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.

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Individual animals species can alter ecosystem functioning, such as nutrient cycling and storage, both directly, by altering carbon (C) or nitrogen (N) flux through grazing or excretion of ammonium (NH_4^+) (Grimm 1988; Frank *et al.* 1997; Vanni 2002), or indirectly via predation (Schindler *et al.* 1997). Despite numerous examples linking animal species with ecosystem processes such as nutrient fluxes, there have been only a few examples showing how invasives may affect ecosystem processes or overall functions (Strayer *et al.* 1999; Lovett *et al.* 2003). Exotic animals may provide a model system for examining single-species impacts on ecosystem processes for several reasons. They may have strong ecosystem-scale impacts because they can sometimes dominate invaded ecosystems in terms of biomass. They might also bring a new trait to the invaded ecosystem, for instance that of generalist predator. However, there have been few generalizations about how an exotic animal will impact native ecosystems; although many impact studies have been carried out, these have mostly been at the population or community level (Parker *et al.* 1999; Byers *et al.* 2002).

Parker *et al.* (1999) presented a framework for considering exotic species impact as $I = RAE$, where R = range (unit area), A = biomass per unit area, and E = impact per unit of biomass. Local-scale impact can be determined by either high biomass (Strayer *et al.* 1990), or high per-biomass impact relative to native species, which may include an exotic species that brings a novel trait (Vitousek 1990; Byers 2000). Despite the existence of this framework, we do not know how much either high biomass or high per-biomass impact contributes to the overall ecosystem-scale 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/m^2 (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 uninvaded 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.*

Parkway 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 m^3/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 NH_4^+ ion in stream water prior to incorporation by benthic microbes (Newbold *et al.* 1981). We describe the detailed methods in Hall and Tank (2003), but here we explain the conceptual approach. We added a small amount of ammonium (12 µgN/L) for 2 hours and measured its concentration decline downstream, and calculated NH_4^+ uptake length as $\ln N_x = \ln N_0 - ax$, where N_x and N_0 are dilution-corrected NH_4^+ concentrations at x m downstream from the addition site (0 m), a is a per-meter uptake rate (1/m), and 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) = vda, where d is stream depth (m) and v is water velocity (m/min), and is conceptually considered as the demand for ammonium relative to its water-column concentration. Finally, we calculated area-specific NH_4^+ uptake as U ($mgN/m^2/h$) = $V_f N_a$ 60 min/h (Newbold *et al.* 1981), where N_a 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.

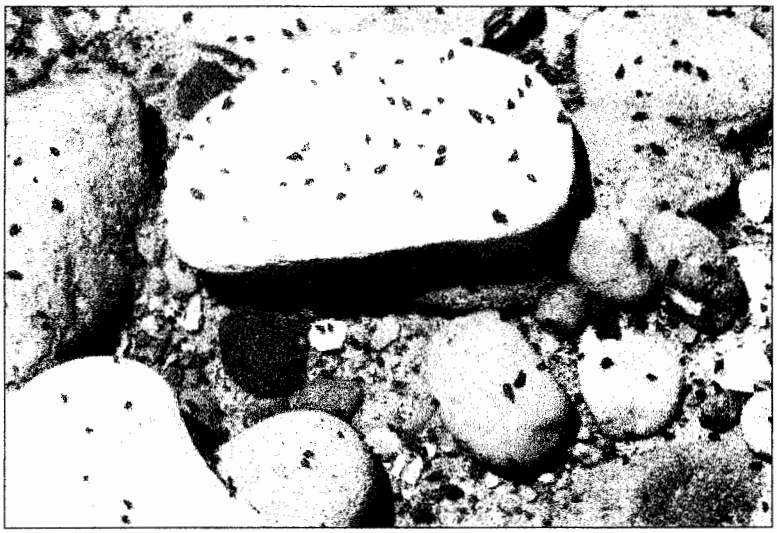

Figure 2. Potamopyrgus antipodarum *is easily visible on cobbles, in the Snake River in Yellowstone National Park.*

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 m^2. 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/m^2/d, which was about 75% of daily GPP, which averaged 7.9 gAFDM/m^2/d (Table 2). This consumption rate of GPP may be overestimated because algae respire some fraction of GPP (usually assumed to be 50%) for their own metabolism; error in measuring snail biomass and ingestion rate may contribute to this overestimation. However, we can conclude that snails consumed a large proportion of daily primary production.

We compared snail NH_4^+ excretion to both the measured net NH_4^+ uptake from water column to benthos and the estimated gross NH_4^+ uptake calculated from primary production measurements. Nitrogen cycling was rapid in Polecat Creek. Ammonium concentrations were extremely low, NH_4^+ uptake lengths were short (mean 65 m) (Table 2), and residence time of NH_4^+ 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 NH_4^+ uptake velocity found to be higher than Polecat Creek was a section of the Kuparuk River in Alaska (V_f = 120 mm/min), which has been experimentally fertilized with phosphorus since 1983 (Wollheim *et al.* 2001).

Despite this high demand for NH_4^+, area-specific uptake of NH_4^+ was merely average because of the extremely low NH_4^+ concentration (Table 2). Because nitrate uptake lengths were 5–17 times longer than NH_4^+ 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 NH_4^+.

It is possible that much of the demand for NH_4^+ was met by recycling within the thick algal/vascular plant mat in this stream. We can roughly estimate net demand for N

Table 1. Mean abundance, biomass, secondary production, and scaled excretion and egestion fluxes of *Potamopyrgus antipodarum* relative to native invertebrates in Polecat Creek, WY, during July and August 2001

	Abundance	Biomass	Production	Excretion	Egestion	
	indiv/m^2	gAFDM/m^2	mgAFDM/m^2/d	mgN/m^2/h	gAFDM/m^2/d	mg/Nm^2/d
Potamopyrgus	48 3000	34.5	1490	7.8	4.1	190
Native primary consumer taxa	950	0.95	41	0.17*	**	8.7*

*Estimates based on Grimm (1988) **Not estimated

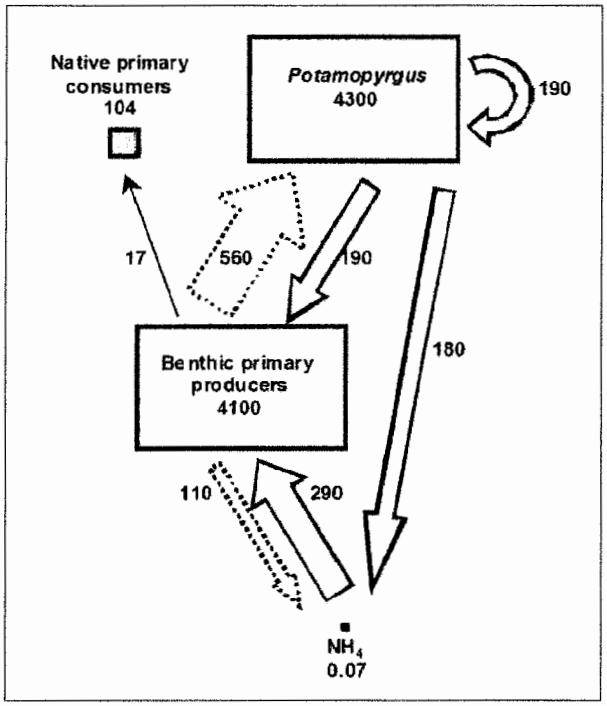

Figure 3. *Stocks and fluxes of N in Polecat Creek, WY. Stocks of N (mg/m^2) are shown with boxes, and N fluxes (mg/m^2/d) are shown with arrows. Box area and arrow width are proportional to these values. The circular arrow represents secondary production. Estimate of native invertebrate consumption of N is based on Grimm (1988). The flux from NH_4 to benthic algae and detritus includes an estimate of 50 mgN/m^2/d from water and 240 mgN/m^2/d from within the algal mat. Grey arrows are fluxes calculated by difference; regeneration of NH_4 is calculated as the difference between efflux and influx, and consumption of N by* Potamopyrgus *is calculated as the sum of egestion, excretion, and production, all of which are measured directly.*

based on estimated primary production (Hall and Tank 2003). Assuming net primary production (NPP) is 50% of GPP, and converting O_2 evolution to C fixation, we estimate NPP to be 2.0 gC/m^2/d. Given 14 h of daylight, our calculated hourly rate of C fixation is 0.14 gC/m^2/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 NH_4^+ uptake should be 12 mgN/m^2/h, suggesting that recycling of NH_4^+ 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 NH_4^+ demand. Excretion rates of NH_4^+ 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/m^2/h (Table 1), which was almost four times higher than the average NH_4^+ flux from the water column to the benthos (2.1 mgN/m^2/h). However, given our predicted gross NH_4^+ uptake of 12 mgN/m^2/h within the algal mat, *Potamopyrgus* excreted about 65% of the estimated total NH_4^+ 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 NH_4^+ 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-

Table 2. Ammonium uptake and metabolism estimates for Polecat Creek WY

		Ammonium				Matabolism			
	Discharge	NH+ concentration	Uptake length	Uptake velocity	Area-specific N uptake	Gross primary production		Community respiration	
Date	m^3/s	µgN/L	m	mm/min	mgN/m^2/h	gO$_2$/m^2/d	gAFDM/m^2/d	gO$_2$/m^2/d	gAFDM/m^2/d
28 Jul 2000	1.9	0.37	75	93	2.1	11.9	8.9	10.3	7.7
13 Jul 2001	1.3	0.5	38	126	3.8	9.3	7.0	11.7	8.8
26 Jul 2001	1.3	0.35	100	48	1.0	*	*	*	*
8 Aug 2001	1.3	0.3	45	107	1.6	10.5	7.9	14	10.5

*Not estimated

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, uninvaded 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-specific rates of N excretion from all types of freshwater animals averaged 1.9 mg $N/m^2/h$ (range 0.2–9.3) (Vanni 2002), which is on average lower than our estimate of 7.8 $mgN/m^2/h$. 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 estimated 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 that one organism that achieves high biomass can dominate fluxes; zebra mussels can filter the entire water column in 1–4 days (Strayer 1999), which is analogous to our finding that *Potamopyrgus* 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 very well have community-level impacts beyond the direct interactions with native species because they have altered ecosystem functioning 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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