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Complex impacts of an invasive omnivore and native consumers on stream communities in California and Hawaii

Kristie Klose · Scott D. Cooper

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Abstract The effects of invasive species on native communities often depend on the characteristics of the recipient community and on the food habits of the invasive species, becoming complicated when the invader is omnivorous. In field enclosure experiments, we assessed the direct and interactive effects of an invasive omnivorous crayfish (*Procambarus clarkii*) and either native herbivorous snails (*Physella gyrina*) or shrimp (*Atyoida bisulcata*) on stream communities in California and Hawaii, respectively. Based on literature data and the characteristics of each study site, we predicted that crayfish would affect primarily algal-based trophic linkages in an open California stream but detritus-based trophic linkages in a shaded Hawaiian stream, with trophic cascades mediated through crayfish effects on primary consumers being observed in both systems. As predicted, crayfish in California directly reduced periphyton, filamentous algae, sediment, and snail levels, but generated a cascade by decreasing snail densities and increasing periphyton biomass. Contrary to prediction, crayfish did not reduce total invertebrate biomass. As predicted, crayfish in Hawaii reduced leaf litter,

filamentous algae, and benthic invertebrate biomass. Contrary to our predictions, however, a trophic cascade was not observed because shrimp did not affect periphyton levels, crayfish did not reduce shrimp abundance, and crayfish had greater negative impacts on filamentous algae than did shrimp. Our findings highlight that the same invasive species can generate different effects on disparate systems, probably as mediated through the availability of different food types, flexibility in the invasive species' food habits, and complex pathways of trophic interaction.

Keywords Invasive species · Omnivory · Trophic cascade · *Procambarus clarkii* · *Physella gyrina*

Introduction

Although covering only a minute proportion of the Earth's surface (<2 %), freshwater systems contain 6 % of all described species, but have extinction rates five times higher than terrestrial and marine systems combined (Ricciardi and Rasmussen 1999; Sala et al. 2000; Dudgeon et al. 2006). The introduction and spread of invasive species, and their impacts on native ecosystems, rank second only to habitat degradation as a threat to global biodiversity (Sala et al. 2000). In some cases, invasive species may remain undiscovered for many years with few discernible ecological impacts; however, in other cases, the invasion and spread of introduced species result in profound biological and economic changes (Herbold and Moyle 1986; Kolar and Lodge 2000). As a consequence, scientists and managers are interested in determining the attributes of invasive species and recipient communities which allow invaders to thrive and greatly affect native communities, including reductions or extinctions of native taxa.

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The characteristics of invasive species that determine their persistence and expansion in novel communities have been postulated to include: (1) broad physiological tolerances, (2) high genetic variability, (3) high fecundity, rapid growth and early maturity, (4) rapid dispersal, and (5) generalist habitats and diets (e.g., omnivory) (Kolar and Lodge 2001). Regarding the last point, some invasive omnivores pose multiple threats to native species through competition for shared resources, predation on native taxa, and alteration of environmental conditions and native prey behavior (Polis et al. 2000; Turner et al. 2000; Vandermeer 2006; Thompson et al. 2007). The broad diets and habitat tolerances of invasive omnivores often also dictate that their impacts depend on recipient community attributes such as: (1) the degree to which areas are affected by human disturbance, (2) the comparability of new environments to the alien species' habitat of origin, (3) low or high native species richness, and (4) the relative availability of different food sources (Hobbs and Huenneke 1992; Levine and D'Antonio 1999; Stohlgren et al. 1999; Naeem et al. 2000; Fridley et al. 2007). Likewise, systems affected by changing land use patterns, such as those in California, as well as native ecosystems with high levels of endemism, such as island ecosystems (e.g., Hawaii), may be particularly vulnerable to invasions (Elton 1958; Vitousek and Walker 1989; Nichols et al. 1990; Levine and D'Antonio 1999; Holway et al. 2002). Although many previous studies have focused on the effects of invasive species on specific native taxa, species invasions, particularly by omnivores, can affect entire food webs via direct and indirect interactions through multiple trophic levels.

Several studies have documented the importance of omnivores in structuring lake and pond communities, focusing on the effects of omnivorous crayfish on food webs (Lodge et al. 1994; Nyström et al. 1999). As generalized omnivores, crayfish typically influence the biomass, abundance, and species composition of algae, macrophytes, detritus, and other benthic invertebrates; however, these impacts are often specific to the taxa or system under consideration. For example, the direct effects of crayfish on highly mobile taxa (e.g., baetid mayflies) may be weak relative to their impacts on slow-moving invertebrates, such as snails (Parkyn et al. 1997; Nyström 2005). Although omnivorous invasive decapods are often abundant in streams with a diversity of food resources, including algae and leaf litter, only a few studies have assessed their separate and joint impacts with native grazers and detritivores on stream communities (Hart 1992; Creed 1994; Usio and Townsend 2004; Nilsson et al. 2008).

Here, we compare the impacts of the same invasive crayfish species and native primary consumers (grazers, detritivores) on the community of a temperate stream with

an open canopy in California (Ventura River) to their impacts on a forested tropical stream community in Hawaii (Waiau Stream). Unlike open California streams, Hawaiian streams contain few invertebrate species (Ziegler 2002) and receive substantial leaf litter inputs from abundant riparian vegetation. We focused on the effects of an invasive omnivore in temperate mainland and tropical island systems because of the omnivore's importance in influencing benthic food webs (invertebrates, algae, leaf litter), its potential to affect native consumers through both competition and predation (Usio 2000; Klose and Cooper 2012), and the paucity of information about the effects of an invasive omnivore on depauperate native stream invertebrate communities on islands (Larned et al. 2003).

The red swamp crayfish, *Procambarus clarkii* (Girard), is native to the south central United States and is currently the most broadly distributed crayfish species in the world, reaching high densities in streams in southern California and Hawaii (Gamradt and Katz 1996; Huner 2002; Riley et al. 2005; Klose and Cooper 2012). The dominant macroinvertebrate primary consumer in the southern Californian stream we studied was the herbivorous snail *Physella gyrina* (Say), whereas the atyid shrimp *Atyoida bisulcata* (J.W. Randall), which primarily functions as a collector/gatherer (Resh et al. 1990), was the most abundant large macroinvertebrate in the Hawaiian stream. The Ventura River had an open canopy and substantial biomasses of both filamentous algae (*Cladophora* Kützing) and invertebrate taxa (i.e., baetid mayflies, chironomids, philopotamid caddisflies), moderate microalgae (primarily diatoms) and physid snail biomass, and negligible leaf litter inputs. The shaded Waiau Stream, on the other hand, contained moderate levels of filamentous algae (*Spirogyra* C.G. Nees) and invertebrate biomass (i.e., hydropsychid caddisflies, nematodes, oligochaetes), abundant atyid shrimp, a low biomass of microalgae (i.e., periphyton), and high leaf litter levels (i.e., *Hibiscus tiliaceus* L., *Schizotachyum glaucifolium* (Rupr.) Munro). To examine the direct, indirect, and interactive community impacts of the invasive red swamp crayfish, *P. clarkii*, and two native consumers in disparate systems, we experimentally manipulated crayfish and snails or shrimp in a cross-classified design in field enclosures in streams in southern California and Hawaii to address the following two questions. (1) What are the individual and combined effects of crayfish and snails (California) or shrimp (Hawaii) on inorganic sediment, leaf litter mass, algal biomass, invertebrate densities and biomass, and snail microdistributions in systems which differ in abiotic and biotic characteristics? (2) What do the individual and combined effects of an invasive omnivorous crayfish and two native consumers in dissimilar stream communities indicate about the direct and indirect effects of crayfish on different food webs?

Because the red swamp crayfish is omnivorous and typically reduces the biomass of both filamentous algae and slow-moving benthic invertebrates (e.g., snails), we predicted that crayfish in the unshaded California stream would affect primarily the components of algal-based food webs by directly grazing periphyton and filamentous algae, and consuming aquatic insects and herbivorous snails, the latter leading to a trophic cascade with increased microalgae biomass (Fig. 1a) (Hart 1992; Creed 1994; Lodge et al. 1994; Nyström et al. 1999; Klose and Cooper 2012). In the Hawaiian stream, on the other hand, we hypothesized that crayfish would reduce both filamentous algae, which were patchily distributed on the stream bottom, and atyid shrimp densities (Banha and Anastácio 2011), the latter resulting in increases in the biomasses of filamentous algae and periphyton (primarily diatoms), as well as reduce components of the detritus-based food web (i.e., collectors, leaf litter, fine particulate organic matter) (Fig. 1b; Pringle et al. 1993; Usio 2000; Schofield et al. 2001; Ziegler 2002). We did not expect to see trophic cascades in the detritus-based food chain because shredders, except for the omnivorous crayfish, were virtually absent in Hawaii. Among invertebrates, we predicted that crayfish would primarily reduce large, slow-moving or sedentary prey (e.g., snails, oligochaetes, odonates), but would have little direct effect on evasive, mobile, and/or small prey (microcrustaceans, amphipods, baetid mayflies) (Parkyn et al. 2001; Stenroth and Nyström 2003; Nyström 2005). We examined our hypotheses by manipulating the densities of crayfish and two primary herbivorous/detritivorous consumers (snails or shrimp) in enclosures in a Californian and a Hawaiian stream.

Materials and methods

Invasion and natural histories

Ventura River and Waiau Stream

The precise timing and location of red swamp crayfish (*P. clarkii*) introductions into southern California, including the Ventura River, are unknown; however, this crayfish species was first documented from a southern California stream (near Pasadena, Los Angeles County) in the 1920s (Holmes 1924). Based on historical records, it is likely that *P. clarkii* spread into rivers and streams from reservoirs where they escaped or were deliberately released as bait for recreational sport fishing (Riegel 1959). Stomach content and stable isotope analyses show that crayfish feed on detritus, algae, plants, invertebrates (including other crayfish), and vertebrates (including fish and amphibians) (Guan and Wiles 1997; Parkyn et al. 2001; Stenroth and

Nyström 2003), and become key shredders in systems receiving high inputs of allochthonous material (Ilheu and Bernardo 1993). The distribution of the freshwater gastropod *P. gyrina* extends from California to the Gulf of Mexico, and northward to Quebec and the Northwest Territories (Dillon and Wethington 2004). *P. gyrina* consumes detritus, algae, fungi, and living animal and vascular plant material, but is primarily a herbivore (Sheldon 1987).

P. clarkii was first introduced to the Hawaiian Island of Oahu in 1934 then spread rapidly, invading Kauai and Maui by 1954 and Molokai and Hawaii shortly thereafter, becoming a pest which damaged both taro plants and irrigation levees (Huner 1977). The mountain atyid shrimp, *A. bisulcata*, is an algivore/detritivore endemic to the Hawaiian Islands, functioning as a collector/gatherer at low flow velocities and as an omnivorous filter feeder at high current speeds (Resh et al. 1990; Ziegler 2002).

The design of field experiments in California and Hawaii

Because the Waiau Stream site was remote and difficult to reach, we could not use the same experimental enclosures in the Ventura River and Waiau Stream. Although we manipulated the presence-absence of crayfish and dominant primary consumers (snails in the Ventura River, shrimp in Waiau Stream) in a cross-factorial design in both systems, we used rectangular stream channels (2 m long × 0.31 m wide × 0.15 m high) in the Ventura River and smaller cylindrical enclosures (0.30 m diameter × 0.37 m high) in Waiau Stream. Despite differences in the size and shape of experimental arenas used at these sites, the results suggest that these differences probably did not affect experimental outcomes because crayfish effects were most manifest on sedentary resources in both systems (Englund et al. 2001). Nevertheless, the methods and results for both systems are presented separately here, as two independent experiments, but the results from the two systems are compared to each other and to those from other systems in the “Discussion”.

Study sites

Ventura River

This experiment was conducted for 12 days in a third-order section of the Ventura River, southern California, during July 2004. The Ventura River flows southward 26 km from an elevation of >1,400 m in the Transverse Ranges to the Pacific Ocean, draining a 590-km² catchment. The Ventura River is alkaline (pH 8.0) and mesotrophic (NH₄⁺ = 0.1–0.6 μmol L⁻¹, NO₃⁻ = 31.3–37.7 μmol L⁻¹, SRP = 1.2–1.9 μmol L⁻¹). The study section was 6–8 m wide

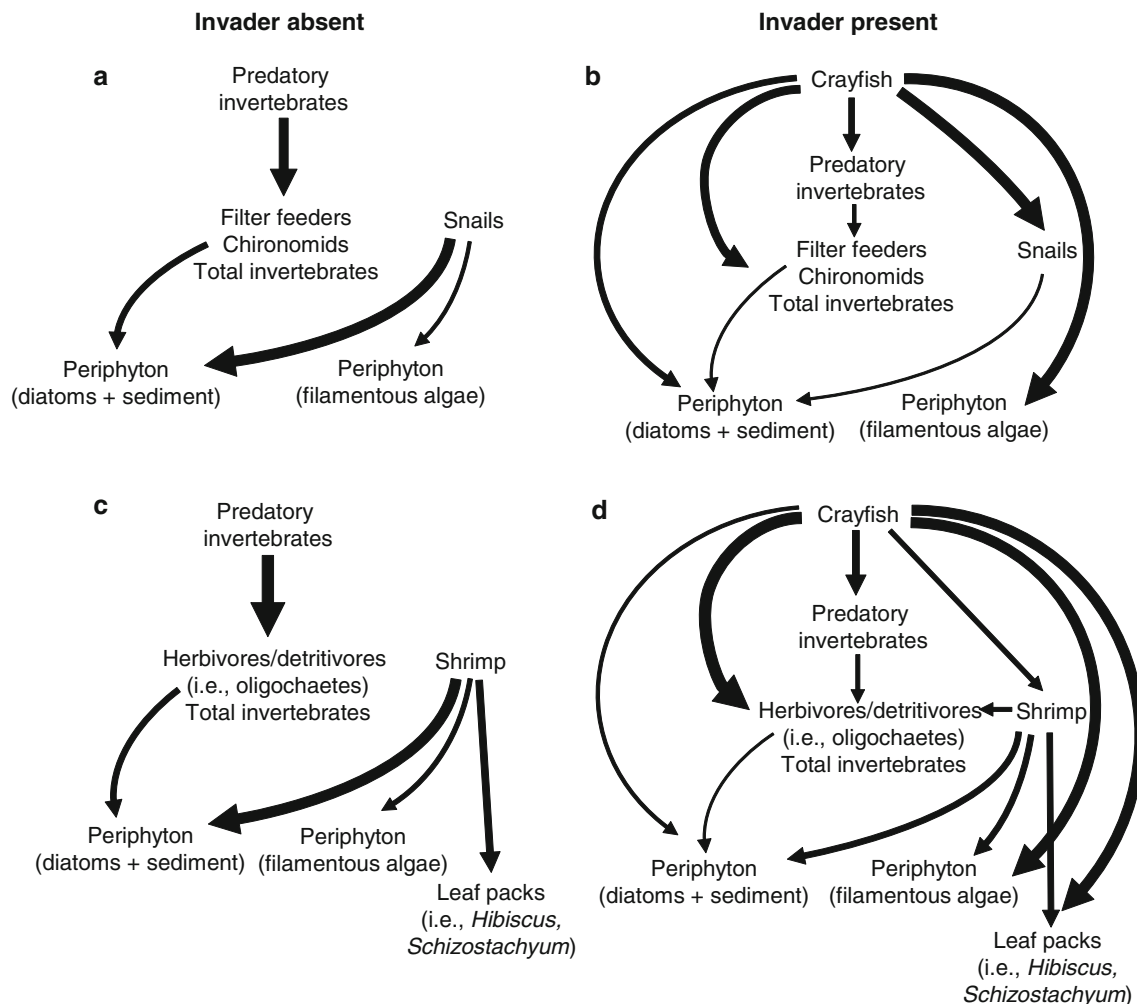


Fig. 1 Postulated pathways of interaction in: **a, b** the Ventura River, California, and **c, d** Waiiau Stream, Hawaii, in the absence or presence of invasive crayfish. Hypothesized food web links are based on literature results (Creed 1994; Lodge et al. 1994; Nyström et al. 1999;

Usio 2000; Larned et al. 2003; Klose and Cooper 2012) and the availabilities of different food sources in the different systems. *Arrow thickness* indicates the strength of direct effects and point from consumers to resources

with a 25 % riparian canopy represented by giant reed (*Arundo donax* L.), western sycamore (*Platanus racemosa* Nutt), and willow (*Salix* spp. L). Current velocities and water temperatures ranged from 4 to 25 cm s⁻¹ and 18 to 22.5 °C during the study period, average water depth was 0.3 m in riffles and ranged from 1 to 4 m in pools, and substrata consisted largely of sand and gravel in pools, and medium to large cobbles in riffles. *Cladophora* sp. (Kützing) was the dominant macroalga, microalgae were represented by diatoms, and common benthic invertebrates included mayflies (*Tricorythodes* Ulmer), chironomids (Chironomidae: Chironominae, Orthoclaadiinae), worms (oligochaetes), crustaceans (*Hyalella azteca* Saussure), microcrustaceans (ostracods, chydorid cladocerans, copepods), and gastropods (*P. gyrina*). The density of *P. clarkii* was estimated on two occasions using night visual counts within a modified quadrat sampler. Ten 1-m² areas were

delineated with four re-bar posts driven into substrata and extended above the water line (0.3–0.4 m water depth). Immediately prior to the visual count of each area, the re-bar was surrounded on all sides by 0.4 cm mesh netting forming a quadrat. Crayfish density was estimated by using a headlamp and scanning the stream bottom within the delineated area at night, turning over all large rocks and cobbles and counting all crayfish on the stream bottom. The *P. clarkii* density estimate was 3.7 ± 1.2 individuals m⁻² (mean ± 1 SE) over the two sampling occasions, agreeing with estimates obtained in other years (Klose 2007). Fish species occurring in the study reach, based on minnow trap catches (20 baited traps set out overnight; each 42 cm long × 23 cm diameter, with a 4-cm-deep funnel) and direct observations, included threespine stickleback (*Gasterosteus aculeatus* L.), arroyo chub (*Gila orcuttii* Eigenmann and Eigenmann), prickly sculpin

(*Cottus asper* Richardson), and rainbow trout (*Oncorhynchus mykiss* Walbaum).

Waiau Stream

Fieldwork was conducted during September 2004 in Waiau Stream, a second-order stream on the island of Hawaii, located 5 km east of the Hilo Forest Reserve. Waiau Stream flows eastward 3.5 km before discharging into Hilo Bay. The stream is slightly alkaline (pH 7.6) and oligotrophic ($\text{NO}_3^- = 9.1 \mu\text{mol L}^{-1}$, $\text{SRP} = 1.7 \mu\text{mol L}^{-1}$). During the 12-day study period, the study reach was 10–11 m wide, average water depths were 0.35 m in riffles and 1.5 m in pools, current velocities ranged from 0 to 100 cm s^{-1} and water temperatures from 20 to 23 °C, and stream substrata were diverse, including bedrock and basaltic boulders in riffles, and coarse gravel and small cobbles in pools. Riparian canopy cover was 68 % and represented by guava (*Psidium guajava* L.), hau (*H. tiliaceus*), bamboo (*S. glaucifolium*), siris (*Albizia lebbek* (L.) Benth.), false heather (*Cuphea hyssopifolia* Kunth) and Job's tears (*Coix lacrymajobi* L.). *Spirogyra* was the dominant filamentous algal genus present, microalgae included epilithic diatoms, and the benthic invertebrate community was comprised of worms (oligochaetes, nematodes, and polychaetes), flatworms (*Dugesia* sp.), microcrustaceans (ostracods, copepods, chydorid cladocerans), and introduced caddisflies (Hydropsychidae: *Cheumatopsyche pettiti* (Banks), Hydroptilidae: *Oxyethira mira* (Morton) and *Hydroptila arctia* (Ross)). Decapod and fish species present included Tahitian prawns (*Macrobrachium lar* J.C. Fabricius), red swamp crayfish (*P. clarkii*), mountain shrimp (*A. bisulcata*), and guppies (*Poecilia reticulata* Peters). Based on one night's visual survey (using methods described previously for the Ventura River), and another survey that included hand-netting and mark–recapture methods (Ricker 1975), *P. clarkii* average density was calculated to be 1.2 ± 0.3 crayfish m^{-2} and *A. bisulcata* density was estimated to be 22 ± 7.5 shrimp m^{-2} .

Experimental methods

Ventura River

Sixteen parallel stream channels constructed from polyvinyl chloride (PVC) pipe cut longitudinally in half were placed in a low velocity riffle in an unshaded stream reach with high background densities of adult crayfish, with channel environments closely mimicking the biotic and abiotic (e.g., water temperature, substrata) conditions in the reach. Two (2 m long \times 0.31 m wide \times 0.15 m high) stream channels were mounted onto each of eight 1.2×2.4 m plywood sheets coated with water resistant

Varathane, which were then placed on the stream bottom. The channel top edges protruded 2–3 cm above the water's surface and the ends of each channel were fitted with plastic screens (0.3 cm mesh width) which were cleaned daily, allowing continuous water flow and colonization by invertebrates while preventing the escape or entry of crayfish and snails. Natural substrata from an area of stream bed equal to the total area of all channels combined were elutriated to separate invertebrates from substrata, then substrata were scrubbed and carefully selected to mimic natural stream conditions, with an equal number of very small (24), small (12), medium (5), and large (3) substrata placed into each channel (mean circumferences 7, 21, 36, and 58 cm, respectively), along with sand and gravel to an average depth of 2.5 cm. Four open-ended PVC cylinders (20 cm long \times 8 cm diameter) were placed on the bottom of each stream channel at equally spaced intervals to provide shelter for crayfish and reduce intra-specific interactions. Current velocities within each channel ranged from 0 to 3 cm s^{-1} . Invertebrates and algae collected from the elutriated substrata were combined, mixed thoroughly in a bucket, then equal aliquots were added to each stream channel, ensuring that initial abundances of invertebrates and algae were similar among enclosures. Square unglazed ceramic tiles (2.3 cm on each side \times 0.5 cm thick) were placed on the stream bed for 4 weeks for periphyton colonization, then 25 preconditioned tiles were placed along the bottom of each stream channel at equally spaced intervals at the beginning of the experiment. A standardized mass of *Cladophora* (81.2 ± 2.85 g wet mass) was bound and tethered in the center of each channel, producing *Cladophora* coverage similar to that measured in the Ventura River (Klose, unpublished data). We have often observed *P. clarkii* actively foraging in the Ventura River and similar nearby streams, often in stagnant pools during the summer and fall dry season, at depths similar to those in our stream channels both at night and during the day (Klose and Cooper 2012).

Four treatments were randomly assigned to channels with each replicated four times in a fully factorial design as follows: *P. clarkii* only (2 crayfish per channel, 3.2 crayfish m^{-2}), *P. gyrina* only (100 snails per channel, 127 snails m^{-2}), both *P. clarkii* and *P. gyrina* (2 crayfish and 100 snails per channel), and neither *P. clarkii* or *P. gyrina* (control). All individual crayfish were of similar length and mass (8.8 ± 0.14 cm TL and 22.3 ± 1.3 g wet mass). Natural densities of *P. gyrina* ranged from 0 to 321 snails m^{-2} (9.9 ± 0.25 mm TL) (Klose, unpublished data). Channel tops were covered with thin, transparent netting (0.4 cm mesh) and secured every 10 cm with removable metal clips to exclude avian and mammalian predators and to prevent crayfish and snail escape. Light

levels measured as photosynthetically active radiation (PAR) were recorded below the water's surface within each stream channel, both with and without the netting in place, producing an estimate of the amount of light reduction by the netting of 4.5 %.

Day and night visual surveys were performed 5 days following the start of the experiment in channels which contained snails to determine the number of *P. gyrina* on the tops of substrata, on the walls of stream channels both above and below the water line, and on crayfish shelters. Two researchers counted all snails on each of these surfaces, and data from the two observers were averaged. Night visual counts were conducted using flashlights and began 1 h after sunset (2115 hours PST) and were completed at 2300 hours. Four ceramic tiles were collected at the beginning and end of the experiment from each channel for periphyton biomass estimates [as ash free dry mass (AFDM) and chlorophyll *a* concentrations], then frozen on return to the laboratory. Initial invertebrate densities were sampled using a 0.041-m² Surber sampler (250 µm mesh size, 3 Surber samples per channel), and final sampling was performed by washing the entire contents of each stream channel into a 250-µm mesh drift net at the channel outflow. Invertebrate samples were preserved in the field in 75 % ethanol. All crayfish were recovered at the end of the experiment.

Waiiau Stream

Sixteen cylindrical plastic containers (0.30 m diameter × 0.37 m high) were placed 8 cm apart on the stream bottom along a pool-riffle transition zone at a water depth of 30 cm, and covered with transparent netting (0.4 cm mesh width). Each container had 20 holes (0.7 cm diameter) on opposite sides toward the top which allowed continuous water flow through the containers. Current velocities within each enclosure ranged from 0 to 1 cm s⁻¹. Elutriated stream gravel to a depth of 5 cm and ten small, three medium, and one large cobble (circumferences 5, 10, and 22 cm, respectively) from the streambed were placed on the bottom of each enclosure. One open-ended PVC cylinder (13 cm long × 4 cm diameter) was placed on the bottom of each enclosure as a crayfish refuge, then enclosures were stocked with natural densities of benthic invertebrates and algae collected from Waiiau Stream using the same procedures described for the Ventura River study.

The presence and absence of *P. clarkii* and *A. bisulcata* were manipulated in enclosures in a factorial design with each treatment being replicated four times: one *P. clarkii* only (14 crayfish m⁻²), three *A. bisulcata* only (42 shrimp m⁻²), both *P. clarkii* and *A. bisulcata* (1 crayfish and 3 shrimp), and neither *P. clarkii* or *A. bisulcata*

(control). The density of crayfish used in the enclosures was higher than natural densities; however, it was impossible to add fewer than one crayfish per enclosure. All experimental crayfish were of similar length and mass (7.4 ± 0.24 cm TL and 15.1 ± 1.4 g wet mass, respectively), and *A. bisulcata* averaged 3.6 ± 0.1 cm TL. All *P. clarkii* were recovered at the end of the experiment.

To examine the effects of consumers on periphyton biomass, two initial and two final periphyton samples were collected from the top of a cobble placed in each experimental container by scrubbing, brushing, and washing a 6.2-cm² cobble area into a pan of water, then filtering the suspension through A/E filters which were frozen for later analysis. *Hibiscus* and *Schizostachyum* leaf packs (initial wet masses 4.2 ± 0.18 and 1.8 ± 0.05 g, respectively) and a clump of the filamentous green alga, *Spirogyra* (initial wet mass 3.8 ± 0.07 g) were bound and tethered to the bottom of each enclosure and weighed at the beginning and end of the experiment, including any loose fragments observed at the end of the experiment. Invertebrates were sampled at the end of the experiment by washing and elutriating all substrata in each container through a 250-µm mesh net, then preserving samples in 75 % ethanol.

Laboratory methods

Invertebrates were identified to the lowest practical taxonomic level (generally family or genus for insects and mollusks, coarser levels for other taxa) and counted under a dissecting microscope at ×12 magnification. Average individual dry mass for each taxon within each channel was determined by averaging the lengths of ten individuals of each taxon from each channel which were measured to the nearest 0.01 mm using digital calipers, then calculating dry weights using length–weight relationships (Meyer 1989). Invertebrate taxa were assigned to functional feeding or size categories, including herbivores/detritivores, predatory invertebrates, meiofauna, and filter feeders using designations in Merritt and Cummins (1996) and Thorpe and Covich (2001) (ESM Appendices D, E). Owing to their broad range of feeding modes and diets, Chironominae (here Chironominae and Orthocladiinae combined) were excluded from functional feeding group categorizations, but chironomids belonging to the Tanypodinae were treated separately as small predators. Chironomids (Chironominae, Orthocladiinae), however, were included in total invertebrate density and biomass calculations.

Ceramic tiles from the Ventura River experiment were brushed clean and rinsed with distilled water. The resulting slurry was split into two equal aliquots which were filtered onto separate A/E filters, then stored at –20 °C until AFDM and chlorophyll *a* determinations. In both experiments, filters were extracted at 4 °C in 90 % acetone for 24 h, then

chlorophyll *a* concentrations were measured by fluorometry using the acidification method (Sartory and Grobbelaar 1986). For AFDM analysis, samples were dried at 60 °C for 24 h, weighed to the nearest 0.1 mg, then reweighed following combustion at 500 °C for 2 h. AFDM was determined as the difference between initial and final dry weight following ignition (Steinman and Lamberti 1996).

Statistical analyses

Statistical analyses were conducted using the mean value for each response variable from each stream channel or enclosure as a replicate value. We compared the final mean levels of chlorophyll *a*, AFDM, and inorganic sediment in control treatments of the Ventura River and Waiau Stream using Student's *t* tests ($n = 4$ from each stream). Effects of treatment on initial chlorophyll *a* and AFDM levels, and initial masses of filamentous algae and leaf packs, were determined using two-way ANOVAs. If no initial differences between treatments were detected then the final effects of treatments were determined by applying two-way ANOVAs to final response variable values only. If there were significant associations between treatment and initial levels of these variables, then two-way ANOVAs were performed on proportional changes (final/initial) in the values of these variables. Independent variables in all two-way ANOVAs were the presence versus absence of crayfish and snails (Ventura River) or shrimp (Waiau Stream). In the Ventura River study, where the densities and microdistributions (proportion observed above the water line) of snails were monitored during the day and night, the effects of crayfish and time of day on *P. gyrina* densities and microdistributions were evaluated using repeated measures ANOVAs.

Prior to all analyses, normality was tested using the Kolmogorov–Smirnov test and residuals from analyses were plotted and examined. If assumptions of normality and homogeneity of variances could not be met, then values of count or continuous variables were \log_{10} -transformed. When variables included zero values, then one or the smallest detectable unit for that response variable was added to all values for that variable prior to transformation (Quinn and Keough 2002). All statistical analyses were performed with JMP v.6.0.0 for Windows™ (SAS Institute, Cary, NC, USA).

Results

Ventura River

In general, our enclosure experiment supported some but not all of our predictions of crayfish effects on components of

the California stream food web. We hypothesized that, in the absence of crayfish, snails would reduce periphyton biomass (as chlorophyll *a* and AFDM), and inorganic sediment levels, but that crayfish, when present, would reduce snails which would release periphyton from grazing pressure, leading to increases in periphyton biomass. These predictions were supported by the experimental results, because snails significantly reduced periphyton and sediment levels when crayfish were absent, crayfish reduced snail densities and drove them into refugia above the water line, particularly at night, and periphyton biomass and sediment levels were higher in the presence than absence of crayfish when snails were present (Figs. 2, 3; Table 1). Although crayfish reduced periphyton and sediment levels, their effects were not nearly as pronounced as those for snails, and periphyton biomass and sediment levels were similar in treatments with crayfish regardless of the presence of snails (Fig. 2). Further, in support of our predictions, crayfish, but not snails, significantly reduced the biomass of *Cladophora* (Fig. 2; Table 1; ESM Appendix A).

Invertebrate biomass and abundance across all treatments in the Ventura River were dominated by Chironominae (51 % of total biomass, 15 % of total density), Ostracoda (11, 31 %), Cyclopoida (8.1, 28 %), *Wormaldia* (7.1, <1 %), and *Baetis tricaudatus* (6.2 %, 1.2 %). Herbivores/detritivores comprised 16 %, predatory invertebrates 1.1 %, meiofauna 24.2 %, and filter feeders 7.1 % of total invertebrate biomass and 13.6, 0.05, 71.1, and 0.16 %, respectively, of total invertebrate density (ESM Appendix D). There were significant crayfish \times snail interaction effects on the biomasses of total invertebrates, filter feeders, and Chironominae, and densities of Chironominae, because levels of these variables were higher in the snail alone and crayfish alone treatments than in the control or crayfish + snail treatments (Table 2). Crayfish reductions of the densities of predatory invertebrates (i.e., Tanypodinae, *Graptocorixa*, *Enallagma*) were marginally significant (Fig. 4; ESM Appendices B, D). Other feeding groups or size categories, such as total invertebrate and filter feeder densities, herbivore/detritivore and meiofauna biomasses and densities, and taxon diversity, richness and evenness were unaffected by treatment (ESM Appendices B, D).

Waiau Stream

We predicted that crayfish effects on periphyton biomass and inorganic sediment levels when alone would be minimal owing to low periphyton and sediment levels in this shaded stream, and that crayfish consumption would be directed at more abundant resources such as filamentous algae, leaf litter, and benthic invertebrates. Many of our predictions were confirmed because crayfish had no effects on periphyton and sediment levels, but reduced filamentous

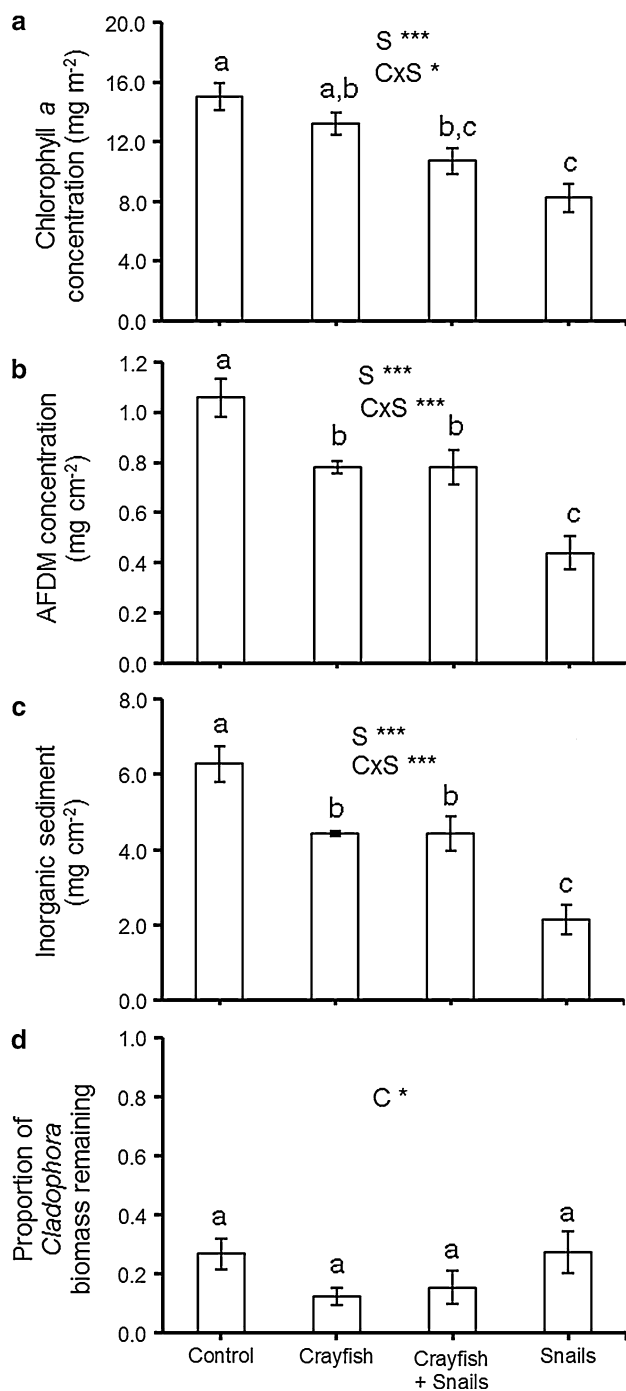


Fig. 2 Final **a** chlorophyll *a* (chl *a*) concentration, **b** ash-free dry mass (AFDM), **c** inorganic sediment levels, and **d** the proportion of *Cladophora* biomass remaining in stream channels in the Ventura River at the end of the experiment for each treatment (mean \pm 1 SE). Uppercase letters represent the results of two-way ANOVAs performed on log-transformed chl *a*, AFDM, and inorganic sediment levels and arcsine square root-transformed proportion of *Cladophora* biomass remaining; bars with the same lowercase letters are not significantly different from one another based on Tukey's post hoc comparison at $P > 0.05$. Significance levels: * $P < 0.05$, *** $P < 0.001$ with *C* indicating a significant crayfish effect, *S* indicating a significant snail effect and *C* \times *S* indicating a significant crayfish \times snail interaction effect

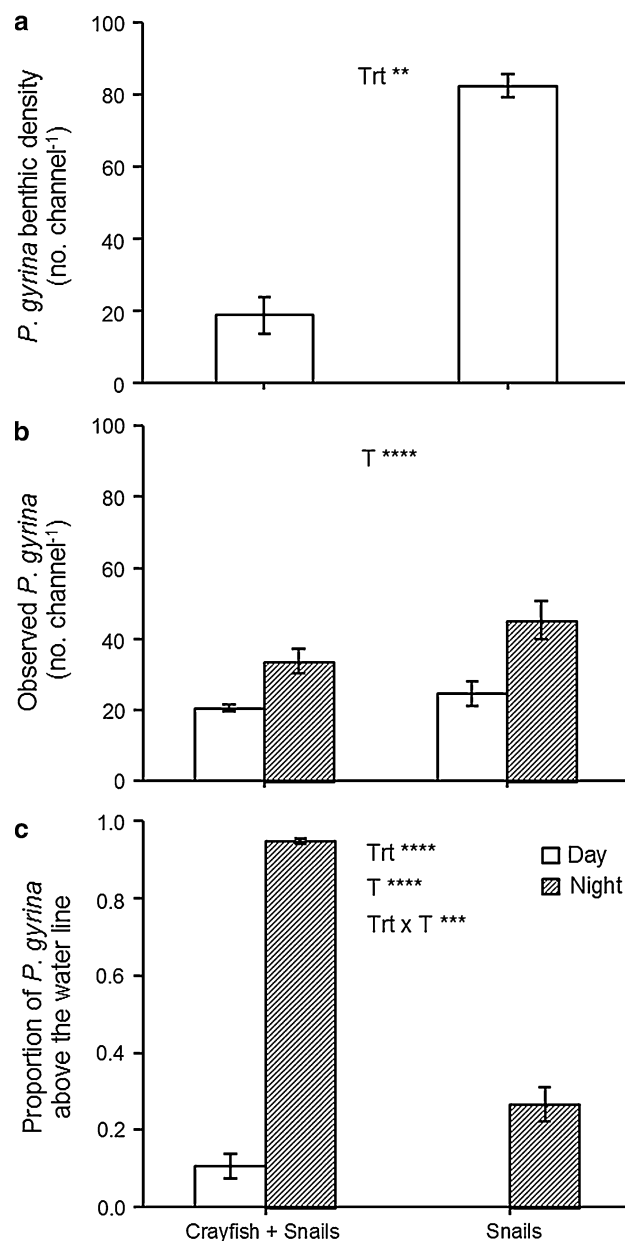


Fig. 3 **a** Final snail benthic density, **b** density of snails observed during the day (open) versus night (shaded) and **c** proportion of observed snails above the water line during the day (open) versus night (shaded) (mean \pm 1 SE) in treatments containing both crayfish and snails versus snails alone in the Ventura River. Treatment differences (crayfish + snail vs. snail, *Trt*) were determined by a *t* test on log-transformed snail benthic densities and repeated measures ANOVAs of treatment, time (day vs. night, *T*) and their interaction on log-transformed observed snail numbers and the arcsine square root-transformed proportion of snails above the water line. Significance levels: ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$; only significant interactions are listed

algae, benthic invertebrate, and leaf litter levels (Figs. 5, 6; ESM Appendices A, C). However, we also hypothesized that shrimp would reduce periphyton, filamentous algae, and sediment levels, and that crayfish, when present, would

Table 1 Summary of significant or marginally significant results from two-way ANOVAs testing for the direct and interactive effects of *P. clarkii* presence/absence and *P. gyrina* or *A. bisulcata* presence/absence on log-transformed final chlorophyll *a*, AFDM, inorganic sediment levels, arcsine square root-transformed proportion of*Cladophora* remaining (Ventura River), and arcsine square root-transformed proportions of inorganic sediment, *Hibiscus*, *Schizostachyum* and *Spirogyra* biomass remaining (Waiau Stream) at the end of the experiments

Response variable Source of variation	MS	$F_{1,12}$	<i>P</i>
Ventura River			
Final chlorophyll <i>a</i>			
<i>P. clarkii</i>	0.37	0.12	0.74
<i>P. gyrina</i>	86.3	28.0	<0.001
<i>P. clarkii</i> × <i>P. gyrina</i>	18.5	5.99	0.03
Final AFDM			
<i>P. clarkii</i>	0.004	0.26	0.62
<i>P. gyrina</i>	0.38	24.8	<0.001
<i>P. clarkii</i> × <i>P. gyrina</i>	0.38	25.0	<0.001
Final inorganic sediment			
<i>P. clarkii</i>	0.19	0.32	0.58
<i>P. gyrina</i>	17.0	29.3	<0.001
<i>P. clarkii</i> × <i>P. gyrina</i>	17.0	29.2	<0.001
Proportion of <i>Cladophora</i> remaining			
<i>P. clarkii</i>	0.071	6.17	0.03
<i>P. gyrina</i>	0.001	0.11	0.74
<i>P. clarkii</i> × <i>P. gyrina</i>	0.001	0.06	0.81
Waiau Stream			
Proportion of inorganic sediment remaining			
<i>P. clarkii</i>	0.23	1.94	0.19
<i>A. bisulcata</i>	0.001	4.21	0.06
<i>P. clarkii</i> × <i>A. bisulcata</i>	0.004	2.05	0.18
Proportion of <i>Hibiscus</i> remaining			
<i>P. clarkii</i>	0.09	5.10	0.04
<i>A. bisulcata</i>	0.01	0.02	0.91
<i>P. clarkii</i> × <i>A. bisulcata</i>	0.01	0.09	0.78
Proportion of <i>Schizostachyum</i> remaining			
<i>P. clarkii</i>	0.49	6.86	0.02
<i>A. bisulcata</i>	0.12	0.78	0.39
<i>P. clarkii</i> × <i>A. bisulcata</i>	0.21	0.43	0.52
Proportion of <i>Spirogyra</i> remaining			
<i>P. clarkii</i>	0.20	15.6	0.002
<i>A. bisulcata</i>	0.44	3.84	0.07
<i>P. clarkii</i> × <i>A. bisulcata</i>	0.21	6.52	0.02

Only significant results are reported. All results (including non-significant results) are reported in ESM Appendices

consume shrimp leading to increases in the levels of these variables. Somewhat contrary to our predictions, shrimp had no significant effect on periphyton biomass, but did marginally reduce sediment levels and *Spirogyra* biomass (Fig. 5; Table 1; ESM Appendix A). Regarding the hypothesized trophic cascade, we found that crayfish had no effect on shrimp density, that there were no effects of shrimp or crayfish, alone and together, on periphyton

biomass, and that crayfish caused larger reductions in filamentous algae biomass than did shrimp, but that average sediment levels were marginally higher in the presence versus absence of crayfish when shrimp were present (Fig. 5; Table 1; ESM Appendix A).

More specifically, final numbers of shrimp remaining in enclosures at the end of the experiment were not significantly different between treatments with and without

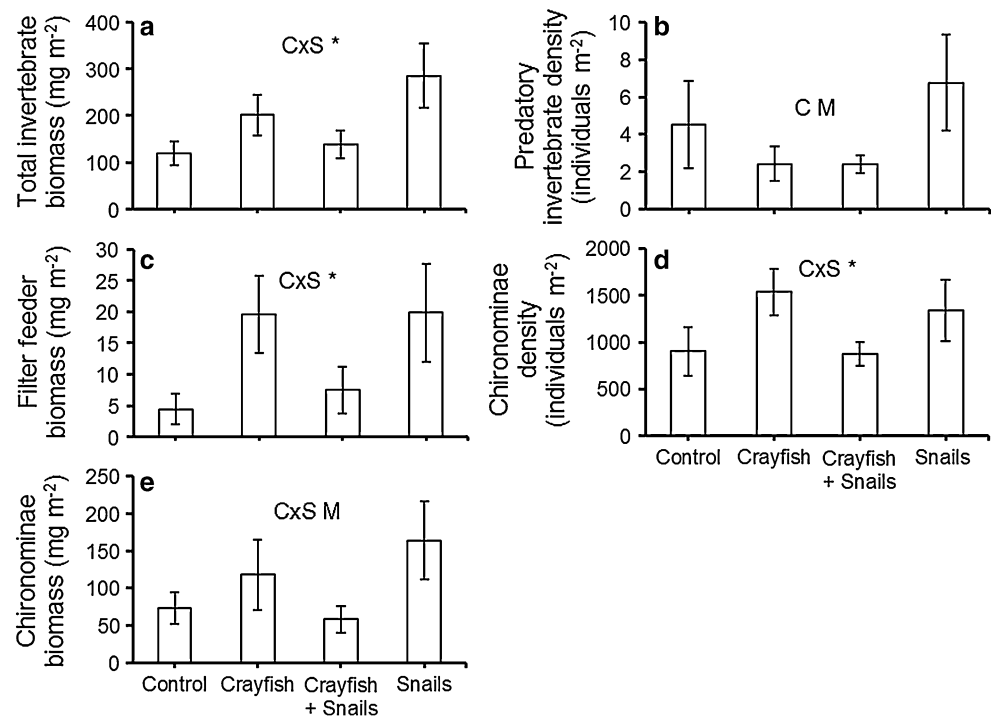
Table 2 Summary of the significant or marginally significant results from two-way ANOVAs testing for the direct and interactive effects of *P. clarkii* presence/absence and *P. gyrina* or *A. bisulcata* presence/absence on log-transformed final biomass for filter feeders, chironomids and total invertebrates for all taxa, and log-transformed final

density of chironomids and predatory invertebrates (Ventura River); and on log-transformed final biomass and density for herbivores/detritivores and total invertebrates for all taxa, and on log-transformed final density of predatory invertebrates (Waiau Stream) at the end of the experiments

Response variable Source of variation	MS	$F_{1,12}$	<i>P</i>
Ventura River			
Invertebrate biomass			
Filter feeders			
<i>P. clarkii</i>	6.92	0.05	0.82
<i>P. gyrina</i>	10.6	0.08	0.78
<i>P. clarkii</i> × <i>P. gyrina</i>	696	5.44	0.04
Chironomids			
<i>P. clarkii</i>	3,357	0.97	0.35
<i>P. gyrina</i>	879	0.05	0.82
<i>P. clarkii</i> × <i>P. gyrina</i>	20,708	4.27	0.06
Total invertebrates			
<i>P. clarkii</i>	3,858	0.46	0.51
<i>P. gyrina</i>	9,747	1.15	0.31
<i>P. clarkii</i> × <i>P. gyrina</i>	48,352	5.70	0.04
Invertebrate density			
Chironomids			
<i>P. clarkii</i>	25,548	0.11	0.75
<i>P. gyrina</i>	46,239	0.19	0.67
<i>P. clarkii</i> × <i>P. gyrina</i>	1,121,014	4.65	0.05
Predatory invertebrates			
<i>P. clarkii</i>	38.2	3.40	0.09
<i>P. gyrina</i>	4.7	0.42	0.53
<i>P. clarkii</i> × <i>P. gyrina</i>	4.7	0.42	0.53
Waiau Stream			
Invertebrate biomass			
Herbivores/detritivores			
<i>P. clarkii</i>	23,946	8.77	0.01
<i>A. bisulcata</i>	383	0.14	0.72
<i>P. clarkii</i> × <i>A. bisulcata</i>	5,219	1.91	0.19
Predatory invertebrates			
<i>P. clarkii</i>	260	1.89	0.19
<i>A. bisulcata</i>	164	1.19	0.30
<i>P. clarkii</i> × <i>A. bisulcata</i>	602	4.38	0.06
Total invertebrates			
<i>P. clarkii</i>	35,847	9.27	0.01
<i>A. bisulcata</i>	344	0.09	0.77
<i>P. clarkii</i> × <i>A. bisulcata</i>	8,565	2.21	0.16
Invertebrate density			
Herbivores/detritivores			
<i>P. clarkii</i>	1,602,534	8.04	0.02
<i>A. bisulcata</i>	39,212	0.20	0.66
<i>P. clarkii</i> × <i>A. bisulcata</i>	369,912	1.86	0.20
Total invertebrates			
<i>P. clarkii</i>	5,463,162	4.85	0.05
<i>A. bisulcata</i>	475,456	0.42	0.53
<i>P. clarkii</i> × <i>A. bisulcata</i>	702,325	0.62	0.44

Only significant results are reported. All results (including non-significant results) are reported in ESM Appendices

Fig. 4 Biomass of **a** total invertebrates, **c** filter feeders, and **e** Chironominae, and densities of **b** predatory invertebrates and **d** Chironominae (mean \pm 1 SE) in stream channels assigned to each treatment at the end of the experiment in the Ventura River. *Uppercase letters* represent the results of two-way ANOVAs performed on log-transformed response variables with *C* indicating a significant crayfish effect and *C* \times *S* indicating a significant crayfish \times snail interaction effect; there were no significant differences among treatments based on Tukey's post hoc comparisons at $P > 0.05$. Significance levels: $^M P < 0.10$, $^* P < 0.05$



crayfish (shrimp density when alone $35 \pm 7.1 \text{ m}^{-2}$; shrimp density with crayfish $28 \pm 5.8 \text{ m}^{-2}$; mean \pm 1 SE) (*t* test comparing shrimp vs. crayfish + shrimp treatments: $t = -0.77$, $P = 0.50$). Invertebrate biomass and density were dominated by Oligochaeta (65 % of total biomass, 27 % of total density), Hydrachna (8.9, 9.1 %), Ostracoda (8.1, 25 %), *C. pettiti* (7.7, <1 %), and *Dugesia* (4.3, 1.3 %). Herbivores/detritivores comprised 67.4 %, predatory invertebrates 4.7 %, meiofauna 20.2 %, filter feeders 7.8 %, and Chironominae <1 % of total invertebrate biomass and 28.1, 1.4, 69.7, <1, and <1 %, respectively, of total invertebrate density (ESM Appendix E). As predicted from the known feeding habits of crayfish and *A. bisulcata*, total invertebrate and herbivore/detritivore biomasses and densities (primarily oligochaetes) were reduced by crayfish, but not by shrimp (Fig. 6; Table 2; ESM Appendix C). Both crayfish and shrimp appeared to marginally reduce predatory invertebrate (primarily flatworm) levels, but their effects when together were similar to their individual effects when alone (Fig. 6; ESM Appendix C). Taxon diversity, richness, and evenness, and the biomasses and densities of Chironominae and meiofauna were unaffected by treatment (Fig. 6; ESM Appendix E).

Discussion

The results of this study provide experimental support for the hypothesis that the biological and physical characteristics of recipient ecosystems, such as autochthonous

production and allochthonous input rates, and consumer behavioral characteristics, drive an invasive omnivore's consumption patterns, ultimately influencing food web structure and function. Based on literature information, we predicted that crayfish would primarily affect components of an algae-based food web in an open California stream but components of a detritus-based food web in a shaded Hawaiian stream. More specifically, we predicted that crayfish would have strong effects on filamentous algae, periphyton (diatoms), sediment, total invertebrates, and snails in the Ventura River, and strong effects on shrimp, total invertebrates, filamentous algae, and leaf litter, but weak effects on periphyton, in Waiiau Stream. We also predicted that snails and shrimp would reduce periphyton and sediment levels and that the addition of crayfish would reduce these primary consumers leading to increases in periphyton and sediment levels. Finally, we expected that, among invertebrates, crayfish would have the greatest impacts on large, slow-moving or sedentary prey because these prey are easiest to catch and handle.

There was mixed confirmation for our predictions. In this study, crayfish reduced large, slow-moving invertebrates (e.g., snails, odonates, oligochaetes) and had few effects on active, mobile prey (e.g., shrimp, amphipods, baetid mayflies), consistent with literature data indicating that large, slow-moving or sedentary prey are most vulnerable to crayfish predation (Lodge et al. 1994; Parkyn et al. 1997; Nyström et al. 1999; Klose and Cooper 2012). We predicted that crayfish would reduce snails in California and shrimp in Hawaii (Banha and Anastácio 2011;

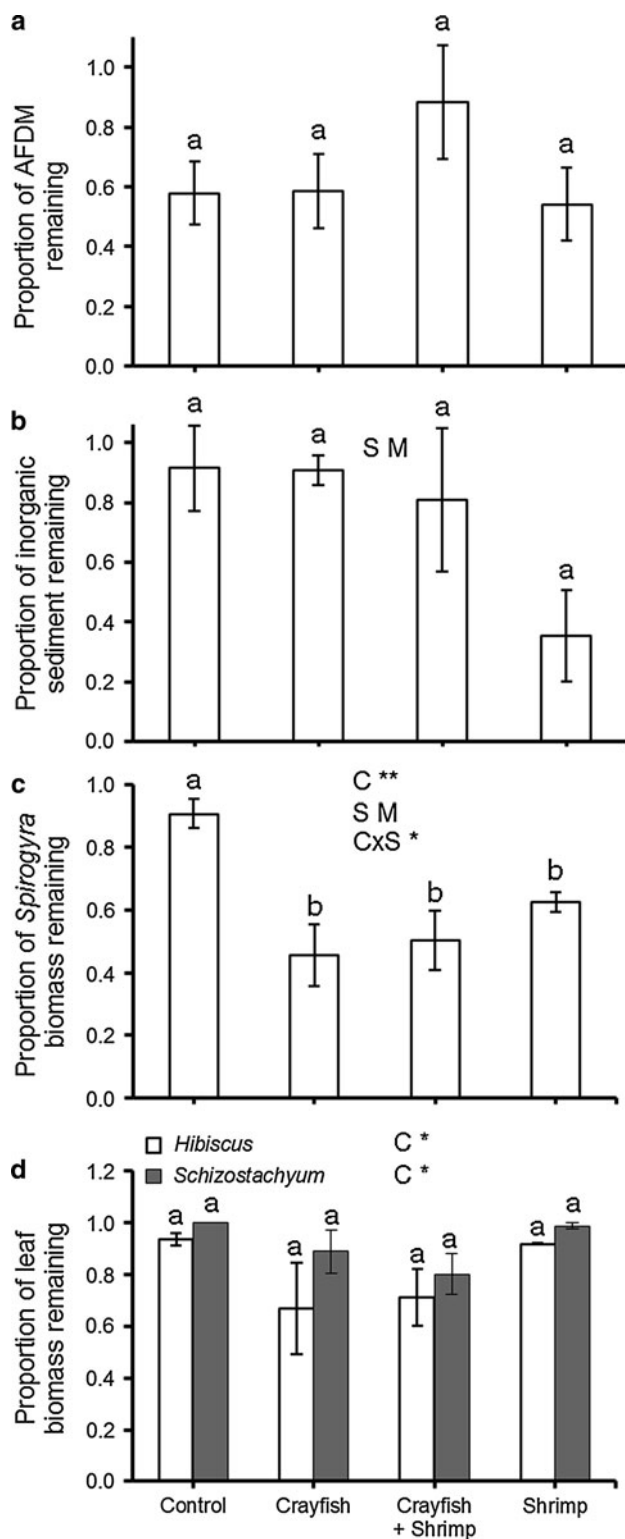


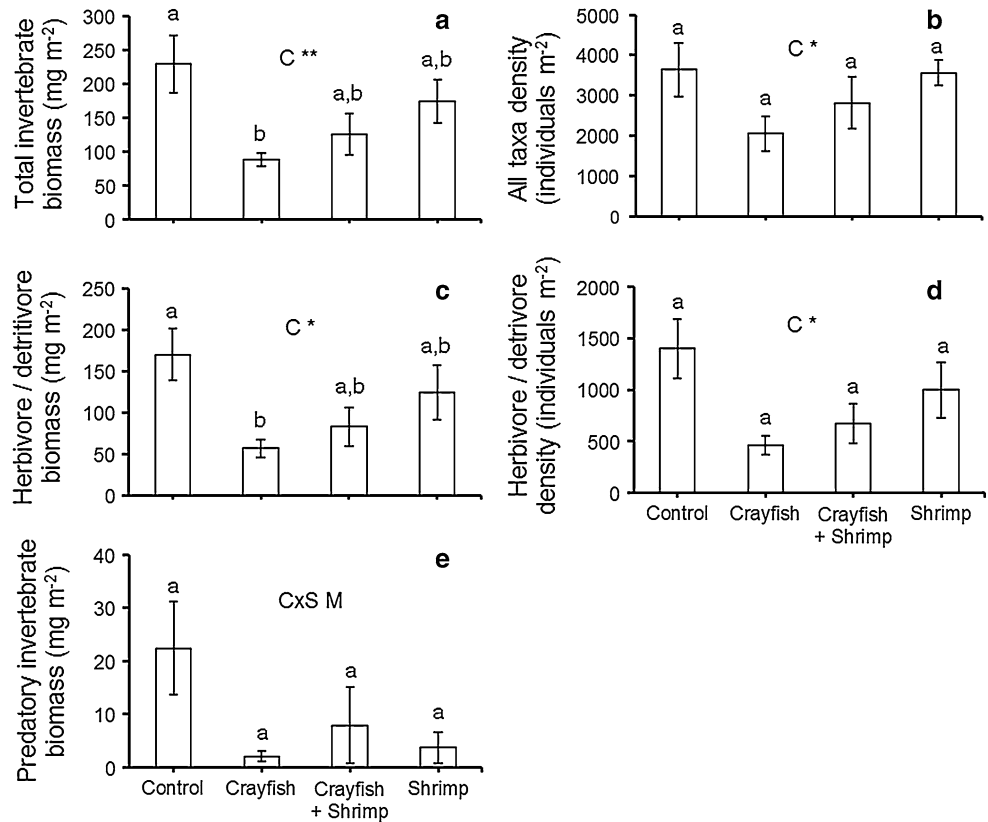
Fig. 5 Final proportions of **a** ash-free dry mass (AFDM), **b** inorganic sediment levels, and biomass of **c** *Spirogyra* and **d** *Hibiscus* and *Schizostachyum* remaining (i.e., final value/initial value) in experimental enclosures in Waiau Stream at the end of the experiment for each experimental treatment (mean \pm 1 SE). Uppercase letters represent the results of two-way ANOVAs performed on log-transformed response variables with *C* indicating a significant crayfish effect, *S* indicating a significant shrimp effect and *C* \times *S* indicating a significant crayfish \times shrimp interaction effect; bars with the same lowercase letters are not significantly different from one another based on Tukey's post hoc comparison at $P > 0.05$. Significance levels: ^M $P < 0.10$, * $P < 0.05$, ** $P < 0.01$

densities of the endemic mountain atyid shrimp in Hawaii. This contrast between crayfish effects on primary consumers in California versus Hawaii likely arose from differences in the vulnerabilities of fast-moving, evasive shrimp versus slow-moving snails to crayfish predation. Crayfish in California, and both crayfish and shrimp in Hawaii, marginally reduced the biomass or density of large, slow-moving predatory invertebrates, primarily odonates in California and flatworms in Hawaii, congruent with the results of previous experiments conducted in southern California (Klose and Cooper 2012). In contrast, total invertebrate and small herbivore/detritivore biomass and abundance were reduced by crayfish in Hawaii but not California, presumably because the dominant herbivores/detritivores were large oligochaetes in Hawaii, but smaller chironomids in California (chironomid mean length 6.4 ± 0.12 mm). In addition, oligochaetes were larger in Waiau Stream than the Ventura River (mean length 8.5 ± 1.4 vs. 5.2 ± 0.09 mm, respectively; t test: $t = -1.95$, $P < 0.05$), perhaps accounting for differences in the susceptibilities of this taxon to crayfish predation. Further, oligochaetes may have occupied refugia by burrowing into sand in California, but remained vulnerable to crayfish among the coarser substrata found in the Hawaiian stream.

Literature data also indicate that crayfish switch from feeding on large, slow-moving invertebrates to filamentous algae, then smaller invertebrates, and finally microalgae as preferred food sources become scarce (Dorn and Wojdak 2004). As predicted, crayfish in the Ventura River, and both crayfish and shrimp in Waiau Stream, reduced the biomass of filamentous algae, similar to previous findings (Hart 1992; Creed 1994; Dorn and Wojdak 2004). Consumption of filamentous algae by decapods can have many repercussions for stream communities, including reductions in the abundance of invertebrates associated with filamentous algae, increases in the abundance of sedentary invertebrate taxa competing with algae for attachment space, and increases in the biomass of microalgae (Creed 1994; Schofield et al. 2008; Klose and Cooper 2012). We did not observe such indirect effects of crayfish on other components of these stream communities; however, we tethered small amounts of filamentous algae in our

Klose 2011; Klose and Cooper 2012). Consistent with the literature, we found that crayfish reduced the abundance and altered the microdistribution of snails in the California stream (Lodge et al. 1994; Nyström et al. 1999; Klose 2011); however, crayfish had no significant effects on the

Fig. 6 Biomass of **a** total invertebrates, **c** herbivores/detritivores, and **e** predatory invertebrates, and the densities of **b** all taxa combined and **d** herbivores/detritivores (mean \pm 1SE) in stream channels assigned to each treatment at the end of the experiment in Waiiau Stream. *Uppercase letters* represent the results of two-way ANOVAs performed on log-transformed response variables with *C* indicating a significant crayfish effect and *C* \times *S* indicating a significant crayfish \times shrimp interaction effect; *bars with the same lowercase letters* are not significantly different from one another based on Tukey's post hoc comparison at $P > 0.05$. Significance levels: ^M $P < 0.10$, * $P < 0.05$, ** $P < 0.01$



enclosures, which replicated natural macroalgal cover in the streams but which may have resulted in muted indirect effects mediated through macroalgae compared to systems where substrata were covered or dominated by filamentous algae. In contrast to shrimp effects in Hawaii, we found that snails had no direct effects on filamentous algae biomass in the California stream, presumably because large filamentous algae are not easily handled or ingested by snails and, in some cases, may even benefit from snail removal of epiphytic diatoms attached to macroalgal filaments (Sarnelle et al. 1993).

Although leaf litter was largely absent from the Ventura River, it was abundant in Waiiau Stream and, as hypothesized, crayfish reduced hau and bamboo leaf litter in the Hawaiian stream. Other studies have shown that crayfish can reduce leaf litter in a variety of stream systems, often being the dominant shredders in systems with substantial allochthonous inputs (Usio 2000; Schofield et al. 2001; Zhang et al. 2004). Native shredders are largely absent in Hawaiian streams, and the invasive red swamp crayfish is often the sole shredder currently found in Hawaiian freshwaters (Larned et al. 2003). Shredders, such as crayfish, directly consume leaf material, reduce organic particle size, and enhance benthic organic matter accumulation (Gulis and Suberkropp 2003; Zhang et al. 2004). Because oligochaetes consume primarily fine particulate organic

matter, their dominance in Waiiau Stream may stem from the accumulation of benthic organic matter in this system; however, they appeared to be vulnerable to crayfish predation.

Although we predicted that crayfish would reduce benthic invertebrates in both systems, this outcome was only observed in Waiiau Stream. Total invertebrate, filter feeder, and Chironominae biomass, and Chironominae density, were higher in the crayfish alone and snail alone treatments than in the control and crayfish + snail treatments in the Ventura River. The mechanisms responsible for these results are unclear; however, it is possible that these taxa may have benefited from the effects of ecosystem engineering via the reduction of sediment levels by crayfish and snails, but with the reduction of sediment levels by snails rendering these taxa vulnerable to crayfish predation when both snails and crayfish were present (March et al. 2002; Mermillod-Blondin et al. 2004). That alteration of sediments by snails and crayfish may have been responsible, at least partly, for the observed responses of these invertebrates to treatment as supported by a negative relationship between total invertebrate biomass and sediment mass (Pearson's $r = -0.56$; $P = 0.03$). Crayfish effects on chironomid abundance reported in the literature have been inconsistent (Creed and Reed 2004; Usio and Townsend 2004; Nyström 2005; Klose and Cooper 2012), and in this

study ranged from complex effects in the Ventura River to no effects in Waiau Stream; however, chironomids were rare in Waiau Stream.

Crayfish reduced periphyton and sediment levels in the Ventura River, but not in Waiau Stream, presumably because of low microalgae and sediment levels and the abundance of alternative food sources (oligochaetes, leaf litter, filamentous algae) in Waiau Stream, consistent with our predictions of different crayfish effects on algal-based versus detrital-based food webs. Although we previously observed, and therefore predicted, that crayfish would decrease total invertebrate biomass and taxon diversity in the Ventura River (Klose and Cooper 2012), we did not observe these crayfish effects on these invertebrate variables in this study. In our previous field experiment in the Ventura River, crayfish reduced periphyton biomass and inorganic sediment, with resultant reductions in the abundance of the meiofauna; however, filamentous algae and snails were largely absent from experimental enclosures (Klose and Cooper 2012; see also Hart 1992; Creed and Reed 2004). In the results reported here, the addition of filamentous algae (*Cladophora*) and snails to experimental arenas apparently resulted in less pronounced effects of crayfish on periphyton biomass, sediment, and associated invertebrates (e.g., meiofauna) (Luttenton et al. 1998).

We also predicted that trophic or behavioral cascades would be observed in both systems, with crayfish-induced reductions in snail or shrimp densities or activity resulting in increases in algal and sediment levels (Fig. 1; Lodge et al. 1994; James et al. 2000). Such cascades assume that dominant primary consumers greatly reduce algal and sediment levels. In the Ventura River, snails greatly reduced periphyton and sediment levels, but had no effects on filamentous algae (see above), whereas in the Waiau Stream, shrimp had no effects on periphyton biomass, but marginally reduced sediment and filamentous algae levels. In California, crayfish greatly reduced snail densities and forced snails into refugia above the water line, precluding their grazing on periphyton, so sediment and periphyton levels increased when crayfish were present. In contrast, we observed no evidence for cascades in the Hawaiian stream, presumably because shrimp had no effects on periphyton biomass and because crayfish did not reduce shrimp densities. Although sediment levels were marginally higher where both shrimp and crayfish were present than where only shrimp were present, this did not appear to have an effect on algal or invertebrate abundances. Finally, it might be predicted that the addition of crayfish would reduce shrimp consumption of filamentous algae (*Spirogyra*), leading to higher filamentous algae biomass where crayfish and shrimp were found together than where shrimp were found alone; however, the negative impacts of crayfish on

filamentous algae biomass appeared to be stronger than the impacts of shrimp on this resource.

Although crayfish densities and the size and shape of experimental units used in the Ventura River and Waiau Stream were different, the results indicate that comparisons of crayfish effects on these two systems are valid. Klose and Cooper (2012) and Matsuzaki et al. (2009) found negative exponential relationships between invertebrate densities and macrophyte biomass, respectively, and crayfish density, suggesting that crayfish effects may have been similar across the range of crayfish densities used in our Californian and Hawaiian experiments. Similarly, McCarthy et al. (2006) found that crayfish effects on invertebrate taxa (i.e., gastropods, odonates, trichoptera, and amphipods) could be extrapolated accurately from small cages (0.2–4.7 m²) with high crayfish densities (0.8–30 individuals m⁻²) to whole lakes. These experimental scales and crayfish densities were comparable to those used in our studies (arena size 0.07 and 0.62 m², crayfish densities 14 and 3.2 m⁻² in Hawaii and California, respectively). Further, dominant crayfish food resources present in both systems were slow-moving or sedentary, including periphyton, filamentous algae, and chironomids in the Ventura River, and periphyton, filamentous algae, leaf litter, and oligochaetes in Waiau Stream. The design of enclosures limited resource exchange between the inside and outside of experimental arenas, with exchange points limited to fine mesh at the ends of long, rectangular channels (Ventura River) or to a limited number of small holes bored into the sides of cylindrical enclosures (Waiau Stream). Because there was limited or no exchange of these resources between the inside and outside of enclosures, crayfish effects would have been affected minimally by resource exchange rates (Englund et al. 2001). In addition, the sizes of end meshes or side holes of enclosures in both streams were fine enough to retain snails in California and atyid shrimp in Hawaii, so experiments constituted closed predation trials for these taxa, showing crayfish impacts on their populations in the absence of prey migration.

Assessments of the effects of a top invasive omnivore on resources in different streams systems (temperate mainland vs. tropical island) represent an important step in developing predictive models of crayfish impacts on different freshwater ecosystems. We suggest that predicting the net effects of omnivorous invaders on native communities, as well as determining the precise mechanisms for these effects, will remain difficult until we determine the vulnerability of different food types and species to invasive taxa as well as the precise composition of the recipient communities. Although short-term food preference trials appear to provide a reliable guide to the immediate effects of an invasive omnivore on native communities, flexibility in the omnivore's food habits, changing food resource

conditions, and longer term and larger scale prey responses to omnivores (e.g., shrimp moving into riffles and runs where fast current speeds exclude crayfish) may make the predictions of long-term impacts problematic.

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