

# Invasion and production of New Zealand mud snails in the Colorado River, Glen Canyon

Wyatt F. Cross · Emma J. Rosi-Marshall · Kathrine E. Behn ·  
Theodore A. Kennedy · Robert O. Hall Jr. ·  
A. Elizabeth Fuller · Colden V. Baxter

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**Abstract** Species invasions are often associated with large-scale human alteration of ecosystems. One classic example is the increasing dominance of non-native taxa below and above dams on large rivers. These dams substantially alter the physical template of river ecosystems, and exotic taxa often proliferate with potentially large impacts on coexisting taxa and ecosystem processes. Here we document the invasion of New Zealand mud snails (*Potamopyrgus antipodarum*) in the Colorado River directly below Lake Powell in Glen Canyon, Arizona, USA. We also quantified the magnitude and variability in growth and secondary production of *P. antipodarum* during 2006–2007 to

gain a functional measure of their role in the ecosystem. Snails were first detected in Glen Canyon in 1995, and have since become a dominant component of the invertebrate fauna. Throughout the invasion of *P. antipodarum*, biomass of other dominant taxa was variable and did not appear to be positively or negatively influenced by the presence of *P. antipodarum*. Specific growth rates of *P. antipodarum* were moderate (0.001–0.030 day<sup>-1</sup>) and strongly related to body size. Mean annual habitat-weighted biomass and production were relatively high (biomass: 4.4 g/m<sup>2</sup>; secondary production: 13.3 g m<sup>-2</sup> year<sup>-1</sup>) and similar among habitats. Mean monthly biomass and daily secondary production were much more variable, with highest values occurring in autumn. We show that invasion of a productive aquatic consumer to a highly disturbed river ecosystem had little detectable influence on the biomass of other invertebrate taxa. However, additional research will be necessary to fully understand and predict effects of *P. antipodarum* on coexisting taxa.

W. F. Cross · K. E. Behn · R. O. Hall Jr.  
Department of Zoology and Physiology, University  
of Wyoming, Laramie, WY 82071, USA

W. F. Cross (✉)  
Department of Ecology, Montana State University,  
Bozeman, MT 59717, USA  
e-mail: wyatt.cross@montana.edu

E. J. Rosi-Marshall  
Department of Biology, Loyola University Chicago,  
Chicago, IL 60626, USA

T. A. Kennedy · A. E. Fuller  
Grand Canyon Monitoring and Research Center,  
USGS, Flagstaff, AZ 86001, USA

C. V. Baxter  
Department of Biology, Idaho State University,  
Pocatello, ID 83209, USA

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## Introduction

Dams are a prominent feature of most rivers in the United States (Benke 1990) and are still being

constructed throughout the world to meet water storage, power, flood control and navigational demands (WCD 2000; Wu et al. 2004; Nilsson et al. 2005). Large dams substantially alter the physical template of river ecosystems through their effects on flow and temperature regimes, water clarity, and sediment delivery (Howard and Dolan 1981; Poff et al. 1997, 2007; Rosenberg et al. 2000; Syvitski et al. 2005). Such changes can strongly affect the structure and function of river biota, and communities below dams are often dominated by a reduced number of taxa that can withstand the new physical regime (Vinson 2001; Olden et al. 2006; Haxton and Findlay 2008). Like many disturbances that occur over large spatial and temporal scales, dams provide unplanned ‘experiments’ in which to examine responses of population, community and ecosystem characteristics to the new physical regime.

Among the species that proliferate below large dams, non-native taxa often attain higher density and biomass than native taxa (Stevens et al. 1997; Vinson 2001). This pattern may result from the fact that many native taxa are adapted to fluctuating environmental cues (e.g., temperature, flow) that are altered or eliminated with river regulation (Vannote and Sweeney 1980; Lytle and Poff 2004; Olden and Naiman 2010). In addition, dam-induced reduction of native taxa may offer niche opportunities that can be exploited by non-native taxa (Shea and Chesson 2002; Olden et al. 2006). Most regulated rivers have also been exposed to repeated deliberate or inadvertent introductions of non-native species via recreational activities (e.g., angling), further contributing to the dominance of non-native taxa below dams.

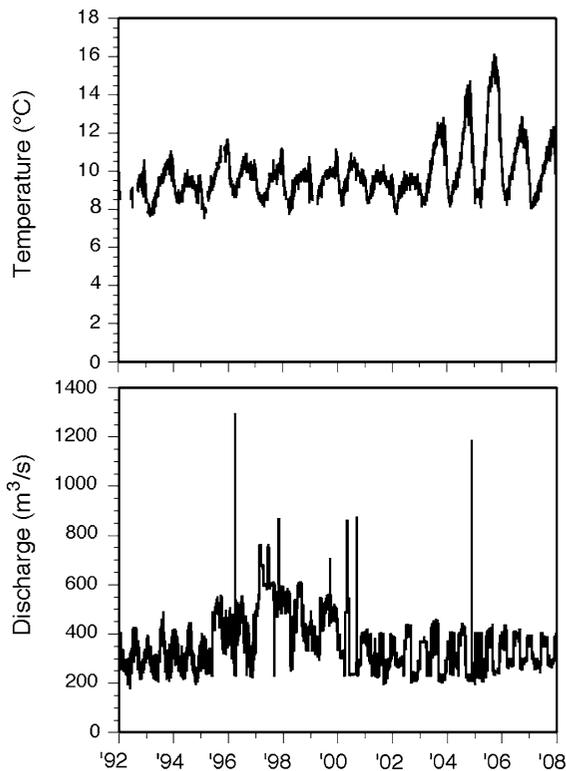
The completion of Glen Canyon Dam in 1963 drastically changed the physical characteristics of the Colorado River in the Grand Canyon by altering temperature, flow regime, and sediment delivery from the upper basin (Howard and Dolan 1981; Andrews 1991; Webb et al. 1999; Topping et al. 2003). Although the effects of these changes on the pre-dam invertebrate assemblage are not clear (i.e., no conclusive data exist), available evidence suggests a decline in native invertebrate diversity. For example, studies upstream of the dam (e.g., the Green and Colorado Rivers in Canyonlands National Park) have reported a diverse fauna consisting of many taxa that do not currently exist below Glen Canyon dam (e.g., mayflies, stoneflies, caddisflies; Haden et al. 1999, 2003).

Available records since the mid-1970s (post-dam construction) indicate that the invertebrate assemblage has been species-poor and dominated by amphipods (*Gammarus lacustris*), oligochaetes, and chironomids (Ward et al. 1986; Blinn and Cole 1991; Stevens et al. 1997; Sublette et al. 1998; Shannon et al. 2001), of which several are non-native. The New Zealand mud snail (*Potamopyrgus antipodarum*), an increasingly ubiquitous invasive species in the US, was first detected in the Colorado River below Glen Canyon Dam in 1995 (Shannon et al. 2003) and has since become a dominant component of the invertebrate assemblage. Here we present a time series of *P. antipodarum* invasion below Glen Canyon dam and examine changes, if any, in populations of resident invertebrate taxa during this time. We also quantified growth rates, biomass and annual secondary production of *P. antipodarum* to gain a functional measure of their potential role in this system. Our results provide general insight for understanding consequences of species invasions in degraded river ecosystems in which non-native taxa dominate total invertebrate biomass.

## Methods

### Study site

We studied a 26-km reach of the Colorado River directly below Glen Canyon Dam (36°56′13″N, –111°29′3″W), near Page Arizona, USA. There are no large tributaries in this reach, and as a consequence, the water is clear for all but a few days of the year. River discharge originates from the hypolimnion of Lake Powell and water temperature at the downstream end of the reach (Lee’s Ferry) is relatively cold throughout the year (1992–2003: mean daily 9.5, range 7.5–11.7; 2003–2008: mean daily 10.8, range 8.0–16.1; Fig. 1) with minimal diel fluctuation (0.5–1°C). River width and thalweg depth average ~120 and 7 m at a discharge of 325 m<sup>3</sup>/s, respectively (Grams et al. 2007; P.E. Grams, unpublished data, USGS, Flagstaff, AZ), but a large amount of variability exists due to fluctuating discharge. Discharge varies widely on a diel, seasonal, and annual basis to meet shifting hydroelectric power demands (Fig. 1), but seasonal and annual variability is considerably lower than



**Fig. 1** River temperature (°C) and discharge ( $\text{m}^3/\text{s}$ ) at Lees Ferry in Glen Canyon of the Colorado River, Arizona (1992–2008). Large peaks in discharge (1996 and 2004) correspond to experimental high flow events

during pre-dam conditions (Topping et al. 2003). For the period of record between 1995 and 2007, mean daily discharge ranged from  $\sim 190$  to  $875 \text{ m}^3/\text{s}$ , with a few periods of relatively steady discharge (Mar–Aug 1997, April–May and Jun–Aug 2000) and two short-term (3–7 days) experimental high flows (1996 and 2004, peak discharge  $\sim 1,300$  and  $1,200 \text{ m}^3/\text{s}$ , respectively). Between July 2006 and July 2007 mean daily discharge during summer and winter months (July–Sept, Dec and Jan) ranged between  $\sim 325$  and  $420 \text{ m}^3/\text{s}$  (Fig. 1). Discharge during other months of this year varied between  $\sim 240$  and  $330 \text{ m}^3/\text{s}$ .

River substrata are dominated by variably sized talus, cobble-gravel bars, cliff faces, and sandy depositional zones. Luxurious algal growth (predominantly *Cladophora glomerata*) dominates river biofilms throughout most the year, and sloughing and transport appear to peak in the spring (Shannon et al. 1996; T.A. Kennedy, USGS, Flagstaff, AZ, unpublished data). Fish species richness in Glen Canyon is

depauperate and numerically dominated by nonnative rainbow trout (*Oncorhynchus mykiss*) (Mckinney et al. 2001).

#### *P. antipodarum* invasion

We compiled data on the abundance and biomass of *P. antipodarum* on cobble/gravel habitat in Glen Canyon between 1992 and 2002 from the database at Grand Canyon Monitoring and Research Center (Benenati et al. 2002; Shannon et al. 2003). These data represent average density and biomass estimates from multiple sampling dates and replicate samples taken each year (see Benenati et al. 2002; Shannon et al. 2003 for details). Sampling methods employed in previous monitoring efforts were different from the sampling we initiated in August 2006. Previous benthic sampling employed a Hess sampler with 1-mm mesh (cited in Oberlin et al. 1999) and samples were picked in the field without magnification (or occasionally with magnification). For our sampling in 2006–2007, we used a modified Hess sampler (mesh size of  $250 \mu\text{m}$ ) and picked samples in the laboratory with a dissecting microscope (at  $10\times$ ). To correct for these methodological differences, we (1) assumed that *P. antipodarum*  $<1 \text{ mm}$  long were not collected in previous samples, (2) calculated the proportion of snails in our current samples that were smaller than  $1 \text{ mm}$  (84%), and (3) added this estimated proportion to previous sample abundances. This correction assumes no change in average annual size frequency distributions of snails between 1995 and 2006. We then used the corrected abundance data to calculate biomass values by applying the typical size distribution from 2006 samples to historic abundance data. Biomass of each size class was estimated with an empirically based shell length-weight (ash-free dry mass [AFDM]) relationship developed from Glen Canyon and Wyoming rivers ( $\text{AFDM} = 0.02 \times (\text{shell length in mm})^{2.4315}$ ;  $r^2 = 0.97$ ; ashed at  $500^\circ\text{C}$  for 4 h), and total corrected biomass was calculated as the summed biomass of all size classes. Although we did not account for the small amount of organic matter may be retained in the shell after ignition (Hunter and Lull 1976), this amount is likely miniscule and would not significantly affect our biomass estimates.

We also examined biomass of other dominant taxa (Lumbricidae, *Gammarus lacustris*, Chironomidae,

and Tubificidae) before and during the *P. antipodarum* invasion (1992–2001 and 2006; Benenati et al. 2002; Shannon et al. 2003, this study). These taxa comprise >80% of the total non-mudsnail biomass. Because we were most interested in inter-annual patterns of biomass, as opposed to their absolute values, we did not attempt to correct these data (i.e., add in missing small individuals) as for *P. antipodarum*. Abundance, and not biomass, was reported for these taxa between 1997 and 2001. For these years, we multiplied the reported abundance by an average individual size. Average size was calculated by dividing total biomass by total abundance with the data collected from 1992 to 1996, which included both biomass and abundance estimates for each taxon. Despite the above issues related to data correction, our goal was to examine the *relative* change (not absolute change) in biomass of coexisting taxa during the *P. antipodarum* invasion. Relationships between biomass of *P. antipodarum* and other dominant taxa across years were examined with ordinary least squares regression.

#### Growth rates

We measured in situ size-specific growth rates of *P. antipodarum* on 3 occasions in February ( $n = 2$ ) and August 2006 ( $n = 1$ ). Snails were hand collected, their shell lengths measured (nearest 0.1 mm), and submerged individually (i.e., one snail per chamber) in mesh-walled chambers (Toby Teaboy, Aldridge Plastics, UK; pore size: 244  $\mu\text{m}$ ) attached to a concrete anchor. A small amount of gravel and *Cladophora* collected from the river was placed in each Teaboy to provide habitat and food. Additional algae could pass through the mesh of Teaboy during the incubation. Growth incubations lasted 2–3 weeks, after which shell length was measured for each individual. Shell lengths were converted to biomass (mg ash-free dry mass; AFDM) as described above. Daily specific growth rates (1/d) were calculated as:  $(\ln W_f - \ln W_i)/t$ , where  $W_i$  is initial individual weight (mg),  $W_f$  is the final individual weight (mg), and  $t$  is the duration of the incubation. Natural log transformations on initial and final weights assume exponential tissue growth over time. The relationship between initial shell size and specific growth rates was analyzed with linear regression, and the resulting equation was used for production estimates (see results). Our method did not account for

potential variation in growth among habitats. Although chamber-based estimates of growth have the possibility of biasing estimates, we feel that conditions of temperature and resource availability in growth chambers were similar to that outside of chambers. Moreover, our estimates were comparable to those found in many other field and laboratory-based studies (Dybdahl and Kane 2005; Hall et al. 2006; Riley et al. 2008). However, small errors in growth rates would not substantially alter our secondary production estimates because production is much more influenced by total snail biomass than size-specific growth rates.

#### Benthic sampling and analysis

We quantitatively sampled multiple benthic habitats approximately monthly between July 2006 and June 2007. Habitat classes included cobble/gravel bars, talus/cliff faces, and fine grained depositional zones (hereafter: cobble/gravel, talus/cliff, and depositional, respectively). The mean number of samples collected from habitats was roughly proportional to their areal contribution based on habitat surveys (cobble/gravel: mean  $n = 5$ , talus/cliff: mean  $n = 5$ , depositional: mean  $n = 10$ ; see *Habitat proportions* below). Cobble/gravel was sampled with a Hess sampler (0.085  $\text{m}^2$ , 250- $\mu\text{m}$  mesh size) to a depth of  $\sim 10$  cm. Depositional zones were sampled with a standard Ponar dredge sampler (0.052  $\text{m}^2$ ) deployed from a motor boat. Talus/cliff habitats were sampled with a custom suction device developed for use in the Grand Canyon (battery-powered submersible pump connected to pool hosing, a Nitex bag and dolphin bucket [250  $\mu\text{m}$  mesh]). Each suction sample consisted of 30 repeated haphazard intakes totaling an average sample area of 0.066  $\text{m}^2$ . We assumed that sampling efficiency was similar among habitats, but this assumption was not tested. All sampling was conducted at times of minimum daily discharge (usually between 06:00 and 09:00) to ensure that samples were collected from the permanently wetted zone.

We preserved samples in the field (70% EtOH) and brought them to the laboratory for subsequent processing. Each sample was rinsed onto nested sieves (pore sizes 1 mm and 250  $\mu\text{m}$ ), and material retained on each sieve was elutriated to separate organic from inorganic material. Snails were removed from the large fraction (>1 mm) at 10 $\times$  magnification, counted, and shell lengths measured (nearest

0.5 mm) on the first 30 individuals encountered. Prohibitively large samples were subsampled using a device similar to the Folsom Plankton Splitter (Wildco, Buffalo, NY USA). Organic material in the smaller fraction (i.e., <1 mm and >250  $\mu\text{m}$ ) was placed in a known volume of water, suspended in a modified Imhoff cone (Wards Natural Science, Rochester, NY; item #18V 1574) with forced air, and subsampled (by volume) with a 60-ml plastic syringe. Snails in subsamples were counted, and the first 30 encountered were measured to the nearest 0.5 mm (15 $\times$  magnification). Snails that were counted, but not measured were assumed to have the same size distribution as those measured. *P. antipodarum* biomass was calculated for each habitat on each date using a shell length-weight relationship as above. Biomass of other dominant taxa during the mudsnail invasion (1995–2002) was quantified by drying (60°C), weighing all individuals collected from each sample and an empirical dry mass-ash-free dry mass relationship (see Shannon et al. 2001).

Daily and annual secondary production of *P. antipodarum* was estimated with the instantaneous growth method (Benke 1993; Benke and Huryn 2006). Bootstrap analysis was used to generate 95% confidence intervals for annual values according to Morin et al. (1987) and Benke and Huryn (2006). Briefly, size-specific abundance data from replicate samples on each date were resampled with replacement 1,000 times to generate estimates of mean size-specific abundance and biomass. Each of these biomass estimates was multiplied by size-specific growth rates and the time interval between sampling dates to generate 1,000 estimates of interval production, which were summed across intervals to calculate annual production. Annual production was estimated on a per square meter basis for each habitat, and weighted according to the relative proportions of each habitat per square meter of river (Huryn and Wallace 1987). Differences in biomass and production among habitats or sampling dates were considered significant if bootstrapped 95% confidence intervals did not overlap.

#### Habitat proportions

We surveyed benthic habitats at 48 linear transects (approximately every 0.3–0.5 km) between 9.7 and 24 km below Glen Canyon Dam in February 2008

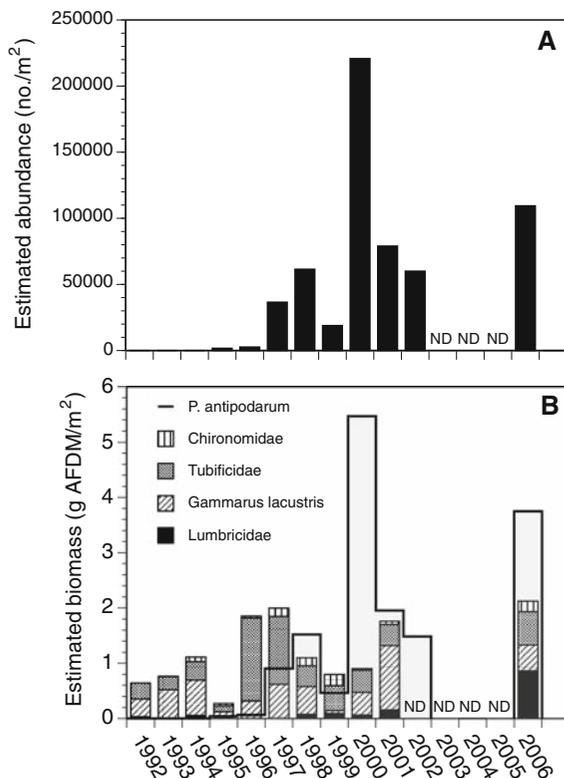
with a motorized boat and an underwater video sled. The video sled consisted of an aluminum housing, a Sony digital video recorder (model: GV-D1000 NTSC; Sony U.S., New York, NY, USA), and two lasers that provided a 2 dimensional reference for measuring grain size of the benthic substrata. A cable connected the video camera to a laptop computer on the boat. At each transect, starting at the shoreline, the video sled was manually lowered by cable until the river benthos was in view on the computer screen. Next, the time of the video was noted and the boat was ferried across the entire width of the river at a constant rate. During the ferry, cable height was constantly adjusted to account for changes in river depth. Videos were recorded on mini-DV tapes and viewed in the laboratory with Final Cut Pro software (Apple Inc., Sunnyvale, CA USA). Transect locations were imported into 2004 river imagery using ArcGIS software, and river width was calculated for each transect. Linear habitat proportions were estimated visually for each transect using timed videos, total ferry time (min), and total river width (m). Our habitat surveys did not account for the vertical cliff habitat on shorelines. Thus, we included this habitat by assuming that transects with cliff shorelines on both sides (19 of 48 transects) had a total of 6 m vertical habitat (3 on each side of the river). This linear amount of cliff habitat was included in the total linear transect dimensions, and habitat proportions were determined accordingly. Although the depth of cliff habitat is variable in Glen Canyon, our observations at transects that intersected cliff habitat suggest that an average of 3 m is a reasonable estimation. In addition, because cliff habitat represents only a portion of the smallest habitat category (talus/cliff; see below), this estimate had very little influence on our final habitat-weighted values. Major qualitative habitat categories used for our analysis corresponded to the 3 major habitats sampled for *P. antipodarum* and accounted for 52% (depositional), 27% (cobble/gravel), and 21% (talus/cliff) of the total surveyed habitat.

#### Results

*P. antipodarum* appeared in samples collected from Glen Canyon in 1995 at relatively low densities (Fig. 2a; see Benenati et al. 2002). By 1997 densities

on cobble/gravel reached 36,500/m<sup>2</sup>, and with the exception of year 2000, remained high through 2006–2007 (average 59,900/m<sup>2</sup> between 1997 and 2006 excluding 2000; no data were available from 2003 to 2005). In 2000, densities of *P. antipodarum* were much higher than other years at 221,000/m<sup>2</sup> (Fig. 2a), and high densities coincided with experimental steady flows from Glen Canyon dam. Biomass of *P. antipodarum* on cobble/gravel followed a similar trend (Fig. 2b), with a maximum of 5.5 g AFDM/m<sup>2</sup> in 2000, and an average of 1.6 g AFDM/m<sup>2</sup> for the period between 1997 and 2006 (excluding 2000).

During the initial invasion of *P. antipodarum* (between 1995 and 2001), total biomass of other

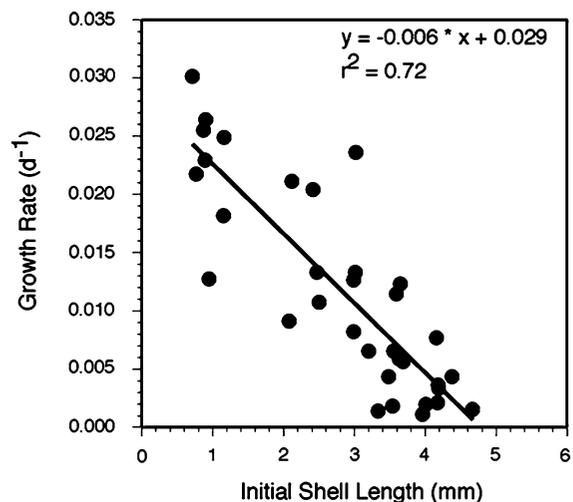


**Fig. 2** *P. antipodarum* was first detected on cobble/gravel habitat in Glen Canyon in 1995 and increased rapidly in abundance (no./m<sup>2</sup>; **a**) and biomass (g AFDM/m<sup>2</sup>; **b**). Biomass of 4 other dominant taxa was variable (**b**), but did not appear to be influenced by the presence of *P. antipodarum* (see text). Data for 1992–2002 are from previous cooperative agreement reports (Benenati et al. 2002; Shannon et al. 2003). ND in **a** = no data available for *P. antipodarum*; ND in **b** = no data available for all taxa except *P. antipodarum*. Note that biomass of dominant taxa (except *P. antipodarum*) was not corrected between 1992 and 2001 (see text)

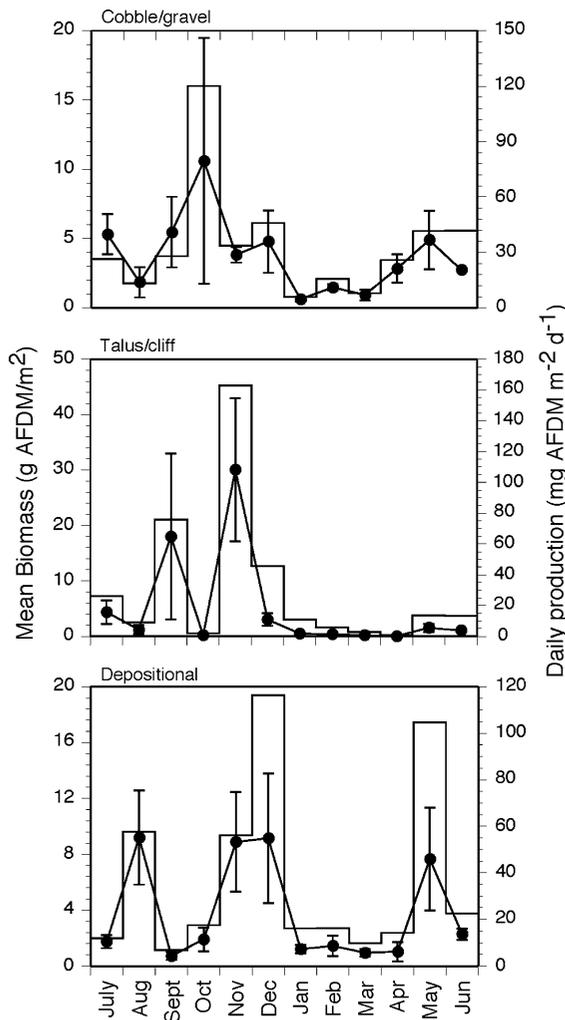
dominant taxa on cobble/gravel ranged from 0.3 g AFDM/m<sup>2</sup> to 2.0 g AFDM/m<sup>2</sup> (Fig. 2b). Total biomass varied strongly (approximately one order of magnitude) among years, as did the contributions to biomass of specific taxa. Yet there was no clear positive or negative effect of the *P. antipodarum* invasion on the biomass of other taxa (Fig 2b; all linear regressions between biomass of *P. antipodarum* and dominant taxa non-significant). In 2006–2007, biomass of other dominant taxa was 2.0 g AFDM/m<sup>2</sup>, and Lumbricidae appeared to constitute a larger proportion of the non-snail biomass in cobble/gravel habitat.

Daily growth rates of *P. antipodarum* ranged from 0.001 to 0.030 day<sup>-1</sup>. Large snails grew more slowly than small snails ( $r^2 = 0.72$ ,  $P < 0.001$ ; Fig. 3). Temperature did not influence growth rates; however, temperature variation was relatively low in this river (Fig. 1).

Mean monthly biomass and daily secondary production varied across habitats and seasons (Fig. 4), and were highest during fall months (Sept–Nov) and lowest during late winter-early spring (Jan–Apr; Fig. 4); this pattern generally followed seasonal patterns of water temperature (Fig. 1). Talus/cliff habitat supported the highest values of *P. antipodarum* biomass and production, where variability among months was also highest (Fig. 4). Mean annual biomass and secondary production were



**Fig. 3** Initial shell length was negatively related to size-specific growth rates (day<sup>-1</sup>) of *P. antipodarum* in Glen Canyon, Colorado River, Arizona. The solid line represents a significant ( $P < 0.001$ ) ordinary least squares linear regression between initial shell size and growth rates



**Fig. 4** Temporal patterns of mean monthly habitat-specific biomass ( $\text{g AFDM/m}^2 \pm 1 \text{ SE}$ ; closed circles and line) and mean daily production by interval ( $\text{mg AFDM m}^{-2} \text{ day}^{-1}$ ; histograms) for *P. antipodarum* on cobble/gravel, talus/cliff, and depositional habitats in Glen Canyon, Colorado River

relatively similar among habitats, with large overlap in bootstrapped 95% confidence intervals (Biomass: cobble/gravel— $3.8 \text{ g AFDM/m}^2$  [95% CI: 2.5–5.4], talus/cliff— $5.2 \text{ g AFDM/m}^2$  [95% CI: 2.5–8.9], depositional— $4.3 \text{ g AFDM/m}^2$  [95% CI: 3.0–6.0]; Production: cobble/gravel— $11.7 \text{ g AFDM/m}^2$  [95% CI: 7.8–16.6], talus/cliff— $11.7 \text{ g AFDM/m}^2$  [95% CI: 7.7–16.4], depositional— $14.7 \text{ g AFDM/m}^2$  [95% CI: 9.8–20.7]), and annual production:biomass ratios averaged 3.0 (95% CI: 2.6–3.4).

Mean annual biomass weighted by habitat proportions in Glen Canyon was  $4.4 \text{ g AFDM/m}^2$  (95% CI:

3.3–5.5) between July 2006 and June 2007. During this same time interval, habitat weighted production was  $13.3 \text{ g AFDM m}^{-2} \text{ year}^{-1}$  (95% CI: 10.3–16.7).

## Discussion

Species-poor communities subject to altered disturbance regimes are particularly susceptible to invasions (Elton 1958). Although the mechanisms for this pattern are debated (e.g., Naeem et al. 2000; Fridley et al. 2007), it is clear that nonnative taxa are often able to establish and thrive in highly disturbed terrestrial, marine, and freshwater ecosystems. In the arid West and southwestern U.S., rivers directly below large dams often exhibit extreme unnatural conditions for regional biota throughout most of the year, and are therefore subject to invasions by species that can tolerate the new physical regime (Stevens et al. 1997; Vinson 2001). Our study documented the invasion of *P. antipodarum* into an ecosystem that has been altered significantly from its pre-dam state. This represented a unique opportunity to examine community-wide effects of an invasive species on a species-poor assemblage dominated (in terms of biomass and production) by non-native taxa. Based on our analysis, it appeared that biomass of dominant resident taxa did not exhibit major changes during the initial invasion of *P. antipodarum* (i.e., between 1995 and 2001). In addition, during 2006–2007, *P. antipodarum* production was relatively high, and coexisting taxa were still a large component of total assemblage biomass. Our research suggests that tailwaters may represent highly invulnerable ecosystems, particularly in geographic areas such as the southwestern US where native taxa that are well adapted to large fluctuations in physical characteristics (i.e., light, discharge, temperature; Lytle and Poff 2004) are virtually absent.

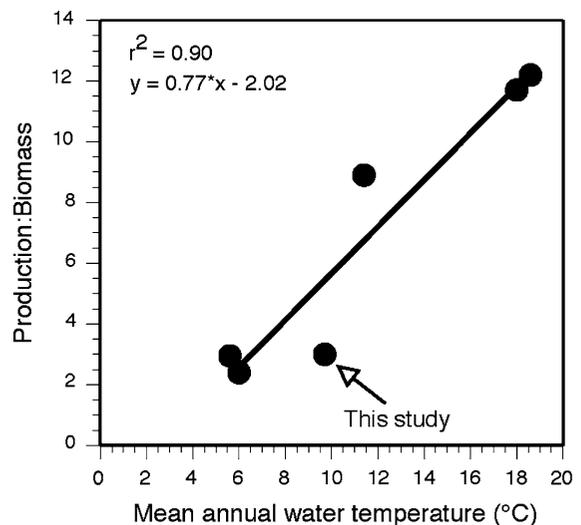
*P. antipodarum* has invaded a large number of streams and rivers in the western U.S., and has now been reported from most western-area states except New Mexico. Although it is still unclear what limits their establishment, temperature, alkalinity, and stable hydrology appear to play important roles, with populations being more common in reaches with moderately high temperatures, high alkalinity, high conductivity and spring-dominated hydrology (Schrieber et al. 2003; Kerans et al. 2005; Hall et al.

2006; Loo et al. 2007; Herbst et al. 2008; Alonso and Díez 2008). However, among aquatic ecosystems where *P. antipodarum* is abundant, there is still considerable uncertainty with regard to their effects on coexisting native taxa. For example, Kerans et al. (2005) found little evidence for negative interactions between *P. antipodarum* and other invertebrate taxa in a broad field survey in Yellowstone National Park. In contrast, colonization experiments in these same systems revealed potential interference competition between these taxa at high densities (Kerans et al. 2005; also see Cada 2004). Other studies have reported mixed results ranging from strongly negative (e.g., Riley et al. 2008) or neutral (e.g., Cope and Winterbourn 2004) to positive (Schrieber et al. 2002) effects of *P. antipodarum* on co-existing taxa. In our study, long-term patterns suggest that biomass of dominant taxa was not altered by the arrival or presence of *P. antipodarum*. Such variation among studies is likely driven by a number of interacting factors including *P. antipodarum* density, basal resource productivity, and the scale at which interactions were examined. Clearly, additional studies are needed to assess when and where competitive interactions between *P. antipodarum* and coexisting taxa are important, as well as how these interactions influence consumers at other trophic positions (Vinson and Baker 2008).

Despite uncertainties regarding interactions with co-existing taxa, there is little doubt that *P. antipodarum* can dominate secondary production and whole ecosystem material fluxes even in highly productive streams. Hall et al. (2006) showed that production of *P. antipodarum* far outweighed that of native taxa in three rivers in Yellowstone National Park, and these production estimates were among the highest ever reported in the literature for a single species of freshwater macroinvertebrate (e.g., 194 g AFDM m<sup>-2</sup> year<sup>-1</sup> in Polecat Creek vs. ~13 g AFDM m<sup>-2</sup> year<sup>-1</sup> in Glen Canyon). *P. antipodarum* also dominated carbon and nitrogen cycling during summer months in Polecat Creek, WY, where they consumed up to 75% of gross primary production and excreted two-thirds of total ecosystem ammonium demand (Hall et al. 2003). In Glen Canyon, the role of *P. antipodarum* in whole-ecosystem material fluxes is likely more modest because of lower secondary production relative to Polecat Creek, colder average temperatures, and

significant fluxes of organic matter and nutrients exiting the dam and passing through the tailwater (Shannon et al. 1996; T. Kennedy, USGS, unpublished data). Nonetheless, because temperature is relatively stable in Glen Canyon compared many other rivers, effects of *P. antipodarum* on ecosystem fluxes, irrespective of magnitude, should be relatively continuous throughout a typical annual cycle.

*P. antipodarum* has a relatively wide range of temperature tolerance (Winterbourn 1969; Cox and Rutherford 2000) and exists in diverse systems that span large variation in diurnal and annual temperature regimes. Although establishment success and densities are highly variable among systems, temperature appears to play a critical role in determining specific growth and turnover rates of established populations. For example, our growth estimates were considerably lower than those measured in geothermally influenced rivers in Yellowstone National Park (Hall et al. 2006), but similar to those in some colder New Zealand streams (estimated from Huryn 1996, 1998). To examine the influence of temperature on population-level turnover rates, we compiled the only existing independent estimates of annual production:biomass ratios for *P. antipodarum* (Fig. 5). Based on these limited data, temperature regulated variation in



**Fig. 5** Mean annual water temperature (°C) was positively related to production:biomass ratios of *P. antipodarum* in six stream reaches. The two low-temperature points are from New Zealand streams (Huryn 1998); the three unmarked high-temperature points are from Wyoming streams with varying amounts of warm-spring inputs (Hall et al. 2006)

biomass turnover rates, which has important implications for identifying where *P. antipodarum* would be expected to most strongly alter ecosystem fluxes and where they should exhibit greatest capacity to increase in abundance and distribution within river networks. Additional variation in biomass turnover rates may be explained by ecosystem-wide differences in food quantity and quality.

We showed that a globally ubiquitous invasive snail can colonize and then dominate invertebrate biomass in a highly altered river, with little detectable influence on biomass of existing invertebrate taxa. During the initial invasion, we did not detect large changes in biomass of coexisting invertebrate taxa. Our estimates of current levels of secondary production showed that *P. antipodarum* represents a substantial contributor to assemblage-wide secondary production (W. F. Cross et al., unpublished data), and is found in all river habitats within Glen Canyon. In highly productive species-poor ecosystems, such as many tailwaters, sufficient resources (e.g., algal production) may support additional taxa that can withstand the altered physical regime. Our example contrasts strongly with other systems that contain a high diversity of native taxa. For example, the invasion of zebra mussels (*Dreissena polymorpha*) in the Hudson River reduced native bivalve diversity and abundance (Strayer and Smith 1996) as well as many other ecosystem components (Strayer et al. 1999; but see Strayer and Malcom 2007). Additional research is needed that examines community and ecosystem-level consequences of invasive taxa in aquatic ecosystems that vary in dominance by non-native taxa.

Because our study was limited to the 26-km reach below Glen Canyon dam, it is still unclear whether the invasion of *P. antipodarum* will have a significant effect on communities downstream in Grand Canyon National Park that contain a modest number of native taxa. Initial observations and preliminary research (Shannon et al. 2003; W. F. Cross et al., unpublished data) show that numbers and biomass of *P. antipodarum* decline precipitously below large tributaries in the Grand Canyon, yet quantitative process-based studies will be required to fully understand their influence on other taxa. In addition, questions remain concerning the potential effect of *P. antipodarum* on near-pristine communities in small tributaries of the Grand Canyon. Such information will be critical for augmenting our ability to predict establishment,

success, and community/ecosystem-level effects of invasive species in freshwater ecosystems.

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