

Before and after the deluge: rain-on-snow flooding effects on aquatic invertebrate communities of small streams in the Sierra Nevada, California

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Abstract. Climate change is predicted to increase the frequency of rain-on-snow events in the winter and spring in mountain streams. Flooding caused by such events can drastically alter stream geomorphology, but much less is known about how such floods affect aquatic life. A record flood in early January 1997 afforded an opportunity to carry out a case study of benthic invertebrate community responses to this flood in 14 eastern Sierra streams sampled in the summers before and after the event. All sites were exposed to the flood. Study sites included 8 exposed to livestock grazing disturbance (test) and 6 where grazing was absent or minimal (reference). Reference sites had more riffle habitat, coarser substrata (cobbles), and greater relative abundances of many Ephemeroptera, Plecoptera, and Trichoptera (EPT) genera, whereas test sites had higher alkalinity, more pool habitats and fine substrata, lower diversity of EPT taxa, and higher densities of chironomid genera and elmids beetles. From 1996 to 1997 (before vs after the flood), the densities of total invertebrates and many taxa increased in most sites, and significantly (10×) more at test than reference sites. At all sites, bank stability and riparian vegetation coverage decreased and roots were exposed on the stream banks. At many sites, fine sediments decreased and average substrate sizes increased. Examination of 1996 to 1997 vectors in nonmetric multidimensional scaling (NMDS) space indicated differences in responses at reference vs test sites. Macroinvertebrate assemblages at reference sites changed relatively little, whereas the relative abundances of certain midges and *Hydropsyche* increased at test sites. Densities of filterers and small gatherers of fine particulate organic matter increased at test sites, and densities of filterers decreased at reference sites. Changes from 1996 to 1997 suggested that the winter rain-on-snow event had little effect in reference streams but increased the densities of small collector invertebrates at disturbed sites where fine sediments were flushed out and particulate organic resources increased. Given the predicted effects of climate change on mountain stream hydrology, these results indicate that benthic invertebrate communities in small pristine streams might be resilient to the effects of large rain-on-snow floods, but that small, mobile collector invertebrates in some degraded streams might increase in response to sediment flushing and increases in particulate organic matter.

Key words: climate change, rain-on-snow, winter floods, macroinvertebrates, Sierra Nevada, hydrologic disturbance, headwater streams.

The effects of global climate warming on many organisms might be related to temperature increases, but many effects on stream communities probably will be mediated through stream hydrology (Poff

et al. 1997). Climate change in montane areas has shifted the form of precipitation from snow to rain, which has reduced snowpack water storage, engendered earlier runoff, raised snow lines, increased the frequency of catastrophic floods through rain-on-snow events, and reduced late-season flows with possible drying of headwater habitats, which are crucial for maintaining watershed hydrological and

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ecological functions (Miller et al. 2003, Knowles and Cayan 2004, Stewart et al. 2005).

One important aspect of these hydrological changes is the increasing likelihood of rain-on-snow events that can trigger catastrophic flooding as rain melts the snowpack and sends torrents of water flowing down steep mountain canyons (Knowles et al. 2006). These torrents scour, transport, and redistribute sediments, organic matter, and benthic life forms. Large floods of this kind are currently rare and unpredictable, but rain-on-snow events are projected to increase with global warming and could have immense ecological importance because they can restructure the physical environment and alter the species composition and interactions of stream communities (Power et al. 1988, Poff and Ward 1990, Poff 2002). Previous studies of flooding have focused mainly on community and ecosystem responses and recovery in rainfall-dominated stream communities (Fisher et al. 1982, Power et al. 2008). However, few studies have examined community responses to rain-on-snow floods, which differ from more typical spring snowmelt floods in their timing, magnitude, and duration. Studies of repeated washouts of a foothill stream in the Sierra Nevada during winter storms showed 95% reductions in benthic invertebrate biomass and losses in species diversity compared to the previous summer and autumn (Siegfried and Knight 1977). Large winter floods in lowland New Zealand rivers reduced densities of more taxa than did smaller floods, but numbers rebounded within weeks to months (Scrimgeour and Winterbourn 1989, Suren and Jowett 2006). In the glacial-fed Rakaia River of New Zealand, persistent low invertebrate densities and diversity were associated with frequent, unpredictable aseasonal floods and unstable substrata (Sagar 1986).

Because large rain-on-snow events are rare, assessments of their effects are difficult and must rely on the fortuitous collection of data before and after such incidents. We surveyed 14 streams in the eastern Sierra Nevada of California in the summers before and after a record rain-on-snow flood in early January 1997. These 14 streams included 8 rangeland streams degraded by substantial livestock grazing (test sites) and 6 reference sites where grazing was minimal or absent. Thus, we were able to compare the responses of disturbed and intact stream habitats and communities to this event.

After polar storm systems covered extensive low-elevation areas of the Sierra Nevada with snow in December 1996, an ensuing January tropical flow of warm, moisture-laden storms (the "pineapple express") produced heavy precipitation in the Sierra. This precipitation fell as rain even at altitudes

>3000 m and melted much of the snowpack below this elevation. Over a 9-d period >50 cm of rain fell near the Sierra crest and, combined with melting snow, resulted in record flooding that broke levees, caused landslides, and scoured river channels with debris flows—perhaps a harbinger of future events with climate change. This flood had profound effects on rivers in the Sierra Nevada, particularly confined main-stem rivers, as evidenced by the destruction of portions of US Highway 395 along the West Walker River and the inundation of much of the Yosemite Valley by the Merced River.

Climate model simulations of changing storm patterns predict that extreme rain-on-snow flood events in the Sierra Nevada probably will increase in frequency and magnitude during the 21st century (Dettinger et al. 2009). Increases in heavy precipitation over broad geographic areas in the past 50 to 100 y and increases in the proportion of precipitation falling as rain rather than snow at middle and high elevations are both associated with climate change. Thus, montane areas at rain-on-snow transitional altitudes might be especially vulnerable to winter flooding (Groisman et al. 2001, 2005, Knowles et al. 2006, McCabe et al. 2007, O’Gorman and Schneider 2009). Another phenomenon that could make a contribution to snowmelt floods is the possibility that snow might melt synchronously over large areas when winters are warmer and the snowpack is more isothermal across elevations (Lundquist et al. 2004).

Our objectives were to: 1) examine the geomorphic and biological responses of small- to moderate-size mid-elevation mountain streams to the large rain-on-snow flood event in January of 1997 and 2) compare the physical, chemical, and biological responses of reference and test streams to this event. We hypothesized that this rain-on-snow flood would scour streams, remove fine substrata and particulate organic matter, and cause decreases in the diversity and abundance of benthic macroinvertebrates. We expected reference streams and their more diverse and sensitive faunas to be more affected by the flood than test streams, where fewer and more tolerant taxa would be able to cope with flood effects.

Contrasts of the responses of invertebrate communities to this winter flood in reference and disturbed streams also provided insights into how bioassessment data are interpreted within the context of climate change effects on hydrological regimes and geomorphological conditions. We recognize that it might be difficult to isolate the effects of the rain-on-snow flood on geomorphic and biological variables in this correlative (before vs after) study, but we think our suggestions are supported by the similarity

between the 1995–1996 and 1996–1997 hydrographs except for the rain-on-snow flood in 1996–1997, by changes in physical and chemical variables from 1996 to 1997 that probably can be attributed to the rain-on-snow flood, and by the temporal coherence of changes among the 14 study streams that indicated the effects of regional weather events on stream communities. Although we examined the effects of just this single storm on stream communities, rain-on-snow floods typically occur as infrequent, isolated storms but are expected to have shorter recurrence intervals under changing climatic conditions.

Methods

Environmental setting of study sites and the rain-on-snow hydrograph

We sampled 14 streams on similar dates in July and August of 1996 and 1997, 4 to 6 mo before and 7 to 9 mo after the 1997 winter flood. These 1st- to 3rd-order streams drain catchments of ~10 to 100 km² in area, and study reaches were at elevations of ~2000 m on the eastern slope of the Sierra Nevada or in adjacent mountain ranges (Fig. 1, Table 1). These small streams (mostly ≤ 2 m in mean width) are similar and occur within a 100-km radius of one another in a semi-arid environment where annual precipitation falls primarily as snow, spring snowmelt typically occurs in May and June, and stream base flows are maintained by groundwater inputs.

Reference streams drained catchments with low levels of human land use where livestock grazing was absent or limited to short periods with cattle access restricted to upland areas (outside the riparian zone). Test streams occurred in catchments with summer-long grazing allotments where cattle had open access to streams, which led to trampled and degraded stream beds and banks, fecal contamination, and fine-sediment deposition.

The abrupt peak in the rain-on-snow event hydrograph was very different from the gradually changing and sustained flows associated with typical spring snowmelt (Fig. 2A). The hydrograph for Convict Creek, representative of the low-order streams in our study, showed very similar discharge patterns for 1995–1996 and 1996–1997, except for the winter 1997 flood, and the winter flood pulse had a similar or lower peak discharge than flows during spring runoff. In contrast, the hydrograph for the West Walker River (to which several of the study streams were tributary) showed the magnifying effects of the rain-on-snow event on rivers with larger catchments. Rain-on-snow discharge was 5 \times larger than the spring snowmelt peaks for these near-average water years (Fig. 2B).

Stream surveys and sampling

We surveyed physical-habitat, water-chemistry, and biological variables (benthic macroinvertebrates, algae, and organic matter) along a 150-m reach in each study stream. We delineated the longitudinal distribution and lengths of riffle and pool habitats in each study reach and used the delineation to determine random riffle locations for benthic macroinvertebrate sampling. At each study reach, we measured slope with a survey transit and stadia rod, estimated sinuosity by comparing thalweg and straight-line distances, and measured physical-habitat variables (water depth, substratum type, current velocity) at 5 equidistant points across each of 15 transects spaced at 10-m intervals along the study reach. We recorded substratum type (fine: <0.25 mm, sand: 0.25–2 mm, gravel: 2–64 mm, cobble: 64–256 mm, and boulder: >256 mm), and measured current velocity with a flow probe (Model FP-101; Global Water Instrumentation, Gold River, California) at $0.6\times$ the depth at each point. We derived median particle size (D50) as the 50th percentile of the substrata size distributions. We also measured or noted stream width, bank structure, riparian canopy cover, bank angle, riparian vegetation composition and density, cobble embeddedness, and discharge at each of the 15 transects. We rated bank structure between the water and bankfull edges as open, vegetated, or armored (by rocks or logs), and as stable or eroded (evidence of collapse or scour scars). We scored bank angles as shallow, moderate, or undercut ($<30^\circ$, $30\text{--}90^\circ$, and $>90^\circ$, respectively) and measured riparian cover at the edges and middle of each channel transect (upstream and downstream) with a concave densitometer. We estimated the type and extent of riparian vegetation visually and the embeddedness of 25 cobbles as the volume of cobbles buried by silt or fine sand. We calculated discharge by combining width, depth, and current velocity measures. We took water-quality measurements, including temperature, pH, alkalinity, dissolved O₂, conductivity, and turbidity, at the upstream end of each study reach with LaMotte field kits (Chestertown, Maryland) and a calibrated Oakton pH/Con 10 meter (Vernon Hills, Illinois).

We took 5 replicate benthic samples, each consisting of three 0.09-m² D-net samples, from riffle zones distributed throughout each study reach (30-cm wide, 250- μ m mesh, D-frame kick-net; 1.4 m² total area sampled per survey). We processed samples in the field by washing and removing large organic matter and rocks from samples placed in buckets followed by repeated elutriation of the sample to separate invertebrates and organic matter and final inspection of

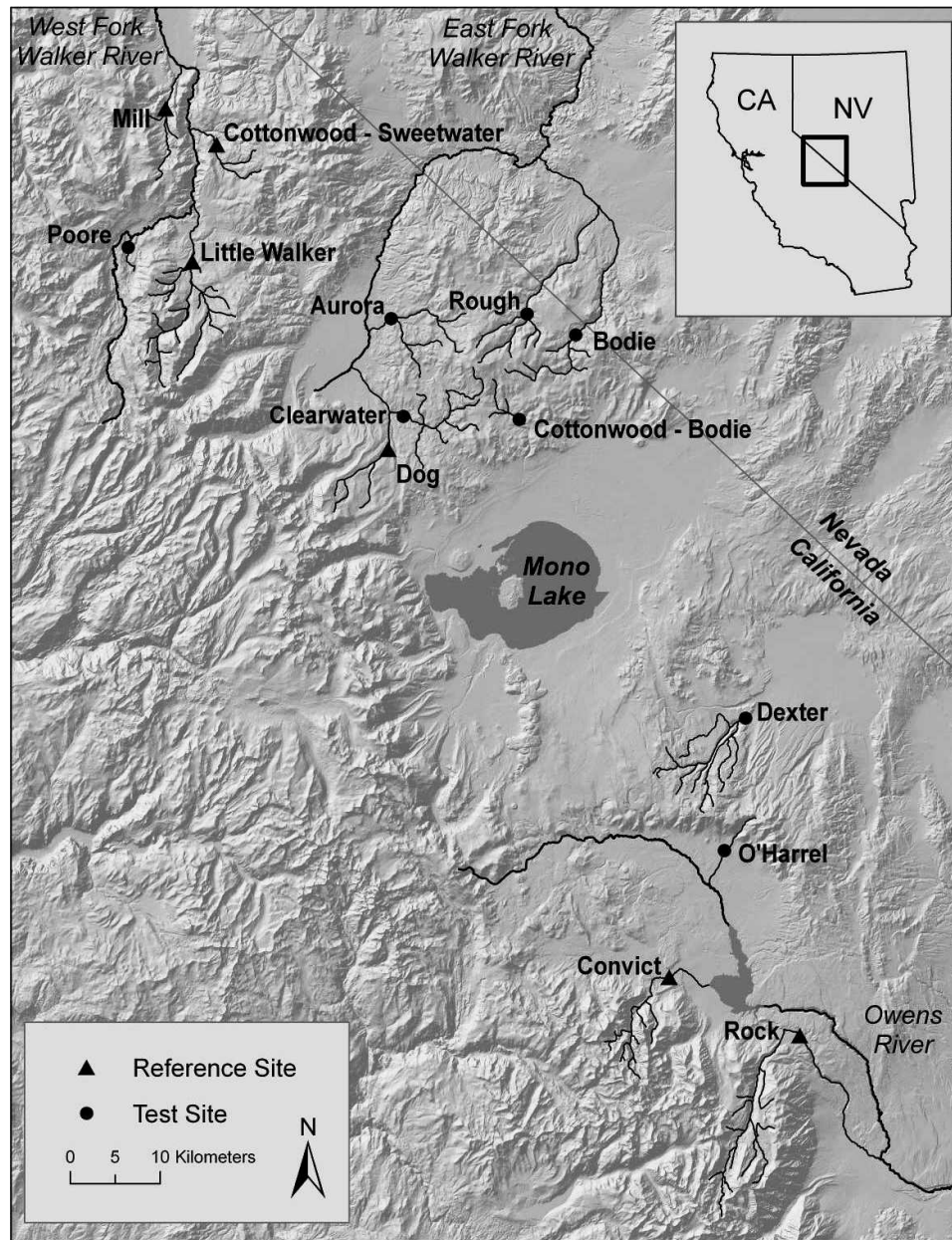


FIG. 1. Locations of study streams on the eastern slope of the Sierra Nevada, the Bodie Hills, the Sweetwater Mountains, and the Glass Mountains, eastern California (US). CA = California, NV = Nevada.

remaining mineral substrata to collect remnant cased caddis larvae or shelled mollusks. We preserved samples in 90% ethanol with rose Bengal stain added to aid in laboratory processing.

In the laboratory, we subsampled invertebrate samples with a rotating drum plankton splitter (usually $\frac{1}{4}$ – $\frac{1}{8}$ split fraction). This process typically yielded 300 to 500 invertebrates in each subsample, which we then identified (to genus or species, when possible, for all insects and water mites, but not oligochaetes, flatworms, and ostracods) and counted

using stereo and compound microscopes. We used combined data from the replicate samples at each site to determine the absolute and relative abundances of individual taxa at each site and time. We calculated a variety of community metrics, such as total density, total and Ephemeroptera, Plecoptera, Trichoptera (EPT) richness, the biotic index (Resh and Jackson 1993), richness and relative abundances of sensitive and tolerant taxa (tolerance values of 0–2 and 7–10, respectively, derived from regional lists of the Southwestern Association of Freshwater Invertebrate

TABLE 1. Coordinates and physical features of eastern Sierra study streams. Cross-sectional area is the average width \times depth of the flowing channel calculated from 1996 and 1997 summer data. These areas serve as proportionate estimates of bankfull area for each stream, which produce nondimensional indices of stream power when multiplied by associated reach slopes. R = reference, T = test.

Stream name	Latitude ($^{\circ}$ N)	Longitude ($^{\circ}$ W)	R or T	Elevation (m)	Reach slope	Sinuosity	Catchment area (km 2)	Cross-sectional area (m 2)	Power index
Convict	37.61540	118.82550	R	2110	1.3%	2.11	64.9	1.87	2.44
Cottonwood-Sweetwater	38.43976	119.42347	R	2158	0.8%	1.21	22.8	0.27	0.22
Dog	38.13821	119.19608	R	2274	2.5%	1.06	31.6	0.74	1.85
Little Walker	38.32074	119.44881	R	2181	1.6%	1.10	98.7	2.53	4.05
Mill	38.47600	119.48767	R	1932	1.8%	1.22	28.4	0.26	0.46
Rock	37.56140	118.66237	R	2140	0.4%	1.38	112.3	1.56	0.62
Aurora	38.27003	119.19621	T	2085	2.5%	1.07	71.4	0.09	0.23
Bodie	38.25775	118.96111	T	2368	0.7%	1.52	68.4	0.22	0.15
Clearwater	38.17142	119.17757	T	2130	1.5%	1.11	80.3	0.22	0.34
Cottonwood-Bodie	38.17117	119.03067	T	2255	2.9%	1.21	27.0	0.07	0.19
Dexter	37.87651	118.73568	T	2066	0.3%	1.53	73.3	0.51	0.15
O'Harrel	37.74326	118.75997	T	2176	4.9%	1.10	8.7	0.03	0.12
Poore	38.33493	119.53186	T	2106	0.6%	1.74	15.8	0.44	0.27
Rough	38.27767	119.02356	T	2292	2.1%	1.11	36.3	0.17	0.36

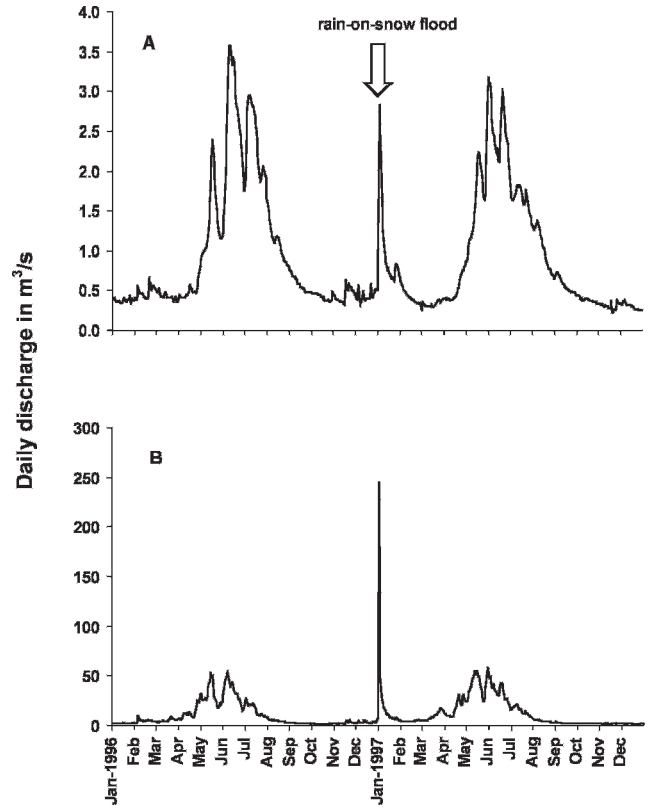


FIG. 2. A.—Hydrograph of Convict Creek (catchment area = 64.9 km 2), which is representative of our study streams, showing the rain-on-snow flood event of early January 1997. B.—Hydrograph for the West Walker River (catchment area = 468 km 2), where combined tributary flows resulted in peak rain-on-snow flood discharge far exceeding spring snowmelt flows. The 1995–1996 and 1996–1997 water years were near-average water years in the eastern Sierra. Convict Creek records are from the Los Angeles Department of Water and Power gauging station 4014, and West Walker River records are from USGS gauging station 10296000.

Taxonomists; <http://www.safit.org/TVFFG.html>), functional feeding groups (following Merritt et al. 2008), and size composition groups based on measurements of the body sizes of the taxa present in each sample (<5 mm, 5–10 mm, and >10 mm).

We measured food-resource levels for benthic macroinvertebrates by collecting 3 replicate riffle samples of both coarse and fine particulate organic matter (CPOM, FPOM, respectively) and periphyton (algal biomass as chlorophyll *a* concentration) from each study reach. The same methods used to collect benthic macroinvertebrates were used to sample particulate organic matter (POM) from riffles. We poured samples through a 1-mm screen and retained wood and leaf debris, which we weighed wet as a measure of CPOM. We collected the fine fraction that

passed through the screen in a 100- μm -mesh net (particle size range 250–1000 μm) and placed it in a sample vial with formalin as a preservative. We dried and weighed each sample, combusted it in a muffle furnace (550°C for 3 h), and reweighed it to quantify the ash-free dry mass (AFDM) of FPOM. We sampled benthic algae by scrubbing 3 cobbles selected randomly from mid-stream riffle habitats with a nylon bristle brush. We rinsed, homogenized, and filtered measured volumes of the algal suspension through a 1- μm pore-size, glass-fiber filter. We extracted chlorophyll *a* with cold ethanol for 24 h and measured concentrations with fluorometry (Sartory and Grobelaar 1984). We estimated the area of each sampled rock from measures of rock length, width, height, and circumference and calculated chlorophyll *a* per unit area.

Data analysis

We did all multivariate analyses with PC-ORD software (version 5; MjM Software, Gleneden Beach, Oregon) and all univariate analyses with JMP 7 software (SAS Institute, Cary, North Carolina).

We used paired *t*-tests on environmental variables, relative and $\log_{10}(x + 1)$ -transformed absolute abundances of common invertebrate taxa, and invertebrate community metrics to determine whether values of biotic and abiotic variables changed consistently across sites from summer 1996 to summer 1997. We defined common invertebrate taxa as those occurring in $\geq 1/2$ of the study sites on ≥ 1 sampling date. We derived taxon richness by rarefaction of combined counts from the 5 replicate samples for each site and time. We used EcoSim software (version 7; Acquired Intelligence and Kesey-Bear, Jericho, Vermont) to provide richness estimates for a fixed total of 1000 individuals. We calculated differences in the values of all variables between 1996 and 1997 and used independent sample *t*-tests on these differences to determine if changes from 1996 to 1997 differed between reference and test sites.

We used multiple regression analyses with backward stepwise elimination of nonsignificant independent variables to examine relationships between changes in composite invertebrate community metrics from 1996 to 1997 and changes in environmental variables from 1996 to 1997. Initial regression models included 1 geomorphic/hydrologic (width/depth ratio), 1 riparian (riparian cover), 1 substratum (proportion of sample locations dominated by fine substrata [silt, clay, and sand]), 1 biotic-resource (mean CPOM as g/m^2), and 1 chemical (conductivity) variable. We chose these variables based on the

correlation matrix for all environmental variables. Each variable was associated with an amalgam of other variables in each of the environmental variable classes (see Results), but changes from 1996 to 1997 in these 5 environmental variables were not correlated with each other (*r* ranged from -0.24 to $+0.36$, all $p > 0.20$).

We used the relative abundances of all invertebrate taxa collected from all sites and times to calculate multivariate distances between all pairs of sample sites and times using the Sørensen dissimilarity index (=Bray–Curtis or % dissimilarity index; Sørensen 1948). We used nonmetric multidimensional scaling (NMDS) to display relationships among sites and times in invertebrate community structure. We determined significant correlations (Pearson's *r*, $p < 0.05$) between NMDS axes and the relative abundances of invertebrate taxa or values for environmental variables. We arrived at a 2-dimensional solution for the NMDS analysis based on the asymptotic behavior of an NMDS scree plot showing a minor reduction in stress from the 2-dimensional (stress 13.4) to the 3-dimensional (stress 9.2) solution. Parameters for the NMDS analysis for a 2-dimensional solution were as follows: number of runs with real data = 150 (no runs with randomized data), stability criterion = 0.00001 (over the last 15 iterations), maximum number of iterations = 250, and initial step length = 0.20. We used paired and independent *t*-tests to determine whether NMDS axis scores differed consistently from 1996 to 1997 and whether the 1996–1997 vectors for NMDS scores for individual sites differed between reference and test reaches, respectively. We used multiple regression analyses to examine further the relationships between 1996–1997 changes in NMDS scores and the battery of environmental variables used in the univariate analyses. We used a Mantel test to examine the relationship between distance matrices for invertebrate relative abundances (Sørensen index) vs values of environmental factors (Euclidean distance). We calculated probability values with Mantel's asymptotic approximation. Results with raw environmental data were the same as results with values for each environmental variable relativized to its mean value. We used Indicator Species Analysis to identify significant associations between invertebrate taxa and reference vs test sites.

Results

Changes in geomorphic features

The trajectories, timing, and magnitude of spring snowmelt flows were remarkably similar in 1996 and 1997, so the major hydrographic difference between

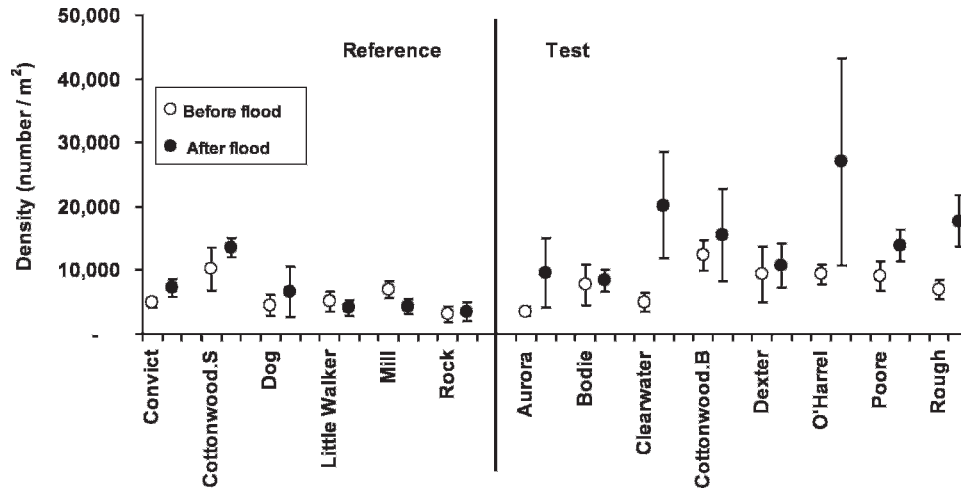


FIG. 3. Mean ($\pm 95\%$ CI) macroinvertebrate densities at reference ($n = 6$) and test ($n = 8$) sites in the summers before (1996) and after (1997) the winter flood. Cottonwood S = in Sweetwater mountains, B = in Bodie Hills.

the 1995–1996 and 1996–1997 water years was the January 1997 flood (Fig. 2A). Between the summers of 1996 and 1997, pool area, open banks, exposed roots, and the amounts of detritus that could have been deposited during falling limbs of the hydrograph increased across all sites (paired t -tests, all $p < 0.05$). Bank-stability ratings and water hardness decreased from 1996 to 1997. Stream power was higher in reference than test sites, and discharge increased more in reference than test sites from 1996 to 1997, whereas water hardness decreased much more from 1996 to 1997 in test than reference sites (independent sample t -tests, all $p < 0.05$).

Benthic macroinvertebrate community responses

More than 170 invertebrate taxa were identified from samples collected at the 14 sites in 1996 and 1997. On average, total densities of invertebrates across sites increased $1.7\times$ from 1996 to 1997 (mean \pm SE, 1996: 6979 ± 744 individuals [ind.]/m², 1997: $11,580 \pm 1830$ ind./m²; paired t -test, $t = 2.9$, $p = 0.012$; Fig. 3). This increase in density was significantly greater at test than at reference sites (t -test on mean increase in $\log_{10}[\text{density} + 1]$, $t = 5.8$, $p = 0.033$). The taxa that were primarily responsible for the increased densities across all sites from 1996 to 1997 included *Serratella*, *Ameletus*, *Cinygmula*, *Cleptelmis*, *Eukiefferiella brehmi* group, *Thienemanniella fusca*, and oligochaetes, but *Sweltsa* decreased. *Serratella* and *Ameletus* increased and *Sweltsa* decreased more at test than at reference sites, and *Bezzia* increased at test sites (especially O'Harrel) but decreased at reference sites.

The NMDS plot showed differences in invertebrate community structure between reference and test sites

and differences in 1996–1997 changes between reference and test sites (Fig. 4A). NMDS Axis 2 primarily distinguished reference from test sites, whereas Axis 1 mainly indicated differing directions of community change from 1996 to 1997 between reference and test sites (as shown in the 1996-centered plot; Fig. 4B). In general, the results for NMDS Axis 2 and the Indicator Species Analysis indicated that reference sites were characterized by more riffle habitat, coarser substrata (cobbles, boulders), and greater relative abundances of mayfly and caddisfly genera and *Doroneuria*, whereas test sites had higher conductivities, fine substrata (sand + fines), more pool habitat, and were inhabited by less diverse EPT taxa, more abundant chironomid and elmidae beetle genera, and greater relative abundances of *Isoperla* and *Sweltsa* (Figs 4A, 5). The NMDS Axis 1 results indicated a slight shift from 1996 to 1997 at reference sites to more tolerant taxa (oligochaetes, *Pisidium*, *Hexatoma*), whereas 1996 to 1997 vectors at most test sites indicated increases in the relative abundances of other taxa, such as *Cricotopus-Orthocladius* complex, *Thienemanniella cf. xena*, *Hydropsyche*, and *Zapada* (Fig. 5). Other widespread opportunistic taxa, such as *Simulium* and *Eukiefferiella* spp., were not significantly correlated with an NMDS axis, but did increase strongly in $>1/2$ of the test sites.

Changes in NMDS Axis 1 scores from 1996 to 1997 differed significantly between reference and test sites (t -test, $p < 0.05$). Each environmental variable represented an amalgam of other environmental variables. Conductivity was positively related to alkalinity, hardness, and Ca²⁺ and Mg²⁺ concentrations ($r = 0.66-0.91$, $p \leq 0.001$) and negatively related to dissolved O₂ concentration ($r = -0.47$, $p \approx 0.012$).

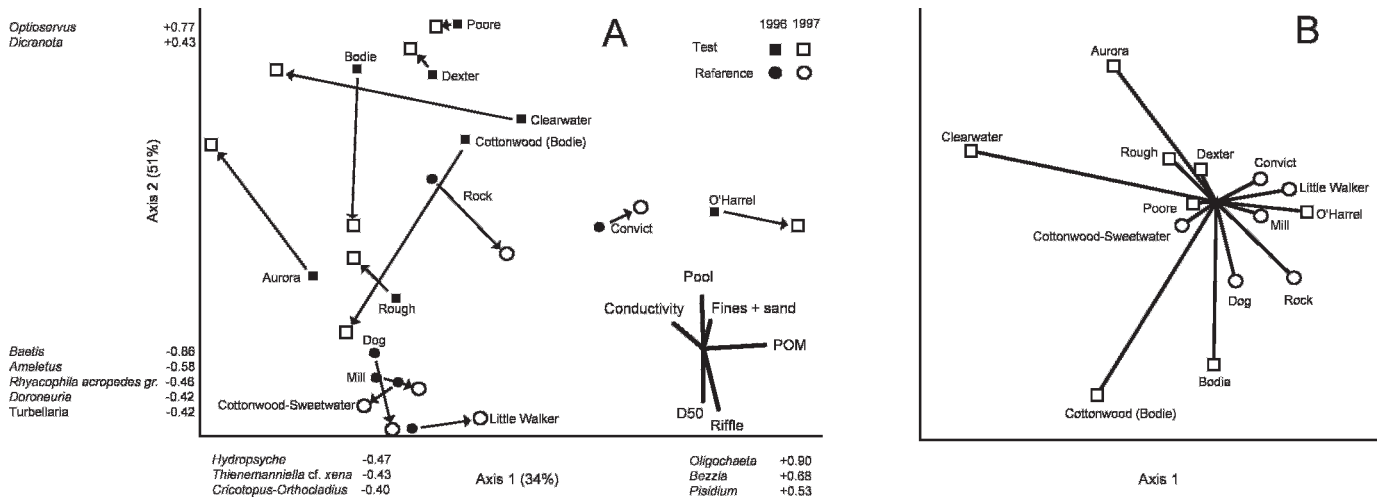


FIG. 4. A.—Results of the nonmetric multidimensional scaling (NMDS) analysis applied to the matrix of the relative abundances of all benthic macroinvertebrate species at all sample times and sites. For the NMDS 2-dimensional solution, final stress = 13.4, % orthogonality for the pair of axes = 99.7, and cumulative R^2 between original and ordination distances = 0.84 (R^2 for axis 1 = 0.34 and for axis 2 = 0.51). Common invertebrate species correlated with each NMDS axis and their correlation coefficients are noted in the margins of the diagram, and the vectors in the lower right-hand inset indicate the environmental factors related to each axis. Common taxa were those that occurred in $\geq 1/2$ of the study sites on ≥ 1 sampling date. Thin arrows connect 1996 to 1997 values for each site. 1996–1997 changes in axis 1 scores but not axis 2 scores were significantly different between reference and test sites (mean change in 1996–1997 axis 1 score for reference sites = 0.19 [SE = 0.18], mean change in 1996–1997 axis 1 score for test sites = -0.33 [0.16], $t = -2.2$, $p < 0.05$). B.—1996 to 1997 changes in NMDS scores for each site represented by vectors whose origins (1996 values) are centered on 0. POM = particulate organic matter, D50 = median particle diameter.

CPOM and FPOM were tightly correlated ($r = 0.91$, $p < 0.0001$; represented by POM in Figs 4B, 5), and both were correlated with proportionate cover by leaves and woody debris ($r = 0.42$ – 0.63 , $p = 0.03$ – 0.0004). D50 was significantly correlated with proportionate coverage by cobbles and boulders ($r = 0.76$ – 0.87 , $p < 0.0001$) and negatively correlated with fine substrata (sand + fines; $r = -0.66$, $p = 0.0001$), gravel ($r = -0.39$, $p = 0.04$), and mean cobble embeddedness ($r = -0.50$, $p = 0.007$). Riffle coverage was negatively related to mean and maximum depths ($r = -0.47$ to -0.57 , $p = 0.01$ and 0.001 , respectively) and positively related to width/depth ratio ($r = 0.52$, $p \approx 0.004$), with pool coverage showing the opposite pattern. All correlation coefficients or environmental vectors shown on Fig. 4A, B were significantly associated with NMDS axes (all $p < 0.05$). Distance matrices for biotic and abiotic variables were significantly correlated (standardized Mantel statistic = 0.23, $t = -2.5$, $p = 0.012$). Multiple regression analyses revealed that 1996–1997 changes in NMDS Axis 1 scores were marginally positively related to 1996–1997 changes in fine substrata, whereas 1996–1997 changes in NMDS Axis 2 scores were marginally negatively related to 1996–1997 changes in riparian cover (in both cases, $R^2 = 0.16$, $F = 3.5$, $p = 0.09$).

Reference sites had higher levels of overall diversity and greater representation of sensitive taxa than did test sites, but no significant differences were found between 1996 and 1997 in many composite community metrics (total and EPT rarefied richness, proportion of total richness composed of EPT taxa, tolerant and sensitive taxon richness and relative abundances, and the biotic index). Changes from 1996 to 1997 in these metrics did not differ between reference and test sites. Moreover, none of the changes in these common bioassessment metrics exceeded the level of interannual variation found in these and other sites of the eastern Sierra during nonflood years (coefficient of variation [CV] = 7–23%; DBH and SDC, unpublished data), and none were related to stream power. However, changes from 1996 to 1997 in the proportions of taxa that were EPT taxa (rarefied) were marginally or significantly negatively related to changes from 1996 to 1997 in fine substrata and conductivity and marginally positively related to changes from 1996 to 1997 in riparian cover (overall $R^2 = 0.36$, $F = 3.4$, $p \approx 0.06$).

Changes from 1996 to 1997 in functional feeding groups and the size composition of the community differed significantly between reference and test sites. Densities of gatherers (paired t -test, $t = 2.6$, $p = 0.022$),

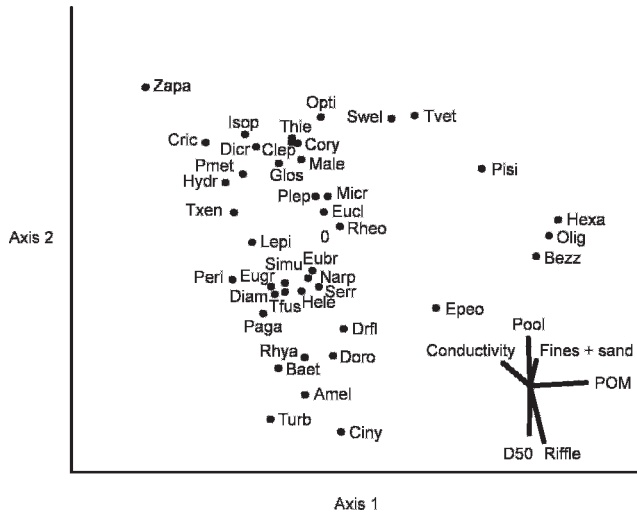


FIG. 5. Weighted average nonmetric multidimensional scaling (NMDS) scores for common taxa. Relationships of environmental factors to each axis are indicated in the inset in the lower right hand corner. Ephemeroptera: Amel = *Ameletus*, Baet = *Baetis*, Ciny = *Cinygmula*, Drfl = *Drunella flavilinea*, Epeo = *Epeorus*, Plep = *Paraleptophlebia*, Serr = *Serratella*; Plecoptera: Doro = *Doroneuria baumannii*, Isop = *Isoperla*, Male = *Malenka*, Swel = *Sweltsa/Suwallia*, Zapa = *Zapada*; Trichoptera: Glos = *Glossosoma*, Hydr = *Hydropsyche/Ceratopsyche*, Lepi = *Lepidostoma*, Rhya = *Rhyacophila brunnea* gr.; Coleoptera: Clep = *Cleptelmis*, Narp = *Narpus concolor*, Opti = *Optioservus*; Diptera: Bezz = *Bezzia/ Palpomyia*, Cory = *Corynoneura*, Cric = *Cricotopus/Orthocladius*, Diam = *Diamesa*, Dicl = *Dicranota*, Eubr = *Eukiefferiella brehmi*, Eucl = *Eukiefferiella claripennis*, Eugr = *Eukiefferiella gracei*, Hele = *Heleniella*, Hexa = *Hexatoma*, Micr = *Micropsectra*, Paga = *Pagastia*, Peri = *Pericoma*, Pmet = *Parametrioctenus*, Rheo = *Rheocricotopus*, Simu = *Simulium*, Tfus = *Thienemanniella fusca*, Thie = *Thienemannimyia* gr., Tvet = *Tvetenia bavarica*, Txen = *Thienemanniella* cf. *xena*; Noninsect invertebrates: Olig = *Oligochaeta*, Pisi = *Pisidium*, Turb = *Turbellaria*. POM = particulate organic matter, D50 = median particle diameter.

filterers (paired *t*-test, *t* = 4.1, *p* = 0.001), and small invertebrates (<5 mm; paired *t*-test, *t* = 2.2, *p* = 0.05) increased significantly at test sites but remained relatively constant (gatherers, small invertebrates) or declined (filterers) at reference sites (Fig. 6). There were no significant overall changes in density of algae or of coarse or fine particulate organic matter between years, although FPOM increased and algae decreased at 6 of 8 test sites.

Discussion

Global warming is expected to shift the more predictable hydrologic regime of snowmelt-dominated temperate streams to the more variable and

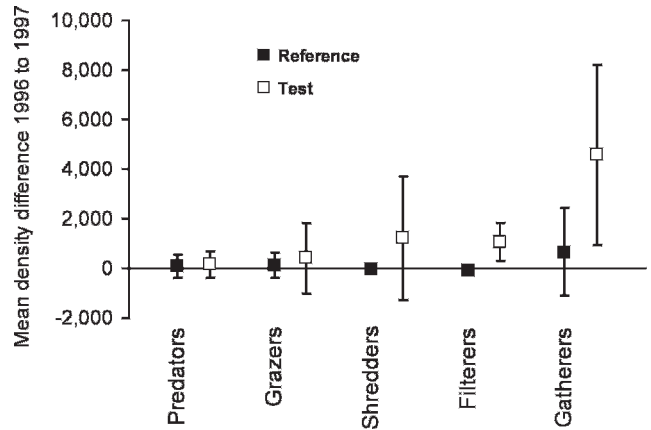


FIG. 6. Mean ($\pm 95\%$ CI) densities of functional feeding groups from 1996 to 1997 in reference vs test sites.

extreme flood–drought conditions of Mediterranean climates (Arnell 1999). Comparisons of stream invertebrates in the Mediterranean basin of Europe with more northern temperate-stream invertebrates suggest that warm-adapted Mediterranean invertebrates are more vagile and are capable of recolonizing stream systems more quickly after hydrologic disturbances than their northern counterparts (Bonada et al. 2007). As temperate climates warm, colonizers from Mediterranean areas could displace components of the northern fauna, with a concomitant loss of temperate taxonomic diversity. This possibility emphasizes the importance of habitats at high elevations and latitudes for preserving taxonomic richness. The resilience or resistance of community diversity to flooding that we found in small, montane reference streams supports the view that these habitats could serve as refugia from the effects of climate change. These headwater streams might act as sources for the recolonization of downstream reaches where floods can have far more destructive impacts on stream habitat (as in the West Walker River; Fig. 2B). Headwater streams protect organisms from temperature and flow extremes and are important sources of biodiversity in river networks (Meyer et al. 2007).

Winter flooding affects the stream biota in the Sierra Nevada. Sampling during and after floods in February 1982 revealed high mortalities and reduced population densities of native Paiute sculpin and nonnative brook trout (Erman et al. 1988). Winter flooding caused by the formation and break-up of dams of anchor ice in Convict Creek in the eastern Sierra increased the drift of benthic invertebrates (Maciolek and Needham 1952). We observed little change in the taxonomic composition of benthic invertebrate assemblages in reference headwater Sierra streams in the summer after the 1997 flood,

although total abundance increased in most streams and trophic structure shifted in streams affected by livestock grazing. Consistent increases in benthic macroinvertebrate densities also were observed from 1996 to 1997 in five 1st- and 2nd-order mid-elevation streams of the western Sierra Nevada that experienced the same winter flood that is the focus of our study (Bêche et al. 2005). After a winter rain-on-snow flood in 1986, a stream in the Oregon Cascades showed only limited geomorphic change in an upstream reach. However, a downstream section was scoured and then dammed by a debris flow originating from a landslide on a logging clear-cut in the basin (Lamberti et al. 1991). Invertebrates were greatly reduced by this flood, but recolonization by high densities of vagile taxa (*Baetis* and midges) occurred within 6 to 12 mo (similar to our study).

We did not observe stream communities until 7 to 9 mo after the rain-on-snow flood, so we did not observe immediate flood effects. However, some effects of this storm could still be detected in the ensuing summer in habitat and benthic invertebrate changes in streams draining these small catchments. Given the much higher magnitude of rain-on-snow flood peaks in downstream, higher-order reaches, such floods probably have a much larger effect on invertebrate communities in downstream areas. We expected that a major winter flood would cause scouring of the stream bed, changes in stream geomorphology, and reductions in benthic invertebrate populations. Both intact reference sites and degraded test sites showed evidence of physical scouring by the rain-on-snow flood event, with eroded and widened channels, exposed stream banks and roots of riparian plants, and increased size of bottom substrata caused by removal of fine sediments. Nevertheless, many composite metrics of the invertebrate community showed little change from 1996 to 1997 and fell within the bounds of interannual variation observed in nonflood years. Long-term studies in other California streams also have shown few consistent relationships between bioassessment metrics and climate-related variables (Mazor et al. 2009). In contrast to these composite metrics, the densities of total invertebrates (primarily small collector-gatherers and filterers) increased in test sites, perhaps because these invertebrates were represented by mobile species that quickly colonized substrata scoured by the flood and that benefited from increased detrital resources. Three of the 4 test sites (Aurora, Bodie, Clearwater) with the largest changes in 1996–1997 NMDS axis 1 scores had the most extensive flushing of fine sediments, and most test sites showed increases in FPOM levels. However,

the smallest test stream with the lowest power, O'Harrel Creek, showed decreases in FPOM and increases in fine sediment, and its 1996–1997 NMDS axis 1 vector shifted in the opposite direction from the other test sites, indicating increased dominance by sediment-tolerant taxa (oligochaetes, *Pisidium*, *Bezzia*).

The timing of the life cycles of stream organisms might be critically important in determining the influence of rain-on-snow floods on stream communities. The success of rainbow trout introductions has been tied to matching the spring-spawning life history of this species to sites with appropriate flood regimes (Fausch et al. 2001). In the western US, eggs of autumn-spawning nonnative brown trout and brook charr can be scoured during winter floods, whereas eggs laid by spring-spawning native cutthroat and rainbow trout are largely unaffected by winter floods (Strange et al. 1992). Similarly, the responses of benthic invertebrate populations to winter floods would be expected to depend strongly on the life-history stages of the invertebrates present during the winter. For example, the aerial adults of many aquatic insect species are not affected by instream disturbances and can be a source of postdisturbance colonists via oviposition. However, adults of most species are absent in the winter, so this path to immediate recolonization is not open. Large insects that require multiple years for larval development can be swept away by floods and fail to mature, whereas small multivoltine species could occupy protected pore spaces, complete their life cycles, and reproduce by the next summer. Consistent with their characterization as opportunistic colonizers, small collector invertebrates dominated the postflood communities of streams disturbed by livestock grazing. This pattern also has been observed in the increased fraction of smaller invertebrates found in streams with more intense and frequent high-flow discharge events (Townsend and Thompson 2007).

Invertebrate communities at reference sites, which had a high diversity and abundance of sensitive species, changed little from summer 1996 to summer 1997. In contrast, invertebrate communities at streams degraded by livestock grazing changed significantly over the same time period. These changes were characterized by large increases in invertebrate abundance, particularly of opportunistic small gatherers and filterers, perhaps because deposited fine sediments were flushed and organic matter from the riparian zone was captured and redistributed. In lower-elevation streams in a part of California with a Mediterranean climate, stream invertebrates with traits related to resilience and resistance to floods (high dispersal, flow-tolerant morphologies) become

more abundant in wet than dry years (Bêche and Resh 2007). Floods often result in transient export of benthic invertebrates, but population recovery from these pulse disturbances is often rapid (Grimm and Fisher 1989, Niemi et al. 1990).

The spatial distribution of flood effects on physical conditions might influence the ecological consequences of winter flooding. Stream power reaches maximum levels in mid-order reaches of mountain streams where both channel size and slope combine to produce the greatest forces (Knighton 1999, but see Fonstad 2003 for the role of local channel features in altering power). Despite steeper gradients, headwater streams might have weaker hydrographic responses to winter floods than downstream reaches because they have small channels and catchment areas and cannot generate as much power (as in this study). In large, low-elevation rivers, flood energy is dissipated by gentle slopes and overflow onto floodplains. Thus, middle reaches of mountain streams might be more ecologically vulnerable because hydraulic geometry, cumulative flows from tributaries, and confined canyons magnify flood effects.

The abrupt peak in the rain-on-snow hydrograph was distinctly different from the gradual rise and sustained flows of spring snowmelt (Fig. 2A). Most sediment transport occurs during the rising limb of flood events, before peak flow (Gordon et al. 2004, pp. 197–198), and rapidly rising flows, such as in flash floods, mobilize bed substrata swiftly and carry large volumes of sediment. However, less sediment movement occurs during subsequent high flows. Despite sustained high stream flows during peak snowmelt, the slow rise in discharge generated by spring runoff does not carry the sediment loads of flashy winter floods. Our observations of stream geomorphology after the winter 1997 flood indicate that the redistribution of substrata and organic matter probably occurred during the winter flood rather than during the subsequent snowmelt flood, a result suggesting that climate change will alter the timing and magnitude of sediment transport.

The disruptions caused by a pulse disturbance, such as a flood, might have very different effects on stream communities than press disturbances, such as livestock grazing, pollution, and other human-induced perturbations that are often the focus of bioassessment. Biological recovery might be rapid after a pulse disturbance has passed, and these perturbations sometimes reset conditions for recolonization. Floods have the potential to destroy and to renew habitats and resources, and the effects of floods are likely to be context-dependent, depending on the timing, frequency, magnitude and duration of floods, and on the size

and environmental setting of recipient bodies of water. Mobile colonizers and low densities of primary producers and consumers often characterize benthic communities of large mountain streams with high flow variability where drag-disturbance forces produce high shear stress and unstable bed conditions (Biggs et al. 2005). In the densely forested, steep, and erosion-prone terrain of the Klamath Mountains of northern California, rainstorm-driven debris flows scour streams, remove coarse organic matter, and reduce large and shredder stoneflies and amphibians, taking many years to recover (Cover, in press). Small headwater streams are more stable environments, with less-frequent bed mobilization than larger, downstream rivers (Power and Dietrich 2002). Thus, headwater streams are protected areas for the biota and are important conservation targets for maintaining regional biodiversity in the face of hydrologic disturbances associated with climate change.

Extreme floods might have larger effects on communities in degraded than in pristine streams. After large spring runoff flows in 1983–1984, grazed streams had increased channel incision and erosion, whereas ungrazed or restored streams with riparian cover maintained stable banks and channel profiles (Platts et al. 1985). More sediment is transported during floods in grazed streams prone to erosion than in ungrazed streams. However, floods of appropriate magnitude can scour substrata and remove fine sediments, and the fauna typical of degraded streams possess life-history traits that allow rapid recolonization and growth and efficient use of FPOM. The absence of responses to winter flooding in reference streams indicates a resistant fauna adapted to periodic high-flow conditions in mountain landscapes. The flow regime of Sierra Nevada streams has been classified as a rain + snow type, defined by predictable snowmelt and rains in the spring, variable flows, and less predictable floods than colder snowmelt stream types (Poff and Ward 1989). Thus, many Sierran streams already are influenced by the mixed snow and rain weather conditions that are expected to increase with global warming. During the long dry season with predictable stable flows, biotic interactions are often primary drivers of community organization. However, increasing frequency of aperiodic floods (Dettinger et al. 2009) might shift these systems to greater regulation by environmental perturbations (Power et al. 2008).

Flood disturbance maintains habitat and biological diversity in streams (Townsend 1989). In general, natural floods regenerate habitat variety, alter nutrient cycling, capture and redistribute organic matter, and rearrange and maintain community diversity.

Conversely, the absence of flood disturbances or irregular peak flows, such as those associated with hydropower dams, can degrade biological integrity (Rehn 2009). Studies of stream community responses to increasing rain-on-snow flooding in combination with warmer temperatures, earlier runoff, loss of late-season flows, and altered riparian communities and fire regimes are needed to understand how to protect and manage montane aquatic biodiversity and ecosystem functions.

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