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 animal 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 (NH4+).1 (Cottingham 1988; Frank et al. 1997; Vanni 2002), and indirectly via predation (Scheiner 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 invasive species may affect ecosystem processes or overall functioning (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 dominate invaded ecosystems in terms of biomass. They might also bring a novel 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 (area 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. 1999), or high per-biomass impact relative to native species, which may include an exotic species that brings a novel trait (Vanni and Byers 2003). 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 species. 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 snail (Potamopyrgus antipodarum) on C and N fluxes in Pelican 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 (Cottingham 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 inputs in the stream. We compared both the per-biomass rates and dominance of ecosystem N fluxes by Potamopyrgus with values for other freshwater invertebrates in the literature.

Study system

Potamopyrgus antipodarum is an herbivorous, dietitiozoan that invades rivers in Yellowstone National Park in 1994, and has rapidly spread within and near the park since then (Figure 1). 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 Lovly 1995), but exotic populations in North America are all-female clones (Dybdahl MF unpublished). Since it has achieved high densities of 20,000–50,000 snails/m2 (Hall RD 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, Pelical Creek, is a geothermal spring stream that flows through the southern area of the park and the John D Rockefeller National
Parkway in northwest Wyoming. We used an 800-m reach approximately 2 km upstream of Flagg Ranch Reservoir. Stream temperature was warm and stable, the average temperature in January 2001 was 14.4°C, and the average temperature for July was 23.5°C. Pocatello Creek is N-limited (Tinkin Jr. 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 Pocatello Creek and compared this uptake with scaled rates of ammonium excretion by snails. First, we estimated uptake length, the average distance traveled by an NH₄⁺ ion in stream water prior to incorporation by benthic microbes (Newbold et al. 1991). We describe the detailed methods in Hall and Tank (2003), but here we explore the conceptual approach. We added a small amount of ammonium (12 mgN/L) for 2 hours and measured its concentration decline downstream, and calculated NH₄⁺ uptake length as LN₄ = ln N₂/N₀ = α, where N₀ and N₂ are dilution-corrected NH₄⁺ concentrations at x km downstream from the addition site (0 m), a is a periwntake rate (1/α), and the uptake length is LN₄ (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 geometric factors on uptake length confound our ability to compare streams with respect to biologically nutrient deprived (Davis and Mitchhall 1999). Therefore, to compare nutrient demand between streams and years with varying discharge, we calculated an ammonium uptake velocity on Vₐ (m/min) = u/N, where u is stream depth (m) and N 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 NH₄⁺ uptake as U (mgN/m²h) = V₀N₀ 60 min/hr (Newbold et al. 1991), where N₀ is ambient ammonium levels averaged from 16 pre-added 8 samples. We measured nitrate (NO₃), uptake using the same methods.

We quantified whole-stream gross primary production (GPP), community respiration (CR), measured as oxygen (O₂) production and consumption, and compared these metabolism rates with organic matter ingestion by snails. We used the open-channel-diel oxygen method (Gelman 1956; Hall and Tank 2003), which integrates GPP and CR over the 800-m stream reach by budgeting fluxes of O₂ 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 O₂ concentrations and stream temperature continuously for two nights and one day at the top and bottom of the 800-m reach using recording O₂ sensors (Hall and Tank 2003). We estimated the exchange of dissolved O₂ with the atmosphere by measuring the rate of loss of solute headspace, a tracer gas that exchanges at a rate proportional to O₂ (Hall and Tank 2003). We then estimated metabolism by difference, CR was measured as metabolism at night, while net ecosystem metabolism (net GPP-CR) was measured during the day. We converted O₂ flux to C by assuming that for every mole of O₂ produced, a mole of C is fixed, and that organic matter contained 50% C.

We measured ingestion rates of organic matter by first estimating on-stream rates of organic matter (on production of fecal pellets) and then converting to in-stream rates by dividing excretion by (1 – assimilation efficiency). We assumed an assimilation efficiency of 0.3 for invertebrates consuming algae (Hall et al. 2004). Excretion was measured by incubating snails in filtered water for 1 h, and collecting and weighing feces. We measured the ratio of CN of fecal pellets and snails with a Carlo-Ebis CN-analyzer to convert excretion to organic matter to an N excretion rate. The N excretion rate was calculated differently than for organic matter, by summing excretion, excretion, and secondary production. To estimate the rate at which snails recycled assimilated N back to the water column, we measured their ammonium excretion rate by measuring NH₄⁺ production of 2–21 snails incubated in 250 mL of filtered O₂ and measured nutrient fluxes at 1 h in the field. Following the incubation, we filtered water samples and immediately analyzed them for NH₄⁺. We converted NH₄⁺ production to perianual excretion rates which we scaled to stream bottom area by multiplying by small biomass.
Small and native invertebrate biomass was measured in July and August 2001 by collecting six benthic samples on each date using a 152-cm diameter strethoscope core. All taxa were counted and weighed (Table 1) to estimate mass using length-mass regressions. Secondary production of mud snails was estimated by multiplying small biomass per-biomass growth rates measured in the field (Dykhuisen MF and Hall RO unpublished). To estimate biomass of the primary producers, we sorted, weighed, and ashed the macroalgae and vascular plant material from each of the cores, and estimated C and N content of primary producers as for snails.

Results and discussion

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

Community respiration and GPP were consistently high in Poletoot Creek (Table 2). In fact, GPP rates were higher than all other whole-stream measurements reviewed by Watt (2001), and were higher than for seven of eight streams in a North American inter-biome study (McKelland et al. 2001). Biomass of macroalgae and vascular primary producers, which probably supports a productive attached macroalgae assemblage, was also large: 170 g of submersed dry mass (AFDM) m-2. Despite high primary productivity in Poletoot Creek, Panopeasqua consumed nearly all of its production. Per-biomass Panopeasqua ingestion rate averaged 0.12±d and ranged from 0.08±0.18±d, which converted to an ingestion rate of 0.17±d. Multiplying per-biomass ingestion rate by small biomass gave an aspecific ingestion rate of 0.16±d, which was about 35% higher than estimates in other streams. This consumption rate of GPP may have overstated the impact because snails require some fraction of GPP (usually assumed to be 50%) for their own metabolism; error in measuring small biomass and ingestion rate may contribute to this overestimation. However, we can conclude that snails consumed a large proportion of daily primary production.

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

<table>
<thead>
<tr>
<th>Abundance</th>
<th>Biomass</th>
<th>Production</th>
<th>Excretion</th>
<th>Egestion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Potamopyrgus</td>
<td>48000</td>
<td>43.9</td>
<td>1490</td>
<td>7.8</td>
</tr>
<tr>
<td>Native primary</td>
<td>950</td>
<td>0.95</td>
<td>41</td>
<td>0.17*</td>
</tr>
</tbody>
</table>

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

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We computed small NH₄⁺ excretion to both the measured net NH₄⁺ uptake from water columns to benthos and the estimated gross NH₄⁺ uptake calculated from primary production measurements. Nitrogen cycling was rapid in Poletoot 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 aquatic birds and coral reefs (Thomas et al. 2003). The only NH₄⁺ uptake velocity found to be higher than Poletoot Creek was a section of the Kuparuk River in Alaska (V = 122 mm/min), which has been experimentally fertilized with phosphorus since 1983 (Wollheim et al. 2001).

Despite this high demand for NH₄⁺, anaerobic uptake of NH₄⁺ was merely average because of the extremely low NH₄⁺ concentration (Table 2). Because nitrate uptake lengths were 5-12 times longer than NH₄⁺ uptake lengths and nitrate concentrations were <1 mg N L⁻¹, 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/macrophyte mat in this stream. We can roughly estimate nutrient demand for N

Figure 2. Potamopyrgus antipodarum is easily visible on cobble, in the Snake River in Yellowstone National Park.
Figure 3. Stocks and fluxes of N in Poclet Creek, WY. Stocks of N (mg/m²) are shown with boxes, and N fluxes (mg/m²d) are shown with arrows. Flux area and arrow width are proportional to these values. The circular arrow represents primary production. Estimate of native invertebrate consumption of N is based on Grimm (1988). The flux from NH₄ to benthic algae and detritus includes an estimate of 50 mg/m²d from water and 245 mg/m²d/yr within the algal mat. Grey arrows are fluxes calculated by difference; regeneration of NH₄ is calculated as the difference between efflux and influx, and consumption of NH₄ by Potamogeton is calculated as the sum of efflux, excretion, and production, all of which are measured directly.

Based on estimated primary production (Hall and Task 2003), assuming net primary production (NPP) is 50% of OPP, and converting O₂ evolution to C fixation, we estimate NPP to be 2.0 gC/m²d. Given 14 h of daylight, calculated hourly rate of C fixation is 0.14 gC/m²h. The rate of N uptake should be stoichiometrically related to C fixation, and measured mean C/N ratio for filamentous algae and seagrasses was 14:1, so N uptake should therefore be 1/14 of NPP. Given these assumptions, we predict that NH₄ uptake should be 12 mgN/m²d, suggesting that recycling of NH₄ within the algal mat was five times higher than the flux from the water column to the algal mat.

Small excursions in a large fraction of ecosystem NH₄ demand. Excursions in N by Potamogeton decreased with increasing small size and ranged from 0.1-0.66 mgN/m²d/AFDM (Table 1). To estimate area-specific excursion fluxes for the entire streambed, we multiplied excursion rate by small biomass. Small excursions 7.8 mgN/m²d/AFDM (Table 1), which was almost four times higher than the average NH₄ flux from the water column to the benthos (2.1 mgN/m²d). However, given our predicted gross NH₄ uptake of 12 mgN/m²d within the algal mat, Potamogeton exceeded about 65% of the estimated total NH₄ demand by microbes and plants. Using these fluxes, we can create an N box model for Poclet Creek that includes the exotic seagrass Potamogeton (Figure 3). The transfer of N from benthic primary producers and detritus to the exotic seagrass represents the largest flux of the element in the stream, and was much higher than the flux to native primary consumers. Potamogeton-dominated fluxes of C and N, despite the fact that Poclet Creek had high rates of primary production and nighth cycling. In effect, smalls were one of the largest components in the Poclet Creek ecosystem, withstanding crop of small N limited benthic plant N, they consumed 37% of OPP, and were responsible for most of the NH₄ regeneration in this stream.

Did smalls dominate these fluxes because they had high biomass or because of their high per-biomass rates of N ingestion and excretion? Excursion 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 excursion rates of 0.045-0.32 mgN/m²d/AFDM (Arcott and Varonis 1996), which are also within the range reported by Grimm (1988). Per-biomass consumption rates were usually two times lower than for primary consumers in two temperate

Table 3. Ammonium uptake and uptake estimates for Poclet Creek WY

<table>
<thead>
<tr>
<th>Date</th>
<th>Discharge</th>
<th>NH₄ concentration</th>
<th>Uptake length</th>
<th>Uptake velocity</th>
<th>Area-specific</th>
<th>Gross primary production</th>
<th>Community respiration</th>
</tr>
</thead>
<tbody>
<tr>
<td>28 Jul 2000</td>
<td>1.9</td>
<td>0.37</td>
<td>75</td>
<td>93</td>
<td>2.1</td>
<td>11.9</td>
<td>8.9</td>
</tr>
<tr>
<td>13 Jul 2001</td>
<td>1.3</td>
<td>0.5</td>
<td>35</td>
<td>126</td>
<td>3.8</td>
<td>9.3</td>
<td>7.0</td>
</tr>
<tr>
<td>24 Jul 2001</td>
<td>1.3</td>
<td>0.35</td>
<td>100</td>
<td>48</td>
<td>1.0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1 Aug 2001</td>
<td>1.3</td>
<td>0.3</td>
<td>45</td>
<td>107</td>
<td>1.6</td>
<td>10.5</td>
<td>7.9</td>
</tr>
</tbody>
</table>

NH₄ = estimated

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Exotic snails and nutrient cycling.

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