Hydrobiologia (2015) 746:375–399
DOI 10.1007/s10750-014-2136-6

INVASIVE SPECIES

Ecology of the invasive New Zealand mud snail, *Potamopyrgus antipodarum* (Hydrobiidae), in a mediterranean-climate stream system

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Received: 16 May 2014 / Revised: 23 November 2014 / Accepted: 27 November 2014 / Published online: 14 December 2014

Abstract The New Zealand mud snail, *Potamopyrgus antipodarum*, is a widely distributed non-native species of management concern on four continents. In a southern California stream, *P. antipodarum* abundance, which ranged from ca. <10 to nearly 150,000 snails m^{-2}, was related to discharge and temperature patterns. Laboratory experiments indicated that *P. antipodarum* (1) survivorship decreased from 13 to 27°C, but its growth rate was higher at 13 and 20°C than 27°C; (2) grazing rates were similar to those of native algivores in short-term trials; (3) grazing impact was greater than that of a native hydrobiid snail in longer-term trials; (4) ingested different diatom sizes than some other grazers; (5) reduced the abundances of medium-sized and large diatoms, and several filamentous cyanobacteria and chlorophytes, while increasing the relative abundances of tough filamentous chlorophytes (e.g., *Cladophora*); (6) impact on other grazing invertebrates was species specific, ranging from competition to facilitation; (7) reduced the survivorship of *Anaxyrus boreas* tadpoles; and (8) was consumed by non-native *Procambarus clarkii* and naiads of *Aeshna* and *Argia*. Ecological effects of introduced *P.antipodarum* are subtle, occurring primarily at transitory high densities, but flow regulation may enhance their effects by eliminating high flows that reduce their population sizes.

Keywords Invasive aquatic species · *Potamopyrgus antipodarum* · Mediterranean-climate stream

Introduction

Like running water systems in many parts of the world, streams in Mediterranean climates are often invaded by non-native plant and animal taxa (Dudley & Collins, 1995; Vila-Gispert et al., 2005; Ribeiro et al., 2008). Also, as in other systems, the impacts of non-native species on native communities will depend on the characteristics of the invader and the invaded community, and on environmental conditions (Poff, 1996). Because climatic, hydrological, thermal, and other environmental conditions will vary across regions, the success and impacts of potentially invasive species also are likely to vary across regions (Dukes & Mooney, 1999), as mediated through the

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Electronic supplementary material The online version of this article (doi:10.1007/s10750-014-2136-6) contains supplementary material, which is available to authorized users.

Guest editors: Sidinei M. Thomaz, Katya E. Kovalenko, John E. Havel & Lee B. Kats / Aquatic Invasive Species

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effects of environmental conditions on disturbance regimes and the life histories, and birth, death, and growth rates, of invasive and native species. Knowledge of the success and impacts of invasive species across different regions and ecosystem types can be useful in developing a more nuanced understanding of invasive species effects on ecosystems, guiding management activities (Meekins & McCarthy, 2001; Vilà et al., 2011). For example, a hydrological regime with periodic flooding can prevent extirpation of a native topminnow (*Poeciliopsis occidentalis*) that is displaced by introduced mosquitofish (*Gambusia affinis*) in stable streams that no longer flood (Meffe, 1984).

The New Zealand mud snail, *Potamopyrgus antipodarum* (Gray, 1843), has been introduced to stream systems throughout the world, including in Europe, Australia, North America, and eastern Asia (Ponder, 1988; Bowler, 1991; Richards et al., 2001; Alonso & Castro-Diez, 2008; Davidson et al., 2011). In the continental U.S., this non-native mollusk is established in a wide range of habitats, encompassing arid desert to high-elevation temperate streams, coastal waterways, and the Great Lakes (ANS, 2007; Levri et al., 2008). As a consequence, *P. antipodarum*'s broad distribution provides an opportunity to compare its ecological relationships and impacts across regions to better understand and predict where and when its impacts rise to the level of management concern (Murria et al., 2008). This diminutive snail (ca. 3–6 mm from shell apex to base in adults) is an opportunistic grazer-detritivore in its native and adventive range (Schreiber et al., 1998; James et al., 2000; Broekhuizen et al., 2001; Hall et al., 2003) and is found in a variety of habitat types, including stream riffles and pools, lentic habitats, drainage ditches, and even high estuarine zones (Schreiber et al., 2003; Brown et al., 2008; Brenneis et al., 2011; Benson, 2011). Because *P. antipodarum* can reach densities of over 300,000 individuals per m^2 (Hall et al., 2003), it has a high potential for affecting benthic food resources and co-occurring organisms (Kerans et al., 2005; Evans, 2012; Alonso & Castro-Diez, 2012). Because of their similarity, invasive *P. antipodarum* might be expected to affect closely related native hydrobiid snails, including threatened species (Richards et al., 2001). Although *P. antipodarum* is now widely distributed in California, few ecological studies have examined its dynamics, success, environmental constraints, and impacts on native communities (Twardochleb et al., 2012; Moore et al., 2012; Krist & Charles, 2012; Kolosovich et al., 2012), although such studies might inform management activities, not only in California but also in other regions with Mediterranean climates that *P. antipodarum* has invaded (e.g., southern Europe, Alonso & Castro-Diez, 2008; Murria et al., 2008).

The objectives of the field and laboratory studies described here were to examine the life history and population dynamics of *P. antipodarum* in a southern California stream, to evaluate its responses to environmental conditions, particularly temperature and flow, and to examine its interactions with native algal communities, native grazer species, and native and non-native predators. This comprehensive battery of studies allowed comparisons to *P. antipodarum*'s dynamics, success, and impacts in other regions, as well as provided scientific evidence to determine if efforts to mitigate *P. antipodarum*'s impacts through traditional or biological control practices were justifiable.

We addressed the following questions:

1. What are the characteristics of *P. antipodarum*'s life cycle, and reproductive and population dynamics, in a southern California stream, and how are its population dynamics related to seasonal changes in abiotic factors? Aquatic invertebrate life histories and population dynamics can be highly variable, depending on climatic and hydrological conditions (Li et al., 2011). Because mediterranean systems are characterized by winter rains, summer droughts, flashy hydrographs, and benign temperatures, the life histories and dynamics of organisms in mediterranean streams are often different from those in other biomes (Gasith & Resh, 1999; Moffitt & James, 2012; Bonada & Resh, 2013).
2. How are the growth and survivorship of *P. antipodarum* affected by temperature? Consistently warmer temperatures in mediterranean compared to other temperate streams can accelerate the growth, development, and reproduction of *P. antipodarum*, potentially leading to more continuous life cycles (Nebeker, 1971). In some cases, *P. antipodarum* may grow faster in shaded habitats with lower temperatures, independent of food quality (Liess & Lange, 2011).
3. How do the grazing rates and diet composition of *P. antipodarum* compare to those of native grazers

and how does *P. antipodarum* alter the physiognomy and species composition of algal assemblages? Owing to its small size, relatively sedentary feeding behavior, and sometimes very high densities, *P. antipodarum* can have substantial impacts on algal biomass and composition, as well as nutrient cycling (McCormick & Stevenson, 1989; Riley et al., 2008; Liess & Kahlert, 2009).

4. Does *P. antipodarum* affect the birth, death, and population growth rates of native grazers and vice versa? By altering algal assemblages, reducing algal biomass, and affecting the behavior of competitors, *P. antipodarum* can affect native grazers, including insect and amphibian larvae, and particularly ecologically similar snails (Cross & Benke, 2002; Riley et al., 2008; Kerans et al., 2010).
5. Can different native and non-native invertebrate predators or omnivores feed on *P. antipodarum* and, if so, do predators prefer particular *P. antipodarum* sizes? Predation has often inhibited the establishment and population growth of non-native organisms, so pre-existing predators, including non-native species, may reduce *P. antipodarum* population size and ecosystem impacts (Baltz & Moyle, 1993; Brenneis et al., 2011; Twardochleb et al., 2012).

Methods

Field studies

Study site

We monitored the densities and size structure of *Potomopyrgus antipodarum* in Piru Creek, a 3rd order tributary of the Santa Clara River in Los Angeles County, California, from 2009 to 2011 (densities: February 2009 to February 2011; size structure: March 2009 to January 2010). Our primary study site on Piru Creek was Frenchman's Flat (118° 44′ 51″W, 34° 37′ 50″ N; elevation ca. 680 m) located approximately 4 kms downstream from Pyramid Reservoir in an area where *P. antipodarum* has been established since at least 2006 (Fig. 1).

This site has a mediterranean climate with a mean annual rainfall of about 40 cm yr^{-1}, which mostly falls between November and April, with hot, dry summers indicative of its inland location (ca. 75 km from the Pacific Ocean). Middle Piru Creek is surrounded by Angeles and Los Padres National Forests and is used primarily for recreation. Pyramid Dam controls water releases into the study section, although some effort is made to simulate natural discharge patterns, with high winter and low summer flows. The study reach flows through a narrow rocky canyon, but has an open canopy with its sandstone banks lined with Fremont cottonwood (*Populus fremontii*), willows (*Salix* spp.), poison oak (*Toxicodendron diversilobum*), and giant reed (*Arundo donax*). The creek between Pyramid and downstream Piru Dams contains arroyo and western toads (*Anaxyrus californicus* and *A. boreas*), California and Pacific tree frogs (*Pseudacris cadaverina* and *P. regilla*), bullfrogs (*Rana catesbeiana*), the pond turtle (*Actinemys marmorata*), and a variety of fish species, including Santa Ana suckers (*Catostomus santaanae*), sticklebacks (*Gasterosteus aculeatus*), arroyo chubs (*Gila orcuttii*), sculpins (*Cottus asper*), largemouth bass (*Micropterus salmoides*), and introduced and wild rainbow trout (*Oncorhynchus mykiss*), among others (Bell, 1978; Swift et al., 1993). The section of Piru Creek extending from Pyramid Dam downstream to near the Frenchman's Flat site is a California-designated Wild Trout area and part of the Heritage and Wild Trout Program.

Field methods

The surface densities of *P. antipodarum* (number of snails m^{-2}) were estimated monthly from February 2009 to February 2011, on soft substrata (mud, sand, and gravel) and hard substrata (rock, cobble, boulder) in riffles and pools, separately, by recording the number of snails observed under a 'viewing bucket' (plastic box with a clear plexiglass bottom gridded into 15 squares (5 × 5 cm each, 375 cm^2 per quadrat)). Five hard and five soft substrata quadrat counts were taken across two riffles and two pools on each sampling date. In addition, we took 5-cm-deep core samples (core surface area = 19.6 cm^2) monthly from five soft and five macroalgae (primarily *Cladophora*, but with occasional vascular plants) substrata from riffles and pools, separately, from March 2009 to January 2010. On each sampling date, we combined the five cores from each substrate type (macroalgae vs. soft substrata) and habitat (pools vs. riffles) in one

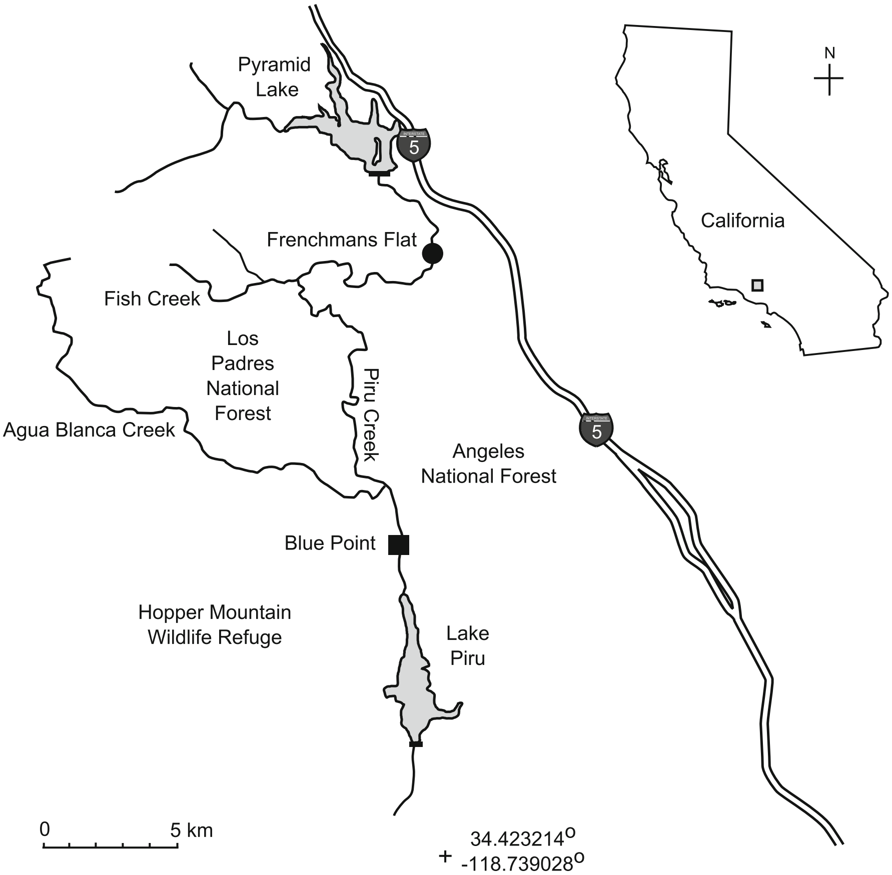


Fig. 1 Map of study reach of Piru Creek, CA, USA, below Pyramid Reservoir and above Piru Reservoir, and location within California (inset). The *dot* represents the location of the New Zealand mud snail (*Potamopyrgus antipodarum*) monitoring site at Frenchman's Flat and the *square* represents the location of the Blue Point collection site, where mud snails and tadpoles were collected for experiments. Map data ©2014, Google maps, terra matrics

container and preserved each composite sample in 75% ethanol.

The size structure of *P. antipodarum* populations was determined from core samples in March 2009 from only riffle macroalgae habitats, in April 2009 from riffle macroalgae and soft sediment habitats, and from June 2009 to January 2010 from macroalgae and soft sediment habitats in both riffles and pools. On each date and for each habitat (soft and macroalgae substrate types in riffles vs. pools), we measured the lengths of 0–150 snails (depending on the numbers in samples), from the shell's apex to the anterior tip of the aperture, under a microscope at ×10 magnification or by analyzing photographs using "Image J" software. In this paper, we primarily distinguish adult snails (length $\geq$ 2 mm) from juvenile snails (length $<$ 2 mm), because *P. antipodarum* reaches reproductive maturity at a length of 2.5–3 mm (Zaranko et al., 1997).

Water temperature, conductivity, pH, and total dissolved solids (TDS) were measured in a pool and a riffle on each date using an Extech digital handheld meter (ExStik MULTI Meter - PH100). Monthly average discharge data were obtained for station PYRAMID (PYM) on Piru Creek below Pyramid Lake from the California Department of Water Resources (California Data Exchange Center: http://cdec.water.ca.gov/selectQuery.html).

Experimental studies

Laboratory experiments were performed to examine the effects of temperature on *P. antipodarum* survivorship and growth and to quantify interactions between *P. antipodarum* and their algal resources, potential competitors, and potential predators. Experiments were conducted in glass or plastic containers filled with stream water collected either from Piru Creek, Ventura County, or from Mission Creek, Santa Barbara County, then filtered through a 50-µm sieve. Experimental units were exposed to fluorescent light on a 12-h light/12-h dark regime. With the exception of the experiment where we manipulated temperatures, most temperatures remained between 17 and 20°C. All containers were aerated using air pumps and 2 mm tubing. *Potamopyrgus* and *Anaxyrus* tadpoles used in these experiments were collected from Piru Creek, whereas other stream insects and snails were collected from coastal streams in Santa Barbara County (Mission, Arroyo Hondo, Carneros, Romero Creeks). With the possible exception of native *Pyrgulopsis*, all taxa co-occur with *Potamopyrgus* in Piru Creek or other southern California streams, and *Pyrgulopsis* was used because it is similar to *Potamopyrgus* and occurs in streams vulnerable to *Potamopyrgus* invasion.

Temperature experiment

In this experiment, 24 glass experimental units (container volume = 473 cm^3, bottom surface area = 0.018 m^2) contained filtered stream water at temperatures of 13, 20, and 27°C, effected using aquarium water heaters, with eight units assigned to each temperature level. Thirty *P. antipodarum* juveniles (average length = 1.3 mm) were placed into each container at the beginning of the experiment. Because snails only grew to a length of 2.1 mm by the end of this 70-day experiment, no reproduction was observed. Snails were fed *Spirulina* throughout this experiment (1.2 teaspoons of powder $week^{-1}$). Dead snails were removed and replaced during the first 48 h of the experiment, but dead snails were removed but not replaced thereafter. The number of live and dead snails, and average snail size, in each container were determined weekly.

Grazing experiments

Grazing experiments were conducted in clear plastic containers (container volume = 131 cm^3, bottom surface area = 0.0025 m^2, water depth = 4 cm) with tiled bottoms covered by diatoms and unicellular green algae. In these experiments, we measured the response of algal biomass (as chlorophyll *a* concentration) to the manipulated densities of *Potamopyrgus antipodarum* (mean length = 3.6 mm) and the snail *Physella gyrina* (Physidae; mean length = 4.8 mm), the snail *Pyrgulopsis* cf. *stearsiana* (a native snail from the same Hydrobiidae family as *P. antipodarum*, mean length = 2.0 mm), late instar nymphs of the mayfly *Centroptilum* sp. (Family Baetidae), and mid- to late-instar larvae of the caddisfly *Gumaga nigricula* (Family Sericostomatidae). In the first 2-day experiment, densities of *Potamopyrgus*, *Physella*, *Pyrgulopsis*, and *Centroptilum* were 5, 10, 15, and 20 per container, respectively, when each species was alone, and were 10 (5 *Potamopyrgus* + 5 of each of the other species), 15 (10 or 5 *Potamopyrgus* + 5 or 10 of each of the other species) and 20 (10 *Potamopyrgus* + 10 of each of the other species) per container when *Potamopyrgus* was combined with each of the other species. In the second grazing experiment, we measured the effects of four densities (2, 4, 6, 8 individuals per container) of *Potamopyrgus* and *Gumaga*, when each was alone, as well as four density combinations of these two species (2 *Potamopyrgus* + 2 *Gumaga*, 2 *Potamopyrgus* + 4 *Gumaga*, 4 *Potamopyrgus* + 2 *Gumaga*, and 4 *Potamopyrgus* + 4 *Gumaga*), on algal biomass over 2 days. Finally, in a third experiment, we measured the effects of four monospecific densities of *Potamopyrgus* and *Pyrgulopsis* (5, 10, 15, 20 per container, same sizes as in the 1st experiment) on algal biomass over 17 days. In all grazing experiments, control containers contained no grazers and three replicate experimental units were assigned to each treatment level (i.e., controls and each monospecific density and each density combination of two species).

At the end of these trials, we sampled algae in each grazing chamber by scraping algae from each tile, stirring the suspension, and then removing 10 ml of algal slurry with a syringe. Syringe samples were filtered through glass fiber filters (Whatman GFF), and chlorophyll on each filter was extracted for 24 h with 10 ml of 90% acetone in a dark freezer. Chlorophyll solutions were centrifuged then read on a Turner 10-AU Digital Fluorometer, both with and without acidification. After the first set of grazing trials, grazers were preserved in 70% ethanol, then guts of individual grazers, except for *Gumaga*, were removed and gut contents were extruded and examined at ×400 under a microscope to enumerate the numbers of recognizable algal species in each gut.

Additionally, we determined the effects of *P. antipodarum* (mean size = 3.6 mm) and Western toad tadpoles (*Anaxyrus boreas*, initial mean body length = 9.8 mm) on algal composition, algal density (number of cells cm^{-2}), and filamentous algal cover

over 27 days by manipulating both initial algal community composition (three types: diatoms, *Cladophora*, *Zygnema*) and the presence or absence of tadpoles (0 or 5 T) and mud snail density (0, 100, 500 S) with the following treatments: 0T/0S, 5T/0S, 5T/100S, 0T/500S, 5T/500S. This experiment was conducted in plastic boxes (container volume = 6,000 cm^3, bottom surface area = 0.0175 m^2, water depth = 12 cm; three replicates per treatment) whose bottoms were covered with cleaned beach sand (3 cm deep). Three initial algal community types were used in this experiment: (1) algal communities dominated by single-celled algae, mostly diatoms (Bacillariophyceae; called the diatom culture), (2) algal communities dominated by filamentous *Cladophora* sp. (Chlorophyceae, called the *Cladophora* culture), and (3) algal communities dominated by other filamentous algae, including *Zygnema* (Chlorophyceae) and *Melosira varians* (Bacillariophyceae) with some *Mougeotia* and *Spirogyra* (Chlorophyceae, hereafter called the *Zygnema* culture). Algal assemblages were sampled by determining percent cover of filamentous algae using a gridded quadrat, then removing overlying filamentous algae and taking three cores (each 2.5 cm diameter, 1 cm deep) from the sand covering each experimental container's bottom at the beginning and end of the experiment. Core samples from each container were agitated thoroughly, the algal suspension was mixed, and then a syringe was used to collect 10 ml of suspension, which was preserved in 10% formalin. Subsamples of preserved samples were identified and enumerated at ×400 under a microscope. Initial characteristics of each algal culture community can be found in Supplementary Materials Table 1.

Competition experiments

In the first competition experiment, we examined the effects of different densities of *Potamopyrgus*, *Pyrgulopsis*, *Centroptilum*, *Physella*, and *Gumaga*, both alone and together, on the birth, death, and population growth rates of each potential competitor species. We used the same sizes of grazers as used in the grazing trials. We set up three monospecific densities of *Potamopyrgus* (25, 50, 75 individuals/container), *Pyrgulopsis* (15, 30, 45/container), *Centroptilum* (6, 12, 18/container), *Physella* (10, 20, 30/container), and *Gumaga* (9, 18, 27/container), as well as specific combinations of *Potamopyrgus* (Po) (25 and 50 Po/container) with each of the other species (25 and 50 Po with 6 and 25 Po with 12 individuals of *Centroptilum;* 25 and 50 Po with 10 and 25 Po with 20 individuals of *Physella;* 25 and 50 Po with 9 and 50 Po with 18 individuals of *Gumaga*; and 25 and 50 Po with 15 and 25 Po with 30 individuals of *Pyrgulopsis*). Each experimental container had a volume of 1,770 cm^3 and a ceramic tile bottom surface area of 0.023 m^2, three replicate units were assigned to each experimental treatment, and the experiment lasted 55 days. Bottom tiles were colonized primarily by diatoms collected from Piru and Mission Creeks and introduced to containers for 2 weeks before the experiment started. To compensate for mayfly nymph deaths due to handling and losses to adult emergence, we replaced emerged or dead mayflies daily over the first 7 days to maintain preset densities. Snails and *Gumaga* showed no initial mortality and *Gumaga* remained in the larval stage throughout the experiment. We counted the number of dead and live individuals in each container during the experiment, as well as the number of emerged *Centroptilum* in the *Centroptilum* treatments.

In the second experiment, we examined the effects of *Potamopyrgus* and Western toad tadpoles on each other's growth and mortality across three different algal community types (diatoms, *Cladophora*, *Zygnema*, described in grazing impact section, above). In this experiment, the following five treatments were set up in each algal culture type: no tadpoles or snails, 5 tadpoles and no *Potamopyrgus*, 5 tadpoles and 100 *Potamopyrgus*, no tadpoles and 500 *Potamopyrgus*, and 5 tadpoles and 500 *Potamopyrgus*. Each experimental container had a volume of 6,000 cm^3 and a bottom surface area (covered by 3 cm of cleaned sand) of 0.0175 m^2, Three replicate containers were assigned to each treatment, and the experiment ran for 27 days. The number of live and dead tadpoles in treatments with tadpoles was counted weekly, whereas the numbers of dead and live *Potamopyrgus* were counted at the end of the experiment, and the lengths of tadpoles and *Potamopyrgus* were determined at the beginning and end of the experiment using digital images and "Image J" software.

Predation experiments

We conducted predation trials to determine if native and non-native predators commonly found in southern California streams would consume *Potamopyrgus* of different sizes. We examined possible predation by the ephemerillid mayfly *Drunella* sp. (*n* = 4 replicate trials), the perlodid stonefly *Isoperla* sp. (*n* = 1), the dragonflies *Aeshna walkeri* (*n* = 6), *Cordulegaster dorsalis* (*n* = 1), *Octogomphus specularis* (*n* = 7), and *Paltothemis lineatipes* (*n* = 3), the damselfly *Argia vivida* (*n* = 19), the hemipteran back swimmer *Notonecta hoffmanni* (*n* = 3), the hellgrammite *Protochauliodes* (*n* = 2), the caddisflies *Rhyacophila* sp. (*n* = 1), *Lepidostoma* sp. (*n* = 6), and *Gumaga nigricula* (*n* = 3), and three size classes (<5 cm, *n* = 2; 5–10 cm, *n* = 2, and >10 cm, *n* = 3) of the non-native red swamp crayfish (*Procambarus clarkii*) on two (crayfish trials, <2 mm, >2 mm) or three (insect trials, <2 mm, 2–4 mm, and >4 mm) *P. antipodarum* size classes. A single, starved (72 h) predator was used in each trial, and initial densities of *P. antipodarum* were 6 per container (2 of each of 3 size classes) in insect trials and 200 per container (100 of each of 2 size classes) in crayfish trials. Because *P. antipodarum* mortality was negligible in the competition and grazing experiments, we did not include control units with no predators present. Each predation trial container had a volume of 1,770 cm^3 and a tile bottom surface area of 0.023 m^2, and no food was provided to snails during these trials. After 2 days, the number of live snails remaining in each container was counted. Fecal analysis was performed at 10X under a microscope to determine if snails passed viably through predator guts.

Statistical analysis

For the field sampling, we determined if there were consistently different densities of *P. antipodarum* over sampling times between different habitat types (riffle vs. pool, hard vs. soft substrata for quadrat samples, macroalgae vs. soft substrata for core samples) using paired *t* tests. To examine relationships between *P. antipodarum* densities in different habitats and abiotic factors, we performed linear and quadratic (only for water temperature) regressions of *P. antipodarum* densities versus conductivity, water temperature, and discharge, independently, as well as multiple regressions using snail densities as dependent variables and the abiotic factors listed above, including a quadratic term for temperature, as independent variables with the backwards stepwise elimination of non-significant independent variables. Intercorrelations among all abiotic factors were also examined (Pearson's *r*). In all cases, snail densities were $\log_{10}(x + 1)$-transformed and discharge data were $\log_{10}$-transformed before analyses.

For laboratory experiments, we used one-way ANOVAs to examine treatment effects (when designs were asymmetrical) and two-way ANOVAs to examine the effects of manipulated variables (in cross-classified designs), followed by either t tests (two categories) or Tukey's HSD tests (> two categories) to determine which contrasts or treatments were significantly different. Data for all proportionate response variables (proportion surviving, proportionate increases in size, i.e., final length—initial length/initial length, proportion of population in small size classes, proportion filamentous algae cover) were logit-transformed before analyses, with adjustments for extreme 0 and 1 values (Warton & Hui, 2011).

Response variables for the competition, grazing, and predation experiments were derived from an exponential population growth and loss model (similar to Riley et al., 2008), i.e., final biomass or density = initial biomass or density X e^{rt} with r = b−d, which well fit our time series data; r, b, and d represent the per capita population growth, birth, and death rates of each population, respectively, and t represents experiment duration in days, with all vital rates having units of d^{-1}. We used data on total numbers of live and dead individuals of each taxon at the beginning and end of the first competition experiment to calculate r, b, and d rates for each competitor in each experimental container. Because there was no *Centroptilum* and *Gumaga* recruitment in treatments with these species, this collapsed to a calculation of d rates for *Gumaga*; however, because we also tracked emergence numbers for *Centroptilum*, we could partition population losses into per capita losses owing to emergence versus death for *Centroptilum*. Similarly, grazing impact or grazing rate indices in the short-term (2 d) grazing experiments were calculated as [ln (Chl a in control containers without grazers/Chl a in containers with grazers)]/[(time in days) × (number of grazers)], with final dimensions per grazer per day, and predation impact indices were calculated as [(ln (beginning *P. antipodarum* number/final *P. antipodarum* number)]/(time in days), with final dimensions per predator per day because a single predator was used in each trial. In the long-term grazing experiment with *P. antipodarum* and *Pyrgulopsis* in monospecific culture, grazer impact was calculated as [ln (chl a without grazers/chl a with grazers]/(grazer number) to obtain a per grazer impact index for the duration of the experiment. Contrary to typical calculations, we reversed the numerator and denominator of grazer or predator vs. control trial values in grazing and predation impact calculations, so that they would scale positively with increasing grazer or predator impact or feeding rates. Because the short-term grazing experiments used substitutive designs, we compared observed grazing impacts when *Potamopyrgus* was present with another competitor species to predicted grazing impacts derived from grazing rates when each species was alone, at the same total grazer density, weighted by the proportion of total grazer numbers comprised of each species. The means and indices of dispersion for predicted grazing rates were calculated using bootstrapping techniques, where random subsamples with replacement were taken from the population of all combinations of the weighted averages of the grazing rates of each species when alone, then compared to observed grazing rates in mixed culture using t tests. In the competition experiments, we also calculated competition coefficients as growth (r), birth (b), or death (d) rates when a competitor was alone—r, b, or d rates when competitors were added, including conspecific or heterospecific competitors, divided by the added number of competitors. Because the analysis of competition coefficients produced similar conclusions as the analysis of competitor treatment effects on r, b, and d rates, they are only briefly mentioned in the Results.

In examining the effects of *P. antipodarum and Anaxyrus* tadpoles, alone and together, on algal communities, we classified individual algal taxa by life form (unicells, colonies, filaments), taxonomy (diatoms, cyanobacteria, chlorophytes), and size (small = less than 10 μm, medium = 10–100 μm, large = > 100 μm) following Dussart (1965), Patrick & Reimer (1966), Hillebrand et al. (1999), Krammer & Lange-Bertalot (1986, 1988, 1991a, b), Kociolek & Stoermer (1993), and Potapova & Hamilton (2007). We then performed two-way ANOVAs using the population growth rates (r = ln (algal density at the end of the 27-day experiment/algal density at the beginning of the experiment)) for total algae and each algal group as dependent variables and algal culture type and tadpole-snail treatment (0T/0S, 5T/0S, 5T/100S, 0T/500S, 5T/500S), and their interaction, as independent variables. In all cases, the algal culture type X tadpole-snail treatment interaction effect was significant, so we then conducted analyses to determine the effects of competitor treatment on algal community structure for each algal culture type, independently. To examine the effects of competitor treatment on multivariate community structure for each algal culture type, we first performed non-metric multidimensional scaling (NMS) on the matrix of experimental containers by the relative abundances of algal taxa. We then examined the effects of competitor treatment on NMS axes scores, as well as on the population growth rates of total algae and each algal group, using one-way ANOVAs followed by Tukey's HSD tests. To interpret each NMS axis, we determined the percentage of multivariate community variation accounted for by each NMS axis and significant correlations between NMS axes and common (occurring in ca. 50% or more of samples) algal taxa. We also performed multiple response permutation procedures (MRPP) to examine the effects of competitor treatment on multivariate algal community distances between experimental containers.

Results

Population dynamics, life history in Piru Creek, and experimental effects of temperature

Potamopyrgus antipodarum populations reached their highest densities during the summer dry season and occurred at low densities during the winter wet season in Piru Creek (Figs. 2 and 3). Although juvenile (<2 mm) mud snails were collected throughout the year, they reached highest densities in late spring and early summer (Fig. 3). For both quadrat and core samples, there were no consistent differences in *Potamopyrgus* densities or size structure between riffles and pools, or between different substrata types, throughout the year, with the exception that *Potamopyrgus* densities in core samples, primarily the densities of large (>2 mm) *Potamopyrgus*, were higher in macroalgae than soft sediment substrata in riffles (paired t test, $t_{1,\ 10} = 2.3$, $P < 0.05$).

Because environmental variables were intercorrelated, it was difficult to disentangle the effects of different environmental variables on *Potamopyrgus* densities or per capita population growth rates. Piru

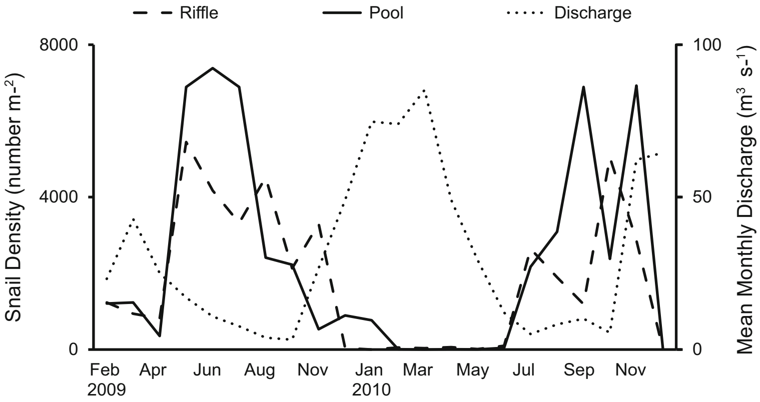


Fig. 2 Discharge (*dotted line*) and *Potamopyrgus* densities in riffles (*dashed line*) and pools (*solid line*), based on quadrat sampling, in Piru Creek from February 2009 to February 2011

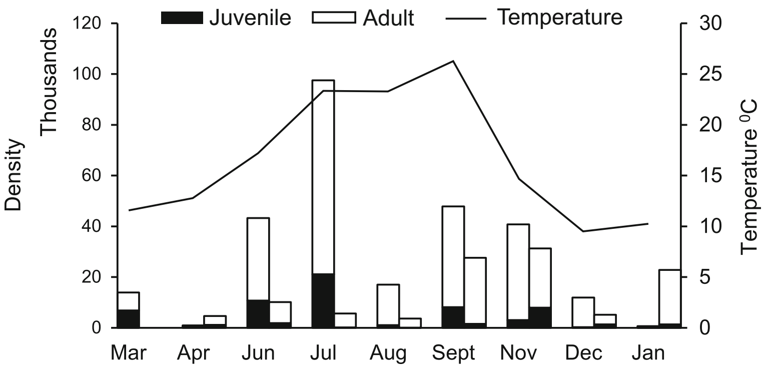


Fig. 3 *Potamopyrgus* densities (number m^{-2}, histograms), based on core sampling, and water temperature (*line*) from March 2009 through January 2010. Histograms are *shaded* to show densities of juvenile (<2 mm, *black*) and adult (>2 mm, *white*) *Potamopyrgus* on each date. For each date, the histogram on the *left* represents *Potamopyrgus* density for macroalgal substrata and the histogram on the *right* is *Potamopyrgus* density for soft sediment substrata. No data on snail densities were collected from soft sediment substrata in March 2009

Creek discharge was negatively related to conductivity ($r = -0.63$, $P < 0.05$), water temperature ($r = -0.76$, $P < 0.0001$), and total dissolved solids ($r = -0.70$, $P < 0.05$) and was positively related to current velocity in both riffles and pools (rs = + 0.87 and +0.72, both ps < 0.001), but was unrelated to pH ($n = 10$–22). Nevertheless, multiple backwards stepwise regression analysis consistently produced models containing only a negative relationship between log *Potamopyrgus* densities and log stream discharge for both quadrat and core samples from both riffles and pools (R^2s = 0.30–0.55, ps < 0.05 to < 0.001).

Although *Potamopyrgus* densities often had positive linear or quadratic relationships with water temperature, these relationships became non-significant when discharge was also entered as an independent environmental variable. For example, the relationship between log *Potamopyrgus* density and water temperature was best fit by a quadratic model, with snail densities peaking at around 17°C (Fig. 4). Only one (marginally) significant relationship was observed between *Potamopyrgus* population growth rates and water temperature, for riffle quadrat samples, and this relationship was also best described by a quadratic model (*Potamopyrgus* growth rate = 0.08 + 0.008* temperature−0.0015 temperature$^{2x;}$ * = $P < 0.05$, ^{x} = $P < 0.10$, peak at ca. 20°C). In the laboratory temperature experiment, *Potamopyrgus* individual growth rates were higher at 13 and 20°C than 27°C, whereas *Potamopyrgus* survival decreased as temperature increased from 13 to 27°C (Fig. 5).

Grazing trials and grazer effects on algal communities

In the first set of grazing trials, different grazer species (*Centroptilum* (Ce), *Pyrgulopsis* (Py), *Potamopyrgus* (Po), and *Physella* (Ph)) showed similar per capita grazing rates per day (no significant grazer species effect; means in monospecific culture ±1 *SE*: Ce $= 0.014 \pm 0.005$, Py $= 0.014 \pm 0.004$, Po $= 0.019 \pm 0.004$, Ph $= 0.008 \pm 0.006$; $n = 12$ per species). Grazing rates declined with increasing total grazer density, being higher at the lowest grazer density (5 per container) than at higher grazer densities (10, 15, 20 per container) (grazer density effect: $F_{1,82} = 17.6$, $P < 0.0001$; $5 > 10, 15, 20$ grazers per container, Tukey's HSD test, $P < 0.05$; Fig. 6a–c). In the second grazing trial, grazing rates of both *Gumaga* and *Potamopyrgus* were low and variable, and there were no significant effects of grazer species or total grazer density on grazing rates (Fig. 6d).

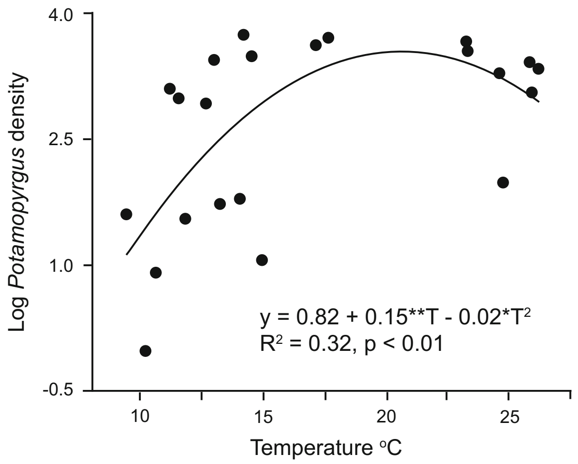


Fig. 4 The relationship between $\log_{10}$ *Potamopyrgus* density (from quadrat sampling) on hard, riffle substrata and water temperature. This relationship was best fit with a quadratic equation, which is shown along with the associated coefficient of determination and probability level. Significant equation terms are indicated as $** = P < 0.01$ and $* = P < 0.05$

At specific total densities, additive expectations based on grazing rates of each grazer species when alone differed from observed grazing rates when both species were together; however, the direction of these differences in expected and observed grazing rates varied with total density and grazer species combination. Observed grazing rates were lower than additive expectations at a total density of 10 grazers per container for *Potamopyrgus* and *Pyrgulopsis* when together and for *Potamopyrgus* and *Centroptilum* when together (Figs. 6a,b) and at a total density of 8 per container for *Gumaga* and *Potamopyrgus* (Fig. 6d) when together, but the reverse was observed at a total density of 10 per container when *Potamopyrgus* and *Physella* were together (Fig. 6c). In the *Physella*–*Potamopyrgus* trials, differences between observed and expected grazing rates were associated with large declines in *Physella* grazing rates from 5 to 10 *Physella* per container (see Fig. 6c).

In the longer-term experiment examining the impacts of *Pyrgulopsis* and *Potamopyrgus* in monospecific culture on algal biomass (as chlorophyll *a*), there were significant effects of species ($F_{1,20} = 3.5$, $P < 0.01$) and grazer density ($F_{1,20} = -4.2$, $P < 0.001$) on per capita grazer impacts, with a marginally significant species X density interaction effect ($F_{1,20} = -1.8$, $P < 0.10$). The interaction effect was owing to a significant difference between *Pyrgulopsis* and *Potamopyrgus* grazing impacts at a density of 10 snails per container, but not at other grazer densities (Fig. 7).

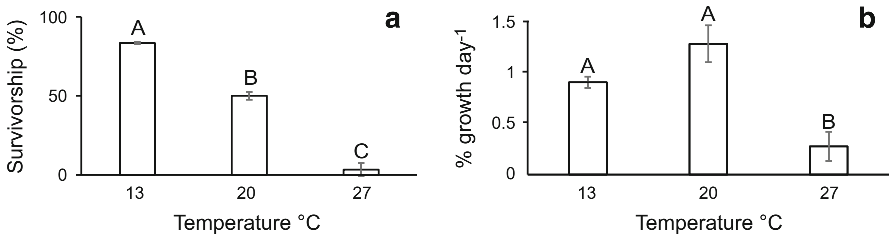


Fig. 5 Responses of *Potamopyrgus* survivorship (% over 70 days) and individual growth (as % length increment over initial length over 70 days) at three experimental temperatures (13, 20, 27°C). Histograms overlain by the same *letter* in each *graph* are not significantly different ($P > 0.05$, Tukey's HSD test)

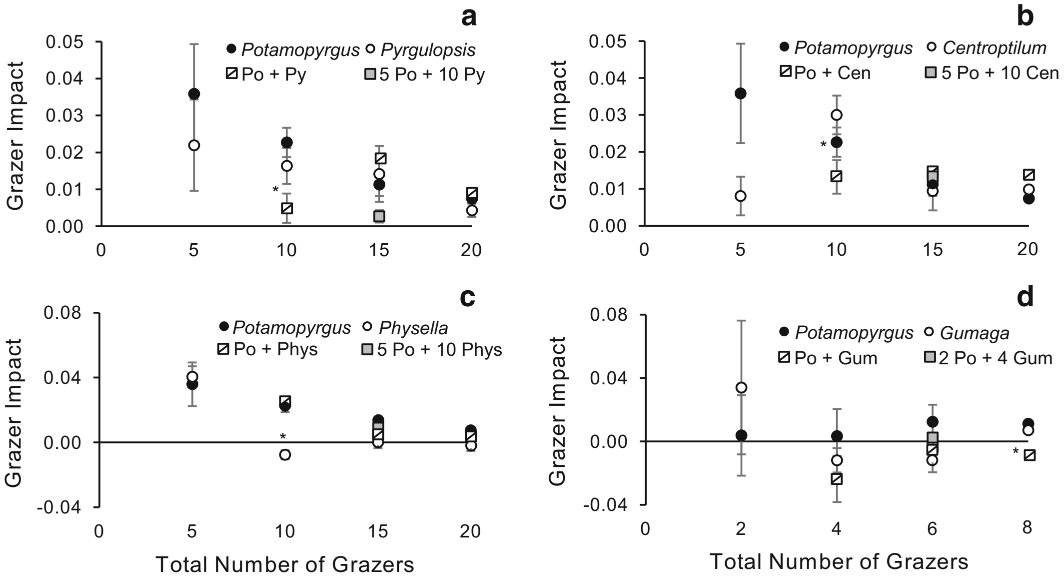


Fig. 6 Grazing impact ((ln (Chl *a* no grazers/Chl *a* with grazers))/grazers per container/time in days) of five grazer species (*Potamopyrgus* (Po), *Pyrgulopsis* (Py), *Physella* (Phys), *Centroptilum* (Cen), *Gumaga* (Gum)), both alone and with *Potamopyrgus*, across four total grazer densities (5, 10, 15, 20 per container for Py, Phys, and Cen, alone and with Po, and for Po alone; 2, 4, 6, 8 per container for Gum and Po alone and together). Values are means ± 1 SE. Grazer impacts for Po (*black circle*) and other grazers (*white circle*) alone are compared to values for species when together (*hatched square* for equal densities of Po and other grazer and for 2/3 Po and 1/3 other grazers at the third highest grazer density; gray square for 1/3 Po and 2/3 other grazers at third highest density). *Asterisks* denote significant differences between observed grazer impacts when different grazer species were together versus additive expectations based on grazer impacts when each species was alone (two-tailed $t_{1,4}$, > 3.0, * = $P < 0.05$)

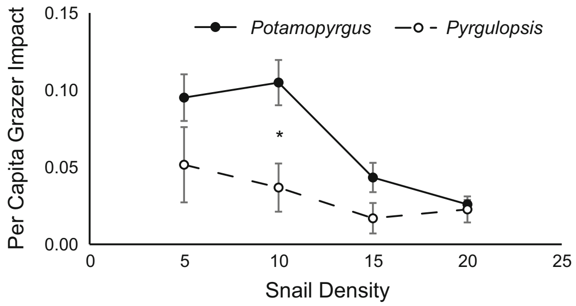


Fig. 7 Grazer impact (means ± 1 SE) per grazer for two snail species (*Potamopyrgus = black dots*, *Pyrgulopsis = white dots*) in monospecific culture across four snail densities (5, 10, 15, 20 per container) over a 17-day experiment. Asterisk denotes a significant difference between species at a snail density of 10 per container (ANOVA, $F_{1,4} = 10.4$, $P < 0.05$)

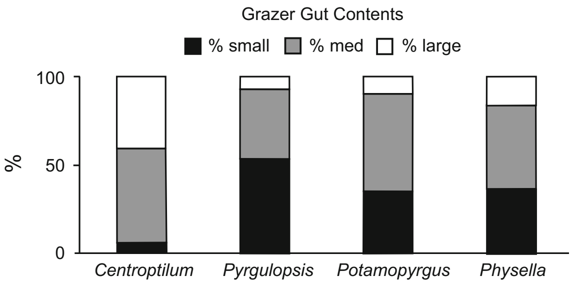


Fig. 8 Percentage contribution of different algal sizes (small, medium, large; see text) to the gut contents of four different grazer species (*Centroptilum*, *Pyrgulopsis, Potamopyrgus*, *Physella*) at the end of the first grazing experiment

Gut content analysis of grazers from the first set of grazing trials revealed differences in the diets of different grazer species (Fig. 8). Although all grazers consumed diatoms (97% of cells ingested), they differed in the sizes of diatoms eaten. *Centroptilum* consumed a greater proportion of large diatoms and a smaller proportion of small diatoms than *Pyrgulopsis*, *Potamopyrgus*, and *Physella* (P's < 0.05, Tukey's HSD test), whereas *Potamopyrgus* consumed a greater proportion of medium-sized diatoms than *Pyrgulopsis* ($P < 0.05$, Tukey's HSD), with *Physella* and *Centroptilum* consuming intermediate proportions of medium diatoms.

We also examined the long-term (27 days) impacts of western toad larval stages (tadpoles) and *Potamopyrgus antipodarum*, both alone and together, on algal community structure across three initial algal community types (dominated by diatoms, *Cladophora* or *Zygnema*). In general, the presence of tadpoles had little effect on algal community structure, but there were large changes in algal community structure with increasing *Potamopyrgus* densities. Further, because initial ANOVAs showed significant interaction effects of grazer treatment and algal community culture type on the population growth rates of different algal groups, we examined the effects of grazer treatment on algal growth rates for each algal culture type independently. Total algal population growth rates declining with increasing snail density in the *Zygnema* culture and were lowest in the 5 tadpole and 100 *Potamopyrgus* treatment in the diatom culture, but were unaffected by treatment in the *Cladophora* culture (Supplementary Materials Table 2). Percent cover by filamentous algae was not significantly different among grazer treatments in the *Cladophora* and *Zygnema* cultures (mean = 87 and 37%, respectively), but was affected by treatment in diatom culture, being significantly higher where *Potamopyrgus* was present (17%) than where it was absent (0%). Among algal categories, the population growth rates (r) of (1) diatoms and other unicellular algae declined with increasing *Potamopyrgus* density across all algal culture types, (2) colonial algae and cyanobacteria were lowest in the 5 tadpole/100 *Potamopyrgus* treatment in diatom culture but not affected by treatment in the other algal cultures, and (3) filamentous algae were highest in the 5 tadpole/500 *Potamopyrgus* treatment in *Cladophora* culture and lowest in the same treatment in *Zygnema* culture, and tended to decline with snail density in diatom culture. Regarding algal size categories, population growth rates of large algae tended to increase with increasing snail density in *Cladophora* culture, were lowest in the 5 tadpole/500 *Potamopyrgus* treatment in *Zygnema* culture, and were unaffected by treatment in diatom culture. Medium-sized algal rs declined with snail density in the diatom and *Zygnema* cultures, and small algal rs increased with snail density in the diatom culture and were higher in the 0 tadpole/500 snail treatment than 5 tadpole/500 snail treatment in the *Zygnema* culture (Supplementary Materials Table 2, all P's < 0.05, Tukey's HSD test). Growth rates of medium and small algae were unaffected by grazer treatment in the *Cladophora* culture.

Potamopyrgus treatments had significant effects on algal community structure in all algal culture types (MRPP test, As = 0.09–0.54, ts = −3.0 to −4.4, P's < 0.01 to < 0.001). Non-metric multidimensional scaling (NMS) on the matrix of the relative abundances of algal species across experimental containers in the diatom culture produced a two-dimensional solution with a stress of 0.005, with scores for both NMS axes being significantly affected by grazer treatment (Figs. 9a, b). The scores for NMS axis 1, which accounted for 76% of the variation in the multivariate dataset, were much greater at high snail densities than where snails were absent (Fig. 9a). Correlations between common algal species and NMS axis 1 scores indicated that high snail densities were associated with high relative abundances of the small, colonial, planktonic green alga *Ankistrodesmus falcatus* and low relative abundances of the medium-sized, filamentous cyanobacterium *Cylindrospermum* spp. and several medium to large benthic diatom species, with the reverse observed in containers where snails were absent (Fig. 9a). Algal taxa relationships with, and grazer treatment effects on, NMS axis 2 scores indicated that *Cladophora* and a number of benthic diatom species showed greatest relative abundances in the 5 tadpole/100 snail than other treatments, and that the relative abundances of these algal taxa also were higher at the highest snail densities than where snails were absent (Fig. 9b). For algal data from the *Cladophora* culture, the two-dimensional NMS solution had a stress of 8.7, with scores for only NMS axis 1, which accounted for 82% of the variation in the multivariate dataset, being significantly affected by grazer treatment (Fig. 9c). Correlations between algal species and NMS axis 1 scores indicated that containers containing snails had higher relative abundances of *Cladophora* and lower relative abundances of the filamentous diatom *Melosira varians* and a number of unicellular, medium-sized benthic diatoms than containers lacking *Potamopyrgus* (Fig. 9c). Finally, for the algal data from the *Zygnema* culture, the two-dimensional NMS solution had a stress of 12.1, with significant grazer treatment effects on only NMS axis 1, which accounted for 47% of the variation in the multivariate dataset (Fig. 9d). Associations between the relative abundances of algal species and NMS axis 1 scores indicated that the filamentous green algae

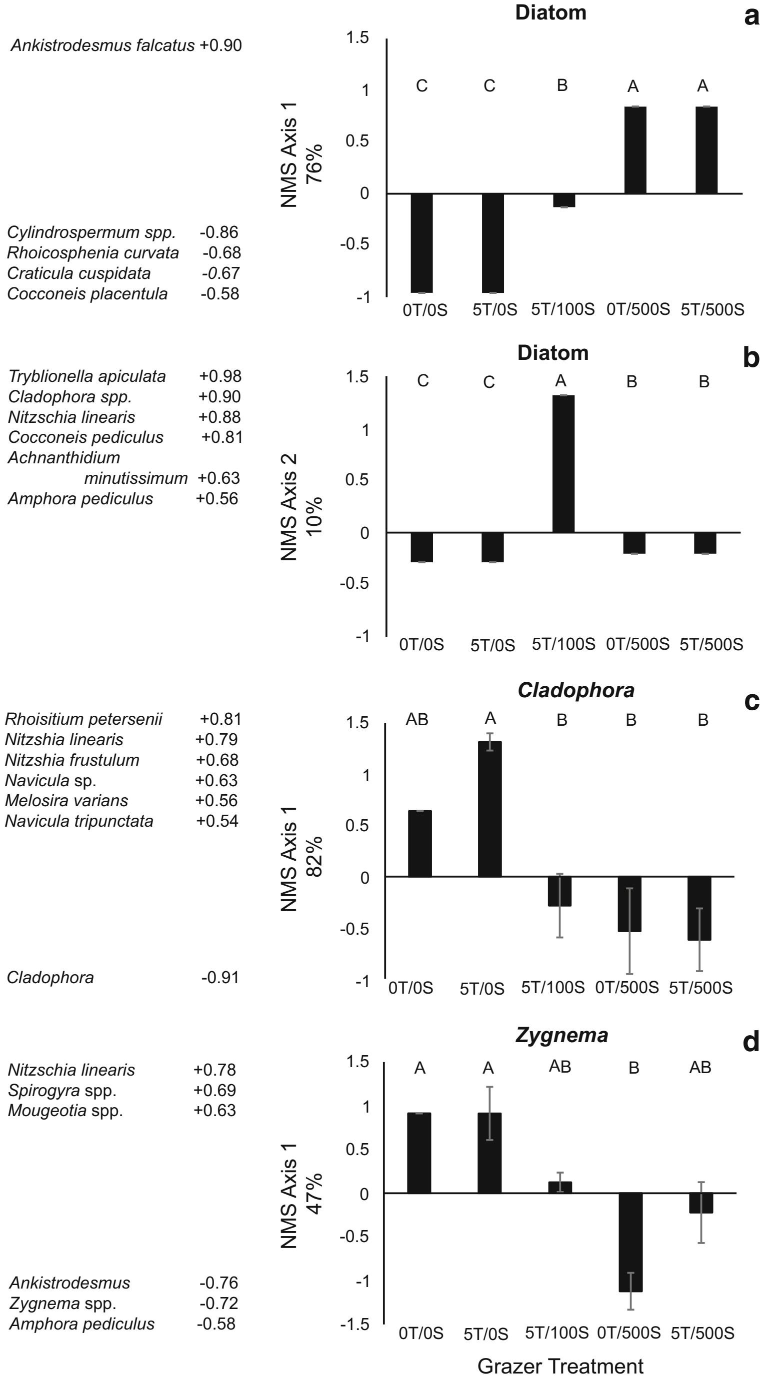


Fig. 9 Mean NMS axis scores (± 1 SE) significantly affected by grazer treatment in the tadpole and *Potamopyrgus* experiment. For each algal culture type (diatoms, *Cladophora*, *Zygnema*) a NMS was conducted on the matrix of experimental containers by the relative abundances of algal species. Final stresses for two-dimensional NMS solutions were: diatom culture = 0.005, *Cladophora* culture = 8.7, *Zygnema* culture = 12.1. Grazer treatments were 0 tadpoles/0 snails (0T/0S), 5 tadpoles/0 snails (5T/0S), 5 tadpoles and 100 snails (5T/100S), 0 tadpoles and 500 snails (0T/500S), and 5 tadpoles and 500 snails (5T/500S). The percentage of the overall variation in the multivariate dataset accounted for by each NMS axis and the algal species significantly ($P < 0.05$, Pearson's r) correlated with each axis are shown. In each *graph*, *bars* overlain by the same *letter* are not significantly different ($P > 0.05$, Tukey's HSD test)

Spirogyra and *Mougeotia* and the medium-sized benthic diatom *Nitzschia linearis/gracilis* had higher relative abundances, while *Ankistrodesmus*, the filamentous green alga *Zygnema*, and the small benthic diatom *Amphora pediculus* had lower relative abundances, where snails were absent than where they occurred at high densities (particularly in the 0 tadpole/500 snail treatment, Fig. 9d). In general, these collective results suggest that *Potamopyrgus* reduces filamentous cyanobacteria, a variety of medium and large benthic diatoms, and the green filamentous algae *Spirogyra* and *Mougeotia*, depending on initial algal conditions, while increasing the relative contributions of small colonial planktonic (*Ancistrodesmus*) and large filamentous benthic green algae (*Cladophora*, *Zygnema*).

Competition experiments

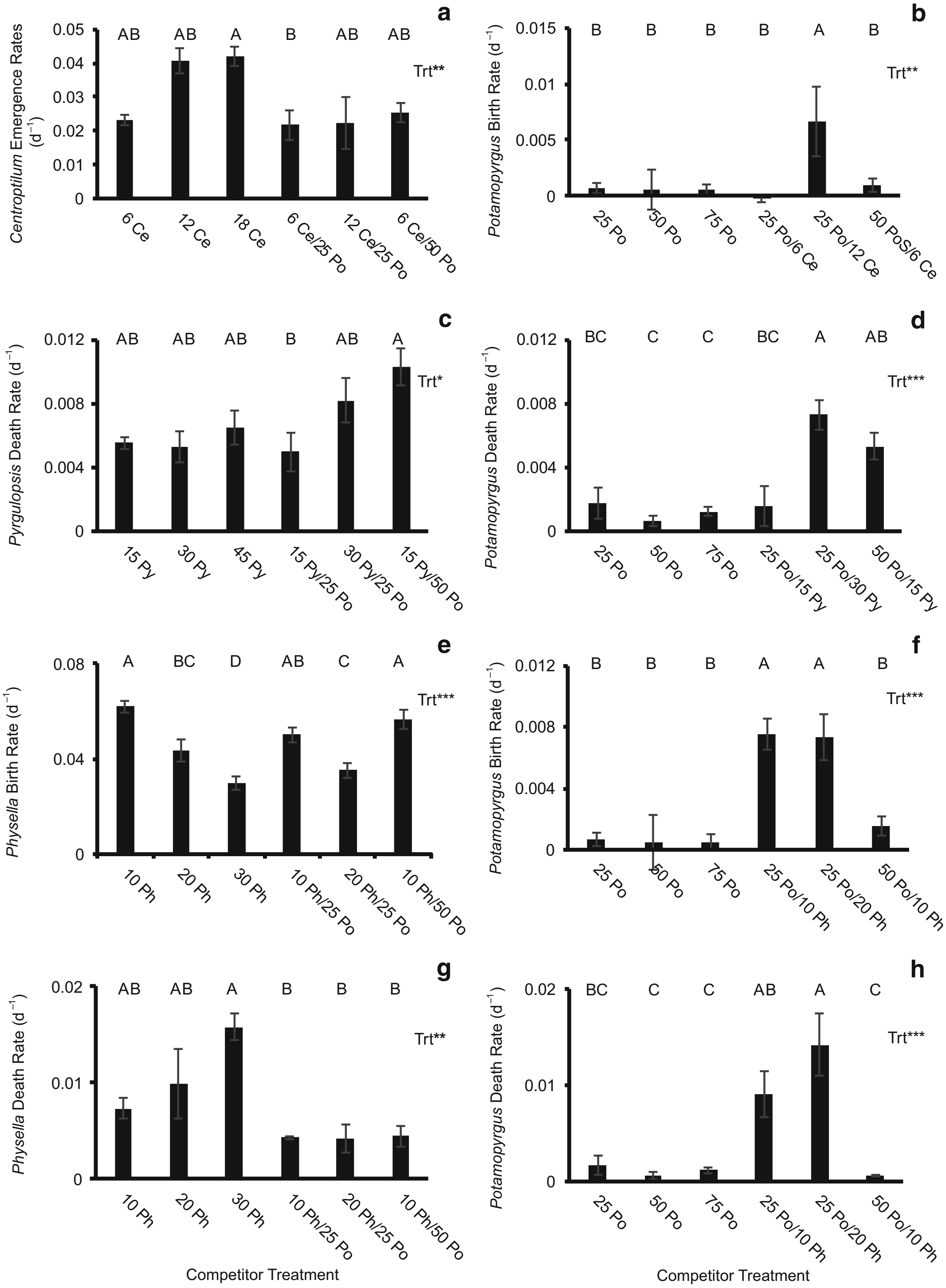
The competition experiments revealed large differences in the birth and death rates of different competitor species, with *Physella* having much higher vital rates ($b = 0.045$ and $d = 0.011$) than *Pyrgulopsis* (0.002, 0.006) and *Potamopyrgus* (0.0006, 0.0012). There was no recruitment to *Gumaga* and *Centroptilum* populations and no *Gumaga* emergence during the experiment. *Gumaga* showed little mortality and remained at constant densities throughout the experiment, whereas *Centroptilum* densities had declined to 0 in most containers by the end of the experiment, owing to emergence and death.

There were no effects of competitor treatments on the population growth (r) and death (d) rates of *Gumaga* and *Potamopyrgus* when these two species were manipulated alone and together. Death rates of *Centroptilum* and *Potamopyrgus* also were unaffected by competitor treatment, but *Centroptilum* per capita emergence rates were higher at the highest monospecific *Centroptilum* density than in the 6 *Centroptilum*/25 *Potamopyrgus* treatment (Fig. 10a). Orthogonal contrasts showed that *Centroptilum* emergence rates were higher in containers where *Potamopyrgus* was absent than where it was present ($F_{1,16} = 8.1$, $P < 0.02$). On the other hand, *Potamopyrgus* birth rates (b) were higher in the 25 *Potamopyrgus*/12 *Centroptilum* treatment than in other treatments (Fig. 10b).

The most intense competitive and facilitative interactions, however, were observed among the snail species. Orthogonal comparisons showed that *Pyrgulopsis* r and b rates ($F_{1,16} = 11.4$ and 10.6, $P < 0.005$ in both cases) were higher and that d rates were marginally lower ($F_{1,16} = 3.4$, $P < 0.10$) where they were alone than with *Potamopyrgus*, whereas *Potamopyrgus* death rates were higher and growth rates lower, where *Pyrgulopsis* was present versus absent ($F_{1,16} = 11.6$ and 7.2, $P < 0.005$ and <0.02). Further, in the *Pyrgulopsis*–*Potamopyrgus* experiment, significant treatment effects were found on *Pyrgulopsis* r and d rates and on *Potamopyrgus* d rates, with d rates tending to be highest at the highest density of heterospecific competitor (Figs. 10c,d). Significant competitor treatment effects also were found in the *Physella*–*Potamopyrgus* experiment with orthogonal comparisons showing significant negative effects of *Potamopyrgus* on *Physella* death rates (facilitation) and significant positive effects of *Physella* on *Potamopyrgus* birth and death rates ($F_{1,16} = 8.8$–15.6, $P < 0.01$ to < 0.005; Figs. 10f–h). *Physella* b rates were strongly, negatively affected by its own densities (Fig. 10e). In examining per capita competition coefficients, *Physella* had the largest competitive effect on its own growth and birth rates and *Physella* had positive per capita effects on both the b (facilitative) and d (competitive) rates of *Potamopyrgus*, translating into little net effect on *Potamopyrgus* population growth rates.

Fig. 10 Effects of competitor treatments on the emergence rate ▶ of *Centroptilum* (Ce) (**a**) in the *Centroptilum*–*Potamopyrgus* experiment, on the birth rates of *Potamopyrgus* (Po) in the *Centroptilum*–*Potamopyrgus* experiment (**b**) and of *Physella* (Ph) (**e**) and *Potamopyrgus* (**f**) in the *Physella*–*Potamopyrgus* experiment, and on the death rates of *Pyrgulopsis* (Py) (**c**) and *Potamopyrgus* (**d**) in the *Pyrgulopsis*–*Potamopyrgus* experiment and of *Physella* (**g**) and *Potamopyrgus* (**h**) in the *Physella*–*Potamopyrgus* experiment. All vital rates have units of d^{-1}. Treatment code *letters* represent grazer species, as outlined in the first sentence of this legend, and grazer numbers (number per container). Trt denotes the effects of competitor treatment on competitor vital rates (ANOVA: * = < 0.05, ** = < 0.01, *** = < 0.001). *Bars* overlain with the same *letter* in each *graph* are not significantly different ($P > 0.05$, Tukey's HSD test)

In the tadpole–*Potamopyrgus* competition experiment, there were no effects of *Potamopyrgus* density on tadpole individual growth rates across algal culture types, but there was a significant algal type X snail density interaction effect on tadpole survivorship (Fig. 11b). Tadpole survivorship declined with increasing *Potamopyrgus* density and was lower in *Cladophora* than other algal cultures at *Potamopyrgus* densities of 0 and 500 per container. There were no effects of algal culture type on snail population and individual growth rates, and the proportions of snail populations that were dead or composed of small individuals (Fig. 12). On the other hand, the individual growth rates and proportions of populations composed of small individuals for *Potamopyrgus* were higher in the 5 tadpole/100 snail treatment than in the 0 tadpole/



500 snail treatment (Figs. 12b,c). The proportions of snail populations that were composed of small individuals and snail population growth rates were positively correlated ($r = +0.54$, $P < 0.005$, $n = 27$), indicating that higher growth rates translated into higher reproductive rates. The proportions of snail

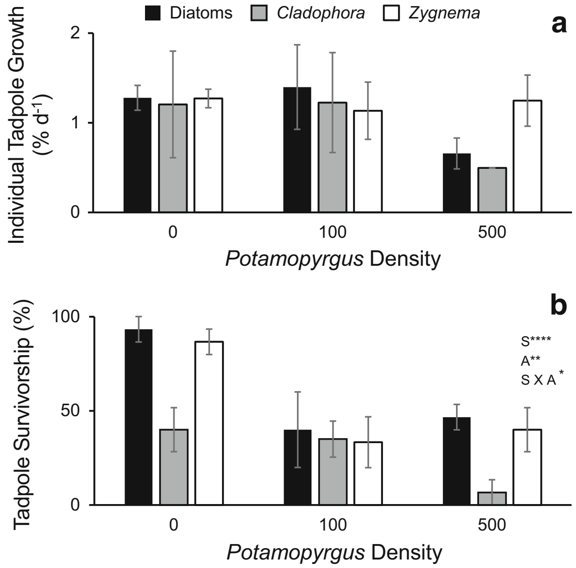


Fig. 11 Effects of algal culture type (dominated by diatoms, *Cladophora, Zygnema*) and *Potamopyrgus* density (number per container) on the percentage individual growth (length increment divided by initial length × 100) and percentage survivorship (over 27 days) of *Anaxyrus boreas* tadpoles. The note in the *bottom graph* indicates significant effects of snail density and algal culture type ($**** = P < 0.001$ and $** = P < 0.01$), and a marginally significant effect of their interaction ($* = P < 0.10$), on tadpole survivorship (two-way ANOVA)

populations that were dead were significantly higher in the 0 tadpole/500 snail and 5 tadpole/500 snail treatments than in the 5 tadpole/100 snail treatment, indicating that *Potamopyrgus* mortality rates increased with increased *Potamopyrgus* density (Fig. 12d).

Predation trials

Large crayfish (*Procambarus clarkii* >10 cm) had the highest predation rates on New Zealand mud snails followed by medium *Procambarus* (5–10 cm), the dragonfly *Aeshna walkeri*, and small *Procambarus* (<5 cm) (Fig. 13). The damselfly *Argia vivida* also had predator impact indices significantly different from zero, but other taxa only consumed mud snails sporadically (*Protochauliodes*, *Cordulegaster dorsalis*, *Octogomphus specularis*, *Notonecta hoffmanni*, *Drunella* sp., *Paltothemis lineatipes*) or not at all (*Rhyacophila* sp., *Isoperla* sp., *Lepidostoma* sp. *Gumaga nigricula*). Some of the predators that consumed substantial numbers of mud snails were size-selective, with *Argia* naiads, for example, largely consuming small (<2 mm) and medium-sized (2–4 mm) snails, but not large snails (>4 mm) (paired t tests on proportions consumed, small $\sim$ medium > large, two-tailed $t_{1,19} = -4.1$ and -4.4, P's < 0.001). Predator impact indices for small *Procambarus* were significantly higher for small (<2 mm) than large (>2 mm) snails, but medium and large *Procambarus* preyed preferentially on large snails (paired t test for medium and large crayfish combined, large snails > small snails, two-tailed $t_{1,5} = -9.7$, $P < 0.001$) (Fig. 14). On the other hand, *Aeshna* naiads preyed on all snail size classes at similar rates.

Discussion

The success and impacts of an invasive species in a new environment depend on its capacity to tolerate novel ecosystem conditions and then attain abundances that alter trophic relationships and/or disturbance regimes (Vitousek et al., 1997). *Potamopyrgus antipodarum* has become established in a wide variety of freshwater and estuarine habitats on four continents, including aquatic systems in mediterranean climates (Ponder, 1988; Alonso & Castro-Diez, 2008, 2012). Although *P. antipodarum* is present in some waterways in California, its impacts are largely unknown and management prescriptions are uncertain (ANS, 2007; Davis and Moeltner, 2010; Brenneis et al., 2011; Moore et al., 2012). To address this knowledge gap, we used a combination of field monitoring and laboratory experiments to evaluate *P. antipodarum* dynamics in a southern California stream and its potential impacts on the native stream biota.

Population dynamics and abiotic regulation of life cycles

Invasive *P. antipodarum* can achieve extremely high densities during summer months in some temperate streams, which has been attributed to the high primary production, stable discharge, and benign summer temperatures found in invaded habitats (Richards et al., 2004; Hall et al., 2006; Kolosovich et al., 2012). In most temperate streams, life cycles are marked by high summer reproductive and growth rates, but little or no production during the winter, presumably owing to low temperatures (Moffitt &

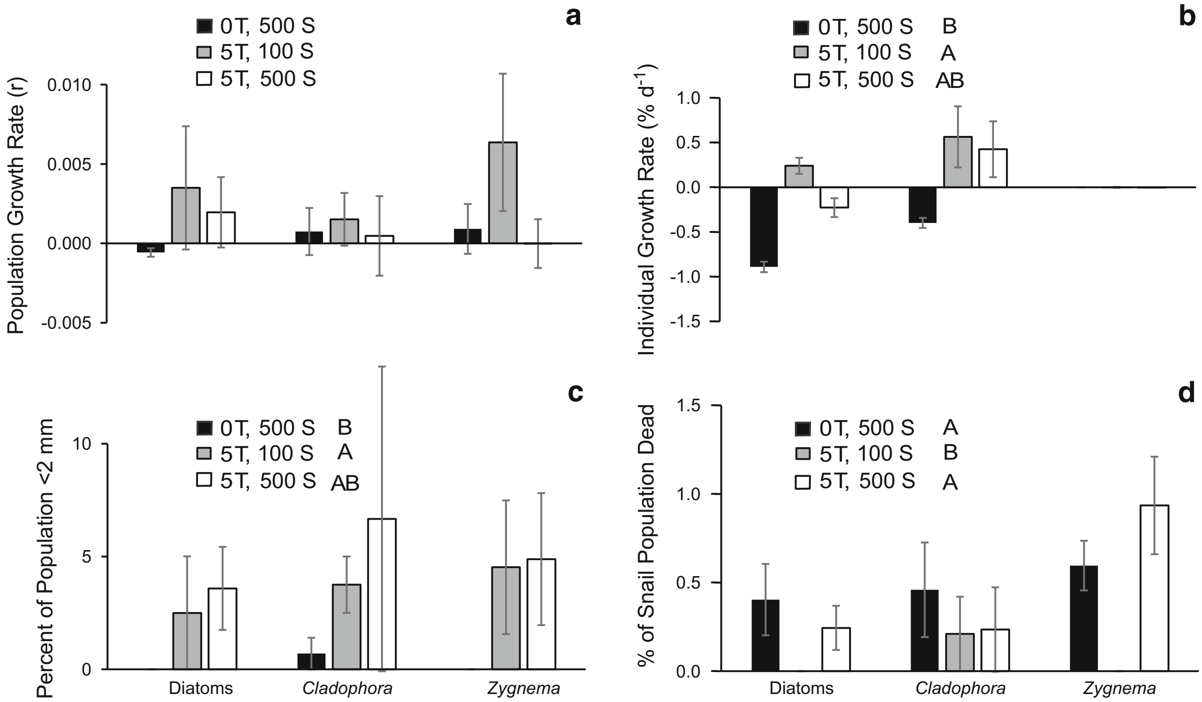


Fig. 12 Effects of competitor treatment (0 tadpoles/500 *Potamopyrgus* (0T/500S), 5 tadpoles/100 *Potamopyrgus* (5T/100Po), 5 tadpoles/500 *Potamopyrgus* (5T/500S)) and algal culture type (diatoms, *Cladophora*, *Zygnema* dominated) on the population and individual growth rates, percentages of populations composed of individuals <2 mm, and percentages of populations that were dead for *Potamopyrgus*. *Heights* of *bars* are means ± 1 *SE*. Algal type had no effect on *Potamopyrgus* responses, but competitor treatment did, as indicated by the *letters* next to the competitor treatment code. For each response variable, competitor treatments with the same following *letter* were not significantly different ($P > 0.05$, Tukey's HSD tests)

James, 2012). In our southern California study stream, *P. antipodarum* populations reached densities as high as 150,000 individuals/m^2 in late spring and summer, but growth and reproduction declined in the winter. In contrast to studies in other temperate regions, some reproduction was observed in winter, presumably because water temperatures remained above 9°C. Population dynamics reflected stream discharge patterns with declines in abundance being associated with winter floods. Although *P. antipodarum* thrives in thermally stable streams with moderate flow variability (Cox & Rutherford, 2000), flow rather than thermal regimes largely drove *P. antipodarum's* dynamics in Piru Creek, consistent with previous results (Holomuzki & Biggs, 1999; Holomuzki & Biggs, 2006; Sepulveda & Marczak, 2011). Most Californian streams known to support high abundances of *P. antipodarum* are at least partially regulated with relatively stable discharge patterns, so we postulate that flashy, unregulated streams in mediterranean climates may be at lower risk for *P. antipodarum* invasion than regulated streams.

In addition, *P. antipodarum* population densities declined during low flow periods in August, when temperatures exceeded 20°C. Population densities tended to peak between 15° and 20°C, congruent with our laboratory results showing that growth rates and survivorship declined as temperatures approached 27°C. Studies in other regions reported *P. antipodarum* at temperatures ranging from 0 to 34°C, with population growth rates falling below ca. 12°C and above 25°C (Cox & Rutherford, 2000; Dybdahl & Kane, 2005; Cejka et al., 2008). Because temperatures are benign during southern California's winters, *P. antipodarum* shows lower seasonality in growth and reproduction, near-continuous reproduction with indistinct cohorts, and greater annual production than in other temperate regions (Evans, 2012).

In Piru Creek, *P. antipodarum* densities were similar in pools and riffles, and on hard versus soft

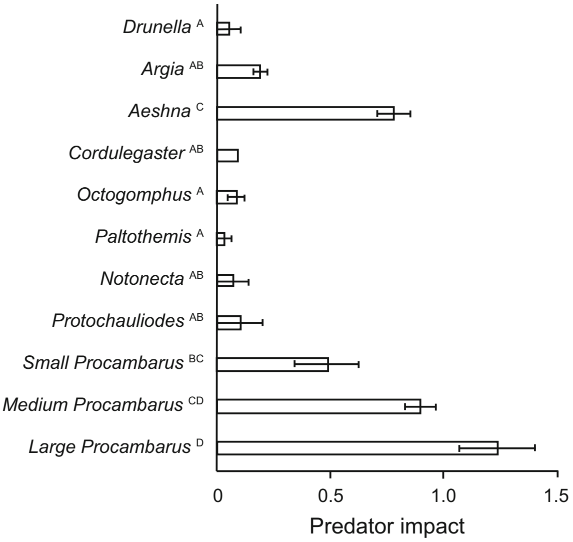


Fig. 13 Predator impact indices (means ± 1 *SE*, per predator per day) for different invertebrate taxa and, in the case of *Procambarus clarkii*, different predator size classes. Invertebrate taxa with the same following *alphabetical letters* were not significantly different ($P > 0.05$, Tukey's HSD test)

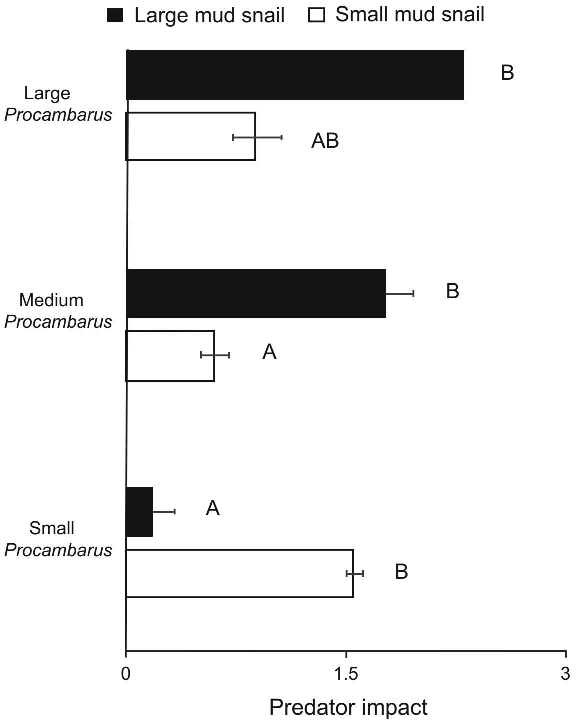


Fig. 14 Size-selective predation on *Potamopyrgus* by different size classes of *Procambarus clarkii*. Predator impact indices (means ± 1 *SE*) are shown for each predator size class feeding on each of two *Potamopyrgus* size classes (small = < 2 mm, *black bar*; large = > 2 mm, *white bar*). Different *letters* next to *bars* for each predator size class indicate significant differences in predator impact on different snail size classes

substrata. On the other hand, *P. antipodarum* was most abundant in filamentous algae, primarily *Cladophora glomerata*, and juveniles were found during peak reproduction periods primarily on macroalgae. Suren (2005) similarly found that *P. antipodarum* showed a preference for filamentous green algae. *Cladophora* provides increased surface area, reduced flow conditions, and microhabitat and epiphytic resources for many stream invertebrates (Dudley et al., 1986a, b; Dudley, 1992), perhaps accounting for the increased abundance of *P. antipodarum* in macroalgal habitats.

Beyond these relationships with macroalgae, stream discharge and, perhaps, temperature, no other environmental variables were associated with *P. antipodarum* densities. The conductivities recorded in Piru Creek (>447 µS/cm) were far higher than those proposed to limit *P. antipodarum*'s distribution and abundance (Herbst et al., 2008) and similar to the conductivities recorded in other streams with high *P. antipodarum* densities (Hall et al., 2003, 2006; Kerans et al., 2005).

Grazing effects

Potamopyrgus antipodarum is an opportunistic feeder on fine detritus and microalgae (James et al., 2000; Broekhuizen et al., 2001; Suren, 2005). Given its potential to achieve very high densities, we anticipated that snails would alter algal composition, biomass, and production, with indirect impacts on native grazer species. Prior results have been mixed, however, with some studies showing substantial reductions in primary producers (Hall et al., 2003; Cada, 2004) and changes in algal assemblage composition (Arango et al., 2009), and others showing little impact on algal resources (Welch et al., 2000; Murria et al., 2008; Riley et al., 2008). In our controlled studies, *P. antipodarum* significantly reduced algal biomass at per capita rates comparable to those of native insect and snail grazers. Grazing rates were highest at low grazer densities and declined as grazer density increased. The net impacts of *P. antipodarum* on algal levels were generally low, perhaps owing to grazer excretion of ammonium which would stimulate algal growth (Dorgelo & Leonards, 2001; Riley, 2002). One study also suggested that *P. antipodarum* impacts on algae were modest because of its low energetic requirements and morphological specialization for low profile, adnate algae (Broekhuizen et al., 2002). Conversely, others have reported that high densities of *P. antipodarum* consumed 75% of gross primary production and significantly altered nitrogen dynamics and food web structure (Hall et al., 2003, 2006). In our studies, we found little evidence that *P. antipodarum* has higher grazing rates or can more efficiently convert food to biomass than do native grazers (but see Aberle et al., 2005).

Dietary analysis showed some differences in the algae ingested by different grazers. Nymphs of the mayfly *Centroptilum* consumed a greater proportion of medium-sized and large diatoms than did snails. Although the snail species had similar diets, *P. antipodarum* ingested a greater proportion of medium-sized diatoms than *Pyrgulopsis*, which favored small diatoms. Despite some evidence for slightly different food habits, grazing rates of different grazer species when together were sometimes lower than those predicted from grazing rates when each species was alone. These results for *Potamopyrgus* with *Pyrgulopsis*, *Centroptilum*, or *Gumaga* could be attributed to interference between species, a contention supported by Kerans et al.'s (2010) observations of mutual interference between *P. antipodarum* and baetid mayflies. They also found that *Brachycentrus*, a filter-feeding caddisfly larva, reduced the use of tile surfaces by *P. antipodarum*, illustrating that interference interactions can occur between species with different feeding modes or food habits (Dudley et al., 1990), similar to what we observed between *Gumaga*, a consumer of macroalgae and detritus (Feminella et al., 1989), and *P. antipodarum* at high densities.

In our studies, high densities of *P. antipodarum* altered the composition and physiognomy of algal assemblages consistently reducing the abundances of larger unicellular diatoms and several soft-tissue filamentous taxa including cyanobacteria (e.g., *Cylindrospermum*), green algae (e.g. *Spirogyra*, *Mougeotia*,), and the colonial diatom, *Melosira varians* (Holomuzki & Biggs, 2006; Arango et al., 2009). On the other hand, the relative and absolute abundances of tough macroalgae, such as *Cladophora* and *Zygnema*, increased with increasing *P. antipodarum* density, presumably by snails removing epiphytic diatoms which can compete with host algae for common resources (Dudley, 1992). Explanations for increases in planktonic *Ankistrodesmus* with increasing *P. antipodarum* densities are more problematic, but also could involve nutrient regeneration by the snails. We conclude that high densities of *P. antipodarum* have substantial effects on algal assemblages, but that those effects will depend on the structure of the primary producer community and the relative importance of snail effects mediated through direct feeding versus nutrient regeneration.

Grazer–Grazer interactions

Literature results indicate that the effects of *P. antipodarum* on native grazers can range from reductions (Richards, 2004; Kerans et al., 2005, 2010; Murria et al., 2008; Riley et al., 2008; Schmidlin et al., 2012) to little or no impact (Cada, 2004; Brenneis et al., 2010) to increases in native grazer densities (Schreiber et al., 2002; Cope & Winterbourn, 2004). In our study, *P. antipodarum* competitive impacts depended on the identity and density of competitors. *P. antipodarum* and *Gumaga* had no effects on each other's vital rates, presumably because they had different diets. *Centroptilum* mayflies have greater dietary overlap with *P. antipodarum* and, as expected, showed reduced per capita emergence rates when *P. antipodarum* was present, but this could be attributed to both interference and exploitative competition (Kerans et al., 2010). Conversely, *P. antipodarum* birth rates were greatest at high mayfly densities, presumably because dead mayflies augmented *P. antipodarum* food supplies either directly or via nutrient regeneration leading to enhanced algal growth.

Competitive interactions between *P. antipodarum* and native snails, particularly with the hydrobiid *Pyrgulopsis*, were expected to be intense owing to similarity in their diets. The death rates of both *P. antipodarum* and *Pyrgulopsis* were higher and birth rates of *Pyrgulopsis* were lower, at the highest densities of the heterospecific competitor, indicating competition between these species. Riley et al. (2008) reported that *P. antipodarum* and native *Pyrgulopsis robusta* reduced periphyton to the same degree, but that the introduced snail depressed the population growth of the native species, consistent with our results, and that the native species promoted the growth of *Potamopyrgus*, contrary to our results. Riley et al. (2008) suggested that these asymmetrical interactions accounted for the dominance of the exotic species where it was present and the restriction of native *Pyrgulopsis* to reaches without *Potamopyrgus*.

We also observed complex interactions between *P. antipodarum* and *Physella* not readily explained by overlap in their food habits or microhabitat use. *Physella* increased both the birth and death rates of *P. antipodarum* at intermediate densities, but *Physella* mortality declined in the presence of *P. antipodarum*. Furthermore, *Physella* had the greatest negative impacts on its own feeding, birth, and population growth rates, and greatest positive effect, when alone, on its own death rates. Previous studies indicated that *P. antipodarum* had weak competitive interactions with other native gastropods in New Zealand, but that it enhanced the growth and fecundity of the introduced *Physella acuta* (Cope & Winterbourn, 2004).

Interactions between *P. antipodarum* and *Anaxyrus boreas* larvae (western toad tadpoles) were also complex. Over two months, tadpoles had little effect on algal community structure, but high *Potamopyrgus* densities reduced the abundances of medium to large diatoms and soft filamentous taxa while promoting the growth of filamentous *Cladophora*. Tadpole development tended to be slowed by high *P. antipodarum* densities, particularly when fed *Cladophora* and diatom food sources, although this trend was not statistically significant. On the other hand, tadpole survivorship decreased with increasing *P. antipodarum* density and was lower with *Cladophora* than other food types. In general, then, *P. antipodarum* appeared to negatively affect tadpole survivorship by facilitating inedible *Cladophora* growth, which also inhibited tadpole movement, and reducing the growth rates of edible algae. Conversely, *P. antipodarum* individual growth, reproductive, and death rates were related more strongly to their own densities than to the presence of tadpoles. Competitive interactions between snails and tadpoles have been documented in other systems (e.g., Holomuzki & Hemphill, 1996; Smith et al., 2012). These results carry management implications because Piru Creek provides critical habitat for the endangered arroyo toad, (*A. californicus*); a congener of the western toad also present in this system. Because high *P. antipodarum* densities can reduce edible algae while enhancing *Cladophora* cover in the sand-silt feeding habitats of arroyo toad tadpoles (Sweet & Sullivan, 2005), they may affect arroyo toad populations, posing problems for the management of this species.

Interactions with predators

The introduction of a new species into an ecosystem can provide a new food resource for secondary consumers (predators) and alter predator–prey relationships, and native or non-native predators may inhibit the establishment and expansion of introduced species, sometimes below thresholds of management concern (ANS, 2007; Dzialowski, 2007; Ricciardi & MacIsaac, 2011; Montserrat et al., 2012; Twardochleb et al., 2012). Because of the possible importance of predators in regulating the population growth of invasive species, we examined the potential for non-native crayfish (*Procambarus clarkii*) and a variety of native insects to consume *P. antipodarum*. Crayfish were the most effective predators on *P. antipodarum*, with small individuals (<5 cm) consuming primarily small snails (<2 mm) and larger (>5 cm) crayfish consuming large snails (>2 mm). Other studies have shown that crayfish can consume *P. antipodarum* at high rates, with the signal crayfish, *Pacifastacus leniusculus*, consuming over 900 snails in 12 h (Twardochleb et al., 2012; also see Brenneis et al., 2011).

Predatory insects, namely naiads of the dragonfly *Aeshna walkeri* and the damselfly *Argia vivida*, consumed snails at significant rates, in the case of *Aeshna* at rates comparable to those for small crayfish. *Aeshna* is a large-bodied, active predator found in stream pools, whereas *Argia* is found primarily in slow-flowing sections of small and medium-sized streams, a microhabitat favored by the snail. *Argia* also can be found in macroalgal mats and prefers small snails, so may pose a predatory bottleneck for developing *P. antipodarum*. Although not addressed in this study, fish impacts on *P. antipodarum* populations in southern California are likely to be minimal, either because fish are uncommon in many *P. antipodarum* habitats or because fish rarely ingest and often cannot digest *P. antipodarum*, obtaining little nutritional benefit from this invasive species (Haynes et al., 1985; Cada, 2004; Bersine et al., 2008; Vinson & Baker, 2008; Brenneis et al., 2011). Generalist predators are often poor regulatory agents for invasive species, so the control of *P. antipodarum* populations may require introduction of specialized parasites, such as the trematode *Microphallus*, which infects *P. antipodarum* in its native habitat (Winterbourn, 1970; Jokela & Lively, 1995; Dybdahl et al., 2005; Hechinger, 2012).

The New Zealand mud snail as an invasive species

P. antipodarum has successfully invaded aquatic ecosystems in many regions of the world, engendering concern from conservationists, water managers and wildlife protection agencies (Ponder, 1988; ANS, 2007; Davis & Moeltner, 2010). Of particular concern is that this invasive species is capable of achieving very high densities (Hall et al., 2006), with possible impacts to fisheries via reductions in the quantity and quality of fish food resources (Vinson & Baker, 2008). As a consequence, considerable effort has been devoted to preventing its establishment and spread, although success may be low because this species is already widespread and easily dispersed (Richards et al., 2004; California Department of Fish and Game, 2005).

Potamopyrgus antipodarum possesses a number of traits (Kolar & Lodge, 2001) that make it an effective invader, including early reproductive maturity, high dispersal and population growth rates, phenotypic plasticity and tolerance of a broad range of environmental conditions. It also uses a variety of food types and benefits from humans as dispersal vectors. Although fecundity for this ovoviviparous species is low (ca. several dozen embryos per female (Richards, 2002)), *P. antipodarum*'s ability to reproduce parthenogenetically and produce multiple generations in a season enables high population growth under suitable conditions. Furthermore, by attenuating peak flows in streams and rivers, humans create conditions conducive to the establishment of non-native species not adapted to flashy hydrographs (Baltz & Moyle, 1993).

The reasons for the invasion success of *P. antipodarum* have been reviewed by Alonso & Diez-Castro (2008), but we lack guidelines for determining when its impacts reach levels necessitating control efforts (National New Zealand Mudsnail Conference, 2011). Our experimental results indicate that *P. antipodarum* and native grazing invertebrates affect primary producers and consumers in similar ways under laboratory conditions. Because these experiments often dealt with two trophic levels or pairs of species, it is not clear how *P. antipodarum* will affect stream communities with multiple trophic levels and many species (Murria et al., 2008).

The impacts of *P. antipodarum* invasion on stream communities in this region may be short in duration, because *P. antipodarum* populations reached high levels in Piru Creek for fairly brief periods owing to the effects of periodic high flow events. Accumulating evidence (Hall et al., 2006, Moore et al., 2012) also indicates that *P. antipodarum* may exhibit the 'boom-bust' population dynamics observed in numerous invasive species populations, with initially high densities during early establishment followed by a decline to more moderate, sustained levels (Simberloff & Gibbons, 2004). Recent surveys of Piru Creek seem to corroborate this trend (Bennett & Wood, unpublished data), although it is difficult to differentiate long-term declines from the effects of the current drought in the western U.S. If *P. antipodarum* declines are sustained, their impacts may be transitory. This population expansion–contraction pattern can be driven by several mechanisms, including depletion of food resources, alterations in environmental conditions, and increased predation or parasite pressure (Sakai et al., 2001; Simberloff & Gibbons, 2004; Strayer & Malcolm, 2006). Given the breadth of *P. antipodarum*'s food habits and environmental tolerances (temperature, salinity, water quality), it is unlikely that snail populations would be reduced in the long term by these factors. Invertebrate predators, particularly crayfish, consumed large numbers of *P. antipodarum* (Brenneis et al., 2011; Twardochleb et al., 2012; this study), but could not account for long-term snail declines because they were absent from some invaded systems (Moore et al., 2012) and, as generalist predators, were unlikely to provide sustained population regulation. It is possible that naturally occurring parasites or pathogens are infecting *P. antipodarum*, as observed in Europe (Gerard et al., 2003), thereby causing snail population declines which may preclude the need for biocontrol development.

Although our investigations indicate significant impacts of *P. antipodarum* on native algae and invertebrates, the likely vulnerability of *P. antipodarum* to high flows, drought and high temperatures suggest that it might not have large, long-term impacts on natural stream ecosystems in southern California. In streams where moderate flows are maintained by dams or other structures, however, *P. antipodarum*'s populations may thrive and pose risks to co-occurring native species. The need for management actions may be mitigated by the moderate effects of *P. antipodarum* on native species, which are similar to the effects of other native species, and their long-term population declines; however, their likely impacts on endangered species, such as the arroyo toad, suggest management action may be needed in special cases.

Acknowledgments We thank Sean Anderson (California State University – Channel Islands), Sabrina Drill (University of California Cooperative Extension) and Curt Lively (University of Indiana, Bloomington) for advice, support, and cooperation during these studies. We gratefully acknowledge the assistance of numerous students at the RIVRlab who assisted in both lab and field adventures: Mara Evans, Alan Wood, Niko Hartline, Kristen Hewett, Vivian Hurtado, Heather Martin (CSUCI), Devyn Orr, Faris Shalan, Cassidy Anton, Beau Tindall, Kellyn Dott, Ryan Hazelton, Samira Spantman, Mariah H. Edmonds, Jordan Senia, and Devin Barry. We also thank Janice Jones from the Marine Sciences Institute for technical assistance in chlorophyll analyses. We extend a special thank you to Sheila Wiseman for creating all the figures that appear in the paper.

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