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Cumulative Effects of Riparian Disturbances along High Desert Trout Streams of the John Day Basin, Oregon

HIRAM W. LI

National Biological Survey, Oregon Cooperative Fishery Research Unit[1]
Oregon State University, Corvallis, Oregon 97331, USA

GARY A. LAMBERTI,[2] TODD N. PEARSONS,[3] CYNTHIA K. TAIT, AND JUDITH L. LI

Department of Fisheries and Wildlife, Oregon State University

JOHN C. BUCKHOUSE

Department of Rangeland Resources, Oregon State University

Abstract.—In a study of cumulative effects of riparian disturbance by grazing on the trophic structure of high desert trout streams, watersheds with greater riparian canopy had higher standing crops of rainbow trout *Oncorhynchus mykiss*, lower daily maximum temperatures (range, 16–23°C compared with 26–31°C), and perennial flow. Watershed aspect influenced the response of trophic structure to grazing influences. Standing crops of rainbow trout were negatively correlated with solar radiation and maximum temperature in watersheds flowing northward. A different relationship was observed for a set of watersheds with a southern aspect, perhaps due to the presence of spring seeps and stream desiccation in the heavily grazed stream. Trout biomass was negatively correlated with solar radiation, whereas positive relationships were found for discharge and depth. Algal biomass was positively correlated with solar insolation ($r = 0.91$), total invertebrate biomass ($r = 0.77$), and herbivorous invertebrate biomass ($r = 0.79$) in all watersheds. Invertebrate biomass was not significantly correlated with rainbow trout standing crop. High irradiance apparently resulted in increased algal biomass and invertebrate abundance. However, temperature elevations to levels close to lethal may impose high metabolic costs on rainbow trout, which may offset higher food availability and affect the availability of prey.

The John Day River is one of only 42 streams exceeding 200 km that remain unimpounded in the contiguous United States (Benke 1990). It is one of the few drainage systems in the Columbia River basin that still supports entirely wild runs of fall and spring chinook salmon *Oncorhynchus tshawytscha* and summer steelhead (anadromous rainbow trout *O. mykiss*). However, for various reasons, all related to human disturbance, numbers of returning spawners have diminished greatly. In 1990, the sizes of fall chinook salmon, spring chinook salmon, and summer steelhead runs were estimated at 3,000, 6,000, and 35,000 fish, respectively; from 1969 to 1985, the average runs of the same fishes were estimated at less than 150, 4,000, and 12,000–15,000 fish (Oregon Water Resources Department 1986).

The most obvious human disturbance in the John Day River basin is cattle grazing (Oregon Water Resources Department 1986). This region is particularly sensitive to overgrazing by exotic ungulates because the native vegetation of the grasslands west of the Rocky Mountains evolved in the absence of large herbivores for the past 2,500 years (Mack and Thompson 1982). In contrast, grasses east of the Rockies evolved with *Bison* sp. and the impact of exotic ungulates on the vegetative community was less severe. Overgrazing on riparian vegetation increases the amount of insolation reaching streams, resulting in cumulative increases of stream temperatures downstream (Barton et al. 1985), especially in high desert watersheds of the intermountain West (Platts and Nelson 1989). However, reduced abundance and distribution of riparian vegetation can have positive effects on salmonids by stimulating the auto-

[1] Cooperators are the National Biological Survey, the Department of Fisheries and Wildlife of Oregon State University, and the Oregon Department of Fish and Wildlife.

[2] Present address: Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556, USA.

[3] Present address: Department of Wildlife, Yakima Species Interactions Study, 801 South Ruby, Ellensburg, Washington 98926, USA.

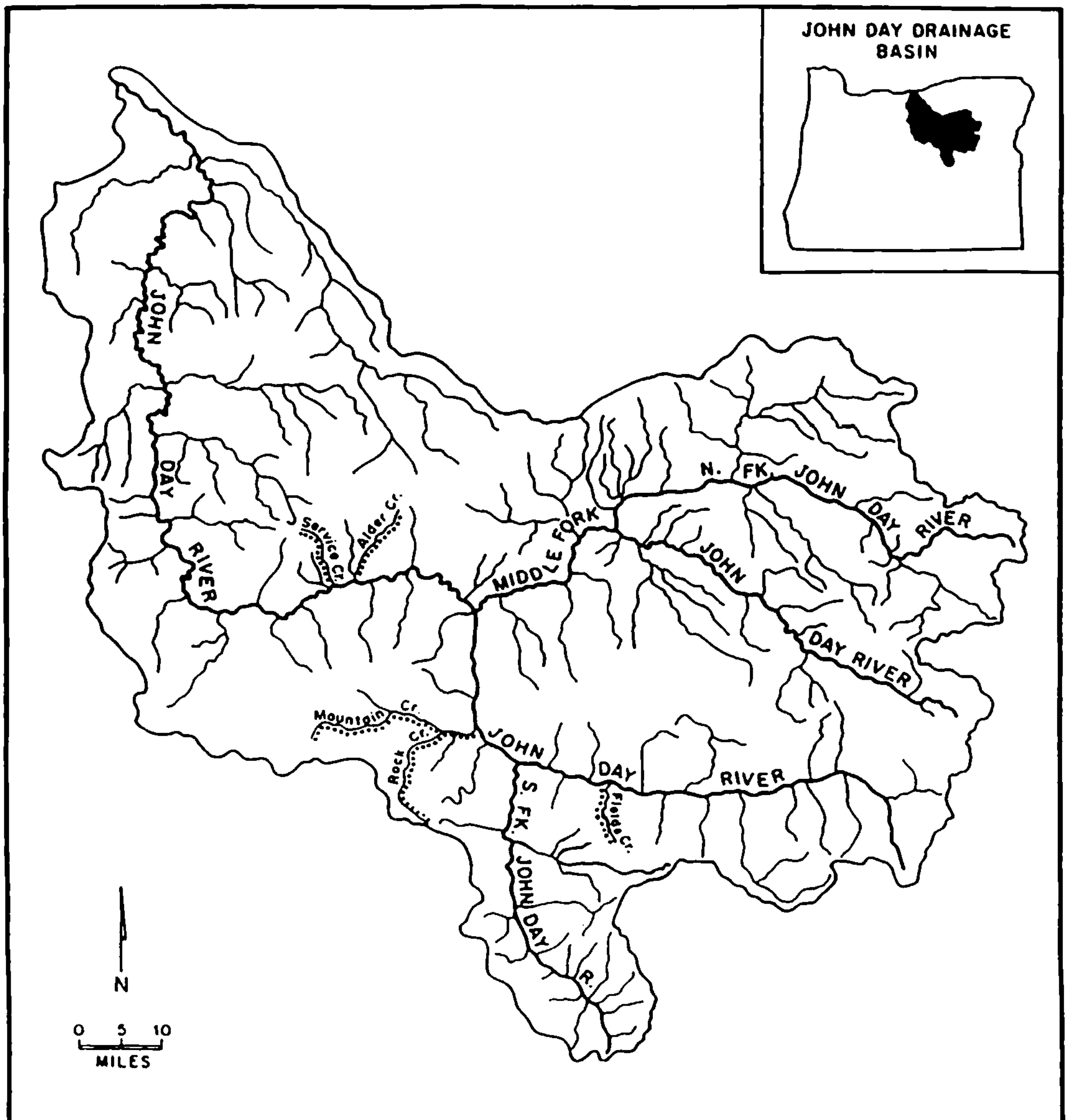

FIGURE 1.—Location of study streams within the John Day basin, Oregon. The mouth of the John Day River at the Columbia River is at the northwest corner of the map. The dotted lines denote each study drainage.

trophic food base (Murphy and Hall 1981; Murphy et al. 1981; Hawkins et al. 1983; Bilby and Bisson 1987). Alternatively, Platts and Rinne (1985) and Platts and Nelson (1989) suggested that temperature increases could offset any potential benefits to salmonids from increased invertebrate abundance generated from stimulated primary production. To our knowledge, no careful trophic studies similar to those conducted in west-slope Cascade Mountain streams (e.g., Murphy et al. 1981; Hawkins et al. 1982, 1983) have been conducted in high desert trout streams to verify this hypothesis.

The purpose of our study was to test the hypothesis proposed by Platts and his coworkers. We examined the cumulative effect of riparian canopy on standing crops of rainbow trout in high desert trout streams by asking the following questions.

(1) Are there differences in standing crops of rainbow trout between similar watersheds differing primarily in the distribution and extent of riparian canopy?

(2) Do rainbow trout standing crops differ among unshaded and shaded reaches of stream along a longitudinal profile?

(3) What is the relationship of riparian canopy and solar insolation to maximum and average daily temperature along the longitudinal profile of a stream?

(4) Are trout populations inhabiting watersheds with different compass aspects affected similarly by disturbance of the riparian canopy?

(5) What effect does solar insolation have on the biomass and standing crop of algae and aquatic invertebrates?

(6) What correlative relationships exist among solar insolation, water temperature, trophic structure, and standing crops of rainbow trout?

Study Area

The John Day River basin is on the southern flank of the mid-Columbia group of basins. It drains 21,702 km^2 (Figure 1), an area approximately the size of Massachusetts, and contains a diversity of landscapes (Oregon Water Resources Department 1986). The major physiographic provinces are the Deschutes-Umatilla Plateau and the Blue Mountains (Hughes et al. 1987). Our study was conducted in the Blue Mountain province. This part of the basin is physiographically diverse, containing high mountain meadows, alluvial valleys, mountains, hills, and rimrock plateaus. Below 1,200 m, the terrestrial vegetation is dominated by bunch grasses *Festuca* sp., bitter brush *Pursia tridentata*, mountain mahogany *Cercocarpus* sp., junipers *Juniperus* sp., and sagebrush *Artemesia* sp. At higher elevations, vegetation is dominated by lodgepole pine *Pinus contorta*, white fir *Abies concolor*, ponderosa pine *Pinus ponderosa*, and Douglas fir *Pseudotsuga menziesii*. Most of the drainage is xeric; however, annual precipitation in different subbasins ranges from 3.9 to 15.8 cm, 90% of which is snow. Most of the basin receives less than 7.9 cm of precipitation per year. The 40-year mean annual flow (1950–1989) measured at the lowest gauging station near Service Creek (river kilometer 252) is 15.6 m^3/s, ranging from a low of 5.4 to a high of 34.2 m^3/s. On average, peak discharge occurs in April (37.3 m^3/s), and low flow occurs during August (1.7 m^3/s).

Methods

Assumptions.—A traditional problem with the study of habitat conditions for stream fishes is proper replication. As water flows downstream, upstream influences preclude the use of "replicate" reaches of stream in studies that involve discharge and temperature. Choosing replicate streams is also difficult because no two systems are exactly alike. We made the following assumptions to partly accommodate these problems.

We assumed that effects of upstream disturbances accrued downstream and were thus cumulative; therefore, downstream study sites were selected on the basis of the degree of disturbance in the upper watershed. As a corollary, spatial distribution of a disturbance along the stream may be as important as its magnitude; that is, the location of canopy removal in the drainage (upstream versus downstream) may be as important as the longitudinal extent of canopy removal. This led to using focal reaches in our sampling design. Focal reaches were located near the lower margins of shaded and unshaded "patches" of stream. This design allowed for the full expression of cumulative effects of riparian cover upstream. We also assumed that watersheds could be grouped by ecological potential, and that this ecological potential could be indexed by selected physical characteristics through a classification process (Frissell et al. 1986). Our design for comparative watershed studies was to match focal reaches by elevation and relative position of the reach within each basin. These sites were located near the bottom of each watershed.

Habitat classification.—Habitat classification was used to match streams for study. We used two methods to classify stream systems: cluster analysis of watersheds based on their physical characteristics and the Rosgen stream classification system (Rosgen 1985). The classifications served to identify similar watersheds based upon climatic, geomorphic, and geological factors. We assumed that watersheds falling into the same class would have similar ecological potentials based upon these intrinsic characteristics. Land use patterns were not used as characters of classification to define potential, but were used to sort out the realized capacity of each watershed in a cluster with similar potentials. Therefore, once a cluster was identified, we searched for watersheds in it that differed in riparian zone condition, ranging from relatively intact to highly abused. Final selection of study sites from the range of possibilities was based on field inspections.

We estimated the ecological potential for 27 subbasins on the basis of the following physical characteristics: mean annual precipitation within the watershed, water storage capacity (inferred

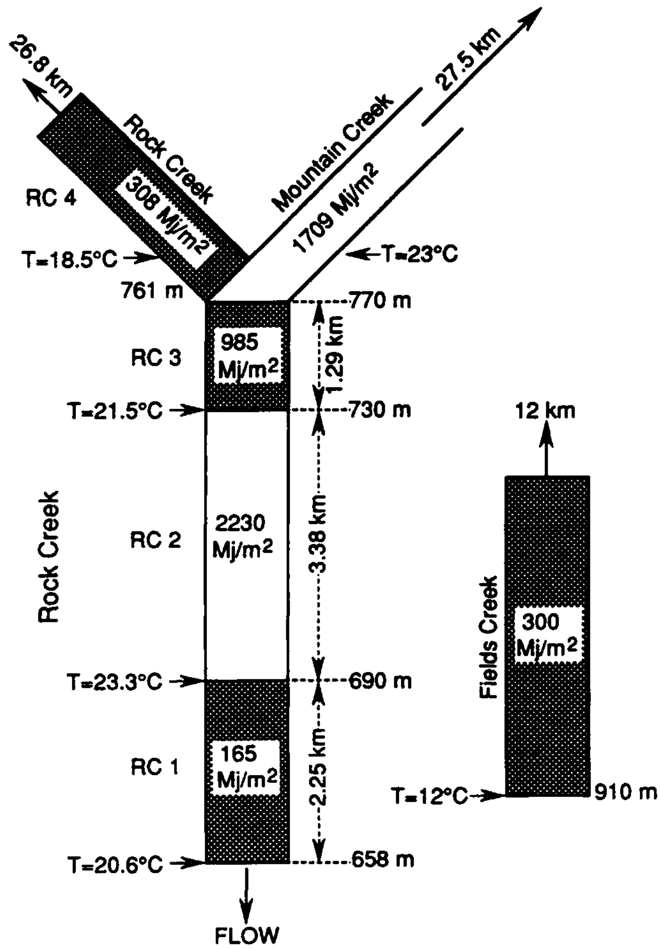

FIGURE 2.—The distribution of riparian canopy in reaches of Rock and Mountain Creeks. Stippling denotes reaches of stream shaded by riparian canopy. Blank areas represent reaches exposed to solar input. Solid arrows running counter to stream flow refer to the length of stream above the focal reach. Dashed arrows to the right of each stream indicate the lengths of stream reaches. Numbers within the stream reach are the solar inputs for the months of June, July, and August in megajoules per square meter. Elevations and mean daily water temperatures during the study are shown at the lower border of each reach.

from local geology), watershed area, length of the major stream, total length of all streams of the basin, drainage density, stream gradient, compass aspect (scored to adjust for solar insolation and transpiration), highest elevation, lowest elevation, soil composition, and mean annual runoff. A digitizer was used to integrate areas from various maps describing these characteristics (U.S. Geological Survey 7.5-minute and 15-minute maps, Oregon Water Resources Board). Different groupings of watersheds resulted from an agglomerative clustering technique that employed unweighted pair-groups and group mean averages (UPGMA technique, see Gauch 1982). Euclidean distance was used as a measure of dissimilarity among clusters.

We selected two clusters for comparison. Mountain, Rock, and Field Creeks formed cluster N; all drain in a northerly direction and Mountain Creek joins Rock Creek (Figure 1). The major difference among these creeks was the type and distribution of riparian canopy (Figure 2). The upper portion of Rock Creek is shaded with alders *Alnus* sp., willows *Salix* sp., and ponderosa pine, whereas the lower portion of Rock Creek, below the confluence of Mountain Creek, has an intermittent canopy. Mountain Creek is virtually devoid of riparian canopy. Fields Creek has an extensive canopy of alders, willows, and ponderosa pine from the sampling site to its headwaters. These watersheds were sampled during July 12–17, 1988. Mean

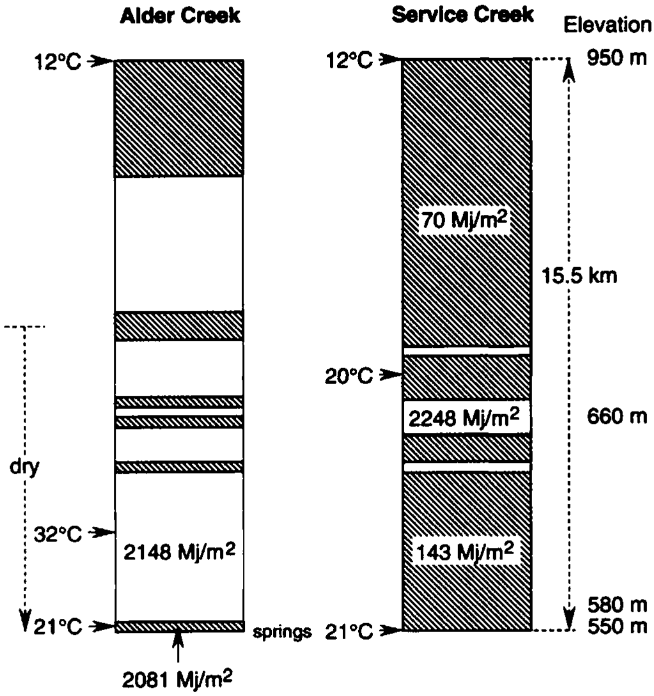

FIGURE 3.—The distribution of riparian canopy in Service and Alder Creeks. Crosshatching denotes reaches of stream shaded by riparian canopy. Blank areas represent reaches exposed to solar input. Numbers within the stream reach are the solar inputs for the months of June, July, and August in megajoules per square meter. Temperatures are daily maxima in stream reaches. Focal reaches were at 580 m elevation. The scale on the right refers to the elevation and the linear extent of each stream. Alder Creek goes dry, as denoted by the dashed arrow. Springs markedly lower water temperature at 550 m in Alder Creek.

discharge of the John Day River recorded at the Service Creek gauging station during this period was 6.39 m^3/s.

Service and Alder creeks formed cluster S, a set of streams with a southern aspect (Figure 1). Both streams have headwaters at an elevation of about 950 m and both have similar-sized watersheds. Service Creek has an extensive but incomplete riparian canopy, whereas Alder Creek is almost devoid of trees in the riparian zone over much of its length (Figure 3). These two watersheds were sampled during July 17–23, 1989. Mean discharge of the John Day River recorded at the Service Creek gauging station during this period was 11.9 m^3/s.

The Rosgen stream classification system (Rosgen 1985) was used as an independent check on our clustering classification of study sites. The Rosgen stream classification system is based upon the following factors: stream gradient, sinuosity, width : depth ratio, dominant substrate particle size, valley constraint, and soil stability aspects. The Rosgen method confirmed that our classification approach was a good method for identifying similar streams from which to sample. The channel segments were remarkably similar: 22 were B1, 11 were B2, and 1 was C1. A B1 stream segment has a moderate gradient (2.5–4%) and a stable channel with small boulders, large cobbles, and coarse gravels. A B2 stream also has a moderate gradient (1.5–2.5%) and a stable channel composed of large cobbles, coarse gravels, and sand. A C1 reach has a gentle gradient (1.0–1.5%) with cobble beds and meanders.

Field sampling.—Sampling was conducted in mid-July of 1988 and 1989. At this time of the year, young-of-the-year (age-0) rainbow trout have been in the water column for 2–4 weeks, water temperatures reach their maxima, and flows decline to base levels. We conducted intensive physical inventories of representative stream units and the riparian zone within different focal reaches using the protocol of Platts et al. (1983). Discharge, stream unit area, stream unit volume, stream unit depth, maximum and minimum temperatures, and bank angles were measured. Indices of bank stability, soil alteration, vegetative use, and substrate embeddedness were categorially ranked. Parametric statistics were used to analyze the continuous data, whereas Spearman's rank correlation method was used to analyze the categorical information. As previously described, a focal reach was situated to maximize the signal of upstream influences on water quality and was composed of an array of stream units. Stream units are hydrogeomorphic features (e.g., pools, riffles) that extend the full width of the stream (Gregory et al. 1991).

We used a Solar Pathfinder to measure insolation at several transects within shaded or unshaded stream reaches. A Solar Pathfinder is used by solar engineers to site active and passive solar energy collectors. It resembles a densiometer, an instrument used by foresters to measure canopy closure. It differs from that instrument in that it has a graphical capacity. The graph takes into account latitude, compass bearing, azimuth, and the distribution of energy through the average day for different months. Riparian and topographic features that cast shade, not the shade itself, are scribed onto the surface of the graph. Solar energy is estimated by determining the percent of solar input unimpeded by shading structures and by determining the number of cloud-free days each month at that locale (nearest local airport). Therefore, insolation for any month, for the season, or for the year can be determined with a single measurement irrespective of the time of day or month (see Platts et al. 1987). We expressed insolation as megajoules per square meter integrated for the months of June, July, and August. Weekly measurements of maximum and minimum water temperatures were taken at the lower margins of shaded and unshaded reaches over a 10-week period for streams in cluster N (Rock, Mountain, and Fields Creeks). We found that maximum water temperatures occurred during the last 2 weeks in July and that maximum daily water temperatures were attained during 1200–1400 hours. Therefore, maximum water temperatures of watersheds in cluster S (Alder and Service Creeks) were taken by parallel survey teams moving down each watershed at the lower margins of canopied and exposed reaches of stream during 1200–1400 hours on July 27, 1989.

Algal standing crops.—We determined standing crops of benthic plants by analysis of algal biomass (Strickland and Parsons 1968). We used the method of Lamberti et al. (1991). At each site five flat, symmetrical rocks (5–10 cm in diameter) were selected from pool, riffle, and backwater or stream margin habitat units. Algae were removed from each rock with a stiff brush, diluted to a 1.0-L slurry, and split into two equal portions. Each portion was filtered onto a separate Whatman GF/C glass microfiber filter. For determination of algal biomass as ash-free dry mass, one filter was dried at 55°C for 24 h, weighed, combusted at 500°C for 24 h, and reweighed. Surface area of algal cover for all rocks sampled per habitat unit was estimated by molding aluminum foil to the surface of each rock, weighing the foil, and converting foil weight to surface area by a known foil weight : area ratio. Estimated surface areas were halved to represent the upper portion of the rocks where most algal growth occurs.

Invertebrate standing crops.—Invertebrate abundances were measured for each site by taking five 0.1-m^2 benthic samples from riffles. Hess samplers were used in watersheds of cluster N; Surber samplers were used in watersheds of cluster S. Both samplers had 250-μm-mesh nets. All invertebrates were preserved in 95% ethanol, identified to genus, and counted. Taxa were also assigned to functional feeding groups (Merritt and Cummins 1984). Biomasses of individual taxa for each habitat unit were determined by weighing after preserved specimens were dried for 24 h in a temperature-controlled oven set at 50°C.

Rainbow trout standing crops.—Rainbow trout were inventoried by snorkeling in watersheds of cluster N (Rock, Mountain, and Fields Creeks). Fish were counted by two divers moving upstream in lanes. Age-class or size-class distinctions were made using calibrated markers on diving gloves as references. Two snorkeling passes of the same stream unit were made whenever accuracy of the census was questionable (about 60% of the units were recensused). Counts on the second pass ranged between 91 and 99% of counts on the first. Due to shallow depths that prevented snorkeling, standing crops of rainbow trout in cluster S (Alder and Service Creeks) were calculated from DeLury depletion estimates after three electroshocking passes. Intracluster comparisons for cluster N and cluster S were made on the basis of snorkeling counts and DeLury depletion estimates, respectively. An analysis of stream reaches among clusters N and S was made by calibrating DeLury depletion estimates to snorkeling counts at seven stream units in cluster N. These units were blocked with seines, snorkeled twice, and then electrofished with successive passes until no fish were captured. The number of passes ranged from 3 to

TABLE 1.—Elevations of and maximum and minimum temperatures in study reaches of cluster N (Rock, Mountain, and Fields Creeks) during July 12–17, 1988.

Site	Elevation (m)	Temperature (°C)	
		Maximum	Minimum
Mountain Creek	770	28	18
Fields Creek	910	16	8
Rock Creek 1	658	26	16
Rock Creek 2	690	30	16
Rock Creek 3	730	27	16
Rock Creek 4	761	23	14

8 for each census. Ratios between DeLury estimates and snorkeling counts were averaged, and standing crops of cluster N were adjusted to DeLury estimates by the following conversions:

Age-class	DeLury : snorkel ratio, mean (SD)	
0	1.19	0.21
1	3.45	1.18
2	0.89	0.29

Samples of each age-class from the different streams were captured for weight measurements and scale confirmations of age. Biomass estimates were made by multiplying average weight for each age-class by the age-class population estimate for the appropriate habitat.

Trophic comparisons.—We combined data sets of both clusters of watershed to examine the correlations among solar insolation, water temperature, discharge, and standing crops. Because the two clusters of watersheds were physically different, combining the data sets expanded the range of physical gradients, increasing the power of regression analyses.

Results

Riparian Influences on Fish Habitat

The effect of disturbed riparian canopy on solar input and stream temperatures in watersheds of cluster N was striking (Figure 2, Table 1). Reaches of stream with extensive riparian shading were cooler than those exposed to the sun. This was particularly evident in patterns of solar input for the upstream tributaries in the Rock Creek–Mountain Creek complex. The two drainages have approximately the same size and length, yet Mountain Creek was nearly 5°C warmer than Rock Creek (reach RC4) just above the confluence of the two streams. Below the confluence, the stream either heats or cools, depending on the extent of riparian canopy within the reach upstream. Fields Creek was substantially cooler than Rock Creek (reach RC4), although the solar pathfinder recordings were similar; however, the focal reach at Fields Creek was 140 m higher than reach RC4 of Rock Creek.

TABLE 2.—Bank angles of habitat units in study streams. Angles less that 90° indicate undercut banks, 90° indicates a vertical bank, 180° denotes a flat bank (an incline of 0°), and angles from 91° to 179° denote sloping banks with inclines of 89 to 1°, respectively (see Platts et al. 1987 for further details).

Sampling site	Mean	SD	*N*
Watershed cluster N			
Mountain Creek	168	8	22
Fields Creek	150	37	18
Rock Creek 1	162	10	10
Rock Creek 2	162	9	12
Rock Creek 3	160	15	14
Rock Creek 4	164	9	14
Watershed cluster S			
Alder Creek 550 m	149	16	6
Alder Creek 580 m	172	5	6
Service Creek 580 m	137	48	8

The contrasts between watersheds of cluster S were even more striking than those of cluster N, reflecting the great difference in density and extent of riparian canopies between Service and Alder Creeks (Figure 3). Exposed Alder Creek was 11°C warmer than shaded Service Creek at elevations of 580 m. Cold spring water lowered stream temperatures in Alder Creek at an elevation of 550 m to levels identical to those in the focal reach of Service Creek. Unshaded Alder Creek regularly becomes intermittent during summer. Within 2 weeks after sampling, Alder Creek was dry 200 m above the study reaches; by September 21, 1989, all but the lower 20 m of the reach at 550 m was dry. By contrast, Service Creek is a perennial stream. An analysis of stream bank conditions based upon the slopes of the banks indicated no significant differences among reaches of different watersheds (Table 2).

The two watershed clusters exhibited different correlations between trout density and seven out of eight variables of riparian and stream condition (Table 3). Trout abundances were negatively correlated with solar input within both watershed clusters. Over all age-classes, trout densities in watersheds of cluster N were negatively correlated with temperature and solar input and positively associated with substrates free of silt (high embeddedness index scores). Densities of trout of all age-

TABLE 3.—Correlation matrices of densities (g/m^2) of age-classes of rainbow trout versus habitat factors. Pearson's r was calculated from continuous data; Spearman's r_s was calculated from categorical data. Asterisks denote $P < 0.05$*, $P < 0.01$**, or $P < 0.001$***.

Age-class	Pearson's r^a: Maximum temperature	Solar insolation	Discharge	Depth	Spearman's r_s^b: Vegetative use	Bank stability	Soil alteration	Substrate embeddedness
Watershed cluster N (Rock, Mountain, and Fields Creeks)								
Age 0	−0.80***	−0.52**	−0.23	−0.18	0.30	0.28	0.17	0.69**
Age 1	−0.61**	−0.41*	0.01	−0.26	0.41	0.28	0.01	0.75***
Age 2	−0.34	−0.09	−0.04	−0.03	0.23	−0.21	−0.04	0.09
All ages	−0.68**	−0.45*	−0.04	−0.25	0.39	0.17	0.00	0.81***
Watershed cluster S (Alder and Service Creeks)								
Age 0	−0.59	−0.63*	0.68*	0.68*	0.80*	0.69*	0.74*	0.40
Age 1	−0.15	−0.95***	0.96***	0.49	0.74*	0.44	0.43	0.29
All ages	−0.44	−0.85**	0.87**	0.69*	0.93**	0.73*	0.74*	0.48

[a] N = 24 for watershed cluster N and 10 for cluster S.
[b] N = 19 for watershed cluster N and 10 for cluster S.

classes in watersheds of cluster S were negatively correlated with solar input, but positively associated with discharge and depth and three indices of streambank condition. Positive correlations of these indices indicate that higher densities were found where riparian and bank conditions were of higher quality. Curiously, densities of age-1 fish did not correlate well with indices of bank stability

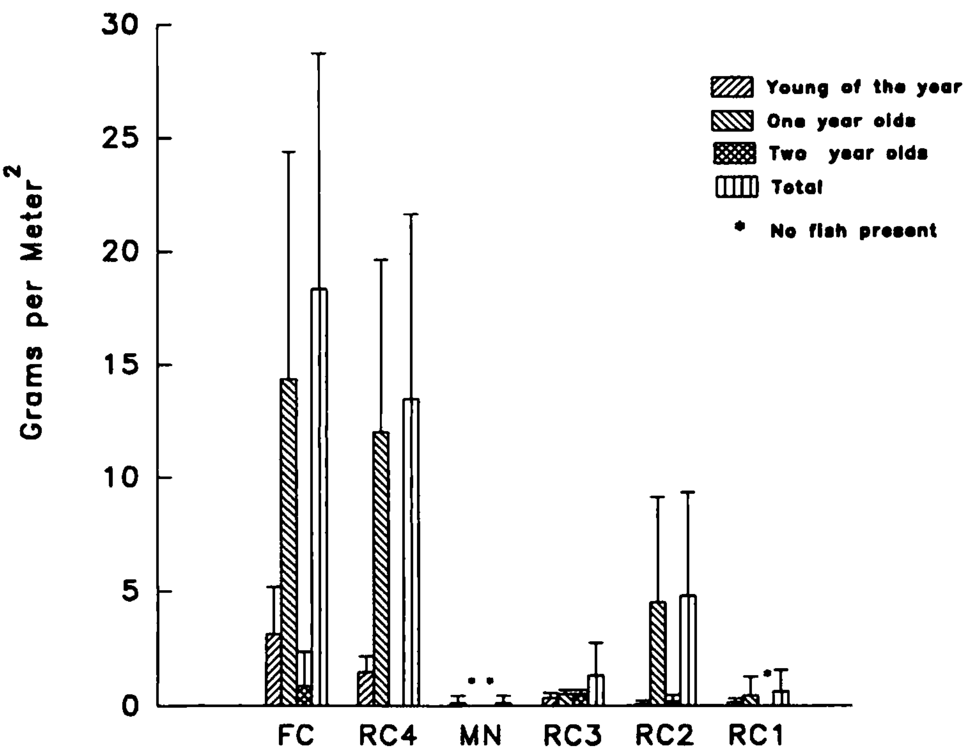

FIGURE 4.—Rainbow trout biomass (mean, 1 SD) by age in reaches of stream in cluster N (Rock, Mountain, and Fields Creeks); FC = Field Creek, MN = Mountain Creek, and RC1–RC4 = different reaches of Rock Creek. Asterisks indicate that no fish of that age-class are present.

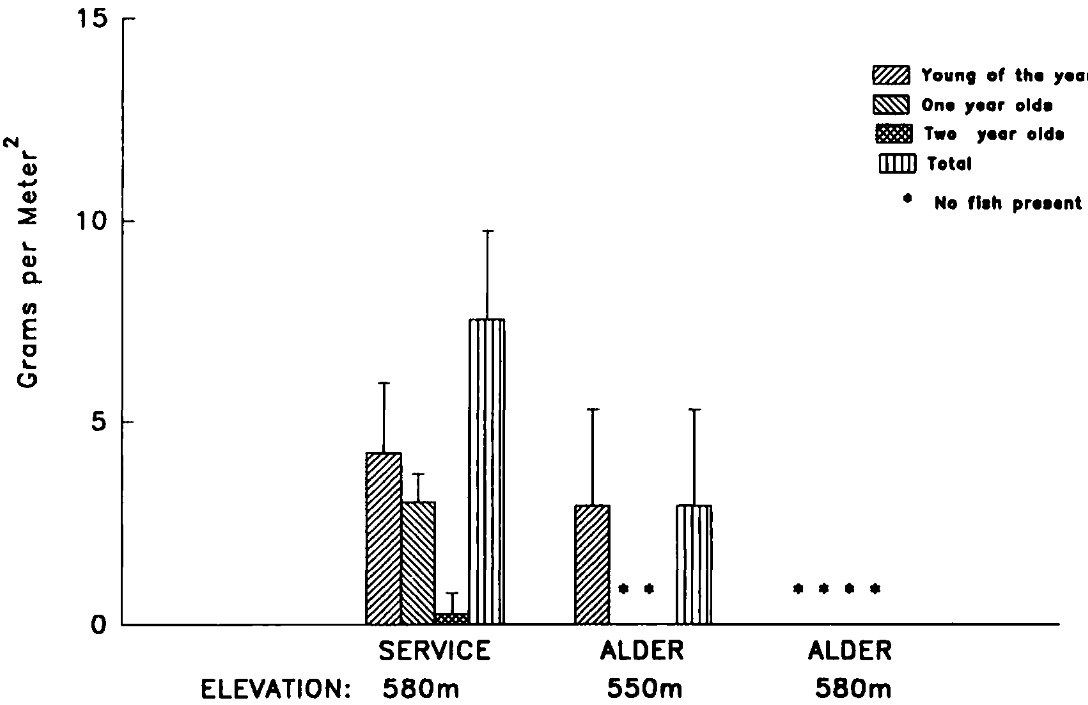

FIGURE 5.—Rainbow trout biomass (mean, 1 SD) by age in reaches of streams in cluster S (Alder and Service Creeks). Asterisks indicate that no fish of that age-class are present.

or soil alteration. Age-2 trout were scattered in too few locations in both drainages to make correlations meaningful.

Trophic Structure

Focal reaches of watersheds used more intensively for cattle production (Mountain and Alder Creeks) were greatly different biologically from focal reaches in reference watersheds within their respective clusters (Rock and Fields Creeks and Service Creek, respectively). Trout density in Mountain Creek was the second lowest recorded, whereas a few meters away above the confluence of the two creeks, reach RC4 of Rock Creek supported the highest trout density in the Rock Creek–Mountain Creek watershed complex (Figure 4). Fields Creek, the most pristine of the watersheds in cluster N, supported the highest trout biomass in its cluster. The difference between focal reaches at 580 m elevation in Alder and Service Creeks was even greater: Service Creek supported trout, whereas no fish of any species was found in Alder Creek (Figure 5). There was no significant difference in the standing crops of age-0 rainbow trout between the focal reach in Service Creek and the spring-fed reach of Alder Creek (550 m elevation). However, age-1 trout were present only in Service Creek.

Significant positive correlations were found between solar input and algal biomass, algal biomass and total invertebrate biomass, algal biomass and herbivorous invertebrate biomass, and total invertebrate biomass and herbivorous invertebrate biomass (Figure 6). Data from Alder Creek were excluded from correlation analyses because Alder was the only intermittent stream in the study. Excluding these data increases the correlation coefficients for the following relationships: total invertebrate biomass versus algal biomass from 0.59 ($P < 0.12$) to 0.77 ($P < 0.04$); herbivorous invertebrates biomass versus algal biomass from 0.66 ($P < 0.07$) to 0.79 ($P < 0.03$) (Figure 6B, C). There was no significant correlation, however, between trout biomass and either total invertebrate biomass or herbivorous invertebrate biomass (Figure 6E, F). The correlation of the ratio of trout : stream invertebrate standing crops (Table 4) versus temperature was −0.71 ($P < 0.5$); therefore, as temperature increased, the amount of trout biomass in relation to invertebrate biomass decreased (Figure 7).

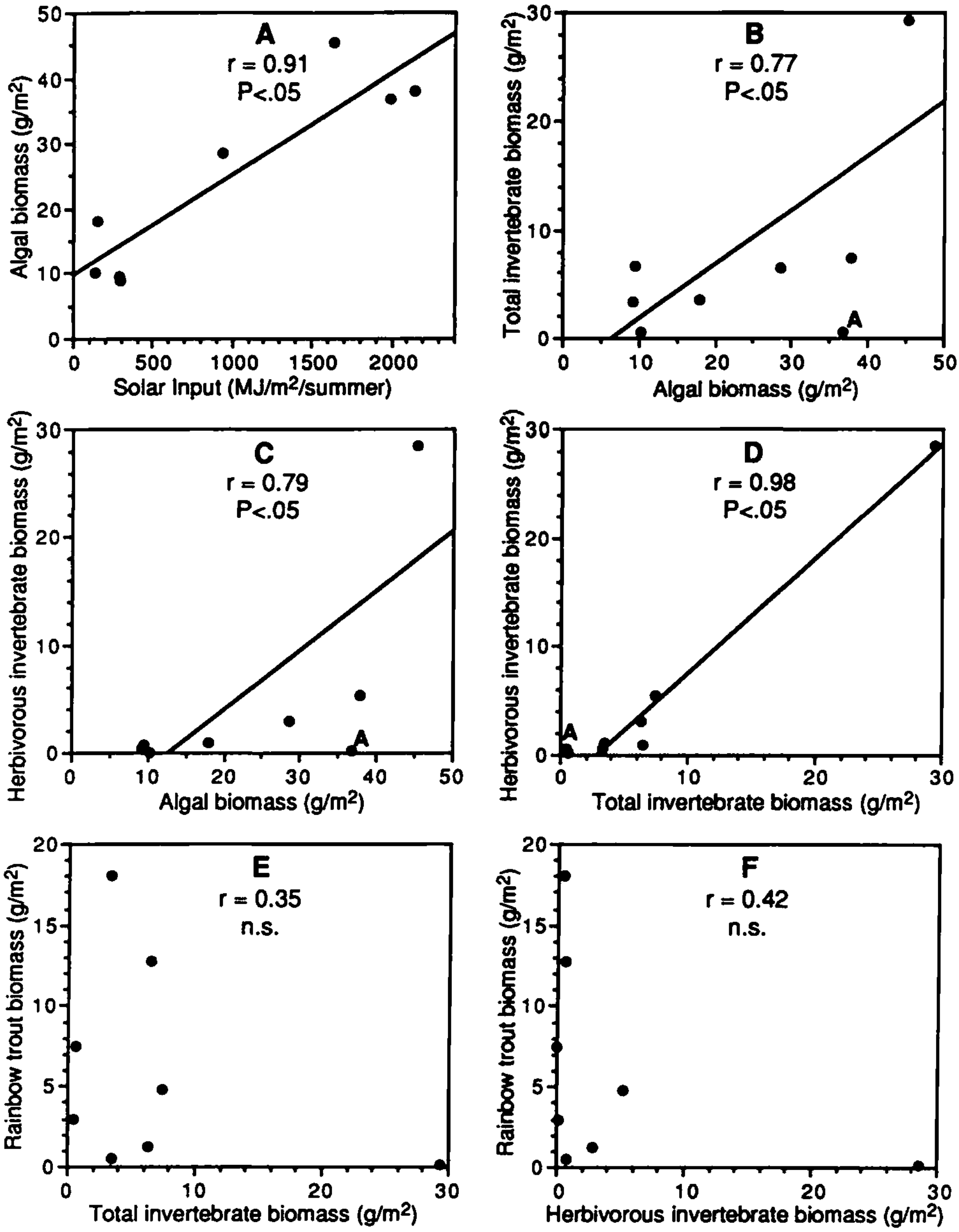

FIGURE 6.—Correlations among trophic components for all study reaches combined: (A) algal biomass versus solar insolation, (B) total invertebrate biomass versus algal biomass, (C) herbivorous invertebrate biomass versus algal biomass, (D) herbivorous invertebrate biomass versus total invertebrate biomass, (E) rainbow trout biomass versus total invertebrate biomass, (F) rainbow trout biomass versus herbivorous invertebrate biomass. The letter A in panels B, C, and D are data from the reach at an elevation of 550 m in Alder Creek.

Discussion

Our results differed from those of Murphy and Hall (1981), Murphy et al. (1981), Hawkins et al. (1983), and Bilby and Bisson (1987), who found that removal of riparian vegetation increased trout production. There are several reasons for the differences: (1) temperature and metabolic trade-offs, (2) trophic interactions, (3) impacts related to streambank–riparian conditions, and (4) cumulative effects of stream disturbance that accrue downstream.

TABLE 4.—Ratios of rainbow trout biomass to stream invertebrate biomass (both g dry weight) at study sites.

Sampling site	Biomass ratio (trout : invertebrate)
Watershed cluster N	
Fields Creek	5.44
Mountain Creek	<0.01
Rock Creek 1	0.18
Rock Creek 2	0.65
Rock Creek 3	0.21
Rock Creek 4	2.05
Watershed cluster S	
Alder Creek 550 m	5.46
Alder Creek 580 m	0.00
Service Creek 580 m	11.47

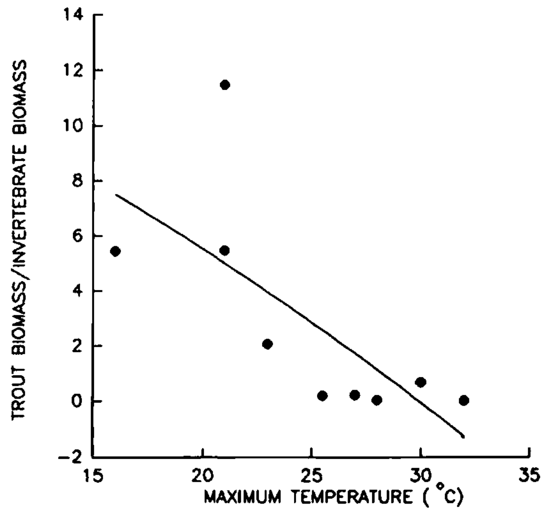

FIGURE 7.—Regression of trout biomass : invertebrate biomass ratio on maximum daily temperature for all reaches combined; $r = -0.71$, $P < 0.05$.

Removal of the riparian canopy in mesic environments on the west side of the Cascade Mountains did not result in elevated stream temperatures stressful to salmonids (Murphy and Hall 1981; Murphy et al. 1981; Hawkins et al. 1982, 1983; Bilby and Bisson 1987). In contrast, maximum daily temperatures at five of our study sites exceeded published values of upper incipient lethal temperatures for rainbow trout, about 26°C (e.g., Bidgood and Berst 1969; Jobling 1981). Maximum daily temperatures were so high at the 580-m sampling site in Alder Creek that it was devoid of fish of any species. If we presume that the thermal limits of inland populations of rainbow trout are similar to those of other rainbow trout stocks, then the mathematical relationship between temperature and maintenance ratios for steelhead derived by Wurtsbaugh and Davis (1977) may be applicable to our study. Based on their model, it would take a ration increase of 43% to support maintenance functions of trout in the warmest section of Rock Creek (23.3°C average temperature) relative to maintenance rations in Fields Creek (12°C average temperature). The actual situation might even be worse than this because Wurtsbaugh and Davis (1977) found that rainbow trout fed less as temperatures approached 22.5°C than did trout held at a temperature 3°C lower. They proposed that temperature stress inhibited the appetite of rainbow trout. We suspect that appetite suppression occurred in the warmer study sites during the hours between 1400 and 1700, when daily temperatures exceeded 23.5°C. We believe that the Wurtsbaugh and Davis model is applicable to rainbow trout of the John Day basin. We found that inland rainbow trout behaviorally thermoregulate when temperatures approach 23–25°C (Pearsons and H. Li, unpublished data). Persistence of inland rainbow trout in warm reaches of a stream may be due to behavioral thermoregulation and the availability of coldwater microhabitats. We do not have to appeal to stock adaptation to warm water, although this has yet to be tested.

Unlike studies in mesic streams, rainbow trout inhabiting streams exposed to high solar input in the high desert face unfavorable energetic tradeoffs, according to Platts and Nelson (1989). Our work supports this hypothesis. Greater insolation causes higher temperatures, which induce greater metabolic expenditures than can be offset by incrases in food supply. We inferred this from the correlation analysis through the trophic network. As one would expect, algal biomass was associated with solar input. Likewise, invertebrate biomass was positively correlated with algal biomass. However, there was no significant correlation between invertebrate abundance and trout density. This may be explained as follows: at high temperatures (1) shifts in the trophic network make the food base more limited and (2) metabolic demands may exceed food supply. Two findings from our study illustrate these two processes. (1) Less palatable trout prey dominate the food base in warmwater reaches exposed to sunlight (Tait et al. 1994). Bisson and Davis (1976) reported similar findings from their laboratory stream studies. (2) The coldest streams supported the highest standing crops of trout and had the most favorable trout : invertebrate standing crop ratios, suggesting that colder streams have a greater trophic efficiency leading to trout production. Elevated stream temperatures may increase competition for food among fishes (e.g., Baltz et al. 1982; Reeves et al. 1987). However, we cannot address this question yet because we have not finished the analyses of our competition experiments.

Elevated stream temperature is not the only impact of grazing riparian zones. Streambank erosion, stream siltation, and stream intermittency are problems in severely grazed riparian systems. In watershed cluster N, stream units with the highest trout carrying capacities are those with the lowest deposits of silt. In cluster S, stream units with the highest trout carrying capacities are associated with streambanks with the least grazing, the most stable and least erodible banks, and the lowest solar input. Along Alder Creek, cattle grazing was so severe that the stream is now intermittent, whereas its reference stream, Service Creek, has permanent flow. Cattle grazing can cause streams to become intermittent through lowering of the water table due to diminished interaction of the stream channel with the riparian vegetation, lowered water permeability of riparian soils due to compaction, and dewatering. We suspect that the lack of older age-classes of trout in Alder Creek was the result of annual patterns of desiccation. Habitat was unavailable for holding larger fish during late summer, and aquatic insect biomass in Alder Creek was substantially less than would have been predicted from solar input. We suspect that annual desiccation forces the aquatic invertebrate community to recolonize yearly. Channel structure becomes more simple when riparian vegetation is removed because inputs of large woody debris and their influence on channel structure are diminished (Gregory et al. 1991). Cumulative losses of habitat complexity can make fish populations more vulnerable to flash floods (Fausch and Bramblett 1991). This is certainly true for the Rock and Mountain Creek watersheds, which are regularly subjected to flash floods from convective storms during the summer (Pearsons et al. 1992).

Rainbow trout populations appeared to be limited by different factors in the two watershed clusters. We hypothesized that this might be true because the two clusters represented different environmental settings. Watersheds of cluster N are higher in elevation and larger in drainage size; because they have a northern aspect, they are exposed to less sunlight. Normally, the discharge of the north-draining watersheds should be greater than that of the south-draining watersheds. However, when we sampled the south-flowing streams, the discharge was double that of the north-flowing streams at the time we studied them. Therefore, habitat differences between the northern and southern clusters were less dramatic than would have been expected. Riparian and streambank conditions were more important factors in cluster S than in cluster N because of Alder Creek. Alder Creek was more badly overgrazed than any other stream in the study, and the contrast with its reference stream was more striking than contrasts between the grazed watersheds and their reference sites in cluster N.

The ecological response to a watershed disturbance depends upon the position of the study site relative to the extent and distribution of the perturbation. Our study sites were positioned to detect the cumulative effects of disturbed riparian zones over stream reaches extending several kilometers. The reaches perturbed by clear-cut logging over riparian zones in the studies of Aho (1977), Murphy and Hall (1981), Murphy et al. (1981), and Bilby and Bisson (1987) were measured in hundreds of meters. Perturbed sites were situated below undisturbed reaches and in at least one case (Hawkins et al. 1983), perturbed and control study sites were selected to minimize temperature differences among sites. In essence, these clear-cut sites received the benefits of cold, high-quality water from the old-growth reaches upstream, and the increased primary productivity from greater solar input in clear-cut areas increased the prey base for trout. Water flowing into our study sites was degraded by elevated temperatures, was physiologically stressful to trout, and changed prey composition to a less favorable mix. We believe that temperature was more detrimental than increased silt for invertebrates in our unshaded stream reaches. Siltation in the low-gradient reaches studied by Murphy et al. (1981) and Hawkins et al. (1983) did not appear to affect invertebrate standing crops. Bisson and Davis (1976) observed that invertebrate biomasses were lower in heated laboratory streams than the controls and cited Iverson (1972), who suggested that invertebrates were physiologically taxed by elevated laboratory stream temperatures. However, as in our study, Bisson and Davis (1976) found increased sedimentation rates in heated streams.

The rangelands of eastern Oregon and Washington are badly overgrazed. About half the federal rangelands are rated in poor condition (GAO 1988). It is obvious that improper livestock and grazing practices can limit trout production in streams throughout the intermountain West (Platts and Rinne 1985; Platts and Nelson 1989). Gross impacts of overgrazing by livestock in riparian ecosystems have been well documented, and land management agencies understand, based on their own reports, that impacts on fishes are negative (Kauffman and Krueger 1984). Why have changes in livestock management not been enforced if the end result of overgrazing is obvious even to the casual observer? Simply put, the problem is a political and economic rather than an ecological one. Why then is this study important? We need to think of a suite of restoration strategies. However, there has been relatively little understanding of how riparian and stream systems interact and react to disturbances at the watershed level (Elmore and Beschta 1987; Elmore 1988; Wissmar and Swanson 1990). In the long term, documenting how the disturbance functions at a community and ecosystem level is important. If we understand why a system is "broken," we should understand how healthy systems function. In the short term, ecological analysis of overgrazed systems clarifies the debate between range and fisheries managers.

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