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The Influence of Introduced Trout on Native Aquatic Invertebrate Communities in a Paired Watershed Study of High Sierran Streams

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Executive Summary:

Resource management agencies are often confronted with conflicts between natural resource protection and public recreation in wildland areas. An example of such a conflict is the stocking of non-native trout for recreational fisheries versus the protection of unaltered freshwater habitat for native wildlife. Declines and losses of over half the species of native amphibians and fish found in the Sierra Nevada have been attributed to the introduction of exotic species, especially trout. Although the effects of non-native trout on native biodiversity have been documented for many Sierran lakes, there is practically no information on their impact on Sierran stream ecosystems and communities, which evolved in the absence of fish. These mountain streams harbor high proportions of endemic species in insect groups such as stoneflies and caddisflies, and these insects potentially are vulnerable to direct and indirect effects of fish predation. Inadequate data on the distribution and diversity of stream invertebrates is a major obstacle to evaluating and monitoring the health of native aquatic species and habitats in the High Sierra.

The objective of this research has been to compare the composition of invertebrate communities in streams lacking introduced trout with paired nearby streams containing trout. The studies involved surveys of aquatic invertebrate diversity in riffle and pool habitats of first and second order streams in Yosemite National Park, at elevations from 1350 to over 3000 meters. Invertebrate samples were collected along with an inventory of their food resources, water chemistry and physical habitat. Analyses of the data emphasizes contrasts of the impacts of trout on the organization and diversity of stream communities.

Fish stocking and its impacts on high elevation aquatic ecosystems is a controversial topic currently under review in California by a variety of public and private organizations. The research results presented here provide essential scientific input to policy development through (1) the evaluation of the impact of non-native trout on the biodiversity and ecological integrity of Sierran streams, (2) the development of criteria for identifying aquatic diversity management areas for conserving native species, and (3) the establishment of baseline biological indicators for the monitoring of programs designed to restore stream biodiversity.

The introduction of non-native trout into the Sierra Nevada mountains of California, USA, has caused important changes in the densities of many invertebrate and vertebrate species

inhabiting lakes of this region. Researchers, however, know little about the effects of trout introductions on invertebrates in streams of the Sierra Nevada. In this report, we present the results from surveys of 21 fishless streams and 21 paired streams containing introduced trout in Yosemite National Park.

Results show that environmental conditions did not differ between the fishless and trout streams, but that algal biomass and macroalgal cover were significantly higher in the streams containing trout. The majority of taxa were unaffected by trout presence in Yosemite streams but enough were affected that we conclude trout have caused changes in benthic stream community structure and function in many but not all streams to which trout have been introduced. Moderate effects of trout on the structure of the invertebrate community were evident in significant and/or consistent changes in the density of 26 different taxa (20 decreasing and 6 increasing in the presence of fish). Among common taxa, trends were statistically significant for 10 taxa and qualitatively consistent for 8 taxa (statistical power insufficient). This represents 18 of 43 common taxa groups (over 40%). Another 8 uncommon taxa also showed distinct patterns of association with fishless or trout streams but were not abundant enough for statistical tests. The strongest effects of trout appeared to be on endemic taxa (such as the caddisfly *Neothremma* spp., the mayfly *Edmundsius agilis*, Triclad flatworms, and others), which may be vulnerable because of the absence of evolved selection for mechanisms of coexistence with fish predators.

The effects of trout on the function of benthic communities were also evident in increased (1) algal density and cover, (2) abundance of midges (which play dominant roles in the consumption of organic matter and algae and as prey to invertebrate predators), and (3) reduced density of the most common large predator (*Doroneuria baumanni*, likely the dominant aquatic predator prior to trout introductions). These changes suggest that trout alter the resource production and transformation in high Sierra streams.

Because the strongest effects from trout fell primarily on endemic species, we recommend that managers first focus on endemic invertebrates by conducting taxonomic verifications, detailed surveys of species-specific distributions and, when necessary, eradicating trout to increase and recover populations of threatened invertebrates. In addition, experimental removals of trout from stream segments should be combined with benthic invertebrate community monitoring before and after treatments to evaluate the potential for recovery.

Background

In 1993 Congress funded the Sierra Nevada Ecosystem Project (SNEP), which was a scientific review and study of ecosystems of the entire Sierra Nevada, to document the status of old-growth forests and to prepare inventories and management recommendations for natural resources. Watersheds provided an important organizing theme for this report and the report's analyses concluded that aquatic ecosystems were the most altered and impaired habitats in the Sierra (SNEP 1996). Degraded ecological conditions in rivers and streams have resulted from a century and a half of alterations in stream flows and water quality caused by mining, dams, diversions, and the loss of riparian areas to reservoirs, road building, logging, and overgrazing, as well as from the development of a major recreational economy based on the introduction of non-native fishes to aquatic ecosystems (Mount 1995, SNEP 1996, Knapp 1996).

The introduction of non-native fish species, primarily trout, to Sierran lakes and streams has been cited as one of the leading causes of declines and losses in over half the 70 species of native amphibians and fish in the Sierra (Jennings 1996, Knapp 1996, Moyle et al. 1996a). Because most aquatic invertebrate and amphibian assemblages in the High Sierra evolved in the absence of fish predators, these systems may be particularly vulnerable to the introduction of fish. Recent studies indicate that introduced fish have had a large effect on frogs and toads at mid to high elevations and introduced fish also may be affecting other components of the aquatic fauna in areas of the Sierra Nevada historically lacking fish. Historically, nearly all drainages above 6,000 feet lacked fish, and these fishless areas comprised nearly one-third of the Sierran ecoregion. Current estimates indicate that 90% of Sierran streams outside of National Parks contain introduced trout populations, whereas inside Parks the figure is at least 60% (Moyle et al. 1996a). In addition to the impacts of exotic fishes on native fish and amphibians, other effects on aquatic ecosystems have been documented. In a survey of Sierran lakes, Stoddard (1987) found that most large zooplankton species were absent in stocked lakes compared to fishless lakes, and that the phantom midge, *Chaoborus americanus*, may have been extirpated from most of the Sierra Nevada by introduced fish. Bradford et al. (1998) surveyed high-elevation lakes in Kings Canyon National Park and reported that large and/or mobile, conspicuous taxa, including tadpoles, large-bodied microcrustaceans (*Hesperodiaptomus*, *Daphnia middendorffiana*), and many epibenthic or limnetic macroinvertebrates (baetid and siphonurid mayfly nymphs,

notonectids, corixids, limnephilid caddis larvae, and dytiscid beetles), were rare or absent in trout lakes, but were relatively common in lakes lacking trout, and that the taxon richness of macroinvertebrates was reduced by trout. Preliminary results from a more comprehensive survey of fish and fishless lakes in the High Sierra, i.e. the Sierra Lakes Inventory Project (SLIP) of the U.S. Forest Service, reported similar results (Knapp pers. comm). Although the status of many lakes has now been documented, biodiversity in Sierran streams is still poorly known. The only reported information on the effects of exotic trout on stream communities in the Sierra comes from a single study of the outlet streams of lakes with and without fish (Melack et al. 1989). This study indicated alterations in stream community structure, primarily through reductions in dytiscid beetles and true bugs (Hemiptera: Corixidae, Notonectidae) in trout versus troutless streams.

Most Sierran fish stocking has been carried out under the direction of the California Department of Fish and Game (CDFG) and this agency has begun to re-examine its stocking policies. The general intent of current management planning within the National Park Service and U.S. Forest Service is to protect and restore Sierra Nevada habitats and biodiversity. Although the existing management direction of Forest Plans includes standards and guidelines for aquatic conservation, the Forest Service has not yet adopted a policy on fish stocking (USFS 1998). Since 1972, Park Service policy has not allowed the stocking of exotic species in Parks; however, an agreement with CDFG to discontinue fish stocking was not concluded until 1991. In some Sierran lakes experimental removals of trout are currently underway to determine how native lake communities recover after trout are removed. To provide state and federal agencies with guidance in formulating management policies for Sierran streams, it is necessary to investigate the effects of trout on the diversity and structure of stream invertebrate communities, because invertebrates are the dominant, and often only, visible organisms in fishless Sierran streams. An inventory of stream invertebrates will also provide an index of native aquatic resources in the Sierra Nevada, as well as a baseline for evaluating environmental health and the impacts of possible future changes in environmental conditions.

The SNEP report compiled existing information and directed attention to gaps in resource inventory information. Biological resource inventories are useful for evaluating the condition and trends of different habitat types according to their constituent inhabitants. One of the most useful ecological indicators of the status and recovery of aquatic habitats in the Sierra Nevada is

the diverse and abundant invertebrates found in streams and lakes. Invertebrate communities are often composed of dozens of species with different sensitivities to environmental degradation and which occupy central roles in stream food webs. As a consequence, benthic invertebrates have been used widely in water quality monitoring in Europe and other parts of the U.S., a procedure often known as bioassessment. Despite their diversity, important ecological roles, and potential for application in environmental assessments, aquatic invertebrates are the most poorly known of all faunal groups in the Sierra Nevada (Erman 1996). Data for stream invertebrates are especially incomplete, with most collection records coming from intensively studied locales or taxonomic groups. Levels of endemism are high among well-known taxa such as stoneflies (25% of the species in the Sierra are endemic) and caddisflies (19% endemic species). Undocumented but likely species losses due to human-induced disturbance argue for an inventory and biological monitoring program for stream invertebrates, particularly in sensitive headwater stream systems. The goal of the proposed research is to integrate biogeographical and distributional information on Sierra Nevada aquatic invertebrates with data that will permit an evaluation of the effects of exotic predatory trout on the organization of mountain stream communities. The objective of the research is to compare the structure and diversity of benthic invertebrate communities of fishless streams each paired with adjacent, historically fishless drainages now containing introduced trout (located in Yosemite National Park). The results should have wide implications for conserving native aquatic biodiversity in the entire Sierran ecoregion.

The SNEP report identified a strategy for the conservation of natural resources through the establishment of Aquatic Diversity Management Areas (Moyle et al. 1996b). The criteria for defining such areas were based primarily on the presence of rare/endangered fish and amphibians, and on the proportions of native fish and amphibian species in the community. This approach fails to use aquatic invertebrates in identifying ADMA watersheds and so ignores the greatest reservoir of native aquatic biodiversity in the Sierra Nevada. Because most of the High Sierra was historically devoid of trout, and because many amphibian species are patchily distributed, criteria based on fish and amphibians often don't work in High Sierra waters. Targeting watersheds that have been free of exotic trout could provide criteria for the designation of areas containing unaltered community diversity. The present study will provide a foundation

for the use of this strategy in defining ADMAs and their boundaries in parts of Yosemite National Park and this strategy will be applicable to watersheds throughout the Sierra Nevada.

Fish Predation and Stream Communities

Information on the role of predation in regulating the structure of stream communities has been derived from both experimental manipulations and natural comparisons. These studies have often produced contradictory results (Reice and Edwards 1986, Thorp 1986, Cooper et al. 1990, Flecker 1992, Power 1990, 1992, Englund 1997). The importance of fish in altering community structure appears to be contingent on the spatial and temporal scales at which observations are made, the characteristics of predators and prey, and the environmental setting. Although experiments in small-scale exclosures and microcosms often demonstrate local effects of predators on prey, results are difficult to extrapolate to larger, natural areas and longer amounts of time, precisely the large scales affected by management practices (Peckarsky et al. 1997, Cooper et al. 1998). The relative body sizes, behaviors, life histories, identities, diversity, and habitat affinities of predators and prey will all influence the direct and indirect effects of fish predation on aquatic invertebrate assemblages (Allan 1995). Rapid movements of prey into and out of stream habitats, e.g., as drifting aquatic stages, may also alter the impacts of predators, particularly at local scales (Cooper et al. 1990, Wooster and Sih 1995, Englund 1997). The degree of habitat heterogeneity, which affects the availability of prey refugia, will further determine the degree of prey exposure to predators and the potential for predator-prey coexistence (Macan 1977, Power 1992).

Experimental manipulations of trout predators in large stream channels (1 X 50 m) at the Sierra Nevada Aquatic Research Laboratory (SNARL) have revealed that a primary effect of trout is to increase the drift and hiding behaviors of common *Baetis* mayflies (Cooper et al. 1998, Diehl et al. 2000). Trout reduce the grazing activity of mayfly nymphs resulting in increased amounts of algae growing on rock surfaces. Using experimental manipulations of top trout predators in a northern California river, Power (1990) reported that trout reduced small predators (fish fry, damselfly naiads) causing an increase in invertebrate grazers and a consequent decline in algal biomass on boulder surfaces. In subsequent experiments, Power et al. (1995) reported considerable year-to-year variation in the presence and intensity of these “cascading effects”, presumably owing to the effects of interannual variation in flood timing and intensity on the

abundance and identity of different types of grazers. These results indicate that trout effects on prey can have knock-on effects on the prey's food (e.g. algae) and that these effects may be influenced by physical conditions and the vulnerability of intermediate to top predators.

Stonefly predators were also manipulated in a variety of arenas of different size at SNARL, ranging from small cages (0.04 m²) to large channels (20 m²) (Cooper et al. 1998). Only at small scales of manipulation were the impacts of stonefly predators pronounced (spatial heterogeneity provided refugia at larger scales) indicating that the impacts of predators may depend critically on the scale of experiments or observations (Cooper et al. 1998). It should be recognized that the SNARL communities have been exposed to introduced trout predators for many decades, so the structure of these communities may have been altered already by fish predation. The composition and structure of invertebrate communities in streams that have always lacked fish are likely to be different than those in streams that have contained fish for some time. In order to detect long-term effects of introduced fish on native benthic communities in whole streams it is necessary to compare formerly fishless streams now containing established populations of introduced trout to streams that have never contained trout.

Research Introduction

The introduction and invasion of non-native species constitutes one of the primary threats to world biodiversity (Czech and Krausman 1997, Vitousek et al. 1997, Wilcove et al. 1998). Global introductions of Salmonidae fishes, especially trout in the genera *Salmo*, *Salvelinus*, and *Oncorhynchus*, have led to the decline of many vertebrate species in lakes and streams (Krueger and May 1991, Crowl et al. 1992, Bradford et al. 1993, Brana et al. 1996, Delacoste et al. 1997, Cambray 2000, Knapp and Matthews 2000, McIntosh 2000, Gillespie 2001). Like with many conservation issues worldwide, however, the effects of exotic trout on invertebrates have not been a priority for either resource managers or conservation organizations, and little is known about how trout introductions have affected native invertebrate populations.

In the Sierra Nevada mountains of California, USA, nearly all streams and lakes above 1800 m (6000 ft) originally lacked fish, presumably representing one of the largest contiguous areas of fishless streams and lakes in North America (Knapp 1996, Moyle et al. 1996a). Beginning in the mid-1800s, however, Euro-Americans introduced trout into the aquatic habitats of this region, with the result that nearly all lakes and perennial streams currently contain trout (Knapp 1996, Moyle et al. 1996a). Although some of the negative effects of exotic trout on lake invertebrates

have been known for decades (Reimers 1979, Stoddard 1987), only recent evidence for trout impacts on the mountain yellow-legged frog (*Rana muscosa*) have motivated management agencies to both re-evaluate trout stocking programs and begin extirpating introduced trout from a few lake basins (Knapp and Matthews 1998, Pister 2001, CDFG 2002). Except for a few streams that could provide trout colonists to lakes where trout are being removed, research studies and management practices have not targeted the streams of the Sierra Nevada because no native vertebrates require streams for the completion of their life cycles. Thus, any threats from exotic trout to stream invertebrate populations have been ignored when considering the management of trout in the Sierra Nevada.

Compounding the indifference toward invertebrate conservation in this region is a lack of consensus on how trout affect stream invertebrate populations in all regions of the world. Nearly all research on trout-invertebrate interactions has been conducted at small temporal and spatial scales where invertebrate responses primarily reflect behavioral changes, and not demographic responses, to trout presence (see review by Englund et al. 2001). The few large-scale studies that have been conducted, however, have provided inconsistent conclusions about how trout affect invertebrate population sizes. A number of studies have found that trout have no strong impacts on stream invertebrate densities (Jacobi 1979, Allan 1982, Andersen et al. 1993, Diehl et al. 2000, Peckarsky et al. 2001). In marked contrast, a few studies have found large differences in the densities of stream invertebrates between sites containing and lacking trout, including local extirpation (Feltmate and Williams 1991, Harvey 1993, McIntosh 2002, Silldorff *in review*). These variable results may simply reflect the variable responses of different invertebrate species and assemblages to trout predation. Such a conclusion, however, provides little guidance for predicting how trout introductions in the Sierra Nevada have affected stream invertebrate densities and diversity.

Ideally, trout impacts on stream invertebrates in the Sierra Nevada could be determined by experimentally adding or removing trout from a number of Sierra Nevada streams and monitoring invertebrate responses. Such studies, however, are difficult to conduct because of logistical (e.g., time, money) and ethical limitations. Because we could not overcome these constraints, we conducted three complementary observational studies that could collectively provide a rigorous indication of the effects of trout introductions on Sierra Nevada stream invertebrate assemblages. In two other studies, we compared invertebrate assemblages in stream

reaches above and below waterfalls that acted as barriers to trout invasion (see Silldorff et al. - Report 2; and Silldorff, Report 3, *in review*). Even using strict criteria for selecting the stream reaches, however, we could not eliminate the possibility that observed upstream to downstream differences in invertebrate assemblages were caused by natural longitudinal changes in both environmental conditions and invertebrate populations.

In this report, we present a study whose results provide complementary evidence for how trout affect stream invertebrate populations in the Sierra Nevada. In this study, we selected 21 fishless streams in Yosemite National Park and identified nearby, paired streams with similar environmental characteristics but which contained introduced trout. We then measured environmental conditions and invertebrate population densities in these 42 streams to determine if there were consistent biotic and abiotic differences between streams with and without introduced trout. Because we did not manipulate trout directly, the primary limitation of this third study is the possibility that some unmeasured environmental, biotic, or historical variables differed in consistent ways across pairs of streams and, thus, that these natural differences led to consistent differences in the densities of a number of invertebrate taxa between fishless and trout streams. In contrast to our barrier waterfall studies, however, paired fish and fishless reaches occurred at similar distances from stream headwaters. Consequently, any differences in invertebrate populations between fish and fishless sites could not be explained by natural longitudinal changes, and the results of this study are unaffected by the primary limitation of the waterfall studies. On the other hand, numerous environmental, biological, or historical factors may differ considerably between our paired streams for the current study, obscuring any effects of trout presence. In this case, the waterfall comparisons, because they are conducted in the same stream, provide estimates for the effects of trout which are unclouded by the limitations of the paired watershed study. Together, consistent differences in invertebrate assemblages across all 3 studies can be clearly linked to trout presence because of the complementarities.

The goals of this report are: 1) to determine whether differences existed in the densities of stream invertebrates between 21 fishless and trout stream pairs in Yosemite National Park; 2) to examine if observed differences in the invertebrate assemblages could be explained by consistent environmental differences between fishless and trout streams; and 3) to identify consistent patterns in the results of our 3 studies that provide strong evidence for the effects of exotic trout on Sierra Nevada stream invertebrates.

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. We first surveyed more than 100 streams in Yosemite National Park to identify streams which lacked fish but which could potentially support trout populations (i.e., perennial, wide, deep pools). From these surveys, we identified 68 fishless streams in the Park and selected 21 of these streams for detailed study. From topographic maps, we then identified candidate trout streams for pairing with these 21 fishless streams based on stream elevation, watershed aspect and area, proximity of suitable sites to stream headwaters, and proximity to one of the 21 fishless streams. We then selected a single trout stream for each of the 21 fishless streams via field observations of stream width, depth, and gradient for the possible stream pairs.

Field Sampling

Sampling began with the delineation of a 150-m stream reach from which all samples were taken. Each meter of stream was classified as Riffle, Pool, or Other (e.g., waterfall, bedrock chute, shallow run) habitat and, simultaneously, semi-quantitative visual fish surveys were conducted. Two individuals worked together on fish surveys, with one individual spotting fish, flushing fish from hiding locations with a stick or rod, and estimating fish sizes while the other worker recorded fish and habitat information. Each survey lasted approximately ½ hour and was conducted a single time by proceeding from the lower to the upper end of each reach. Although our census methods likely will underestimate the densities of trout in these streams, these censuses were conducted in a standard way across all study streams and should provide a relative index of fish densities.

Water chemistry samples were taken immediately upstream from each delineated reach to eliminate the possibility of contamination of samples by sampling activities. We measured stream pH, temperature, and conductivity in the field using an Oakton model pH/Con10 meter. Alkalinity was measured using a standard LaMotte titration kit. A single 60ml water sample was taken from the stream and returned to the laboratory for analysis of turbidity. Two 175-ml water

samples were taken above each reach and returned to the laboratory for duplicate measurements of nutrient chemistry. For these nutrient samples, sample bottles were acid-washed then rinsed and stored with DI water. Stream water was filtered through a glass fiber filter (GF/F), and filtered samples were acidified with concentrated sulfuric acid to a pH of 2.0.

Invertebrate samples were taken with a kick net (30 cm opening, 250 μ m mesh) from habitats classified as either riffles or pools, with 5 samples from each habitat and a total of 10 invertebrate samples per reach. The 5 pool and 5 riffle sampling locations were initially selected at random, then redistributed so that samples covered the entire 150 m length of stream. For each riffle sample, we sampled at 3 locations across each riffle site (edge, middle, and in between) to produce a single overall composite riffle sample. For streams with widths too narrow to sample across the channel, the three samples composited into each riffle sample were collected sequentially by moving upstream and sampling near the middle of the channel. At each location, the bottom of the kick net frame was placed against substrata and all material in the 30 cm x 30 cm area immediately upstream from the kick net was disturbed by hand and foot for approximately 30 seconds, with dislodged invertebrates and organic material drifting into the net. For each pool sample, a single location in the center of each identified pool was selected and sampled. The bottom of the kick net frame was placed against the substrata and over a period of approximately 60 seconds material in the 30 cm x 30 cm area upstream from the net was alternately disturbed by hand or foot then “pushed” into the net by creating a water current into the net by hand. For a small number of samples (9 of the 210 total), two kick samples were taken in each pool to increase the number of invertebrates collected from pool habitats. All material in the sampling net from each pool sample or composite riffle sample was washed into a small bucket, stirred, and filtered through a 100 μ m mesh net, then placed into a sample bottle and preserved in 95% ethanol. Where large amounts of gravel and sand were present in the sampling net, all material was washed into a small bucket and repeatedly elutriated to separate gravel and sand from biological materials before filtering and preservation.

Coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) were sampled using the same technique used for riffle invertebrate samples. We took a total of three samples for CPOM/FPOM, including one each from a riffle in the lower, middle, and upper 50 m of each sampling reach, avoiding locations already sampled for invertebrates. Each CPOM/FPOM samples consisted of a composite of samples from three locations within each

riffle. All material collected in the kick 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. Large invertebrates were removed from the material collected on the 1 mm net for 3 minutes to minimize the contribution of invertebrates to the overall estimate of organic matter. The remaining material in the net was weighed using a small Pesola scale and the tare weight of the net was subtracted from this measurement to obtain an estimate of CPOM wet weight. Material passing through the 1 mm net was collected in a second bucket, moderate to large invertebrates were removed for 3 minutes, and the remaining material was filtered through a 100 μm net. All material collected on this net was transferred to a 20-ml vial containing stream water and 2 ml of formaldehyde, then transported to the laboratory for measurements of FPOM.

A single algal sample was taken from each riffle sampled for CPOM/FPOM (avoiding locations already sampled for POM or invertebrates) to estimate algal biomass (3 total algal samples per reach). In each sampled riffle, a single cobble was selected from the center of the channel and removed, the cobble was scrubbed with a wire brush, and both the cobble and the brush were rinsed with stream water into a small plastic tray. The material was then washed through a fine net (100 μm) into a graduated cylinder, and large macroalgae collected in the net was crushed and added to the cylinder. The total volume of algae and water in the graduated cylinder was measured and recorded. A small, homogenized subsample of this material was then drawn into a 50 ml syringe, the syringe sample was filtered through a small, pre-weighed glass fiber filter (GF/F), and the sample volume filtered was recorded. The material collected on the filter was then preserved using a small drop of formalin, and the filter stored within a piece of aluminum foil. Finally, the length, width, height, and longest circumference of the stone were measured to obtain estimates of stone surface area. For stone height measurements, we used only the height of the stone that was not embedded in surrounding, fine stream substrata.

Stream depths, wetted stream widths, substrate particle sizes, macroalgal cover, and overhead canopy cover were measured at 15 meter intervals beginning at the 0 m mark and continuing to the 150 m mark. Stream depth and substrate particle size were measured at 3 equally-spaced positions across the wetted stream width (i.e., $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$ width). At each of these cross-stream positions, we also recorded the presence or absence of macroalgae to estimate macroalgal cover. Canopy cover by forest and riparian vegetation was measured at 4 locations for each transect (left bank, center of stream facing upstream, center of stream facing

downstream, right bank) using a spherical densiometer (Platts et al. 1987). Maximum stream depth was measured by taking depth readings in the deepest locations in all large pools, then selecting the maximum value. Stream gradient was measured with a clinometer by measuring the vertical drop in stream elevation along the six 25-m intervals in each 150-m reach. Finally, latitude and longitude were measured using a hand-held GPS unit, and the elevation of each reach was determined from USGS topographic maps (1:24000 scale).

Laboratory Methods

Ash-free dry mass (AFDM) of fine particulate organic matter (FPOM) was determined by drying FPOM samples overnight at 75° C, then measuring the weight lost from these samples after 3 hours at 550° C in a muffle furnace. Chlorophyll *a* was measured on a Turner Model No. 110 Fluorometer using a 90% ethanol extraction method (Sartory and Grobbelaar 1984). We measured soluble reactive phosphorus (SRP) using the ammonium molybdate method, nitrate-nitrite (NO₃+NO₂) using cadmium reduction columns, and ammonia (NH₃) using the phenol-hypochlorite method for each of the duplicate samples from each stream (APHA et al. 1992). Turbidity was measured on an Orbeco-Hellige Model 966 Turbidimeter.

When we estimated that the abundance of invertebrates in a sample exceeded 800 organisms, invertebrate in that sample were subsampled using a Folsom plankton splitter with a minimum of 300 invertebrates sorted and identified in each sample that was subsampled. Samples and subsamples were sorted under a dissecting microscope at a minimum of 10x magnification, and invertebrates identified to the lowest practical taxonomic level (usually genus or species). We also searched the portion of each sample that was not subsampled for large and/or rare organisms at 3–5x magnification for up to 10 minutes, and these large/rare organisms were added to the sample.

Two characteristics of the upstream catchment were measured for each stream based on USGS topographic maps (1:24000 scale). The cumulative length of perennial streams in the watershed (Upstream Length) was measured as the sum of 1) the perennial length of the main stem and 2) the perennial length of all tributaries upstream of the sampled reach. The average gradient of perennial streams in the watershed (Upstream Gradient) was measured as the cumulative elevation loss divided by the Upstream Length. We measured the cumulative elevation loss for each catchment by adding 1) the elevation loss from the headwaters of the

main stem to the sampling reach, and 2) the elevation loss from the headwaters of each perennial tributary to its confluence with the main stem.

Data Analysis

Mean values of environmental measurements (i.e., organic matter, nutrients) were used to represent conditions for each stream reach. We adjusted invertebrate abundances to numbers per square meter, taking into account the proportion of each sample which was sorted and the bottom area sampled. Large/rare organisms were not distinguished from the subsampled organisms and their densities were overestimated in the final sample (though overestimates are unbiased between stream pairs because all large/rare searches were treated equally). We report mean densities for each invertebrate taxon across the 10 replicate samples (5 riffle, 5 pool) to characterize invertebrate population sizes in each stream reach. In these initial analyses, we did not distinguish between pool and riffle population estimates to concentrate on relationships between invertebrate densities and fish presence for whole streams. However, we did analyze, but do not report, pool versus riffle results separately and found that our overall conclusions were not affected by this decision.

For statistical analyses, we used paired t-tests for environmental variables and paired Wilcoxon signed-rank tests for biological response variables (algae, invertebrate metrics, densities of 43 “common” invertebrate taxa; see Table 2). We defined “common” as invertebrates having a mean relative abundance across all streams greater than 0.1%, although *Yphria californica* was included in this “common” group because of its high densities in fishless streams. We used t-tests for most environmental variables because environmental differences between fishless and paired fish streams typically had distributions close to normal whereas invertebrate differences between fish and fishless streams were often highly non-normal. We examined the sensitivity of our conclusions to the choice of statistical test and found that the statistical results of both t-tests and signed-rank tests were similar for both environmental and invertebrate variables, and that the results of two-sample parametric and non-parametric tests typically agreed with the results of the paired tests that we report here.

We used an absolute (rather than a relative) difference for invertebrate responses between fishless and trout streams. Although relative differences (e.g., ratios of abundance or percent change in trout versus fishless streams) are often used as response variables when evaluating

experimental results, the choice of response metric should match the study question (Osenberg et al. 1997, Osenberg et al. 1999). Because we are primarily interested in the size of invertebrate populations in these streams and the effect of trout on these populations, we have focused on absolute differences in abundance.

Differences in the broad invertebrate assemblages between trout and troutless streams were examined using univariate and multivariate summary methods. For univariate measures, we used the average densities of common invertebrate taxa (excluding Chironomidae), taxa richness, and community evenness (J' ; Pielou 1966) for each sampled reach in statistical analyses. For multivariate analyses, we qualitatively examined patterns in the similarity matrix within and among different groups of fishless and trout streams. We also used Non-Metric Multidimensional Scaling (NMDS, Sammon's algorithm implemented in S-Plus; Insightful 2001) to display relationships among streams in two-dimensional space based on the similarity in stream invertebrate assemblages. For all multivariate analyses, mean abundances of all invertebrates in each stream were standardized to proportional abundances and a Bray-Curtis distance between streams was based on these proportional data (excluding Chironomidae). The Bray-Curtis metric provides linear increases in weighting as the abundance of component species increases and has been shown to perform as well or better than comparable similarity measures when used with proportional data (Faith et al. 1987).

Results

Environmental Conditions

All physical, chemical, and habitat variables were similar in fishless and trout streams (Table 1 and Appendix). The close matching of environmental conditions is apparent when comparing all trout to all fishless streams as well as when examining the distribution of differences between paired trout and fishless streams, even for variables (e.g., stream width, depth, gradient, and temperature) that might be expected to differ between streams with and without trout in the Sierra Nevada (Figure 1).

Algal Response

Algal biomass (as measured by chlorophyll *a* standing crop density) and macroalgal cover were both significantly higher ($p < 0.02$) in streams with introduced trout compared to paired fishless streams (Table 2, Figure 2). Algal biomass was typically 57% (median) to 98% (mean) higher in trout streams, although algal biomass was higher in the fishless stream in 6 of the 21 pairs. Macroalgae cover increased from an average of 4% in fishless streams to 22% in trout streams, but the values for median cover for fishless and trout streams were only 0% and 4%, respectively. Thus, the large difference in average macroalgal cover primarily reflects the dramatic increases in 6 pairs where cover differences ranged from 40 to 80% (see Figure 2). In 5 of these 6 stream pairs, macroalgal cover was 0% in the fishless streams and 40-80% in the trout streams. In the 6th pair, the fishless stream had 13% macroalgal cover and the trout stream had 80% cover.

Invertebrate Abundance

Densities of 7 common invertebrate taxa consistently declined across all but 1 or 2 stream pairs (Table 2, Figure 3). These 7 common taxa included 1 mayfly (*Ameletus*), 2 Perlidae stoneflies (*Doroneuria baumanni* and *Hesperoperla*), 3 cased caddisflies (*Anagapetus*, *Yphria californica*, and *Neothremma*), and 1 non-insect (Tricladida flatworms). For 3 of these invertebrate taxa (*Ameletus*, *Doroneuria baumanni*, and Tricladida flatworms), declines in abundance in the fish vs. fishless streams are statistically significant using a conservative Bonferroni adjustment of critical values for the 43 statistical tests of “common” taxa. For the 4

remaining taxa, p-values for tests of differences between trout and troutless streams lie between 0.05 and the Bonferroni-adjusted critical alpha of 0.001 (0.05/43). The increases or decreases for these remaining 4 taxa are therefore not unambiguously non-random, but the consistent patterns in the data and the low probability of seeing such differences by chance alone suggest that these are biologically meaningful differences in abundance between the streams with and without introduced trout. In particular, *Neothremma* densities drop from an average of 150 individuals/m² in the fishless streams to just 3 individuals/m² in streams containing introduced trout, with a total of over 1600 larvae found in fishless streams but only 55 larvae found across all trout streams.

Strong differences between trout and fishless streams in the densities of 3 other common invertebrate groups were observed across most stream pairs (Figure 4). The mayfly *Paraleptophlebia* and the caddisfly family Hydropsychidae both declined in a large majority of trout streams in our pairings, and nymphs of the mayfly *Centroptilum* increased in trout streams for all but 3 stream pairs where it was found. For these 3 taxa, moderately strong evidence of statistical differences ($0.001 < p < 0.05$) and consistency in density differences between trout and troutless streams suggest that these differences are biologically meaningful.

We also found suggestive patterns for 8 other common invertebrate taxa (Figure 5). Although differences in the densities of these taxa between trout and fishless streams were statistically inconclusive, the patterns were strong and consistent enough to warrant consideration given the low statistical power of the current analyses. For example, the power of a paired t-test for differences in Chloroperlidae densities between stream types would be 0.41 (alpha=0.05) or 0.06 (alpha=0.001). Thus, depending on our choice of Type I error (alpha) level, there is a 60% to 94% chance of accepting the null hypothesis of no density difference between stream types even if it is false.

Consistent increases or decreases in the densities of 8 uncommon invertebrate taxa were observed across multiple fishless-trout stream pairs (Figure 6). We collected only a limited number of individuals of these taxa in this study (i.e., range of 7 to 139 total individuals for the 8 taxa in Figure 6) and thus did not conduct statistical analyses on their density patterns. The dobsonfly *Dysmicohermes ingens*, the crane fly *Hesperoconopa*, the two largest Dytiscidae beetle genera, *Agabus* and *Agabinus*, and the water boatman *Graptocorixa californica* were all found only in fishless streams. We note, too, that two other species in the water boatman family

Corixidae, *Cenocorixa wileyae* and *Hesperocorixa*, were found in only 1 fishless stream each. In addition, the mayfly *Attenella* and the stonefly *Moselia infuscata* were found predominantly in fishless streams in this study, with very few individuals collected from streams with introduced trout. Finally, the caddisfly *Glossosoma* was found almost exclusively in a small number of trout streams.

There also are suggestive but inconclusive differences in the densities of 5 other uncommon invertebrate taxa between trout and troutless streams (*Edmundsius agilis* (rank=78), *Chyranda centralis* (rank=86), *Dicosmoecus* (rank=58), *Neophylax* (rank=66), and *Gumaga* (rank=51); see Table 2). These suggestive differences may be biologically meaningful but are difficult to assess because of the rarity of these taxa. A detailed study of *Edmundsius agilis*' distribution indicates that this endemic mayfly is currently limited to a few fishless headwater streams because of trout introductions (Silldorff Report 3, *in review*). The patterns in these other invertebrates may likewise indicate strong relationships with introduced trout.

Finally, we highlight a few common taxa that showed no density differences between fishless and trout streams (Figure 7). The *Baetis*-group mayflies, the mayfly *Serratella*, the predatory stonefly *Calineuria californica* (family Perlidae), the predatory stonefly family Perlodidae, the shredder stonefly family Nemouridae, the predatory caddisfly genus *Rhyacophila*, and the grazing caddisfly *Micrasema* all showed no differences in density or frequency of occurrence between fishless and trout streams in this study.

Invertebrate Assemblage

The total abundance of invertebrates (excluding the dominant Chironomidae) and the total number of invertebrate taxa collected per sample were very similar in trout and troutless streams, although both variables tended to have slightly lower values in the trout streams (Table 2, Figure 8). Community evenness, however, was significantly lower in the streams with than without introduced trout (Table 2, Figure 8).

Depending on the strength of the response detected, the data show that a moderate to substantial fraction of the common taxa (10 to 18 or 23 to 42% of 43) were affected by the presence of trout (Figures 3-5). Reductions in both evenness and richness components of diversity further indicate modest but detectable effects of trout on the overall invertebrate community assemblage. Although these observations show components of the community are altered, the majority of benthic invertebrates

do not appear to be affected by trout. Multivariate ordination of the invertebrate assemblage data (excluding Chironomidae) revealed no clear patterns in the distribution of fishless and trout streams in two-dimensional ordination space (Figure 9, stress=0.09), although most trout streams fell above a diagonal (16 of 21) and most fishless streams below (12 of 21). The overall dissimilarity of streams is shown by stream pairs being neither closer together (similar), or further apart from one another than they were to other streams. Detailed examination of the Bray-Curtis distance similarity matrix revealed no patterns indicating differences between trout and fishless streams, and the results from these analyses are omitted. Together, the multivariate analyses suggest that invertebrate assemblages in fishless and paired trout streams were for the most part as similar to each other as they were to other fishless and trout streams. In summation, some taxa in the assemblage were changed, most were not.

Discussion

Evidence for Trout Effects in the Current Study

The goal of our overall research program was to examine relationships between trout and invertebrate distributions and abundances in Sierra Nevada streams in an effort to determine how trout introductions have affected native stream invertebrates. In the work presented here, we used independent paired streams to estimate differences in invertebrate populations sizes between trout and fishless streams whose biological and environmental characteristics were closely matched. In addition, we measured values of algal variables in these streams to determine if trout had indirect effects on primary producers in Sierra Nevada streams.

Our results indicate that both algae and a number of invertebrate taxa differed in abundance between fishless and trout streams. Specifically, both algal biomass and macroalgal cover were higher in streams with introduced trout, and the community evenness of invertebrates (J') was consistently lower in trout streams. In addition, specific mayflies (*Ameletus*, *Paraleptophlebia*), stoneflies (*Doroneuria baumanni*, *Hesperoperla*), caddisflies (*Anagapetus*, *Neothremma*, *Yphria californica*, Hydropsychidae), and non-insect invertebrates (flatworms) had lower abundances in streams with than without trout. One genus of mayflies (*Centroptilum*) also had higher abundances in trout streams. Particularly striking among these consistent changes were the declines by 1 to 2 orders of magnitude in the abundance of 2 primarily endemic groups of invertebrates (*Neothremma* and Tricladida flatworms; see Silldorff et al. Report 2) and a similar decline for *Yphria californica*, a species endemic to the Sierra Nevada of California and Cascade mountains of Oregon (Wiggins 1998). In addition to these clear differences between trout and fishless stream pairs, our results provide preliminary evidence that densities of a number of other invertebrate taxa were consistently higher in either fishless or trout streams (see Figures 5-6).

Because we did not manipulate trout in this study and cannot unambiguously link trout to the observed differences, we systematically examine and evaluate alternative explanations for the differences between trout and fishless streams. The primary alternative explanation for observed differences in both algae and invertebrate abundances is that confounding differences in abiotic or other biotic conditions between trout and fishless streams might have driven the observed patterns. Data on environmental conditions (Table 1) show no such consistent differences in the environmental characteristics of fishless and trout streams. It is possible, however, that observed patterns were driven by consistent fishless-trout stream differences in an unmeasured variable.

The variables that we measured in each reach include most known factors which influence invertebrate and algal assemblages, including nutrients, organic matter, substrata, habitat refuges, light, stream size, depth, temperature, water chemistry, and gradient (Allan 1995, Giller and Malmqvist 1998). The literature and our data suggest that any unmeasured but consistent differences in environmental conditions between trout and fishless streams would be related to variables which have only weak effects on invertebrate and algal assemblages and which would be unlikely to produce the consistent and strong invertebrate and algal patterns observed.

On the other hand, it is possible that differences in algal biomass and macroalgal cover between trout and fishless streams could be due to natural differences in algal production or loss between stream pairs rather than responses to trout introduction. In turn, differences in invertebrate densities between fishless and trout streams could be viewed as responses to these important food and habitat resources. We argue that this is not the case using three lines of reasoning. First, we found no differences between paired fishless and trout streams in any of the resources potentially limiting algal growth, including carbon (as measured by alkalinity and pH), nutrients (nitrate/nitrite, ammonia, phosphate), or light (as measured by canopy cover and water turbidity). Second, experimental manipulations of trout in streams worldwide have found that the addition of trout to fishless streams or stream channels typically causes increases in algal biomass (Bechara et al. 1992, Flecker and Townsend 1994, McIntosh and Townsend 1996, Dahl 1998b, Huryn 1998, Peckarsky and McIntosh 1998, Dahl and Greenberg 1999, Nakano et al. 1999, Diehl et al. 2000, Rosenfeld 2000a, 2000b, Shurin et al. 2002, but see Power 1990, 1992). Prior research, then, indicates that algal abundance should be higher in streams with trout even if there are no differences in algal resources and even if trout have no effect on grazer densities or biomass.

Finally, the patterns for grazing invertebrates are inconsistent with the hypothesis that the observed differences in invertebrate density are driven by responses to natural algal differences. The strongest patterns among grazing invertebrates were the large declines in trout streams for the mayfly *Ameletus* and the caddisflies *Neothremma* and *Anagapetus*, as well as the large increase in trout streams for the mayfly *Centroptilum*. Weaker patterns of increased abundance in the trout streams were also observed for the Chironomidae midges and the caddisfly *Glossosoma*, while many of the most common grazing invertebrates showed no consistent difference between trout and fishless streams (e.g., *Baetis* group, Heptageniidae, *Micrasema*,

Serratella, *Caudatella*). With most of the strongest patterns indicating decreased abundance in trout streams, and with inconsistent patterns among the majority of grazers, the density patterns for grazing invertebrates provide no support for the hypothesis that invertebrate differences simply reflect responses to natural differences in algae between trout and fishless streams.

In fact, these invertebrate grazer patterns provide further support that algal resources increased in streams with trout because of reduced grazing pressure (i.e., a trophic and/or behavioral cascade). In this study, some grazers declined in abundance in the presence of trout (*Ameletus*, *Neothremma*, *Anagapetus*) and other grazers likely foraged less in the presence of trout (Kohler and McPeck 1989, McIntosh and Townsend 1994, 1995, 1996, Peckarsky and McIntosh 1998, Diehl et al. 2000). Combined, these shifts in density and grazing behavior could have resulted in higher algal biomass and cover in trout streams. The increase in *Centropilum* and the tendency for increases in Chironomidae and *Glossosoma* in trout streams, we suspect, indicate grazer taxa which were able to track increased algal levels but which were unable to compensate fully for trout-induced reductions in grazing by other invertebrate groups (see below).

There is therefore little or no evidence supporting the alternative explanations that: 1) differences in algae and invertebrate abundances were caused by other biotic/abiotic differences between fishless and trout streams; or 2) that invertebrates differences simply reflected the tracking of natural algal differences between trout and fishless streams. Although we cannot conclusively demonstrate that trout caused observed differences between trout and fishless streams in this study, we have shown that trout presence is strongly related to observed patterns in algae and invertebrate abundances and that the evidence supporting trout presence as the cause of observed differences between trout and fishless streams is much stronger than for any alternative hypothesis.

Combined Results from Waterfall and Watershed Studies

We have used two observational approaches to measure the large-scale effects of trout introductions on stream invertebrate assemblages in the Sierra Nevada mountains: paired comparisons of stream reaches lacking and containing trout above and below barrier waterfalls (Silldorff et al. Report 2) and comparisons of independent pairs of trout and fishless streams with similar environmental characteristics (current study). Because trout were not manipulated in

these studies, however, it is difficult to show, unequivocally, that trout caused the observed patterns because other factors may have differed between trout and fishless streams or stream reaches. By combining data from the two studies, however, we can overcome many of the individual limitations of each observational study.

The primary alternative hypothesis for differences in invertebrate abundances above and below barrier waterfalls relates to the confounding influence of natural longitudinal changes in invertebrate abundances. As Table 1 shows, longitudinal effects cannot explain differences observed in the paired watershed study because fishless streams occurred at similar elevations and distances from headwaters as trout streams. Likewise, alternative explanations for patterns emerging from the paired watershed study (above) primarily relate to consistent differences between fishless and trout streams in each pair, such as natural differences in algal productivity. These alternatives, however, cannot explain invertebrate patterns observed in the barrier waterfall study because fishless and trout reaches were conterminous and no tributaries entered the stream between trout and fishless reaches. Therefore, consistent invertebrate differences across both studies cannot be explained by the most plausible alternative explanations for each component study. As a result, the only viable explanation for consistent invertebrate differences in our two studies is that trout directly or indirectly affected the distribution and/or abundance of these stream invertebrates. We therefore identify which patterns were observed consistently across the two types of studies.

Densities of 7 invertebrate taxa (*Ameletus*, *Edmundsius agilis*, *Paraleptophlebia*, *Doroneuria baumanni*, *Anagapetus*, *Neothremma*, Tricladida) and 1 community metric (evenness, J') consistently declined from fishless to trout sites in both studies (Table 3, Figure 10). We conclude that these 7 invertebrate taxa and community evenness declined because of interactions with introduced trout, and we discuss the implications of these changes below. The primary criteria for including a taxon on this list was the presence of statistical evidence ($p < 0.05$) for density differences in trout versus fishless reaches in one of the two studies and then either statistical evidence ($p < 0.05$) for density differences or consistent patterns across pairs of streams in the other study. Two taxa (*Edmundsius agilis* and *Doroneuria baumanni*) were included in this list based on slightly different criteria. *Edmundsius agilis* nymphs were found in only a small number of fishless reaches or streams in each study; consequently, there was inadequate information to draw conclusions about the effects of trout on this endemic mayfly's abundance.

A more detailed study of 3 streams with populations of this uncommon mayfly, however, revealed that abundant populations dropped to zero or near zero immediately below barrier waterfalls, providing clear evidence that trout presence was a critical factor driving the distribution of this mayfly in Sierra Nevada streams (Silldorff Report 3, *in review*). For densities of *Doroneuria baumanni*, the paired watershed study indicated clear declines from fishless to trout streams but the barrier waterfall study found less convincing evidence for declines using the broader grouping of *Doroneuria baumanni* with *Calineuria californica* (5 of 7 reach pairs above versus below waterfalls showed declines, $p=0.08$). Because the current paired watershed study showed that *Calineuria californica* did not show density differences between fishless and trout streams, we believe that the barrier waterfall study produced less convincing data on density differences between trout and fishless reaches for *Doroneuria baumanni* both because this taxon was lumped with *Calineuria californica* and because of the smaller sample size in the waterfall study.

In addition to these 7 invertebrate taxa whose abundances clearly have been reduced by trout introductions, and the consistent declines in community evenness, we highlight 10 additional taxa and one additional community metric with less consistent patterns across the 2 studies but whose patterns, we believe, may reflect actual biological responses to trout introductions (Table 3, Figures 11-12). Other invertebrate taxa not highlighted in Table 3 also showed patterns indicating that their densities may have been altered by trout introductions, but our data were too inconclusive for us to make any broader statements about their responses to trout. Additional investigations are needed to determine if observed differences in the densities of these 10 taxa (and others highlighted in each individual study) between trout and fishless sites are caused by the introduction of trout.

Two broad patterns emerge from the combined results of these two studies. First, the strongest effects from trout introductions that we could unambiguously identify are the reduction or elimination of invertebrates endemic to the Sierra Nevada (Table 3). Silldorff (Report 3, *in review*) presented data indicating that the endemic mayfly *Edmundsius agilis* has been essentially eliminated from streams because of trout introductions. In addition, the common rheophilic caddisfly *Neothremma*, which has a single known endemic species in the central Sierra Nevada (see Silldorff et al. Report 3), declined by 98-99% in trout relative to fishless sites in both of our studies. Finally, the Tricladida flatworms declined by 80-90% in trout relative to fishless sites in

both of our studies, and limited research indicates that nearly all flatworms at higher elevations in the Sierra Nevada are endemic species (Hampton 1988). These patterns suggest that endemic invertebrates are particularly vulnerable to trout because they lack an evolutionary history with fish and, hence, effective defenses for counteracting fish predators (see McPeck 1990a, 1990b, McPeck et al. 1996).

Second, comparisons of responses by closely related or morphologically similar taxa suggest that invertebrate responses to trout introduction are remarkably species-specific. Among predators, both the most and least abundant of the three Perlidae stonefly taxa (*Doroneuria baumanni* and *Hesperoperla*) were less abundant in trout streams, whereas *Calineuria californica*, with intermediate densities and a similar size to the other two Perlidae taxa, showed no relationship with the presence of introduced trout (Figure 3, Figure 7). Similarly, the two largest invertebrates found in this study were the predaceous dobsonfly larvae, *Dysmicohermes ingens* and *Orohermes crepusculus*. Both were uncommon, being collected in 6 streams each, but *Dysmicohermes* was found in only 6 fishless streams whereas *Orohermes* was collected at similar densities from 3 trout and 3 fishless streams. Finally, two of the predaceous diving beetle taxa (family Dytiscidae) we collected were found only in fishless streams (*Agabus* and *Agabinus*) whereas three others were collected with similar frequencies and densities in both fishless and trout streams (*Hydroporus*, *Oreodytes*, *Stictotarsus*). Unlike the taxa discussed above, *Agabus* and *Agabinus* adults (7-11 mm and 5-7 mm, respectively) are typically larger than adults of the other three genera (2 to 6 mm), indicating that trout effects on Dytiscidae density may be related to beetle size (Usinger 1956, Larson et al. 2000). Among these large stream predators, only *Dysmicohermes ingens* is endemic to high elevations in the Sierra Nevada (Usinger 1956, Evans 1972, Stewart and Stark 1988, Larson et al. 2000), so apparent declines in stream predators occurred in both the lone endemic as well as in other non-endemic large predators.

Among non-predaceous taxa, the two common turtle-cased caddisfly larvae (*Anagapetus* and *Glossosoma*) exhibited opposite patterns with respect to trout: *Anagapetus* was less abundant in trout streams, whereas *Glossosoma* was apparently more abundant in trout streams. For two small and abundant rheophilic caddisflies in these streams, the densities of *Neothremma* were much lower in trout streams, whereas the densities of *Micrasema* did not differ between fishless and trout streams. The two largest mayflies in our study, both occurring in pool habitats and

belonging to the family Siphonuridae, showed distinct relationships to trout presence, with *Edmundsius agilis* essentially absent in trout streams and *Siphonurus* occurring at similar densities in trout and fishless streams. Observations of the habitat preferences and physiological tolerances of these taxa suggest that this pattern may have resulted from *Siphonurus*' ability to shift its distribution to areas of the stream channel inaccessible to fish (e.g., detached pools with lower oxygen levels and higher daytime water temperatures than the main channel) whereas *Edmundsius agilis* has always been found only in well-aerated, cool pools in the main channel (Day 1956, E.L. Silldorff *personal observation*). Finally, two groups of small swimming mayflies in the family Baetidae, which often are dominant components of trout diets in streams (e.g., Allan 1978), exhibited different response patterns to trout presence. The *Baetis* group mayflies (*Baetis bicaudatus*, *Baetis tricaudatus*, *Dipheter hageni*; species could not be distinguished for all individuals; all widespread species) were the second most abundant invertebrate taxon in our streams and were 10 times more abundant in riffle than pool habitats (mean abundance in fishless stream riffles in this study = 1800 / m², mean abundance in fishless stream pools = 19 / m²). Although other research in the Sierra Nevada clearly indicates that these mayfly nymphs are an important component of trout diets (e.g., Diehl et al. 2000), there was no difference in their abundance in trout and fishless streams. By contrast, the less common, pool-dwelling baetid mayfly, *Centroptilum*, (mean abundance in trout stream riffles = 1 / m², mean abundance in trout stream pools = 305 / m²) was more abundant in trout than fishless streams, a remarkable result given the strong preference of this genus for slow-flowing pool habitats where trout are more common and abundant. Among these non-predatory invertebrate taxa, the mayfly *Edmundsius agilis* is endemic, and the species of *Anagapetus*, *Glossosoma*, and *Neothremma* collected in this study are all taxa likely endemic to the Sierra Nevada (Usinger 1956, Meyer 2001, Silldorff et al. *in prep*). Again with these non-predaceous taxa, the largest declines are among endemic groups, although it is noteworthy that *Glossosoma* apparently increased with trout.

Only for the water boatmen family Corixidae do we have evidence that all species within the family have similar responses to trout introductions. Specifically, we collected three water boatmen in this study (*Cenocorixa wileyae*, *Graptocorixa californica*, *Hesperocorixa*) and all were found only in fishless streams. Although this pattern is moderately strong for *Graptocorixa*

californica (found only in 6 fishless streams), the other two taxa were each found in only a single fishless stream. All of the collected Corixidae taxa are widespread (Menke 1979)

Ecological Role of Trout in Streams

Salmonidae fishes are the dominant, and often only, fish present in cold-water streams throughout much of North America and Eurasia, and these fishes have now been introduced to all continents of the world save Antarctica (MacCrimmon and Marshall 1968, MacCrimmon 1971, Welcomme 1992, Moyle and Cech 1996). Because of their heavy reliance on stream invertebrates for food, trout and other Salmonidae have the potential to play a major role in the ecology and evolution of stream invertebrates worldwide. Extensive research has clearly shown that trout can strongly influence the behavior and life history of stream invertebrates (Cooper 1984, Malmqvist 1988, Flecker 1992, Wiseman et al. 1993, Douglas et al. 1994, Forrester 1994, McIntosh and Townsend 1995, McIntosh and Townsend 1996, Dahl 1998b, Peckarsky and McIntosh 1998, McIntosh et al. 1999, Miyasaka and Nakano 1999, Diehl et al. 2000, Peckarsky et al. 2001, Peckarsky et al. 2002) and trout may affect the evolution of invertebrate behaviors in areas where they have been introduced (McIntosh and Townsend 1994). It also is clear that trout can be important consumers of stream secondary production (Allen 1951, Huryn 1996, 1998).

Considerable controversy exists, however, about the role that trout play in the population biology and community ecology of stream invertebrates. Part of this controversy arises because of conflicting results between small and large-scale research. The work on the *Baetis* group mayflies illustrates this controversy well. Most research at small spatial and temporal scales suggests that densities of these mayflies decline when trout are present (Culp 1986, Bechara et al. 1992, 1993, Dahl 1998a, 1998b, Dahl and Greenberg 1999, Rosenfeld 2000a). Combined with the fact they are often a dominant component of trout diets (e.g., Allan 1978), these experimental results have been interpreted as relatively clear evidence that trout cause direct negative effects on population sizes for *Baetis* mayflies (Bechara et al. 1992, Dahl 1998b, Rosenfeld 2000a). Yet most research at larger scales (i.e., reach, whole stream) has either failed to find any relationship between *Baetis* density and trout presence or has found suggestive evidence that these mayflies are more abundant in the presence of trout (Allan 1975, Allan 1978, Jacobi 1979, Harvey 1993, Diehl et al. 2000, Peckarsky et al. 2001, Silldorff et al. Report 2, this study). Recent modeling of predation experiments in open systems indicates that such reversals

in results across scales may arise through a switch from dominance by behavioral responses at small scales to dominance by demographic responses at large scales, with the large scale research providing the only reliable estimates for population-level effects from direct predation in these open systems (Englund et al. 2001). Furthermore, research at large spatial and temporal scales reveals that trout have complex indirect effects on the life history of *Baetis* with nymphs exposed to trout completing their immature life cycle more quickly, emerging at a smaller size, and having lower female fecundity (McPeck and Peckarsky 1998, Peckarsky et al. 2001, 2002). An additional, but unexplored, interaction may be an net indirect positive effect on *Baetis* through enhancement of their food resources (see Peacor 2002). As in this study, many researchers working at various scales have reported that the combined reduction in grazer density and/or grazer feeding on the surfaces of stream substrates causes increases in algal abundance and algal productivity (Bechara et al. 1992, Flecker and Townsend 1994, McIntosh and Townsend 1996, Dahl 1998b, Huryn 1998, Peckarsky and McIntosh 1998, Dahl and Greenberg 1999, Nakano et al. 1999, Diehl et al. 2000, Rosenfeld 2000a, 2000b, Taylor et al. 2002, Shurin et al. 2002). The enhancement of their primary food resource (i.e., algae) may lead to increased growth rates and lower mortality for *Baetis* (and other grazers), thus canceling or even reversing the direct negative effects from trout predation and the indirect negative effects on individual growth and fecundity. Finally, the decreased abundance in trout streams of predatory flatworms and the dominant large stonefly predator (*Doroneuria baumanni*) may indicate that decreased mortality from invertebrate predators compensates for increased mortality from trout (Dahl and Greenberg 1997, Soluk and Richardson 1997, Peckarsky and McIntosh 1998). We suspect that these indirect positive effects may explain the suggestive positive relationship between trout presence and *Baetis*-group densities in a number of large-scale studies (Jacobi 1979, Peckarsky et al. 2001, Silldorff et al. Report 2, this study)

Clearly, complex direct and indirect effects from trout not only are possible in these systems but actually occur for at least some stream invertebrates (see also Feltmate and Williams 1991). Predicting, *a priori*, the net effect from these complex interactions for any invertebrate population will be very difficult. Indeed, the results from our surveys suggest that the net effects on closely related or morphologically similar taxa are strongly divergent. Nevertheless, a few general patterns emerge from comparisons of our results to previous research on trout-invertebrate interactions in streams.

As expected with visual, size-selective predators, trout can reduce or eliminate large and conspicuous invertebrates in streams (Hemphill and Cooper 1984, Cooper 1988, Wiseman et al. 1993, McIntosh 2002). In our current work, the largest Dysticidae beetles (*Agabinus*, *Agabus*), all Corixidae water boatmen, and 3 of the 4 largest swimming mayflies (*Edmundsius agilis*, *Ameletus*, *Paraleptophlebia*) showed patterns of lower abundance and restricted distribution in streams with introduced trout. As noted above, however, an invertebrate's size and conspicuousness provides only limited insight into how it will respond to trout. We found that organisms with similar sizes, behaviors, and (presumably) conspicuousness showed different responses to the presence of trout in the current study (i.e., *Edmundsius* vs. *Siphonurus*, *Baetis* group vs. *Centroptilum*, *Doroneuria* and *Hesperoperla* vs. *Calineuria*, *Dysmicohermes* vs. *Orohermes*, *Anagapetus* vs. *Glossosoma*, *Neothremma* vs. *Micrasema*). Our results suggest that such distinctive responses may, in part, be related to different evolutionary exposure to trout and other fish.

Large predaceous stoneflies, in particular, appear to be highly vulnerable to trout predation in a number of studies. Research in Utah, USA, and Ontario, Canada, both found large reductions in Perlidae stoneflies in streams or stream channels with trout (Harvey 1993, Feltmate and Williams 1991). Our results for the Sierra Nevada clearly indicate that the dominant of the 3 Perlidae stoneflies in these streams (*Doroneuria baumanni*) declined because of trout introductions, while a second Perlidae stonefly (*Herperoperla*) exhibited patterns suggesting it, too, may have declined because of trout introductions. However, the third Perlidae stonefly in these streams (*Calineuria californica*) exhibited no association with trout presence, indicating that large predatory stoneflies can show highly individualistic responses to trout presence, a pattern supported by work in streams of Colorado, USA (Peckarsky et al. 2001). Harvey's (1993) research in Utah also found apparently compensatory increases in the combined abundance of 2 smaller predatory stoneflies in the Utah streams he studied (*Cultus aetievalis* and *Skwala parallela*, both Perlodidae). In our work in the Sierra Nevada, however, we found that neither the Chloroperlidae nor the Perlodidae stoneflies increased in abundance in streams with trout (Silldorff et al. Report 2, Table 2). The differences between our findings and those of Harvey may stem from distinct responses by the particular species of Perlodidae in Utah streams compared to Sierra Nevada streams. Alternatively, because Harvey sampled from only the tails of pools within a narrow range of substrate, depth, and flow characteristics, it is possible that his

results for both Perlidae (*Hesperoperla pacifica*) and Perlodidae stoneflies reflect shifts in microdistributions rather than changes in population sizes in these streams. Thus, the net effects of trout on smaller predatory stoneflies remain ambiguous.

We found 2 apparently indirect, positive effects from trout which also are consistent with previous studies. First, algal abundance tends to increase in the presence of trout in most studies which examine algal responses (Bechara et al. 1992, Flecker and Townsend 1994, McIntosh and Townsend 1996, Dahl 1998b, Huryn 1998, Dahl and Greenberg 1999, Nakano et al. 1999, Peckarsky and McIntosh 1998, Diehl et al. 2000, Rosenfeld 2000a, 2000b, Shurin et al. 2002). This increased algal abundance likely stems both from decreased abundance of grazers and from decreased feeding activity of grazers (Flecker and Townsend 1994, McIntosh and Townsend 1996, Peckarsky and McIntosh 1998, Diehl et al. 2000). Furthermore, this increased algal abundance may be the proximate cause for a number of positive relationships we observed between invertebrates and trout. Foremost among these is the tendency for Chironomidae midges to be more abundant in trout streams. Although this pattern has been commonly observed, it is also typically inconsistent across replicate treatments (Jacobi 1979, Culp 1986, Bechara et al. 1992, Andersen et al. 1993, Bechara et al. 1993, Harvey 1993, Huryn 1998, Rosenfeld 2000a, 2000b, Silldorff et al. Report 2, this study). The primary hypothesis posed to explain increased midge abundance suggests that trout either reduce the abundance and/or the activity of grazing invertebrates in streams, which leads to increased algal biomass and/or productivity, followed by increases in some groups of common grazing Chironomidae as they track this increased food resource. Observing an increase in midges is therefore contingent both on 2 initial responses to trout presence (an invertebrate grazer response and an algal response) as well as food limitation in common Chironomidae. When all of these processes occur in the same stream, midge larvae will likely increase their abundance. The number of studies finding such results suggests that these processes do indeed occur simultaneously in many streams. Yet our result that only 13 of the 21 stream pairs showed increased Chironomidae abundance, and the inconsistent pattern in earlier studies, indicates that it is nearly as common for one or more links in this chain to be broken, which results in little or no response by the midges to trout presence. An alternative explanation to the increase in midges as a response to algae as a food resource is that many midges also use algae as habitat cover.

In addition to the indirect positive effects on algae and Chironomidae midges, trout may also be having indirect positive effects on *Centroptilum* mayflies in these systems (Figure 4), a perplexing pattern not found prior to this work (but see Cooper 1988). Because this mayfly has a strong preference for pool habitats (see above) where trout are more common and abundant, and because these mayflies are active swimmers with similar size to other Baetidae mayflies, it seems reasonable that they would be highly vulnerable to trout predation. But in both components of our study, we found that their average abundance more than doubled in streams or stream reaches with trout. We hypothesize 2 complementary reasons why such large increases may occur. First, as with the *Baetis* group mayflies, the indirect positive effects of increased food resources (i.e., algae) may cancel or even override the negative direct and indirect effects from trout. Second, we found a suggestive pattern for habitat shifts in the *Baetis* group mayflies, with densities lower in pool habitats with trout than in pools without trout (median density in fishless pools = 76 / m², median density in trout pools = 40 / m²). Combined with increased algal resources, this decrease in the abundance of confamilial (and likely competitive) mayflies may have provided additional positive indirect effects for *Centroptilum*. It is also possible that *Centroptilum* is released from invertebrate predation in trout streams where abundance of the large stonefly predator *Doroneuria baumanni* is greatly reduced.

We also found dramatic declines in 2 cased caddis larvae (*Neothremma*, *Anagapetus*, both likely endemic to the Sierra Nevada), a surprising results from a group of stream invertebrates typically less vulnerable to fish predation than other invertebrates (Kohler and McPeck 1989). Suggestive patterns for declines in 2 other more widely distributed cased caddis (*Yphria californica*, *Apatania*) indicate that negative effects to cased caddisflies may not be uncommon. Harvey's (1993) research in Utah found similar, 90+% declines in *Neothremma* in streams with trout. Work in New Zealand has also found that trout cause declines in the abundance of a large cased caddis, *Zelandopsyche ingens*, through indirect effects on foraging and growth (McIntosh et al. 2002).

Finally, the strong declines in Tricladida flatworms provide a surprising result which has generally not been reported in the literature but which may also have occurred with trout introductions to New Zealand (A.R. McIntosh *personal communication*). It is not clear whether the 80-90% reductions in flatworm density are caused by direct predation on these soft bodied invertebrates or by some indirect interaction. Although flatworms are not abundant in samples

of stream drift, they do drift in the water column at appreciable rates (Dendy 1944, Waters 1972, Turcote and Harper 1982, Brittain and Eikeland 1988). Furthermore, their large size (5-20 mm) and their poor ability to return to the substrate may make them particularly vulnerable to drift-feeding fish such as trout (Pennak 1953, Elliott 1971, Kenk 1972, Kolasa 1991). Alternatively, trout may indirectly affect flatworms because the increased algal abundance and macroalgal cover on the upper surfaces of stones in trout streams may structurally interfere with their mucus trail locomotion and thus inhibit their ability to move or effectively capture prey (Pennak 1953, Kolasa 1991). More mechanistic research about this interaction would be needed to clarify the processes leading to our dramatic results.

Although we have found large changes in the distribution and abundance of some stream invertebrates associated with trout introductions into the Sierra Nevada, the majority of stream invertebrates do not change between fishless stream assemblages and trout stream assemblages. We did find consistent decreases in community evenness in trout streams. However, this shift in evenness primarily reflects the increased abundance of the dominant Chironomidae, with little change in the absolute abundance for most invertebrate taxa. Similarly, we found moderately consistent declines in the taxa richness for a typical sample, but the changes were both small (less than 10%) and primarily reflect the loss of a few invertebrate groups from trout streams. Multivariate analyses were ambiguous in evaluating differences in the invertebrate assemblages between fishless and trout streams. Nonetheless, a substantial fraction of common taxa, and uncommon taxa, showed responses to trout suggesting that moderate changes in community structure have occurred as a result of trout introductions. Our earlier study looking at reach-to-reach variability across waterfalls also found that there were moderate changes in the invertebrate assemblage found in downstream trout reaches when compared to upstream fishless reaches (Silldorff et al. Report 2). The broader conclusion that trout streams support largely the same invertebrate fauna as fishless streams has been the finding of nearly all large-scale research examining trout-invertebrate interactions (Allan 1975, Jacobi 1979, Allan 1982, Andersen et al. 1993, Huryn 1996, Huryn 1998, Diehl et al. 2000, Peckarsky et al. 2001).

Conclusions

The combined results from our work in the Sierra Nevada indicate that trout cause important reductions in the abundance and the distribution of a number of stream invertebrate taxa. The negative effects on endemic invertebrates (*Edmundsius agilis*, *Ameletus*, *Neothremma*, Tricladida flatworms) appear to be particularly pronounced. Moderate changes in the structure of the invertebrate community associated with trout were also evident in significant and/or consistent changes in the density of 10-18 common taxa (13 decreasing and 5 increasing in the presence of fish). Among these taxa, trends were statistically significant for 10 taxa and qualitatively consistent for 8 taxa (statistical power insufficient). Of 43 taxa designated as common (>0.1%) this represents 23-42% of these taxa responding to fish. Another 8-13 uncommon taxa also showed distinct patterns of association with fishless or trout streams but were not abundant enough for statistical tests. The abundances of 9 invertebrate taxa (*Ameletus*, *Paraleptophlebia*, *Doroneuria baumanni*, *Hesperoperla*, *Neothremma*, *Anagapetus*, *Yphria californica*, Hydropsychidae, and Tricladida) were consistently lower in trout streams, with dramatic declines in the caddisfly *Neothremma* and the Tricladida flatworms. Furthermore, densities of the Baetidae mayfly *Centroptilum* were higher in the trout streams. A synthesis of the results from the current study and other stream surveys above and below barrier waterfalls provide the clearest evidence that trout introductions are related to declines in at least 7 invertebrate groups: the mayflies *Ameletus*, *Edmundsius agilis*, and *Paraleptophlebia*; the stonefly *Doroneuria baumanni*; the caddisflies *Anagapetus* and *Neothremma*; and the Tricladida flatworms. The most severely affected taxa (*Edmundsius agilis*, *Neothremma*, Tricladida) contain primarily endemic species in the Sierra Nevada mountains, suggesting that a lack of evolutionary exposure to trout and other fishes may increase the likelihood and severity of effects from these introduced fishes. We also found remarkably distinct responses to trout introductions from taxonomically related and morphologically similar invertebrate groups, even those with similar evolutionary exposure to trout. The effects of trout on invertebrate populations therefore appear to be highly species specific.

The probable effects of trout on the function of High Sierra benthic stream communities were also evident in (1) increased algal density and cover, (2) a greater abundance of midges (which play dominant roles in the consumption of organic matter and algae and as prey to invertebrate predators), and (3) reduced density of the most common large predator (*Doroneuria*

baumanni) in the presence of trout. These changes suggest that trout alter the trophic organization and resource production and transformation in high Sierra streams. Trout may cause indirect positive effects on a few invertebrate groups in these streams (e.g., Chironomidae, *Centroptilum*) and an increase in algal biomass and productivity. Trout can clearly play an important role in the population biology of stream invertebrates in the Sierra Nevada and in regions around the world where they are both native and introduced (Feltmate and Williams 1991, McIntosh 2002, Silldorff Report 3 *in review*).

The results of this study argue that the management of introduced trout in Sierra Nevada streams should focus first on endemic invertebrates impacted by trout. Where introduced trout threaten the survival of an endemic invertebrate species, trout should be extirpated from sufficient lengths of streams to insure that multiple, large populations of these invertebrates may persist in expanded headwater habitats protected by natural trout migration barriers (waterfalls and steep cascades). In addition, there may be benefits to recovery of native biodiversity in creating expanded fishless habitat that could restore altered structure and function of stream communities. The broader conclusion of our studies that most taxa appear to be unaffected by trout has been the finding of nearly all large-scale research examining trout-invertebrate interactions (Allan 1975, Jacobi 1979, Allan 1982, Andersen et al. 1993, Huryn 1996, Huryn 1998, Diehl et al. 2000, Peckarsky et al. 2001) and suggests that management should be carefully targeted at those streams where trout removals could provide the greatest benefit to enhanced biodiversity.

Our results provide additional guidance in criteria for selection of Aquatic Diversity Management Areas (ADMAs) that would serve as habitat and geographic regions for sustaining native biodiversity of the Sierra Nevada (Moyle et al. 1996b). Fishless habitat is clearly rare and supports an unaltered native community, so primary criteria might be: (1) any fishless stream reaches and especially those with contiguous areas of fishless habitat, (2) fishless locations with known endemic invertebrate populations, and (3) streams that are manageable for trout removal because of natural migration barriers and demonstrated alteration of benthic community structure and function. With additional biological survey data, streams with diverse assemblages of invertebrates (with or without exotic trout), endemic species, and distinctive community types will also need to be represented within ADMAs. Headwater streams, including intermittent channels, may provide important habitat refugia from trout predation, and may harbor many rare

or endemic species. These small drainages should be the emphasis of survey and inventory studies that can then be used to help delineate ADMAs.

Future Research

Our research in Yosemite National Park has demonstrated that introduced trout cause significant changes in the ecology of high-elevation streams. Although removing introduced trout from high-elevation lakes has been shown to reverse their effects on native amphibians, we do not know if removing trout from high-elevation streams will reverse their effect on native invertebrate communities. Planned management actions in Sequoia-Kings Canyon National Park provide an opportunity to evaluate the potential for recovery of streams after the removal of introduced trout. Trout removals from lakes and a connecting stream segment in the Center Basin are planned for 2004 or 2005, and under a cooperative agreement with the Park Service, David Herbst and a crew from the Sierra Nevada Aquatic Research Laboratory will conduct two seasons of both pre-treatment and post-treatment invertebrate sampling to evaluate recovery. These surveys will be combined with control studies of benthos from 2 streams containing trout that will not be removed, and one fishless stream that will serve as a target condition. This information will allow SEKI to quantify the potential recovery rate of native biodiversity in high-elevation streams, consider the inclusion of stream habitat in parkwide restoration planning, and obtain a baseline for future invertebrate monitoring.

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Table 1. Summary of the environmental characteristics of surveyed fishless and trout streams.

Variable	Mean (s.e.) for Fishless Streams		Mean (s.e.) for Trout Streams		Range for Fishless Streams	Range for Trout Streams	Mean Difference (Trout - Fishless)	Range of Differences	Paired t-test (p-value)
	Mean	(s.e.)	Mean	(s.e.)	Min - Max	Min - Max	Mean	Min - Max	
Elevation (m)	2258	(112)	2258	(100)	1348 - 3165	1433 - 2976	0	-256 - 543	0.99
Average Wetted Stream Width (cm)	203	(17)	222	(21)	89 - 471	69 - 447	19	-114 - 137	0.22
Average Stream Depth (cm)	13	(1)	14	(1)	7 - 22	6 - 34	1	-8 - 22	0.59
Maximum Stream Depth (cm)	39	(3)	42	(4)	20 - 85	15 - 97	2	-26 - 66	0.61
Length of Headwaters (km)	3.1	(.5)	3.6	(.5)	0.6 - 7.1	0.7 - 9.7	0.5	-5.7 - 5.6	0.38
Gradient of Sampled Reach (%)	5.7	(.6)	5.3	(.5)	0.9 - 13.7	0.7 - 11.9	-0.4	-7.4 - 2.6	0.47
Average Gradient of Headwaters (%)	10.9	(1.4)	10.7	(1.1)	3.0 - 29.3	3.0 - 18.6	-0.1	-18.9 - 10.7	0.94
Canopy Cover (%)	35	(5)	40	(6)	10 - 80	1 - 89	5	-25 - 34	0.21
Water Temperature (C)	13	(1)	12	(0)	8 - 17	8 - 17	0	-5 - 4	0.41
pH	6.0	(.1)	6.0	(.2)	4.7 - 7.2	4.3 - 7.8	0.0	-1.9 - 1.9	0.92
Conductivity (µS)	27	(4)	30	(7)	5 - 55	5 - 162	3	-40 - 117	0.63
Alkalinity (mg/L CaCO ₃)	25	(2)	27	(4)	12 - 49	6 - 96	3	-31 - 64	0.52
Turbidity (NTU)	1.6	(.2)	1.5	(.2)	0.2 - 2.6	0.3 - 2.7	0.0	-0.7 - 0.9	0.51
Soluble Reactive Phosphorus (µM)	33	(5)	30	(7)	2 - 84	0 - 153	-3	-84 - 75	0.60
Nitrate + Nitrite (µg/L)	10	(3)	15	(6)	0 - 57	0 - 105	5	-40 - 96	0.78 *
Ammonia (µM)	24	(3)	27	(4)	0 - 46	1 - 69	3	-24 - 69	0.43
Fine Particular Organic Matter (g AFDM)	1.5	(.2)	1.6	(.2)	0.2 - 4.5	0.3 - 3.5	0.1	-1.3 - 2.4	0.71
Coarse Particulate Organic Matter (g wet weight)	394	(98)	410	(97)	15 - 1651	116 - 1759	16	-1170 - 1370	0.90
Riffle Area (%)	39	(3)	38	(3)	15 - 59	7 - 66	-1	-35 - 17	0.84
Pool Area (%)	28	(3)	30	(3)	14 - 75	14 - 59	2	-16 - 33	0.41
Fine substrate (% , size < 1 mm)	2	(1)	2	(1)	0 - 18	0 - 12	-1	-18 - 7	0.79 *
Sand Substrate (% , 1 mm < size < 3 mm)	13	(2)	16	(3)	0 - 32	0 - 40	3	-16 - 27	0.21
Gravel Substrate (% , 3 mm < size < 65 mm)	30	(3)	27	(3)	10 - 53	8 - 60	-3	-37 - 10	0.22
Cobble Substrate (% , 6.5 cm < size < 25 cm)	26	(3)	29	(3)	7 - 50	0 - 58	4	-27 - 40	0.38
Boulder Substrate (% , size > 25 cm)	29	(4)	26	(4)	0 - 68	0 - 60	-3	-40 - 30	0.55
Trout Density (# / m ²)	0	(0)	0.11	(.02)	0 - 0	0.01 - 0.30			

* Statistical results from a Wilcoxon signed ranks-test. Differences in the fishless vs. trout values for these two variables did not follow a normal distribution.

Table 2. Summary of values for algal and invertebrate response variables. The order for each insect taxon is given in parentheses: C=Coleoptera, D=Diptera, E=Ephemeroptera, H=Hemiptera, M=Megaloptera, P=Plecoptera, T=Trichoptera. Rank orders are based on the means of the proportional abundances for each taxon in each stream out of a total of 110 taxa. Figure # indicates the graph where data are displayed. Declines are the number of stream pairs where the abundances of a taxon decreased from fishless to trout streams out of the total number of stream pairs where this taxon was found. Fishless and Trout Streams represent the total number of streams of each type where that taxon was found. Results from the Wilcoxon signed-rank test are provided for algal responses, invertebrate assemblage metrics, and for the densities of all invertebrates with percent abundances greater than 0.1%. Statistical tests were also performed on *Yphria californica* because of its high abundance and frequent occurrence in fishless streams.

Variable	Rank	Percent Abundance	Figure #	Declines	Fishless Streams	Trout Streams	Mean Density (s.e.) in Fishless Streams (# / m ²)	Mean Density (s.e.) in Trout Streams (# / m ²)	Median Density in Fishless Streams (# / m ²)	Median Density in Trout Streams (# / m ²)	Median Difference in Density (Trout - Fishless, # / m ²)	Wilcoxon Signed-Rank Test (p-value)
Algal Biomass (mg / m ²)		-	2	6 of 21	21	21	6.7 (1)	13.3 (3)	4.7	7.4	4.4	0.018
Macro-Algae (% Cover)		-	2	2 of 21 of	21	21	4 (2)	22 (6)	0	4	3	0.007
Total Abundance (except Chironomidae)		-	8	13 of 21	21	21	6179 (1047)	5501 (750)	4638	4250	-453	0.47
Richness (average # of taxa per sample)		-	8	13 of 21	21	21	22.5 (1.1)	21.2 (1.1)	21.6	22.0	-1	0.10
Evenness (Pielou's J')		-	8	17 of 21	21	21	0.54 (.02)	0.45 (.02)	0.55	0.44	-0.09	0.0005
Chironomidae (D)	1	59.9	5	8 of 21	21	21	8609 (1,320)	12235 (2,229)	7165	9937	2935	0.10
Baetis-group (E)	2	5.4	7	9 of 21	21	21	996 (246)	892 (186)	500	634	124	0.52
Acari	3	5.0		12 of 21	21	21	754 (112)	783 (92)	672	787	-27	1.00
Nemouridae (P)	4	4.1	7	8 of 21	21	21	704 (215)	714 (124)	387	553	73	0.41
Heptageniidae (E)	5	2.4	5	14 of 21	21	21	612 (272)	220 (41)	183	166	-41	0.27
Ostracoda	6	2.2		8 of 18	13	15	267 (102)	662 (396)	3	19	3	0.65
Micrasema (T)	7	1.6	7	9 of 20	17	19	426 (239)	244 (83)	58	117	4	0.62
Paraleptophlebia (E)	8	1.5	4	15 of 21	20	18	321 (67)	158 (33)	231	150	-30	0.02 *
Serratella (E)	9	1.4	7	8 of 20	17	19	235 (71)	279 (85)	56	189	36	0.57
Capniidae (P)	10	1.3		8 of 20	18	20	133 (40)	177 (54)	50	89	4	0.57
Chloroperlidae (P)	11	1.2	5	14 of 21	21	21	161 (19)	120 (18)	142	103	-27	0.11
Oligochaeta	12	1.2		10 of 21	21	20	142 (21)	202 (47)	131	133	20	0.43
Bezzia/Palpomyia (D)	13	0.9		8 of 21	19	20	131 (28)	258 (139)	96	63	9	0.54
Ameletus (E)	14	0.9	3	19 of 21	21	21	181 (28)	64 (10)	161	64	-86	0.00001****
Rhyacophila (T)	15	0.8	7	10 of 21	21	21	136 (27)	127 (17)	104	98	3	0.79
Tricladida	16	0.7	3	20 of 21	21	17	177 (45)	34 (13)	101	12	-87	0.000003****
Simuliidae (D)	17	0.6	5	8 of 21	18	20	87 (28)	127 (37)	33	70	23	0.19
Neothremma (T)	18	0.6	3	12 of 14	12	7	150 (72)	3 (3)	25	0	-65	0.003 *
Doroneuria baumanni (P)	19	0.6	3	15 of 16	16	12	132 (31)	30 (8)	90	12	-72	0.00006****
Apatania (T)	20	0.5	5	11 of 19	19	18	110 (33)	51 (10)	76	46	-9	0.13
Elmidae (C)	21	0.5		9 of 17	15	13	38 (18)	122 (75)	6	5	-3	0.92
Hydropsychidae (T)	22	0.5	4	14 of 19	18	17	117 (38)	38 (13)	45	10	-27	0.03*
Caudatella (E)	23	0.4		9 of 19	14	16	65 (26)	51 (15)	9	22	9	0.98
Lepidostoma (T)	24	0.4		9 of 16	14	15	85 (38)	89 (55)	38	21	-17	0.90
Perlodidae (P)	25	0.4	7	9 of 21	20	21	51 (9)	70 (15)	44	51	14	0.43
Yoraperla (P)	26	0.4	5	11 of 19	15	16	83 (26)	38 (13)	64	6	-24	0.21
Drunella spinifera/grandis (E)	27	0.4	5	9 of 20	18	16	27 (8)	80 (26)	12	40	20	0.18
Centroptilum (E)	28	0.4	4	3 of 13	10	11	17 (9)	153 (106)	0	4	41	0.03 *
Hydroptilidae (T)	29	0.4		5 of 16	9	13	60 (37)	43 (13)	0	13	15	0.32
Hexatoma (D)	30	0.3		9 of 21	21	19	48 (9)	34 (7)	41	26	1	0.42
Drunella doddsi (E)	31	0.2	5	5 of 17	13	15	16 (8)	40 (13)	2	16	9	0.14
Ecdisionia (T)	32	0.2		8 of 15	14	12	28 (8)	31 (15)	9	3	-8	0.51
Chelifera (D)	33	0.2		9 of 21	18	19	43 (14)	33 (7)	14	25	9	0.75
Polycentropus (T)	34	0.2		8 of 15	12	12	35 (15)	19 (7)	4	3	-4	0.49
Dicranota (D)	35	0.2		8 of 21	19	20	22 (5)	26 (5)	20	21	5	0.45
Anagapetus (T)	36	0.2	3	9 of 11	11	8	43 (15)	24 (10)	4	0	-20	0.03 *
Calineuria californica (P)	37	0.2	7	10 of 16	12	14	26 (10)	22 (8)	3	11	-8	0.44
Leuctridae (P)	38	0.2		9 of 15	13	11	17 (5)	18 (7)	9	3	-6	0.64
Sialis (M)	39	0.2		6 of 16	12	14	26 (15)	17 (6)	3	4	2	0.76
Dolophilodes (T)	40	0.1		7 of 8	7	6	24 (13)	16 (10)	0	0	-28	0.14
Pisidium	41	0.1		11 of 17	14	12	22 (8)	11 (6)	4	3	-4	0.12
Hesperoperla (P)	42	0.1	3	9 of 11	10	9	28 (11)	10 (4)	0	0	-16	0.02 *
Hydroporus (C)	43	0.07		3 of 8	4	5	6 (4)	7 (5)	0	0	3	
Mosella infuscata (P)	47	0.05	6	8 of 10	9	7	8 (3)	3 (2)	0	0	-4	
Oreodytes (C)	49	0.05		7 of 12	9	5	6 (3)	10 (8)	0	0	-3	
Gumaga (T)	51	0.04		1 of 4	2	4	4 (3)	10 (7)	0	0	9	
Stictotarsus (C)	52	0.04		4 of 7	4	3	3 (2)	5 (4)	0	0	-3	
Yphria californica (T)	54	0.03	3	10 of 11	11	4	11 (5)	2 (1)	2	0	-7	0.02 *
Dicosmoecus (T)	58	0.02		5 of 6	5	1	4 (3)	0 (0)	0	0	-1	
Hesperoconopa (D)	59	0.02	6	4 of 4	4	0	2 (1)	0 (0)	0	0	-5	
Siphonurus (E)	60	0.02		3 of 5	3	2	9 (8)	4 (4)	0	0	-1	
Attenella (E)	62	0.02	6	4 of 4	4	2	5 (3)	0 (0)	0	0	-17	
Glossosoma (T)	63	0.02	6	1 of 6	1	5	0 (0)	6 (3)	0	0	21	
Neophylax (T)	66	0.01		4 of 5	5	3	4 (3)	1 (0)	0	0	-2	
Graptocorixa californica (H)	69	0.008	6	6 of 6	6	0	3 (2)	0 (0)	0	0	-3	
Orohermes crepusculus (M)	70	0.008		3 of 5	3	3	2 (1)	1 (1)	0	0	-2	
Dysmicohermes ingens (M)	72	0.007	6	6 of 6	6	0	3 (2)	0 (0)	0	0	-5	
Agabus (C)	76	0.004	6	5 of 5	5	0	1 (1)	0 (0)	0	0	-1	
Edmundsius agilis (E)	78	0.004		2 of 2	2	0	2 (1)	0 (0)	0	0	-17	
Agabinus (C)	81	0.004	6	5 of 5	5	0	2 (1)	0 (0)	0	0	-4	
Chyranda centralis (T)	86	0.002		3 of 3	3	0	0 (0)	0 (0)	0	0	-4	

Table 3. Summary of consistent and suggestive patterns in both the current paired watershed study and the earlier barrier waterfall study (Silldorff et al. *in prep*). Observed change is the average percent increase or decrease across the two studies in the mean abundance change from troutless to trout streams (i.e., the plotted values in Figures 10-12). For *Dysmicohermes ingens*, *Graptocorixa californica*, and *Glossosoma*, observed change is based solely on the paired watershed study because these taxa were not collected in the barrier waterfall study.

Taxon	Observed Change	Evidence from Barrier Waterfall	Evidence from Paired Watershed
Taxa with Consistent Change			
<i>Ameletus</i>	46% decline	6 of 7	p<0.001
<i>Edmundsius agilis</i> ***	100% decline	3 of 3	2 of 2
<i>Paraleptophlebia</i>	51% decline	6 of 7	p<0.05
<i>Doroneuria baumanni</i>	53% decline	p=0.08	p<0.001
<i>Anagapetus</i>	51% decline	p<0.05	p<0.05
<i>Neothremma</i>	99% decline	5 of 6	p<0.05
Tricladida	84% decline	p<0.05	p<0.001
Evenness (J')	16 % decline	p<0.05	p<0.001
Select Taxa with Weaker Evidence for Change			
<i>Centroptilum</i>	400% increase	-	p<0.05
<i>Drunella spinifera/grandis</i>	172% increase	p<0.05	-
<i>Hesperoperla</i>	59% decline	-	p<0.05
<i>Dysmicohermes ingens</i>	100% decline	-	6 of 6
<i>Graptocorixa californica</i>	100% decline	-	6 of 6
<i>Apatania</i>	37% decline	5 of 6	-
<i>Glossosoma</i>	600% increase	-	5 of 6
Hydropsychidae	70% decline	-	p<0.05
<i>Yphria californica</i>	88% decline	3 of 3	p<0.05
Chironomidae	68% increase	6 of 7	p=0.10
Taxa Richness	8% decline	p<0.05	p=0.10

*** *Edmundsius agilis* included in table because of conclusive evidence from Silldorff (*in review*)

Figure 1. Mean values (± 1 s.e.) for 4 environmental variables for fishless (NF) and trout streams (T) are shown on the left side of each figure. Ordered absolute differences (trout-fishless) for the 21 stream pairs are shown on right part of each figure, with higher values in the trout stream indicated by positive values (dark bars) and lower values in the trout stream indicated by negative values (open bar).

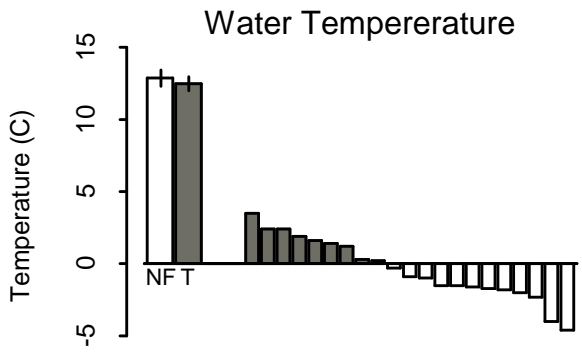
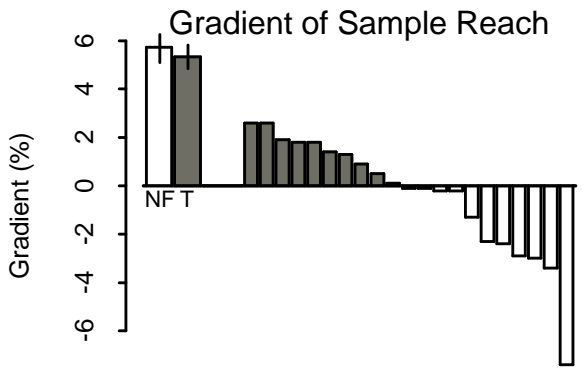
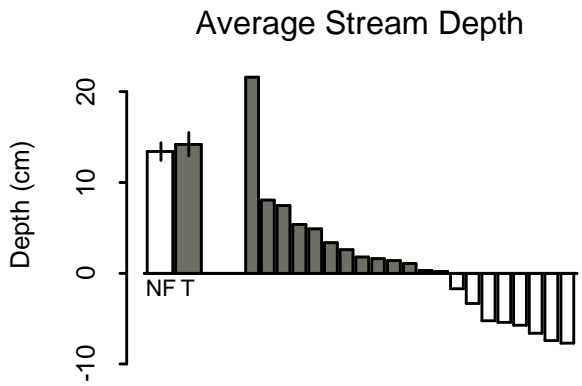
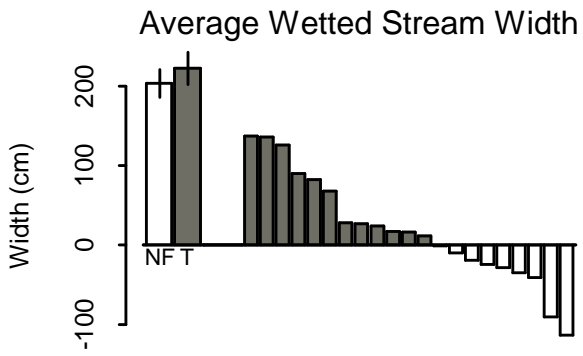


Figure 2. Means (\pm s.e.) and ordered differences for algal variables in fishless and paired trout streams (see Figure 1).

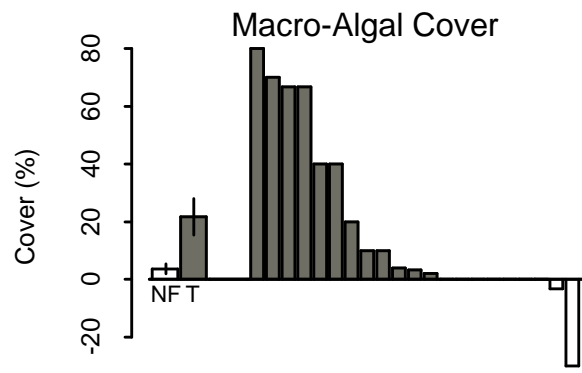
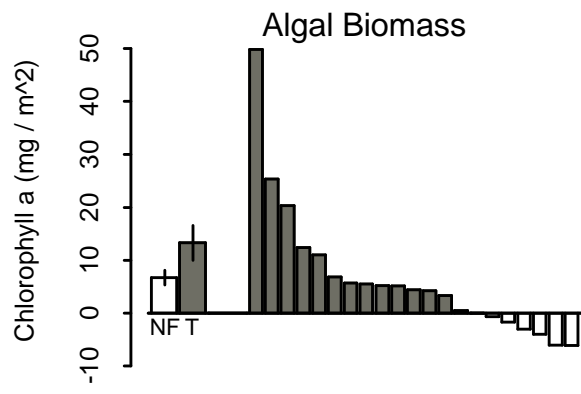


Figure 3. Mean invertebrate densities (± 1 s.e.) in fishless (NF) and trout streams (T) are shown on the left side of each figure. On the right side of each graph is shown the ordered absolute differences in invertebrate density (trout-fishless) for those stream pairs where each invertebrate taxon was collected in either the fishless or the trout stream (the number of difference bars corresponds to the total number of pairs indicated in Table 2). The rank abundance of each invertebrate taxon is indicated in parentheses for cross-reference to Table 2.

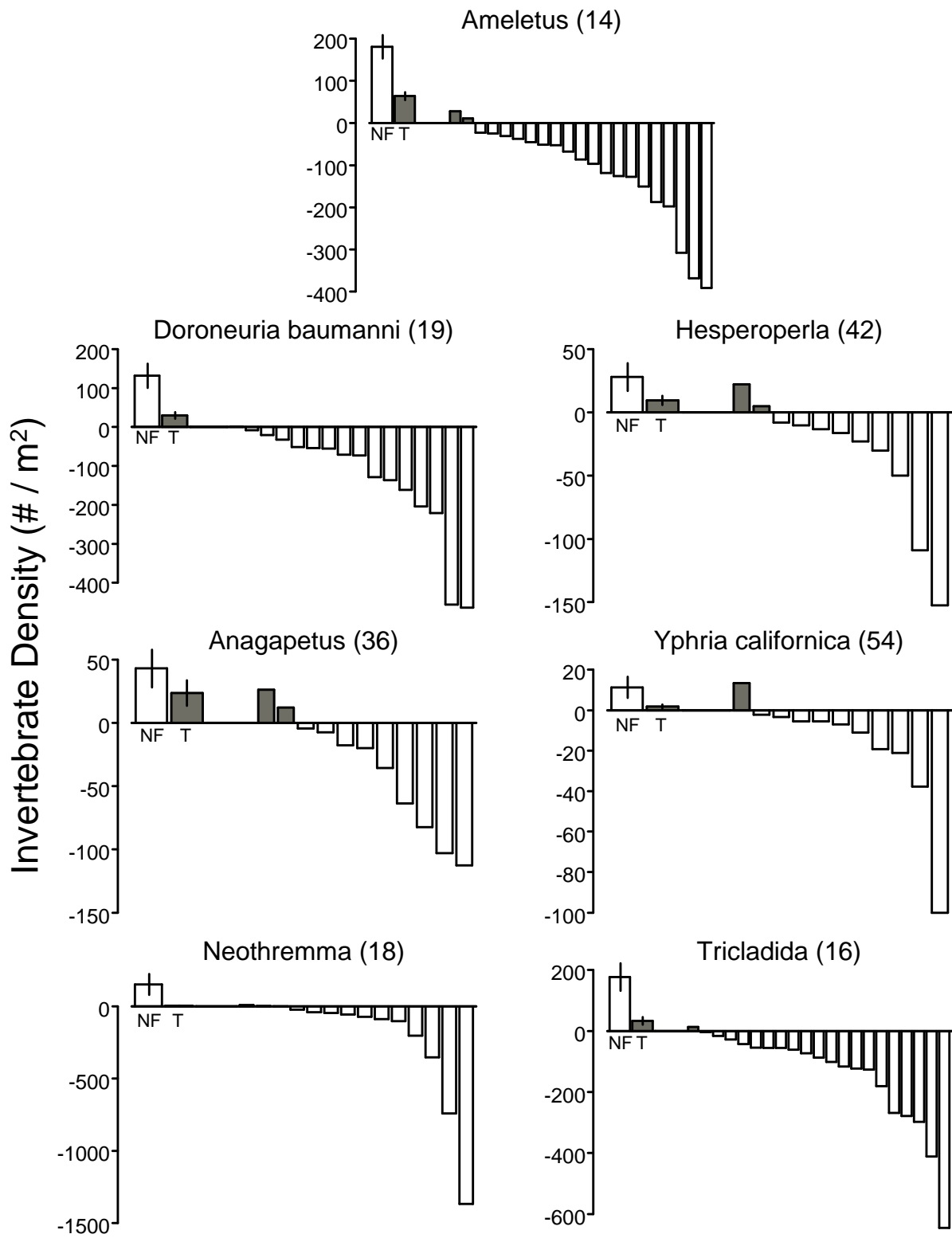


Figure 4. Mean invertebrate densities (± 1 s.e.) and ordered absolute differences in density for fishless and paired trout streams (rank abundance for each taxon given in parentheses; see Figure 3).

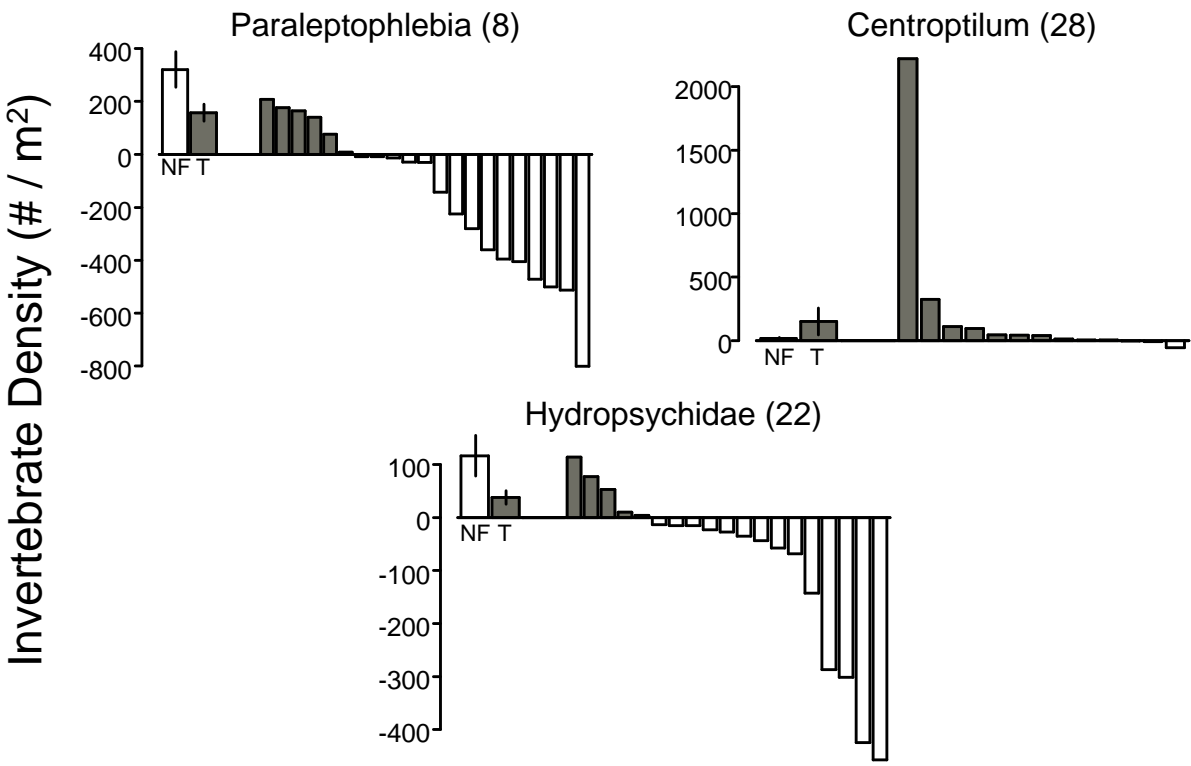


Figure 5. Mean invertebrate densities (± 1 s.e.) (left) and ordered absolute differences in density between fishless (NF) and paired trout (T) streams (right) (rank abundance of each taxon is given in parentheses; see Figure 3).

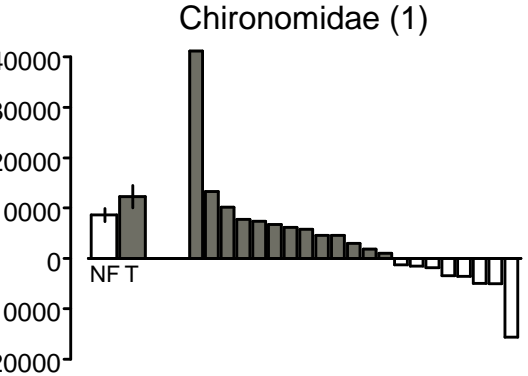
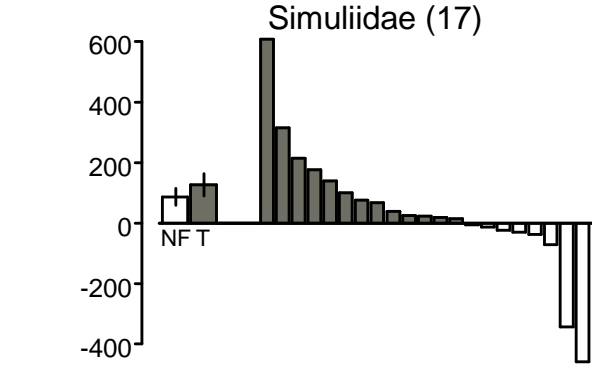
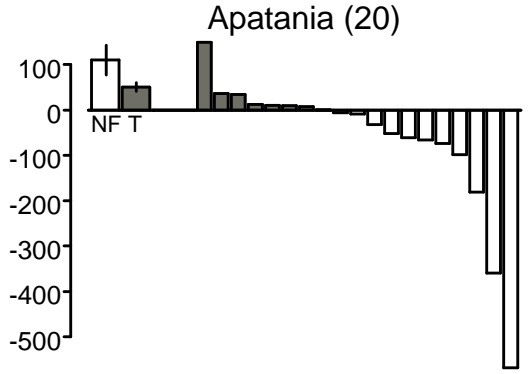
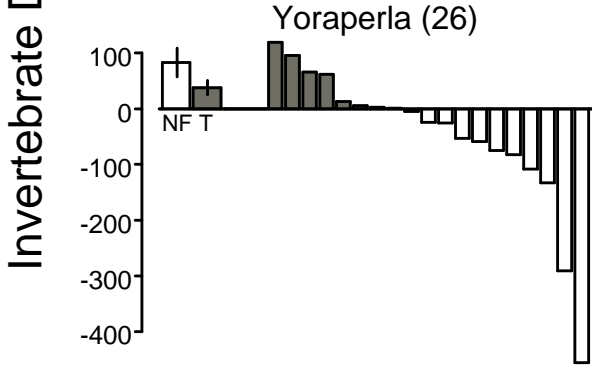
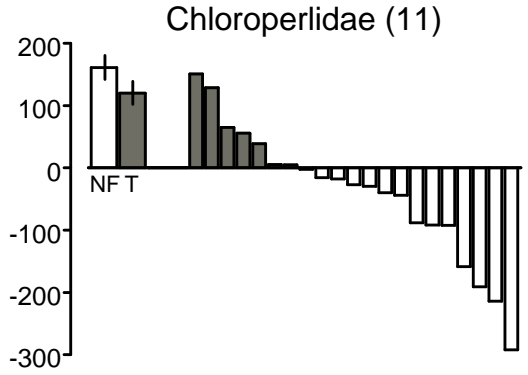
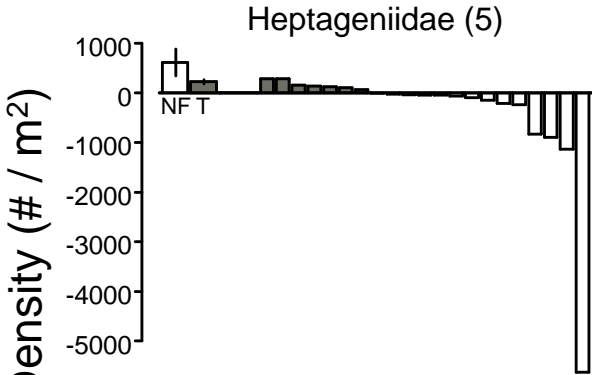
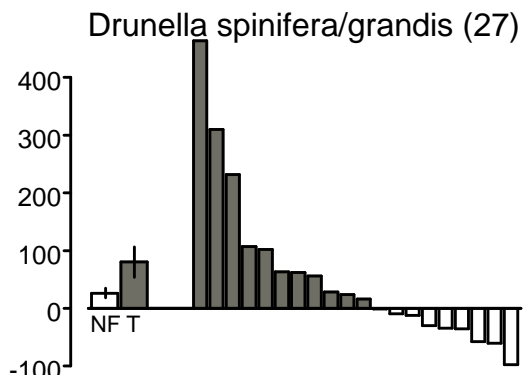
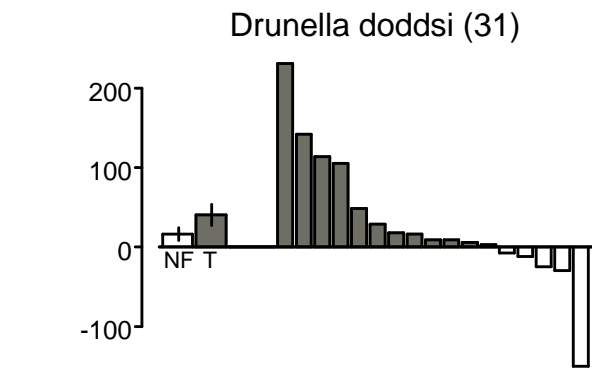


Figure 6. Mean invertebrate densities (± 1 s.e.) in fishless and trout streams and ordered absolute differences in invertebrate density between fishless and paired trout streams (rank abundance for each taxon given in parentheses; see Figure 3).

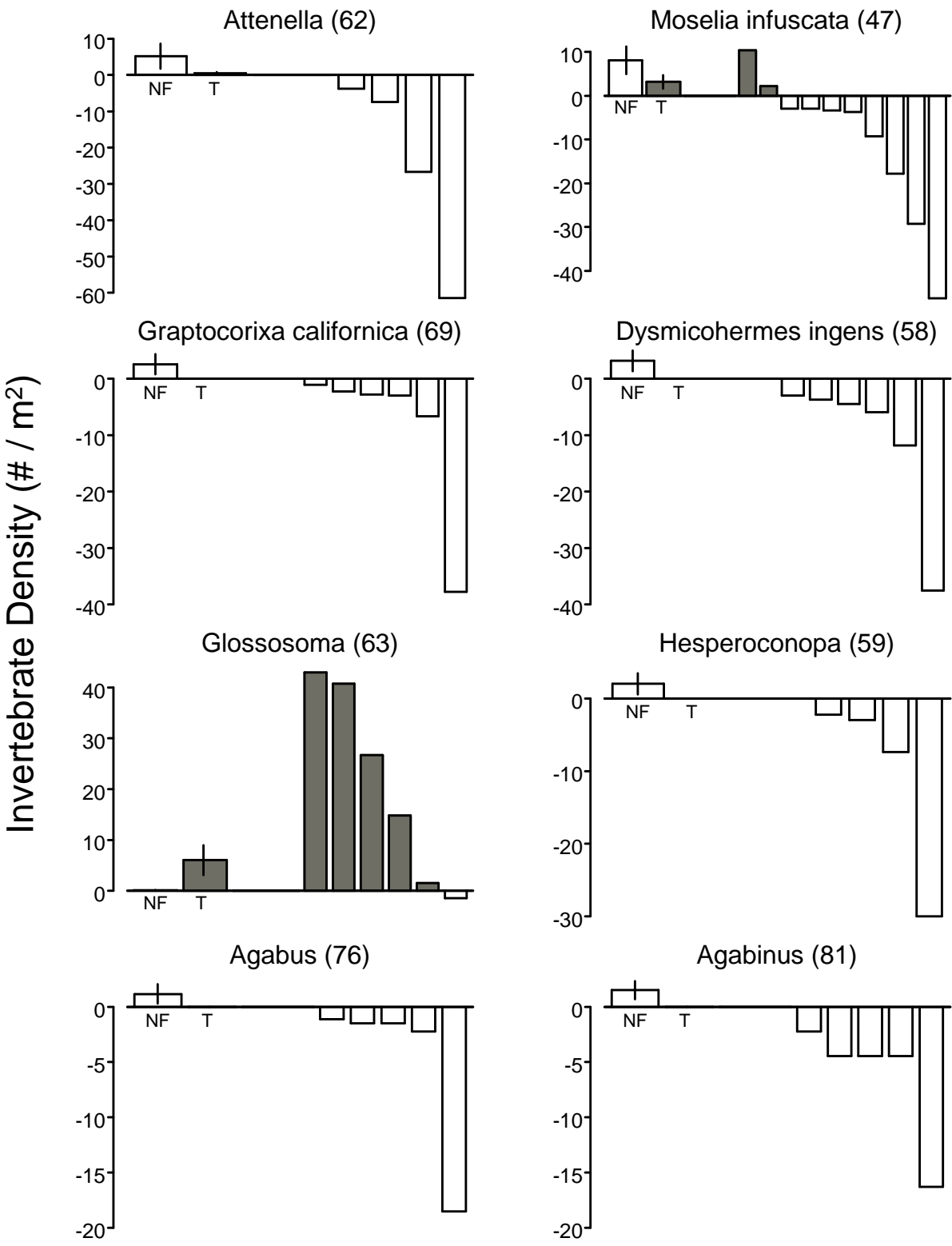


Figure 7. Mean invertebrate densities (± 1 s.e.) in fishless and trout streams and ordered absolute differences in invertebrate density between fishless and paired trout streams (rank abundance for each taxon given in parentheses; see Figure 3).

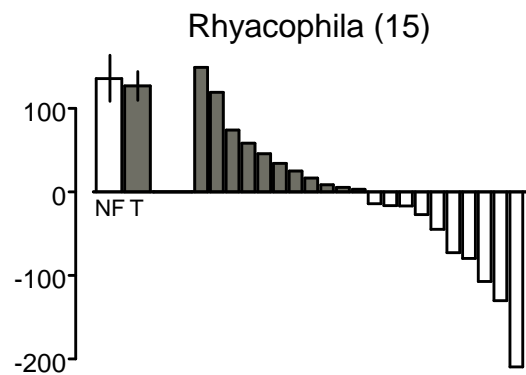
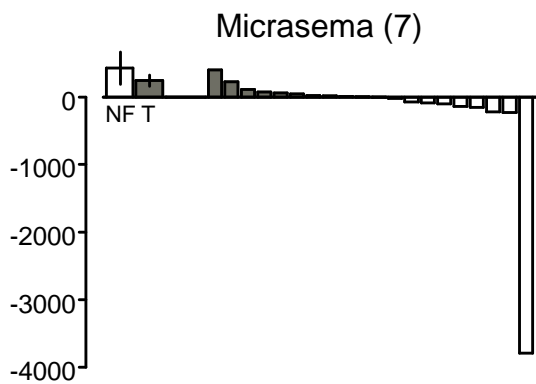
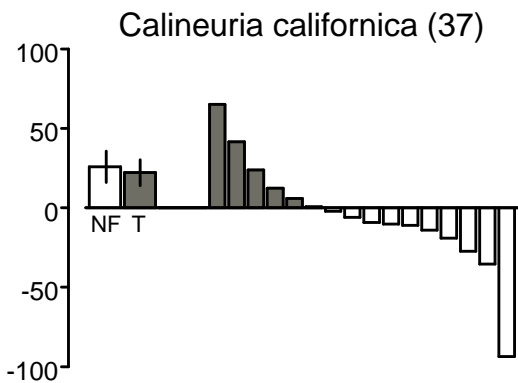
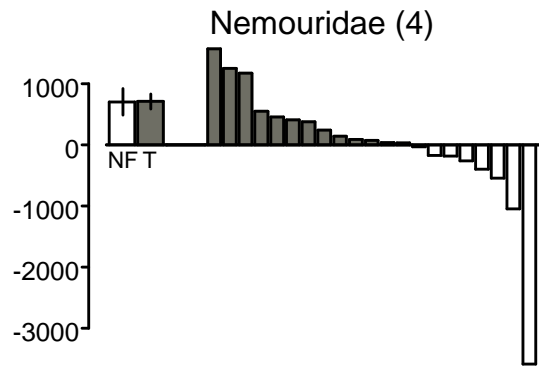
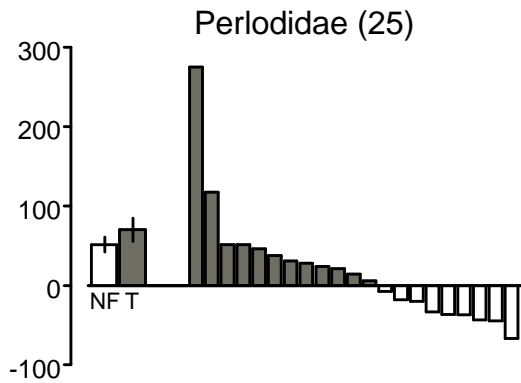
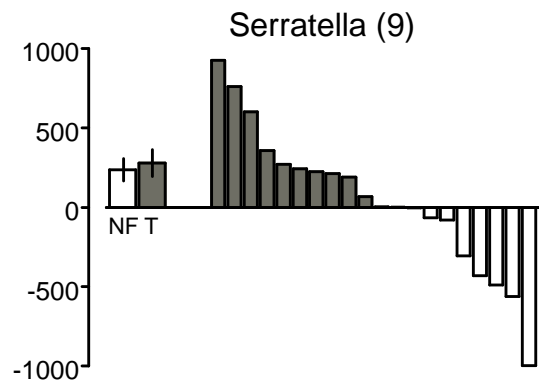
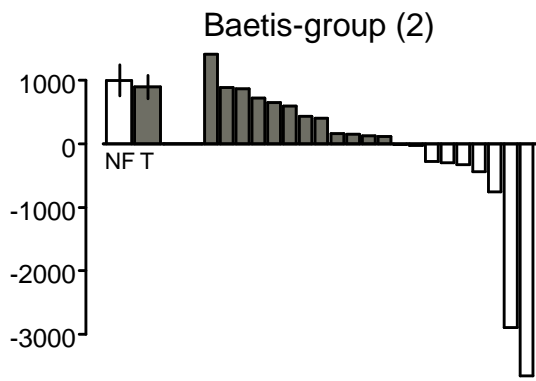


Figure 8. Mean values (\pm s.e.) of invertebrate assemblage metrics for fishless and trout streams and ordered absolute differences in these three summary metrics between fishless and trout streams (see Figure 3).

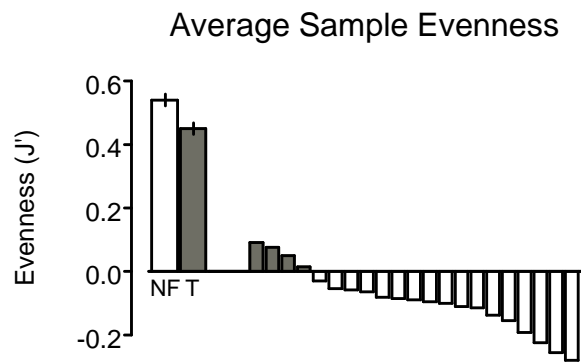
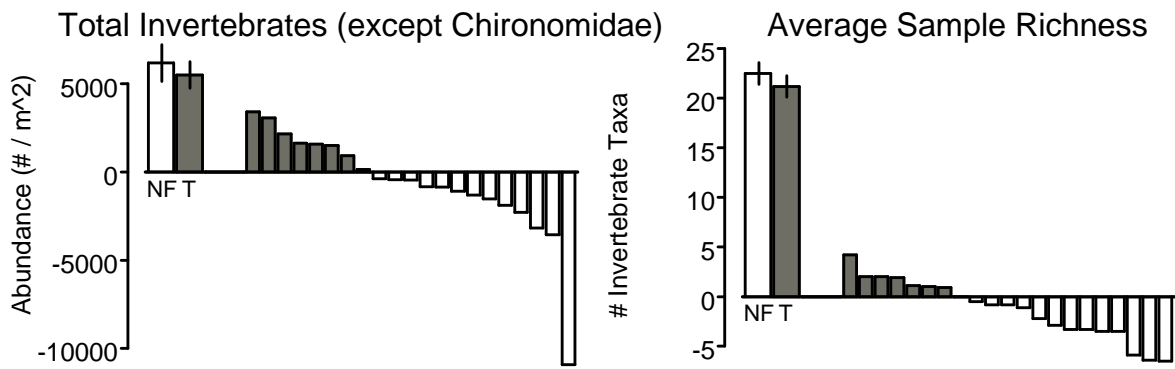


Figure 9. Non-metric multidimensional scaling (NMDS) ordination of Bray-Curtis distances among mean stream vectors (stress=0.09; proportional abundance used; all taxa except Chironomidae included in analysis). The stream pair number is indicated for each stream with trout streams indicated with small font and an asterisk (*), and fishless streams indicated with large font.

1 Fishless Stream

1* Trout Stream

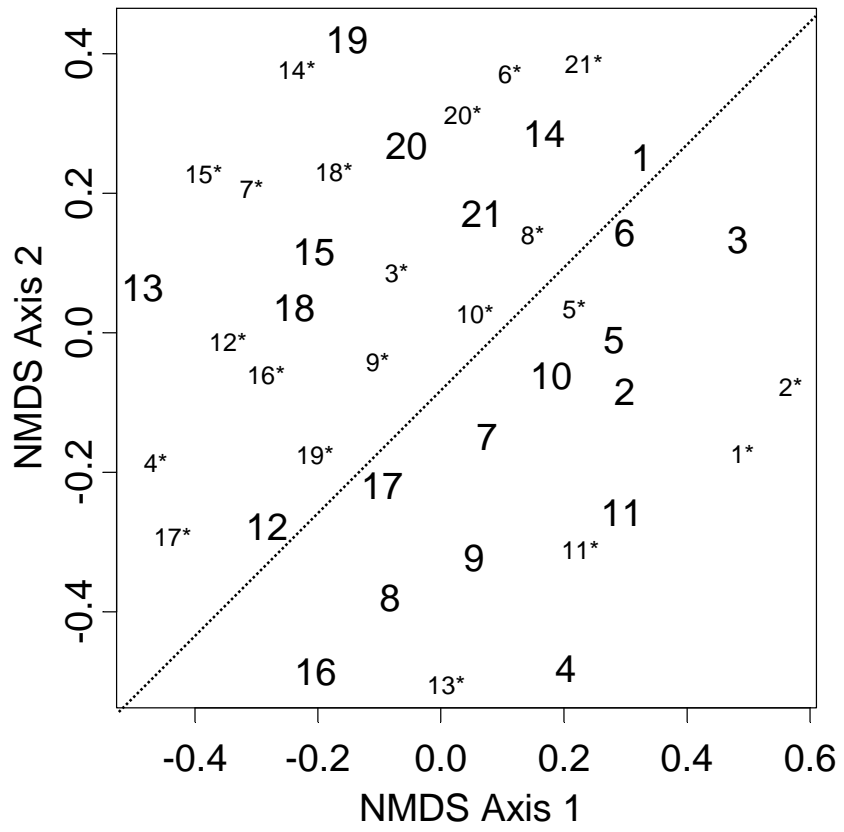


Figure 10. Mean invertebrate densities and community evenness (± 1 s.e.) in fishless (open bars) and trout streams (shaded bars) for the paired watershed study and the earlier barrier waterfall study (Silldorff et al. *in prep*). Two graphs are shown for the paired watershed study: the left graph includes means for all 21 fishless and trout streams; the right graph (paired watershed (indep)) includes means for the 14 independent fishless and 19 independent trout streams not included in the barrier waterfall study (note: streams sampled for both the barrier waterfall study and the paired watershed study were sampled at different times for the 2 studies).

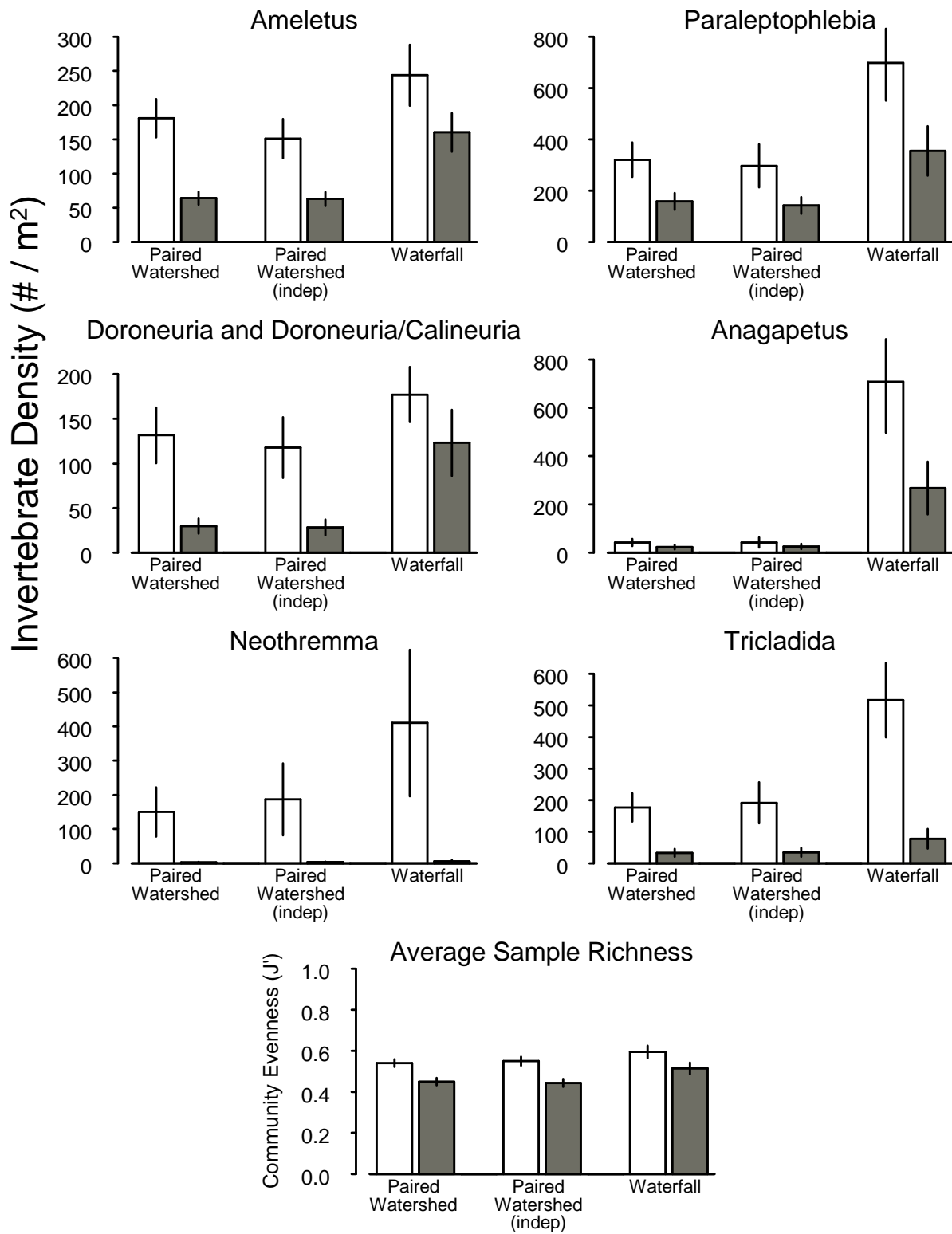


Figure 11. Mean invertebrate densities (± 1 s.e.) in fishless (open bars) and trout streams (shaded bars) in the paired watershed study (results presented for all 42 streams as well as the 33 streams not sampled in the waterfall study) and the earlier barrier waterfall study (Silldorff et al. *in prep*). See Figure 10 for a detailed description.

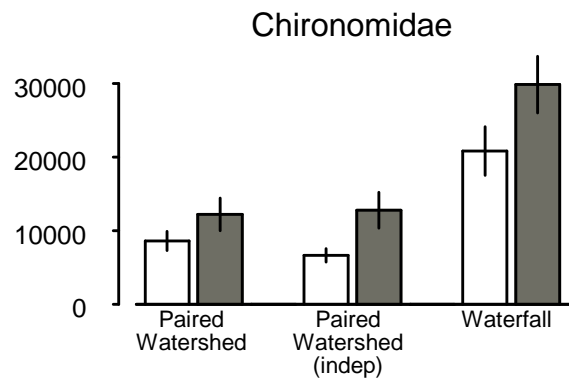
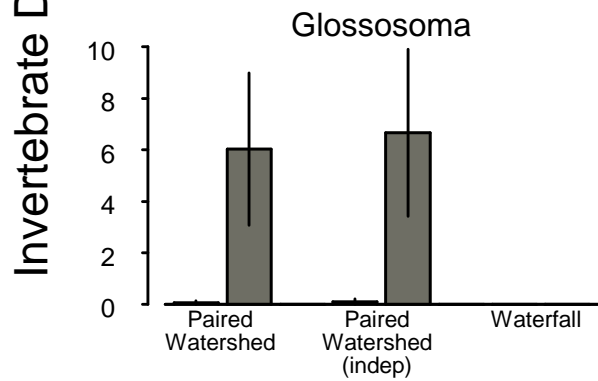
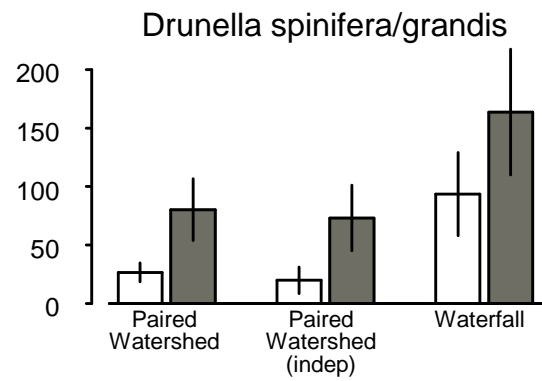
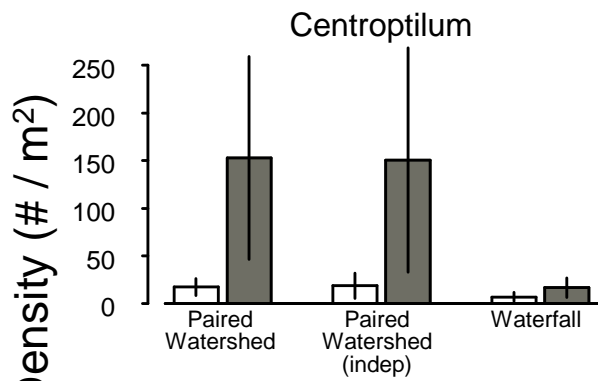


Figure 12. Mean invertebrate densities and taxa richness (± 1 s.e.) in fishless (open bars) and trout streams (shaded bars) in the paired watershed study (results presented for all 42 streams as well as the 33 streams not sampled in the waterfall study) and the earlier barrier waterfall study (Silldorff et al. *in prep*). See Figure 10 for detailed description.

