Ecological Applications, 16(3), 2006, pp. 1121–1131

EXTREMELY HIGH SECONDARY PRODUCTION OF INTRODUCED SNAILS IN RIVERS

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Abstract. The functional importance of invasive animals may be measured as the degree to which they dominate secondary production, relative to native animals. We used this approach to examine dominance of invertebrate secondary production by invasive New Zealand mudsnails (*Potamopyrgus antipodarum*) in rivers. We measured secondary production of mudsnails and native invertebrates in three rivers in the Greater Yellowstone Area (Wyoming, USA): Gibbon River, Firehole River, and Polecat Creek. *Potamopyrgus* production was estimated by measuring in situ growth rates and multiplying by monthly biomass; native invertebrate production was estimated using size frequency and instantaneous growth methods. Mudsnail growth rates were high (up to 0.06 d^{-1}) for juvenile snails and much lower for adult females (0.003 d^{-1}). *Potamopyrgus* production in Polecat Creek (194 $g \cdot m^{-2} \cdot yr^{-1}$) was one of the highest values ever reported for a stream invertebrate. Native invertebrate production ranged from 4.4 to 51 $g \cdot m^{-2} \cdot yr^{-1}$. *Potamopyrgus* was the most productive taxon and constituted 65–92% of total invertebrate productivity. Native invertebrate production was low in all streams. Based on a survey of production measures from uninvaded rivers, the distribution of secondary production across taxa was much more highly skewed toward the invasive dominant *Potamopyrgus* in the three rivers. We suggest that this invasive herbivorous snail is sequestering a large fraction of the carbon available for invertebrate production and altering food web function.

Key words: biological invasion; Firehole River; Gibbon River; Greater Yellowstone Area; invasive species; invertebrates; New Zealand mudsnail; Polecat Creek; Potamopyrgus antipodarum; *secondary production.*

Introduction

Measuring and predicting the impact of invasive species is centrally important so that managers can prioritize efforts to prevent invasion or control the invader. Yet few species introduced outside their endemic range produce dramatic ecological changes (Williamson 1996). Obvious cases include exotic plants that dominate communities as virtual monocultures and thereby disrupt ecosystem processes (e.g., Sala et al. 1996) or invasive species that bring a novel trait (Vitousek 1990). Consistent with these cases, invasive species dominance, measured as relative biomass, is often a better metric of invasion success than absolute cover or biomass, as in plant studies (Lundholm and Larson 2004). Even though invasive animals do not often form monocultures, their dominance of communities might be an indicator of impact within and between trophic levels. Within a trophic level, animals that achieve higher biomass or production relative to their competitors are sometimes considered successful invasives (Simon and Townsend 2003). As consumers, the impact of an invasive animal might be best measured as the level of dominance of production in food webs, compared to that of native consumers. A notable example of dominance in biomass and production associated with invasive species impact, in terms of material flow through the food web, is the zebra mussel (*Dreissena polymorpha*) (Strayer et al. 1999, Strayer and Smith 2001).

Dominance within an animal assemblage likely represents a large impact on either native consumers and/or ecosystem functioning. At one extreme, a dominant invader might add to community production without depressing native production and thereby impact ecosystem function via the additional secondary production (Strayer et al. 1999). At the other extreme, a dominant invader might be highly productive and reduce production of native consumers without necessarily changing overall ecosystem function (no net change in total production). Regardless of where an invader lies on the continuum between these two extremes, dominance in biomass and production serves as a useful metric to estimate impact. Secondary production is a useful way to measure dominance because it combines animal biomass, growth rates, and population dynamics, thus integrating the functional performance of an animal population (Benke 1993). Secondary production estimates of introduced species

Manuscript received 3 June 2005; accepted 25 August 2005; final version received 4 November 2005. Corresponding Editor: J. Elser.
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are comparable with those of (1) native members from the invaded community, (2) other invasive species, and (3) members from uninvaded communities. This comparability is particularly valuable in situations where preinvasion data or reference sites do not exist.

Our objective was to measure secondary production of an invasive snail to estimate the degree to which it dominated the invertebrate assemblage. We compared dominance by exotics with secondary production data from the literature to show that exotic snails constituted a larger fraction of secondary production than uninvaded ecosystems. The New Zealand mudsnail (*Potamopyrgus antipodarum*) is endemic to New Zealand, but is a worldwide invader that spread in the 1800s in Europe and Australia, and since 1985 in North America (Zaranko et al. 1997). In the western United States, it reaches extremely high densities in geothermally influenced rivers in the Greater Yellowstone Area (GYA, Wyoming, USA) (Kerans et al. 2005) and plays a large role in ecosystem processing of nitrogen and carbon (Hall et al. 2003). However, attempts to study community-level effects in this important conservation region are hampered by the existence of only a few preinvasion data sets and the lack of suitable, uninvaded reference sites. (All warm rivers in the GYA have been invaded and colder rivers have dramatically different physical conditions and benthic invertebrate assemblages [Armitage 1961].) By measuring secondary production among invertebrate consumers in these rivers, we show that *Potamopyrgus* dominated production relative to native invertebrates and that this level of dominance was extreme compared to other published production estimates. This approach revealed the functional importance of an invasive animal and its alteration of food web structure.

Study sites and invasion

The New Zealand mudsnail (*Potamopyrgus antipodarum*) was discovered in rivers in the GYA in 1994 and rapidly spread throughout and beyond Yellowstone National Park, USA. The snails asexually reproduce (Dybdahl and Lively 1995) and the Yellowstone population comprises only female individuals of the same clonal lineage (M. F. Dybdahl, *unpublished data*). Females are ovoviviparous; brood sizes can be up to 80 juvenile snails (all female) (M. F. Dybdahl, *unpublished data*). They are herbivorous/ detritivorous scrapers.

We used three rivers for this analysis: Firehole River, Gibbon River, and Polecat Creek. Firehole River and Gibbon River drain the major geothermal features of Yellowstone National Park. We used four sites in total; two were highly vegetated with macrophytes and macroalgae, while the other two were riffles with little vegetation. We used two sites on the Firehole River representing two habitat types, an armored sediment riffle and vegetated depositional zone. These sites were near the Fountain Freight Bridge (at Ojo Caliente Spring) at the downstream end of the Lower Geyser basin. This site corresponded to the "Ojo Caliente" site from Armitage (1958). The riffle site ("Firehole riffle"; Universal Transverse Mercator [UTM] coordinates 12 513020E, 4934180N) had bedrock-like, silicate-armored sediment that covers much of the site. This section was a deep riffle with few macrophyte beds and some large cobbles. The vegetated site (Firehole vegetated; UTM 12 512650E, 4934220N) was downstream of a deep pool and ~200 m below the riffle site. Substratum at this site was gravel and sand covered with extensive macrophyte beds. The Gibbon River site (UTM 12 511470E, 4942930N) was ~200 m upstream from the bridge at Madison Junction. Substratum was mixed pebble, gravel, and sand with nearly no macroalgae or vascular plants. Polecat Creek is a geothermal spring stream near the South Boundary area of Yellowstone Park. Our site (UTM 12 525010E, 4883960N) was 300 m upstream of Huckleberry Hot Springs outlet (2 km from Flagg Ranch) in the John D. Rockefeller National Parkway. Substratum was pebble-gravel overlain by extensive macrophyte beds (Hall et al. 2003).

Methods

We sampled each river approximately monthly from August 2000 to August 2001. We did not sample in August 2000 at Polecat Creek because of a nearby wildfire or on 6 April 2001 at Firehole River because of bear management closure of the area. In depositional sites with high vegetation mass (Firehole vegetated site and Polecat Creek), we used a 15.2 cm diameter stovepipe corer to collect invertebrates. All plants, sediment material ($\leq$5 cm), and overlying water were removed from the corer; organic matter and invertebrates were elutriated from the mineral sediment and collected on a 250-μm sieve. In the two sites with mineral substrate (Gibbon River and the Firehole riffle site), we used a 250-μm mesh Hess sampler following Hall et al. (2001). We collected six samples in Polecat Creek and Gibbon River, five samples in the vegetated reach of Firehole River, and eight samples in the riffle reach of Firehole River: four samples from low-velocity areas near the bank and four samples near the deeper thalweg. Visual surveys of the Firehole riffle reach showed that ~50% of the area was in low-velocity bank zones with the remainder in fast-moving, deeper areas.

We preserved samples in 95% ethanol, stained them with Phloxine B, and separated them into a >1-mm size fraction and a fraction of 250 μm–1 mm for sorting. We picked all invertebrates from the >1-mm sample, except when there were >500 snails or amphipods in a sample. In that case, we subsampled the snails and amphipods after picking all other invertebrates by evenly distributing them on a 250-μm sieve and removing a fraction (one-eighth to one-half) of this material for sorting and counting. We subsampled all 250 μm–1 mm samples by removing a weighed fraction of the wet mass of each sample. We identified insects and macrocrustaceans to the level of genus, except for chironomids, which we identified as tanypodine and non-tanypodine. Oligo-

chaetes were separated into two categories: Tubificidae and other oligochaetes. Native snails were identified to the level of family. All individuals for most taxa were measured to the nearest millimeter. Exceptions were amphipods, for which we measured a subsample of 30 individuals when they were common. For mudsnails, we measured a subsample of >30 individuals from each size fraction to the nearest 0.1 mm to more precisely estimate the biomass.

We used length–mass regressions to estimate ash-free dry mass (AFDM) for each taxon. For most taxa, we used published equations (Benke et al. 1999). Three common taxa, *Potamopyrgus*, *Hyalella*, and tubificid oligochaetes, had no published regressions, so we developed our own. The regression for *Potamopyrgus* is mass $= 0.0199L^{2.375}$ ($n = 46$, $r^2 = 0.96$), where mass is measured in milligrams (AFDM) and L is shell length in millimeters. This mass includes organic matter in the shell, but not the inorganic shell itself. *Hyallela* regression is $0.0024L^{3.15}$ ($n = 53$, $r^2 = 0.91$), and the tubificid regression is $0.0124L^{1.05}$ ($n = 27$, $r^2 = 0.73$), where L is length in millimeters.

Estimating secondary production

We estimated annual secondary production for most common taxa using the size-frequency method, corrected for cohort production interval (CPI) (Benke 1984). The CPIs were estimated by examining size distributions of invertebrates through the one-year sampling period and by examining insect emergence patterns based on observation (Benke 1984). For the amphipod *Hyalella*, observation of size-frequency patterns suggested two cohorts per year; this corresponded to those found by Pickard and Benke (1996) for *Hyalella* in a warm southeastern United States wetland. For rare taxa, we multiplied biomass by an assumed production : biomass (P:B) ratio of 10, (for assumed bivoltine taxa), 5 (for univoltine taxa) or 2.5 (for some rare semivoltine taxa with life cycles >1 yr) (Benke 1984). For taxa with unknown life cycle lengths, we multiplied biomass by a P:B ratio of 5. Errors from calculating total invertebrate production by using these methods for rare taxa are small, since they accounted for only 2–6% of total secondary production in these streams. Non-tanypodine chironomid production was estimated using the assemblage level, instantaneous growth method (Huryn and Wallace 1986), correcting for water temperature. We used regression equations in Huryn and Wallace (1986) to estimate growth rates, which were multiplied by monthly chironomid biomass. This method was originally created for forest streams, but the equations work in other, warmer systems (Stagliano and Whiles 2002). For example, in a warm prairie stream in Kansas, USA, the size-frequency method and the instantaneous growth method (Huryn and Wallace 1986) equations gave similar results (Stagliano and Whiles 2002). We recorded water temperature hourly in each stream using Hobo StowAway temperature loggers (Onset Computer Corporation, Bourne, Massachusetts, USA). There are few in situ studies on oligochaete production, so we used published laboratory growth rates and applied them using the instantaneous growth method. We estimated growth rates as [ln (mature mass) − ln (initial mass)]/maturation time. Maturation time was estimated from data in Poddubnaya (1980), and mature mass and initial mass were estimated based on the largest and smallest size class of tubificids found in our samples.

We measured mudsnail production by measuring their growth and fecundity rates and multiplying by monthly biomass (instantaneous growth method, Benke 1984). Because mudsnail production was so large, errors in estimating production would be large if we had assumed their growth rates. We measured growth rates in small cages placed in GYA streams during summer 2001. Mark–recapture methods used in other studies (e.g., Huryn et al. 1994) did not work for these tiny, abundant snails (R. O. Hall, *personal observation*). We measured growth rates and fecundity of snails in seven 0.5-mm size classes at various temperatures and locations throughout the GYA (cf. Huryn et al. 1994). For each snail growth measurement, we placed 15 snails for each size class in three replicate 3-cm stainless steel mesh round cages (tea balls, Lund Distributing, Lansing, Michigan, USA) wrapped in 154-μm Nitex mesh. There was only one size class per cage. We tethered these cages to a spike in the stream bottom, and left them in place for ~14 days, after which we measured all snails. For each fecundity measurement, we caged 15 snails in three replicate 50-mL centrifuge tubes with three windows cut into the sides. The windows were covered with 154-μm Nitex mesh to allow water circulation but prevent escape of newborn snails. Centrifuge tubes were mounted in plastic brackets and spiked together to the stream bottom for ~2 days. To obtain snails for the cages, we collected from the nearest population and sorted the snails into a maximum of seven shell length size classes (1.75, 2.25, 2.75, 3.25, 3.75, 4.25, and 4.75 mm) using a digital micrometer. Snails in each size class varied by <0.25 mm from the mean length for each size class. The larger size classes were used if enough snails of that size were present in a population. For fecundity estimates, the smallest size class of brooding snails was 2.75 mm. Biofilm-coated pebbles were added to each cage. For each size class, we made 37–42 growth estimates, except for the 4.25-mm growth class and the 4.75-mm fecundity classes, where we only had 12 and 16 estimates. Biomass-specific somatic growth rates (d^{-1}) were estimated as $(\ln M_t - \ln M_0)/t$, where M_t was the average mass of a snail after t days and M_0 was the average mass of a snail at the onset of the growth measurement. For the contribution of fecundity to biomass growth, we counted all juvenile snails hatched, and based on their mass (0.0033 mg AFDM/juvenile snail; M. F. Dybdahl and R. O. Hall, *unpublished data*), calculated fecundity as Pickard and Benke (1996) did for amphipods. Biomass-specific fecundity rates (d^{-1}) were calculated

as the $M_{juv}/(M_0 \cdot t)$, where M_{juv} was the mass of all juvenile snails produced during interval t.

We predicted snail growth rates as a function of shell size and temperature. We estimated somatic growth for each 0.1-mm size class by fitting a multiple linear regression of snail size (1.5–4.75 mm) and mean temperature to predict snail growth rate. For snails <1.5 mm, we assumed that growth rates were equal to the rate for snails in the 1.75-mm size class. Given the allometry of growth (Fig. 1), this assumption will underestimate actual snail production, but we did not want to extrapolate that relationship. Thus, our estimates of production are probably lower than actual production. We estimated fecundity rate for each size class of >2.75 mm by fitting a linear model of fecundity vs. snail size. Total growth rate for each 0.1-mm snail size class was estimated by summing somatic growth and fecundity rates.

We used our tea-ball growth estimates to measure production; because production is sensitive to these growth rates, we examined production rates using growth estimates from two independent sources. One was growth from much larger cages that were designed to measure competition between mudsnails and a native snail in 2002 (L. A. Riley, M. F. Dybdahl, and R. O. Hall, *unpublished data*). These cages were made from 256-cm^2 sandwich trays with screened openings on top and sides to allow light and water through and were filled with 5–6 algae-coated rocks. They were located much upstream from our site in Polecat Creek and in an unnamed tributary spring, both in Yellowstone National Park, USA. The other growth data set was from laboratory studies (Dybdahl and Kane 2005). For each growth vs. size relationship (Fig. 1), we calculated production, ignoring temperature for the sole purpose of comparing how different methods of measuring growth affected our production estimates.

To estimate snail production, we multiplied growth rate by the biomass of that size class at each field site and for each collection date. For each site, we summed production for all size classes to estimate monthly production, and summed monthly production to estimate annual production.

Results

Water temperatures were relatively warm in Polecat Creek and Firehole River compared to Gibbon River. Polecat Creek was warm in winter (mean January temperature = 14.4°C) and summer (mean July temperature = 22.1°C), with an annual average of 18.0°C. Firehole River had a similar annual average (18.6°C), but was cooler in winter (mean January temperature = 12.6°C) and hotter in summer (July mean = 26.1°C) than Polecat Creek. Firehole River and Polecat Creek accumulated nearly the same number of degree-days from 1 Aug 2000 to 31 July 2001: 6597 degree-days in Firehole River vs. 6539 degree-days in Polecat Creek. Gibbon River was much cooler and more variable than either stream with annual average of 11.4°C and larger annual variation (January mean = 5.1°C, July mean = 20.1°C). The 4135 accumulated degree-days in Gibbon River were fewer than in the other two rivers.

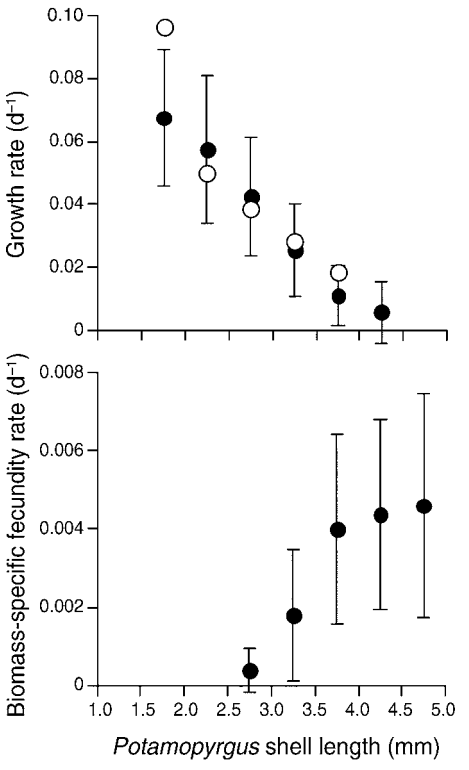

FIG. 1. Shell length is the primary predictor of *Potamopyrgus* growth (top) and fecundity rates (bottom). Solid circles are growth estimates from several rivers in Yellowstone National Park. Open circles are growth data measured in larger cages as part of a competition study in an upstream reach and tributary spring of Polecat Creek. Data are means ± SD. Note the smaller axis scale for fecundity; these rates were much lower than somatic growth.

Potamopyrgus biomass-specific growth rates were high, and strongly varied as a function of snail size class (Fig. 1) and mean temperature (multiple regression, growth rate [d^{-1}] = (0.0775 − 0.0293)[shell size] + 0.0024 [temperature], with size in millimeters and temperatue in °C, $n = 225$, adjusted $r^2 = 0.68$, $P < 0.001$). Most of the variation was explained by shell size class alone in the model ($r^2 = 0.59$). Small snails grew quickly, while snails >4.25 mm did not grow in our incubations, as expected (Winterbourn 1970). These growth rates were similar to those measured independently as part of a competition study with larger cages (Fig 1).

Fecundity rates increased as growth rates decreased with snail size (Fig. 1). Large snails produced 0.1–1.3 daughters/d (snails are asexual), which corresponded to biomass-specific fecundity rates that varied from 0.0004 to 0.0045 d^{-1}. Fecundity rates were not a function of temperature, only of shell size (in millimeters) (regression, biomass-specific fecundity rate [d^{-1}] = −0.00603 +

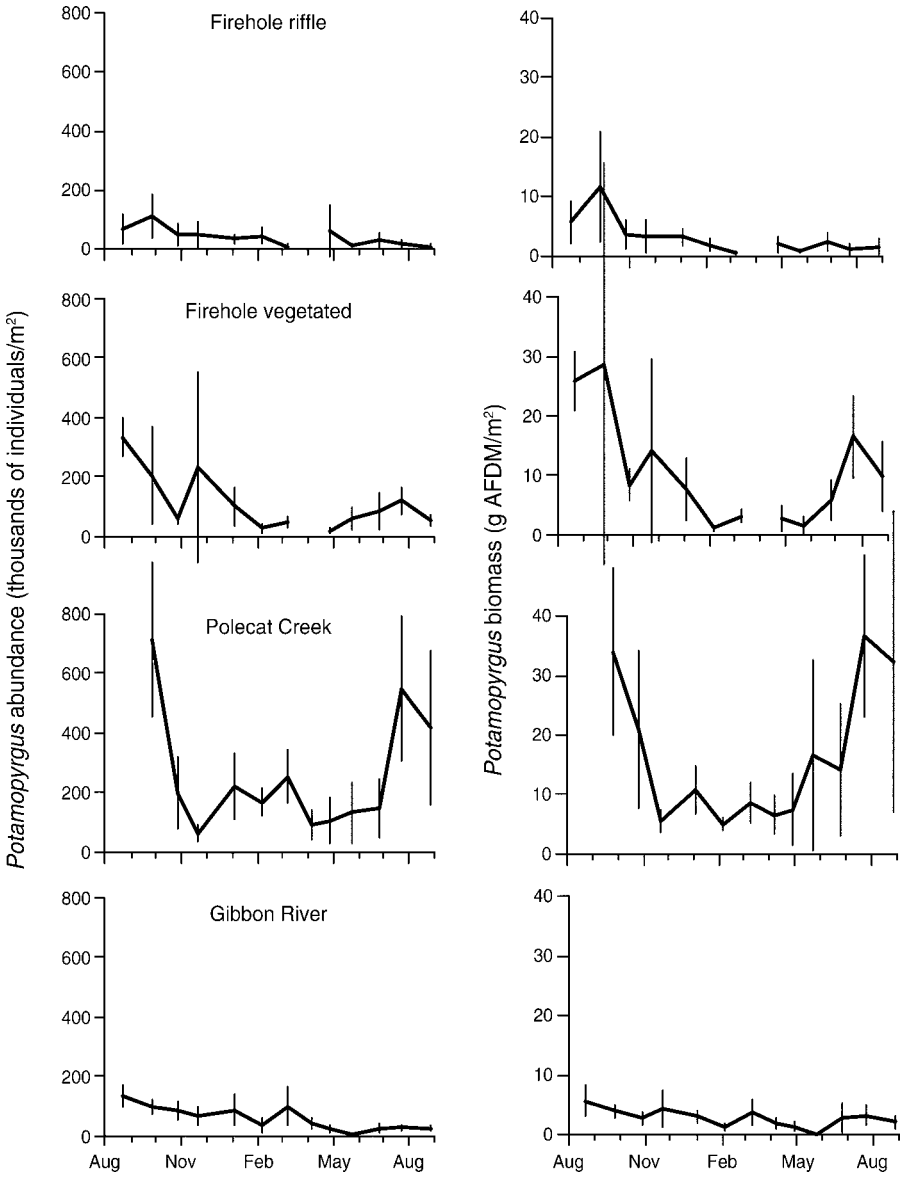

FIG. 2. *Potamopyrgus* abundance and biomass from monthly benthic samples in each of the four study sites; data are means and 90% confidence intervals.

0.00244[shell size], $n = 179$, $r^2 = 0.37$, $P < 0.001$). These biomass-specific fecundity rates were much lower than somatic growth rates for small snails.

Abundance and biomass of snails varied throughout the year in all streams with summer maxima and winter minima (Fig. 2) in the vegetated habitats, although there was less seasonal periodicity in the riffle habitats of Firehole River and Gibbon River. Polecat Creek had the highest average biomass, followed by Firehole River, and then Gibbon River. Gibbon River had much lower average biomass than either of the warmer streams. The highest biomass was in Polecat Creek during late summer and reached 36 g AFDM/m^2, with abundance >500 000 individuals/m^2 (Fig. 2). Mudsnail biomass and abundance from the Firehole riffle section and the Gibbon River varied less during the year and had lower abundance and biomass than Polecat Creek or the vegetated section of Firehole River. Biomass tracked abundance, except in late summer when biomass was higher than expected from abundance.

High biomass combined with high growth rates led to extremely high estimates of annual snail production in Polecat Creek and the vegetated habitat of Firehole (Fig. 3, Appendix). Monthly secondary production during summer from Polecat Creek was much higher than the annual average due to higher biomass then. During July 2001, daily *Potamopyrgus* production was 1.5 g AFDM·m^{-2}·d^{-1}. Production to biomass ratio

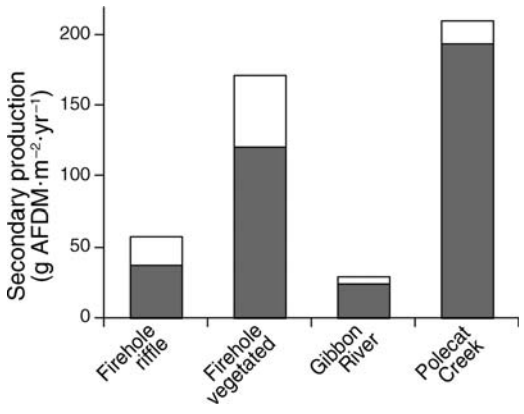

FIG. 3. *Potamopyrgus*-dominated total invertebrate secondary production in Firehole River, Gibbon River, and Polecat Creek in 2000–2001. The open portion of each bar is production of native invertebrates; the shaded portion is production of *Potamopyrgus*.

(*P*:*B*) was 12 yr^{-1} in Polecat Creek and both habitats of Firehole River, and 9 yr^{-1} in Gibbon River (Appendix). Production in all but Gibbon River was relatively even across size classes of snails; in Gibbon River, however, most of the production was in the smallest size classes (Fig. 4). The vast majority of the secondary production was via somatic growth, and not production of juvenile snails (Fig. 4). We recalculated production for Polecat Creek using our field data from this paper, data from larger cages, and laboratory growth rates (Dybdahl and Kane 2005). We did not use temperature as a covariate just so we could compare among these different growth rates. Production using our field growth rates was 188 g AFDM·m^{-2}·yr^{-1} (lower than our reported value because we did not include temperature). Estimated production using laboratory growth rates was 171 g AFDM·m^{-2}·yr^{-1}, and using growth rates from the larger competition cages, was 201 g AFDM·m^{-2}·yr^{-1}.

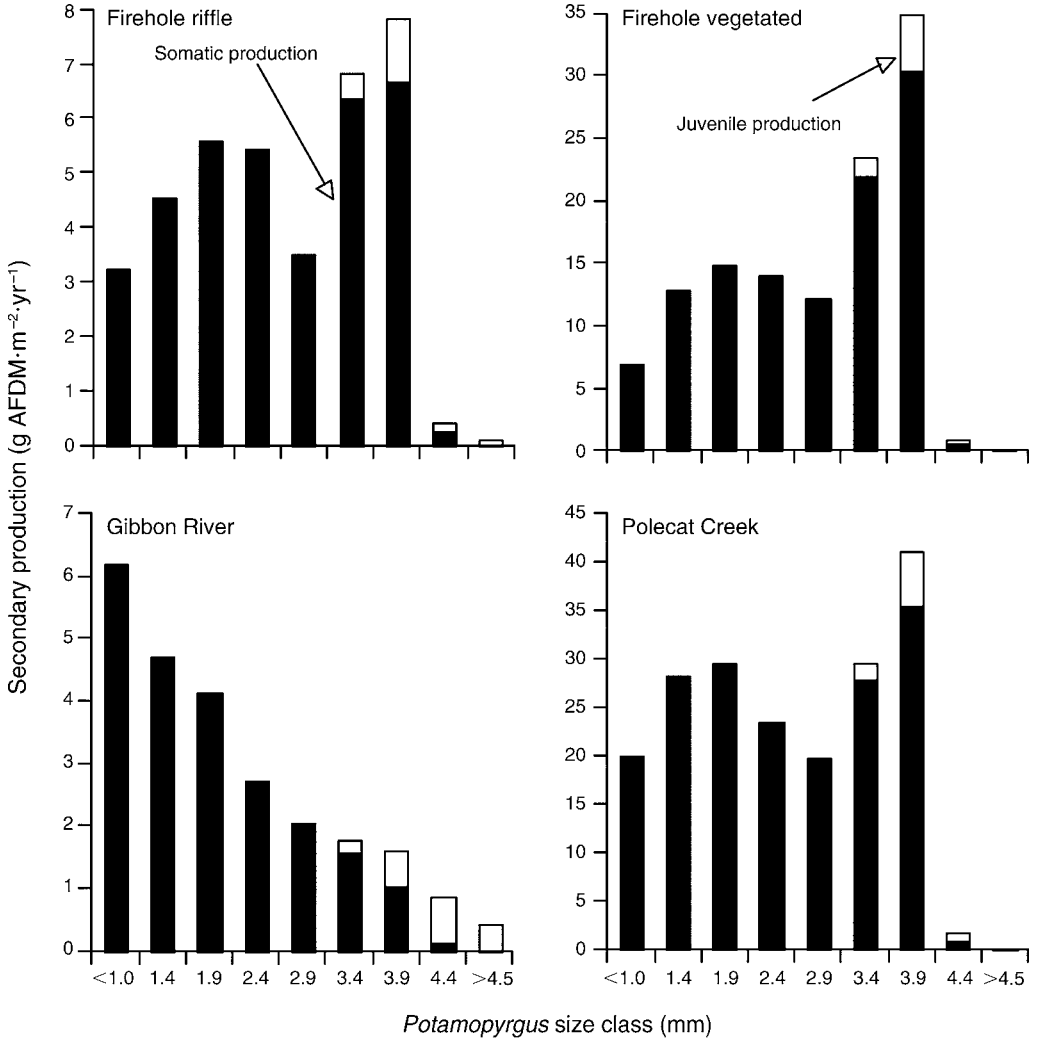

FIG. 4. Distribution of *Potamopyrgus* secondary production in Firehole River, Polecat Creek, and Gibbon River across a range of snail shell size. Most production is somatic (solid bars) relative to juvenile production (open bars). Note the different *y*-axis scales.

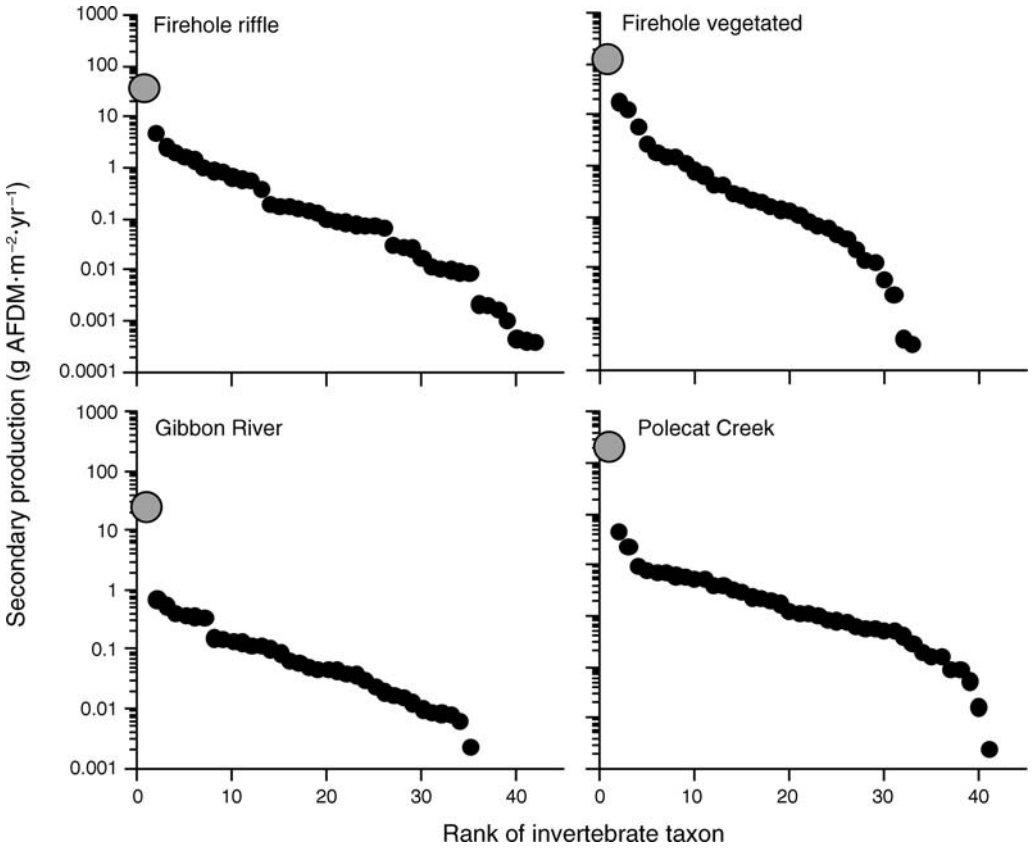

FIG 5. Annual secondary production of *Potamopyrgus* was 7–40 times higher than any other taxon in Firehole River, Gibbon River, and Polecat Creek in 2000–2001. Large gray circles are secondary production of *Potamopyrgus*. Small black circles are secondary production for native invertebrate taxa ranked from highest to lowest production.

Production of native invertebrate assemblages was much lower than for mudsnails in each stream (Fig. 3; Appendix). Production of native invertebrates constituted 30% of total production in the Firehole River vegetated reach, 35% in the Firehole River's riffle reach, 8% in Polecat Creek, and 15% in the Gibbon River. Despite low mudsnail production in the Gibbon River relative to the vegetated streams, production of native invertebrates was so low (4.4 g AFDM·m^{-2}·y^{-1}) that mudsnails dominated the secondary production of the entire assemblage. When considered on a taxonomic basis, mudsnails in riffle sections were 7.5 times more productive in the vegetated section and 6.5 times more productive than the next most productive taxon in Firehole River. Mudsnails were 34 times more productive than the next most productive taxon in Gibbon River, and 40 times more productive in Polecat Creek (Fig. 5). The distribution of ranked production values of native taxa in those streams was approximately lognormal, but the production values for mudsnails were strong positive outliers (Fig. 5).

DISCUSSION

Potamopyrgus dominated secondary production in all three streams and had extremely high rates of secondary production. In fact, these rates are among the highest recorded for stream benthic invertebrates. Native invertebrate production was a small fraction of total production. The vast majority of total organic matter flow through the invertebrate assemblage was through these invasive snails vs. native benthic invertebrates. The dominant role of the invasive snail was strongly influenced by their high biomass, and to a lesser extent, by their high growth rates.

While abundant and widespread in their native New Zealand habitats, *Potamopyrgus* does not reach biomass levels as high as those measured in the geothermal streams in their invasive range. Abundances in a 48-stream survey in New Zealand rarely exceeded 1000 individuals/m^2 (Holomuzki and Biggs 1999). In their native range, they can numerically dominate the invertebrate assemblages in lowland streams containing lots of macrophytes, habitats that are ecologically similar to our sites (Duggan et al. 2002). However, even in these types of habitats their densities reached only

4000 individuals/m^2 (Collier et al. 1998). In contrast, outside of their native range, *Potamopyrgus* can achieve higher densities. They dominate native snail assemblages (Strzelec 1999), and their success might be facilitated by human disturbance, as abundance was positively correlated with human land use and flow disturbance in several Australian streams (Schreiber et al. 2003). Even in relatively pristine conditions in the western United States, *Potamopyrgus* abundance exceeds 30 000 individuals/m^2 in Snake River Springs, Idaho, USA (Richards et al. 2001). Additionally, the Madison River in Yellowstone has reported 300 000 individuals/m^2 (Kerans et al. 2005). These extremely high abundances would produce high secondary productivity even at low or moderate growth rates.

The growth rates we measured for *Potamopyrgus* were high compared to published growth rates of other freshwater snails, but were similar to growth rates measured for snails and other invertebrates from warm waters. Growth rates measured in this study seemed to be generally accurate estimates for *Potamopyrgus,* since they were repeatable and closely matched by growth rates measured from larger cages and laboratory growth rates. Recalculated production for Polecat Creek from these alternate growth rate data sets shows that estimates of production varied ~16%, showing that differences in estimating growth rates cause only small variation in production estimates. Most production for larger, brooding snails was derived from their continual production of juvenile snails; their somatic growth rates were very low. Our estimates of production : biomass (*P*:*B*) ratios for *Potamopyrgus* (8–12 yr^{-1}) were higher than estimates for *Potamopyrgus* in New Zealand (3.0 yr^{-1}; Huryn 1996), perhaps because the New Zealand streams were much colder (average = 6.2°C) than the geothermal streams in our study (Polecat Creek average = 18°C). *Potamopyrgus P:B* estimates were also much higher than estimates for a temperate marsh population of *Lymnaea* (3.2 yr^{-1}; Hunter 1975), and for two prosobranch snails from a southeastern United States coastal stream (2–3 yr^{-1}; Richardson and Brown 1989). On the other hand, in an artificially warmed pond, *Physa* grew at rates approximately equal to *Potamopyrgus* growth rates in our study (0.03–0.04 d^{-1}; McMahon 1975). Indeed, our *Potamopyrgus* annual growth rate estimates were about equal to the average of the native invertebrate assemblage (Appendix). Thus, high *Potamopyrgus* productivity measures were driven by high biomass, but high growth rates also contributed.

The production estimate of 194 g AFDM·m^{-2}·yr^{-1} for *Potamopyrgus* in Polecat Creek is one of the highest published for a freshwater invertebrate; only production by filter feeders from lake outlet streams is higher, e.g., 8 g DM·m^{-2}·d^{-1} (~5 times higher than *Potamopyrgus*) (Wotton 1988). In that case, secondary production is high in lake outlets because high-quality food is generated in a larger, adjacent ecosystem and focused on the filter-feeding assemblage right at the lake outlet. In the case of *Potamopyrgus*, the food resources (i.e., epiphyton) are generated in the same location as the snails. Nevertheless, *Potamopyrgus* production (121–194 g AFDM·m^{-2}·yr^{-1}) in the two most productive sites was comparable to aquatic invertebrates in highly enriched ecosystems, such as sewage ponds. For example, secondary production of *Glyptotendipes* (Diptera, Chironomidae) was 161 g DM·m^{-2}·yr^{-1} at the edge of a sewage pond (Kimerle and Anderson 1971). Total tubificid oligochaete secondary production was 268 g DM·m^{-2}·yr^{-1} in an organically enriched moat (Lazim and Learner 1986). Still, the highest production rate for a single species in that system (139 g DM·m^{-2}·yr^{-1}), was lower than that of *Potamopyrgus*. Production of mudsnails by themselves was higher in Polecat Creek than all community-level estimates of production except for four studies (three lake outlets and one moat) reviewed by Huryn and Wallace (2000) and Benke (1993). Production estimates for Firehole River and Gibbon River, although lower than for Polecat Creek, were also high relative to estimates reviewed by Benke (1993).

Why was secondary production so high in Polecat Creek and Firehole River? Both rivers are spring fed and thus have low discharge fluctuation relative to runoff streams in the area. Additionally, they are warm compared to streams in New Zealand and have high primary production. Low discharge variation may increase the competitive ability of this armored grazer, similar to its effects on stone-cased caddisflies (Wootton et al. 1996), because mudsnails are not as successful in frequently disturbed habitats (Holomuzki and Biggs 1999, but see Schreiber et al. 2003). Polecat Creek had very high gross primary production, up to 8 g AFDM·m^{-2}·yr^{-1} (Hall et al. 2003). We do not have annual estimates for primary production in these streams, but daily estimates collected in July in Polecat Creek suggested that *Potamopyrgus* consumed nearly 75% of daily gross primary production (Hall et al. 2003). This high primary production may largely be due to the high surface area for epiphytic algae growing on macrophytes and the macrophytes themselves. We suggest that high secondary production of snails is sustained by high rates of primary production, stable hydrology, and warm temperatures.

Potential impact of Potamopyrgus *on the rivers*

The optimal method for estimating invasive species' impact incorporates before–after control–impact (BACI) experimental designs (Underwood 1994). However, for many established invasives, such approaches are difficult due to a lack of preinvasion data or suitable reference sites. In our case, there were few preinvasion data on invertebrate assemblages in GYA rivers from which to estimate the impact of mudsnails. Potential control sites differ ecologically and suitable sites are already invaded. For example, upstream of major geothermal water inputs, Firehole River has no *Potamopyrgus* (R. O. Hall and M. F. Dybdahl, *personal*

observation) and has a wholly different insect assemblage (Armitage 1958, 1961, Kerans et al. 2005, R. O. Hall, *unpublished data*). Given these limitations, we suggest that impact has been large for several reasons. First, the vast majority of invertebrate secondary production was contributed by mudsnails. Second, production by mudsnails was comparable to that of dominant taxa in highly eutrophic habitats, like sewage ponds and enriched moats. Third, in Polecat Creek and Gibbon River, production of native invertebrates was lower than in some unproductive streams. Gibbon River native invertebrate secondary production was similar to that in a cold, slightly acidic, forest stream (Bear Brook, New Hampshire, USA; Hall et al. 2001) and a forest stream following one year of leaf litter exclusion (Wallace et al. 1999).

Potamopyrgus invasion of geothermally influenced rivers in our study area has likely altered ecosystem function and community structure. For example, high-density populations of zebra mussels in the Hudson River have produced measurable impacts on the native animals (Strayer and Smith 2001). Additionally, the huge amount of zebra mussel secondary production and filter-feeding capacity has dramatically altered ecosystem processes, such as decreasing primary production (Caraco et al. 1997). If *Potamopyrgus* has increased overall secondary production in these rivers by exploiting an unfilled niche, then there might be a strong effect on ecosystem processes without a major influence on community structure. We know that ecosystem processes are strongly influenced by *Potamopyrgus*; mudsnails consumed nearly all daily gross primary production and constituted the largest nitrogen flows in Polecat Creek (Hall et al. 2003), suggesting a strongly altered ecosystem.

There is some evidence to suggest that the alteration of ecosystem processes is associated with changes in the river benthic assemblage, based on a limited set of preinvasion data from the Firehole River and Gibbon River. In the Firehole River, the average annual biomass of insects in the riffle habitat at the Ojo Caliente site in 2000–2001 was about half that at the same site in 1952 (810 g AFDM/m^2 vs. 1775 g DM/m^2 using data from Armitage (1958) and assuming dry mass = 0.3 × wet mass). Similarly, for the Gibbon River, the total annual biomass of insects in 2000–2001 was about half (0.52 g AFDM/m^2 vs. 1.2 g DM/m^2) that of a site 7 km upstream in 1963–1965 (estimated by biovolume displacement by Vincent [1966]). The mechanism for their ecological dominance may be that mudsnails are superior competitors, either because they are better at exploiting resources (e.g., McAuliffe 1984, Byers 2000) or because their density is so high that they actually interfere with the ability of native invertebrates to acquire resources. Small-scale experiments with *Potamopyrgus* showed facilitation, not depression, of native invertebrates in an Australian stream (Schreiber et al. 2002), although they used densities (10 000 snails/m^2) that were much lower than those in GYA rivers. However, in Polecat Creek and a tributary, *Potamopyrgus* competes asymmetrically for algal resources with a native hydrobiid snail, which may be one mechanism causing its dominance in this stream (L. A. Riley, M. F. Dybdahl, and R. O. Hall, *unpublished data*). Given that invertebrate production can be determined by the amount of basal food resources (Peterson et al. 1993, Wallace et al. 1999), consumption of available food by *Potamopyrgus* may have lowered production rates of native invertebrates.

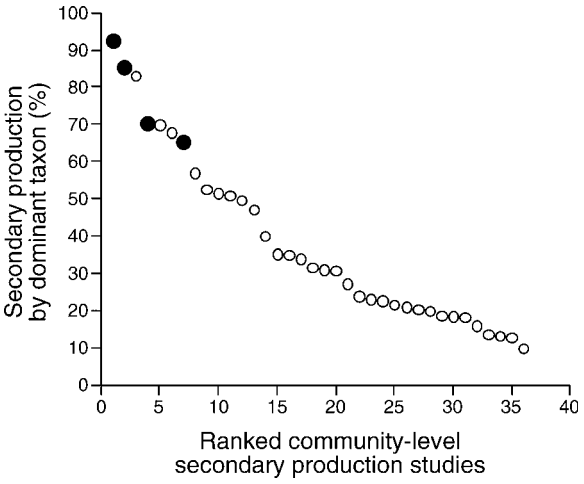

FIG. 6. Relative to other secondary production studies, *Potamopyrgus* constituted a large fraction of total overall production. The *y*-axis represents the percentage contribution of the dominant taxon from 32 community-level secondary production studies in streams (open circles) and our sites with *Potamopyrgus* (solid circles). Studies are ranked from highest to lowest percentage contribution. Data are from Benke (1993) and others that followed (Smock et al. 1992, Grubaugh and Wallace 1995, Huryn 1996, 1998, Grubaugh et al. 1997, Rameriez and Pringle 1998, Hall et al. 2001, McCutchan and Lewis 2002, Stagliano and Whiles 2002). We did not include studies from anthropogenically impacted streams, nor those studies where the dominant taxon was Chironomidae, which may include tens of species.

Potamopyrgus dominated total invertebrate production in these rivers to an extremely high degree (Fig. 5). To what degree does a single taxon dominate production in undisturbed ecosystems? We recorded the fraction of total secondary production by the most productive taxon for 32 studies from the literature (Fig. 6). Of the 36 total studies, Polecat Creek and Gibbon River were the two highest, in terms of percentage dominance by one taxon (Fig. 6). Firehole River was in the top one-fifth. This finding is accentuated by the fact that species are often lumped into genera in secondary production analysis, so that the fraction of production dominated by a single taxon may actually be lower for these other studies, while in our study it is a single species. We suggest that undisturbed ecosystems have more evenly distributed secondary production across taxa (possibly lognormal, Hall et al. 2001), but that rivers invaded by

mudsnails fall on the extreme edge of this distribution, due to the dominance of secondary production by *Potamopyrgus*.

Estimating impact from invasions is important, as many invaders have minimal impact while others will require aggressive management actions if they strongly affect native species or economic interests. Currently, there is no way to eradicate these snails from rivers. Given the high rates of secondary production and the high degree of dominance by this invasive snail, preventing the spread and future introductions of this snail into rivers should be a high priority. *Potamopyrgus* dominated native consumer secondary production in three Yellowstone rivers. They had among the highest secondary production rates ever measured for a river animal, and were responsible for 65–92% of total invertebrate production; this strongly indicates altered invertebrate assemblages and/or ecosystem function (Hall et al. 2003). With little preinvasion data or suitable reference habitats, such secondary production estimates of established invaders and their coexisting native assemblage indicates impact as the degree to which total organic matter in the invertebrate assemblage flows through an invader. This measure of dominance may be useful for measuring invasive impact because it integrates the relative performance of animal consumer populations by combining population dynamics, animal size, and individual growth rates (Benke 1993). Secondary production allows an estimation of how patterns of energy flow have been altered and can complement the more commonly studied population-level interactions (e.g., Hill and Lodge 1999, Grosholz et al. 2000, Kerans et al. 2005).

Acknowledgments

Thanks to Robin Anderson who assisted with the picking and counting of 92 000 snails and fewer native invertebrates. Jack Downs and Monique Lai helped with field sampling. Leslie Riley, Stephanie Fahrney, and Lauren Harvey assisted with snail growth measurements, and Leslie kindly supplied an alternate growth vs. size data set. Brad Taylor, Ben Koch, and three anonymous reviewers read and commented on early drafts of the manuscript. This research was funded by an NSF EPSCoR grant to the University of Wyoming, a National Park Service grant to Billie Kerans, M. F. Dybdahl, and R. O. Hall, and by NSF DEB 9907373 to M. F. Dybdahl. This manuscript is a contribution to the University of Wyoming/National Park Service Research Station.

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APPENDIX

A table showing abundance, biomass, and secondary production of individual taxa from Firehole River, Gibbon River, and Polecat Creek in the Greater Yellowstone area, Wyoming, USA (*Ecological Archives* A016-041-A1).