Exotic snails dominate nitrogen and carbon cycling in a highly productive stream

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Individual animal species can impact ecosystem processes, but few exotic invaders have demonstrated ecosystem-scale impacts, even when population sizes are large. We combined whole-stream measures of carbon and nitrogen fluxes with rates of consumption and ammonium excretion to show that an exotic freshwater snail, *Potamopyrgus antipodarum*, dominated these fluxes in a highly productive stream. The snails consumed 75% of gross primary productivity, and their excretion accounted for two-thirds of ammonium demand. Such large fluxes were due to high snail biomass rather than high rates of excretion or consumption. This exotic species may dramatically alter ecosystem function in rivers, with potential consequences for food web structure and element transport.

Impact of an invading animal. Separating these two will allow us to predict impacts better, in that we can focus research and management on understanding either specific traits or the invaders’ potential maximum biomass.

We studied the role of the exotic New Zealand mud snail (*Potamopyrgus antipodarum*) on C and N fluxes in Polecat Creek, WY (Figure 1). We scaled the snails’ per-biomass rates of organic matter consumption and ammonium excretion to whole-stream rates in an 800-m reach. We then compared these scaled estimates with whole-stream measures of C fixation and N cycling to estimate the snails’ contribution to stream C and N cycling (Grimm 1988; Vanni 2002). Because we scaled the impact of snails by multiplying per-biomass rates by snail biomass, we were able to estimate the degree to which high biomass or high per-biomass rates contributed to the dominance of C and N fluxes in the stream. We also compared both the per-biomass rates and dominance of ecosystem N fluxes by *Potamopyrgus* with values for other freshwater invertebrates from the literature.

### Study system

*Potamopyrgus antipodarum* is an herbivore/detritivore that invaded rivers in Yellowstone National Park in 1994, and has rapidly spread within and near the park since then (Figure 2). The snail is native to lakes and streams in New Zealand, where females may be sexual or parthenogenetic clones (with individuals developing from unfertilized eggs) (Dybdahl and Lively 1995), but exotic populations in North America are all-female clones (Dybdahl MF unpublished). Since it has achieved high densities of 20 000–500 000 snails/m² (Hall RO unpublished) in all geothermal spring streams in and around the park, there are no suitable reference sites with which to compare invaded and unininvaded warm spring streams. Our study site, Polecat Creek, is a geothermal spring stream that flows through the southern area of the park and the John D Rockefeller National
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Figure 1. Polecat Creek, in the John D Rockefeller National Parkway, WY.

Polecat Creek in northwest Wyoming. We used an 800-m reach approximately 2 km upstream of Flagg Ranch Resort. Stream temperature was warm and stable; the average temperature in January 2001 was 14.4°C, and the average temperature that July was 23.5°C. Polecat Creek is N-limited (Tank JL and Hall RO unpublished), and the stream bottom is carpeted by filamentous algae and vascular plants, with few open areas of cobble and gravel. The average channel width was 16 m, and summer discharge was 1.3–1.9 m³/s.

Methods

We measured ammonium uptake by benthic algae and microbes in Polecat Creek and compared this uptake with scaled rates of ammonium excretion by snails. First, we estimated uptake length, the average distance traveled by an ammonium molecule before it is taken up by the streambed. This uptake length, $x$, is given by

$$ x = \ln(N_x - N_0)/\alpha $$

where $N_x$ and $N_0$ are dilution-corrected ammonium concentrations at $x$ m downstream from the addition site (0 m), $a$ is a per-meter uptake rate (1/m), and $\alpha$ is a per-minute uptake rate (1/min). Thus, the uptake length is $1/a$ (Newbold et al. 1981). Uptake length will vary with water depth and velocity, so that fast, deep streams will carry a nutrient molecule further before it has the opportunity to contact the streambed.

Such hydrologic and geomorphic controls on uptake length confound our ability to compare streams with respect to biological nutrient demand (Davis and Minshall 1999). Therefore, to compare nutrient demand between streams and years with varying discharge, we calculated an ammonium uptake velocity as $V_f (m/min) = \alpha a$, where $d$ is stream depth (m) and $\alpha$ is water velocity (m/min), and is conceptually considered as the demand for ammonium relative to its water-column concentration. Finally, we calculated areal-specific $NH_4^+$ uptake as $U (mgN/m^2/h) = V_f N_x 60 \text{ min/h}$ (Newbold et al. 1981), where $N_x$ is ambient ammonium levels averaged from 16 pre-addition samples. We measured nitrate ($NO_3^-$) uptake using the same methods.

We quantified whole-stream gross primary production (GPP) and community respiration (CR), measured as oxygen ($O_2$) production and consumption, and compared these metabolism rates with organic matter ingestion by snails. We used the open-channel diel oxygen method (Odum 1956; Hall and Tank 2003), which integrates GPP and CR over the 800-m stream reach by budgeting fluxes of $O_2$ based on upstream inputs, downstream losses, exchange with the atmosphere, and metabolism. To estimate fluxes of oxygen from upstream and out to downstream, we recorded dissolved $O_2$ concentrations and stream temperature continuously for two nights and one day at the top and bottom of the 800-m reach using recording $O_2$ sensors (Hall and Tank 2003). We estimated the exchange of dissolved $O_2$ with the atmosphere by measuring the rate of loss of sulfur hexafluoride, a tracer gas that exchanges at a rate proportional to $O_2$ (Hall and Tank 2003). We thus estimated metabolism by difference; CR was measured as metabolism at night, while net ecosystem metabolism (ie GPP-CR) was measured during the day. We converted $O_2$ flux to C by assuming that for every mole of $O_2$ produced, a mole of C is fixed, and that organic matter contained 50% C.

We measured ingestion rates of organic matter by first estimating egestion rates of organic matter (as production of fecal pellets) and then converting to ingestion rates by dividing egestion by (1-assimilation efficiency). We assumed an assimilation efficiency of 0.3 for invertebrates consuming algae (Hall et al. 2001). Egestion was measured by incubating snails in filtered water for 1 h, and collecting and weighing feces. We measured the ratio of C:N of fecal pellets and snails with a Carlo-Erba CN analyzer to convert egestion as organic matter to an N egestion rate. The N ingestion rate was calculated differently than for organic matter, by summing egestion, excretion, and secondary N production.

To estimate the rate at which snails recycled assimilated N back to the water column, we measured their ammonium excretion rate by measuring $NH_4^+$ production of 7–21 snails incubated in 20-ml vials filled with filtered stream water for 1 h in the field. Following the incubation, we filtered water samples and immediately analyzed them for $NH_4^+$. We converted $NH_4^+$ production to per-biomass excretion rates, which we scaled to stream bottom area by multiplying by snail biomass.
Snail and native invertebrate biomass was measured in July and August 2001 by collecting six benthic samples on each date using a 15.2-cm diameter stovepipe corer. All taxa were counted and measured to estimate mass using length–mass regressions. Secondary production of mud snails was estimated by multiplying snail biomass by per-biomass growth rates measured in the field (Dybdahl MF and Hall RO unpublished). To estimate the combined biomass of the primary producers, we sorted, weighed, and ashed the macroalgal and vascular plant material from each of the cores, and estimated C and N content of primary producers as for snails.

Results and discussion

*Potamopyrgus* had high densities and biomass during July and August 2001 (Table 1). Snails dominated the invertebrate assemblage during these months, while native invertebrate biomass constituted only 3% of total biomass.

Community respiration and GPP were consistently high in Polecat Creek (Table 2). In fact, GPP rates were higher than all other whole-stream measurements reviewed by Wetzel (2001), and were higher than for seven of eight streams in a North American inter-biome study (Mulholland et al. 2001). Biomass of macroalgal and vascular primary producers, which probably supports a productive attached microalgal assemblage, was also large: 170 g of ash-free dry mass (AFDM) per m². Despite high primary productivity in Polecat Creek, *Potamopyrgus* consumed nearly all of primary production. Per-biomass *Potamopyrgus* egestion rates averaged 0.12/d and ranged from 0.09–0.18/d, which converted to an ingestion rate of 0.17/d. Multiplying per-biomass ingestion rate by snail biomass gave an area-specific ingestion rate of 5.9 gAFDM/m²/d, which was about 75% of daily GPP, which averaged 7.9 gAFDM/m²/d (Table 2). This consumption rate of GPP may be overestimated because algae respiration and nutrient uptake contribute to this overestimation. However, we can conclude that snails consumed a large proportion of daily primary production.

We compared snail NH₄⁺ excretion to both the measured net NH₄⁺ uptake from water column to benthos and the estimated gross NH₄⁺ uptake calculated from primary production measurements. Nitrogen cycling was rapid in Polecat Creek. Ammonium concentrations were extremely low, NH₄⁺ uptake lengths were short (mean 65 m) (Table 2), and residence time of NH₄⁺ in the water column averaged only 1.7 min. Ammonium uptake velocities were high (Table 2), among the highest previously published for any aquatic ecosystem, including seagrass beds and coral reefs (Thomas et al. 2000). The only NH₄⁺ uptake velocity found to be higher than Polecat Creek was a section of the Kuparuk River in Alaska (Vf = 120 mm/min), which has been experimentally fertilized with phosphorus since 1983 (Wollheim et al. 2001).

Despite this high demand for NH₄⁺, area-specific uptake of NH₄⁺ was merely average because of the extremely low NH₄⁺ concentration (Table 2). Because nitrate uptake lengths were 5–17 times longer than NH₄⁺ uptake lengths and nitrate concentrations were < 1 µg N/L, nitrate was probably not a substantial source of N to the benthic assemblage relative to NH₄⁺.

It is possible that much of the demand for NH₄⁺ was met by recycling within the thick algal/vascular plant mat in this stream. We can roughly estimate net demand for N

<table>
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<th>Potamopyrgus</th>
<th>Abundance</th>
<th>Biomass</th>
<th>Production</th>
<th>Excretion</th>
<th>Egestion</th>
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<td>gAFDM/m²</td>
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<td>0.95</td>
<td>41</td>
<td>0.17¹</td>
<td>**</td>
</tr>
</tbody>
</table>

¹Estimates based on Grimm (1988)    ²Not estimated
based on estimated primary production (Hall and Tank 2003). Assuming net primary production (NPP) is 50% of GPP, and converting O2 evolution to C fixation, we estimate NPP to be 2.0 gC/m2/d. Given 14 h of daylight, our calculated hourly rate of C fixation is 0.14 gC/m2/h. The rate of N uptake should be stoichiometrically related to C fixation, and measured molar C/N ratio for filamentous algae and epiphytes was 14, so N uptake should therefore be 1/14 of NPP. Given these assumptions, we predict that NH4+ uptake should be 12 mgN/m2/h, suggesting that recycling of NH4+ within the algal mat was five times higher than the flux from the water column to the algal mat.

Snail excretion was a large fraction of ecosystem NH4+ demand. Excretion rates of NH4+ by Potamopyrgus decreased with increasing snail size and ranged from 0.1–0.46 µgN/mgAFDM/h, resulting in a biomass-weighted mean excretion rate of 0.23 µgN/mgAFDM/h (Table 1). To estimate area-specific excretion fluxes for the entire streambed, we multiplied excretion rate by snail biomass. Snails excreted 7.8 mgN/m2/h (Table 1), which was almost four times higher than the average NH4+ flux from the water column to the benthos (2.1 mgN/m2/h). However, given our predicted gross NH4+ uptake of 12 mgN/m2/h within the algal mat, Potamopyrgus excreted about 65% of the estimated total NH4+ demand by microbes and plants.

Using these fluxes, we can create an N box model for Polecat Creek that includes the exotic snail Potamopyrgus (Figure 3). The transfer of N from benthic primary producers and detritus to the exotic snail represents the largest flux of the element in the stream, and was much higher than the flux to native primary consumers. Potamopyrgus dominated fluxes of C and N, despite the fact that Polecat Creek had high rates of primary production and tight N cycling. In effect, snails were one of the largest components in the Polecat Creek ecosystem; the standing crop of snail N equaled benthic plant N, they consumed 75% of GPP, and they were responsible for most of the NH4+ regeneration in this stream.

Did snails dominate these fluxes because they had high biomass or because of their high per-biomass rates of N ingestion and excretion? Excretion rates were in the middle of the range found for invertebrates in a desert stream (Grimm 1988). Zebra mussels (Dreissena polymorpha), another invasive exotic species, have slightly lower excretion rates of 0.045–0.32 µgN/mgAFDM/h (Arnott and Vanni 1996), which are also within the range reported by Grimm (1988). Per-biomass consumption rates were nearly two times lower than for primary consumers in two temper-
ate forest streams (0.31–0.32/d) (Hall et al., 2001), and about 12 times lower than periphyton removal predicted by Cattaneo and Mousseau (1995). Since *Potamopyrgus* had excretion and consumption rates equivalent or lower than other animals, we conclude that it dominated the N cycle in Polecat Creek because of its high biomass, not because it had particularly high rates of N ingestion and excretion.

Are ecosystem processes dominated by animal-derived fluxes in other ecosystems? We had no suitable site, unin- vaded by *Potamopyrgus*, with which to compare invaded streams, but it is possible to compare *Potamopyrgus*-derived fluxes with those from animals in other systems. Area-spe- cific rates of N excretion from all types of freshwater ani- mals averaged 1.9 mg N/m²/h (range 0.2–9.3) (Vanni 2002), which is on average lower than our estimate of 7.8 mgN/m²/h. Interestingly, the only value higher than ours was for exotic zebra mussels in Lake Erie (Arnott and Vanni 1996). Animal excretion can meet a substantial fraction of ecosystem N demand; Vanni (2002) found a range of 0.5–70% (mean 25%), a value much lower than our esti- mated percentage of 65%. Vanni’s high values of near or above 50% were for entire animal assemblages, whereas in Polecat Creek the high proportion of ecosystem N demand met by animal excretion is from only one species.

*Potamopyrgus* dominated flows of N and C in Polecat Creek, relative to other animals, despite the fact that the rates of primary production and N cycling were extremely high. The impacts of this invasion are similar to zebra mussel invasions in Lake Erie (Arnott and Vanni 1996). Exotic snails can consume nearly all primary production. Even in terrestrial habitats, the exotic gypsy moth (*Lymantria dispar*) can accelerate N cycling in forests (Lovett et al., 2003), which is similar to impacts by *Potamopyrgus*, given their high rates of N regeneration.

*Potamopyrgus* dominated N fluxes in Polecat Creek, and it has therefore probably altered ecosystem functions of storage and fluxes of N. This snail may well have community-level impacts beyond the direct interactions with native species because they have altered ecosystem function- ing at the base of the food web (Vitousek 1990). Species that dominate ecosystem function in rivers may affect processes beyond the ecosystem by altering nutrient retention and export to downstream ecosystems.

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### References


