Title

Effect of Stream Flow Regulation and Absence of Scouring Floods on Trophic Transfer of Biomass to Fish in Northern California Rivers

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Effect of Stream Flow Regulation and Absence of Scouring Floods on Trophic Transfer of Biomass to Fish in Northern California Rivers

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ABSTRACT

Scouring winter floods strongly influence the structure and dynamics of food webs in rivers with winter flood, summer drought hydrographs. Reduction or elimination of scouring floods, in addtition to altering physical conditions within rivers, may negatively affect salmonid populations by reducing energy flow to them from lower trophic levels. We compared food webs of two northern California rivers with drastically different flow regimes to assess the effects of differences in food web structure on the distribution and growth of juvenile steelhead trout. The upper Mad River has a highly regulated flow regime and rarely experiences scouring winter floods, while the upper Van Duzen River is free-flowing and experiences frequent scouring floods. Thrroughout spring and summer 1994 densities of the large, grazing caddisfly Dicosmoecus gilvipes exceeded $80/m^2$ in the Mad River, but were $< 2/m^2$ in the Van Duzen. Consequently, filamentous green algae was nearly absent in the Mad from June through September, but was relatively abundant in the Van Duzen. Densities of other stream-dwelling insects (primarily Chironomids and mayflies, which are the preferred prey of juvenile salmonids) and juvenile steelhead were consistently much lower in the Mad than the Van Duzen. At the end of the summer, Dicosmoecus pupated, and thus became inactive, which resulted in a large bloom of filamentous green algae (primarily Oedogonium and Cladophora) and a several-fold increase in the densities of Chironomids and mayflies in the Mad but not the Van Duzen. River flows in 1995 were much higher than in 1994 and both rivers experienced a number of scouring floods. As a consequence, Dicosmoecus densities were reduced to $< 2/m^2$ in both rivers throughout the spring and summer. The Mad experienced a large Cladophora bloom, and densities of Chironomids and mayflies were several times higher in 1995 than 1994. These observations support our hypothesis that eliminating scouring floods favors large, slow-growing benthic insect taxa over smaller, faster-growing taxa whose populations build up rapidly after floods. Since the former are invulnerable to predation by juvenile salmonids, energy flow is reduced and juvenile salmonid populations decline.

Experimental manipulation of juvenile steelhead in artificial channels with and without Dicosmoecus allowed us to test this hypothesis more directly and without potential influences from factors other than food web structure that may have varied between regulated and unregulated rivers. Experimental results revealed that Dicosmoecus significantly reduced the availability of small prey, which resulted in negative juvenile steelhead growth. Together, our surveys and experimental results show that elimination of scouring floods alters energy pathways in river food webs resulting in reduced biomass available to fish populations. Modifying flow regimes regulated by dams, so they more closely resemble natural hydrographs, may be an important step in restoring salmonid populations in some rivers.

Key Words: Algae, Aquatic Insects, Benthos, Fish Ecology, Flood Control, Geomorphology, River Beds, Water Diversion, Watershed Management.

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PROBLEM AND RESEARCH OBJECTIVES

Development of water resources throughout the western United States has resulted in the damming of most large streams and rivers (Behnke 1990; Palmer 1996). These impound large volumes of streamflow that is subsequently diverted from natural channels, through systems of canals and pipelines, to agricultural and municipal users often far outside the boundaries of the watershed. In California more than 1,400 private and federally-operated dams impound and regulate the distribution of over 60% of the state's average annual runoff (Mount 1995). As the world's largest water engineering program, "...the development of the modern water system in California presents one of the most massive rearrangements of the natural environment that has ever been attempted" (Kahrl 1979). As a consequence of this rearrangement, resources associated with natural stream channels have been drastically reduced or eliminated from large regions of the state, resulting in frequent conflicts over protection of remaining resources and supply of water to cities and farms.

Native fish populations, particularly economically important salmon and steelhead, are a natural resource that has been damaged by current water resource management (Moyle and Williams 1990; Lufkin 1991; Nehlsen et. al. 1991; Moyle 1994). Dams often block migratory routes preventing access to spawning areas, create reservoirs that inundate extensive areas of riverine habitat, and modify flow regimes and sediment transport which, in turn, alters channel morphology and habitat availability within downstream reaches (Parker 1980; Burt and Mundie 1986; Ligon et. al. 1995). Reservoirs and tailwaters are also common sites for introductions of non-native fishes that can spread throughout watersheds and compete with and prey upon native species (e.g., Brown and Brasher 1995). Many studies reporting effects of flow regulation on fish populations have focused on direct effects of such modifications to their habitat (e.g., Nelson et. al. 1987; Lisle 1989; Shirvell 1994). In addition, a large number of studies have shown that altered flow regimes, and associated channel modifications, can strongly affect the distribution and abundance of organisms at lower trophic levels (algae and benthic invertebrates) from which fish derive their food (e.g., Armitage 1978; Ward and Stanford 1979; Radar and Ward 1988). Surprisingly few studies have examined the link between effects of flow regulation on lower trophic levels and the transfer of energy to fish populations.

The purpose of this study was to examine the effects of flow alteration, specifically the reduction or elimination of scouring floods, on food web structure and energy transfer to juvenile steelhead trout populations in northern California rivers. Our focus on the effects of bed scour stems from two important observations. First, flow regulation by dams on many California rivers has caused a distortion of the natural winter-flood, summer-drought hydrograph. Runoff from winter storms and spring snowmelt is stored in reservoirs and is released during the summer for irrigation or municipal use. As a consequence, peak winter storm flows, particularly flows competent to mobilize river bed substates, are much reduced and summer base flows are artificially enhanced (Mount 1995). Second, previous research funded by the WRC (WRC-726; Power 1992) alerted us to the possibility that when bed scour is eliminated in rivers, by impoundments or diversions, or during drought in natural channels, successional changes at lower trophic levels may reduce energy flow to fish. Shortly after flood scour stream insects are dominated by fast-growing taxa (e.g., chironomids and mayflies) vulnerable to predation by juvenile fish. Over time (many months) densities of early successional species are reduced as larger, slow-growing taxa, which are much less vulnerable to predators, come to dominate river invertebrate assemblages. Field surveys suggested that in impounded rivers with regulated flows, predators (fish and invertebrates) were present but much less abundant than in rivers with natural hydrographs and winter scour (Power 1992). We hypothesized that in regulated channels the natural succession pattern is eliminated and the persistance of late successional, invulnerable taxa reduces prey availability and is responsible for differences in predator densities.

To test this hypothesis we surveyed regulated and unregulated rivers over two summer seasons, one a dry year in which the unregulated channel experienced scouring winter flows but the regulated river did not, and the other a wet year in which both rivers experienced multiple scouring floods. We compared differences (between rivers and within rivers between years) in the densities of large benthic invertebrate taxa invulnerable to predation by juvenile salmonids and small, mobile invertebrate taxa susceptible to predation. We also compared differences in the distribution and abundance of juvenile steelhead. In addition, we conducted a field experiment in which we manipulated densities of Dicosmoecus gilvipes, a large stone-cased caddisfly, to simulate differences between food webs that assemble under regulated and unregulated flows, and monitored the effects on predator-susceptible invertebrates and on the growth of juvenile steelhead. Based on the results of these surveys and experiments, we show that there is a strong link between flow regulation, the elimination of scouring floods, and the structure of food webs that support juvenile salmonids in California rivers.

METHODS

Study Sites

Regulated vs. Unregulated Rivers -- We compared food web structure and the abundance of juvenile steelhead trout in the upper Mad and Van Duzen Rivers, Trinity County, California (figure 1), from June through September, 1994 and 1995. The Mad River is impounded by the Robert W. Mathews Dam, which is owned and operated by the Humboldt Bay Municipal Water District, primarily to supply water to municipal and industrial users in the Humboldt Bay region. The dam was completed in July 1961 and began storing water in Ruth Reservoir and regulating river flows. The Van Duzen river is undammed its entire length. Both rivers originate in the Coast Range of northern California and flow in a northwesterly direction. The Van Duzen River is a major tributary of the Eel River, and joins it approximately 24 km upstream from its mouth. The Mad River flows directly into the Pacific Ocean approximately 10 km north of the town of Arcata, California. We surveyed upper reaches of these rivers in an area where they flow nearly parallel to each other, separated by a narrow mountain ridge. We selected sample sites so that watershed areas, gradients, and flow directions were similar between

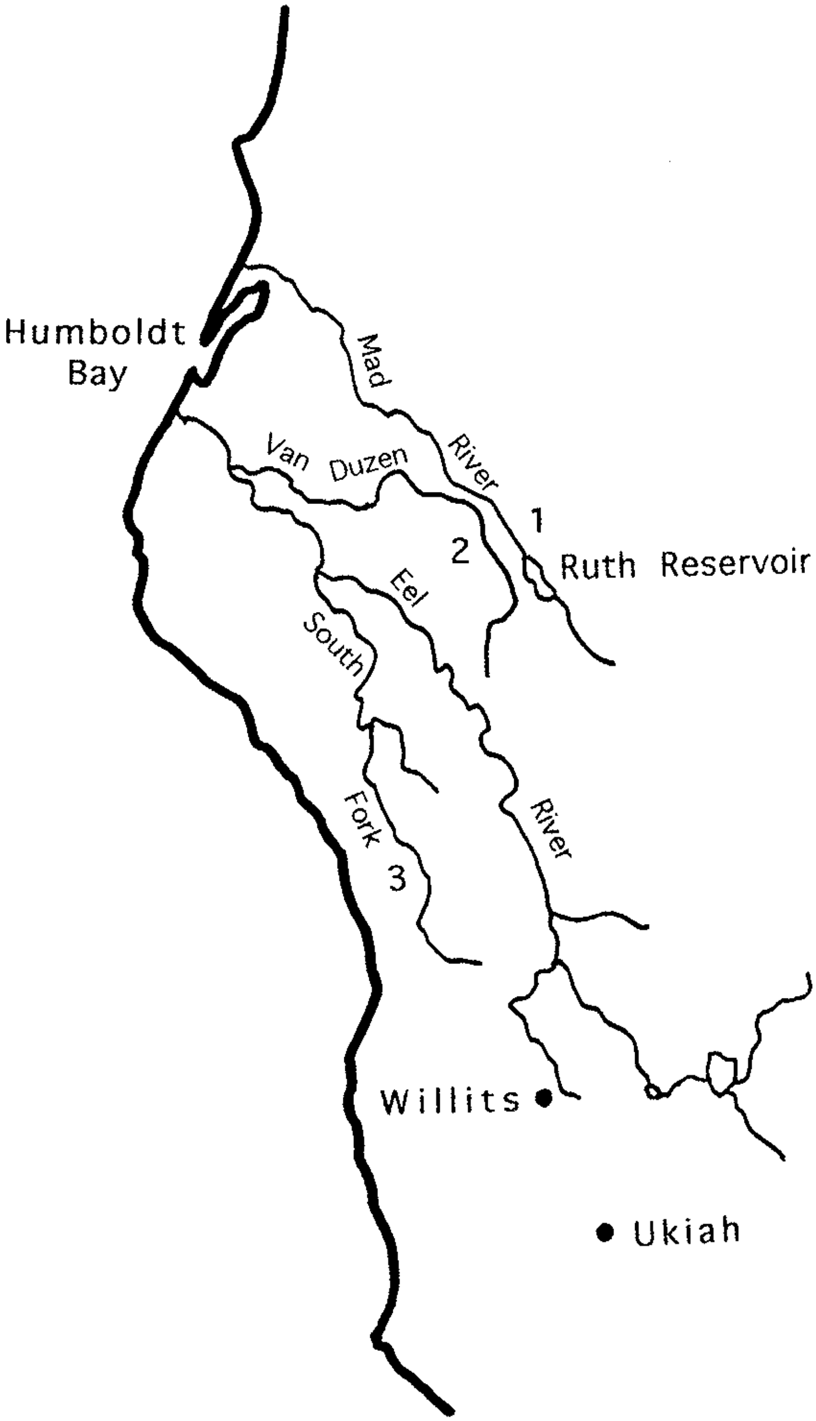


Figure 1. Map of a portion of coastal northern California showing approximate study site locations on the Mad (1), Van Duzen (2) and South Fork Eel (3) rivers.

the two rivers. On the Mad our sites were approximately 1, 2 and 7 km downstream from the dam (40°22-27'N, 123°30"'W), and on the Van Duzen our sites were located between 12 and 15 km upstream from highway 36 along the Van Duzen River Road (40°24-27'N, 123°32'W). Both rivers are gaged by the United States Geological Survey (USGS); the Mad approximately 0.5 km upstream and 2 km downstream of our sampled reach (USGS 11480410 and 11480500 respectively), and the Van Duzen approximately 55 km downstream from our sampled reach (USGS 11478500).

To estimate and compare relative intensities of streambed scour in the two rivers, we used two empirical generalizations about gravel-bedded rivers: first, bankfull discharge has a recurrence interval of approximately 1.5 years (e.g., Dunne and Leopold 1978), and second, significant mobilization of bed materials does not occur until streamflow is close to bankfull (Parker 1978). Using flow records for years prior to the completion of Mathews Dam, we conducted flood frequency analyses (Dunne and Leopold 1978) for both rivers to determine flows with 1.5 year recurrence intervals. We used these values to estimate the proportion of years following dam completion in which each river experienced bankfull or greater, and thus potentially bed-scouring, flows. The proportion of post-dam years in which scouring flows occurred were 42.4% and 68.2% for the Mad and Van Duzen respectively, indicating that the Mad River downstream of the dam typically experiences a lower frequency and magnitude of scouring winter floods than does the Van Duzen. These values may overestimate the actual frequency of scouring floods in the Mad, though, because substrate particles on the surface of its streambed are dominated by large cobbles and boulders, a large proportion of which are embedded. In contrast, bed materials of the Van Duzen River are less embedded and consist of a higher diversity of particles ranging from pebbles to bedrock (figure 3). In addition, both rivers have well-developed riparian vegetation zones, dominated by white alder (Alnus rhombifolia) and willows (Salix spp.), but differences in proximity to, and density along, river margins during summer low flow further indicate differences in the frequency and magnitude of flooding. Along the Mad River, dense riparian vegetation grows up to the margin of the wetted channel during low flow, but along the Van Duzen there is an intervening space of exposed streambed, typically several meters wide, between the rivers edge and the densest riparian vegetation.

During the two years of our study runoff differed considerably within and between rivers. The winter of 1994 was one of the driest on record and the winter of 1995 was among the wettest. Dividing discharge by watershed area shows that flows released into the Mad River were reduced compared to runoff in the unregulated Van Duzen in both years (figure 2). Winter storms in December and January 1994 produced runoff sufficient to scour portions of the streambed of the Van Duzen, but the majority of runoff into the Mad was stored in Ruth Reservoir, preventing scouring of the downstream channel. During winter 1995 both rivers experienced scouring flows on numerous occasions. With regard to our study design, this large difference in scouring flows betweeen years was fortuitous because it allowed us to compare food web responses to bed scour in both a regulated and unregulated river. Originally, during the second year of the study we had intended to simulate a scouring flood in portions of the regulated river using a hydraulic gravel-cleaning machine. The naturally high flows of 1995 accomplished this manipulation for us.

In addition to differences in scouring flows, summer base flows and water temperatures differed considerably between the two rivers (figure 4) . Mean daily discharge in the Van Duzen dropped throughout the summer in both years, reaching its lowest volume in September when the river consisted primarily of long, slow flowing pools connected by much shorter riffles. In contrast, discharge in the Mad was artificially maintained by dam releases, even increasing slightly over the course of the summer, which also maintained higher average current velocities within the channel than were observed in the Van Duzen (figure 5). Because the dam has a hypolimnetic release, the Mad experiences relatively constant, artificially-maintained low temperatures (12-14°C) throughout the summer, whereas maximum summer temperatures (20-22°C) and both daily and seasonal temperature fluctuations are much greater in the Van Duzen. Thus, differences in both flow regimes and temperatures were likely to have strong effects on life histories, and thus distibutions and abundances of aquatic organisms in the two rivers.

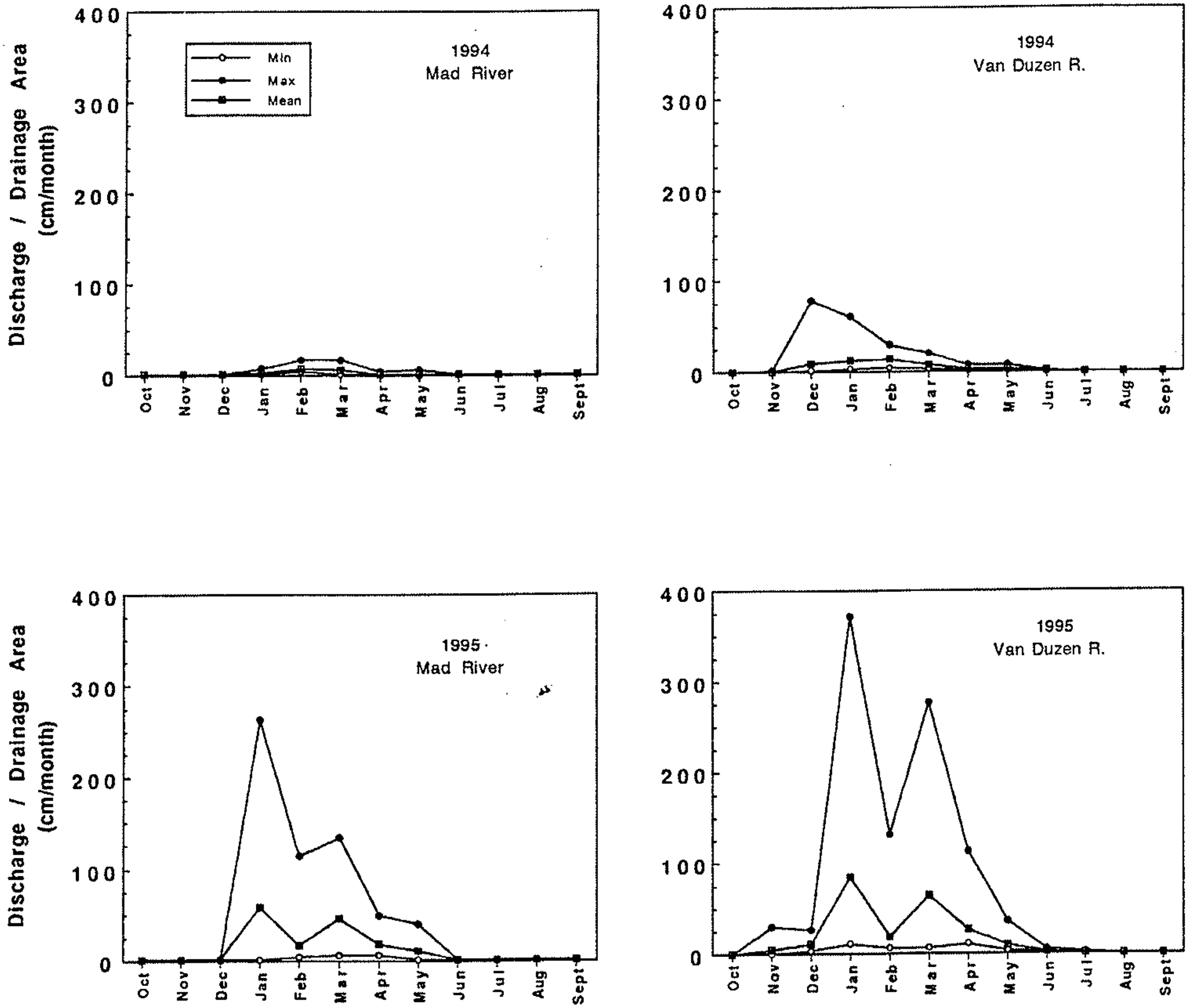


Figure 2. Monthly discharge from river channels, divided by their drainage areas, to compare amounts of precipitation discharged as runoff, and to show effects of storage by Robert W. Mathews Dam on downstream flows in the Mad River relative to natural flows in the Van Duzen River.

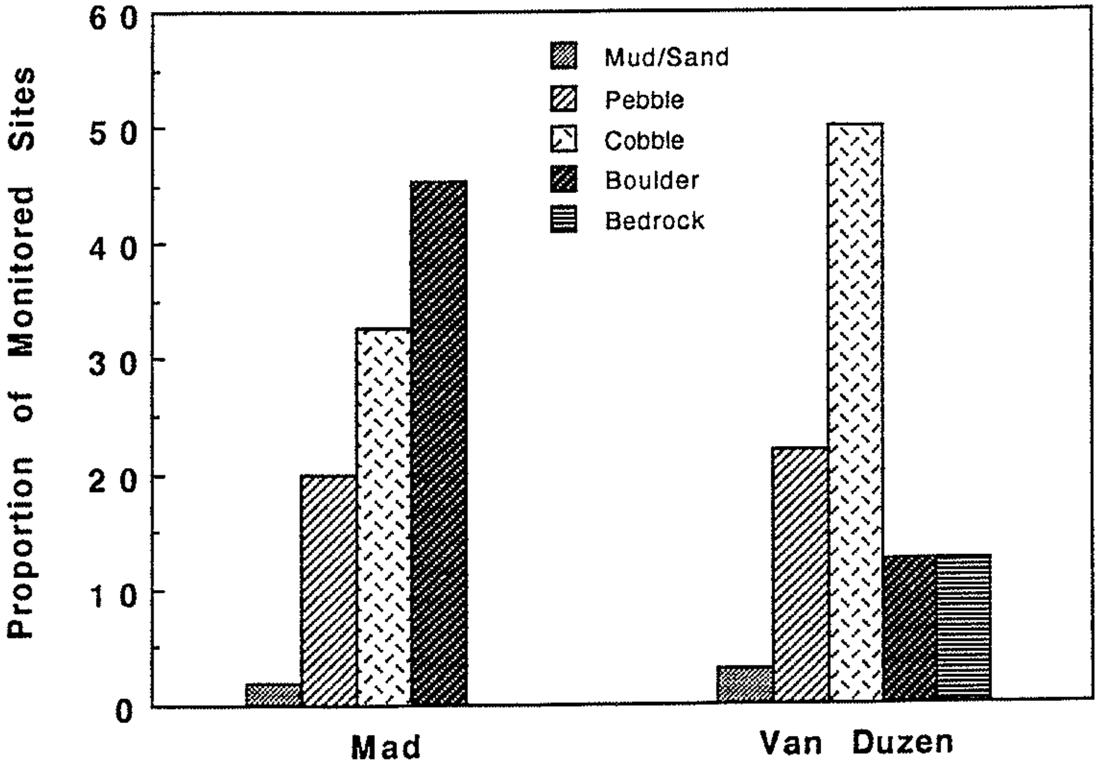


Figure 3. Distribution of bed sediments in the Mad and Van Duzen Rivers, June 1994, as a percent of the total sites sampled (Van Duzen: N=32; Mad: N=55). Mud/sand median diameter < 2mm; pebble median diameter 2-64mm; cobble median diameter 65-256 mm; boulder and bedrock > 256mm.

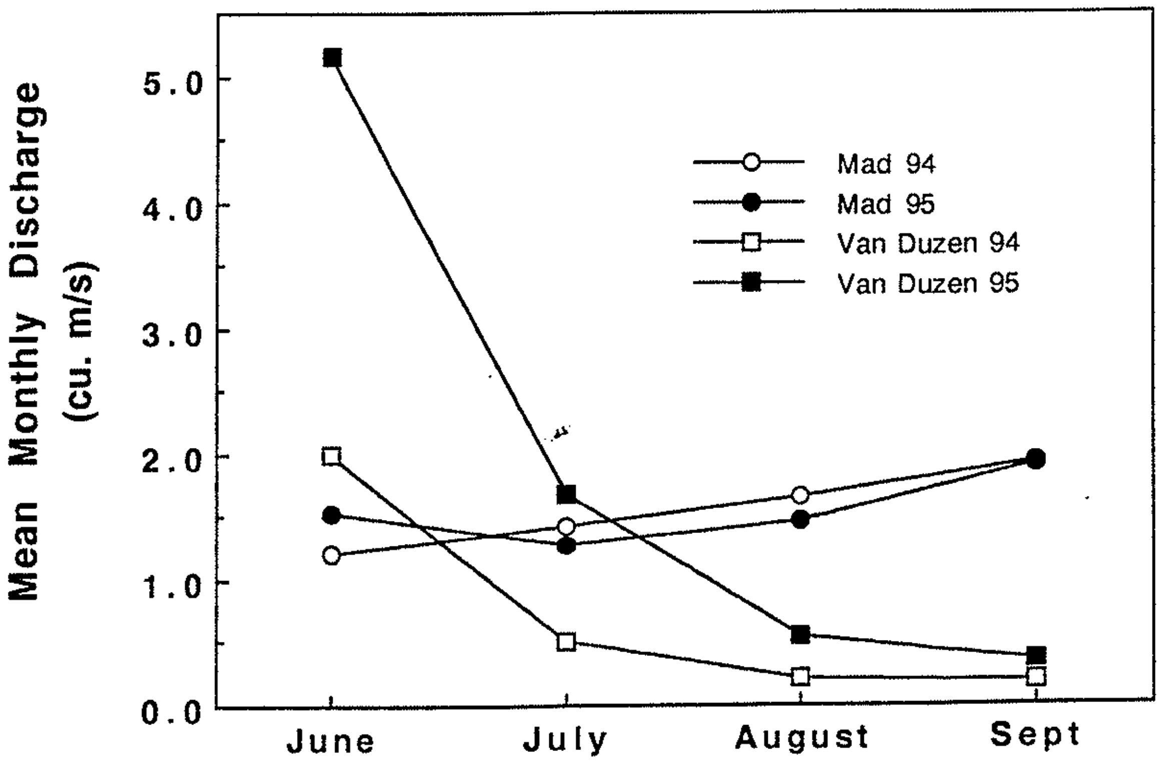
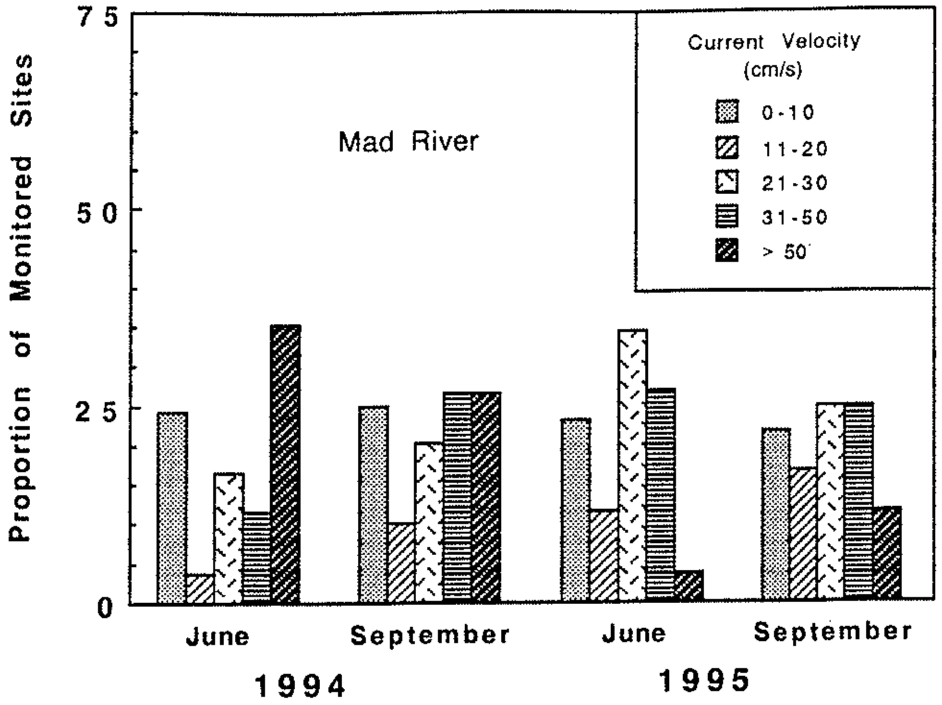


Figure 4. Mean monthly discharge during summer low flow periods of 1994 an d 1995 in the Mad and Van Duzen rivers.



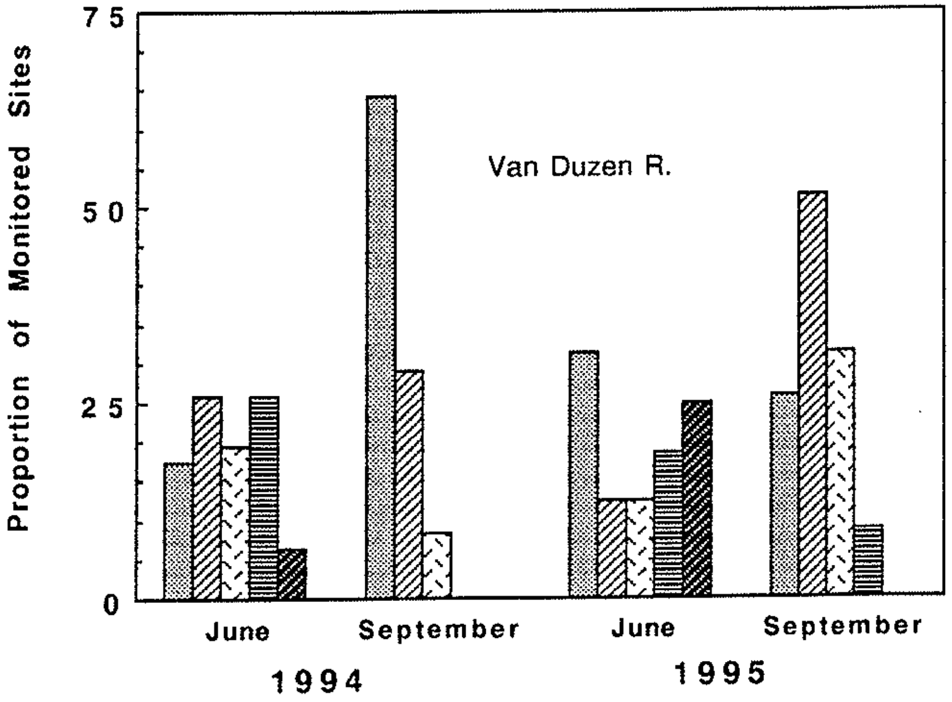


Figure 5. Proportional distribution of current velocities in the Mad and Van Duzen rivers in early (June) and late (September) summers 1994 and 1995. Sample sizes were Mad: 55 and 60 in 1994 and 26 and 60 in 1995 (June and September respectively); Van Duzen: 32 and 48 in 1994 and 24 and 45 in 1995 (June and September respectively).

Food Web Experiment -- This portion of our study was conducted in the South Fork Eel River near Branscomb, Mendocino County, along a reach within the boundaries of the Angelo Coast Range Reserve. This reach of the South Fork Eel has been the site of ongoing field research on river food webs for nearly a decade, and has been described in detail elsewhere (Power 1990a, b). Most importantly, this river is undammed and relatively undisturbed by other human activities.

Survey of Regulated vs. Unregulated Rivers

At each of three sites on each river we established permanent cross-stream transects for monitoring physical characteristics of the channel and densities of algae, benthic macroinvertebrates and fish. At 0.5 m intervals along each transect on the Van Duzen and 1.0 m intervals on the Mad, we measured water depth and current velocity (with a Flow Probe current meter) and visually estimated substrate composition. Using a plexiglass view box for underwater observation, we examined an area approximately 10 by 10 cm at each transect point and recorded the dominant algal type present and its height and density (on a scale of 1 [= majority of substrate bare] to 5 [= complete coverage of the substrate]). We made a distinction between two general algal categories based on growth pattern and height above the substate. Filamentous algae that extended 0.5 cm or more above the substrate was considered macro-algae, and algae closely adherent, and thus not extending above the substrate, was considered adnate or micro-algae. The macroalgae category was dominated by Cladophora glomerata, but on occasion also included Oedogonium and Zygnematales. The microalgae category was typically a diverse organic layer, less than 2 mm thick, covering the surface of substrate particles. This category was dominated by diatoms, but also frequently included cyanobacterial filaments and basal portions of green algae filaments. In addition to our visual estimates of algal distribution, we collected three samples from each transect to determine algal biomass. These samples were obtained from the surfaces of large cobbles collected at equally spaced intervals along the transect. We used a circular rubber template (3.2 cm diameter) to delineate the sample area, scraped the cobble surface within the template with a stiff brush, suspended the loosened material in water, and collected the slurry with a Pasteur pipet. Three such subsamples were collected from each of three cobbles at each transect, placed in plastic vials, preserved with 2% formalin, and returned to the laboratory where they were collected on individual glass fiber filters (0.45 micron effective pore size), dried to constant weight (48 hr at 60°C), weighed, then ashed (4 hr at 485°C), and reweighed.

To estimate densities of large, conspicuous macroinvertebrates, at each point along a transect we placed a 25 x 25 cm metal template on the streambed and recorded the number of individuals within it. To determine densities of other benthic macroinvertebrates we collected five cobble samples along each transect. These samples were collected by placing a large dipnet (0.3 mm mesh netting) immediately downstream of an individual cobble, rolling the cobble into the net, and disturbing the sediments directly below the cobble to suspend and wash into the net any organisms that had been dislodged. Contents of the net were washed into a bucket of water, and invertebrates clinging the cobble surface were removed and also placed into the bucket. Bucket contents were retained on a 0.3 mm mesh sieve, preserved with 70% ethyl alcohol and returned to the laboratory where all organisms were separated from debris under 10X magnification, identified to the lowest possible taxonomic level, and counted. We attempted to standardize cobble size (160 - 200 mm maximum diameter) among sites so invertebrate densities could be reported as number per cobble, and thus be directly compared between rivers. On two dates in 1994 (23 June and 09 September), in conjunction with sampling our permanent transects, we also collected 5 cobble samples at a site 3 km upstream of Ruth Reservoir. This allowed us to compare macroinvertebrate densities and relative abundances between regulated and unregulated sections of the Mad, and compare both sites with the unregulated Van Duzen.

To compare juvenile steelhead densities between rivers, and years within rivers, we conducted visual surveys by swimming three cross-stream transects at each site and counting the number of fish observed in a 2 m wide band. The product of channel and band widths was used to estimate the area surveyed, and thus fish densities. On a given sampling date, all snorkel surveys were conducted by the same observer to minimize variation among counts.

Effects of Food Web Structure on Energy Flow to Fish: a Field Experiment

This experiment was designed to assess effects of food web structure, as determined by differences in densities of Dicosmoecus gilvipes, on food availability to, and short-term growth of, juvenile steelhead. Dicosmoecus dominated the benthic invertebrate assemblage in the Mad River in 1994, and is abundant in the S. F. Eel. during drought years without scouring winter floods. Because of its large size and bulky stone case, Dicosmoecus is invulnerable to predation by junveile salmonids but experiences high mortality during scouring floods. Moreover, grazing by Dicosmoecus has been shown to dramatically reduce algal standing crop (Lamberti et. al. 1987) and thus food availability and habitat (Dudley et al. 1986, Power 1990) for smaller, predator-susceptible invertebrates.

Manipulations were conducted in experimental stream channels consisting of large plastic troughs (1.8 m long, 0.4 m wide, 0.35 cm tall) with open ends covered with rigid plastic screen (6.35 mm mesh openings). When placed in the river, water flowed through the channels at a depth of 10-20 cm. End screens allowed movement into and out of the channels by most benthic invertebrates, but prevented movements of Dicosmoecus and most juvenile steelhead. Sides of the channels extended above the water surface approximately 5 cm and to each we attached a screen barrier which extended an additional 25 cm and prevented fish from jumping in or out and restricted access by predators such as garter snakes and dippers. To each channel we added a 10 cm thick layer of gravel taken directly from the river bed. Care was taken to remove all large caddisfly larvae before placing gravel in the channels. We then placed 8 cobbles (140 - 180 mm diameter), also collected from the nearby river bed, haphazardly along the length of each channel. These cobbles served as sampling units for algae and benthic invertebrates. Twenty channels were used in this experiment, placed at five sites each with four channels. Within a site, channels were placed in riffle-run habitats that had similar depth, flow, and cover. Channels were placed in the river 14 days prior to the start of the experiment to allow colonization by algae and invertebrates.

At the start of the experiment (08 July) each channel within a site was randomly assigned one of four treatments: (1) 50 late instar Dicosmoecus, (2) 3 steelhead parr (38-53 mm Standard Lenth (SL)), (3) 50 Dicosmoecus plus 3 steelhead, and (4) no Dicosmoecus or steelhead. In Dicosmoecus treatments, resulting densities were $69.4/m^2$ which is within the range of densities observed in the South Fork Eel during years without scouring flows, and is lower than densities typically observed in the regulated Mad River. Experimental steelhead densities ($4.1/m^2$) were high relative to average densities typically encountered in the S. F. Eel and much higher than densities in either the Mad or Van Duzen. Juvenile steelhead are generally not evenly distributed among habitats within a stream, however, and the density established in these treatments was within the range typically observed in favorable habitats. Juvenile steelhead introduced into the channels were individually measured (SL to the nearest 0.5 mm) and weighed (to the nearest 0.1 g) and were size-matched as closely as possible among channels. Fish lengths within a given channel differed enough to allow identification of individuals at the end of the experiment.

The experiment ran 21 days (08 - 29 July 1995), and was terminated prior to the period of pre-pupation diapause in Dicosmoecus. At the end of the experiment we collected samples to assess differences in the algal standing crop and distribution, and benthic macroinvertebrate density. We also removed and counted all Dicosmoecus remaining and collected remaining juvenile steelhead by electroshocking. Juvenile fish were again individually measured and weighed and differences in short-term growth were estimated as the difference between initial and final weights.

One day prior to the end of the experiment we collected samples of insects drifting out of the channels using conical drift nets (0.3 mm mesh openings) that filtered the entire discharge of the channels. Upstream ends of the channels were blocked with 0.3 mm mesh, allowing water to pass through but filtering out insects. Thus, downstream drift nets collected only the organisms emigrating from the channels. Drift samples were collected for one hour at midday and again during the hour after sunset. The volume of water filtered by each net was estimated by measuring current velocity into the net and cross-sectional area of the net mouth. Drift net contents were washed into a sample container and preserved with 70% ethyl alcohol. In the lab organisms were sorted from debris, identified and counted.

We collected and processed algal biomass samples using the same methods described above for our river surveys. Three cobbles were randomly selected from each channel and a composite of three subsamples was collected from the surface of each. In addition, we estimated the distribution and abundance of Cladophora, the dominant macroalga present, by conducting visual surveys prior to destructively sampling the algae. Within each channel we determined the density (ranked, as above, from 0-5) and modal height of Cladophora filaments on the surfaces of each of the eight cobbles. We sampled benthic macroinvertebrates by randomly selecting three of the remaining six cobbles and collecting and processing them individually as described above during our river surveys.

We removed an average of 45.9 (±3.81; 1 S.D.; range 39-51) Dicosmoecus from channels to which they were added and none from the other channels, showing that our manipulation was maintained over the course of the experiment. There was no difference in the number of Dicosmoecus remaining between treatments with (46.0 ± 3.43; mean ± 1 S. D.) and without steelhead (45.8 ± 4.15), showing that Dicosmoecus were not eaten by the juvenile fish during the experiment even thought they were very conspicuous on the substrate surface. We removed fewer than three steelhead from some of the channels to which they were added suggesting that some of the fish escaped or were eaten by predators. At one site all three fish from one treatment were missing so we did not include in our analysis data from either fish treatment at this site. At each of the other sites, at least two of the three fish remained in both fish treatments including a total of 10 of the original 12 fish in the steelhead only treatments and 8 of 12 from the steelhead plus Dicosmoecus treatments. Differences in weight change between the two groups of fish were compared using a Mann-Whitney U test after data were pooled. All other response variables were analyzed by Analysis of Variance (ANOVA) followed by Fisher's Protected Least Squares

Difference (PLSD) tests to determine differences among treatment means. Data transformations were preformed if assumptions of equal variance were violated (log transformation for count data and arcsine transformation for proportions).

PRINCIPAL FINDINGS AND SIGNIFICANCE

Results and Discussion

Our surveys revealed striking differences in physical conditions and in the distributions of algae, benthic macroinvertebrates and juvenile steelhead trout between a regulated river, in which the frequency and magnitude of bed-scouring flows has been reduced, and a river with a natural winter flood-summer drought hydrograph, which experiences frequent scouring flows. In summer 1994, densities of the large, case-building caddisfly Dicosmoecus gilvipes remained very high in the Mad River, which did not experience scouring winter flows, but remained quite low in the Van Duzen, which did experience some bed scour during the winter (figure 6). In contrast, during summer 1995, following a winter when both rivers experienced scouring floods, Dicosmoecus densities remained low in both rivers.

In response to differences in Dicosmoecus densities, algae distribution and abundance also differed considerably between the two rivers. During mid-summer (June-August) 1994, the proportion of sample sites with macroalgal growth was higher in the Van Duzen than in the Mad (figure 6). Over the same period, however, similar differences in total algal biomass were not observed. Although macroalgae was much reduced in the Mad River, there was a relatively thick (1-2mm) layer comprised of diatoms, cyanobacteria and associated organic matter covering the streambed that was not present in the Van Duzen. As is typical for rivers receiving hypolimnetic releases from dams, the Mad River probably has much higher nutrient concentrations than the Van Duzen, which maintain the rapid growth of this dense organic layer, even under intense grazing pressure from Dicosmoecus. In September after Dicosmoecus larvae pupated, and were

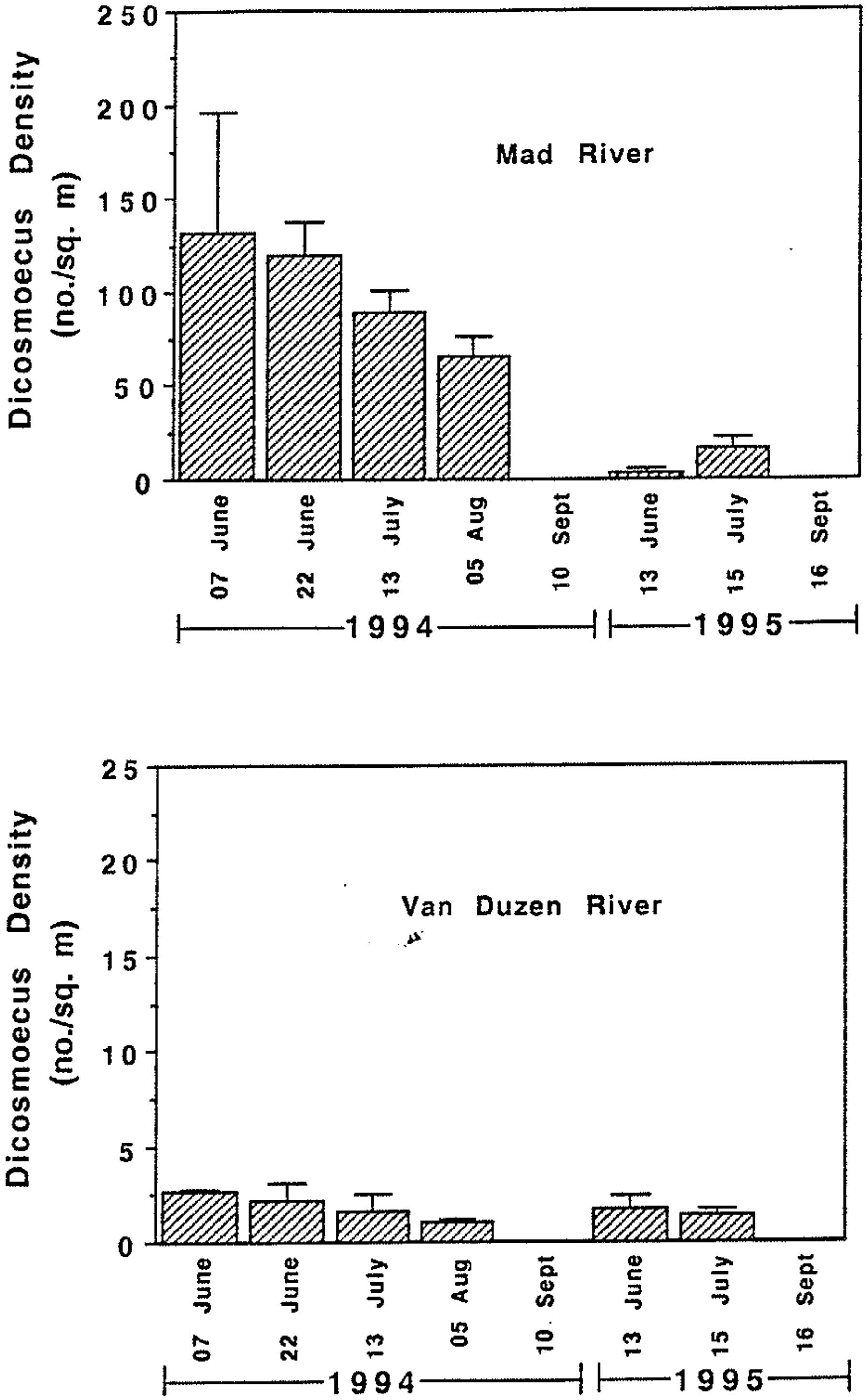


Figure 6. Comparison of Dicosmoecus gilvipes densities (means ± 1 S.E.) in the Mad and Van Duzen rivers, summers 1994 and 1995. Note scale differences of the Y-axes between the two graphs.

no longer active on the streambed surface, the Mad River experienced an extensive bloom of the green alga Oedogonium and algal biomass was several times higher than in the Van Duzen which did not experience such a bloom.

During summer 1995, algal distribution patterns were considerably different than observed in 1994. In June there was an extensive bloom of Cladophora in the Mad River but not in the Van Duzen (figure 7) and macroalgae was much more prevalent, and total algal biomass was much higher (figure 8), throughout the summer in the Mad. Higher nutrient concentrations and lower temperatures of the Mad compared to the Van Duzen, and a large reduction in Dicosmoecus densities likely contributed to this dramatic shift in algal distribution and abundance.

Effects of the differences in Dicosmoecus densities due to flood scour following high flow releases, and resultant changes in algal distribution, were observed in the distribution and abundances of other benthic invertebrates, particularly midges (Chironomidae) and mayflies (Ephemeroptera, dominated by Baetidae). During summer 1994, when Dicosmoecus densities were high and macroalgae sparse in the Mad River, macroinvertebrate densities were 2 - 6 times lower than in the Van Duzen (figure 9). Also at this time macroinvertebrate densities and taxonomic composition in an unregulated reach of the Mad River upstream of the dam were much more similar to those observed in the Van Duzen than in the regulated reach of the Mad (figure 10). Similarity between the upper Mad and Van Duzen included very low densities of Dicosmoecus ($< 1/m^2$ based on visual estimates). In September 1994 the pattern shifted. With Dicosmoecus no longer present, and algal density having increased several-fold, macroinvertebrate density, particularly the Chironomidae, increased to nearly twice that in the Van Duzen or upper Mad (figure 10). In 1995, macroinvertebrate densities, again dominated by the Chironomidae, were consistently several times higher in the Mad than in the Van Duzen (figure 9). From these observation it seems apparent that Dicosmoecus plays an important role in regulating the distribution and abundance of other invertebrates, particularly small-bodied taxa with rapid generation times like midges and some mayflies. These two taxonomic groups are

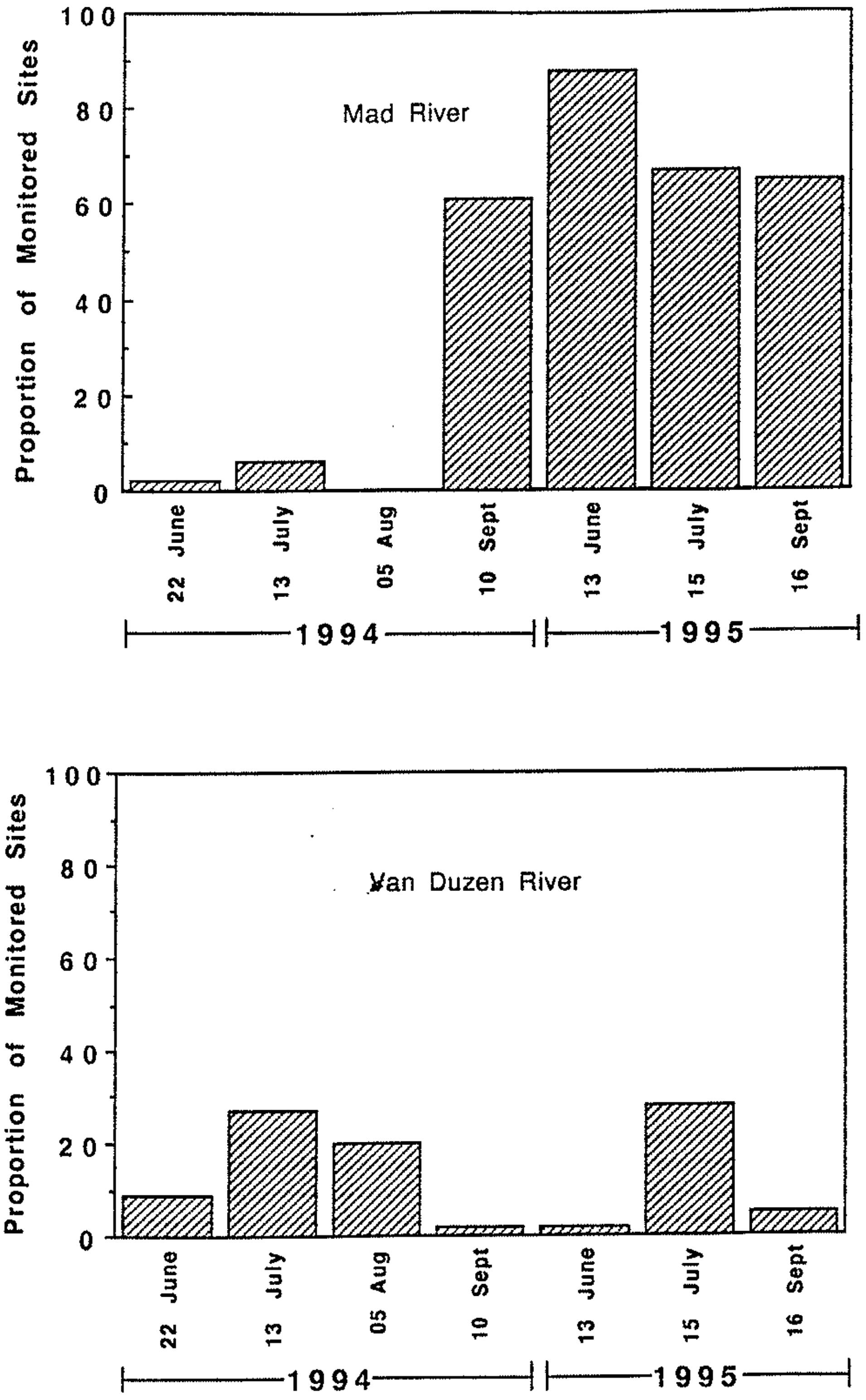
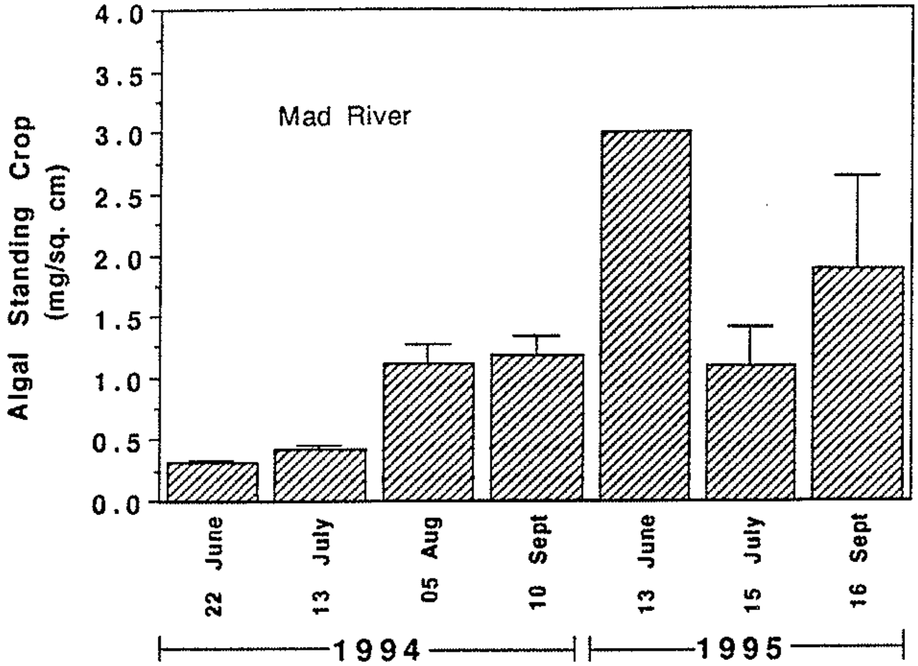


Figure 7. Proportional distribution of macroalgae (defined as extending greater than 0.5 cm above the substrate surface) on substrate surfaces in the Mad and Van Duzen Rivers.



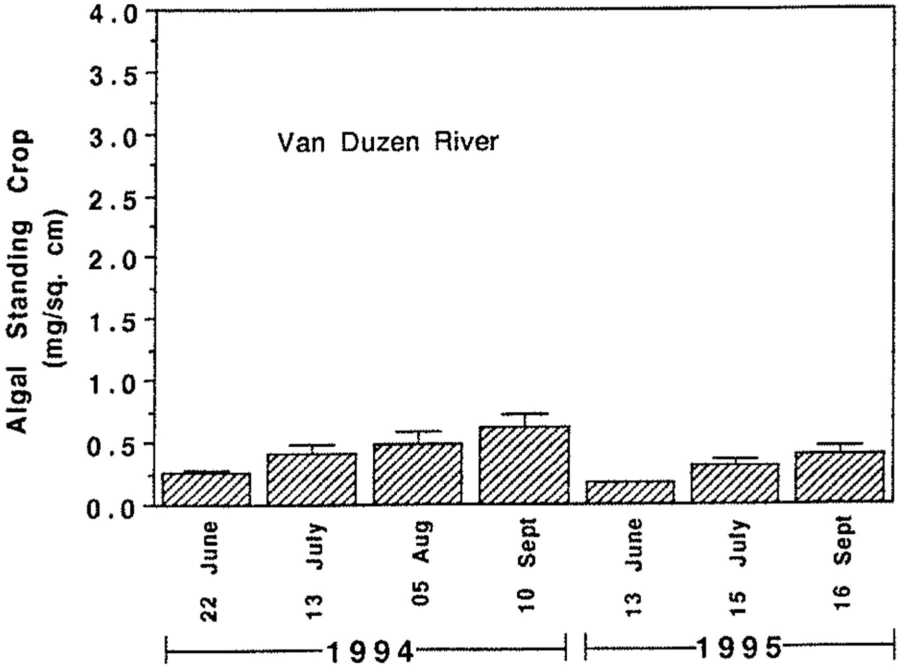


Figure 8. Algal biomass on cobble surfaces of the Mad and Van Duzen rivers, summers 1994 and 1995 (values are means ± 1 S.E.).

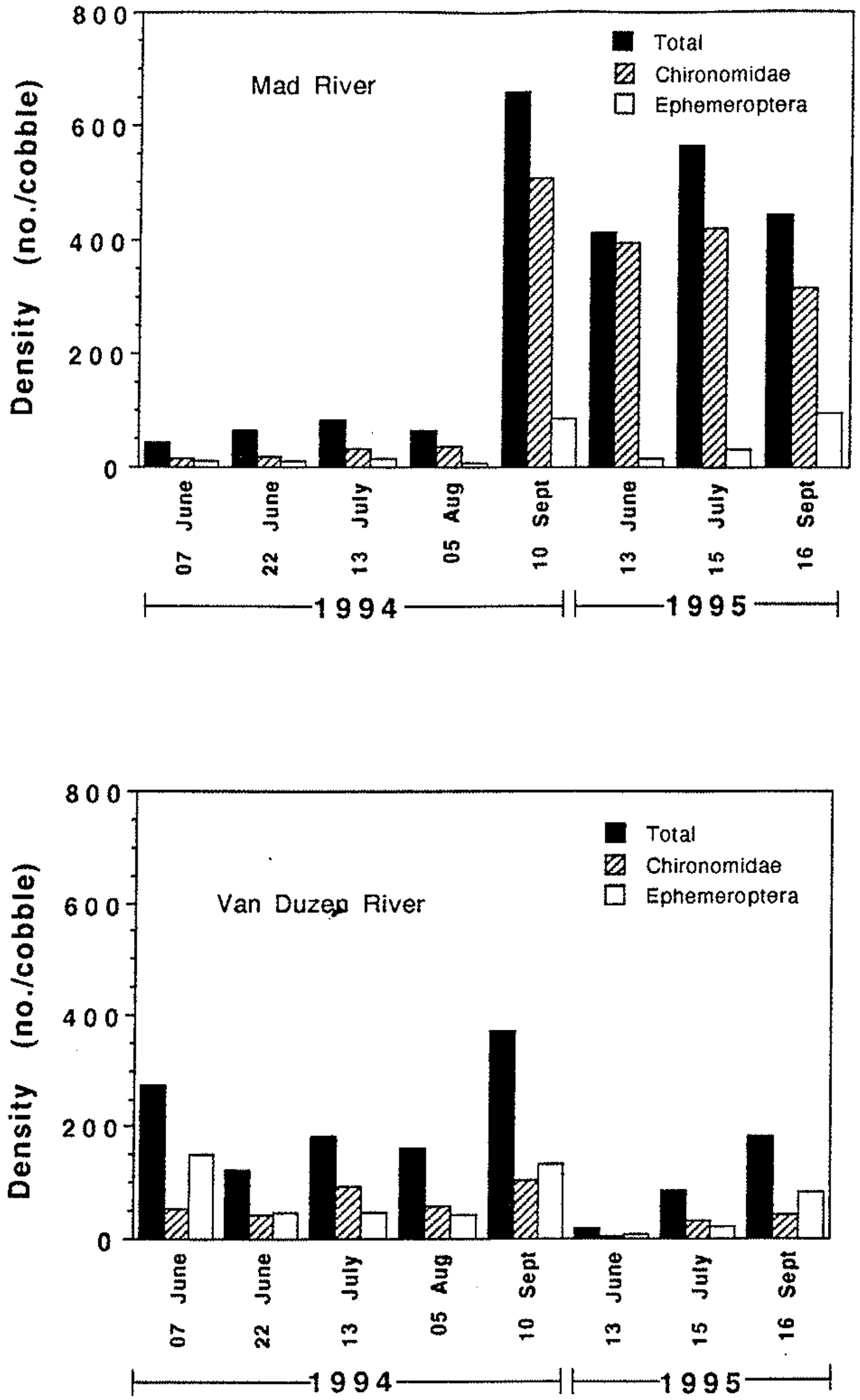


Figure 9. Comparisons of total macroinvertebrate densities (excluding Dicosmoecus) and the densities of the two most abundant taxonomic groups, midges (Chironomidae) and mayflies (Ephemeroptera), in the Mad and Van Duzen rivers, summers 1994 and 1995.

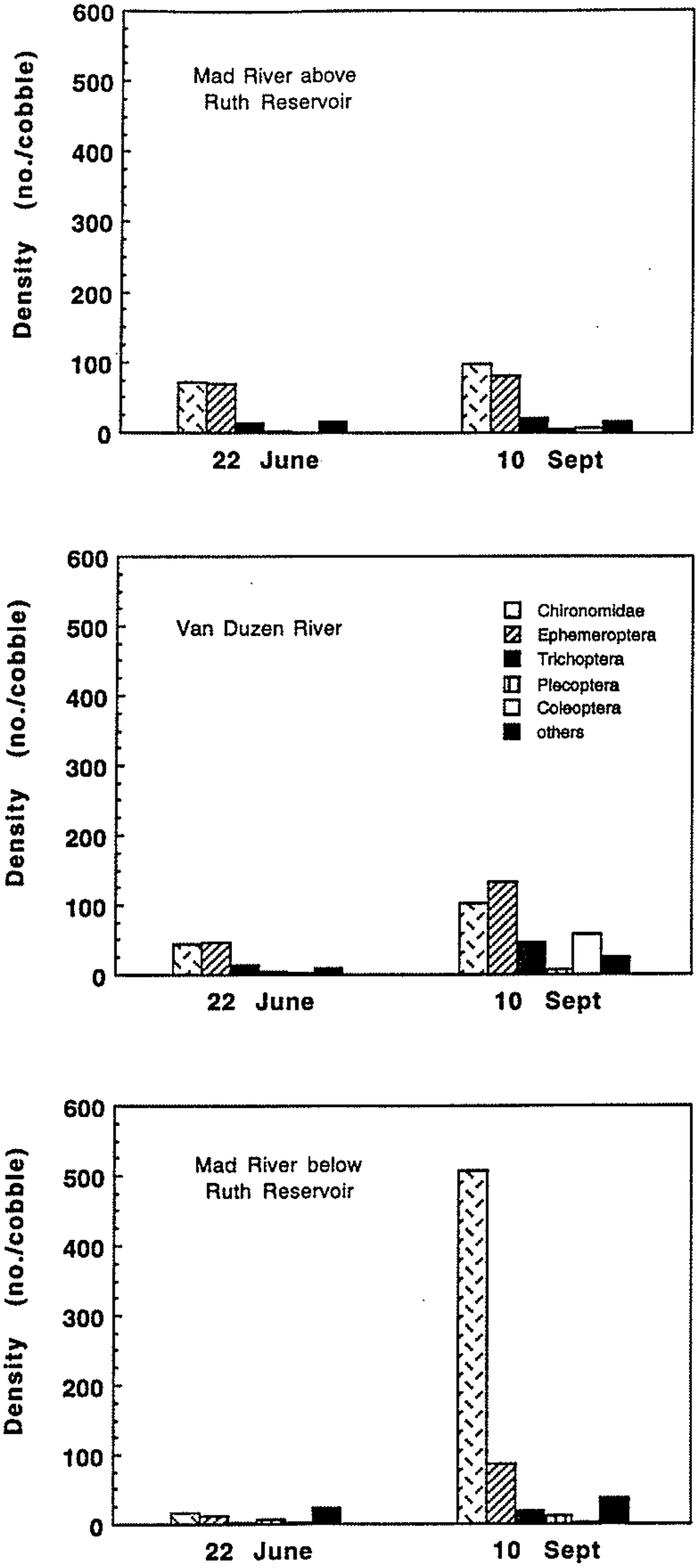


Figure 10. Comparisons of benthic macroinvertebrate distributions and abundances in the Van Duzen River and at sites upstream (unregulated) and downstream (regulated) of Ruth Reservoir on the Mad River.

important members of early successional invertebrate communities that develop following winter floods, and are among the most important food sources for juvenile salmonids (e.g. Johnson and Ringler 1980; Johnson and Johnson 1981).

Juvenile steelhead trout densities varied as predicted by differences in prey availability. Densities were low in both rivers during 1994, and were much lower in the Mad than in the Van Duzen (figure 11). In July we observed a total of two fish among nine transects in the Mad and observed no fish on any transect in August. At the same time we observed high densities of juvenile steelhead in pools of small tributary streams (Hale and Grace creeks) that entered the Mad River near our transects, indicating that fish had successfully spawned but juveniles were rearing in tributaries rather than in the river. The slight increase in fish observed in September is likely due to drying of tributary streams causing fish to move into the river, but may also indicate that fish moved into the river in response to increased prey availability. On both dates fish were censused in 1995, their densities were over twice as high in the Mad than in the Van Duzen, while fish densities in the Van Duzen.were several times higher than in the Mad in 1994. In additiion to differences in prey availability between rivers, and within the Mad River between years, the increase in macroalgae in the Mad may have provided a greater amount of cover for juvenile fish.

Several important conclusions regarding effects of flow regulation on river food webs are suggested by these results. Seasonal fluctuations in distributions and abundances of organisms appeared to be much greater in the regulated versus the unregulated river, in spite of reduced variation in flow and temperature. A major reason for such variation was linked to responses of Dicosmoecus populations to differences in the occurrence of scouring floods. Dicosmoecus over-winter as larvae, and because of their relatively large size and bulky case are susceptible to being crushed as large sediment particles move along the streambed during scouring flows (Wootton et. al. 1996). In the absence of scouring flows, Dicosmoecus densities reamain high, and these grazers can reduce standing crops of filamentous algae and other macorinvertebrates. Their negative effects on other macroinvertebrates may be indirect, through exploitation of the

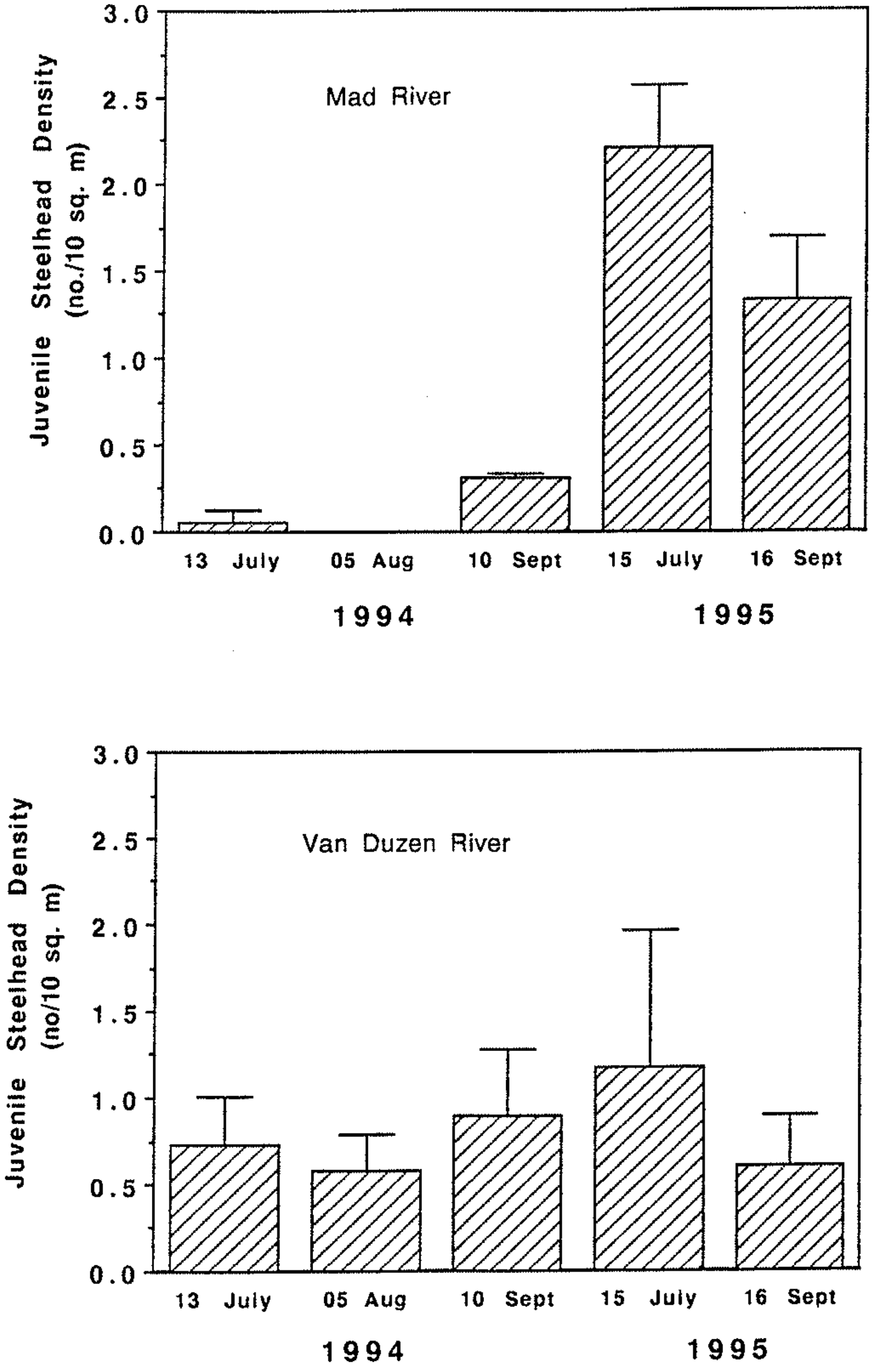


Figure 11. Densities of juvenile steelhead trout observed in the Mad and Van Duzen rivers (means ± 1 S. E.)

algal food resource and reomval of cover, or direct, by physically displacing or eating them. Regardless of the mechanism, high densities of Dicosmoecus, and perhaps other late successional species in other rivers (e.g, Power 1992), reduce densities of prey taxa preferred by junvenile steelhead, and may thus be contribute to low densities of juvenile fish downstream of dams.

Our experimental results largely support the above inferences from survey observations, but also allowed us to directly test the effects of Dicosmoecus on juvenile steelhead growth without potential confounding variables. Juvenile steelhead experienced negative growth over 21 days in the presence of Dicosmoecus, but had positive growth in the absence of Dicosmoecus (figure 12; $p < 0.025$, Mann-Whitney U). As we observed in the river survey, macroalgal distribution and total algal biomass were significantly reduced by Dicosmoecus in our experimental channels (figure 13). Densities of other macroinvertebrates on cobble surfaces, particularly mayflies and midges, were also significantly lower in Dicosmoecus treatments (figure 14). In contrast, densities of drifting invertebrates did not differ among treatments (ANOVA, $p>0.45$). Due to significantly lower invertebrate densities within the streambed in Dicosmoecus treatments, however, per capita emigration rates were proportionally much higher. This result indicates that strong negative effects of Dicosmoecus on benthic invertebrate distribution, are due in part to increased emigration.

Conclusions and Significance

The continuing decline of fish populations in rivers throughout our region (e.g., Moyle and Williams 1990) requires that steps be taken to better manage their habitats if they are to be restored and maintained. Understanding the multitude of ways human alterations of riverine environments affect fish populations, and other important features of river ecosystems, is an important step toward identifying methods to minimize our impacts. Too narrow a focus on physical characteristics of river channels often ignores biological processes that may play as important a role in the growth and survival of juvenile fish. Here we provide evidence that when dams or diversions reduce or eliminate scouring floods, resultant changes in food webs can

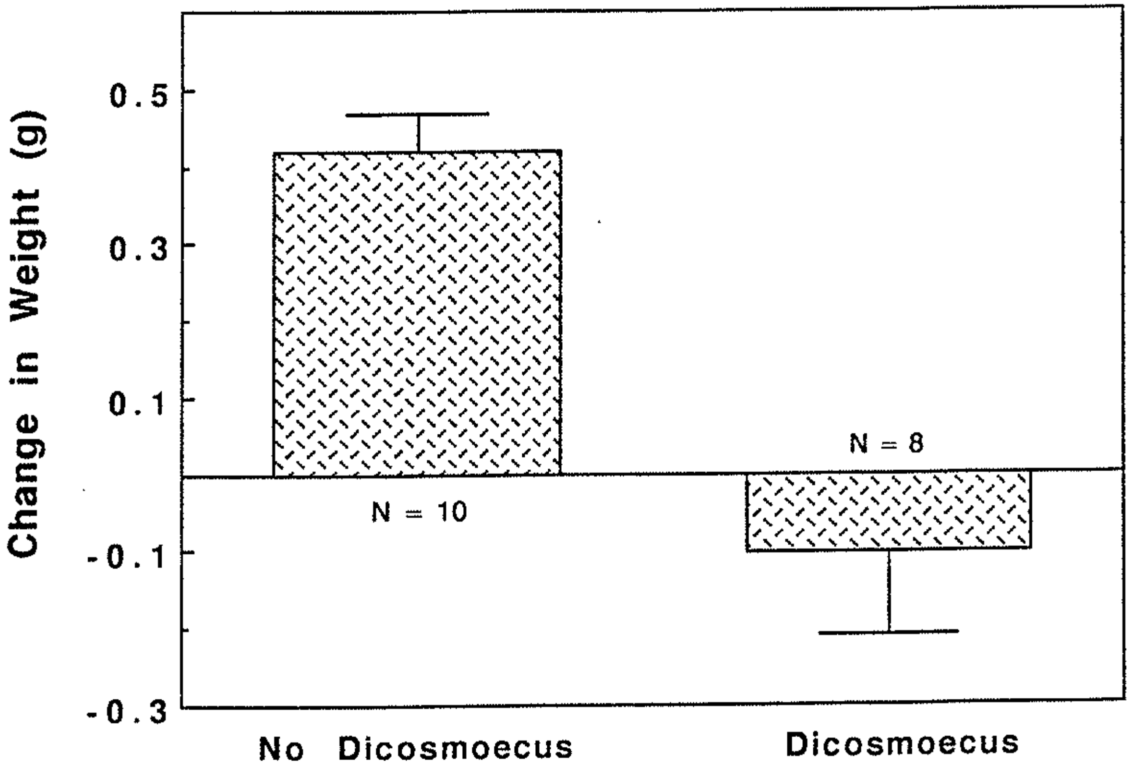


Figure 12. Change in the weight of juvenile steelhead after 21 days in channels with and without Dicosmoecus (means ± 1 S. E.).

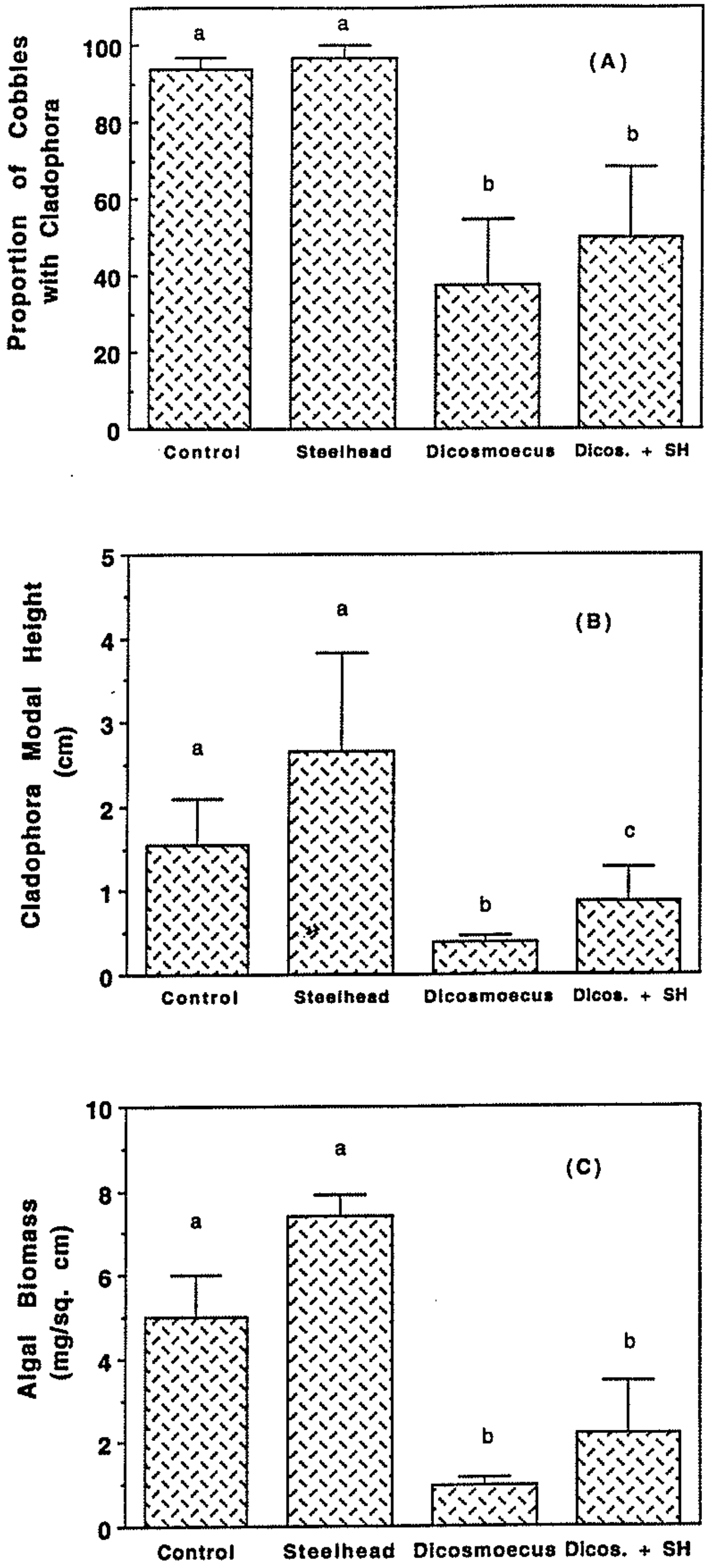


Figure 13. Algal responses to manipulation of Dicosmoecus and juvenile steelhead: (A) Proportions of cobbles within each treatment on which Cladophora filaments (> 0.5 cm long) were observed; (B) Modal height of Cladophora filaments extending from cobble surfaces; (C) Total algal biomass (AFDM) collected as composite samples from cobble surfaces. All values are means ± 1 S. E. and bars with different superscripts differ significanly from each other ($p < 0.05$).

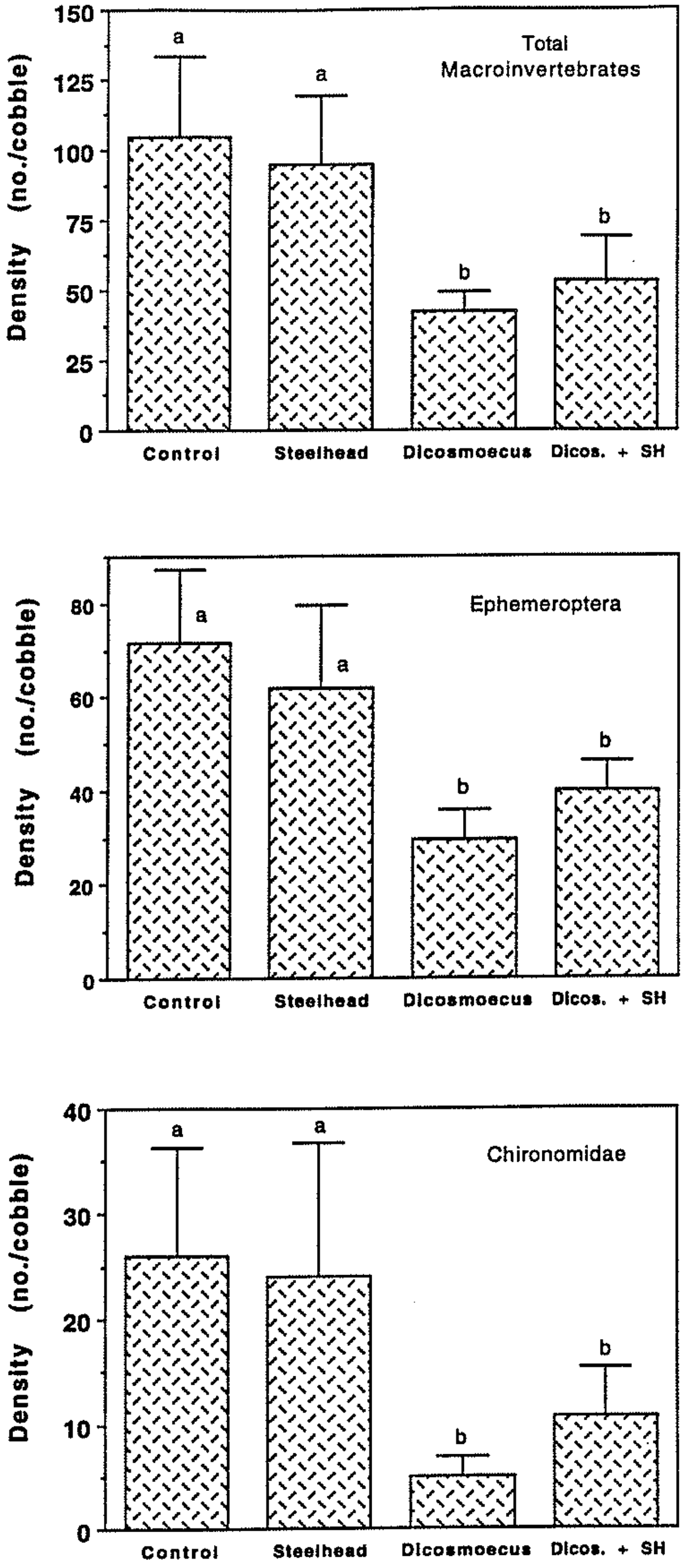


Figure 14. Effects of experimental treatments on densities of total macroinvertebrates (excluding Dicosmoecus), Chironomidae and Ephemeroptera. All values are means ± 1 S. E. and bars with different superscripts differ significantly from each other (Fisher's PLSD; $p < 0.05$).

reduce energy flow to fish. These results suggest that managing flows out of dams so they more closely mimic natural conditions, including allowing flows that result in streambed scour in rivers with winter flood, summer drought hydrographs, may benefit steelhead and salmon populations. Releasing flushing flows from dams has been suggested as a means of redistributing sediments to improve spawning habitat for salmonids (Nelson et. al. 1987; Reiser et. al. 1989a,b). Our results suggest that release of flushing flows at appropriate times may also enhance prey availability to juvenile fish. In addition, our study suggests a potential approach to monitoring the effects of flow modifications on river food webs, to indirectly assess potential prey availability. Populations of large benthic invertebrates, such as <u>Dicosmoecus</u>, are relatively easy to visually census (e.g., Lamberti and Resh 1979; Hart 1981) and could thus be used to assess responses of benthic communities to river flow manipulations. Caution must be exercised in returning flushing flows to regulated rivers, however, so they correspond as closely as possible to natural flow regimes (particularly with regard to seasonal timing) and are minimally disruptive to other organisms that reside and reproduce along river channels (e.g., Lind et. al. 1996).

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