

Research Article

Establishment and ecological integration of the New Zealand mud snail in Spirit Lake, Mount St. Helens, Washington State, USA

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Abstract

Mount St. Helens National Volcanic Monument was designated by the U.S. Congress in 1982 to conserve the landscape for natural regeneration, scientific research, education, and cultural resource preservation. However, this designation has not eliminated threats from the introduction of non-native species. The non-native New Zealand mud snail (NZMS), *Potamopyrgus antipodarum*, was first observed in 2016 along the SW shore of Spirit Lake at the foot of Mount St. Helens, despite the lake's closure to public recreation and isolation from other known sites harboring NZMS. Our study mapped native and non-native snails on aquatic macrophytes in Spirit Lake, analyzed NZMS eDNA in Spirit Lake and surrounding waters, measured stable isotopes in snails and their food sources, and analyzed rainbow trout (*Oncorhynchus mykiss*) gut contents from a twenty-year survey to examine the patterns of spatial distribution, habitat occurrence, and resource use. Our results show that NZMS colonies were likely first established along the SW shore of Spirit Lake in 2015, and presently remain largely confined to the vegetated littoral zone along this same shoreline. The native snail species *Gyraulus deflectus* and NZMS co-occur on multiple macrophyte species, and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope data reveal they are consuming the same food sources, but no evidence was seen for competitive exclusion. The abundance and frequency of NZMS found in rainbow trout gut contents have increased since 2015 with a significant portion undigested. In addition, stable isotope analysis shows a negligible trophic tie between snails (both NZMS and *G. deflectus*) and rainbow trout, which may signal longer-term impacts on fish populations. Characterizing this invasion spatially and temporally elucidates the factors facilitating and hindering the spread of NZMS in a relatively young and dynamic subalpine lake ecosystem closed to public recreation, and may inform current and future management decisions.

Key words: rainbow trout, *Potamopyrgus antipodarum*, aquatic macrophyte, stable isotope analysis, *Gyraulus deflectus*

Introduction

Globally, invasive species such as New Zealand mud snails (NZMS), *Potamopyrgus antipodarum* (Gray, 1843), have proven to decrease biodiversity and threaten the overall health of invaded ecosystems (Gallardo et al. 2016). First documented in the Western U.S. in 1987 (Bowler 1991), NZMS are now common in western freshwater systems and can exceed densities of 500,000 individuals m⁻² (Richards et al. 2001; Hall et al. 2003). NZMS are parthenogenetic and oviparous with invasive communities consisting entirely of clonal females able to brood live young; a single snail has the potential to colonize a new ecosystem (Winterbourn 1970; Jokela et al. 1997). Once established, NZMS can dominate secondary production (Hall et al. 2006), nitrogen and carbon cycling (Hall et al. 2003), and the total biomass of macroinvertebrates in freshwater systems (Kerans et al. 2005). NZMS have high dietary plasticity; grazing on periphyton, macrophytes, benthic detritus, fungi, etc. (Rakauskas et al. 2017; Geist et al. 2022), and therefore may compete with an array of native macroinvertebrates for resources and habitat (Kerans et al. 2005). Their ability to survive desiccation, wide temperature ranges (Alonso and Castro-Diez 2012), and digestion (Vinson and Baker 2008), in addition to their reproductive capacity, makes them a formidable invasive species to manage.

Disturbed landscapes, like Spirit Lake in Mount St. Helens National Volcanic Monument, are especially vulnerable to invasion. Spirit Lake was in the direct path of the massive debris avalanche, explosive lateral blast, and subsequent pyroclastic flows of the cataclysmic May 18th, 1980 eruption of the Mount St. Helens volcano (Swanson and Major 2005). The cumulative volcanic deposits dramatically changed the morphometry of the lake, creating a shallower basin with a larger surface area (Dahm et al. 2005). Elevated lake temperatures and anoxia resulting from the eruption effectively depopulated the lake as all oxygen-dependent organisms perished (Wissmar 1990; Larson 1993; Larson 1994; Larson et al. 2006). Today many species have returned to Spirit Lake, but the ecosystem as a whole remains permanently altered, with trophic state index (TSI) (Carlson 1977) in the lower mesotrophic to upper oligotrophic range (Gawel et al. 2018). The post-eruption expanded shallows fostered the development of a macrophyte-rich littoral ecosystem which has provided food and habitat for grazers, both native and non-native. This created an ideal habitat for NZMS. This invasive, non-native species was first seen in Spirit Lake along the lake's southwestern shore in 2016, and thus a new species was inserted into the lake's food web.

Rainbow trout (*Oncorhynchus mykiss*) were first discovered to have repopulated Spirit Lake in 1993 (Lucas and Weinheimer 2003), and were well-established by 2000 when annual rainbow trout growth measurements and diet studies began (Blackman et al. 2018). Rainbow trout currently occupy the role of apex aquatic predator in Spirit Lake and are a keystone species connecting aquatic and terrestrial food webs (Bisson et al. 2005). The diet of rainbow trout in Spirit Lake consists primarily of large quantities of small macroinvertebrate prey (Blackman et al. 2018). In previous gut content studies of post-eruption Spirit Lake rainbow trout, three snail species, *Gyraulus deflectus* (native), *Lymnaea humilis* (native), and *Lymnaea auricularia* (non-native), comprised a significant portion of sampled fish diets (Blackman et al. 2018). Fish have been shown to consume prey in proportion to their abundance in an environment (Bres 1986). Thus, NZMS may represent an increasingly abundant prey item in the Spirit Lake rainbow trout diet if their population expands, with potentially negative consequences for fish condition and fitness. Vinson and Baker (2008) found rainbow trout feeding on NZMS in laboratory studies and in the field in Utah had decreased body mass and poorer condition than those not feeding on NZMS.

Spirit Lake serves as a unique setting to study NZMS invasion because it is a relatively new, intensely disturbed ecosystem that is isolated from the typical industrial (transporting of aquaculture products, including fish hatchery stocking) and recreational activities (boating and fishing) often associated with the spread of NZMS (Alonso and Castro-Díez 2008; Geist et al. 2022). In this study, we mapped the distribution and corresponding abundance of NZMS in Spirit Lake through visual detection surveys, aquatic macrophyte sampling, fish gut contents, and eDNA analysis in order to establish the current spatial extent of NZMS habitation and provide a baseline from which to monitor future spread. We also conducted carbon and nitrogen stable isotope analysis of native and non-native snail specimens, as well as other abundant and common aquatic taxa, including rainbow trout, to determine the potential for resource competition between snail species and elucidate the integration of NZMS into the Spirit Lake food web (McCue et al. 2019).

Methods

Site characterization

Spirit Lake is located 8 km northeast of the summit of Mount St. Helens in southwestern Washington State, USA (Fig. 1). Following the 1980 eruption of the volcano the altered lake now has a surface area of 11 km² (more than twice pre-eruption) and a mean depth of 23 m (38% less than pre-eruption; Gawel et al. 2018). The lake's drainage area was reduced 32% to 26.4 km² by landscape changes to the flanks of the volcano and from the resulting eruptive deposits (Dahm et al. 2005; Swanson and Major 2005; Gawel et al. 2018). In addition, deep volcanic deposits obliterated the pre-eruption North Fork Toutle River that was the outlet for discharging water from Spirit Lake. In the absence of an outlet the lake's level rose creating the potential for a catastrophic breach. In order to mitigate the risk of a breach of the volcanic debris dam and the potentially catastrophic flooding of downstream communities the US Army Corps of Engineers installed an emergency pumping station to temporarily maintain safe water levels in the lake. As a longer-term solution a tunnel outlet through the ridge in the NW quadrant of the basin was completed in 1985 to reconnect the lake to the Toutle River (via South Coldwater Creek), which then drains through the Cowlitz River to the Columbia River beyond (Fig. 2). Spirit Lake continues to be managed by the US Forest Service as part of Mount St. Helens National Volcanic Monument (created in 1982), with restricted public access to the lake, including a prohibition on boating, swimming, and public fishing (Public Law 97-243 §4, 1982: <https://uscode.house.gov/statutes/pl/97/243.pdf>).

eDNA Sampling

On two dates in October 2019 we gathered water samples from 18 sites for eDNA testing (Fig. 2). Sites included nearshore waters along the SW shore of Spirit Lake (where NZMS had been observed annually since 2016), tributary streams flowing into Spirit Lake along this shoreline, nearby isolated ponds, and downstream in Coldwater Creek and Coldwater Lake. Flow rates in the tributary streams entering Spirit Lake were generally low in October (0.5–90 L s⁻¹ measured in 2008; Gawel et al. 2018). Flow rates exiting the tunnel outlet and into Coldwater Creek were approximately 2800 L s⁻¹ at the time of sampling (Gawel et al. 2018; US Geological Survey 2024). At each site two replicate 1000 mL samples were collected in sterile one-liter Nalgene bottles following published protocol (Goldberg and

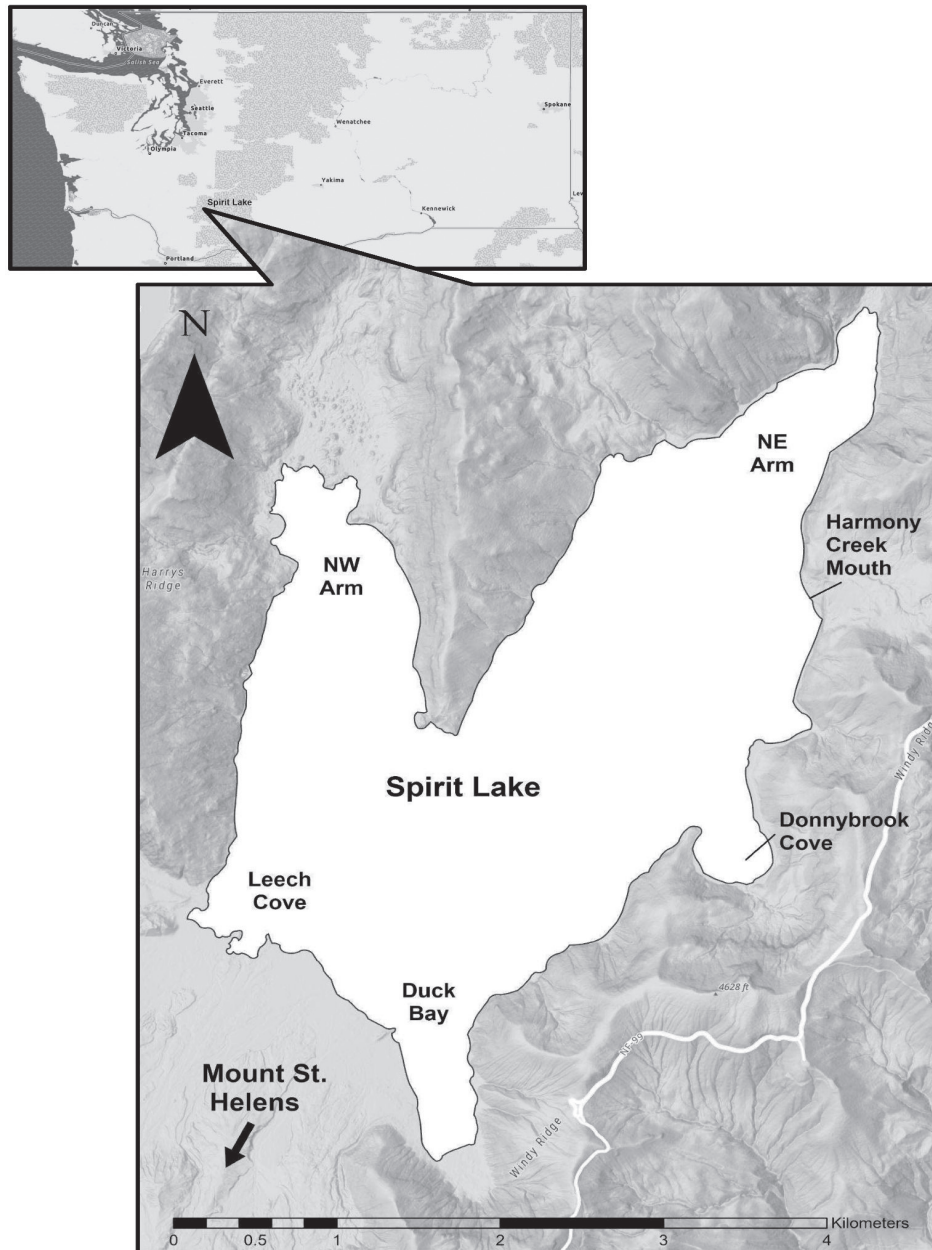


Figure 1. Map of Spirit Lake, Washington State, USA, with embayments indicated.

Strickler 2017). Samples were placed on ice and filtered within 12 hours of collection. Both replicates were analyzed for 13 of the sampling sites with single samples run for the remaining 5 sites, in addition to 2 field blanks. Filtered samples and field blanks were delivered to Dr. Caren Goldberg at Washington State University for analysis using published methods (Goldberg et al. 2013).

Aquatic macrophyte and snail sampling

Sampling for aquatic macrophytes with attached snails occurred on multiple dates during the summers of 2021 and 2022. Samples of common and abundant macrophyte taxa (*Myriophyllum spicatum*, Charales (Class, Charophyceae), *Ceratophyllum demersum*, *Potamogeton amplifolius*, and filamentous algae) were gathered using a plant rake at water depths ranging from 1 to 5 m. Macrophyte samples were floated in water in a clear plastic tub and agitated by hand for 30 s to release any attached

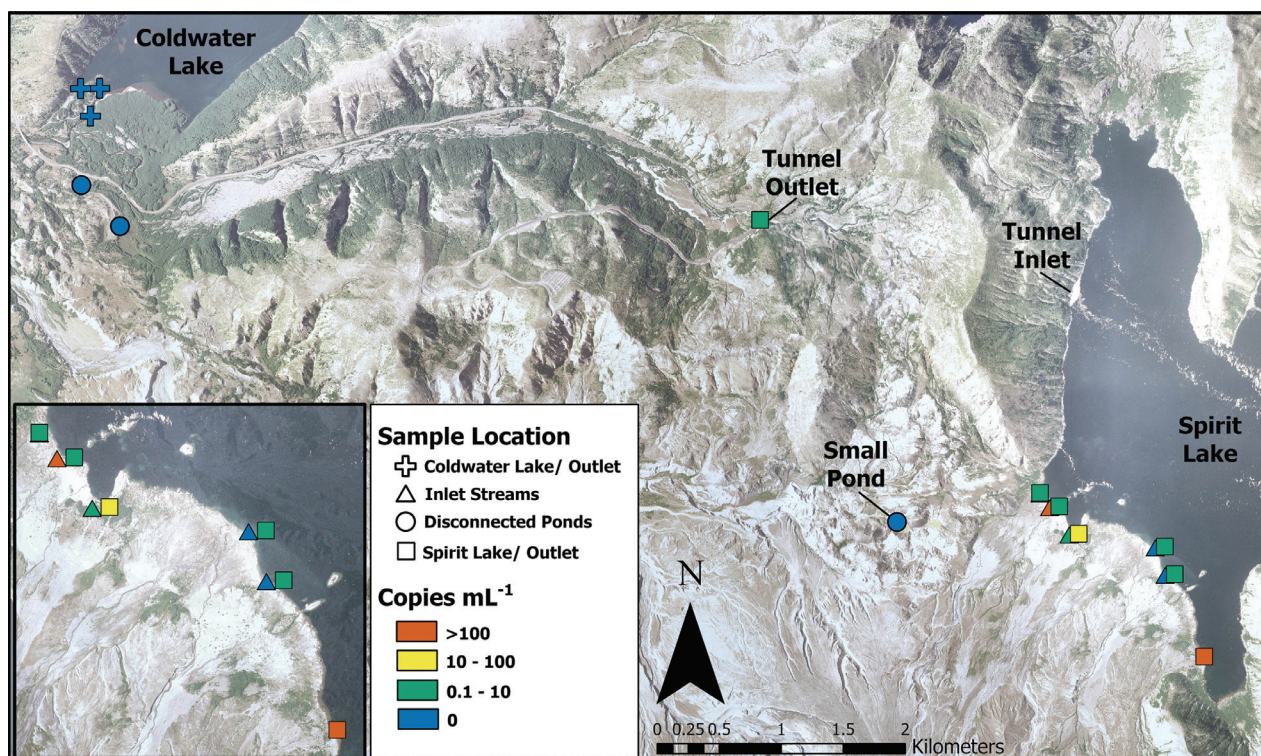


Figure 2. Concentrations (copies mL⁻¹) of NZMS eDNA measured at sampling sites in and around Spirit Lake in 2019. Each symbol represents the mean of paired samples.

snails from the vegetation. Snails were allowed to sink to the bottom and separated from the vegetation. Subsequent periodic examination of the vegetation after agitation showed this method to be very effective at separating snails from vegetation, with < 1% of total snail abundance remaining on any vegetation sample. Any additional snails found in rechecked samples were not included in sample totals for method consistency. Macrophytes were then removed by hand, identified, and vegetation volume was estimated using a graduated beaker. The area of vegetation sampled was estimated using the diameter of the rake head, which was rotated on the pole axis to collect a circular sample of macrophytes. The remaining solids and detached snails were then transferred to plastic containers on ice for transport to University of Washington Tacoma for analysis. Snails were separated from any remaining solids, identified, and manually counted under a dissecting microscope. A subset of macrophyte and snail samples collected in 2021 were kept for stable isotope analysis.

Fish sample collection and gut content analysis

Annual sampling of rainbow trout began at Spirit Lake in 2000 using hook and line and gillnet methods (Suppl. material 1: table S1; Blackman et al. 2018). Due to the unpredictability of weather and the Spirit Lake log mat the majority of these surveys took place in Duck Bay in the SW quadrant of the lake (Fig. 1). However, in 2021 additional hook and line sampling was conducted in locations paired with macrophyte surveys to provide more insight into snail distribution throughout Spirit Lake. Rainbow trout caudal fins from fish collected in 2021 (n= 42) were removed, transported on ice, and dried for stable isotope analysis. Gastrointestinal tracts (fish guts) were collected (Suppl. material 1: table S1) from destructive hook and line sampling, gill netting, and opportunistically from catch-and-release sampling when fish perished unintentionally. Rainbow trout gut sam-

ples were transported to our lab in 90% ethanol where they were dissected, with contents removed from the entirety of the gastrointestinal tract and stored again in 90% ethanol. Snails were then separated from the gut contents, identified, and counted under a dissecting microscope. *P. antipodarum* and *G. deflectus* individuals from a subset of rainbow trout guts sampled in 2021 containing both species ($n = 10$ fish) were stored after counting in 90% ethanol for stable isotope analysis (Suppl. material 1: table S2). Midge larvae (Chironomidae) were also present in the gut contents of 9 of these 10 trout, and they were also stored in 90% ethanol for stable isotope analysis (Suppl. material 1: table S2).

Arthropod and amphibian sample collection

Aquatic insect larvae samples (Ephemeroptera, Plecoptera, Trichoptera, Odonata), aquatic mite samples (*Hydrachna* species), and amphibian tadpole samples (*Anaxyrus boreas*) were collected from benthic (log mat and littoral) substrates in the summers of 2018 and 2021. Arthropod specimens were scraped off submerged substrates with a modified brush and picked off substrates with forceps, and amphibians were captured with handheld dip nets. Emergent Ephemeroptera were collected from emergence traps (amphibious emergence trap - black and white, BugDorm, Mega-View Science Co.) over logs and the lake surface. All samples were transported on ice, and stored frozen until they were prepared for stable isotope analysis.

Stable isotope sample preparation

Macrophyte samples were dried at 40 °C to a constant weight, and then pulverized in a mortar and pestle. Aquatic arthropod samples that were large enough were dissected, and head, thorax and legs were preferentially subsampled for analysis. Smaller arthropods, including mites and midge larva, were kept as intact individuals, and whole snail bodies were carefully extracted from their shells. Kiljunen et al. (2006) found no relationship between the change in $\delta^{13}\text{C}$ values after lipid extraction and the original carbon (C) to nitrogen (N) ratios for aquatic invertebrates so, to avoid sample loss, invertebrates were not lipid-extracted. Tadpole tails and caudal fins were subsampled and sonicated in a 2:1 chloroform and methanol solution twice for 30 minutes to remove lipids. Graham et al. (2016) determined that there was minimal benefit to decalcifying caudal salmonid fins to remove potential inorganic carbon, so rainbow trout samples were not acid-treated, but were wiped with methanol to clean surface contaminants. The distal 1–2 mm tip of the fin was subsampled for analysis since it represented the most recent period of growth, and because the tip has the highest membrane relative to ray tissues, which reduces the variability among individual trout due to sample composition (Hayden et al. 2015). All animal samples were dried at 40 °C to a constant weight. Macrophyte and animal samples were weighed into tin capsules to a target mass of 1–3 mg, and multiple individuals ($n = 3\text{--}5$) were combined into composited samples for the snails and the smaller arthropods. Stable isotope analysis samples are summarized in Suppl. material 1: table S2.

Stable isotope sample analysis

All samples were analyzed for carbon and nitrogen stable isotope ratios (reported as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) at the University of Colorado Earth Systems Stable Isotope Laboratory using an elemental analyzer coupled to a Thermo Delta V Isotope Ratio Mass Spectrometer. Sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are reported relative to Vienna Pee Dee Belemnite and air N_2 standards, respectively.

Stable isotope data analysis

We assumed that the isotopic values of all samples were seasonally comparable and reflected the spring and summer growth season (May–September) in Spirit Lake. We used elemental C and N content to verify that invertebrate samples (comprised of chitin, proteinaceous materials, and soft tissues) were comparable among individuals; weight percent C/N ratios were within the range of 3.2 – 5.5 (except for 6 samples with higher ratios that were not isotopically anomalous and thus retained in the dataset). The tadpole tail and fin samples were fleshy and assumed to be primarily composed of skin, muscle, and connective tissues, and all C/N ratios fell within a range of 4.2–4.3. The rainbow trout fin tip sample C/N ratios were relatively invariant (range = 2.9–3.4), which suggested there were not substantial differences in tissue composition. We confirmed that the larval and emergent Ephemeroptera $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were not significantly different (t-test, $p > 0.05$) and combined these into a single dataset for that taxon. We used data collected from the few 2021 macrophyte samples to supplement a published Spirit Lake 2018 macrophyte dataset (Shinneman et al. 2024) and confirmed that the isotopic values were comparable, with only one $\delta^{15}\text{N}$ value slightly outside the range of the published values. We also used isotopic values for Spirit Lake periphyton reported in Shinneman et al. (2024). We used average isotopic trophic discrimination factors ($\delta^{13}\text{C} = 1.5\text{‰}$, $\delta^{15}\text{N} = 1.3\text{‰}$) calculated from a snail feeding study (Li et al. 2018) to directly compare snail isotopic values to those of their most abundant diet sources (periphyton and macrophytes). Since this was not a comprehensive dietary analysis for either snail species, we did not attempt to quantitatively estimate the contributions of diet sources with an isotopic mixing model. We used isotopic trophic discrimination factors determined experimentally from trout ($\delta^{13}\text{C} = 1.0\text{‰}$, Jensen et al. 2012 and $\delta^{15}\text{N} = 1.7\text{‰}$, Heady and Moore 2012) to directly compare trout and snail values and demonstrate the improbability of snails as a substantial assimilated diet source. Our study was not a dietary analysis for the rainbow trout and future research may focus on determining the relative contributions of diet sources in Spirit Lake.

Results and discussion

Temporal distribution of NZMS

Rainbow trout sampling was performed from 2000–2021 along the SW shore of Spirit Lake (Fig. 3; Suppl. material 1: table S1). This choice of sampling location was due to ease of researcher access and initially conducted to follow changes in fish population structure and diet, but it may have been fortuitous in recording the colonization of the lake by NZMS as their population has since been found to be concentrated along this shore. Although NZMS were first detected visually along the SW shore of Spirit Lake in 2016, subsequent analysis of preserved rainbow trout gut content samples found the presence of NZMS in the lake starting in 2015 (Fig. 3), providing the earliest evidence of NZMS invasion of Spirit Lake. The mean abundance of NZMS in gut samples in 2015 and 2016 was very low, but that number increased substantially in 2017 and subsequent years. Annual NZMS abundance in rainbow trout guts in Spirit Lake likely represents a combination of differences in sampling date, macroinvertebrate emergence timing, macrophyte abundance, and individual fish foraging preferences (Bres 1986; Bennett et al. 2015; Blackman et al. 2018) all in conjunction with year-to-year snail population changes. Therefore, although our fish gut content data provides clear evidence of

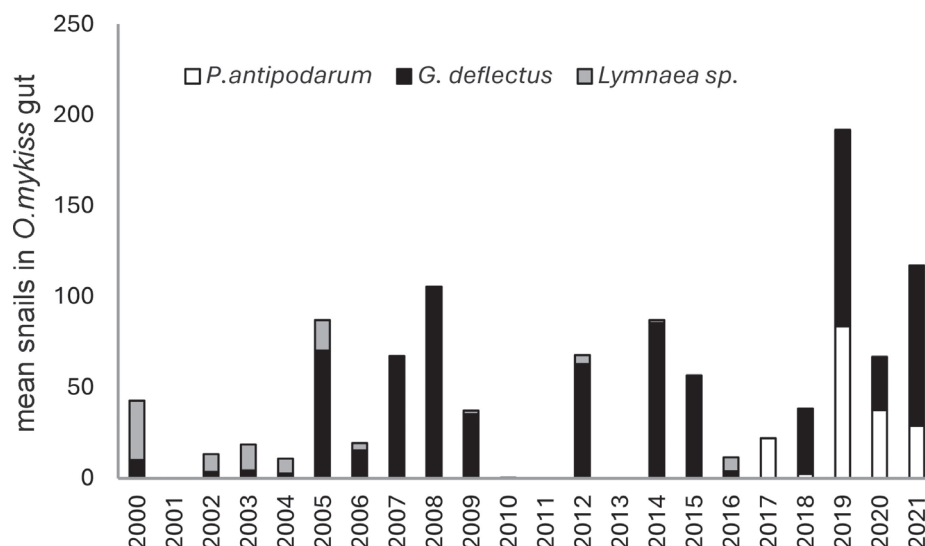


Figure 3. Mean number of snails by species in rainbow trout (*O. mykiss*) gut collected in Duck Bay along the SW shore of Spirit Lake ($n \geq 6$, except $n = 0$ in 2011 and 2013, $n = 1$ in 2001 and 2017).

significantly higher numbers of NZMS in the diet of rainbow trout individuals in more recent years (2019–2021) compared to early years (2015–2016), it is difficult to translate this pattern more broadly to accurately estimate temporal NZMS demographic trends in the lake as sampling intensity and timing was not consistent over this time.

Spatial distribution of NZMS

Our eDNA results showed non-zero concentrations ranging from 2.37–173.31 copies mL^{-1} of NZMS DNA in all samples collected in shallow waters along the SW shore in Spirit Lake, while no detectable DNA copies were measured in field blanks. Concentrations ranging from 1.74–102.32 copies mL^{-1} were found in slower-moving tributaries feeding into the SW shore of the lake, while no detectable DNA copies were measured in the faster-moving, unstable Willow Springs tributary (the second southernmost inlet stream along SW shoreline; Fig. 2). Very low DNA concentrations (0.12–0.35 copies mL^{-1}) were found immediately downstream of the outflow tunnel in S. Coldwater Creek. However, DNA was not detected in the remainder of S. Coldwater Creek further downstream, Coldwater Lake, or in the isolated pond SW of Spirit Lake in the debris avalanche deposit. Therefore, our data support the assertion that in 2019 NZMS invasion was limited to Spirit Lake and its lower velocity tributary streams.

eDNA results were consistent with multiple visual presence/absence surveys conducted in 2019–2021 that confirmed the presence of NZMS along the SW shoreline of Spirit Lake and in slow-moving, vegetated tributaries flowing into the lake. NZMS were not visually detected in surveys conducted in the fast-moving Willow Springs tributary, nor in Coldwater Creek or Coldwater Lake. A previous study using eDNA for detecting NZMS (Ponce et al. 2021) found a significant correlation between eDNA concentrations and NZMS abundance, although sample size was small and heavily weighted by one sampling site. The very low concentration of DNA found downstream of the outflow tunnel may have signaled DNA escaping the tunnel and does not necessarily require animals to have been present. Goldberg et al. (2013) showed that eDNA was still detectable in water that contained a single NZMS snail 21–44 days after snail removal, and based

on these data, it is plausible that DNA was flushed from Spirit Lake and detected downstream. Thus, eDNA data and visual surveys corroborate the presence of NZMS along the SW shore of Spirit Lake and some of the connected tributaries, but also that the invasion was limited to Spirit Lake and its lower tributary reaches in proximity to the lake.

Like many benthic aquatic macroinvertebrates, stable substrates and limited flow velocities are required for NZMS population establishment (Holomuzki and Biggs 2000; 2007). The Willow Springs tributary is prone to seasonally high velocities and stream channel avulsion. The Spirit Lake outflow channel also has high velocities. Therefore, the distribution of NZMS throughout the Spirit Lake tributary/outflow system is consistent with studies of NZMS habitat preferences and flow velocity tolerance. Although the Spirit Lake outflow velocity likely decreases the likelihood of NZMS establishment within the outflow channel, it would not inhibit their potential to become suspended and spread downstream of the lake (Geist et al. 2022).

Macrophyte-associated sampling of NZMS and other resident snails was performed in 2021–2022 to create a finer scale map (Fig. 4) of the spatial extent and density of snail species in the littoral zone of Spirit Lake. Our results show that NZMS were concentrated primarily along the SW shore in Leech Cove and Duck Bay (mean densities 252,632 and 104,463 individuals m^{-3} , respectively; Table 1) with nearshore densities of NZMS declining quickly away from the SW shore. NZMS were not detected on macrophytes from any samples in the NE or NW arms of the lake, including near the outlet tunnel, in Donnybrook Cove, or near the one public access point to Spirit Lake at the outlet of Harmony Creek (Fig. 1).

In 2021, examining rainbow trout gut contents as a spatially-linked bioindicator of NZMS presence/abundance, we sampled rainbow trout at four locations around Spirit Lake to see how fish consumption (Fig. 5; Suppl. material 1: table S3) paired with direct snail-vegetation sampling (Fig. 4). We found that NZMS abundance in fish guts was lowest in rainbow trout in Donnybrook Cove (<1 snail per fish), where vegetation sampling did not detect NZMS in 2021–2022. The other locations sampled for fish in 2021 were either along the SW shore, or nearby, and the elevated numbers of NZMS in fish guts in these locations (Fig. 5; Suppl. material 1: table S3) is consistent with vegetation sampling. Fish sampling in other locations in 2021 was prevented by weather, log mat location interference, and boat motor malfunction. Gut contents provide only surrogate data for actual snail densities in the lake, however, previous studies have found that rainbow trout consume prey in proportion to their relative abundance in relation to other prey species (Bres 1986). Although in our study we only have three regions delineated that have overlap between vegetation and fish gut data (NW Arm, Duck Bay, and Leech Cove), and thus low statistical power, we do find a positive correlation between snail abundance on vegetation and in *O. mykiss* digestive tracts for NZMS and for all three snail species (Suppl. material 2: fig. S1 (a) and (b), respectively) across the 3 sampling regions, although with large variation. This suggests that rainbow trout individuals frequent more localized feeding ranges within the lake, limiting their potential as a vector of NZMS spread in Spirit Lake. Supporting this idea, a study by Watson et al. (2019) found relatively small daytime home ranges for adult rainbow trout in Gnawed Lake (mean 1300 m^2). However, as NZMS reproduce asexually and quite readily survive passage through fish guts (Vinson and Baker 2008), even the small number of NZMS found in fish in Donnybrook Cove would suggest that transport to other locations in the lake by rainbow trout as a vector is likely. Since this has not occurred yet, it is possible that other factors are preventing NZMS colonization in other areas of the lake.

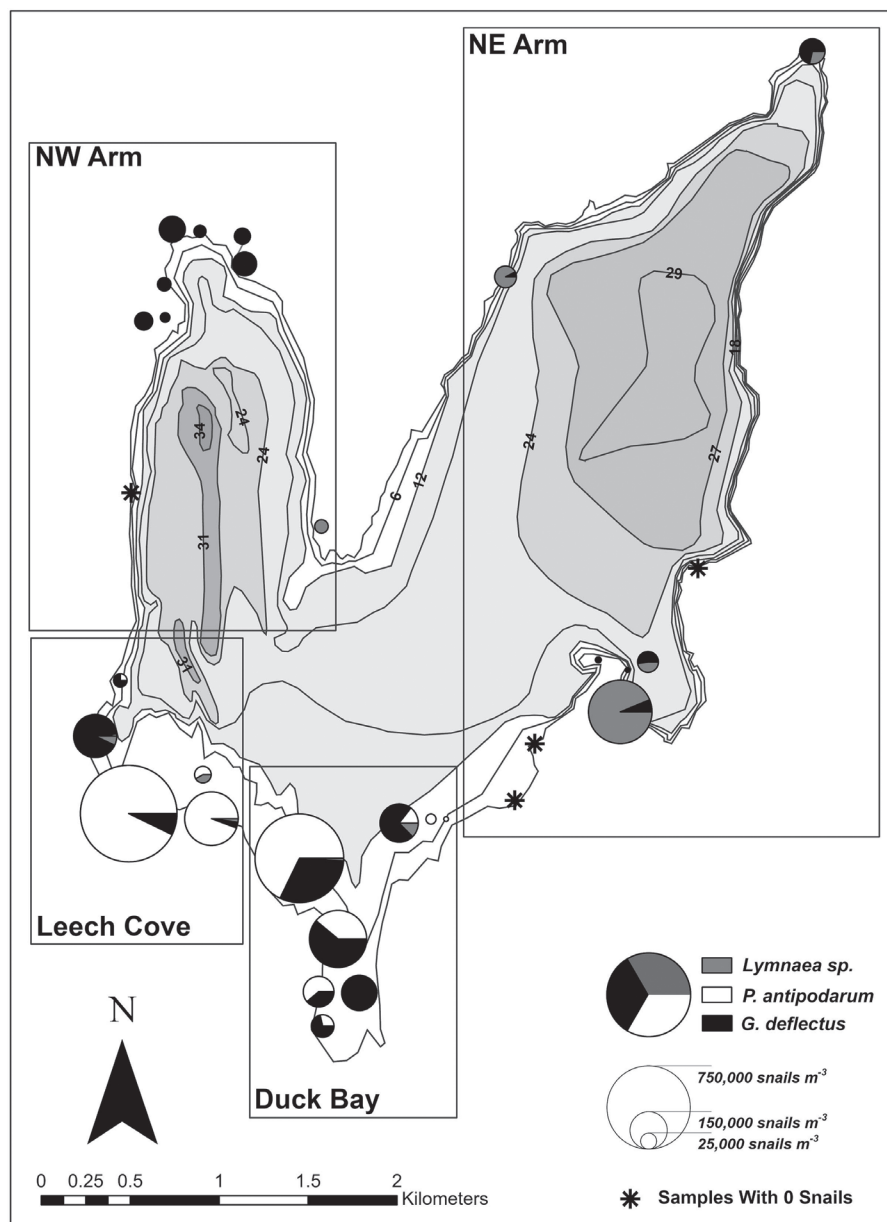


Figure 4. Spirit Lake bathymetric map with aquatic vegetation sampling locations for snail abundance (snail individuals m^{-3} fresh vegetation). Pie charts show the percentage of each species and are scaled in size by the total number of snails at each site.

Table 1. Mean densities (snail individuals m^{-3} fresh vegetation) and standard deviations by lake quadrant for snail species collected on aquatic macrophytes in Spirit Lake in 2021–2022.

Quadrant	n	<i>P. antipodarum</i> m^{-3} veg	<i>G. deflectus</i> m^{-3} veg	<i>Lymnaea</i> sp. m^{-3} veg
NW	9	ND	27,230 $\pm$ 25,938	2,222 $\pm$ 6,667
NE	10	ND	11,633 $\pm$ 16,922	51,856 $\pm$ 127,679
Leech Cove	5	252,632 $\pm$ 405,529	57,065 $\pm$ 77,359	6,676 $\pm$ 6,726
Duck Bay	8	104,463 $\pm$ 198,131	102,321 $\pm$ 100,573	3,500 $\pm$ 7,231

Both our eDNA and snail-macrophyte sampling results point to the SW shore of Spirit Lake as the initial point of NZMS colonization, as evidenced by the highest concentrations of NZMS in the study area. The SW shore of Spirit Lake has no established public access points and off-trail travel is discouraged. It is, however,

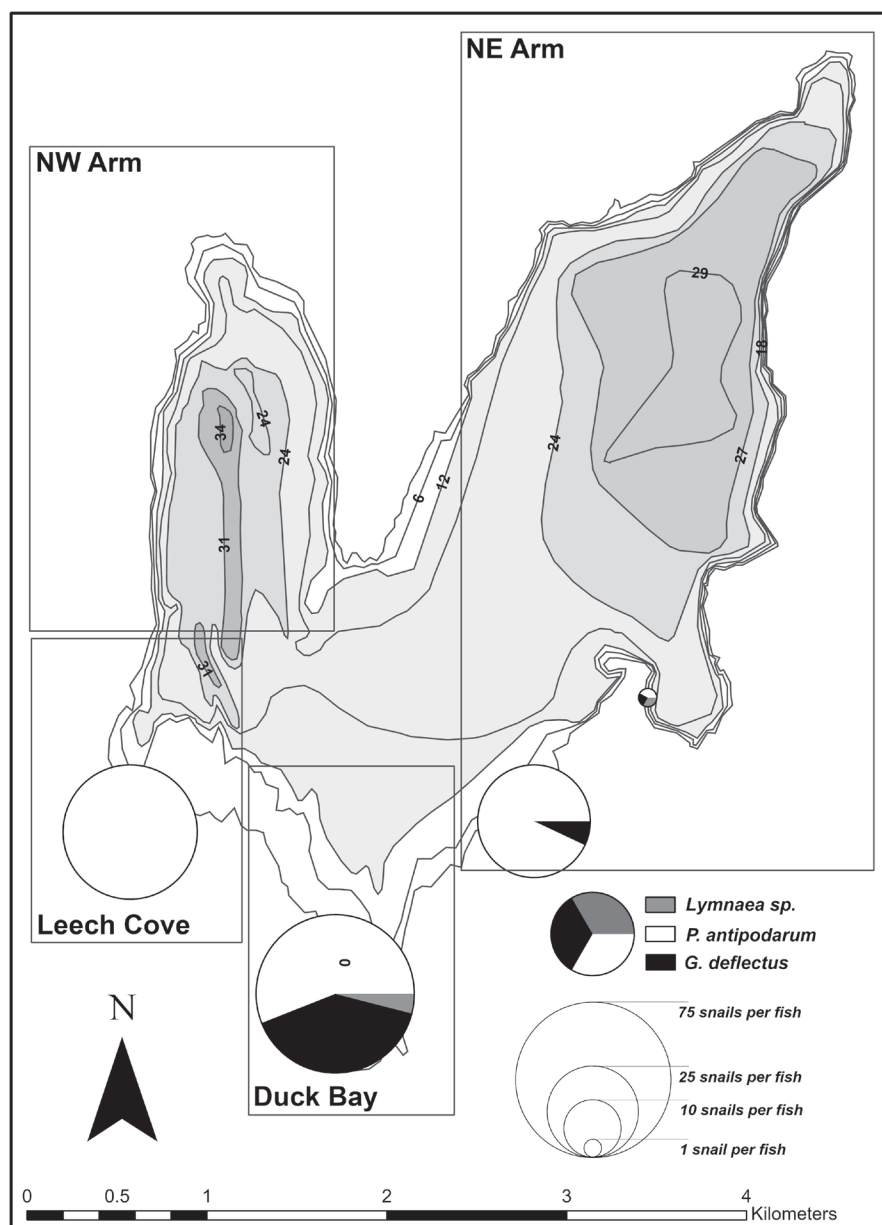


Figure 5. Mean snail abundance (snail individuals per fish) in rainbow trout (*O. mykiss*) gut contents collected at four locations in Spirit Lake in 2021 ($n = 6$ –24 fish). Pie charts show the percentage of each species and are scaled in size by the mean number of snails at each site.

the access point for lake researchers and tunnel maintenance work. Owing to the degree of this area's isolation, it is likely that NZMS were introduced either by wildlife vectors (i.e., ducks/geese frequenting the area of the lake with highest macrophyte density; Butkus et al. 2012) or anthropogenically during research or maintenance visits. The apparent isolated distribution of NZMS along the SW shore in Spirit Lake could be due to a lack of habitat connectivity, insufficient time since introduction, lack of migration pressure, sub-optimal water chemistry, or a combination of these factors.

A 2010 survey of aquatic macrophyte distribution in the lake showed only sparse aquatic vegetation between the SW shore and the NW arm (Gawel et al. 2018), therefore suitable habitat could be limiting the effective spread of NZMS into the quadrant near the outlet tunnel. Geist et al. (2022) suggested that macrophytes provided refuge for NZMS on substrates subjected to high velocity waters,

and Levri et al. (2008) found that NZMS were absent in shallow shoreline areas in Lake Ontario subject to wave action. Thus, it is possible that the low density of macrophytes along the steep-sided west shore of Spirit Lake does not provide adequate refuge on unstable substrate subjected to waves for NZMS to colonize. However, that same survey (Gawel et al. 2018) showed contiguous macrophyte habitat from the SW shore to Donnybrook Cove, although there is presently limited NZMS colonization of the east shore of Spirit Lake (Fig. 4). This may be due to the short time since first colonization or a lack of migration pressure due to plentiful resources (Sepulveda and Marczak 2012) along the SW shore. If NZMS population densities increase, we may see greater spread of the species up the east side of Spirit Lake.

In terms of water chemistry, Spirit Lake specific conductivity has been declining since the eruption, decreasing from $793 \mu\text{S cm}^{-1}$ in 1980 to $100 \mu\text{S cm}^{-1}$ in 2014; pre-eruption values of $19\text{--}27 \mu\text{S cm}^{-1}$ in 1974 may indicate specific conductivity values for the lake in the future (Gawel et al. 2018). In previous studies, lower conductivities in the range of $100 \mu\text{S cm}^{-1}$ resulted in very low NZMS birth rates but little mortality (Vazquez et al. 2016). A summary of the literature on the topic by Geist et al. (2022) found optimal specific conductivity for NZMS to be $200\text{--}800 \mu\text{S cm}^{-1}$, which is higher than that measured in Spirit Lake. However, Vazquez et al. (2016) also found that the negative influence of low specific conductivity was offset by higher calcium concentrations. Calcium concentrations in Spirit Lake were last measured in 1994, and found to be 27.1 mg L^{-1} , decreasing from 31.7 mg L^{-1} in 1986 (Dahm et al. 2005). Assuming that calcium concentrations are relatively proportional to specific conductivity in Spirit Lake over time, the current specific conductivity of $100 \mu\text{S cm}^{-1}$ would suggest a calcium concentration in the range of 14 mg L^{-1} . This concentration is still in the “optimal” range for NZMS growth and survival (Geist et al. 2022). Thus, it is unclear whether water chemistry in Spirit Lake limits NZMS growth and spread currently.

Impact of NZMS on macroinvertebrate species

Comparing NZMS to native snail species abundances in rainbow trout guts (Fig. 3; Suppl. material 1: table S1), we did not see evidence that the introduction of NZMS resulted in a competitive decline in *G. deflectus* populations. Although *Lymnaea* sp. abundance in fish guts along the SW shore of Spirit Lake declined temporally in our fish diet study, this decline seemed to occur prior to the NZMS invasion and was possibly linked to increasing *G. deflectus* abundance or to other ecological changes in the lake. From snail-vegetation sampling, along the SW shore in Leech Cove the mean density of NZMS ($252,632 \text{ individuals m}^{-3}$) exceeded that of *G. deflectus* ($57,065 \text{ individuals m}^{-3}$; Fig. 4), although the sample-to-sample variation was very large (Table 1) and *G. deflectus* were more abundant than NZMS in 40% of samples. *G. deflectus* were found at highest mean densities along the SW shore, even in the presence of NZMS, suggesting higher habitat quality or abundance. A previous lake-wide macrophyte survey showed much greater macrophyte density and coverage along the shallower SW shore (Gawel et al. 2018). Moreover, our measurements showed comparable densities of both NZMS and *G. deflectus* on all macrophyte species (Table 2) suggesting that NZMS are not currently competitively excluding the native species, and that both snail species are opportunistic colonizers of many macrophyte species. The highest mean densities of both NZMS and *G. deflectus* were found on *Ceratophyllum demersum*. With both NZMS and *G. deflectus* co-occurring on the same macrophyte species, there is potential for future interspecies competition between the non-native and native snails. On the

other hand, *Lymnaea* sp. reached their highest densities (51,856 individuals m⁻³) in the absence of NZMS and with lower *G. deflectus* numbers (Fig. 4) and were found in greater numbers on the non-native *Myriophyllum spicatum* (Table 2). Fish gut sample data (Fig. 3), all collected from the SW shore of Spirit Lake, and snail-vegetation sampling data (Table 2) both suggest that all three snail species can colonize the same habitat and the same vegetation types. Therefore, the low numbers of *Lymnaea* sp. in the presence of either NZMS or higher *G. deflectus* numbers along the SW shore suggests that *Lymnaea* sp. may decline further in overall abundance if NZMS colonizes more of Spirit Lake where *Lymnaea* sp. are still found. However, we do recognize that this conclusion relies only on snail abundances on vegetation in the lake, and that all three snail species may exist on sediments in different proportions than on vegetation. Future studies should work to overcome methodological difficulties in sorting snails from sediments, which consist of colors and particle sizes that effectively camouflage snails from the eyes of researchers.

Table 2. Mean densities (snail individuals m⁻³ fresh vegetation) of snail species collected on aquatic macrophyte species in Spirit Lake in 2021–2022. Within a given raked sample, all snail species in that sample are considered associated with all macrophyte species identified within that same sample.

snails m ⁻³ vegetation	n	<i>P. antipodarum</i>	<i>G. deflectus</i>	<i>Lymnaea</i> sp.
<i>Myriophyllum spicatum</i> L. (ITIS)	16	125,556	69,185	32,274
Charales (Order)	13	81,260	35,076	5,231
<i>Ceratophyllum demersum</i>	3	509,175	175,683	7,429
<i>Potamogeton amplifolius</i>	13	85,193	54,618	6,949
Filamentous Algae	4	34,706	89,412	–

Stable isotope analyses are routinely used to unravel aquatic food webs, and several studies have employed isotopic datasets to investigate the ecological role of NZMS in invaded ecosystems (Larson and Ross 2016; Rakauskas et al. 2018). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the Spirit Lake aquatic taxa analyzed here reflect trophic and environmental variability within the Spirit Lake ecosystem (Fig. 6). Specifically, taxa that were most likely to be primary consumers, based upon our *a priori* assumptions about trophic position, had lower $\delta^{15}\text{N}$ values than secondary or tertiary consumers (Peterson and Fry 1997), and the range in $\delta^{13}\text{C}$ values across feeding groups reflects the differences in $\delta^{13}\text{C}$ values of primary producers (Shinneman et al. 2024). Since snail samples for stable isotope analysis were collected haphazardly from shoreline habitat, or indirectly via mobile rainbow trout predators, we assumed that our samples incorporated substantial spatial and temporal averaging. Spirit Lake NZMS and *G. deflectus* occupied an isospace that was distinct from other taxa, and the two snail species had indistinguishable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (MANOVA - Pillai = 0.0068425, approx. $F_{1,27} = 0.089565$, $p > 0.05$; Fig. 7). Trophically-corrected individual snail $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were plotted with values of probable diet sources (periphyton and macrophytes) and most snails had intermediate values (Fig. 7).

As the scope of stable isotope sample collection for this study did not exhaustively sample all possible diet sources, we did not endeavor to quantify interactions between NZMS and other taxa in the Spirit Lake ecosystem. Even so, the degree of isotopic overlap between recently arrived NZMS and the resident *G. deflectus* demonstrated that both species were generalists whose diets similarly reflected resource availability. If either snail species were specialists of a particular resource, or combination of resources, we would expect a lower intraspecific variance primarily in $\delta^{13}\text{C}$ values. Likewise, if the snail species were specialists of different resources,

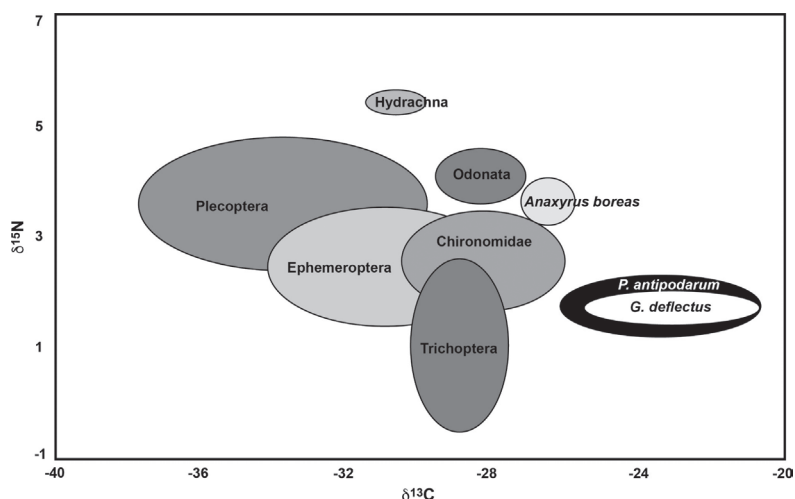


Figure 6. Carbon and nitrogen stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values of abundant and common groups of aquatic organisms in the Spirit Lake food web. Snail species = invasive, non-native NZMS (*P. antipodarum*) and native *G. deflectus*. Insect larva = Chironomidae, Ephemeroptera, Odonata, Plecoptera, Trichoptera. Aquatic mites = *Hydrachna* sp.. Amphibian tadpoles = *Anaxyrus boreas*. Ellipses are defined by mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values $\pm$ standard deviations.

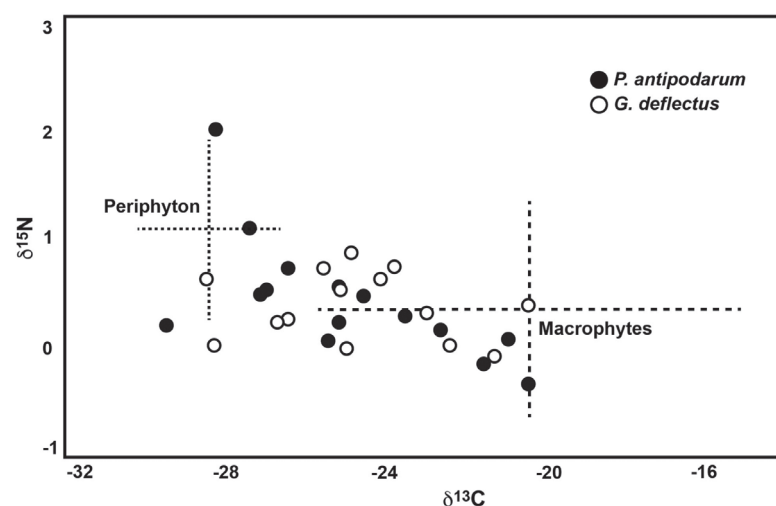


Figure 7. Carbon and nitrogen stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values of individual *P. antipodarum* and *G. deflectus* snails, and their primary diet sources in Spirit Lake. Periphyton and macrophyte ellipses defined by means $\pm$ standard deviations. Snail $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values have been adjusted to account for isotopic trophic differences (mean $\Delta^{13}\text{C}_{\text{snail-diet}} = 1.5\text{‰}$, mean $\Delta^{15}\text{N}_{\text{snail-diet}} = 1.3\text{‰}$, Li et al. 2018). The two snail species have overlapping distributions of $\Delta^{13}\text{C}_{\text{snail-diet}}$ and $\Delta^{15}\text{N}_{\text{snail-diet}}$ values [MANOVA; Pillai = 0.0068425, approx. $F_{1,27} = 0.089565$, $p > 0.05$].

we would expect interspecific differences primarily in $\delta^{13}\text{C}$ values. Thus, the isotopic data complement the snail-vegetation data which showed shared habitat use by the snail species, and together these results suggest that interspecies competition between the snails may increase in the future.

The modest isotopic datasets presented for the common groups of aquatic organisms in the Spirit Lake ecosystem (Fig. 6) provide a frame of reference for the NZMS data, and a baseline for future studies of Spirit Lake food web dynamics with NZMS present. It is clear from the isotopic data of the sampled groups of organisms that the Spirit Lake aquatic food web has assembled into a not uncommon food web in the 40+ years since the 1980 eruption. It will be important and interesting to monitor how this relatively new lake ecosystem and food web respond to the NZMS over time. Other

studies have shown NZMS to have a varied influence on invaded ecosystems. They can shift community structures, improving conditions for some taxa while degrading them for others (Kerans et al. 2005; Riley et al. 2008; Bennett et al. 2015; Rakauskas et al. 2017). In other studies, NZMS have not detectably influenced coexisting invertebrate populations at all when resources were sufficiently abundant, even at high population densities (Cross et al. 2010; Brenneis et al. 2010). The presence of NZMS, however, does have the potential to shift whole macroinvertebrate community structures (Rakauskas et al. 2017). As opportunistic feeders, foraging on detritus and plant material, NZMS may compete for food resources with many taxa. NZMS are also flexible in their habitat, occupying aquatic macrophytes as well as shoreline debris and lake-bottoms, and so their competitive impact spans the Spirit Lake ecosystem. Negative impacts on native macroinvertebrates by NZMS are more likely to occur when food resources are limited (Brenneis et al. 2010; Riley and Dybdahl 2015). Therefore, while it is clear from our work that NZMS and *G. deflectus* share resources and habitat, it is too early to say whether NZMS presence is detrimental and what their future impact on the Spirit Lake macroinvertebrate community will be.

Impact of NZMS and native snails on fish diet

As NZMS and native snails (*G. deflectus*) were found in significant numbers in trout guts (Fig. 3), we examined the nutritional contribution of snails to trout diet in Spirit Lake. Blackman et al. (2018) showed that snails represent a significant portion of rainbow trout gut contents (ingested material) in Spirit Lake. We performed stable isotope analysis of trout fin tissue in 2021 to elucidate the contribution of snails to the fish diet. Fig. 8 illustrates where snail measured and trophically-adjusted (predicted) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values lie with probability ellipses. As shown, rainbow trout values do not at all overlap with the predicted snail ellipses, even though the majority of our snail samples for isotope analysis were obtained from trout guts. Our results show a negligible trophic tie between both snail species and rainbow trout. The fact that we observed undigested snails in the trout guts aligns with the isotopic data. Both observations provide evidence that minimal snail-derived resources are assimilated into trout tissues, and thus snails do not provide dietary nutrients or energy to the trout.

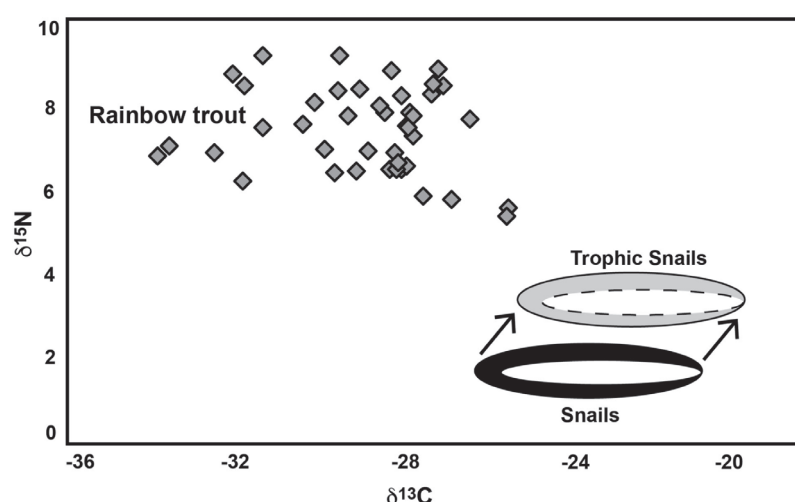


Figure 8. Carbon and nitrogen stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values of individual Spirit Lake rainbow trout (*O. mykiss*). “Snails” ellipses are defined by means $\pm$ standard deviations of *P. antipodarum* (black), and *G. deflectus* (white). “Trophic snails” ellipses and arrows represent the values for the same snail species after they have been adjusted to account for isotopic trophic differences between trout fin and snail tissue samples (mean $\Delta^{13}\text{C}_{\text{snail-trout}} = 1.0\text{‰}$, Jensen et al. 2012; mean $\Delta^{15}\text{N}_{\text{snail-trout}} = 1.7\text{‰}$, Heady and Moore 2012).

Vinson and Baker (2008), in a lab study, found that NZMS were largely indigestible by rainbow trout, with 91.5% undigested (whole animal present in stool samples) and 53.8% percent of NZMS surviving digestion (living animal present), and they saw the eventual starvation of the subject rainbow trout when the fish were fed nothing but NZMS. Spirit Lake rainbow trout historically foraged on large quantities of small macroinvertebrate prey with snails comprising a significant percentage of their intake (Blackman et al. 2018). Rainbow trout have been found to consume prey relative to prey abundance and not caloric content (Bres 1986). Once introduced, NZMS can multiply to dominate macroinvertebrate biomass and establish high density populations (Kerans et al. 2005; Rakauskas et al. 2017). Thus, if there is an increase in the relative abundance of non-nutritious prey items such as NZMS, overall fish health (Geist et al. 2022) and, more largely, the health of the ecosystem could be affected.

Conclusions

The 1982 Congressional designation of the Mount St. Helens National Volcanic Monument limited future development and access to conserve the landscape for natural regeneration, scientific research, and cultural resource preservation (Public Law 97-243 §4, 1982: <https://uscode.house.gov/statutes/pl/97/243.pdf>). This designation has not meant that the Spirit Lake ecosystem has remained unimpacted by outside influences. The introduction of non-native aquatic macrophytes and now NZMS have all undoubtedly changed the ecology of the lake. However, this designation is meant to inform management actions to decrease the likelihood of altering the ecosystem through direct anthropogenic activities. For example, currently public access to Spirit Lake is limited to the Harmony Falls Trail #224 on the NE arm of the lake (Fig. 1), and fishing and other forms of recreation in the lake are prohibited to minimize anthropogenic influences.

For NZMS, management decisions should seek to minimize the likelihood of increasing the speed or geographic extent of the invasion. NZMS have been found in Spirit Lake osprey droppings (vitality/mortality unknown; Gawel, unpublished data) and rainbow trout stomachs (alive), so wildlife spread is a possibility. However, in flowing waters downstream drift is a viable and significant means of transport for NZMS into new habitats (Holomuzki and Biggs 1999; Bennett et al. 2015), and “...an order of magnitude more rapid than volitional movement (Geist et al. 2022).” Recently, the US Forest Service proposed the installation of an in-water construction staging area in Leech Cove, an area of the lake with some of the highest NZMS densities. Boats/barges would ferry equipment and materials from Leech Cove to the outlet tunnel in the NW Arm of the lake, an area that has not been invaded yet, potentially acting as a vector for the spread of NZMS downstream into Coldwater Creek. While NZMS were not present in S. Coldwater Creek during our 2019 eDNA sampling or found in visual surveys conducted in 2019–2021, incidental observation in the summer of 2022 found a new and well-established population of NZMS in the Creek. Because a full-scale survey has not yet been conducted, it is not possible to state whether this population remains novel and localized or whether it represents an invasion throughout Coldwater Creek waters. Nor is it possible to be certain of the mechanism of their arrival, but further actions that would potentially hasten the direct transport of NZMS to the area of Spirit Lake near the tunnel outlet would very likely result in further transport of NZMS downstream into the Toutle River and Cowlitz River systems and beyond.

More broadly, our field data support the lab results of Vinson and Baker (2008) and point to the nutritional deficit posed by NZMS for rainbow trout and other fish populations that are important for recreation or conservation goals. An increase in NZMS density may decrease fish growth rates, especially if they compete with other aquatic macroinvertebrates thus replacing species important to fish diet with an indigestible alternative. Our comparison of NZMS abundances on aquatic vegetation and in fish guts, although limited statistically by our number of sampling regions in the lake, provides field evidence that increasing NZMS densities will likely result in a proportional increase in ingested (but not assimilated) snails, potentially starving the fish. Our results also highlight the need to consider geographic differences in NZMS distribution in lakes rather than considering the entire lake infested when NZMS are detected. Lake management decisions related to aquatic macrophyte controls, fish stocking, and public access, to name a few, are all critical to limiting the further spread of NZMS within a lake and downstream.

Authors' Contribution

SRM: Formal analysis, Investigation, Writing - Original draft, Visualization; HG: Investigation, Visualization, Funding Acquisition; MM: Methodology, Investigation, Funding Acquisition; WC: Investigation, Funding Acquisition; CMC: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data Curation, Writing - Review and Editing, Visualization, Supervision, Funding Acquisition; KFD: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing - Review and Editing, Visualization, Supervision, Funding Acquisition; JEG: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data Curation, Writing - Review and Editing, Visualization, Supervision, Project administration, Funding Acquisition

Funding Declaration

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Ethics and Permits

All sample collection was completed following ethical practices and with the required permits or permission. Our research was approved and permitted by the US Forest Service and Washington Department of Fish and Wildlife, and permits are on file with co-author CM Crisafulli.

Data Accessibility

All data are available through Dryad (<https://doi.org/10.5061/dryad.6t1g1jx71>).

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Supplementary material 1

Number of samples and year collected for stable isotope analyses, fish gut content analysis; and plant samples by lake region (tables S1–S3)

Authors: Shaina R. Myers, Hailey E. Germeau, Meghan McCann, Wyatt Cranston, Charles M. Crisafulli, Kena Fox-Dobbs, James E. Gawel

Data type: xlsx

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Supplementary material 2

Comparison of mean snail abundance on vegetation and in *O. mykiss* guts sorted by sampling region (fig. S1)

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Data type: docx

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