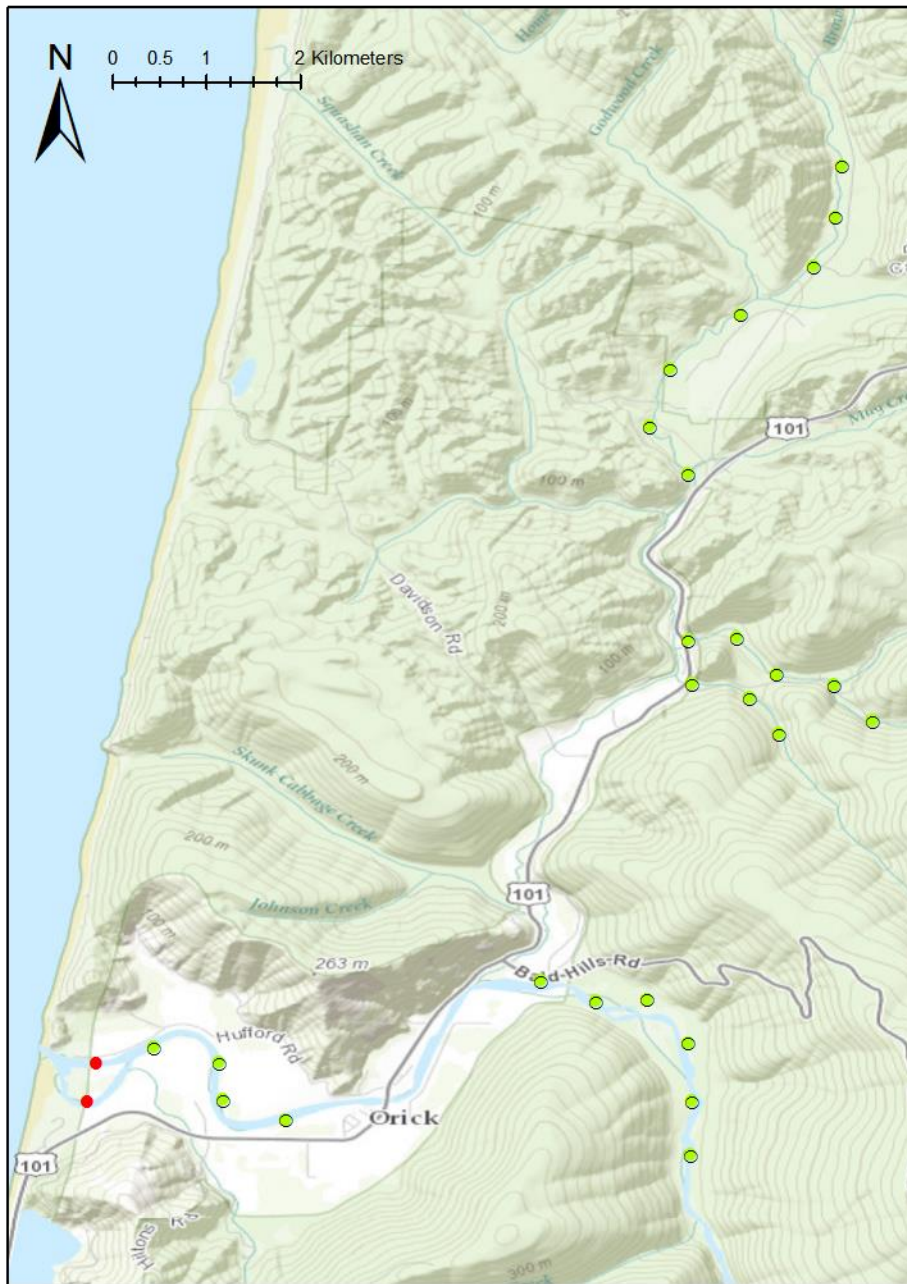


Figure 1 Survey sites and New Zealand mud snail distribution in Redwood Creek and tributaries in 2011 and 2012. Each point is the downstream end of a 500 m survey reach. Red points indicate that New Zealand mud snails were detected in the reach; green points indicate that New Zealand mud snails were not detected in the reach. Starting from the north, the streams with sample sites are Prairie Creek, Lost Man Creek, Little Lost Man Creek, and main stem Redwood Creek.

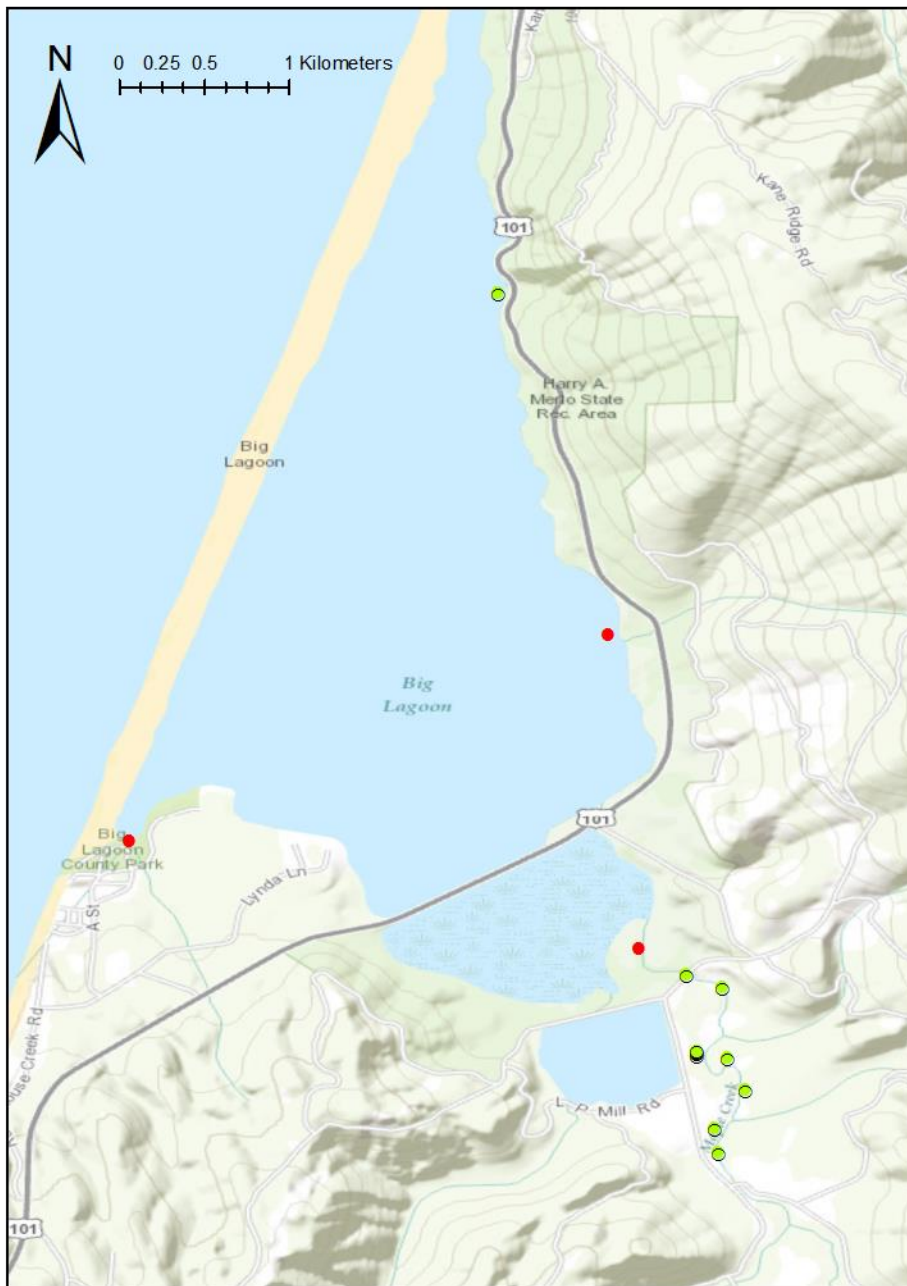


Figure 2 Survey sites and New Zealand mud snail distribution in Maple Creek and other tributaries of Big Lagoon in 2012. Each point is the downstream end of a 200 m survey reach. Red points indicate that New Zealand mud snails were detected in the reach; green points indicate that New Zealand mud snails were not detected in the reach. For small tributaries with only a single sample reach, NZMS were only detected at the downstream end proximate to the lagoon.

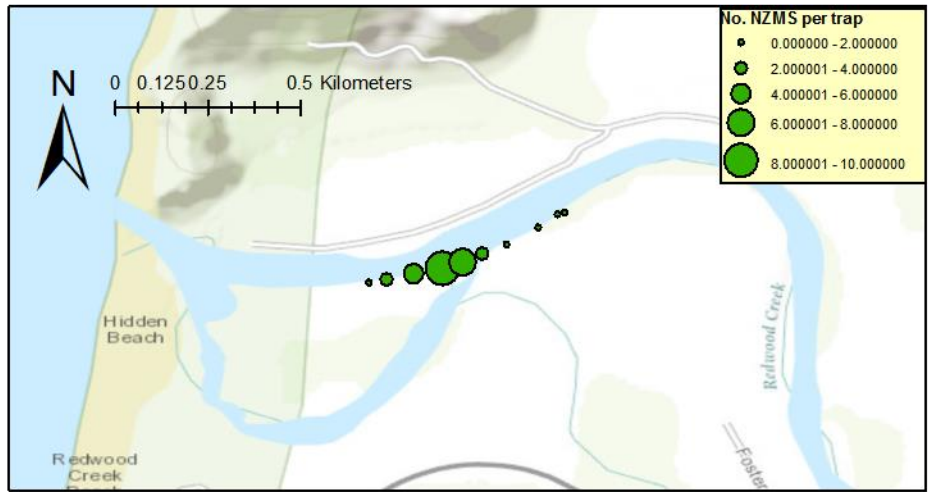


Figure 3 Abundance of New Zealand mud snails in the estuary/lagoon of Redwood Creek. The abundance shown is the average number of snails captured on two replicate Hester-Dendy passive samplers at each location from September-October 2012.

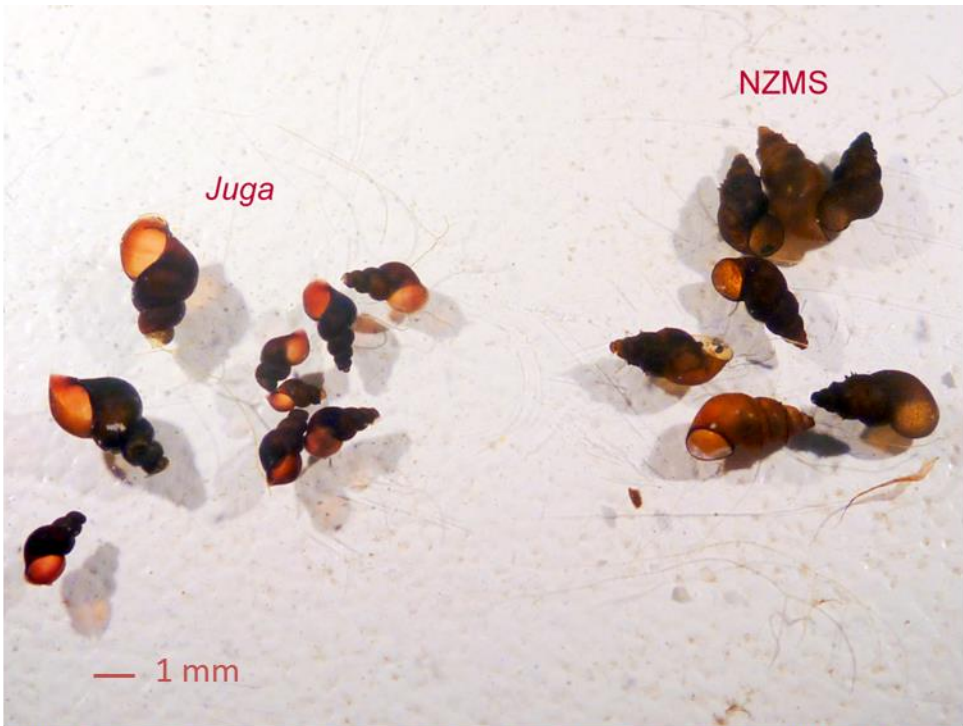


Figure 4 Juvenile *Juga* spp. snails and similar-sized adult New Zealand mud snails (NZMS) from Redwood Creek. Note the small spiny ridge along the whorl of the NZMS shell. In life, both species have an operculum that closes over the shell aperture. Photo by Darren Ward.

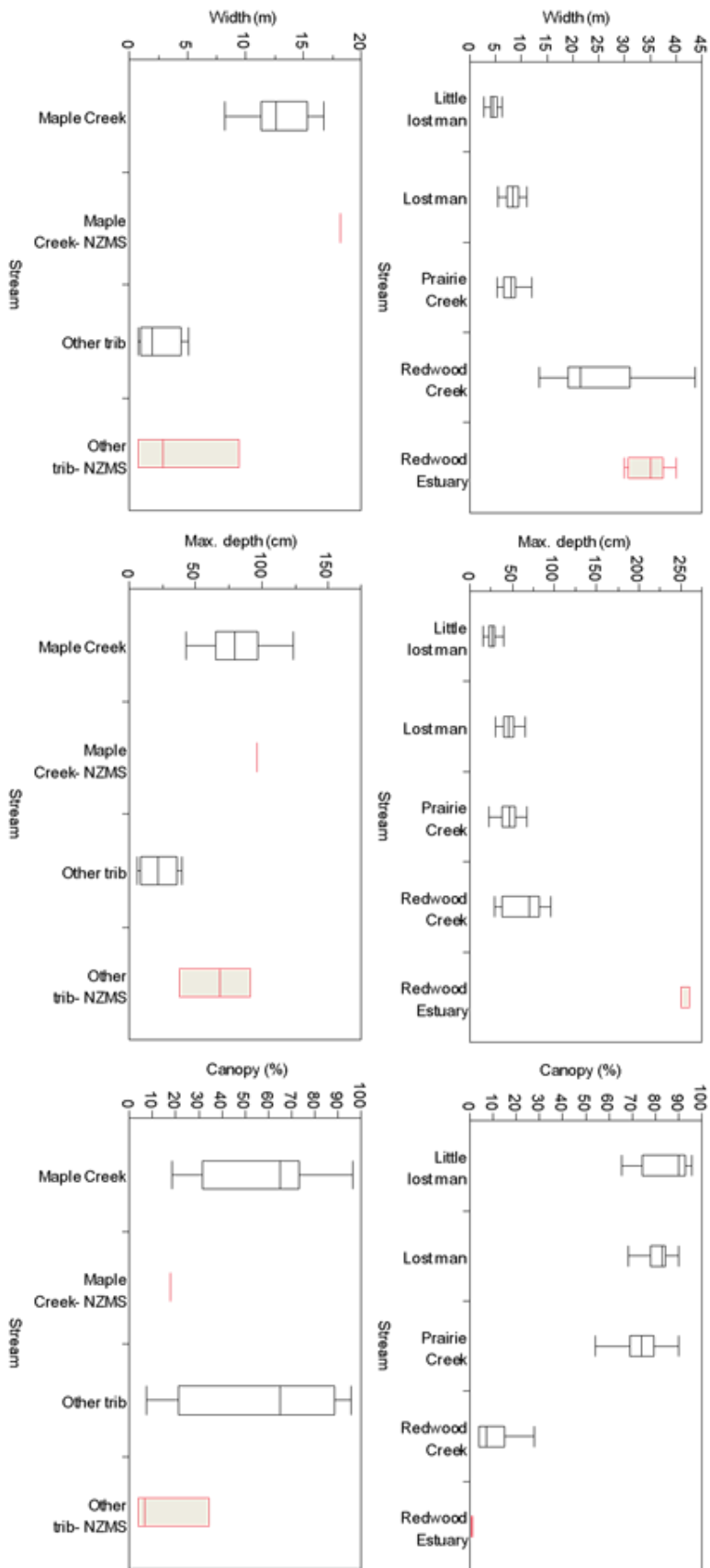


Figure 5 Habitat characteristics at sample sites where New Zealand mud snails were not detected (black box plots, no fill) and sites where they were detected (red box plots with gray fill) in the Redwood Creek basin (top row) and Maple Creek and other tributaries of Big Lagoon (bottom row).



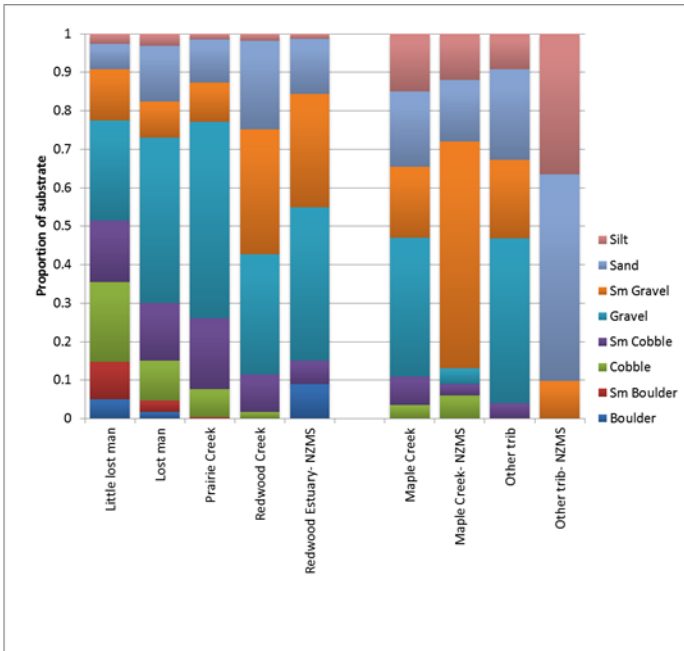


Figure 6 Substrate composition at survey sites.

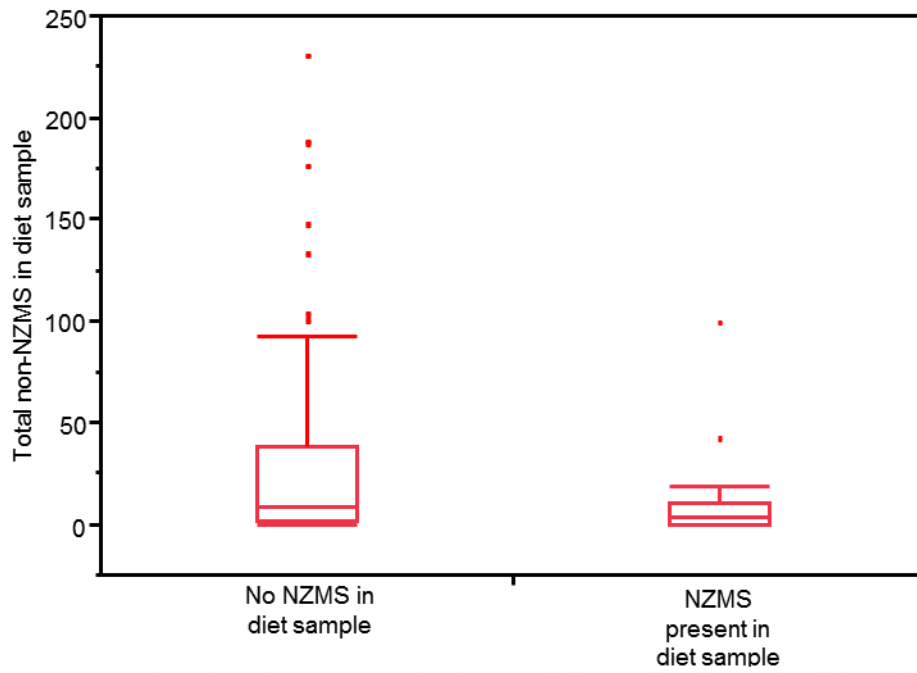


Figure 7 Total number of prey items in the diet sample for steelhead trout that did or did not have New Zealand mud snails (NZMS) in the sample. Mean values are significantly different (Analysis of square-root transformed data;  $F_{1,148}=5.6$ ,  $P=0.02$ )

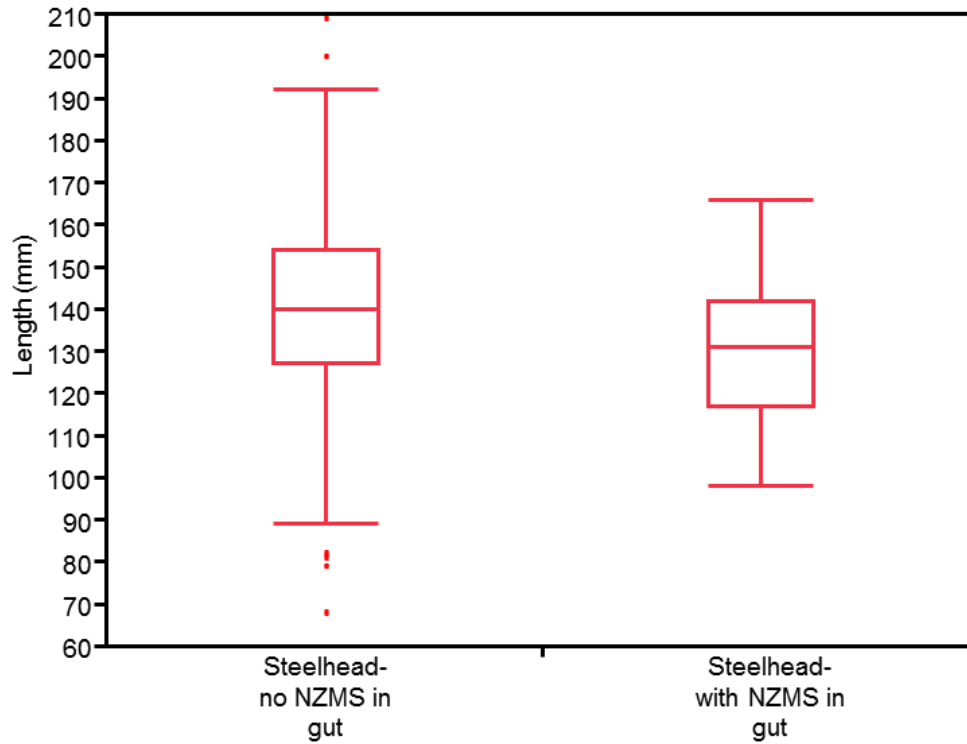


Figure 8 Size distribution of steelhead trout from the Redwood Creek lagoon that did and did not have New Zealand mud snails in their stomach during diet sampling in 2011 and 2012. There is no significant difference in the means ( $F_{1,148}=2.2$ ,  $P=0.14$ )

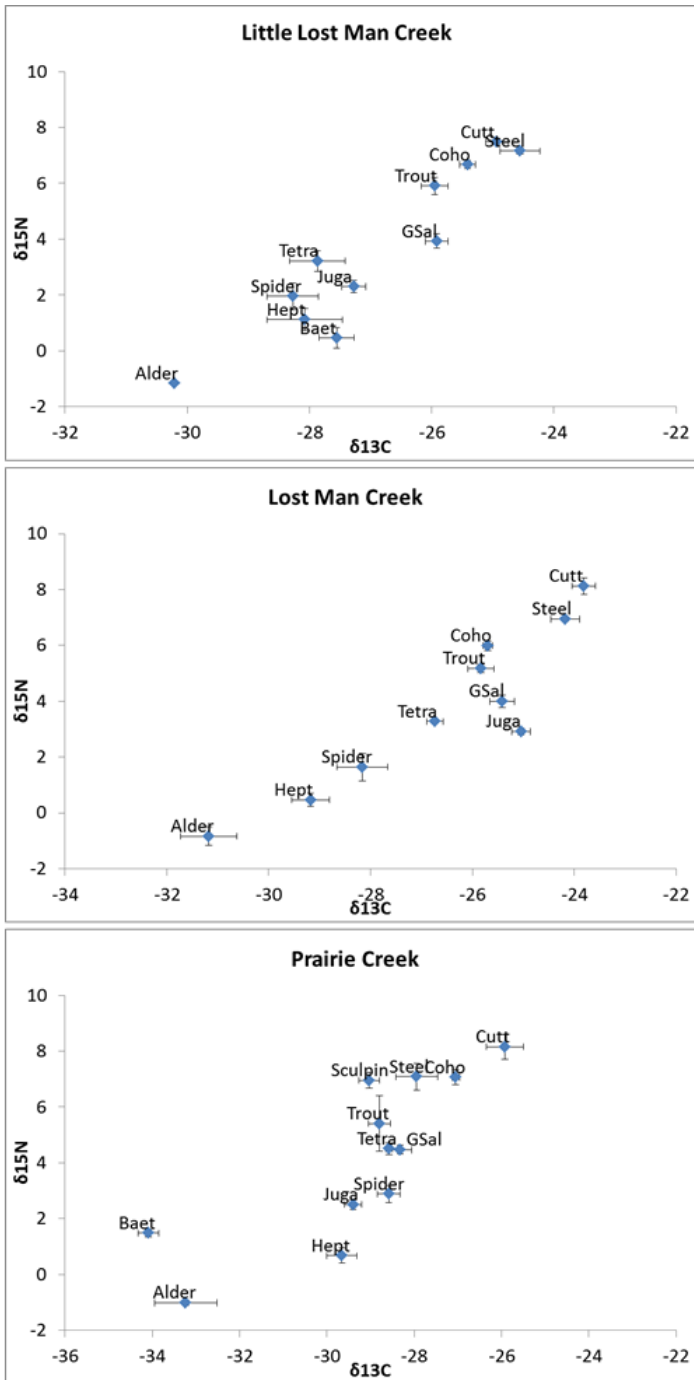
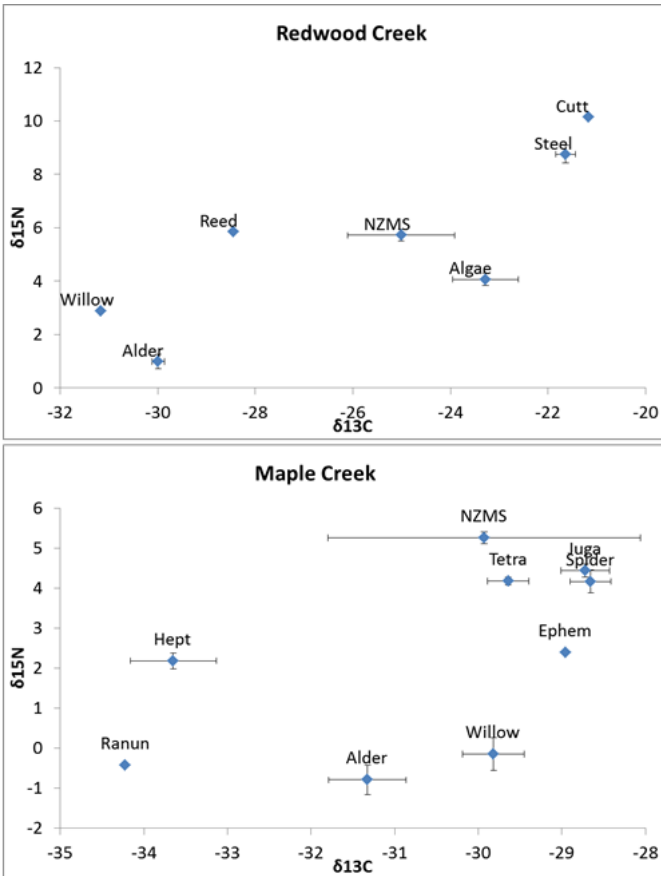


Figure 9 Mean  $\pm$ SE stable isotope ratios for organisms at tributary sites in the Redwood Creek basin. Points are labeled with abbreviated taxa codes: Alder=alder trees, Baet=baetid mayflies, Coho=juvenile coho salmon, Cutt=cutthroat trout, Ephem=ephemerellid mayflies, GSal=coastal giant salamander, Hept=heptegeniid mayflies, Juga=juga snails, Sculpin=prickly sculpin, Spider=riparian spider (excluding tetragnathids), Steel=steelhead trout, Tetra=tetragnathid spider, trout=juvenile trout (species unknown).



**Figure 10** Mean  $\pm$ SE stable isotope ratios for organisms at tributary sites in the Redwood Creek and Maple Creek basins where NZMS are established. Points are labeled with abbreviated taxa codes: Alder=alder trees, Baet=baetid mayflies, Coho=juvenile coho salmon, Cutt=cutthroat trout, Ephem=ephemerellid mayflies, GSal=coastal giant salamander, Hept=heptegeniid mayflies, Juga=juga snails, Sculpin=prickly sculpin, Spider=riparian spider (excluding tetragnathids), Steel=steelhead trout, Tetra=tetragnathid spider, trout=juvenile trout (species unknown), Willow=willow tree.