

Potamopyrgus antipodarum: distribution, density, and effects on native macroinvertebrate assemblages in the Greater Yellowstone Ecosystem

B. L. KERANS¹

Department of Ecology, Montana State University, Bozeman, Montana 59717 USA

M. F. DYBDAHL²

School of Biological Sciences, Washington State University, PO Box 644236,
Pullman, Washington 99164 USA

M. M. GANGLOFF³ AND J. E. JANNOT⁴

Department of Ecology, Montana State University, Bozeman, Montana 59717 USA

Abstract. Invasive species can have large effects on freshwater communities and ecosystems. *Potamopyrgus antipodarum*, a snail indigenous to New Zealand, has recently colonized North America. We documented the distribution and density of *P. antipodarum* in the major tributaries of the Madison River in the Greater Yellowstone Ecosystem, examined associations between *P. antipodarum* and native macroinvertebrates, and experimentally examined how *P. antipodarum* affected colonization of substrates by other macroinvertebrates. In 1997 and 1998, we sampled benthic macroinvertebrates in the Madison, Firehole, and Gibbon Rivers and Nez Perce Creek in 3 seasons. In 1999, we examined colonization of *P. antipodarum* and other macroinvertebrates in a field experiment using slate tiles in the Madison River. In September 1997, we found *P. antipodarum* at 23 of 32 locations. Where they were present, *P. antipodarum* densities ranged from 22 to 299,000 ind./m². Densities of *P. antipodarum* declined between September 1997 and March 1998 and increased between March and July 1998. The composition and structure of native macroinvertebrate assemblages covaried with *P. antipodarum* densities. Whether the differences in macroinvertebrate communities among sites were related to differences in physical characteristics of streams or to interactions with *P. antipodarum* was unclear. However, in the field experiment, high densities of *P. antipodarum* were associated with low colonization of other macroinvertebrates; thus, negative interactions between native macroinvertebrates and *P. antipodarum* may have the potential to influence the large-scale distribution of other macroinvertebrates.

Key words: snail, Yellowstone National Park, biotic interactions, colonization, exotic species, *Potamopyrgus antipodarum*.

Invasive nonindigenous species often have serious economic and ecological costs (Mack et al. 2000, Pimentel et al. 2000, Kolar and Lodge 2001). Invasive species are now viewed as a major component of global change (Vitousek et al. 1996, Sala et al. 2000), but the specific ecological effects of invasive species on native biota are often unpredictable and depend on the properties of the invading species and the invaded ecosystem (Parker et al. 1999, Sakai et al. 2001, Crooks 2002). In fresh waters, invasive species have had large effects on community structure and eco-

system function (e.g., Lodge et al. 1998, Strayer 1999, Ricciardi 2003). For example, nonindigenous species dominate the food web of the Great Lakes (Ricciardi and MacIsaac 2000) and have changed the food web structure of communities in Canadian lakes (Van der Zanden et al. 1999) and the community composition of macroinvertebrates in the Hudson River (Strayer and Smith 2001).

Potamopyrgus antipodarum, an aquatic snail indigenous to New Zealand and its adjacent islands (Winterbourn 1970), colonized freshwater habitats in Australia (Ponder 1988) and Europe (Bondesen and Kaiser 1949) during the 19th and 20th centuries. During the last 15 y, *P. antipodarum* invaded several locations in North America. It was first documented in the Snake River, Ida-

¹ E-mail addresses: bkerans@montana.edu

² dybdahl@wsu.edu

³ ganglmm@mail.auburn.edu

⁴ jjannot@bilbo.bio.purdue.edu

ho (Bowler 1991, Langenstein and Bowler 1991, Bowler and Frest 1992, Richards et al. 2001), but populations have recently been discovered in the Great Lakes (Zaranko et al. 1997), the Owens River in California, the Colorado River in Colorado, and the Madison and Yellowstone basins in the Greater Yellowstone Ecosystem (GYE) in Montana and Wyoming (D. L. Gustafson, Montana State University, personal communication).

We predict that the ecological effects of *P. antipodarum* on aquatic communities will be large, at least locally, for several reasons. In general, snails are *strong interactors* because they are important links between primary producers and higher consumers, and they often play key roles in structuring aquatic communities (Hawkins and Furnish 1987, Feminella and Hawkins 1995). In addition, populations of *P. antipodarum* may reach densities as high as 800,000 ind./m² (Dorgelo 1987). High abundance is one characteristic that often is shared by invaders with profound ecosystem-level impacts (Simon and Townsend 2003). Nonindigenous populations of *P. antipodarum* can build rapidly to large sizes because individuals typically are female and reproduce through parthenogenesis (Wallace 1992, Schreiber et al. 1998).

The effects of *P. antipodarum* on aquatic communities and ecosystems may be complex and variable. Schreiber et al. (2002) found that low densities of *P. antipodarum* (2000–4500 ind./m²) facilitated colonization of native stream fauna in short-term experiments in Australia. However, densities of *P. antipodarum* are often higher than the densities in the Schreiber et al. (2002) study. At high densities, *P. antipodarum* may compete with native macroinvertebrates for food or space. *Potamopyrgus antipodarum* is a generalist feeder (i.e., both grazing herbivore and detritivore; Haynes and Taylor 1984) that uses the same food as many other macroinvertebrates. *Potamopyrgus antipodarum* depressed periphyton biomass in New Zealand streams (Winterbourn and Fegley 1989, Death 1991), and this result suggests that *P. antipodarum* is likely to compete with other grazers through exploitation. Given the remarkably high densities that *P. antipodarum* can reach, it also may compete through interference with macroinvertebrates that attach to rock surfaces (e.g., net-spinning caddisflies). Competition among *P. antipodarum* and native species could reduce the abundances and

change the distributions of native species. *Potamopyrgus antipodarum* also appears to be a poor food resource for secondary consumers such as fishes because it provides little energy and may pass through the gut undigested (Ryan 1982, Haynes et al. 1985, McCarter 1986). Thus, effects of its presence may propagate through food webs and change community structure and function (Carpenter et al. 1985). Moreover, the spread of *P. antipodarum* in the GYE may threaten endemic Yellowstone cutthroat trout and the animals that depend on fish as a food resource (Varley and Schullery 1998).

Our objectives were to: 1) document the distribution and density of *P. antipodarum* in major tributaries of the Madison River in the GYE, 2) examine associations between *P. antipodarum* and native macroinvertebrates, and 3) experimentally examine colonization of *P. antipodarum* and other macroinvertebrates.

Methods

Study area

We conducted surveys and an experiment in the Madison River basin in Montana and Wyoming (Fig. 1). The Madison River is formed by the confluence of the Gibbon and Firehole Rivers within Yellowstone National Park. The Gibbon River originates at an elevation of 2486 m above sea level (asl) and flows 45 km to the Firehole River. The Firehole River originates at an elevation of 2560 m asl and flows ~40 km to the Madison River. Nez Perce Creek is a major tributary of the Firehole River. The Madison River flows freely for ~25 km before entering Hebgen Reservoir just outside Yellowstone National Park.

Heated discharges from geothermal features are released into the Gibbon and Firehole Rivers and Nez Perce Creek (Allen and Day 1935, Fournier 1989). Most thermal additions occur downstream of the Upper Geyser Basin on the Firehole River and downstream of Norris Geyser Basin on the Gibbon River (Allen and Day 1935) (Fig. 1). Nez Perce Creek receives thermal effluent in its headwaters, whereas the Madison River receives little direct thermal discharge (Allen and Day 1935). Physicochemical features differ extensively within and among streams because of the influence of the hot springs and geysers (Table 1). In the Firehole and Gibbon Rivers, wa-

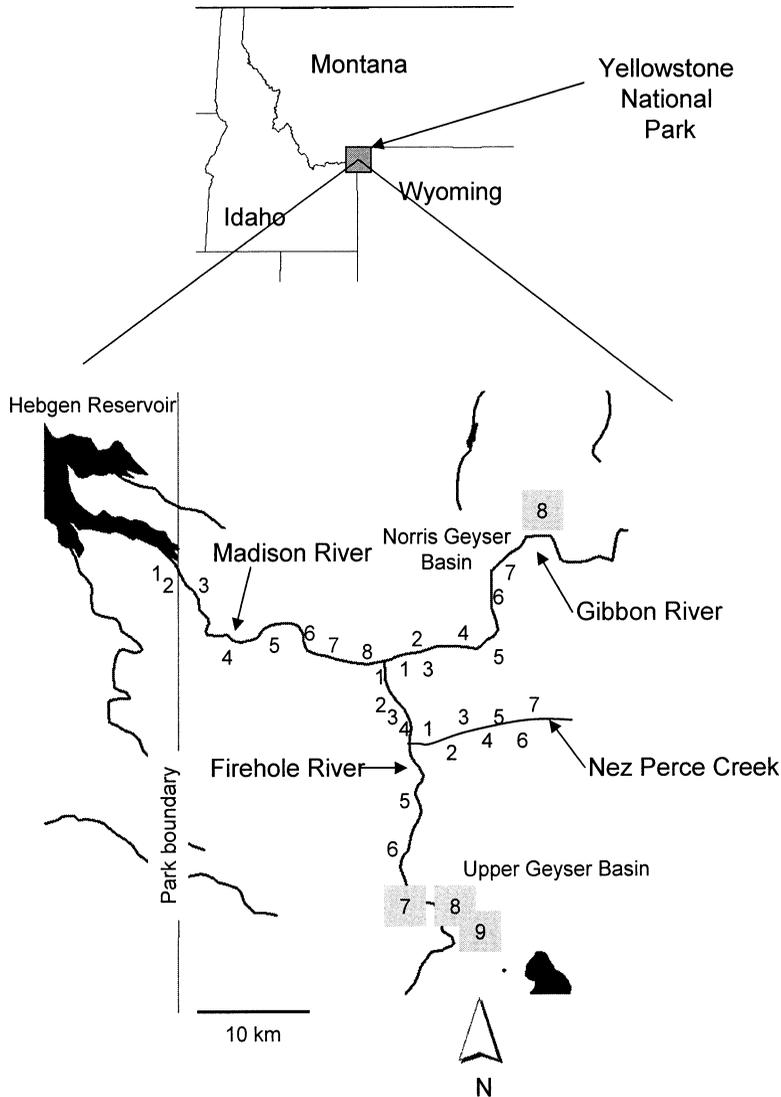


FIG. 1. Approximate locations and identification numbers of the 32 sampling sites in the Madison River basin, Greater Yellowstone Ecosystem. Numbers in shaded boxes indicate locations upstream of most geothermal activity.

ter temperatures and dissolved constituents are higher in reaches below thermal additions than above them (Table 1). Algal standing crops also tend to be higher below thermal discharges than above them (Boylen and Brock 1973). Water chemistry differs between the thermal reaches of the Gibbon and Firehole Rivers because of the chemical composition of the thermal discharges (Allen and Day 1935, Fournier 1989). Thermal reaches of the Gibbon River have higher dissolved SO_4 concentrations than thermal reaches

of the Firehole River (Table 1). Water temperatures, chemical constituents, and algal productivity decline in a downstream direction in the Madison River (Wright and Horrall 1967, Wright and Mills 1967).

Distribution and density of P. antipodarum and other macroinvertebrates

We documented the distribution and density of *P. antipodarum* and other macroinvertebrates

TABLE 1. Mean (SE) selected physical and chemical characteristics of Firehole, Gibbon, and Madison Rivers and Nez Perce Creek in the Greater Yellowstone Ecosystem. Data for mean annual discharge from US Geological Survey, Water Resources of Wyoming, water years (1984 to 1985 and 1989 to 1995 (<http://waterdata.usgs.gov/wy/nwis/annual>); data for remaining variables from Thompson (1979), samples taken 18 October 1975. — = no data.

Stream	Mean annual discharge (m ³ /s)	Location relative to thermal inputs	Water temperature (°C)	pH	Dissolved constituents ^a					
					Ca	Na	HCO ₃	SO ₄	Cl	As
Firehole	8.8	Above	5.6	7.0	3.3	13.0	24.5	5.0	9.5	0.17
		(n = 2) ^b	(0.6)	(0.3)	(0.05)	(2.0)	(4.5)	(0)	(1.5)	(0.16)
Gibbon	3.4	Below	18.0	8.0	4.1	81.0	121.7	9.0	68.7	0.29
		(n = 3) ^b	(2.5)	(0.09)	(0.43)	(19.8)	(22.3)	(2.5)	(14.3)	(0.09)
Nez Perce	—	Above	8.5	6.9	5.7	10.0	40.0	9.0	5.0	0.01
		(n = 1) ^b								
Madison	13.9	Below	12.0	7.4	6.9	55.0	99.0	25.7	42.0	0.13
		(n = 3) ^b	(1.0)	(0.2)	(0.4)	(5.8)	(19.1)	(1.9)	(2.5)	(0.01)
Nez Perce	—	—	15.0	7.8	6.6	70.0	98.0	28.0	74.0	0.13
		(n = 1) ^b								
Madison	13.9	—	12.3	7.6	5.7	81.0	126.0	15.5	51.0	0.23
		(n = 2) ^b	(0.8)	(0)	(0)	(1.0)	(4.0)	(0.5)	(1.0)	(0)

^a mg/L except for pH

^b For each variable

in the upper Madison basin by sampling the benthos in riffles at 32 locations in 1997 and 1998 (Fig. 1). In September 1997, we collected single Surber samples (153- μ m mesh) at 8 locations on the Madison River, 8 locations on the Gibbon River, 9 locations on the Firehole River, and 7 locations on Nez Perce Creek (Fig. 1). We sampled locations above and below major geothermal discharges on the Gibbon (Norris Geyser Basin; location 8 was above the discharge) and Firehole (Upper Geyser Basin; locations 7, 8, and 9 were above the discharge) rivers. In March and July 1998, we collected 3 Surber samples at a subset of the locations that we visited in September 1997 to examine temporal variation in densities of *P. antipodarum*. We sampled 3 locations on the Firehole River (1, 5, and 7), 2 locations on the Madison River (4 and 7 [in March] or 4 and 8 [in July]), and 2 locations on the Gibbon River (4 and 8) (Fig. 1). We chose locations based on ease of access, and we collected samples haphazardly in cobble and pebble sediments. We preserved samples in the field in Kahle's solution (11% formalin, 28% ethanol, 2% glacial acetic acid, 59% water) and transferred them to 70% ethanol after 1 wk. We counted all *P. antipodarum*, and we identified all other invertebrates to family, and counted them. We excluded small noninsect and nonmollusc

taxa (e.g., mites, copepods) from analyses because their ecological associations with the insects and molluscs are not well understood, and they rarely colonized the tiles in the experiment (see below). We used a plankton splitter to obtain random subsamples ($\frac{1}{4}$ or $\frac{1}{8}$ of the total sample) in some instances when invertebrate abundances were extremely high.

Colonization experiment

We conducted an experiment to examine colonization of *P. antipodarum* and other macroinvertebrates. On 29 July 1999, we placed 30 slate tiles (10 \times 10 \times 0.5 cm; surface area = 220 cm²) at random locations in each of 2 sites (n = 60 tiles) along the banks of the Madison River near location 4 (Fig. 1). We placed tiles on the sediment at each site and allowed them to condition for 1 mo prior to the beginning of the experiment. At the beginning of the experiment, we removed all macroinvertebrates from the tiles and attached the tiles to bricks. We elevated $\frac{1}{2}$ of the tiles (raised tiles) 17 mm above the surfaces of the bricks on stainless steel bolts attached to each corner of the tiles. We attached the remaining tiles (benthic tiles) directly to the bricks. We placed the bricks on the surface of the sediment in the river. We used raised and

benthic tiles to determine whether interactions between *P. antipodarum* and other macroinvertebrates differed when modes of colonization (floating/drifted in the water column or crawling on the sediment) differed. We placed hardware cloth (~5-mm mesh) on the upstream sides of the tiles in an attempt to keep floating algal mats from fouling the tiles. The hardware cloth could have reduced colonization of all macroinvertebrates directly from floating algal mats, but we assumed that potential reductions were similar for both raised and benthic tiles because hardware cloth was placed in front of both types of tiles. We removed 1/2 of the tiles (chosen randomly) in each treatment from each site on 27 August, and we removed the remaining tiles on 17 September. We placed a Surber sampler (153- μ m mesh) downstream of each tile to collect any organisms that were dislodged during the lifting process. We removed all organisms from tiles in the field, preserved them, and returned them to the laboratory, where we identified them to family and counted them. We collected periphyton samples from a ~5-cm² area of each tile and determined ash-free dry mass (AFDM) by drying the sample to a constant mass at 105°C for 24 h and combusting the sample at 500°C for 1 h (Stevenson 1996).

Statistical analyses

We examined the distribution of *P. antipodarum* using the samples collected in September 1997 because these samples represented the greatest number of locations. To examine seasonal variation, we plotted mean density of *P. antipodarum* as a function of time using samples from September 1997 and March and July 1998 from 4 locations (2 from the Madison and 2 from the Firehole Rivers) because these were the only locations with *Potamopyrgus* that were sampled seasonally.

We used SAS (version 8.2, SAS, Cary, North Carolina) for all statistical analyses. We examined the associations among *P. antipodarum* and other macroinvertebrates using the data from the September 1997 samples in 3 ways. First, we determined whether the composition and structure of macroinvertebrate assemblages covaried with the density of *P. antipodarum*. We characterized the among-location differences in macroinvertebrate assemblages using principal components analysis (PCA) based on a correla-

tion matrix of the taxon densities (excluding *P. antipodarum*). We reduced the number of taxa in the PCA by including only those families with densities >0.5% of the mean total density of macroinvertebrates. We combined rare families (densities <0.5% of the mean total density) into higher taxonomic groupings (e.g., other Ephemeroptera). We calculated Pearson correlation coefficients between the PCA axis scores and densities of *P. antipodarum* at each location (including locations with and without *P. antipodarum*). Second, we calculated a simple regression equation to determine the relationship between the density of *P. antipodarum* and that of all other macroinvertebrates combined at locations where *P. antipodarum* was present. We used only locations where *P. antipodarum* was present because its absence from a location could have been related to factors (e.g., lack of colonization) other than interactions with other macroinvertebrates. Third, we calculated Pearson correlation coefficients between the densities of macroinvertebrate families and *P. antipodarum* at locations where both *P. antipodarum* and the target families were present (Ludwig and Reynolds 1988). We used only locations where *P. antipodarum* and target families were present because the absence of a family could have been related to factors (e.g., inappropriate habitat) other than interactions between taxa.

To examine colonization, we used 3-way analysis of variance (ANOVA) to compare numbers of *P. antipodarum* on tiles among treatments (raised/benthic tiles, sites, date of tile removal). We used analyses of covariance (ANCOVA) with *P. antipodarum* numbers as the covariate to compare macroinvertebrate numbers and periphyton AFDM on tiles among treatments (raised/benthic tiles, site, date of tile removal) and to determine whether macroinvertebrate numbers and periphyton AFDM on tiles covaried with the numbers of *P. antipodarum* on tiles. We included all interactions among the covariate and other factors in the first models and then removed nonsignificant, higher-order interactions with the covariate for the final models. Sites were treated as blocks in the analysis. We followed this analysis with Pearson correlations between numbers of individual taxa (>0.5% of mean number) and numbers of *P. antipodarum* on tiles. We examined the residuals from regressions, ANOVAs, and ANCOVAs for normality and heterogeneity of variances. We test-

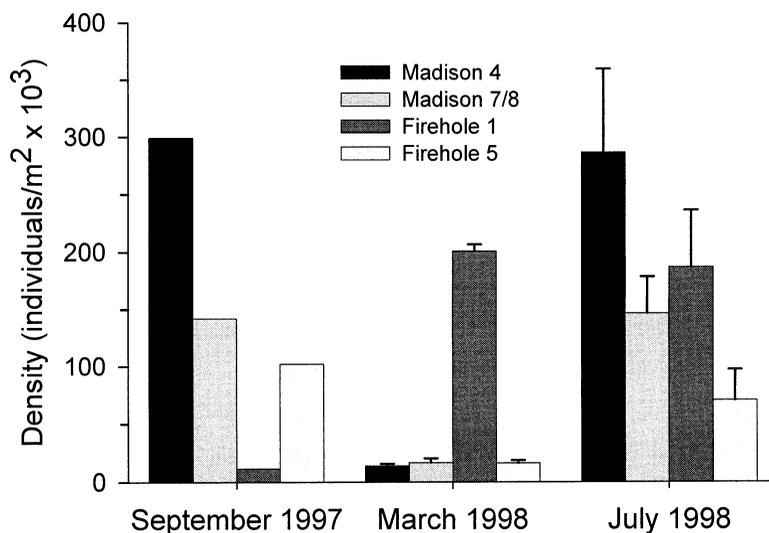


FIG. 2. Seasonal variation in densities of *Potamopyrgus antipodarum* at locations where samples were taken in all 3 seasons and where *P. antipodarum* was present. Error bars are +1 SE.

ed the normality of the taxon densities that were included in the PCA. We transformed densities and numbers of all macroinvertebrates and periphyton AFDM logarithmically (\ln or $[\ln + 1]$) before analyses to stabilize variances and improve normality. Statistical significance of all results was judged at $\alpha = 0.05$.

Results

Distribution and density of P. antipodarum and other macroinvertebrates

In September 1997, we found *P. antipodarum* at 23 of 32 locations. *Potamopyrgus antipodarum* were present at all locations in the Madison River, Nez Perce Creek, and the Firehole River downstream of the Upper Geyser Basin (locations 1–6, Fig. 1). We found *P. antipodarum* in only 2 of the 3 most downstream locations in the Gibbon River (locations 1 and 3, Fig. 1). In March and July 1998, we found *P. antipodarum* at 4 of the 7 locations sampled. *Potamopyrgus antipodarum* had been present at all 4 locations in September 1997. We did not find *P. antipodarum* in any locations where it had been absent in September 1997, except for a few individuals in one sample from the Firehole River above the Upper Geyser Basin (location 7) in July 1998.

In September 1997, densities of *P. antipodarum* ranged from 22 ind./m² (location 3, Gibbon Riv-

er) to 299,000 ind./m² (location 4, Madison River). In 3 of the 4 locations where *P. antipodarum* was present, densities declined between September 1997 and March 1998 and then increased dramatically between March 1998 and July 1998 (Fig. 2). In the other location (Firehole 1), densities were low in September 1997 and then increased between September 1997 and March 1998.

Nineteen macroinvertebrate taxa were included in the PCA (Table 2). The first 3 principal component (PC) axes explained ~50% of the among-location variation in macroinvertebrate assemblages. PC1 separated locations at which Brachycentridae, Baetidae, Ephemerellidae, and other Diptera were common (positive scores, Table 2) from locations where these taxa were uncommon (negative scores, Table 2). PC1 separated most locations on the Gibbon and the upper Firehole Rivers, where these taxa were common, from most locations on the Madison and the lower Firehole Rivers, where these taxa were uncommon (Fig. 3A, B). Locations on Nez Perce Creek were distributed across the entire axis (Fig. 3A, B). PC2 separated locations at which Glossosomatidae and Hydroptilidae were common (negative scores, Table 2) from locations where these taxa were uncommon (positive scores, Table 2). PC2 separated most locations on the Firehole River and Nez Perce Creek,

TABLE 2. Mean (SE) density and principal component (PC) scores for each taxon on the first 3 PC axes in September 1997. The % of total variation explained by each PC axis is at the bottom of the table. $n = 32$.

Taxon	Density (ind./m ²)	PC score		
		PC1	PC2	PC3
Plecoptera	237 (118)	0.2597	0.1278	0.0039
Baetidae	1796 (696)	0.3136	-0.2243	-0.0988
Ephemereillidae	639 (211)	0.3052	-0.1011	0.0632
Heptageniidae	114 (54)	0.1949	-0.2182	-0.1067
Other Ephemeroptera	75 (65)	0.0847	0.2298	0.0700
Glossosomatidae	4184 (1114)	0.1295	-0.4877	0.1167
Lepidostomatidae	606 (195)	0.2418	0.2599	0.2290
Brachycentridae	503 (170)	0.3531	0.2858	-0.1668
Hydroptilidae	768 (218)	-0.1032	-0.3235	0.4195
Hydropyschidae	364 (107)	0.2372	0.0317	0.2433
Limnephilidae	135 (65)	-0.0847	0.1760	0.3736
Other Trichoptera	631 (186)	0.1834	-0.0423	-0.0991
Elmidae	1806 (285)	0.2882	0.1816	0.2500
Chironomidae	7752 (2280)	0.0062	0.2730	0.3984
Tipulidae	394 (164)	0.2933	-0.1615	0.0342
Other Diptera	204 (61)	0.3689	0.1179	0.0111
Odonata and Lepidoptera	70 (24)	-0.1063	-0.1525	0.5116
Physidae	171 (161)	-0.2424	0.2941	-0.0285
Other Mollusca	41 (17)	-0.1125	0.1998	-0.0805
% total variation explained		22.4	14.0	12.2

where these taxa were common, from most locations on the Gibbon and Madison Rivers, where these taxa were uncommon (Fig. 3A). PC3 separated locations at which Hydroptilidae, Limnephilidae, Chironomidae, and Odonata and Lepidoptera were common (positive scores, Table 2) from locations where these taxa were uncommon (negative scores, Table 2). PC3 separated locations on Nez Perce Creek, where these taxa were common, from locations on the

Gibbon River, where they were uncommon (Fig. 3B). Locations on the Madison and Firehole Rivers were distributed across the entire axis (Fig. 3B).

Densities of *P. antipodarum* were significantly correlated with PC1 ($r = -0.5665$, $p = 0.0007$, $n = 32$) and PC3 ($r = 0.5738$, $p = 0.0006$, $n = 32$) (Fig. 3). The most striking pattern was that the assemblages on the Gibbon and upper Firehole Rivers, where *P. antipodarum* has not invaded,

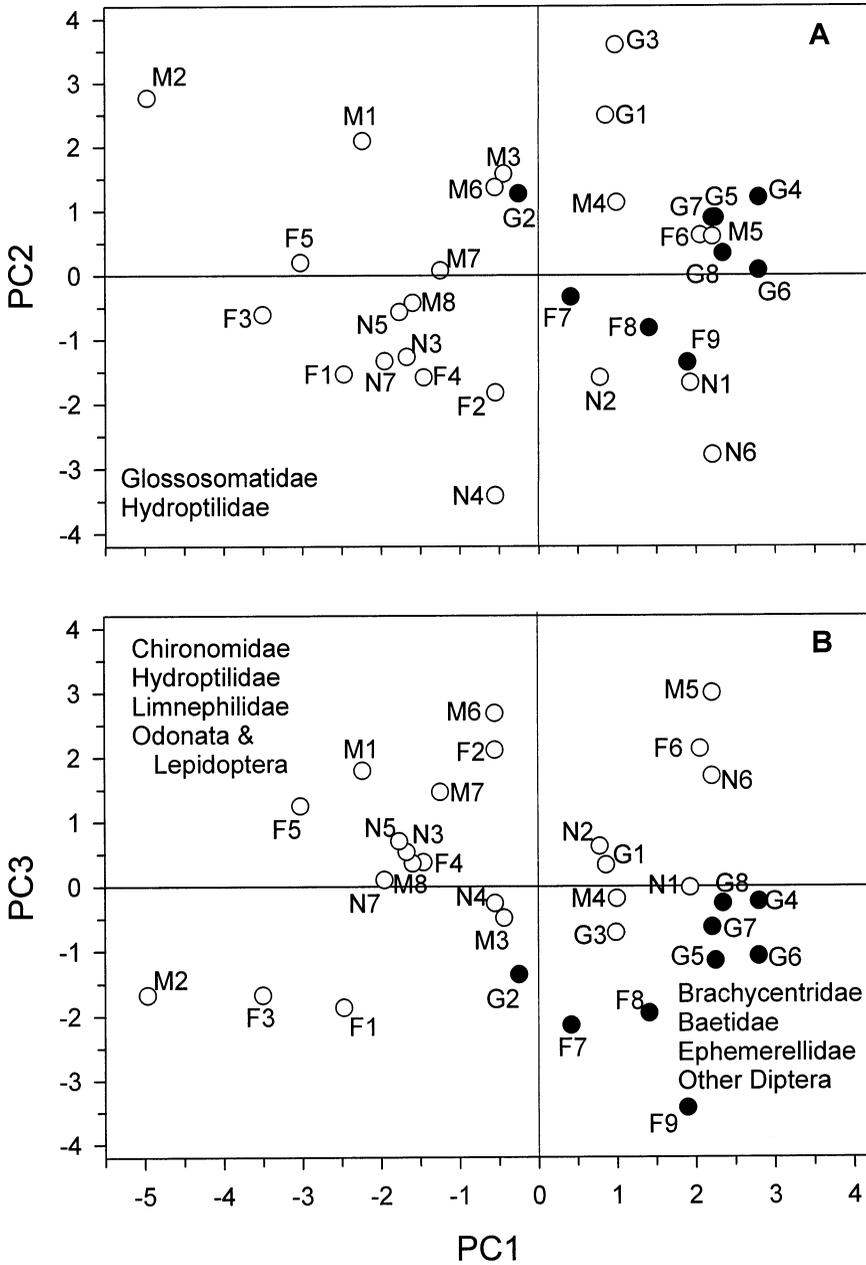


FIG. 3. Plots of principal component (PC) scores for macroinvertebrate assemblages in 32 sampling locations in the Madison River basin in the Greater Yellowstone ecosystem. Analysis was based on macroinvertebrate densities (exclusive of *Potamopyrgus antipodarum*) in fall 1997. A.—PC2 vs PC1. B.—PC3 vs PC1. Taxa with strong correlations with the axes are listed next to the appropriate axis. Sampling locations indicated by letter (F = Firehole, G = Gibbon, M = Madison, N = Nez Perce) and number (see Fig. 1). Open symbols = *P. antipodarum* present; closed symbols = *P. antipodarum* absent.

TABLE 3. Analysis of variance (ANOVA) table for the number of *Potamopyrgus antipodarum* on tiles in the colonization experiment. – = site effect not tested.

Source	df	F	p
Date (27 August vs 17 September)	1	5.07	0.0285
Site (1 vs 2)	1	–	–
Position of tile (raised vs benthic)	1	1.17	0.1969
Date × position of tile	1	0.72	0.3993
Date × site	1	2.59	0.1135
Site × position of tile	1	7.75	0.0075
Date × position of tile × site	1	0.93	0.339
Error	52		

clustered together on PC1 and PC3 (Fig. 3B). Thus, the macroinvertebrate assemblages at locations where *P. antipodarum* was not found were dominated by Brachycentridae, Ephemerelellidae, and Baetidae, and lacked Chironomidae, Hydroptilidae, and Limnephilidae.

The slope of the regression of the density of all other macroinvertebrates combined against the density of *P. antipodarum* was negative, but the slope was not significantly different from 0 ($t_{21} = -1.38$, $p = 0.1814$). In general, correlations between the density of *P. antipodarum* and the densities of individual families were not statistically significant. The strongest correlation observed was between the densities of *P. antipodarum* and Ephemerelellidae ($r = -0.4653$, $p = 0.0805$, $n = 15$).

Colonization experiment

The number of *P. antipodarum* on tiles was significantly higher in September than August (Table 3, Fig. 4A, B). The significant interaction between site and position of tile (Table 3) occurred because more *P. antipodarum* were found on raised tiles than benthic tiles at site 2, whereas the number of *P. antipodarum* was similar on raised and benthic tiles at site 1 (Fig. 4).

The mean total number of macroinvertebrates (excluding *P. antipodarum*) on tiles was significantly higher in September (10.53 ± 1.67 [1 SE]) than in August (9.13 ± 2.29) and tended to be higher on raised (10.17 ± 2.43) than benthic (9.50 ± 1.56) tiles (Table 4). The total number of macroinvertebrates on tiles was negatively related to the number of *P. antipodarum* (Table 4, Fig. 5). However, a significant interaction between the number of *P. antipodarum* on a tile and

the position of the tile (Table 4) indicated that the number of macroinvertebrates on a tile declined with increasing numbers of *P. antipodarum* on raised tiles ($\ln[\text{macroinvertebrate abundance} + 1] = 6.207 + 0.834 \ln[P. \textit{antipodarum} \textit{ abundance}]$) but not on benthic tiles ($\ln[\text{macroinvertebrate abundance} + 1] = 1.692 + 0.086 \ln[P. \textit{antipodarum} \textit{ abundance}]$). The number of *P. antipodarum* on tiles spanned the widest range and was highest on raised tiles (Fig. 5). We removed the tile that had the highest number of macroinvertebrates and lowest number of *P. antipodarum* from the analysis to check its impact on the regression. The numbers of *P. antipodarum* and macroinvertebrates on tiles remained significantly and negatively related, but the interaction between the number of *P. antipodarum* and position of the tile was no longer significant. Thus, the interaction appeared to have been driven by one datum. Eight of the 13 correlations between the number of *P. antipodarum* and the number of individuals in each family on a tile were negative and significant on raised tiles (Table 5). No correlations were significant on the benthic tiles.

Periphyton AFDM was higher in August 1998 (3.44 ± 0.21 g/m², $n = 30$) than in September 1997 (2.59 ± 0.15 g/m², $n = 30$; ANCOVA, $F_{1,51} = 18.86$, $p < 0.0001$) but was not related to the number of *P. antipodarum* on a tile (ANCOVA, $F_{1,51} = 2.62$, $p = 0.1119$) or any other factors in the model.

Discussion

Distribution and abundance of *P. antipodarum*

Potamopyrgus antipodarum was widely distributed and extremely abundant in the Madison River, Nez Perce Creek, and in reaches of the Firehole River downstream of thermal effluents. The densities of *P. antipodarum* in these locations were similar to those reported for other invasive populations of *P. antipodarum* in Europe, Australia, and other streams in Yellowstone National Park (Heywood and Edwards 1962, Dorgelo 1987, Schreiber et al. 1998, Hall et al. 2003). Moreover, the densities of *P. antipodarum* in our study were higher than typical densities in its native range (Talbot and Ward 1987, Death 1991, Scott et al. 1994). Conversely, we rarely found *P. antipodarum* above the geothermal discharges in the Gibbon and Firehole Rivers. Thus, *P. anti-*

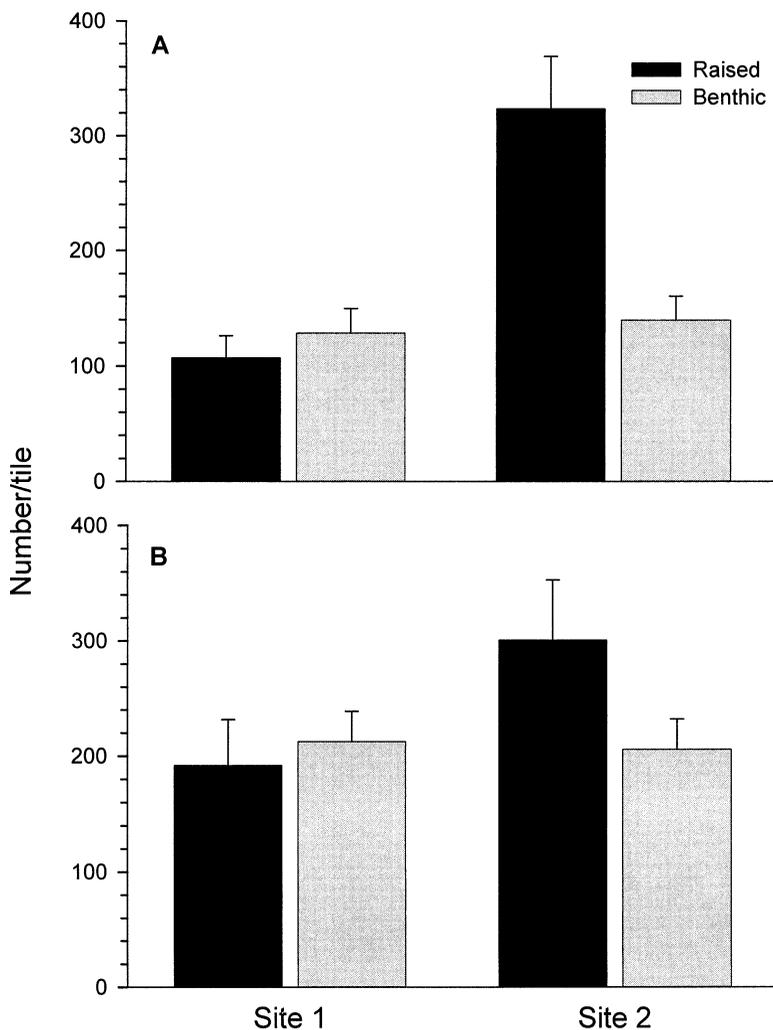


FIG. 4. Mean (+1 SE) number of *Potamopyrgus antipodarum* on raised and benthic tiles sampled from 2 sites on the Madison River in August (A) and September (B) 1999.

TABLE 4. Analysis of covariance (ANCOVA) table for the total number of macroinvertebrates (excluding *Potamopyrgus antipodarum*) on tiles in the colonization experiment. – = site effect not tested.

Source	df	F	p
Number of <i>P. antipodarum</i>	1	7.50	0.0085
Date (27 August vs 17 September)	1	4.77	0.0337
Site (1 vs 2)	1	–	–
Position of tile (raised vs benthic)	1	3.75	0.0585
Date × position of tile	1	0.37	0.5459
Date × site	1	1.07	0.3051
Site × position of tile	1	2.38	0.1295
Date × position of tile × site	1	2.36	0.1306
Number of <i>P. antipodarum</i> × position of tile	1	4.06	0.0494
Error	50		

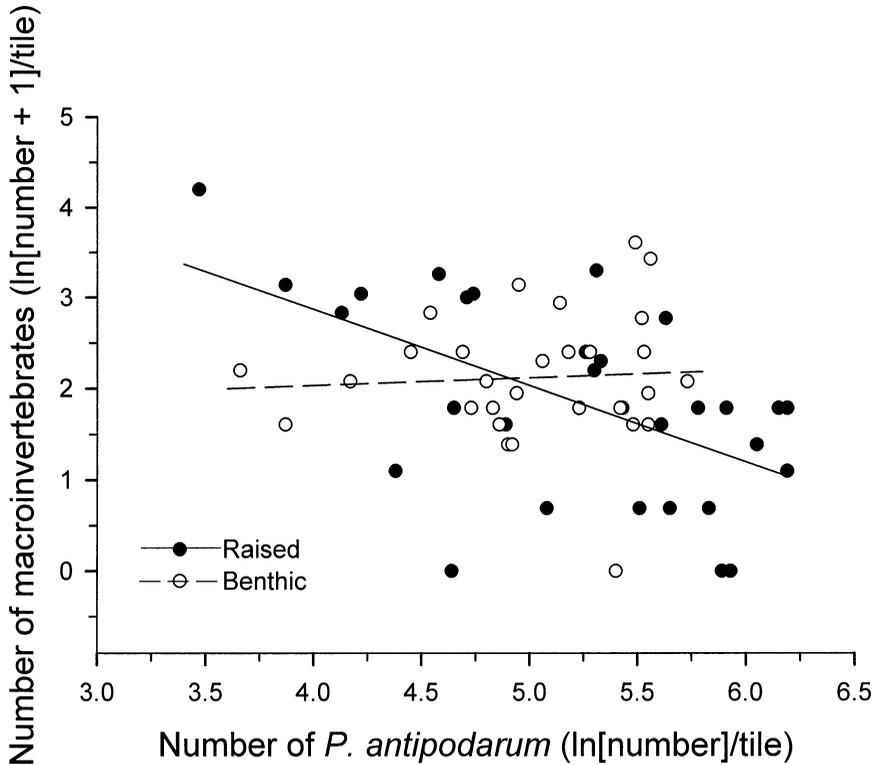


FIG. 5. Relationship between number of macroinvertebrates (excluding *Potamopyrgus antipodarum*) and *P. antipodarum* on raised and benthic tiles from August and September 1999.

podarum has successfully invaded and is abundant in some areas of the upper Madison basin in the GYE, but is absent or uncommon in others.

We may have observed these patterns of distribution and density because *P. antipodarum* is continuing to disperse within the stream system. Thus, our results could have shown an invasion in progress. *Potamopyrgus antipodarum* is a relatively new invader to the GYE (ca 1994), and the areas on the Gibbon and Firehole Rivers where abundances decline upstream may have been invasion fronts. Dispersal of *P. antipodarum* within systems is rapid and occurs via both active and passive mechanisms (Ribi 1986, Holomuzki and Biggs 2000). *Potamopyrgus antipodarum* colonized 640 km of the Snake River in 10 y (Zaranko et al. 1997), and it dispersed 20 km from the location where it was first observed in Lake Zurich in 10 y (Ribi 1986). Downstream dispersal is probably faster than upstream dispersal; *P. antipodarum* has been observed drifting downstream on floating algae in the Madison

basin (BLK, personal observation) and in other systems (Ribi 1986). In addition, humans may have aided in the spread of *P. antipodarum* in the Madison and lower Firehole Rivers because the rivers are used extensively for recreation and follow major tourism routes. Ribi (1986) suggested that distribution patterns of *P. antipodarum* in Lake Zurich could be explained by dispersal of snails by humans. Thus, if the original point of introduction of *P. antipodarum* was somewhere in the Firehole River above Nez Perce Creek, downstream dispersal into the lower Firehole and Madison Rivers should have occurred quickly via drift and human activities. In this scenario, the Gibbon River and Nez Perce Creek could not have been colonized by downstream drift. Upstream dispersal into the Gibbon River should have been slower than upstream dispersal into Nez Perce Creek because the confluence of the Gibbon River with the Firehole River is farther downstream than the confluence of Nez Perce Creek and the Firehole River. Moreover, the Gibbon River has higher

TABLE 5. Mean number (± 1 SE) of macroinvertebrates on tiles, and Pearson correlations between the number of macroinvertebrates and the number of *Potamopyrgus antipodarum* on raised and benthic tiles in the colonization experiment. Significant correlations ($p < 0.05$) are indicated in bold. – = too few individuals to analyze.

Taxon	Raised		Benthic	
	No./tile	<i>r</i>	No./tile	<i>r</i>
Plecoptera	0	–	0.033 \pm 0.033	–
Baetidae	0.667 \pm 0.161	–0.2092 <i>p</i> = 0.2672	0.767 \pm 0.202	–0.0002 <i>p</i> = 0.9990
Ephemerelellidae	0.367 \pm 0.148	–0.4809 <i>p</i> = 0.0071	0.467 \pm 0.261	0.2126 <i>p</i> = 0.2594
Heptageniidae	0.933 \pm 0.209	–0.2619 <i>p</i> = 0.1620	2.667 \pm 0.399	–0.0477 <i>p</i> = 0.8025
Other Ephemeroptera	0.067 \pm 0.046	0.2003 <i>p</i> = 0.2886	0.300 \pm 0.098	0.1568 <i>p</i> = 0.4080
Glossosomatidae	0.033 \pm 0.033	–	0.400 \pm 0.156	–0.0560 <i>p</i> = 0.7690
Brachycentridae	0.400 \pm 0.195	–0.4944 <i>p</i> = 0.0055	0.033 \pm 0.033	–
Hydroptilidae	0.067 \pm 0.067	–0.4481 <i>p</i> = 0.0130	0.067 \pm 0.046	0.1007 <i>p</i> = 0.5964
Hydropyschidae	1.800 \pm 0.923	–0.3796 <i>p</i> = 0.0385	0.300 \pm 0.128	0.0587 <i>p</i> = 0.7582
Other Trichoptera	2.500 \pm 0.882	–0.1940 <i>p</i> = 0.3044	0.500 \pm 0.133	–0.0326 <i>p</i> = 0.8641
Elmidae	0.100 \pm 0.074	–0.2203 <i>p</i> = 0.2421	0.200 \pm 0.074	0.2177 <i>p</i> = 0.2478
Chironomidae	2.467 \pm 0.786	–0.5933 <i>p</i> = 0.0005	3.133 \pm 0.756	0.2580 <i>p</i> = 0.1687
Other Diptera	0.500 \pm 0.213	–0.4343 <i>p</i> = 0.0165	0.300 \pm 0.119	–0.1104 <i>p</i> = 0.5614
Mollusca (excluding <i>P. antipodarum</i>)	0.200 \pm 0.088	–0.3736 <i>p</i> = 0.0420	0.300 \pm 0.109	–0.0947 <i>p</i> = 0.6187
Lepidoptera	0.067 \pm 0.046	–0.5227 <i>p</i> = 0.0030	0.033 \pm 0.033	–

discharges than Nez Perce Creek. We have recently found *P. antipodarum* farther upstream on the Gibbon River than in 1998, but still below the thermal effluents (BLK, personal observation), adding further support that the distribution pattern we observed on the Gibbon River may have reflected an invasion front in 1997 and 1998.

Alternatively, the distribution and density of *P. antipodarum* may be limited by physicochemical conditions and algal productivity. The areas on the Firehole, Gibbon, and Madison Rivers and Nez Perce Creek below the major thermal discharges differ markedly in physicochemical features and productivity from the upper Firehole and Gibbon Rivers (Table 1). Above the thermal discharges, the upper Firehole and Gibbon Rivers are typical mountain streams—water

temperatures and concentrations of most dissolved constituents are low and the rivers can be ice- and snow-covered in the winter (Roeder 1966). In addition, the standing crops of benthic insects (Armitage 1958) and algae (Boyley and Brock 1973) are lower in reaches above than in reaches below thermal discharges. In the Madison River, algal productivity is high and declines downstream (Wright and Horrall 1967).

Potamopyrgus antipodarum has wide temperature tolerances (0–30°C) (Winterbourn 1969, Hylleberg and Siegmund 1987) indicating that water temperature alone probably does not limit its distribution. Densities as high as 180,000 ind./m² have been reported from vegetation in a cold-water spring in New Zealand (Michaelis 1977). In addition, the species' ability to survive in continental fresh waters of northern Europe

(Bondesen and Kaiser 1949), where mean temperatures are $\leq 0^{\circ}\text{C}$ for 3 to 4 mo, suggests that *P. antipodarum* is capable of acclimating to temperatures below those encountered in the GYE.

Potamopyrgus antipodarum is most successful in productive streams. Schreiber et al. (2003) suggested that *P. antipodarum* populations may increase in response to increased food resources that result from agricultural disturbances in Australian streams. Moreover, Death (1991) found that *P. antipodarum* densities were highest in stable rivers with high productivity in New Zealand. Thus, low productivity may limit the upstream population sizes and distribution of *P. antipodarum* in the GYE. Further research examining the relationships among productivity, water temperature, and densities of *P. antipodarum* are warranted.

Densities of *P. antipodarum* declined over the winter in most locations and then rebounded the following summer. Other such precipitous declines have been reported for populations of *P. antipodarum* that have invaded temperate zones (Heywood and Edwards 1962, Dorgelo 1987). Low temperatures and low food availability during cold winters have been suggested as possible reasons for fluctuating snail populations (Dahl and Winther 1993). Smaller population fluctuations have been observed in Australia where climates and water temperatures were more stable (Quinn et al. 1996, Schreiber et al. 1998). Our results suggest that the seasonal decline does not result from low water temperatures because populations declined in the thermally influenced reaches of the Firehole River where water temperatures typically remain $\gg 0^{\circ}\text{C}$ in winter (Goldstein 1999).

Covariation between macroinvertebrate assemblages and the density of P. antipodarum

One of the most striking patterns that we observed was covariation in the composition and structure of the macroinvertebrate assemblages and the density of *P. antipodarum*. For example, Brachycentridae, Baetidae, Ephemerellidae, and nonchironomid Diptera dominated the assemblages in the upper Firehole River and most of the Gibbon River where *P. antipodarum* was absent or rare. At least 2 nonmutually exclusive hypotheses could explain these results. First, taxon distributions could reflect the wide variation in physicochemical characteristics of the

streams. For example, *P. antipodarum* may prefer the habitat types available in the Firehole River below the geothermal discharges, whereas the macroinvertebrate taxa that dominate locations on the upper Firehole River and most of the Gibbon River prefer the habitats available there.

Second, a complex array of direct and indirect interactions among the organisms may have caused the distribution pattern. For example, macroinvertebrates that dominate the assemblages of the upper Firehole River and most of the Gibbon River may prevent the colonization of *P. antipodarum*, or *P. antipodarum* could reduce the abundance of these organisms through competition in areas where it has colonized. Historical data on the macroinvertebrate assemblages of these streams are not directly comparable to our data because of different sampling and data analyses protocols, but they do suggest that some of the patterns we found existed prior to the invasion of *P. antipodarum*. For example, Armitage (1961) and Vincent (1967) found that mayflies, primarily *Baetis tricaudatus*, *Ephemerella* spp., and *Epeorus* spp. were more important components of macroinvertebrate assemblages in the reaches of the Firehole and Gibbon Rivers above most thermal discharges than in areas below the thermal discharges. Thus, our results were concordant with the historical pattern of macroinvertebrate assemblages on the Firehole River, and this concordance suggests that *P. antipodarum* has not caused major shifts in the macroinvertebrate assemblages there. However, on the Gibbon River, we found that Baetidae and Ephemerellidae dominated all but the 3 most-downstream locations, 2 of which had been invaded by *P. antipodarum*. This pattern suggests that *P. antipodarum* may have had an effect on macroinvertebrate assemblages in the Gibbon River. The large-scale patterns of macroinvertebrates and *P. antipodarum* also clearly warrant further investigation.

Interactions between P. antipodarum and other macroinvertebrates

We found little evidence for negative interactions between *P. antipodarum* and other macroinvertebrates in the field survey; however, negative associations occurred between *P. antipodarum* and macroinvertebrates in the colonization experiment. In the field survey, the only significant association was a weak negative correla-

tion between the densities of *P. antipodarum* and Ephemerelellidae. However, in the experiment, the strongest predictor of the number of other macroinvertebrates colonizing the tiles was the number of *P. antipodarum*. The general trend was that the number of other macroinvertebrates declined as the number of *P. antipodarum* increased on a tile. Moreover, the numbers of many taxa with various habits and feeding mechanisms were negatively correlated with the number of *P. antipodarum*. This pattern suggests that *P. antipodarum* interfered with colonization of tiles by other macroinvertebrates. Abundances of *P. antipodarum* and other taxa colonizing tiles were positively correlated in an experiment in Australian streams (Schreiber et al. 2002). The highest densities of *P. antipodarum* colonizing tiles were much higher in our experiment than in the experiment conducted by Schreiber et al. (2002) (~20,000 vs 4500 ind./m², respectively). The contrasting results of the 2 experiments suggest that interactions between *P. antipodarum* and other macroinvertebrates are complex and may shift from facilitation to competition as snail densities increase. The possible occurrence of facilitation at low density adds even more complexity to the interactions between *P. antipodarum* and other macroinvertebrates (Bruno et al. 2003).

In the colonization experiment, abundances of *P. antipodarum* and other macroinvertebrates were negatively associated; however, we detected little solid evidence suggesting that these negative interactions had consequences for the large-scale distribution and abundance patterns of other macroinvertebrates in the field. Other factors such as large-scale variation in environmental characteristics, variation among habitat preferences of macroinvertebrate taxa, and an invasion in progress may have interfered with our ability to detect evidence of small-scale interactions at larger spatial scales. Alternatively, large-scale environmental variation may have been more important to community composition and structure than small-scale competitive interactions. More detailed study is needed to determine the consequences to aquatic communities of the invasion of *P. antipodarum* into aquatic ecosystems in North America.

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