

Stream community and ecosystem responses to the boom and bust of an invading snail

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Abstract Invasive species can fundamentally change ecosystems, but there remains surprisingly little understanding of how they alter ecosystems through time. New Zealand mudsnails (NZMS, *Potamopyrgus antipodarum*) are invading North American aquatic ecosystems with potentially enormous impacts on stream communities and ecosystems. Here we present a unique 10 year time series of stream benthic invertebrates in two sites in a California stream—one invaded site where NZMS populations boomed and then busted, and one upstream reference site that was not invaded to the same degree. As NZMS populations rose and fell, the abundance of native grazing herbivores crashed and then recovered, evidence of direct negative competitive impacts of

NZMS. However, NZMS had a positive indirect effect on piercing herbivores, probably mediated by a shift in the dominant algal type. Retrospective stable isotope analyses and Bayesian isotopic mixing models revealed that NZMS invasion decreased the reliance of native taxa, from a variety of functional feeding groups, on periphyton-derived carbon. Furthermore, NZMS invasion was associated with depleted nitrogen stable isotope signatures, evidence that NZMS alter stream ecosystem nitrogen cycling. The reference site did not exhibit these community- or ecosystem-level dynamics. Thus, invasive herbivores can have strong top-down and bottom-up influences on invaded ecosystems, but these impacts can be extremely temporally dynamic.

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Introduction

Invasive species are a major driver of global change, yet understanding their impacts remains a critical challenge (Parker et al. 1999; Strayer et al. 2006; Simberloff 2011). While there are many examples of invasive predators driving widespread ecological change (e.g., Fritts and Rodda 1998; Croll et al. 2005; Herbst et al. 2009), there are arguably fewer examples of widespread impacts of invasive

herbivores. Invasive herbivores can drive ecological change both by their direct consumption of plants but also through altering biogeochemical cycling. One recent example is that of invasive golden apple snails (*Pomacea canaliculata*), which can control wetland ecosystems by their direct consumption of palatable plants but also through their nutrient excretion which can stimulate phytoplankton productivity (Carlsson et al. 2004). Understanding the impacts of invasive herbivores is especially critical given that the majority of invasive species in some systems belong to these intermediate trophic levels (Byrnes et al. 2007).

The New Zealand mudsnail (NZMS, *Potamopyrgus antipodarum*) is an herbivore that is rapidly invading western North America with the potential to change fresh-water ecosystems and communities fundamentally. Detailed studies, predominantly in the Yellowstone region of the USA, have shown that hyper-abundant NZMS (>500,000 individuals m^{-2}) can excrete enough ammonium to account for 66 % of the stream ammonium demand (Hall et al. 2003) and be responsible for the majority of invertebrate productivity (Hall et al. 2006). Because NZMS can consume the majority of periphyton productivity and are resistant to predation by fish such as trout (Bruce et al. 2009), it is also possible that they act as a trophic dead-end, sequestering periphyton-derived energy and nutrients (Hall et al. 2006). While these studies of high densities of NZMS demonstrate that these grazers can dominate stream ecosystem processes, without pre-invasion data there remains uncertainty about how NZMS change stream processes over the course of their invasion. For example, NZMS could either replace the ecosystem processes performed by displaced native invertebrates or they could change the net ecosystem processes as they invade. Indeed, studies have described mixed impacts of NZMS on stream invertebrate communities. Some studies have found negative impacts of NZMS on native invertebrates at small spatial scales (Kerans et al. 2005; Riley et al. 2008), but another study observed positive associations (Schrieber et al. 2002), and a time-series study did not observe any discernable impact of NZMS invasion on native benthic invertebrates (Cross et al. 2010). Thus, there remains uncertainty over how this invasive herbivore impacts different stream communities and ecosystems, especially how they alter streams over the temporal progression of their invasion.

The vast majority of studies of the impacts of invasive species are snapshots in time (Strayer et al. 2006), even though the most severe impacts of an invasive may be transient (e.g., Morrison 2002). Here we present a unique 10 year time series of stream benthic invertebrates in two sites in a California stream—one invaded site where NZMS populations boomed and then busted, and one upstream reference site that was not invaded to the same degree (Fig. 1a). In the invaded site, NZMS increased from fewer than 500 individuals m^{-2} to almost 100,000 individuals m^{-2} in 7 years. In the next 3 years their populations decreased back to fewer than 1,000 individuals m^{-2} . In contrast, the reference site was not invaded to the same degree, with a maximum of only 2,776 individuals m^{-2} over the 10 year period (Fig. 1a). We hereafter refer to these sites as “invaded” and “un-invaded”. Using functional feeding group composition and retrospective stable isotope analyses of benthic invertebrates from these time series, we asked the question: how does the boom and bust of an invading herbivore alter stream communities and ecosystems? We hypothesized that NZMS would change native communities by outcompeting native grazing invertebrates. Thus, we predicted a negative relationship between annual NZMS abundance and native grazer abundance. In addition, we hypothesized that NZMS would change the flow of energy through the ecosystem by sequestering periphyton-derived resources, driving a shift to a larger reliance on terrestrial resources. Specifically, we predicted that NZMS invasion would lead to depleted carbon stable isotope signatures of native invertebrates as they decreased their reliance on periphyton production.

Materials and methods

This study focused on the invasion of NZMS in the Upper Owens River, California, USA. Biomonitoring surveys have been conducted in the Upper Owens River and tributaries since 1999, when NZMS were first noted in low numbers at only a few locations. We investigated benthic invertebrate communities and stable isotope signatures from 1999 to 2008 in the invaded reach and the un-invaded site that was approximately 20 km upstream. The un-invaded site serves as a reference to examine the possibility that

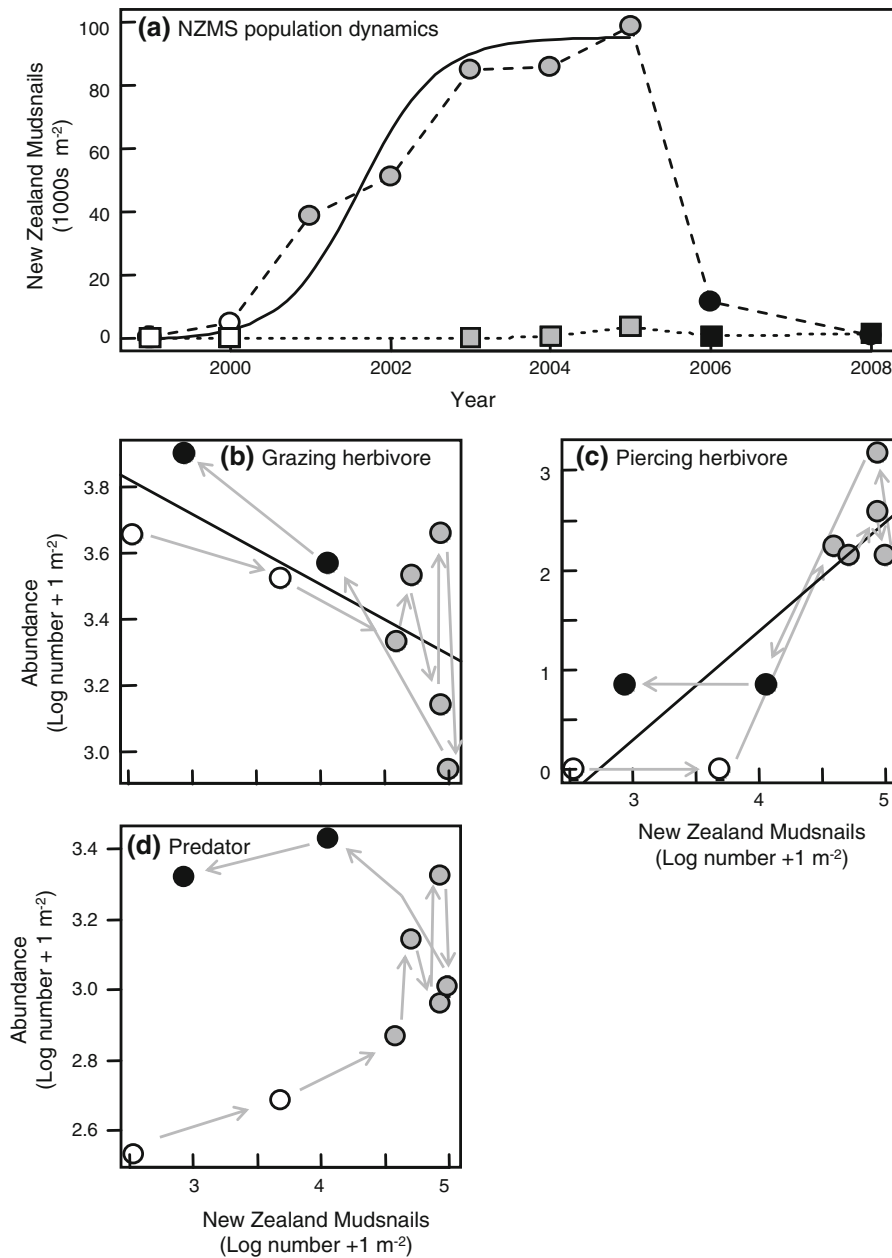


Fig. 1 **a** Time series of average New Zealand mudsnail abundance in the invaded (*circles*) and un-invaded site (*squares*). Also shown is the best-fit logistic model (estimated instantaneous rate of increase, *r*, is 2.09 and carrying capacity, *K*, is 97,100 individuals m⁻²) for the invaded site, restricted to the before and during period. The periods of before, during, and decline are represented with *white*, *gray*, and *black* colors. The

temporal dynamics of benthic invertebrates as a function of NZMS abundance in the invaded site for **b** grazing herbivores (not including NZMS), **c** piercing herbivores, and **d** predators. Each *point* denotes the mean annual abundance of native taxa and NZMS. *Arrows* show the temporal sequence. Also shown is the best fit linear model for significant (*P* < 0.05) relationships

changes in the invaded site were widespread patterns. There were important site differences that may have influenced the relative invasion success of NZMS in

the two sites; specifically, the un-invaded site had a more intact riparian habitat and stable isotope analyses indicated that the benthic community in the invaded

site tended to rely more on periphyton-derived carbon than the un-invaded site (Fig. 2, see below). We used 1999 and 2000 as the “before” invasion period, 2001–2005 as the “during” invasion period, and 2006 and 2008 as the “decline” phase of the invasion. We note that the before period had low abundances of NZMS in the invaded site and the decline period had low abundances in both sites. More information on the study system can be found in Herbst et al. (2008).

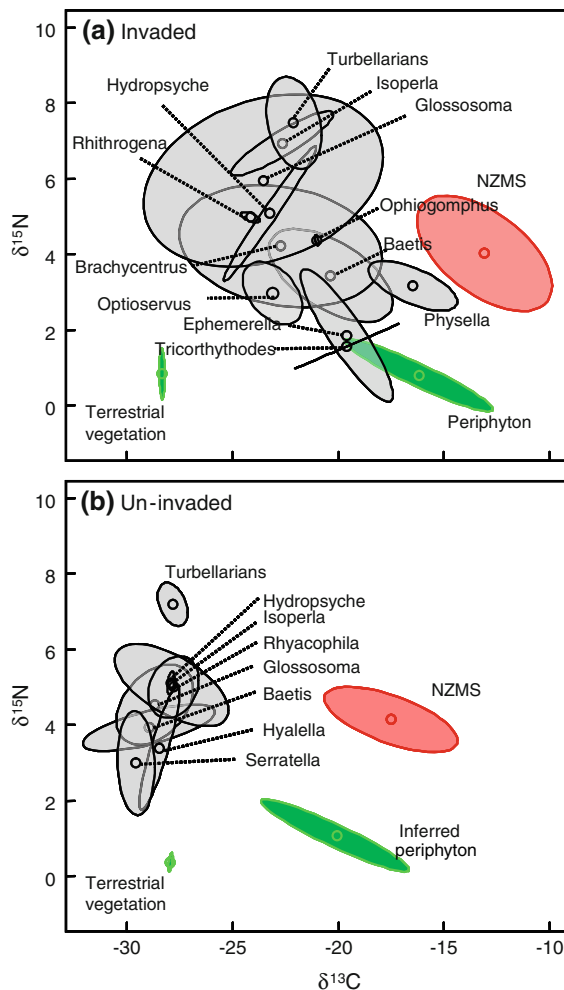


Fig. 2 Stable isotope signatures of stream food webs in the invaded (a) and un-invaded (b) site. We note that the un-invaded site had extremely low densities of NZMS in some years. Shown are means and confidence ellipses at 50 % confidence level for all samples across all years. When necessary, group names are connected to the appropriate mean with a dotted line. For the un-invaded site (b), the periphyton confidence ellipse and mean were inferred based on the relationship between NZMS and periphyton for the invaded site

Benthic invertebrates were sampled from both sites during the summer from 1999 to 2008 (with 1 and 3 years missing from the invaded and un-invaded sites, respectively); each year, five samples were collected from riffle habitats, each sample collected by turning and rubbing substrates over a 0.279 m² area and collecting dislodged invertebrates with a 250 μm D-frame aquatic net. Invertebrates were sorted under a stereomicroscope at 10× magnification, and a minimum subsample of 250 organisms was removed from each replicate for identification. Individuals (including midges and mites) were identified to the lowest practical taxonomic level (usually genus, species, or species group). All identified taxa were classified into functional feeding groups according to the primary designations given by Merritt et al. (2008) and Thorpe and Covich (2009) for analysis of community trophic structure through time. In addition, sub-samples of stored benthic invertebrate samples were used for stable isotope analyses.

Stable isotope analyses

We used stable isotopes of nitrogen (N) and carbon (C) to illuminate changes in the relative flow of these elements through stream food webs. We performed stable isotope analyses on preserved invertebrate samples collected from 1999 to 2008. In addition, we collected samples of terrestrial vegetation, and periphyton during the summer of 2008 from the two sites for stable isotope analyses. A combination of species of terrestrial vegetation was sampled in the riparian area of the sites. We collected periphyton samples by scrubbing rocks with a small brush and rinsing the dislodged algae off with distilled water. Prior to isotopic analyses, periphyton and terrestrial vegetation were frozen and benthic invertebrates were stored in 75 % ethanol. Periphyton, vegetation, and invertebrate samples were dried until a constant dry weight was achieved and homogenized with a mortar and pestle. For small invertebrates, multiple individuals were aggregated (for a total of ~1 mg) for stable isotope analyses. We focused stable isotope analyses on benthic invertebrates for which we could obtain sufficient material for analysis. Given that the taxonomic composition changed through time and was different in the invaded and un-invaded sites, the focal taxa and sample sizes varied somewhat across periods

and sites. In the invaded site these taxa were New Zealand mudsnails (NZMS, *Potamopyrgus antipodarum*, order Neotaenioglossa, family Hydrobiidae), flatworms (class Turbellaria, family Planariidae), *Ephemerella* spp. (order Ephemeroptera, family Ephemerellidae), *Baetis* spp. (order Ephemeroptera, family Baetidae), *Brachycentrus* spp. (order Trichoptera, family Brachycentridae), *Hydropsyche* spp. (order Trichoptera, family Hydropsychidae), and *Optioservus* spp. (order Coleoptera, family Elmidae). In the un-invaded site these taxa were flatworms (class Turbellaria, family Planariidae), *Baetis* spp. (order Ephemeroptera, family Baetidae), *Isoperla* spp. (order Plecoptera, family Perlolidae), *Glossosoma* spp. (order Trichoptera, family Glossosomatidae), *Paraleptophlebia* spp. (order Ephemeroptera, family Leptophlebiidae), and *Serratella* spp. (order Ephemeroptera, family Ephemerellidae).

All samples were then analyzed for $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, $\% \text{C}$ and C:N ratios using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California at Davis Stable Isotope Facility. Samples were compared to in-house standards and international standards of Vienna Pee-Dee Belemnite for C and air for N to account for calibration, quality control, and machine drift. The UC Davis Stable Isotope Facility expresses measuring error as the long term standard deviation of 0.2 ‰ $\delta^{13}\text{C}$ and 0.3 ‰ $\delta^{15}\text{N}$. We present stable isotope values in standard delta notation, δHX (‰) = $[(\text{R}_{\text{sample}}/\text{R}_{\text{standard}}) - 1] \times 1,000$, where X is the element, H is the mass of the heavier isotope, and R is the heavy-to-light isotope ratio of the sample or standard. We note that all benthic invertebrate samples were preserved in 75 % ethanol and that this fixation process can alter isotopic signatures, necessitating the application of a fixation correction factor. The fixation correction factor can be refined through knowing the change in the C:N ratio (Ventura and Jeppesen 2009). However, this requires knowledge of the C:N ratio before and after fixation and we do not have C:N data for our samples before fixation. Accordingly, we used a constant adjustment factor and adjusted for this preservation in ethanol by subtracting 0.39 ‰ from $\delta^{15}\text{N}$ and 1.18 ‰ from $\delta^{13}\text{C}$ (Ventura and Jeppesen 2009). Nonetheless, using a different correction factor would have only slight impacts on our results and would not alter the overall conclusions.

Analytical approach

We compared the isotope signatures of benthic invertebrates before, during, and after NZMS invasion. Through necessity, we restricted this analysis to taxa and years for which we could obtain sufficient tissue for stable isotope analyses across time.

We used circular statistics to quantify changes in stable isotope signatures over the course of the invasion (Zar 1999; Schmidt et al. 2007). Circular statistics facilitate quantification of directional patterns through probability distributions that, in essence, can wrap around a circle. While Schmidt et al. (2007) recommended transforming isotopic axes to niche axes (i.e., benthic vs. pelagic) prior to analysis, this transformation is predicated on accurate characterization of isotopic baselines (Casey and Post 2011). However, if organisms are modifying the biogeochemical cycles that control isotopic baselines (see “Discussion”), such transformations may mask important patterns. For this reason, we performed circular statistics on untransformed isotope data. Specifically, we calculated changes in isotope signatures through time for a given time as angular vectors. We calculated these vectors based on the difference in average isotope signature before versus during invasion and during versus decline phase of the invasion for each taxon in the invaded and un-invaded sites. We performed a Rayleigh’s test (Zar 1999) on these vectors to examine whether the distribution of angles of isotopic change in circular space was significantly different from uniform. We also calculated the average vector of change (Zar 1999). We performed these analyses in R (R Development Core Team 2010).

We used a Bayesian isotope mixing model (MixSIR v1.04, Moore and Semmens 2008) to estimate the contribution of different C sources to benthic invertebrates in the before, during, and decline phases of the invasion of NZMS in the invaded site. We only included C in the mixing model; preliminary data analysis indicated that $\delta^{15}\text{N}$ values were extremely variable through time (see below). This analysis focused on NZMS, *Optioservus*, *Tricorythodes*, *Baetis*, *Brachycentrus*, turbellarians, and *Hydropsyche*. We assumed a $\delta^{13}\text{C}$ trophic discrimination factor of 0.4 ± 1.2 ‰ per trophic level (average ± 1 SD) (McCutchan et al. 2003), this value and the normally distributed uncertainty is incorporated into the mixing model. We assumed invertebrates had a trophic level

of 1, with the exception of turbellarians, for which we used a trophic level of 2. The two sources in this mixing model were from autochthonous production (periphyton: $\delta^{13}\text{C} = -16.2 \pm 2.64 \text{‰}$) or allochthonous production (terrestrial vegetation: $\delta^{13}\text{C} = -28.3 \pm 0.10 \text{‰}$) based on material that we collected in 2008. We note that this approach does not account for the potential for changes in C baselines through time. We specified uninformative priors and used 1,000,000 draws to produce at least 10,000 posterior vectors for all models runs. Model diagnostics all suggested that the models accurately sampled the posterior probability distributions.

We also used a more sophisticated Bayesian mixing model to directly estimate the impact of NZMS on the contribution of periphyton to native invertebrates. The previous mixing model approach estimated contribution of different sources during the different periods of invasion to different invertebrates; however, it doesn't directly estimate the impact of NZMS on this consumption. For this reason, we also ran a stable isotope mixing model in which the impact of NZMS on consumer consumption of periphyton was a factor that was directly estimated. This approach follows that of Semmens et al. (2009) and Francis et al. (2011), in which isotopic mixing models are nested within a more complicated model. In the present study, this more complicated model included taxa as a factor and NZMS invasion as a factor. These factors can be incorporated into mixing models through geometric transformations allowing parameter estimation in the transformed space; parameters are subsequently back-transformed following their estimation. Here we used a logit transformation to normalize the compositional parameter space. The basic model structure was:

$$g(f) = B_0 + B_1 \times X \quad (1)$$

where, in logit space, $g(f)$ is the predicted contribution of periphyton to an invertebrate, B_0 is the taxon-specific average contribution, B_1 is the impact of NZMS on this contribution and is shared across taxa, and X represents the status of NZMS in the system (at an invasive state or before/after invasion). This model also included a normally distributed residual error term. MCMC sampling was performed for each model using three parallel chains in JAGS in R (Plummer 2003), with a burn-in phase of 10,000 vectors, retaining every 2nd sample, for a total iteration

number of 20,000. One of the outputs of this model is a posterior probability distribution of B_1 showing the impact of NZMS on the proportional reliance of native benthic invertebrates on periphyton, and is a direct measure of the influence of NZMS. For more information about these hierarchical Bayesian isotopic mixing models, see Semmens et al. (2009). For this analysis, we focused on how NZMS affected *Tricorythodes*, *Baetis*, *Brachycentrus*, and turbellarians; these species appeared to respond somewhat cohesively to NZMS invasion.

Results

Benthic invertebrate functional group composition changed over the rise and fall of NZMS in the invaded site (Fig. 1). As predicted based on competition with NZMS, the mean annual abundance of native grazers was significantly negatively related to annual NZMS abundance (Fig. 1b, linear model: $R^2 = 0.45$, $P = 0.047$). As NZMS invaded, native grazers decreased by 80 % and then more than doubled when NZMS populations crashed. In contrast, NZMS abundance was significantly positively related to the mean annual abundance of native piercing herbivores, Hydroptilid caddisflies (Fig. 1c, linear model: $R^2 = 0.75$, $P = 0.002$). As NZMS invaded, piercing herbivores increased from 0 individuals m^{-2} to an average of 1,500 individual m^{-2} . As NZMS populations crashed, piercing herbivores decreased back down to an average of <10 individuals m^{-2} (Fig. 1c). Predators, collector-gatherers, and collector-filterers did not exhibit a significant relationship between their annual abundance and the abundance of NZMS ($P > 0.19$ for all). However, the abundance of predatory invertebrates did increase through the entire time period from an average of <500 individuals m^{-2} during the pre-invasion period to over 2,000 individuals m^{-2} (Fig. 1d). In contrast, the abundance of functional feeding groups did not substantially change as a function of NZMS in the un-invaded site ($P > 0.10$ for all), perhaps not surprising given that NZMS didn't reach substantial densities in this site. Furthermore, mean annual abundance of these native taxa in the un-invaded site was not significantly related to annual NZMS abundance in the invaded site ($P > 0.13$ for all), evidence of divergent community dynamics in the invaded and un-invaded sites.

The isotope space of benthic invertebrates across all years in the invaded and the un-invaded sites was substantially different (Fig. 2). Specifically, invertebrates in the invaded site exhibited more variation in both C and N, with greater spread both within and across taxa than in the un-invaded site (Fig. 2a). In contrast, the confidence ellipses around benthic invertebrates in the un-invaded site were smaller, indicating less within-taxa variability within and across years (Fig. 2b). In addition, benthic invertebrates in the un-invaded site were all relatively depleted in $\delta^{13}\text{C}$, with the exception of NZMS, probably reflecting relatively little system-wide dependence on periphyton-derived productivity. The un-invaded site also has an intact riparian ecosystem, with presumably higher allochthonous (i.e., terrestrial

vegetation) inputs. In contrast, benthic invertebrates in the invaded site had a broader range of $\delta^{13}\text{C}$ signatures, and some taxa tended to be more enriched in $\delta^{13}\text{C}$ (Fig. 2).

New Zealand mudsnails invasion corresponded with isotopic change of benthic invertebrates. In particular, during the rapid expansion of NZMS (before vs. during invasion) the isotopes of invertebrates changed cohesively in isotope space in the invaded site ($P = 0.003$, $R_{\text{bar}} = 0.895$, Fig. 3a); benthic invertebrates decreased by an average of 1.7 ‰ $\delta^{15}\text{N}$ (more depleted) and 0.90 ‰ $\delta^{13}\text{C}$ (towards less reliance on periphyton). In contrast, isotopes of invertebrates in the un-invaded site did not change significantly during the same time period (before vs. during) ($P = 0.44$, $R_{\text{bar}} = 0.55$),

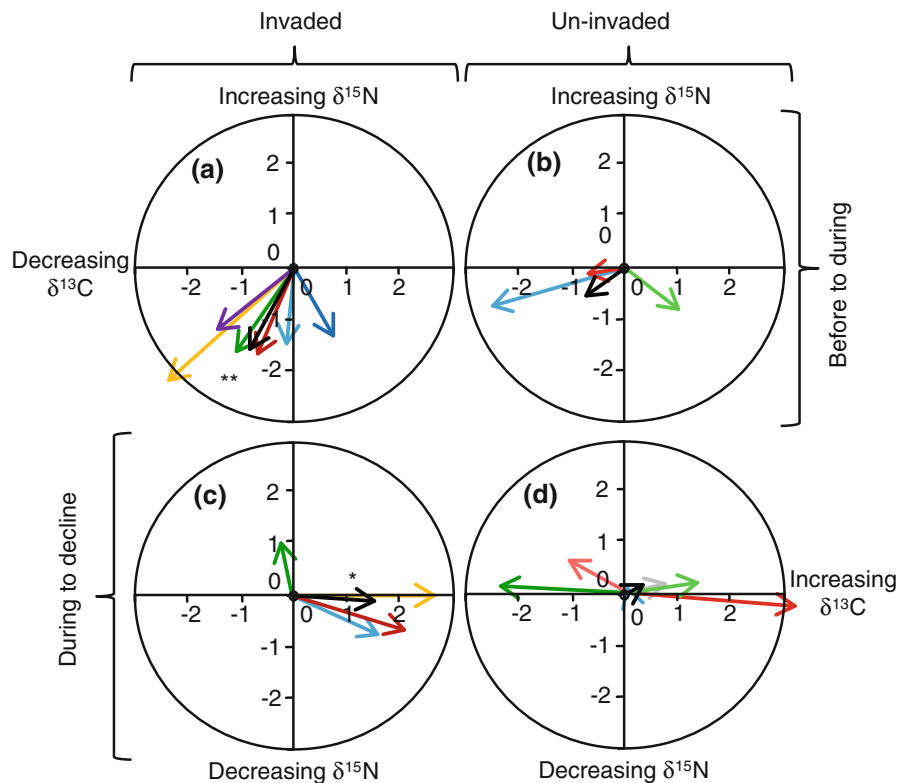


Fig. 3 Temporal changes in isotope signatures of stream invertebrates over the course of the NZMS invasion. *Arrows* point from the isotope signature in the first period, normalized to 0, to the isotope signature in the second period. For all *panels*, the *color-coded arrows* indicate a specific invertebrate taxon and the *black arrow* indicates the average vector of isotopic change (an average of all taxa). Shown are isotopic change for invaded (*left column*) and un-invaded sites (*right column*) from the periods before to during invasion (*top row*, 1999 and 2000

vs. 2001–2005) and the period during to that of the decline of the invasion (*bottom row*, 2001–2005 vs. 2006, 2008). *Vectors* (clockwise from point of $\delta^{13}\text{C} = +2$, $\delta^{15}\text{N} = 0$) for **a** *Optioservus* spp., *Baetis* spp., turbellarians, mean vector, NZMS, *Brachycentrus* spp., *Hydropysche* spp.; **b** *Glossosoma* spp., mean vector, *Baetis* spp., *Isoperla* spp.; **c** mean vector, turbellarians, *Baetis* spp., NZMS, *Brachycentrus* spp.; **d** *Isoperla* spp., NZMS, *Serratella* spp., *Baetis* spp., mean vector, *Paraleptophlebia* spp., *Glossosoma* spp.

decreasing by an average of only 0.59 ‰ $\delta^{15}\text{N}$ and 0.27 ‰ $\delta^{13}\text{C}$ (Fig. 3b). The period of NZMS population crash (during to decline) also corresponded with non-random isotopic change in the invaded site; the native invertebrate taxa exhibited a significantly cohesive isotope shift ($R_{\text{bar}} = 0.982$, $P = 0.0396$) back towards more enriched $\delta^{13}\text{C}$ and higher periphyton reliance with an increase of 2.28 ‰ $\delta^{13}\text{C}$ (Fig. 3c). NZMS did not follow this isotopic trajectory, with consistent $\delta^{13}\text{C}$ signature and $\delta^{15}\text{N}$ increased by 1.12 ‰. The un-invaded site, in contrast, did not exhibit a significant cohesive change in isotope signatures during the period of NZMS decline ($R_{\text{bar}} = 0.298$, $P = 0.61$, Fig. 3d).

While our sampling regime forced us to lump most stable isotope signatures of benthic invertebrates into the three periods of invasion, we obtained five or more years of stable isotope data for three native taxa and NZMS. N isotopes changed cohesively through time; NZMS $\delta^{15}\text{N}$ was significantly positively related to the $\delta^{15}\text{N}$ of *Optioservus* spp. ($R^2 = 0.96$, $P = 0.0006$), not quite significantly related to the $\delta^{15}\text{N}$ of turbellarians ($R^2 = 0.55$, $P = 0.057$), and non-significantly related to the $\delta^{15}\text{N}$ of *Baetis* spp. ($R^2 = 0.23$, $P = 0.4$).

Mixing models on $\delta^{13}\text{C}$ indicated that native consumers shifted their reliance on autochthonous (periphyton) versus allochthonous (terrestrial vegetation) sources of carbon in relation to NZMS boom and bust (Fig. 4). NZMS had consistently high reliance on periphyton across the three phases of the invasion (median contribution of periphyton was >95 % for all periods). Four out of five native taxa used in this analysis exhibited decreases in their direct or indirect reliance on periphyton-derived carbon as NZMS invaded (*Baetis* spp., turbellarians, *Hydropsyche* spp., and *Brachycentrus* spp.), with estimated median contributions that decreased by 9–11 %. Intriguingly, one exception was the grazer *Optioservus*, which increased in their reliance (increased median contribution by 9 %) on periphyton during this same period. Thus, four of five native taxa followed the predicted shift away from periphyton-derived carbon as NZMS invaded. As NZMS populations crashed, native taxa (four out of four) consistently increased their reliance on periphyton, with an estimated contribution of periphyton that increased by a range of 12–42 % (Fig. 4a), following predictions that lower NZMS populations would lead to increased reliance on periphyton.

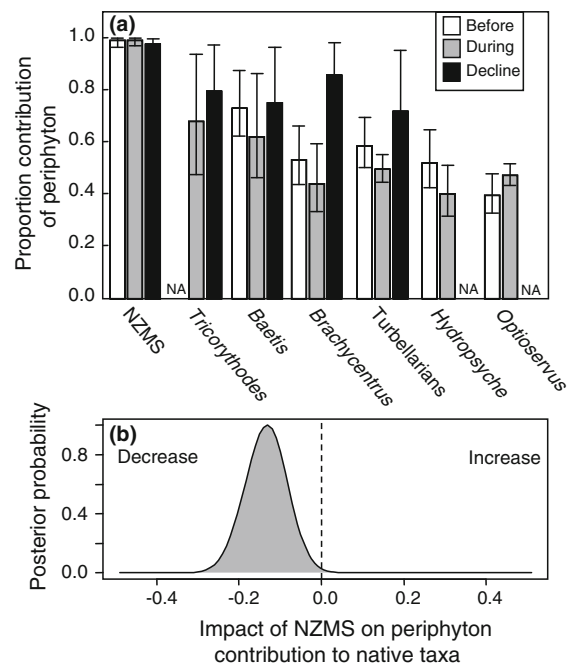


Fig. 4 Shifting proportional reliance on periphyton-derived carbon during the NZMS invasion, as quantified by Bayesian stable isotope mixing models. **a** Estimated proportional reliance of benthic invertebrates on periphyton based on mixSIR mixing models in the before, during, and decline of the invasion. mixSIR was run separately for each taxa and NZMS invasion stage. Shown are the best median estimate of source contribution and 2.5 and 97.5 % credible interval. Lack of data is shown with “NA”. **b** Posterior probability distribution of the impact of NZMS on the proportional reliance of benthic invertebrates on periphyton, as estimated by an integrated Bayesian isotope mixing model. Shown is the posterior probability distribution, back-transformed from logit space, for a consumer with a 69 % reliance on periphyton. The dashed vertical line at zero indicates where NZMS invasion isn’t associated with a change in periphyton reliance, while the positive values indicate an increased reliance and negative values indicate a decreased reliance. This parameter was estimated using a Bayesian isotopic mixing model nested with a model with taxa and NZMS as factors (see “Materials and methods”)

When the impact of NZMS invasion on periphyton contribution was estimated directly with a hierarchical Bayesian stable isotope mixing model (focusing on the four native taxa that shifted cohesively: *Tricorythodes*, *Baetis*, *Brachycentrus*, and turbellarians), the model estimated that NZMS substantially decreased reliance by consumers on periphyton (Fig. 4b). Specifically, the median posterior probability distribution indicated that NZMS decreased native invertebrate periphyton reliance by a proportion of 0.13, with a 95 % credible interval that did not span 0 (Fig. 4b; upper 97.5 % = -0.036, lower 2.5 % = -0.236).

Discussion

In this study, an invasive herbivore, NZMS, boomed and busted in a 10 year period. There are anecdotal reports of other NZMS populations decreasing after their initial invasion in other western U.S. streams (A. Sepulveda, *personal communication*, United States Geological Survey, Bozeman, Montana, USA). There are three main types of mechanisms that could have driven the population decrease. First, the crash could have been driven by bottom-up processes; perhaps the snails outstripped their algal resources. This possibility seems unlikely to have produced the observed sustained decline—populations of native grazing invertebrates rebounded following the crash of NZMS (Fig. 1b), while increasing their reliance on algal resources, evidence that algal resources also rapidly rebounded. Second, environmental variability could have driven the decline in NZMS. Indeed, 2006 was a wet spring; high and prolonged discharge could have diluted dissolved mineral content to levels that were unfavorable for NZMS survival (Herbst et al. 2008). Third, increased mortality of NZMS due to predators or pathogens could have driven the crash of NZMS (e.g., Twardochleb et al., in press). For example, introduced plant species can accumulate predators and pathogens over time (Hawkes 2007) and native predators can adapt to non-native prey over time, leading to increases in predator efficacy over time (Carlsson et al. 2009). The abundance of predatory invertebrates did increase sixfold during the increase of NZMS and predator populations stayed elevated as NZMS populations crashed (Fig. 1d); but these were generally small predators and the efficacy of these predators in feeding on NZMS is unknown. While we do not have data on parasites or other diseases in NZMS, it is also possible that some unknown pathogen caused the observed NZMS population crash. Regardless of the underlying mechanism, this boom and bust pattern has been observed before for other invasive species, ranging from cane toads (*Bufo marinus*) to Least weasels (*Mustela nivalis*), and is a potentially important but poorly understood phenomenon in invasion biology (Simberloff and Gibbons 2004).

The rise and fall of NZMS populations influenced benthic invertebrate community dynamics. As predicted, NZMS abundance was negatively related to native grazing herbivore abundance (Fig. 1b). This

result corroborates previous small-scale experiments that showed that NZMS competition can be detrimental to native grazing invertebrates (e.g., Riley et al. 2008). However, the annual abundance of piercing herbivorous invertebrates (Hydroptilid caddisflies) was positively related to NZMS abundance (Fig. 1c). In contrast to grazing herbivores like NZMS that rasp algae, piercing herbivores feed by puncturing cells in filamentous green algae. These data suggest that NZMS invasion caused a shift in the composition of stream algae; increased grazing pressure by NZMS on palatable periphyton such as diatoms could have allowed for competitive release for grazing-resistant filamentous green algae, thereby benefiting the specialized piercing herbivores. Given that communities in the un-invaded site did not track these changes, our data indicate that NZMS invasion has strong direct and indirect impacts on the trophic organization of stream communities.

New Zealand mudsnails population dynamics influenced stream nitrogen cycling, as evidenced by stable isotopes. During the NZMS invasion, we observed the systematic depletion of $\delta^{15}\text{N}$ signatures of all 6 benthic invertebrate taxa, regardless of their functional role (Fig. 3a). Furthermore, for the few taxa for which annual isotope data were available, N isotopes in the invaded site were remarkably cohesive across years, evidence that isotopic variability is driven probably by bottom-up processes such as alteration of the N-cycle by NZMS. These patterns are predicted based on several mechanisms by which NZMS can impact stream nitrogen cycling. First, NZMS excretion of depleted ammonium could decrease the $\delta^{15}\text{N}$ signature of the periphyton-derived food web because excreted N is generally depleted relative to body tissue (DeNiro and Epstein 1981). Alternatively, NZMS could cause depletion of $\delta^{15}\text{N}$ in the system by driving increases in periphyton N-fixation of atmospheric nitrogen, which is characterized by low $\delta^{15}\text{N}$ (Arango et al. 2009). Lastly, NZMS could lower rates of denitrification and thus enrichment of nitrogen, perhaps by decreasing organic material. Thus, these mechanisms are consistent with our observations that the nitrogen signatures of benthic invertebrates were systematically depleted following invasion of NZMS. This study supports previous findings that NZMS dominate N-cycling when abundant (Hall et al. 2003). Our observations of isotopic change during invasion suggests that NZMS invasion

does not simply replace function of some native species but rather that their invasion changes stream nitrogen cycling. However, the $\delta^{15}\text{N}$ of native invertebrates did not increase again when NZMS populations crashed (Fig. 3c). This lack of response to the crash of NZMS is suggestive that nitrogen biogeochemical cycling was not restored to the pre-invasion state. While we can only speculate on the underlying mechanism, it is possible that this lack of recovery represents hysteresis, with the NZMS invasion pushing the stream nitrogen cycling to an alternate state. Alternatively, the lack of recover may be due to a time-lag in the response to the crash of NZMS and that if NZMS populations remain low, the $\delta^{15}\text{N}$ of native inverts will increase again.

The rise and fall of NZMS also influenced the flow of carbon through the stream food web. As NZMS populations increased, native benthic invertebrates tended to become more depleted in $\delta^{13}\text{C}$ (Fig. 3a), evidence of decreased direct or indirect reliance on periphyton (Fig. 4). As NZMS populations subsequently decreased, native benthic invertebrates shifted back towards enriched $\delta^{13}\text{C}$, evidence of restored transfer of periphyton-derived carbon through the food web (Fig. 4a). These results follow predictions that high abundances of NZMS can sequester periphyton production, driving other benthic invertebrates from a variety of functional feeding groups to shift towards other sources of energy. Thus, NZMS can change carbon cycling in stream ecosystems (see also Hall et al. 2006).

This study examined community and ecosystem dynamics in one site that was heavily invaded and one that was not invaded to the same degree by NZMS. In essence, the un-invaded site served as a reference to assuage the concern that the observed changes in stream communities and ecosystems were indeed associated with the boom and bust of NZMS. However, there was obviously not replication at the site level, a common trade-off with large-scale and long-term studies. While the sites may have had slightly different characteristics, it is unlikely that these site differences directly explained the differences in community and ecosystem dynamics through time. However, site differences probably controlled the differences in invasion success of NZMS. For example, the isotope spaces of the two benthic communities were different, with the un-invaded community more dependent on allochthonous carbon and the invaded

community more dependent on periphyton carbon; a meager periphyton resource base may have even contributed to the poor invasion success of NZMS in the un-invaded site (Fig. 2). Future studies may be able to use stable isotopes to provide insight into whether a site is vulnerable to invasion.

Our study provides an interesting parallel with the extensive research on the invasion of zebra mussels in the Hudson River (Strayer 2009; Strayer et al. 2011). Zebra mussels invaded the Hudson River in 1991 and subsequently reached high densities. Their collectively enormous filtration rate decreased zooplankton abundance (Carlsson et al. 2011) and their high biomass displaced many benthic invertebrates (Strayer 2009; Strayer et al. 2011). Furthermore, zebra mussels dramatically altered biogeochemical cycling (Strayer 2009). However, in some regions, increases in predator numbers or efficiency have driven declines of mussels, thereby allowing their zooplankton prey to rebound (Carlsson et al. 2011; Strayer et al. 2011). Similar to our results, the impacts of zebra mussels on aquatic communities and ecosystems are temporally dynamic and controlled by their population dynamics.

The longer-term patterns of invasive species population dynamics, as well as the ecological causes and consequences of these dynamics, remains an important research frontier (Simberloff and Gibbons 2004; Strayer et al. 2006; Carlsson et al. 2009). Here we show that the invasion of an herbivore can alter ecosystems by top-down control of plant resources, thereby exerting bottom-up control on the flows of carbon and nitrogen through ecosystems. Thus, invasive herbivores can insert themselves into ecosystems with potentially far-reaching consequences. However, the impacts we observed were generally transient over the course of this study, as NZMS rapidly boomed and then busted. Our study provides further support for the notion that the invasion of a non-native species can be a dramatic shock to an ecosystem, but that severe impacts may be fleeting (e.g., Morrison 2002). Given that invasive species are one of the major agents of global change with annual costs to the United States of almost \$120 billion (Pimentel et al. 2005), it is imperative to understand these long-term processes (Strayer et al. 2006).

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