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The influence of introduced trout on the benthic communities of paired headwater streams in the Sierra Nevada of California

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SUMMARY

1. Non-native trout have been stocked in streams and lakes worldwide largely without knowledge of the consequences for native ecosystems. Although trout have been introduced widely throughout the Sierra Nevada of California, U.S.A., fishless streams and their communities of native invertebrates persist in some high elevation areas, providing an opportunity to study the effects of trout introductions on natural fishless stream communities.

2. We compared algal biomass and cover, organic matter levels and invertebrate assemblages in 21 natural fishless headwater streams with 21 paired nearby streams containing stocked trout in Yosemite National Park.

3. Although environmental conditions and particulate organic matter levels did not differ between the fishless and trout streams, algal biomass (as chlorophyll *a* concentration) and macroalgal cover were, on average, approximately two times and five times higher, respectively, in streams containing trout.

4. There were no differences in the overall densities of invertebrates in fishless versus paired trout streams; however, invertebrate richness (after rarefaction), evenness, and Simpson and Shannon diversities were 10–20% higher in fishless than in trout streams.

5. The densities of invertebrates belonging to the scraper-algivore and predator functional feeding guilds were higher, and those for the collector-gatherer guild lower, in fishless than trout streams, but there was considerable variation in the effects of trout on specific taxa within functional feeding groups.

6. We found that the densities of 10 of 50 common native invertebrate taxa (found in more than half of the stream pairs) were reduced in trout compared to fishless streams. A similar number of rarer taxa also were absent or less abundant in the presence of trout. Many of the taxa that declined with trout were conspicuous forms (by size and behaviour) whose native habitats are primarily high elevation montane streams above the original range of trout.

7. Only a few taxa increased in the presence of trout, possibly benefiting from reductions in their competitors and predators by trout predation.

8. These field studies provide catchment-scale evidence showing the selective influence of introduced trout on stream invertebrate and algal communities. Removal of trout from

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targeted headwater streams may promote the recovery of native taxa, community structure and trophic organisation.

Introduction

Although predators are known to have profound effects on the densities, distributions and behaviours of many prey species, others appear to be unaffected. Questions about how and why the influence of predation varies in regulating the population dynamics and community structure of prey have led to an increasing research focus on the factors and circumstances which determine predator impacts (PI) on different prey taxa, and on the trophic organisation of different ecosystems (Sih *et al.*, 1985; Shurin *et al.*, 2002; Englund & Cooper, 2003).

Among the most widespread predators in cold-water streams are salmonid fishes, particularly trout in the genera *Salmo*, *Salvelinus* and *Oncorhynchus*, which have been introduced to streams and rivers around the world (MacCrimmon, 1971; Crowl, Townsend & McIntosh, 1992; Moyle & Cech, 1996; McDowall, 2006). The ecological roles of native and exotic trout have been studied in a variety of settings at differing spatial scales in streams, and study results have ranged from no effects to large impacts on invertebrate and algal abundances (Allan, 1982; Harvey, 1993; Wootton & Power, 1993; Diehl *et al.*, 2000; Nyström, McIntosh & Winterbourn, 2003; McIntosh, Peckarsky & Taylor, 2004). Because of these mixed results, scientists have continued to examine how trout affect lower trophic levels in streams in different regions, to determine if any generalities about the factors influencing trout impacts on prey, and their prey's food, can be derived (Meissner & Muotka, 2006).

Historically, river drainages above waterfall barriers (typically above 1800 m elevation) in the Sierra Nevada of California lacked fish; with extensive fish stocking, however, 90% of Sierra Nevada streams outside of the National Parks, and 60% inside the Parks, currently contain introduced trout populations (Moyle, Yoshiyama & Knapp, 1996a). Although recent studies have shown substantial impacts of introduced trout on zooplankton, benthic invertebrate and amphibian communities in Sierran lakes (Stoddard, 1987; Bradford *et al.*, 1998; Knapp *et al.*, 2005), the effects of trout on Sierran stream communities are unknown. Most high elevation streams in the Sierra lack native vertebrate species, so stream communities are dominated by benthic invertebrates which play central roles in food webs, show high levels of endemism (e.g. 25% of stonefly and 19% of caddisfly species; Erman, 1996), and act as sensitive indicators of environmental change (Herbst, 2004). The objectives of our research, then, were to compare algal biomass and cover, particulate organic matter levels, and the structure and diversity of benthic invertebrate communities in fishless headwater streams to those in paired, nearby, historically fishless streams now containing introduced trout. Because we did not manipulate trout directly, we matched environmental conditions between trout and fishless stream pairs as closely as possible to minimise the effects of confounding variables that could alter or obscure relationships between response variables and trout presence. We hypothesised that trout streams would have a lower diversity of native invertebrates, altered community and trophic structure, and elevated algal biomass compared to fishless streams. By generating data on introduced trout impacts, our results also provide recommendations for the management of native biodiversity and stream ecosystems in the Sierra Nevada.

Methods

Stream selection

Because trout have been stocked extensively in high altitude lakes and streams throughout the Sierra Nevada, few streams exist in their original, fishless state. To select study sites we first surveyed more than 100 headwater streams that we thought lacked trout based, in part, on information on trout distributions in Yosemite National Park (L. Marnell, unpubl. data). From these surveys, we found 68 fishless streams and selected 21 for detailed study. From topographic

maps, we then identified nearby candidate trout streams for pairing with these 21 fishless streams based on stream elevation, catchment aspect and area, location within the catchment, and proximity to the paired fishless streams (Table 1). These small headwater streams (first and second order) were shallow, open and very clear, permitting unobstructed views for confirming the presence or absence of fish. Further, most of these streams were not exposed to fishing or other human disturbances, so trout usually continued normal behaviour during observations. We located possible physical barriers (waterfalls and steep cascades) to trout migration on each fishless stream, then verified through visual observations that trout were found below but not above these barriers (i.e. habitat was appropriate but trout entry was blocked).

Field sampling

Surveys were conducted in early July through late September of the summers of 2000 and 2001, and all our paired sites were exposed to the same antecedent weather because they were always sampled within 1–2 days of each other. Stream sites ranged in elevation from 1348 to 3165 m, and were dispersed throughout the upper catchments of both the Merced and Tuolumne Rivers, the major drainages of Yosemite National Park.

At the upstream end of each 150-m study reach, we measured stream pH, temperature and conductivity using an Oakton model pH/Con10 meter (Oakton Instruments, Vernon Hills, IL, U.S.A.), and alkalinity with a LaMotte titration kit (LaMotte Company, Chestertown, MD, U.S.A.). Water samples were taken

Table 1 List of 21 paired stream study reaches in Yosemite National Park, by UTM coordinates (grid zone 11S) and elevation

Fishless stream name	UTM Northing (m)	UTM Easting (m)	Elevation (m)	Paired stream containing stocked trout	UTM Northing (m)	UTM Easting (m)	Elevation (m)
Eastern tributary to S.Fk. Tuolumne R.	4186313	256686	1689	North Crane Crk	4185241	251193	1433
Central tributary to S.Fk. Tuolumne R.	4185602	254120	1622	Western Trib to S.Fk. Tuolumne R.	4185096	253506	1666
Wildcat Crk	4178616	260536	1348	Coyote Crk - below barrier fall	4180867	261265	1890
S. Fk. Tuolumne River	4186880	262831	2331	Smokey Jack Crk (S. Fk. Tuolumne trib)	4188783	261639	2178
Upper Crane Crk tributary	4181580	254750	1840	Little Crane Crk	4180072	253952	1799
Lower Crane Crk tributary	4180048	256819	1623	Crane Crk	4181373	254385	1834
Gray Crk	4173048	283012	2415	Red Crk	4172687	282120	2326
Tributary to Clark Fork Illilouette Crk	4175373	282241	2549	Clark Fork Illilouette Crk	4173241	282639	2354
Coyote Crk – above barrier fall	4182506	261301	2146	Tamarack Crk	4183350	258511	1945
Avalanche Crk	4172500	261114	1701	Strawberry Crk	4168590	263892	1848
Meadowbrook Crk	4175904	264819	2073	Grouse Crk	4172627	264506	2067
Rock Crk	4214072	282880	2829	Rancheria Crk	4217193	279880	2784
Tributary to Rancheria Crk	4218880	281831	2845	Headwaters to Rancheria Cr.	4220542	283000	2850
Tributary to Chilnualna Crk	4162072	268663	2085	Chilnualna Crk	4163699	273759	2360
Kuna Crk	4184735	302928	3165	Lyell Fk. Tuolumne R.	4183000	300904	2976
Tributary to Conness Crk	4202241	294602	2951	Conness Crk	4203133	293747	2963
S. Fk. Cathedral Crk	4196024	280434	2659	Budd Crk	4193217	290024	2744
Piute Crk	4219120	288627	2957	Matterhorn Crk	4215819	288795	2848
Cascade Crk	4182193	262446	2163	Porcupine Crk	4186361	275675	2384
East Horizon Crk (below Horizon Ridge)	4170361	274422	2220	West Horizon Crk – below barrier fall	4170820	273928	2165
West Horizon Crk - above barrier fall	4170398	273964	2199	Starr King tributary to Illilouette Crk	4174193	276518	2006

for analysis of turbidity and, after filtration through GF/F filters and filtrate acidification, nutrient chemistry. Physical and biological habitat features, including water depth, substrata particle sizes and the presence or absence of macroalgae, were measured at three equally spaced points across the wetted width of each stream at each of 10 transects spaced at 15-m intervals along the reach, beginning at the lowest end and continuing upstream (for a total of 30 point-intercept observations per reach, encompassing both riffle and pool habitats). Riparian canopy cover was measured at the left bank, at the channel center upstream and downstream, and at the right bank using a concave densiometer (Platts *et al.*, 1987). Maximum stream depth was the deepest point recorded among all deep pools in a study reach. Stream gradient was measured with a clinometer over six 25-m intervals in each 150-m reach, latitude and longitude were recorded using a GPS unit, and the elevation of each reach was determined from USGS topographic maps.

Invertebrate samples were taken with a D-frame kick net (250 μm mesh, 30 cm opening, 0.093 m^2 sample area) from five riffles and five pools in each reach. We combined three samples from each riffle into a composite sample, giving 15 total riffle samples from each reach, whereas one sample was taken from each pool, for a total of 20 samples per study reach (*c.* 1.9 m^2). At each riffle sampling point, the bottom of the net frame was placed against the stream bottom and surface substrata within a 30 cm square area above the net were lifted, turned, and rubbed by hand, with dislodged invertebrates and organic material being swept into the net by currents. The length of the net bag (50 cm), and the typically narrow, shallow and swift stream conditions insured efficient collection with little loss of dislodged materials around the sides of the net or from back-wash. In pools, this process was aided by hand sweeping stirred materials into the net, as well as by sweeping the net through dislodged matter in the water column. Sample materials were placed in a small bucket, then repeatedly elutriated and filtered through a 100 μm mesh net, until all light material was removed, and preserved and stored in 95% ethanol. Remaining gravel and sand in elutriated samples was inspected for heavy taxa, such as cased caddisflies and molluscs, which were removed and added to storage bottles.

Each coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) sample consisted of three combined D-frame net collections, as for invertebrate samples, and were taken from each of three riffles in the lower, middle and upper 50 m of each sampling reach (total area per reach sampled = *c.* 0.85 m^2). All material collected in the 250 μm mesh net was washed into a small bucket, repeatedly elutriated to separate gravel and sand from organic material, then filtered through a 1 mm mesh net. After removal of large invertebrates from the 1 mm mesh collection, the CPOM (≥1 mm) material remaining in the net was blotted to remove excess water then weighed on a small Pesola scale (wet mass). The FPOM passing through the 1 mm mesh into a bucket was filtered through a 100 μm net after removal of conspicuous invertebrates, transferred to a storage vial, and preserved with 4% buffered formalin to prevent microbial degradation.

Epilithic algae samples were taken from three cobbles in each stream, with one cobble collected in the center of each of three, separate riffles, avoiding locations already sampled for POM or invertebrates. Each cobble was removed to a pan containing water, brushed with a nylon brush, and rinsed, then suspended material was stirred and passed through a fine net (100 μm) into a graduated cylinder with any macroalgae retained in the net being added to the cylinder. The total volume of the filtered suspension was recorded, then homogenised by repeated suction and expulsion using a 60 mL syringe, and a subsample filtered through a pre-weighed glass fibre filter (GF/F). The filtered material was protected from microbial degradation with a drop of buffered formalin and the filter then folded into aluminium foil to prevent exposure to light, and stored in an ice chest (usually not more than 1 day) before storage in a freezer. The length, width, height and circumference of each sampled cobble were recorded to obtain a measure of the upper cobble surface area so that areal chlorophyll concentration could be calculated.

All field survey and sample processing methods were identical across all of the stream sites surveyed, insuring that the values of all response variables could be rigorously compared between paired streams.

Laboratory methods

The ash-free dry mass (AFDM) of FPOM was determined by drying FPOM samples overnight at 75 °C, then measuring the weight lost from these samples

after 3 h at 550 °C in a muffle furnace. Chlorophyll *a* concentration was measured on a Turner Model No. 110 Fluorometer using a 90% ethanol extraction method (Sartory & Grobbelaar, 1984). We measured soluble reactive phosphorus (SRP) using the ammonium molybdate method, nitrate–nitrite ($NO_3 + NO_2$) using the cadmium reduction column method, and ammonia (NH_3) using the phenol-hypochlorite method for each of the duplicate samples from each stream (American Public Health Association (APHA), American Water Works Association and Water Environment Federation, 1992). Turbidity was measured on an Orbeco-Hellige Model 966 Turbidimeter (Orbeco-Hellige Inc., Sarasota, FL, U.S.A.).

Random subsamples of macroinvertebrates were obtained using a Folsom plankton splitter so that 300–1000 organisms were identified and counted in each subsample. Invertebrates were identified to the lowest practical taxonomic level, usually genus or species, although some taxa represented coarser levels of taxonomic resolution. We also searched the unprocessed remnant of each entire sample for large and/or rare taxa that did not occur in the processed subsample and single specimens of these taxa were included in the count.

The length and gradient of the upstream catchment were estimated for each stream site based on USGS topographic maps (1 : 24 000 scale). The cumulative length of perennial streams above each site (upstream length) was measured as the sum of the lengths of the main stem and all perennial tributaries upstream of the sampled reach. The average gradient of perennial streams in the catchment (upstream gradient) above each study site was measured as the summed elevation gains of the main stem and all tributaries upstream to the headwater origins divided by total upstream length.

Data analysis

Mean values of environmental variables (e.g. nutrient concentrations, physical characteristics, canopy cover) were used to characterise conditions in each stream reach. We calculated invertebrate densities based on the fraction of each sample that was sorted and the bottom area sampled, and used mean densities for each invertebrate taxon from each stream reach as the replicates in statistical analyses. The final mean densities for each study reach were obtained by averaging density estimates for the five composite riffle samples and five pool samples, equalising the representation of riffle and pool habitats so that there was no geomorphic bias when comparing paired sites. Although they usually did not affect conclusions, some pool-riffle differences are presented in more detail later in this paper. We used paired *t*-tests to compare values for most environmental variables in fishless versus paired trout streams and paired Wilcoxon signed-rank tests for comparing biological response variables across paired streams (community metrics, algae and detrital resources, and densities of 50 'common' invertebrate taxa). We used the Wilcoxon signed-rank test for biological data because transformation did not meet parametric assumptions and could not be applied to the positive and negative values found for paired differences in taxa densities between trout and fishless streams. Although sacrificing quantitative information, this test could be applied uniformly across all common taxa and was statistically appropriate for the paired study design. We defined 'common' as invertebrate taxa having a mean relative abundance across all streams greater than 0.1% and/or which were present in at least half of the stream pairs sampled (11 or more of the 21 pairs). Community and resource metrics included the biomass of benthic algae (measured as chlorophyll *a* concentration), macroalgal cover, levels of CPOM and FPOM, the total densities (with and without Chironomidae), richness [standardised via rarefaction using Hurlbert's (1971) formulae], evenness (Pielou, 1966), and Simpson and Shannon diversities of invertebrates, and densities of invertebrate functional feeding groups. We assigned invertebrate taxa to grazer-scraper, predator (not including water mites and ceratopogonids which were classified as micropredators), filterer, shredder and collector-gatherer functional feeding groups based on the designations in Merritt, Cummins & Berg (2008), but excluding undifferentiated Chironomidae because of their possible assignment to multiple functional groups.

We used both absolute and/or relative differences in invertebrate and functional feeding group (FFG) densities, and algal biomass, between fishless and trout streams as indicators of trout impacts. Absolute differences provide a measure of changes in invertebrate taxa or functional feeding group densities in response to trout presence, whereas the log ratio of invertebrate or functional feeding group density in trout versus

fishless streams (i.e. $\ln[(x+1)_{\text{trout}}/(x+1)_{\text{no trout}}]$) provides a standardised index of proportionate trout effects on response variables, has a variety of desirable statistical properties, and can be related to an extensive theoretical and empirical literature on predator effects on prey populations (Hedges, Gurevitch & Curtis, 1999; Osenberg *et al.*, 1999). These measures of cascade strength (for resources) and PI (for invertebrate taxa) were calculated for each stream pair where the resource or taxon was found, and means (±2 SEs, *c.* confidence interval) were calculated from these families of values from paired streams.

Differences in the structure (i.e. taxonomic composition and relative abundances of component taxa) of invertebrate assemblages between trout and troutless streams also were examined using Non-metric multidimensional scaling (NMDS, Sammon's algorithm implemented in S-Plus; Insightful Corp, 2001), which displayed relationships among streams in two-dimensional space based on stream-to-stream similarities in invertebrate assemblages. We calculated Bray–Curtis distances between all pairs of streams using relative abundance data for all taxa collected at each site. The Bray–Curtis metric provides linear increases in weighting as the relative abundances of component species increase and performs as well or better than comparable similarity measures in capturing simulated ecological patterns when used with proportional data (Faith, Minchin & Belbin, 1987).

Results

Environmental conditions

All physical, chemical and geomorphic variables were similar in fishless and trout streams (Table 2). The close matching of environmental conditions in fishless and trout streams was apparent both when comparing the range and mean values of habitat variables over all trout to all fishless streams as well as when examining the differences between paired trout and fishless streams.

Algal and organic matter responses

Algal biomass (measured as chlorophyll *a* concentration) and macroalgal cover were significantly greater

Table 2 Comparisons of the means (±1 SE), ranges, mean differences and statistical differences of values of environmental variables in 21 streams containing trout and 21 paired streams lacking trout (i.e. fishless streams)

Variable	Fishless streams, mean (SE)	Trout streams, mean (SE)	Range in fishless streams	Range in trout streams	Mean difference (trout − fishless)	*P*-value (Paired *t*-test)
Elevation (m)	2258 (112)	2258 (100)	1348–3165	1433–2976	0.4	0.99
Average wetted stream width (cm)	203 (17.5)	222 (20.6)	89–471	69–447	19.0	0.22
Average stream depth (cm)	13 (1.0)	14 (1.3)	7–22	6–34	0.8	0.59
Maximum stream depth (cm)	39 (3.2)	42 (4.4)	20–85	15–97	2.5	0.61
Length of headwaters (km)	3.1 (0.5)	3.6 (0.5)	0.6–7.1	0.7–9.7	0.5	0.38
Gradient of sampled reach (%)	5.7 (0.6)	5.3 (0.5)	0.9–13.7	0.7–11.9	−0.4	0.47
Average gradient of headwaters (%)	10.9 (1.4)	10.7 (1.1)	3.0–29.3	3.0–18.6	−0.1	0.94
Canopy cover (%)	35 (5.1)	40 (5.7)	10–80	1–89	4.5	0.21
Water temperature (°C)	13 (0.6)	12 (0.5)	8–17	8–17	−0.4	0.41
pH	6.0 (0.1)	6.0 (0.2)	4.7–7.2	4.3–7.8	−0.02	0.92
Conductivity ($\mu S\ cm^{-1}$)	27 (3.5)	30 (7.3)	5–55	5–162	3.4	0.63
Alkalinity ($mg\ L^{-1}\ CaCO_3$)	25 (2.0)	27 (4.2)	12–49	6–96	2.6	0.52
Turbidity (NTU)	1.6 (0.2)	1.5 (0.2)	0.2–2.6	0.3–2.7	−0.05	0.51
Soluble reactive phosphorus (μM)	33 (5.4)	30 (7.1)	2–84	0–153	−3.4	0.60
Nitrate + Nitrite ($\mu g\ L^{-1}$)	10 (3.1)	15 (5.8)	0–57	0–105	5.3	0.78*
Ammonia (μM)	24 (3.0)	27 (4.2)	0–46	1–69	3.4	0.43
Riffle area (%)	39 (3.0)	38 (3.4)	15–59	7–66	−0.6	0.84
Pool area (%)	28 (2.8)	30 (2.7)	14–75	14–59	2.2	0.41
% Fine substrata (%, size <1 mm)	2 (1.1)	2 (0.7)	0–18	0–12	−0.7	0.79*
% Sand substrata (1 mm < size <3 mm)	13 (2.2)	16 (2.7)	0–32	0–40	3.2	0.21
% Gravel substrata (3 mm < size < 65 mm)	30 (3.0)	27 (3.2)	10–53	8–60	−3.2	0.22
% Cobble substrata (6.5 cm < size < 25 cm)	26 (2.7)	29 (3.0)	7–50	0–58	3.6	0.38
% Boulder substrata (size > 25 cm)	29 (4.2)	26 (4.4)	0–68	0–60	−2.8	0.55

*Wilcoxon signed-rank tests were used for these parameters because their values were not normally distributed.
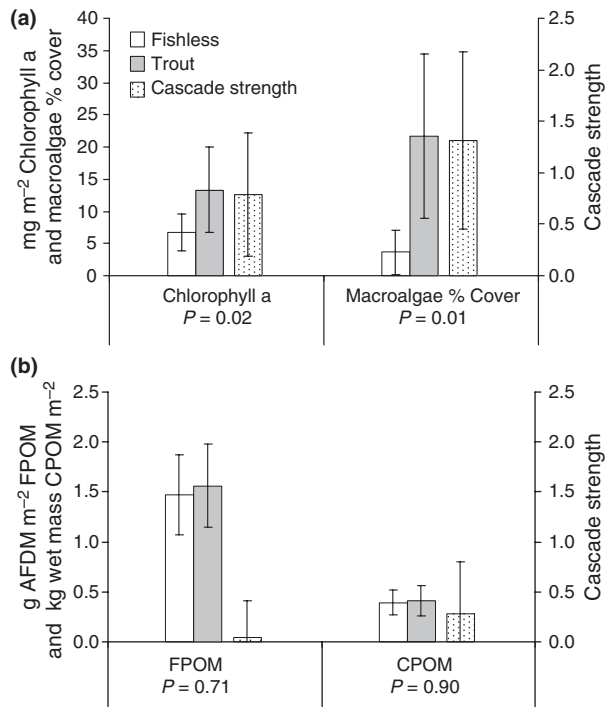
Fig. 1 (a) Average periphyton biomass (as mg chlorophyll *a* m^{-2}) (±2SE) and percent macroalgae cover (±2SE) in fishless and paired trout streams, with associated measures of mean cascade strength (±2SE). (b) Mean FPOM (fine particulate organic matter levels, in g AFDM m^{-2}) (±2SE) and CPOM (coarse particulate organic matter levels, in kg wet mass m^{-2}) (±2SE) in fishless and paired trout streams, with associated measures of mean cascade strength (±2SE). For both panels *n* = 21 for each stream group. Cascade strength was calculated as [ln(value in trout stream/ value in paired fishless stream)], except for macroalgae percent cover, where 3.3%, the lowest observable value, was added to each value. *P*-values refer to the results of paired Wilcoxon signed-rank tests.

in streams with introduced trout than in paired fishless streams (Fig. 1). Algal biomass was typically 57% (median) to 98% (mean) higher in trout than fishless streams, and macroalgae cover increased from an average of 4% in fishless streams to 22% in trout streams, primarily owing to five stream pairs where macroalgal cover was 0% in the fishless streams and 40–80% in the paired trout streams. There were no significant differences in FPOM or CPOM levels between fishless and paired trout streams (Fig. 1).

Invertebrate assemblage and trophic structure

We collected 171 invertebrate taxa across all streams in this study, and have amalgamated those into 109 taxa because an individual taxon dominated a group

or because some taxa within a group could not be easily distinguished (Tables 3 & 4). Of these 109 taxa, 50 were designated as 'common' and another 32 were designated as 'uncommon' (occurring in 3–10 stream pairs and at a relative abundance of <0.1%). The results for the remaining 27 rare taxa, with the exception of one taxon of special interest (i.e. *Edmundsius agilis*), are not treated in this paper.

The total abundance of invertebrates (excluding and including the numerically dominant but small Chironomidae) was similar in trout and troutless streams (Fig. 2a). Community evenness, taxa richness (standardised via rarefaction), and Simpson and Shannon diversities, however, were significantly lower in streams with than without introduced trout.

Although other analyses indicated that portions of the invertebrate community were altered by trout (see below), multivariate ordination of the full invertebrate assemblage data (excluding Chironomidae, which were identified to family) revealed no clear patterns in the distribution of fishless and trout streams in two-dimensional ordination space (Fig. 3, stress = 0.09; ordination similar with Chironomidae included). Paired Wilcoxon signed-rank tests on NMDS axis scores for trout versus paired fishless streams provided little evidence that this pattern was non-random (*P* = 0.22 for axis 1, *P* = 0.16 for axis 2). In general, fishless–trout stream pairs were neither closer together (more similar) or further apart from one another than they were to other streams.

In contrast to the multivariate results, the abundances of some functional feeding groups appeared to be affected by trout presence (Fig. 2b). The abundances of invertebrate grazer/scrapers and predators were reduced, the densities of filterers and shredders were relatively unaffected, and the abundances of collector-gatherers were elevated in the presence versus absence of trout (Fig. 2b).

Invertebrate abundance

Although the densities of several functional feeding groups were different in trout versus fishless streams, we also found substantial variation in the responses of individual taxa to trout presence, even within a functional feeding group. Densities of seven common invertebrate taxa consistently declined from fishless to trout streams across all but one or two stream pairs (Table 3). These seven common taxa included one

Table 3 Common taxa (≥11 pairs, or having >0.1% relative abundance) ordered from most negative (indicating more abundant in fishless than trout streams) to most positive (more abundant in trout than fishless streams) predator impact values (2 SE or *c.* 95% confidence limits). Also presented are the number of stream pairs (out of 21) where a taxon was found, the number of those pairs where density declines were observed in the presence of trout, overall relative abundances of each taxon across all streams, mean (±1 SE) densities (no. m⁻²) of each taxon in fishless and paired trout streams, the results of Wilcoxon paired signed-rank tests on taxon densities in paired trout and fishless streams, and functional feeding group (FFG) designations

Taxon	Average predator impact	2 SE of PI	No. pairs where found	No. pairs where taxon declines with trout	Relative abundance over all streams (Mean %)	Fishless streams		Trout streams		P-value (Wilcoxon sign-rank test)	FFG
						Mean no. m⁻²	SE	Mean no. m⁻²	SE		
Neothremma Dodds & Hisaw (T)	−2.89	1.37	14	12	0.60	150	72	3.2	1.4	0.003	G
Doroneuria baumanni Stark & Gaufin (P)	−2.15	1.03	16	15	0.59	132	31	30	8	0.0001	P
Tricladida	−2.02	0.71	21	20	0.68	177	45	34	13	0.000003	P
Yphria californica (Banks) (T)	−1.70	0.89	11	10	0.03	11	5	1.9	1	0.02	P
Anagapetus Ross (T)	−1.17	0.90	11	9	0.17	43	15	24	10	0.03	G
Hydropsychidae (*Parapsyche* Betten) (T)	−1.16	0.85	19	14	0.47	117	38	38	13	0.03	F
Hesperoperla Banks (P)	−1.08	1.00	11	9	0.10	28	11	10	3.6	0.02	P
Ameletus Eaton (E)	−0.94	0.43	21	19	0.90	181	28	64	10	0.00001	G
Dolophilodes Ulmer (T)	−0.91	1.76	8	7	0.10	24	13	16	10	0.14	F
Yoraperla Ricker (P)	−0.83	1.15	19	11	0.41	83	26	38	13	0.21	Sh
Paraleptophlebia Lestage (E)	−0.77	1.00	21	15	1.48	321	67	158	33	0.02	Cg
Dixa Meigen (D)	−0.67	0.61	16	11	0.03	6.9	2	3.3	1	0.04	Cg
Pisidium L.Pfeiffer (B)	−0.65	1.11	17	11	0.10	22	8	11	6	0.12	F
Hexatoma Latreille (D)	−0.54	0.73	21	9	0.26	48	9	34	7	0.42	P
Ecclisomyia Banks (T)	−0.53	0.76	15	8	0.22	28	8	31	15	0.51	Cg
Cryptochia Ross (T)	−0.47	0.69	12	7	0.02	3.7	1.5	1.2	0.4	0.08	Sh
Heptageniidae (*Cinygmula* McDunnough) (E)	−0.46	0.61	21	14	2.42	612	272	220	41	0.27	G
Polycentropus Curtis (T)	−0.43	1.33	15	8	0.20	35	15	19	7	0.49	P
Apatania Kolenati (T)	−0.43	0.89	19	11	0.51	110	33	51	9.6	0.13	G
Oreodytes Seidlitz (C)	−0.43	1.46	12	7	0.05	5.8	3.1	10	8	0.97	P
Leuctridae (*Despaxia augusta* (Banks)) (P)	−0.36	0.91	15	9	0.16	17	5	18	7	0.64	Sh
Chloroperlidae (*Sweltsa* Ricker) (P)	−0.29	0.44	21	14	1.24	161	19	120	18	0.11	P
Lepidostoma Rambur (T)	−0.16	1.10	16	9	0.44	85	38	89	55	0.90	Sh
Oligochaeta	0.08	0.53	21	10	1.21	142	21	202	47	0.43	Cg

Table 3 (*Continued*)

Taxon	Average predator impact	2 SE of PI	No. pairs where found	No. pairs where taxon declines with trout	Relative abundance over all streams (Mean %)	Fishless streams Mean no. m^{-2}	Fishless streams SE	Trout streams Mean no. m^{-2}	Trout streams SE	P-value (Wilcoxon sign-rank test)	FFG
Elmidae (*Optioservus* Sanderson) (C)	0.08	1.37	17	9	0.49	38	18	122	75	0.92	Cg
Rhyacophila Pictet (mixed groups) (T)	0.09	0.27	21	10	0.83	136	27	127	17	0.79	P
Sialis Latreille (M)	0.10	0.99	16	6	0.15	26	15	17	6	0.76	P
Acari	0.10	0.37	21	12	5.03	754	112	783	92	1.00	mP
Bezzia Kieffer (D)	0.14	0.79	21	8	0.92	131	28	258	139	0.54	mP
Micrasema McLachlan (T)	0.15	0.86	20	9	1.58	426	239	244	83	0.62	Sh
Psychoglypha Ross (T)	0.18	0.95	12	4	0.05	5.7	2.4	4.5	1.5	1.00	Cg
Ostracoda	0.20	1.33	18	8	2.23	267	102	662	396	0.65	Cg
Nemouridae (*Zapada* Ricker) (P)	0.20	0.56	21	8	4.06	704	215	714	124	0.41	Sh
Oreogeton Schiner (D)	0.21	0.90	15	7	0.03	6.2	2.5	4.7	1.3	0.82	P
Calineuria californica (Banks) (P)	0.26	0.92	16	10	0.16	26	10	22	8	0.44	P
Chelifera Macquart (D)	0.29	0.67	21	9	0.22	43	14	33	7	0.75	P
Dicranota Zetterstedt (D)	0.29	0.62	21	8	0.18	22	5	26	5	0.45	P
Chironomidae (D)	0.34	0.40	21	8	59.94	8609	1320	12235	2229	0.10	mix
Baetis Leach (E)	0.35	0.67	21	9	5.37	996	246	892	186	0.52	Cg
Caudatella Edmunds (E)	0.43	1.25	19	9	0.44	65	26	51	15	0.98	Cg
Perlodidae (*Isoperla* Banks, *Cultus* Ricker) (P)	0.52	0.64	21	9	0.43	51	9	70	15	0.43	P
Capniidae (P)	0.55	0.71	20	8	1.29	133	40	177	54	0.57	Sh
Rhabdomastix Skuse (D)	0.57	0.85	11	3	0.01	1	0.4	2.1	0.8	0.33	P
Drunella spinifera (Needham) (E)	0.59	1.35	20	9	0.40	27	8	80	26	0.18	G
Serratella Edmunds (E)	0.63	1.26	20	8	1.40	235	71	279	85	0.57	Cg
Drunella coloradensis (Dodds) (E)	0.79	0.95	11	4	0.05	8.5	4.1	8.4	2.6	0.66	G
Simuliidae (*Simulium* Latreille) (D)	0.84	1.01	21	8	0.63	87	28	127	37	0.19	F
Hydroptilidae (mixed) (T)	0.97	1.48	16	5	0.38	60	37	43	13	0.32	Pi
Drunella doddsi (Needham) (E)	1.08	1.27	17	5	0.25	16	8	40	13	0.14	G
Centroptilum Eaton (E)	1.18	1.11	13	3	0.38	17	9	153	106	0.03	Cg

Functional feeding group (FFG) designations assigned to each taxon are as follows: G, scraper-grazer; Sh, shredder; F, filterer; Cg, collector-gatherer; Pi, piercer; mP, micropredator; and P, predator (macro). The family Chironomidae included taxa from a mix of functional feeding groups. The dominant genus found within the listed families are shown in parentheses, followed by letter abbreviation of order (E, Ephemeroptera; P, Plecoptera; T, Trichoptera; D, Diptera; C, Coleoptera; M, Megaloptera; H, Hemiptera) or class (B, Bivalvia; subclass Lamellibranchia).

Table 4 Uncommon taxa [defined as those present in 3–10 stream pairs and having <0.1% relative abundance, including one taxon of special interest (*Edmundsius*)] ordered from most negative (indicating more abundant in fishless than trout streams) to most positive (more abundant in trout than fishless streams) predator impact values (2 SE or *c.* 95% confidence limits). Also presented are the number of stream pairs (out of 21) where a taxon was found, the number of stream pairs where density declines were observed in the presence of trout, overall relative abundances of each taxon across all streams, mean (and 1 SE) densities (no. m^{-2}) of each taxon in fishless and paired trout streams, and functional feeding group (FFG) designations

Taxon	Average predator impact	2 SE of PI	No. pairs where found	No. pairs where taxon declines with trout	Relative abundance over all streams (Mean %)	Fishless streams Mean no. m^{-2}	SE	Trout streams Mean no. m^{-2}	SE	FFG
Edmundsius agilis Day (E)	−2.76	0.95	2	2	0.004	1.6	1.2	0	0	Cg
Dysmicohermes ingens Chandler (M)	−2.13	0.70	6	6	0.007	3.2	1.8	0	0	P
Hesperoconopa Alexander (D)	−2.03	1.02	4	4	0.02	2	1.4	0	0	Cg
Attenella delantala (Mayo) (E)	−1.94	0.34	4	4	0.016	5.2	3.5	0.5	0.3	Cg
Agabinus Crotch (C)	−1.82	0.55	5	5	0.004	1.5	0.8	0	0	P
Graptocorixa californica (Hungerford) (H)	−1.72	0.85	6	6	0.008	2.5	1.8	0	0	P
Chyranda centralis (Banks) (T)	−1.38	0.63	3	3	0.002	0.5	0.3	0	0	Sh
Agabus Leach (C)	−1.34	0.83	5	5	0.004	1.2	0.9	0	0	P
Neophylax McLachlan (T)	−1.10	0.91	5	4	0.013	4	2.7	0.7	0.4	G
Thaumalea Ruthe (D)	−1.00	2.60	3	2	0.004	1.6	1.5	0.1	0.1	G
Moselia infuscata (Claassen) (P)	−0.85	0.95	10	8	0.055	8.1	3.2	3.2	1.5	Sh
Dicosmoecus McLachlan (T)	−0.83	1.70	6	5	0.021	3.5	3.3	0.4	0.4	Cg
Siphlonurus Eaton (E)	−0.50	3.22	5	3	0.02	8.8	8.3	4.1	4	Cg
Meringodixa chalonensis Nowell (D)	−0.20	1.13	9	5	0.006	1	0.5	1	0.7	Cg
Desmona Denning (T)	−0.19	1.99	5	3	0.01	1	0.5	5.4	5.3	Sh
Glutops *Burgess* (D)	−0.17	0.88	8	5	0.059	6.2	3.6	5.2	2.8	P
Nematomorpha	−0.13	2.52	3	2	0.002	0.3	0.3	0.4	0.4	P
Stictotarsus Zimmermann (C)	−0.11	2.49	7	4	0.036	3.3	1.8	5.3	3.9	P
Orohermes crepusculus (Chandler) (M)	−0.05	1.77	5	3	0.008	1.7	1.2	1.3	0.8	P
Hydraenidae (C)	0.06	1.85	5	3	0.003	0.6	0.6	1	1	P
Heteroplecton californicum McLachlan (T)	0.06	1.07	9	6	0.065	13.6	8	15.6	7.1	Sh
Pedomoecus sierra Ross (T)	0.20	2.48	4	1	0.011	2	1.4	1.7	1.1	G
Tipula Linnaeus (D)	0.20	1.11	4	2	0.002	0.2	0.1	0.2	0.2	Sh
Hydroporus Clairville (C)	0.21	2.17	8	3	0.068	5.7	4	6.9	5.2	P
Atrichopogon Kieffer (D)	0.28	0.95	8	2	0.022	4.7	2.5	3.3	1.5	mP
Hydrophilidae (C)	0.62	1.56	5	2	0.002	0.2	0.1	0.9	0.6	P
Antocha monticola Alexander (D)	0.62	1.38	8	2	0.022	4.6	2.9	4.7	2.5	Cg
Eucapnopsis brevicauda Claassen (P)	0.64	1.65	6	2	0.005	0.5	0.3	1.5	0.9	Sh
Limonia Meigen (D)	0.79	0.97	6	2	0.005	0.3	0.2	0.9	0.4	Sh
Muscidae (D)	1.05	1.51	3	1	0.002	0.02	0.02	0.5	0.4	P
Pericoma Walker (D)	1.17	1.44	9	3	0.063	1.9	0.8	34	26.1	Cg
Gumaga Tsuda (T)	1.54	2.64	4	1	0.044	3.7	2.6	9.8	7	Sh
Glossosoma Curtis (T)	2.27	1.54	6	1	0.015	0.1	0.1	6	3	G

Functional feeding group (FFG) designations assigned to each taxon are as follows: G, scraper-grazer; Sh, shredder; F, filterer; Cg, collector-gatherer; Pi, piercer; mP, micropredator; and P, predator (macro). Taxon names are followed by letter abbreviations of order in parentheses (E, Ephemeroptera; P, Plecoptera; T, Trichoptera; D, Diptera; C, Coleoptera; M, Megaloptera; H, Hemiptera).
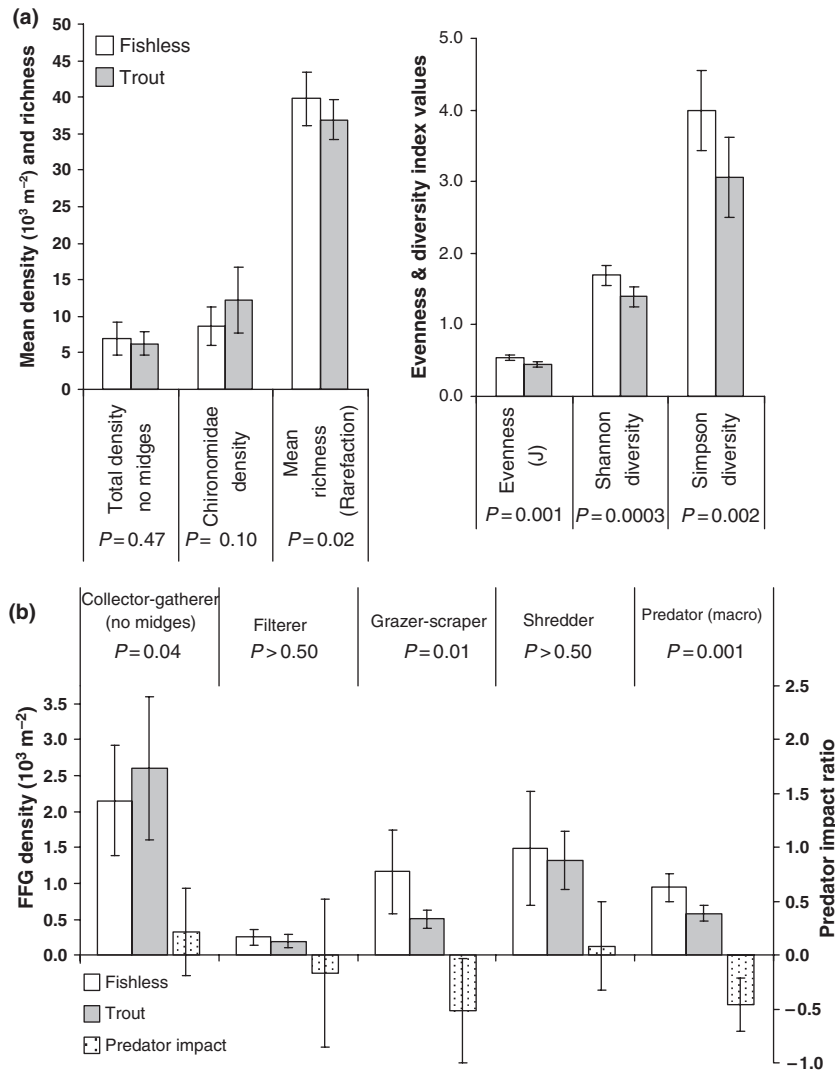
Fig. 2 (a) Comparisons of average community metrics in fishless and paired trout streams (±2SE), including total invertebrate density (without midges), total chironomid (midge) density, invertebrate richness (computed by rarefaction), and evenness and diversity measures. (b) Densities of the primary functional feeding group categories in fishless and paired trout streams (±2SE), as well as the predator impact ratios (PI) for each (±2SE). Mean PIs are significantly ($P < 0.05$) different from 0 if their error bars (±2SE), representing approximate 95% confidence limits, do not overlap zero. Negative PI values indicate taxa with higher densities in fishless than paired trout streams, whereas positive PI values indicate the opposite. The predator category excluded micropredators, such as the Ceratopogonidae and Acari, and Chironomidae were excluded from functional feeding group analyses. *P*-values in both (a) and (b) represent the results of paired Wilcoxon signed-rank tests.

mayfly (*Ameletus*), two Perlidae stoneflies (*Doroneuria baumanni* and *Hesperoperla*), three cased caddisflies (*Anagapetus*, *Yphria californica* and *Neothremma*) and one non-insect taxon (Tricladida flatworms). For three of these invertebrate taxa (*Ameletus*, *Doroneuria baumanni* and Tricladida flatworms), declines in abundance from fishless to fish streams were highly significant ($P < 0.001$), falling below Bonferroni correction thresholds for statistical significance (i.e. 0.05/50 = 0.001 for the 50 'common' taxa evaluated statistically). For the remaining four of these seven taxa, *P*-values for statistical tests fell between 0.05 and 0.001, providing strong evidence that patterns were non-random. Large declines from fishless to trout streams (and *P*-values <0.05) also were observed for the mayfly *Paraleptophlebia*, the net-spinning caddisfly

family Hydropsychidae (mostly *Parapsyche*), and the dipteran *Dixa*, whereas nymphs of the mayfly *Centroptilum* were one of the few taxa found to be more abundant in trout streams compared to paired fishless streams. There were suggestive differences in densities for a number of other taxa between trout and paired fishless streams, including the Chironomidae being higher ($P = 0.10$, Table 3) and the caddisfly *Cryptochia* being lower ($P = 0.08$, Table 3), in trout compared to paired troutless streams.

We note, however, that statistical power was insufficient to detect potential trout effects in a number of these tests because of high variability in the difference estimates among stream pairs. Even relatively large differences between fishless and paired trout streams did not always provide strong ($P < 0.05$) statistical
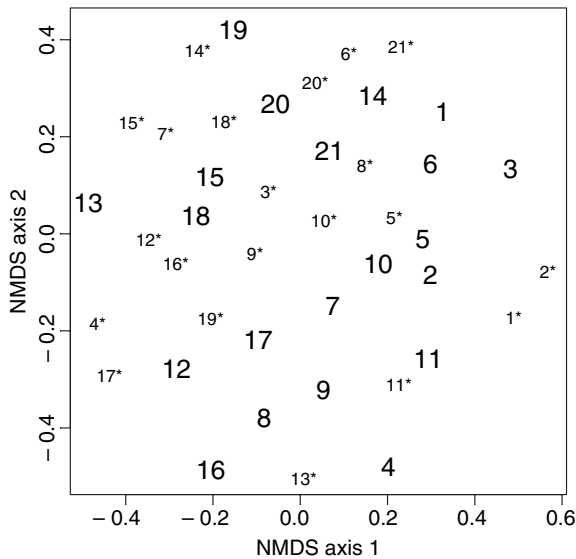
Fig. 3 Non-metric multidimensional scaling (NMDS) ordination of Bray–Curtis distances among mean stream vectors (stress = 0.09; proportional abundances of all taxa except Chironomidae used in analysis). The stream number represents each stream pair with trout streams indicated in small font with an asterisk (*), and paired fishless streams indicated with large, bold font.

evidence that patterns were non-random, and test power was drastically reduced by the application of Bonferroni corrections (Gotelli & Ellison, 2004). For example, the median difference between trout and troutless streams for Chironomidae abundance translates to a 45% increase in this group in trout streams, but the results of the Wilcoxon signed-rank test did not meet either a simple ($\alpha = 0.05$) or comparison-wise adjusted error rate ($\alpha = 0.001$, Bonferroni correction) for rejecting the null hypothesis of no effect. Although *post hoc* power analyses have critical limitations for evaluating the statistical power of such tests (Hoenig and Heisey 2001), confidence intervals around the PI index (Table 3) not only corroborated results obtained from the Wilcoxon signed rank test, but also suggested additional cases (where the confidence limits for PI values barely overlap zero) of trout effects where the tests were equivocal (e.g. increased Chironomidae and Simuliidae, and depleted Heptageniidae). Our data, therefore, cannot conclusively identify the full suite of taxa affected by trout introductions, but instead highlight the largest and most consistent differences associated with trout presence versus absence.

Consistent increases or decreases in the densities of 10 uncommon invertebrate taxa also were observed

(Table 4). Because we collected limited numbers of individuals of these taxa (range of 7–139 total individuals for each of these taxa) in less than half of the stream pairs, the reliability of density estimates was poor and the power of statistical tests was very low, so we did not conduct statistical tests on these taxa. The dobsonfly *Dysmicohermes ingens*, the cranefly *Hesperoconopa*, the two Dytiscidae beetle genera with the largest body sizes, *Agabus* and *Agabinus*, and the water boatman *Graptocorixa californica* were all found only in fishless streams (4–6 streams), and the mayfly *Attenella delantala*, the stonefly *Moselia infuscata*, and the cased caddisfly *Neophylax* were found almost entirely in fishless streams, with these results being generally corroborated by the analyses of PI values and their associated confidence intervals (Table 4). We note, too, that two other species in the water boatman family Corixidae, *Cenocorixa wileyae* and *Hesperocorixa* sp., were found in only one fishless stream each. In contrast, the caddisfly *Glossosoma* was found almost exclusively in trout streams. Finally, we collected the large siphlonurid mayfly, *Edmundsius agilis*, from only two fishless streams. A detailed study of the distribution of this mayfly showed that this endemic species is currently confined to a limited number of fishless headwater streams in the Sierra Nevada and is almost never found with trout (Silldorff, 2003). Hence, the distribution and abundance patterns of these other uncommon invertebrates may also indicate relationships with trout distributions.

Although we found relationships between trout presence and the densities of the taxa noted above, most of the common taxa showed no density differences between fishless and trout streams (Table 3). Among other abundant invertebrates, the *Baetis*-group mayflies, the mayflies *Serratella* and *Caudatella*, the predatory stonefly *Calineuria californica* (family Perlidae), the predatory stonefly family Perlodidae (mostly *Isoperla* and *Cultus*), the shredder stonefly families Nemouridae (mostly *Zapada*) and Capniidae, the predatory caddisfly genus *Rhyacophila* (pooled species groups), the grazing caddisfly *Micrasema*, the dipterans *Bezzia*, *Hexatoma*, *Chelifera*, and *Dicranota*, oligochaetes, and water mites (Acari) all showed no differences in density or frequency of occurrence between fishless and trout streams.

In summary, densities of the grazer and predator guilds, and of 20% of the common taxa (10 of 50), were reduced in the presence of trout, whereas the

collector guild and one taxon increased in the presence of trout (Table 3). Two other common taxa showed suggestive differences in density between trout and fishless streams ($P \leq 0.10$) but interpretation of statistical results for many common taxa was compromised by the low power of statistical tests. In addition, nine uncommon taxa were absent or much less abundant in the presence of fish and one uncommon taxon was found predominately in trout streams (Table 4).

Discussion

We used a paired trout versus fishless stream sampling design to examine relationships between non-native trout introductions and the distributions and abundances of invertebrates and algae in historically fishless Sierra Nevada streams. We used this design because we wanted to focus on the large stream-to-stream scales where introduced species have impacts on recipient communities and populations, which encompass the range of environmental variation (e.g. pools and riffles) found within natural stream reaches, and which represent the scales of interest to managers and policy makers. Although direct inference at these large scales is difficult because of high stream-to-stream variation and the difficulty or impossibility of directly manipulating introduced species, these problems are mitigated by the matched pair design of this study which greatly reduced or eliminated the influence of potentially confounding variables. While there were no differences in the values of measured physicochemical variables in trout versus paired fishless streams, it is possible that an unmeasured variable may have differed between these stream types; however, we measured most factors known to influence invertebrate and algal assemblages, including nutrients, organic matter, substrata, habitat refuges, riparian cover, stream size, depth, temperature, water chemistry, elevation and stream gradient (Allan, 1995; Giller & Malmqvist, 1998), and found no consistent differences in the values of these variables between trout and fishless stream pairs. The results therefore indicate that non-native trout alter invertebrate community structure in historically fishless mountain streams by: (i) reducing the abundances of certain large and/or epibenthic taxa, (ii) producing an increase in periphyton standing stock and cover, and (iii) changing trophic relations by reducing grazers and large invertebrate predators and increasing collector-gatherers.

Community and functional feeding group responses to trout presence

Even though we observed large changes in the distributions and abundances of some stream invertebrate taxa associated with trout introductions in Sierra Nevada streams, the densities of total invertebrates and many common stream invertebrate taxa were not different between fishless and trout streams, generally corroborating results reported by other studies (Allan, 1982; Reice & Edwards, 1986; Reice, 1991; but see Flecker & Townsend, 1994). Although invertebrate community evenness and diversity indices were greater in fishless than trout streams, these results were primarily attributable to the increased relative abundance of the dominant Chironomidae in trout streams, with little change in the relative abundances of the majority of remaining invertebrate taxa. Though the decrease in richness was small (<10%), trout streams did contain significantly fewer taxa than fishless streams (Fig. 2). Across all streams, 154 taxa were collected from fishless sites and 142 from trout sites, with taxa missing from trout streams largely being conspicuous forms (e.g. *Edmundsius*, *Dysmicohermes*, *Agabus*, *Agabinus*, *Chyranda*, *Graptocorixa*).

Multivariate analyses showed little difference in invertebrate community structure between fishless and trout streams, despite our observation that the densities of a substantial fraction of common taxa (20%) showed significant declines in the presence of trout. Exclusion of the Chironomidae in multivariate analyses and weighting of these analyses towards taxa with high relative abundances may explain the lack of clear multivariate responses to trout because we found that trout effects were concentrated on large or epibenthic taxa with low to moderate relative abundances (see Tables 3 & 4).

Our results, however, did show relationships between the abundances of different functional feeding groups and the presence versus absence of trout. Densities of invertebrate predators were reduced and collector-gatherers increased in the presence of trout, similar to results reported by Nyström *et al.* (2003) and Meissner & Muotka (2006). In addition, we found

that grazers were more abundant in fishless than trout streams, but that shredders were relatively unaffected by trout presence (but see Nyström *et al.*, 2003). The invertebrate taxa in the grazer functional feeding guild which were reduced by trout were primarily large mayfly and active caddisfly grazers, consistent with the results of other studies (McIntosh, 2002; Nyström *et al.*, 2003).

Density differences in individual taxa between trout and paired fishless streams

Although trout can have complex direct and indirect effects on stream invertebrate assemblages, comparisons of our results with literature data indicate that some generalities may emerge. As expected with visual, size-selective predators, trout reduced or eliminated many large, active and exposed (i.e. conspicuous) stream invertebrates, including large, predatory dytiscid beetles, water boatmen, dobsonflies, predatory stoneflies, large swimming mayfly nymphs, large, active caddisflies (e.g. *Yphria*) and surface-dwelling dixid larvae (Rosenfeld, 2000; McIntosh, 2002; Meissner & Muotka, 2006). As emphasised by Meissner & Muotka (2006), the vulnerability of predatory macroinvertebrates to trout is largely a function of their exposure, large size, and/or active habits, rather than their functional feeding group designation, *per se*. Nevertheless, an invertebrate's size, mobility and microdistribution provided only partial insight into how it responded to trout introductions because, in this study, some organisms with similar sizes, microdistributions, mobilities, morphologies and (presumably) conspicuousness showed different responses to trout. Although we and others have found reductions in total invertebrate predators by trout (Feltmate & Williams, 1991; Harvey, 1993; Meissner & Muotka, 2006), we found that two abundant stonefly predators in our study streams (*Doroneuria baumanni*, *Hesperoperla*) declined with trout introductions, but that the densities of a third, similar, abundant stonefly predator, *Calineuria californica*, were unrelated to trout presence, indicating that large predatory stoneflies can show individualistic responses to trout presence. We also found that similar predaceous dobsonfly species (family Corydalidae) showed different responses to trout presence, with *Dysmicohermes* being found only in fishless streams and *Orohermes* being found at similar frequencies and

densities in trout versus fishless streams. Grazers as a group were significantly less abundant in trout than fishless streams but we found that pairs of similar grazers, e.g. small turtle-cased caddisflies (Glossosomatidae: *Anagapetus* and *Glossosoma*), rheophilic caddisflies with silk-sand cases (*Neothremma* and *Micrasema*) and large pool-dwelling mayflies (families Ameletidae and Siphlonuridae: *Ameletus*, *Edmundsius* and *Siphlonurus*), often showed very different responses to trout presence, with densities of *Anagapetus*, *Neothremma*, *Ameletus* and *Edmundsius* decreasing, *Glossosoma* increasing, and *Micrasema* and *Siphlonurus* being similar from fishless to trout streams. Because *Siphlonurus* can shift its distribution to stream areas inaccessible to fish (e.g. detached pools with lower oxygen and higher temperature levels than in the main channel) whereas *Edmundsius agilis* is always found only in well-aerated, cool pools in the main channel, these behavioural differences may account for their different associations with trout (Day, 1956; E. Silldorff, unpubl. data).

Although we found strong declines in Tricladida flatworm densities from fishless to trout streams, the mechanisms for this result are unclear. Because flatworms are large (5–20 mm), glide along rock surfaces, and are found in the drift, with a poor ability to return to the bottom, they may be vulnerable to visual predators such as trout (Brittain & Eikeland, 1988; Kolasa, 2001). Alternatively, trout may indirectly affect flatworms because increased macroalgal abundance on the upper surfaces of stones in trout streams may interfere with flatworm locomotion, which is effected via ciliary gliding on mucus trails, and inhibit their ability to capture prey (Kolasa, 2001). We also found that the densities of some caddisfly larvae (*Neothremma*, *Anagapetus*, *Yphria californica*) were much lower in trout than fishless streams, but literature results on trout effects on caddisfly larvae have been inconsistent (Harvey, 1993; Wootton, Parker & Power, 1996; Meissner & Muotka, 2006). Species-specific behavioural differences may account for the different responses of similar taxa to trout as suggested by *Yphria*'s tendency to eject from its case when disturbed, presumably rendering the unprotected larvae vulnerable to trout predation (Wiggins, 1996).

Many of the taxa that were most reduced by trout appeared to be taxa that are found primarily in small high elevation streams in western North America that originally lacked trout [e.g. *Edmundsius agilis*, high

elevation triclads (*Polycelis* spp.), *Neothremma*, *Anagapetus*, *Cryptochia*, *Dysmicohermes ingens*, others], suggesting that the absence of an evolutionary history with trout might render such taxa vulnerable to trout predation (Evans, 1972, 1984; Stark & Gaufin, 1974; Baumann & Stark, 1980; Wiggins, Weaver & Unzicker, 1985; Stewart & Stark, 2002; Meyer, 2001). There were ambiguities in unequivocally assigning taxa to distributional categories that represented allopatry or sympatry with original trout distributions, because of uncertainties in the identity of immature forms, incomplete taxonomic treatments, the high probability of undescribed species (e.g. *Ameletus* spp., J. Zloty, pers. comm), and inadequate information on the elevational and geographical ranges of many taxa. As a consequence, we felt it was premature to quantitatively compare trout impacts on taxa with different distributional patterns and that such an analysis must await more comprehensive information on the larval and adult taxonomy, phylogenies and distributions of the collected taxa. However, we surmise that there is a higher relative risk of extinction for rare taxa which are apparently eliminated by trout, such as *Edmundsius*, *Dysmicohermes*, *Agabus*, *Agabinus* and *Chyranda*.

Indirect effects of trout on stream ecosystems

Consistent with previous studies, we found apparent indirect, positive effects of trout on components of the stream biota. First, algal biomass and macroalgal cover were greater in the presence versus absence of trout, consistent with most studies where algal responses have been examined (e.g. Dahl, 1998; Diehl *et al.*, 2000; Rosenfeld, 2000; Nyström & McIntosh, 2003; Nyström *et al.*, 2003). Because densities of the grazer functional feeding group and component large, active, or exposed grazer species (*Ameletus*, *Paraleptophlebia*, *Neothremma*, *Anagapetus*) were much lower in trout than in troutless streams, we presume that increased algal levels in trout compared to fishless streams were the result of a trophic cascade, whereby trout reduced the densities and foraging activities of grazing insects, resulting in increases in algae, the grazers' food, consistent with the evidence used to infer trophic cascades in other studies (Shurin *et al.*, 2002). Although higher algal biomass in arenas or streams containing versus lacking trout has been commonly observed, there are cases where trout appear to have negative indirect effects on algal

biomass (Power, 1990; Wootton & Power, 1993; McIntosh *et al.*, 2004; Meissner & Muotka, 2006), presumably because these latter studies deal with four-level trophic cascades, where trout reduce invertebrate and small vertebrate predators, and so permit increases in their grazer prey resulting, ultimately, in reduced algal biomass. Most studies, however, have shown increased algal biomass in the presence of trout even though invertebrate predators were present, indicating that trout effects on grazer densities and behaviour which result in algal biomass increases usually override the effects of four-level cascades in determining algal biomass (Shurin *et al.*, 2002). In contrast to algal responses to trout, we found no relationships between the presence or absence of trout and shredder abundance or the levels of particulate organic matter and literature results on trout effects on shredder and detritus levels are mixed and inconsistent (Reice, 1991; Konishi, Nakano & Iwata, 2001; Ruetz, Newman & Vondracek, 2002; Nyström *et al.*, 2003, Greig & McIntosh, 2006).

A second type of indirect trout effect involved increases in the densities of other grazing or collector-gatherer invertebrate taxa in trout streams, such as the mayfly *Centroptilum*, perhaps the Chironomidae midges, and the caddisfly *Glossosoma*, which probably benefited from increases in protective algal cover and food resource availability. Increases in less vulnerable grazing taxa with trout additions, particularly increases in the density of chironomids, also have been reported from experimental studies (reviewed in Englund, Sarnelle & Cooper, 1999; survey and meta-analysis in Meissner & Muotka, 2006). Although trout-induced reductions in large grazers (e.g. some caddisflies and mayflies) may have resulted in increases in algal, and ultimately, small grazer levels, some of these small grazers may have benefited from habitat-specific reductions in dominant grazers induced by trout. For example, densities of the abundant *Baetis*-group mayflies (containing *Baetis bicaudatus*, *Baetis tricaudatus* and *Diphetor hageni*) were similar in the riffles of fishless versus trout streams (mean densities in fishless versus trout riffles = 1805 m^{-2} versus 1678 m^{-2}; Wilcoxon paired (signed rank) test, $P = 0.37$), but their densities in the pools of trout streams were lower than those in the pools of fishless streams (mean densities in fishless versus trout pools = 188 m^{-2} versus 107 m^{-2}; $P = 0.08$, Wilcoxon paired test). This decrease in the abundance of a

confamilial (and likely competitive) mayfly in pools may have benefited the pool-dwelling mayfly, *Centroptilum* [mean densities in fishless versus trout stream riffles = 0.9 m^{-2} versus 0.1 m^{-2} ($P = 0.09$, Wilcoxon paired test); mean densities in fishless versus trout stream pools = 34 m^{-2} versus 305 m^{-2} ($P = 0.03$ Wilcoxon paired test)]. An alternative explanation for increases in some of these taxa (e.g. *Centroptilium*, chironomids) where trout are present is large reductions in the abundances of dominant invertebrate predators (the Perlid stoneflies *Doroneuria baumanni* and *Hesperoperla* spp., Tricladida flatworms), resulting in a release from invertebrate predation pressure on these prey taxa (Peckarsky, 1985; Lancaster, 1990).

Conservation and management

Our results suggest that conservation efforts for native invertebrates that are vulnerable to loss or reductions associated with trout stocking should focus on protecting mid-to-high elevation locations where there are still fishless streams. After verifying the identities of taxa that are rare endemic forms or keystone species for ecological function, managers should also target streams where trout removals would provide the greatest benefit for promoting the recovery of populations of these species. Operationally, these would be streams where trout removal is possible and practical, where trout re-invasion can be prevented by natural trout migration barriers (waterfalls and steep cascades), and where target invertebrate populations are present nearby to provide colonisation sources. In addition, the expansion of fishless habitat through trout extirpations could benefit non-target native taxa and restore the structure and function of stream communities to their original state.

The effects of trout on ecosystem processes in headwater Sierra streams were evidenced here by (i) increased algal biomass and cover, (ii) reduction of the grazer functional feeding group, (iii) the reduced density of the large predator guild, especially the most common perlid stonefly predator (*Doroneuria baumanni*), (iv) increased density of collector-gatherers other than chironomids, and (v) apparent increases in midges in many stream pairs (chironomids play dominant roles in the consumption of organic matter and algae and as prey for invertebrate predators) in the presence of trout. These alterations suggest that trout have changed the trophic organisation, and consequent resource production and transformation dynamics, of many historically fishless high elevation Sierra streams (see also Feltmate & Williams, 1991; Huryn, 1998; McIntosh, 2002).

A major government report, the Sierra Nevada Ecosystem Project report, recommended that Aquatic Diversity Management Areas (ADMAs) be established to conserve aquatic resources in the Sierra Nevada, based primarily on the presence of rare or endangered fish and amphibian species and on the proportions of native fish and amphibian species making up the vertebrate community (Moyle, Randall & Yoshiyama, 1996b). This approach does not use native aquatic invertebrate taxa in identifying ADMA catchments and so ignores the major contributor to native aquatic biodiversity in the Sierra Nevada. Because most of the High Sierra was historically devoid of fish, and because many amphibian species are patchily distributed and largely absent from streams, criteria based only on fish and amphibians are inappropriate for delineating natural headwater habitats which maintain a high level of native biodiversity. We suggest, instead, that invertebrate biodiversity surveys be used as ADMA criteria, and waters devoid of fish in the high Sierra be designated for preservation efforts because they contain a native and, at least partly, vulnerable endemic fauna. Because fishless habitat is rare and supports an unaltered native community, primary criteria for delineating ADMAs in the High Sierra might include: (i) any fishless stream reaches and especially those with contiguous areas of fishless habitat, (ii) fishless locations with known endemic invertebrate populations, and (iii) streams with, or near sources with, a high diversity of native invertebrate species where trout can be removed effectively because of natural barriers to trout migration. Because headwater streams, including intermittent channels, may provide important refuges for native invertebrates from trout predation and may harbour rare and/or endemic species, these small drainages should be the focus of survey and inventory studies that can be used to delineate ADMAs.

Acknowledgments

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