

EXOTIC SNAILS DOMINATE NITROGEN AND CARBON CYCLING IN A HIGHLY PRODUCTIVE STREAM

ROBERT O. HALL, JR.* ✦ DEPARTMENT OF ZOOLOGY AND PHYSIOLOGY
UNIVERSITY OF WYOMING ✦ LARAMIE

JENNIFER L. TANK ✦ DEPARTMENT OF BIOLOGICAL SCIENCES
UNIVERSITY OF NOTRE DAME ✦ NOTRE DAME ✦ IN

MARK F. DYBDAHL ✦ SCHOOL OF BIOLOGICAL SCIENCES
WASHINGTON STATE UNIVERSITY ✦ PULLMAN

✦ ABSTRACT

Individual animal species can impact ecosystem processes, but few exotic animal species have demonstrated ecosystem-scale impacts, in spite of large population sizes. 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 carbon and nitrogen fluxes in a highly productive stream. Exotic snails consumed 75% of gross primary productivity, and their excretion accounted for two-thirds of ammonium demand. These large fluxes were due to high snail biomass rather than high per-biomass rates of excretion or consumption. This exotic snail may dramatically alter ecosystem function in rivers, with potential consequences for food web structure and element transport.

Individual animals species can alter ecosystem functioning, such as nutrient cycling and storage, by directly altering carbon or nitrogen flux through grazing or excretion of ammonium (Grimm 1988, Frank et al. 1997, Vanni 2002), or indirectly via predation (e.g. Schindler et al. 1997). Despite numerous examples linking animal species with ecosystem processes, e.g., nutrient fluxes, there have been only a few examples showing how exotic animals may affect ecosystem processes or overall functions (Strayer et al. 1999, Lovett et al. 2003). Exotic animals might provide a model system for

examining single-species impacts on ecosystem processes for several reasons. There are potentially strong ecosystem-scale impacts from exotic animals because they sometimes can dominate invaded ecosystems in terms of biomass. They also might bring a new trait to the invaded ecosystem, e.g. a generalist predator. However, there are few generalizations about how an exotic animal will impact native ecosystems, in spite of many impact studies which are mostly 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: $I = R \times A \times E$, where R = range (unit area), A = biomass per unit area, and E = per-biomass impact. Local-scale impact can be determined by either high biomass (e.g. Strayer et al. 1990) or by high per-biomass impact relative to native species, which may include an exotic species that brings a novel trait (Vitousek 1990, Byers 2000). Despite this framework, we do not know the degree to which either high biomass or high per-biomass impact contributes to overall ecosystem-scale impact by invading animals. Separating these two will allow better prediction of impacts in that we can focus research and management on understanding either specific traits or potential maximum biomass of invaders.

We studied the role of the exotic New Zealand mud snail, *Potamopyrgus antipodarum*, on

carbon (C) and nitrogen (N) fluxes in Polecat Creek, Wyoming (Fig. 1). We scaled their per-biomass rates of organic matter consumption and ammonium excretion by snails to whole-stream rates in an 800-m reach. We compared these scaled estimates with whole-stream measures of C-fixation and N cycling to estimate the snail's 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 N and C fluxes in this stream. We compared both the per biomass rates and dominance of ecosystem N fluxes by *Potamopyrgus* with literature values for other freshwater invertebrates.



Figure 1. Polecat Creek, located in the John D. Rockefeller National Parkway, Wyoming

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 (Fig. 2). *Potamopyrgus* is native to lakes and streams in New Zealand where females may be sexual or parthenogenetic clones (Dybdahl and Lively 1995), but exotic populations in North America are all-female clones (MF Dybdahl unpublished data). It has achieved high densities, 20,000 - 500,000 snails/m² (RO Hall unpublished data), in all geothermal spring streams in and around the Park; hence, there are no suitable reference sites by 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 Yellowstone National Park and John D. Rockefeller National Parkway, in northwest Wyoming, USA. We used an 800-m reach ~2 km upstream of Flagg Ranch Resort. Stream temperature was warm and stable (average

January 2001 temperature was 14.4°C; average July 2001 temperature was 23.5°C). The stream bottom was carpeted by filamentous algae and vascular plants, with few open areas of cobble and gravel. Polecat Creek is N-limited (JL Tank and RO Hall, unpublished data). Average channel width was 16 m and summer discharge was 1.3-1.9 m³/s.

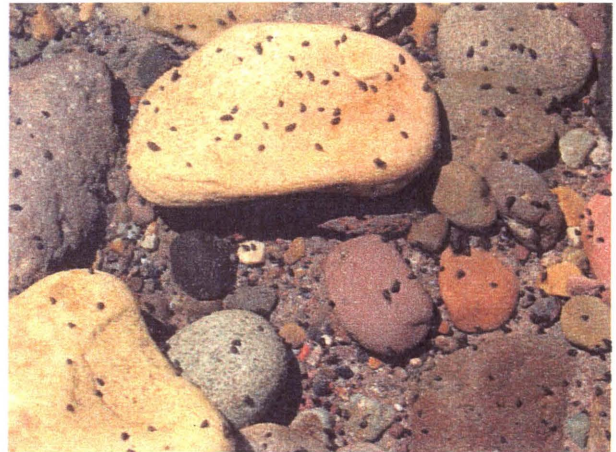


Figure 2. Example of *Potamopyrgus antipodarum* easily visible on cobbles, in the nearby Snake River in Yellowstone National Park

♦ METHODS

We measured ammonium (NH₄⁺) uptake by benthic algae and microbes in Polecat Creek and compared this uptake with scaled rates of NH₄⁺ excretion by snails. First, we estimated NH₄⁺ uptake length, the average distance traveled by a NH₄⁺ ion in stream water prior to incorporation by benthic microbes (Newbold et al. 1981). We added a small amount of NH₄⁺ (12 µgN/L) for 2 h and measured its concentration decline downstream. We calculated NH₄⁺ uptake length as:

$$\ln N_x = \ln N_0 - ax,$$

where N_x and N_0 are dilution-corrected NH₄⁺ concentrations at x m downstream from the addition site (0 m), a is a per-meter uptake rate (1/m), and uptake length, is $1/a$ (Newbold et al. 1981). Uptake length will vary with water depth and velocity; thus fast, deep streams will carry a nutrient molecule farther before it has the opportunity to contact the stream bed. Such hydrologic and geomorphic controls on uptake length confound our ability to compare streams with respect to biological nutrient demand (Davis and Minshall 1999). Thus, to compare nutrient demand among streams and years

with varying discharge we calculated a NH_4^+ uptake velocity (V_f) as

$$V_f (\text{m/min}) = v d a$$

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. Lastly, we calculated area-specific NH_4^+ uptake, U as

$$U (\text{mg N m}^{-2} \text{ h}^{-1}) = V_f \times N_a$$

(Newbold et al. 1981), where N_a is ambient NH_4^+ 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 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 oxygen 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 oxygen concentrations and stream temperature continuously throughout two nights and one day at the top and bottom of the 800-m reach using recording oxygen sensors (Hall and Tank 2003). Exchange of dissolved oxygen with the atmosphere was estimated by measuring the rate of loss of sulfur hexafluoride, a tracer gas that exchanges at a rate proportional to oxygen (Hall and Tank 2003). Metabolism was thus estimated by difference; CR was measured as metabolism at night, whereas net-ecosystem metabolism, (i.e. GPP-CR), was measured during the day. We converted oxygen flux to carbon by assuming that for every mole of O_2 produced a mole of C is fixed, and that organic matter contained 50% carbon.

We measured ingestion rates of organic matter by first estimating egestion rates of organic matter (as fecal pellets), and then converting to ingestion rates by dividing egestion rate 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 organic matter of feces. We measured C:N of fecal pellets and snails with a Carlo-Erba CN analyzer to convert egestion as organic matter to an N egestion rate. Ingestion rate of

nitrogen was calculated differently than for organic matter by summing egestion, excretion, and secondary production of N.

To estimate the rate at which snails recycled assimilated N back to the water column, we measured their NH_4^+ excretion rate by measuring NH_4^+ production of 7-21 snails incubated in 20-ml vials with filtered stream water in the field for 1 h. 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 6 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 (MF Dybdahl and RO Hall, unpublished data). 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.

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

	Abundance	Biomass	Production	Excretion	Egestion	
	ind./m ²	g AFDM/m ²	mg AFDM m ⁻² d ⁻¹	mg N m ⁻² h ⁻¹	g AFDM m ⁻² d ⁻¹	mg N m ⁻² d ⁻¹
Potamopyrgus	483,000	34.5	1490	7.8	4.1	190
Native primary consumer taxa	950	0.95	41	0.17*	ne†	8.7*

* Rates estimated based on Grimm (1988)

† rate not estimated

Gross primary production (GPP) and community respiration were consistently high in Polecat Creek (Table 2). In fact, rates of GPP from Polecat Creek were higher than all other whole-stream measurements reviewed by Wetzel (2001), and were higher than seven of eight streams in an inter-biome study in North America (Mulholland et al. 2001). Biomass of macroalgal and vascular

primary producers, which likely supports a productive attached microalgal assemblage, was also large (170 g AFDM / m). 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/d - 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 g AFDM m⁻² d⁻¹ which was about 75% of daily GPP (average = 7.9 g AFDM m⁻² d⁻¹) (Table 2). This consumption rate of GPP may be overestimated because algae respire some fraction (usually assumed to be 50%) of GPP for their own metabolism and 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.

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

Date	Discharge (m ³ /s)	Ammonium			Area-specific uptake mg N m ⁻² h ⁻¹	Metabolism			
		NH ₄ ⁺ µgN/L (m)	Uptake length mm/min	Uptake velocity mm/min		Gross Primary Production g O ₂ m ⁻² d ⁻¹ / g AFDM m ⁻² d ⁻¹	Community Respiration g O ₂ m ⁻² d ⁻¹ / g AFDM m ⁻² d ⁻¹		
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	ne*	ne*	ne*	ne*
8 Aug 2001	1.3	0.3	45	107	1.6	10.5	7.9	14	10.5

* ne metabolism was not estimated

We compared snail NH₄⁺ excretion to both the measured net NH₄⁺ uptake of 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 and 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 higher than Polecat Creek was a section of the Kuparuk River in Alaska ($V_f = 120 \text{ mm min}^{-1}$) that has been experimentally fertilized with phosphorus since 1983 (Wollheim et al. 2001). Despite this high demand for NH₄⁺, area-specific uptake of NH₄⁺ was 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 not likely 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 nitrogen based on estimated primary production (Hall and Tank 2003). Assuming net primary production (NPP) is 50% of GPP, and converting to O₂ evolution to C fixation, we estimate NPP to be 2.0 g C m⁻² d⁻¹. Given 14 h of daylight, our calculated hourly rate of C fixation is 0.14 g C m⁻² h⁻¹. Nitrogen uptake rate should be stoichiometrically related to C fixation and measured molar C/N ratio for filamentous algae and epiphytes was 14; therefore, N uptake should be 1/14 of NPP. Given these assumptions, we predict that NH₄⁺ uptake should be 12 mg N m⁻² h⁻¹ suggesting that recycling of NH₄⁺ within the algal mat was 5 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 µg N mg AFDM⁻¹ h⁻¹ resulting in a biomass-weighted mean excretion rate of 0.23 µg N mg AFDM⁻¹ h⁻¹ (Table 1). To estimate area-specific excretion fluxes for the entire stream bed we multiplied excretion rate by snail biomass. Snails excreted 7.8 mg N m⁻² h⁻¹ (Table 1) which was almost 4 times higher than the average NH₄⁺ flux from the water column to the benthos of 2.1 mg N m⁻² h⁻¹. However, given our predicted gross NH₄⁺ uptake of 12 mg N m⁻² h⁻¹ within the algal mat, then *Potamopyrgus* excreted about 65% of the estimated total NH₄⁺ demand by microbes and plants.

Using these fluxes we can create a nitrogen box model for Polecat Creek that includes the exotic snail, *Potamopyrgus* (Fig. 3). The transfer of nitrogen from benthic primary producers and detritus to the exotic snail represents the largest flux of N 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 cycling of nitrogen. In effect, snails were one of the largest components in the Polecat Creek ecosystem; 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). Another exotic species, zebra mussels, has slightly lower excretion rates (0.045-0.32 µg N mg AFDM⁻¹

h^{-1}) (Arnott and Vanni 1996), which are also within the range reported by Grimm (1988). Per-biomass consumption rates were nearly 2 times lower than for primary consumers in two temperate 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). We conclude that *Potamopyrgus* had excretion and consumption rates equivalent or lower than other animals; therefore, it dominated the N cycle in Polecat Creek because of its high biomass, not because it had particularly high per-biomass rates.

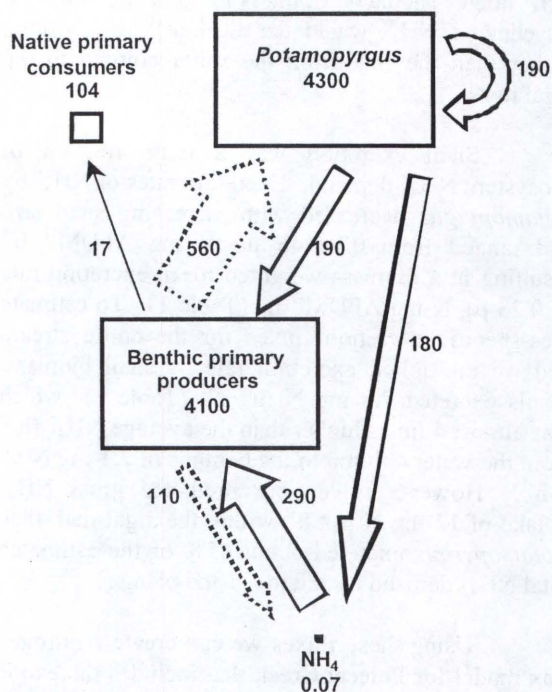


Figure 3. Stocks and fluxes of nitrogen in Polecat Creek. Stocks of N (mg N m^{-2}) are shown with boxes, and fluxes of N ($\text{mg N m}^{-2} \text{d}^{-1}$) are shown with arrows. Box area and arrow width are proportional to these values. The circular arrow on the *Potamopyrgus* box represents their secondary production. Estimate of native invertebrate consumption of N was based on Grimm (1988). The flux from NH_4 to benthic algae and detritus includes an estimate of $50 \text{ mg N m}^{-2} \text{d}^{-1}$ from water and $240 \text{ mg N m}^{-2} \text{d}^{-1}$ from within 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* was calculated as the sum of egestion, excretion and production, which were all measured directly.

Are ecosystem processes dominated by animal-derived fluxes in other ecosystems? We had no suitable uninvaded site which to compare similar streams without *Potamopyrgus*, but it is possible to compare *Potamopyrgus*-derived fluxes with those by animals in other systems. Area-specific rates of N excretion from all types of freshwater animals averaged $1.9 \text{ mg N m}^{-2} \text{h}^{-1}$ (range 0.2-9.3) (Vanni

2002) which is on average lower than our estimate of $7.8 \text{ mg N m}^{-2} \text{h}^{-1}$; 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 (mean = 25% range 0.5-70%) (Vanni 2002); this mean value is lower than our estimated percentage of 65%. High values in Vanni (2002) (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*, relative to other animals, dominated flows of N and C in Polecat Creek, despite the fact that 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; e.g. zebra mussels can filter all of the 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 can accelerate N cycling in forests (Lovett et al. 2003), which we suggest is similar to impacts by *Potamopyrgus* given their high rates of N regeneration.

Potamopyrgus dominated N fluxes in Polecat Creek; thus, it has likely altered ecosystem functions of storage and fluxes of N. This snail will likely 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). Additionally, 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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