AN ABSTRACT OF THE DISSERTATION OF

Cynthia K. Tait for the degree of Doctor of Philosophy in Fisheries Science presented on 12 September 1997. Title: Influences of Riparian Canopy on Aquatic Communities in High Desert Streams of Eastern Oregon.

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Because riparian canopy controls most energy inputs to stream ecosystems, it directly affects the structure of aquatic food webs and the ecological processes that govern interactions among trophic levels. This study addresses the interdependence among riparian canopy, benthic community structure, and the carrying capacity of high desert streams for salmonid fishes. In streams in the lower John Day River Basin in eastern Oregon, algal, invertebrate, and fish communities were compared in reaches with varying densities of riparian canopy. Water temperatures varied with the density and upstream extent of canopy. Densely canopied sites were cool, while sites with high irradiances had temperatures exceeding the upper lethal limit for salmonids. Periphyton and grazer biomasses were greater in well-lighted sites, but 90% of grazer biomass consisted of Dicosmoecus gilvipes, a large caddisfly inedible by juvenile trout. Warmer water increased metabolic demands for salmonids, while the overwhelming dominance of Dicosmoecus in open sites shifted energy flow away from trout and shrunk their food base. High water temperatures, however, provided suitable habitat for many warmwater fishes which would otherwise not enter tributaries of this size. At higher elevation study sites in Camp

Creek, light levels were higher and less variable than at the lower sites. Periphyton and invertebrate abundances were not correlated with irradiance. Rather, periphyton was maintained at low levels by grazers, particularly Dicosmoecus and snails. Manipulations of fish densities in enclosures showed that trout and dace had no negative impacts on numbers of invertebrate prey, and that grazers played a larger role in regulating lower trophic levels than did fish. Dicosmoecus acted as a keystone species in the benthic food web of Camp Creek by simultaneously influencing the trophic level both below and above its own. When irradiance was experimentally reduced under artificial canopies, periphyton standing crops were not different from those in open control pools after 4 wks. However, grazers were more abundant in open pools. The cropping of periphyton to uniform levels in both sunlight and shade indicated that mobile grazers targeted sites of varying productivities. Comparisons between benthic communities in Camp Creek and in a densely canopied reference stream suggested that benthic community structure shifted to accommodate changes in energy resources that occur when canopy density is altered.

Influences of Riparian Canopy on Aquatic Communities in High Desert
Streams of Eastern Oregon

by

Cynthia K. Tait

A DISSERTATION

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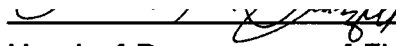presented on September 12, 1997

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CONTRIBUTION OF AUTHORS

Drs. Hiram Li, Gary Lamberti, and Judy Li were involved in experimental design and data collection. Dr. Todd Pearsons assisted with experimental design and data collection, and shared unpublished data.

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DEDICATION

This work is dedicated to Effie Eleanor Tait and George Fulton Tait,
and to Jesse.

INFLUENCES OF RIPARIAN CANOPY ON AQUATIC COMMUNITIES IN HIGH DESERT STREAMS OF EASTERN OREGON

INTRODUCTION

Riparian vegetation is critical to the health and function of streams. Because riparian canopy controls most energy and nutrient inputs to stream communities (Gregory et al. 1991), it directly affects the structure of aquatic food webs and the ecological processes that govern interactions among multiple trophic levels. The relative importance of top-down (consumers) or bottom-up (resources) forces on stream community dynamics has been debated by ecologists for decades. Recently, Hunter and Price (1992) argued that ecosystems are patterned upon the influences of resource heterogeneity that permeate throughout the food web. Plants, by their productivity, control the number of trophic levels possible and ultimately constrain the top-down forces that, in turn, regulate their standing crops (Fretwell 1987; Power 1992b). Depending on its density, riparian canopy admits varying amounts of photosynthetically active radiation (Hill 1996) and nutritive organic matter, and thereby shifts benthic communities between autotrophic and heterotrophic resource bases over space and time (Vannote et al. 1980). This variation in plant productivity imposed by canopy provides the "bottom-up template" for stream trophic dynamics.

By reducing insolation, riparian canopy also modulates water temperature regimes and lowers maximum stream temperatures, especially in aridland systems (Platts and Nelson 1989; Beschta 1997). High water temperatures benefit some algal, invertebrate, and fish species (Lamberti and Resh 1983; Moyle and Cech 1988; DeNicola 1996) but are deleterious

to native salmonids (e.g., Bisson and Davis 1976; Barton et al. 1985; Reeves et al. 1987; Platts and Nelson 1989; Li et al. 1994). With changes in riparian canopy, fish assemblages experience not only alterations to their food base but also changes in their physical environment that constrain their ability to process available energy resources.

In the following studies, I examined the effects of different densities of riparian canopy on trophic processes in small, aridland streams of the John Day River Basin of Oregon. In Chapter 1, seven study reaches were selected from lower basin streams that included riparian areas ranging from denuded by grazing to intact conifer forest. Water temperatures, and the structure of algal, macroinvertebrate, and fish communities, were compared among reaches. In Chapter 2, the study stream, Camp Creek, was located at a higher elevation than the first study area, and all Camp Creek sites were sparsely canopied and well-lighted. Fish enclosures, manipulations of herbivores, and abundances of organisms at each trophic level were used to determine the relative strengths of top-down or bottom-up forces in a stream with high solar inputs. The study described in Chapter 3, also on Camp Creek, examined the effects of artificial shade on the benthic communities observed in Chapter 2. Tents over the streambed were installed for 4 weeks, and changes in community structure caused by shading were measured. In addition, unshaded Camp Creek benthic communities were contrasted with benthic communities in a densely canopied reference stream in order to predict potential food web changes that may occur on Camp Creek if riparian canopy is restored.

Chapter 1

Relationships Between Riparian Cover And The Community Structure Of High Desert Streams

Cynthia K. Tait, Judith L. Li, Gary A. Lamberti,
Todd N. Pearsons, and Hiram W. Li

Abstract

Many studies in cool, forested streams have shown that removal of riparian canopy leads to higher incident radiation, blooms in algal and macroinvertebrate populations, and concomitant increases in salmonid abundance. In warm, high-elevation desert streams, however, an open canopy may not increase salmonid density. Our seven study reaches on 3rd order tributaries of the John Day River in eastern Oregon included riparian areas ranging from denuded, heavily grazed streambanks to intact conifer forest. Average summer solar inputs to these sites varied from 165 to 2230 megajoules/m^2 and stream temperatures were influenced by the density and extent of canopy. Densities of steelhead trout (Oncorhynchus mykiss) and sculpin (Cottus spp.) decreased significantly with increased incident radiation and higher stream temperatures, although many warmwater cyprinids increased in abundance in unshaded sites. Periphyton standing crops (g ash-free dry mass/m^2) closely tracked solar inputs and were, in turn, strongly positively correlated with biomasses of total invertebrates and of grazers. Collector, shredder, and predator biomasses, and numerical abundances of all invertebrate groups, did not change with canopy density. The abundances of chironomids and baetids were unrelated to increases in light or algal resources, in contrast to studies in Cascades and Coast Range streams where irruptions of these taxa occurred in canopy openings. In our streams the large-bodied caddisfly Dicosmoecus accounted for the increase in total invertebrate biomass observed in exposed sites. These insects composed 55-96% of the total biomass in open reaches but only 0-1.4% in the three most shaded sites. Increases in total invertebrate biomass with light levels or periphyton were not observed when Dicosmoecus were

removed from the analysis. <u>Dicosmoecus</u> are consumed infrequently by juvenile trout or other small fish species common in John Day tributaries; consequently, extensive canopy openings appear to produce few advantages to upper trophic levels in these streams.

Introduction

Riparian vegetation plays a crucial role in the productivity and trophic relationships of stream ecosystems (Cummins et al. 1989). Overhanging vegetation (i.e., canopy) filters and absorbs incident radiation, affecting periphyton primary productivity by altering solar inputs and water temperatures (Lyford and Gregory 1975; Towns 1981; Bott 1983). Riparian vegetation also supplies nutritional resources through terrestrial litterfall. Fallen woody debris enhances the retention of organic matter and inorganic sediment by forming debris dams (Speaker et al. 1984; Bisson et al. 1987). These retained materials become sources of habitat and nutrients for the aquatic biota (Benke et al. 1985; Gregory et al. 1991; Prochazka et al. 1991). Variation in the density and extent of the riparian canopy may affect benthic invertebrate production, as well as the abundance and distribution of stream fishes, by modifying nutrient and energy inputs and stream retention (Tschaplinski and Hartman 1983; Gregory et al. 1991; Bilby and Bisson 1992).

For periphyton communities in streams in the Cascade Range (Oregon), Lyford and Gregory (1975) found that increased shade significantly reduced algal standing crops and also lowered their photosynthetic efficiency. Simultaneous studies at these sites indicated that total insect emergence was four times higher in unshaded than in shaded reaches, whereas emergence of shredders was greater under canopy where allochthonous inputs were higher (Grafius 1976). Trout (Oncorhynchus clarki) biomass was greater in unshaded stream sections (Aho 1976).

Many additional studies in the Cascade and Coast Ranges of the Pacific Northwest have documented a stimulation of periphyton growth by

canopy removal and a concomitant increase in macroinvertebrate and salmonid abundance (Newbold et al. 1980; Murphy et al. 1981; Murphy and Hall 1981; Hawkins et al. 1982, 1983). Stream temperatures, however, have not been a significant factor in these studies, i.e., thermal regimes remained within the tolerance ranges of salmonids. Research efforts have focused largely on cool, high-elevation or maritime sites where canopy cover had little effect on water temperatures. In contrast, stream warming is important in reaches lacking canopy in streams flowing through arid or intermountain regions of the western United States (Platts and Nelson 1989).

In warmer climates, riparian vegetation can profoundly influence aquatic communities by altering stream temperature. The presence of canopy can lower water temperatures during summer and reduce heat loss and ice scour in winter (Platts and Nelson 1989). Barton et al. (1985) reported that temperature in southern Ontario streams was inversely related to the fraction of upstream banks covered by forest. The warmer, less forested streams, where mean weekly temperature maxima exceeded 22° C, had few or no trout. Platts and Nelson (1989) proposed that the increase in summer water temperatures in open stream reaches of the Great Basin was more likely to limit salmonid populations than the decline in macroinvertebrate prey associated with closed canopy. Li et al. (1994) found a decline in eastern Oregon trout at high temperatures and linked local thermal conditions to the extent of upstream riparian vegetation.

Although cold stenothermal fishes such as salmonids can be deleteriously affected by the loss of canopy cover in arid systems, less is known about the responses of lower trophic levels to changes in canopy and temperature in these streams. In this paper we describe the

relationships between riparian cover and the community structure of streams in the arid John Day River Basin, Oregon. We examined relationships among periphyton standing crops, macroinvertebrate community structure, fish assemblages and canopy density.

Study Area

The research was conducted on streams in the John Day Basin, Oregon (Fig. 1.1). This semi-arid region encompasses about 120,720 km^2 in northeastern Oregon and is situated primarily on Columbia River basalt overlain with recent alluvium. The study area lies at about 600 m elevation and receives an average of 50 cm of precipitation annually, mostly falling from November to May. Summer low flows occur in August and September, and are usually exacerbated by diversion for agricultural irrigation. Intense livestock grazing has occurred throughout the basin. Typical streamside vegetation, where present, includes grasses (Phalaris spp.), sedges (Carex spp.), willows (Salix spp.), white alder (Alnus rhombifolia), and black cottonwood (Populus trichocarpa). Sagebrush (Artemisia tridentata) and western juniper (Juniperus occidentalis) dominate the uplands, and ponderosa pine (Pinus ponderosa) and Douglas-fir (Pseudotsuga menziesii) occur at higher elevations.

Four similar 3rd-order streams were chosen for study: Rock Creek, Mountain Creek, Fields Creek, and Murderers Creek. These streams were similar physically but differed in density and extent of riparian cover (Table 1.1). Four reaches on Rock Creek (RC1, RC2, RC3, and RC4) and one reach on each of the other three creeks (MTC, FDC, and MUR
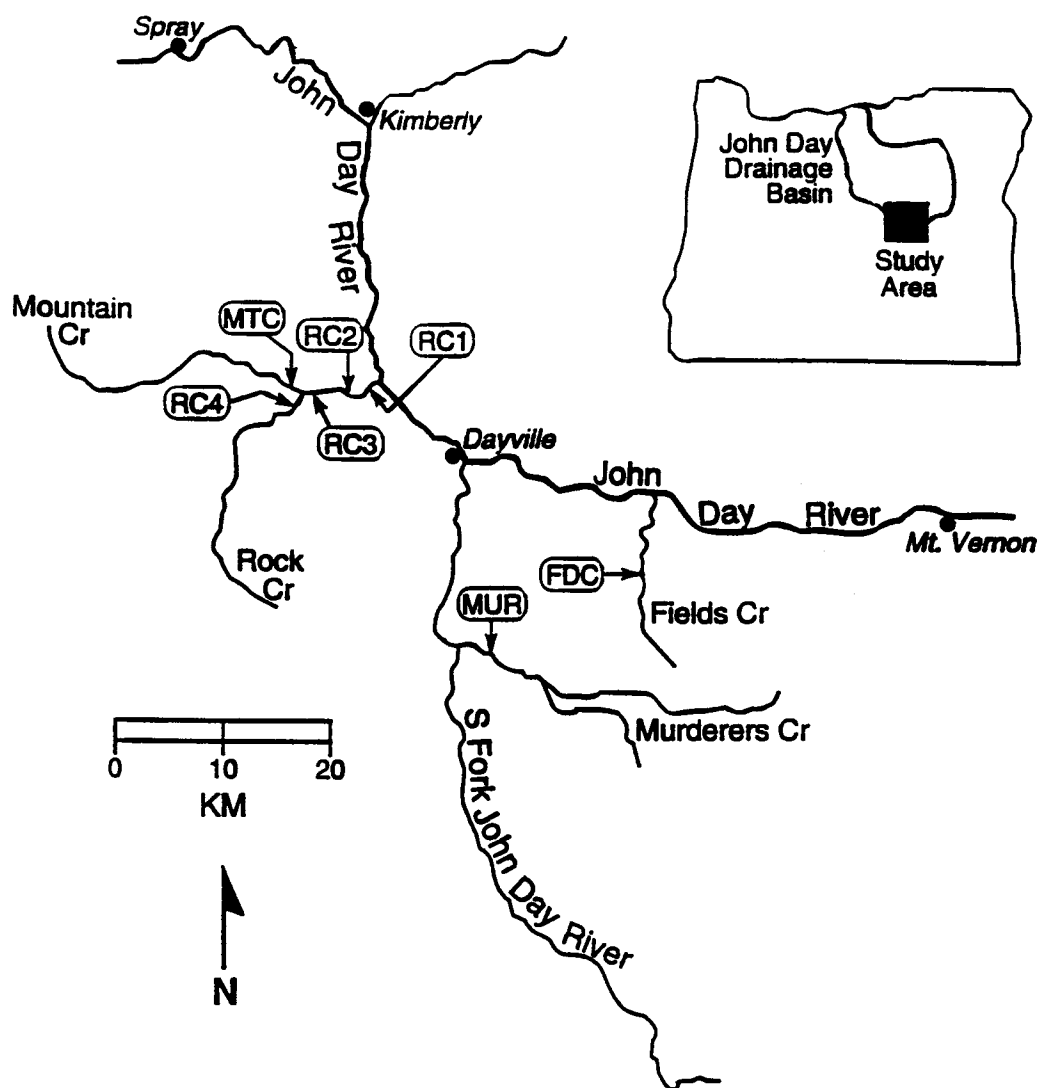
Fig. 1.1 Location of study sites within the John Day Basin, OR.

Table 1.1 Physical characteristics of the seven study reaches. Solar radiation is the cumulative summer average (June, July, and August); discharge, mean daily temperatures, and maximum temperatures are for July 1988.

Sites	RC1	RC2	RC3	RC4	MTC	MUR	FDC
Elevation (m)	658	690	730	761	770	927	910
Discharge (m³/s)	0.28	0.28	0.21	0.21	0.03	0.33	0.03
Reach length (m)	70	182	246	116	220	128	42
Mean reach width (m)	6	7.5	6.5	6	4.5	7	3
Canopy	closed	open	partial	closed	open	open	closed
Solar radiation (Mj/m²)	165	2230	985	308	1709	1994	300
Temperature (°C)							
Mean daily	20.6	23.3	21.5	18.5	23.0	20.5	12.0
Maximum	25.5	30.5	27.2	23.2	28.0	25.0	16.0

respectively) were delineated as research sites (Fig. 1.1). These sites were situated at the lower margin of shaded or unshaded patches of stream and thus were influenced by the full expression of cumulative effects of riparian cover upstream. The upper portion of Rock Creek, including RC4 and extending for 26.8 km upstream, was completely shaded with overhanging alder, pine, and cottonwood canopy and flowed mainly through a high-walled canyon marginally accessible to livestock. Lower reaches of Rock Creek either flowed through open agricultural land or were less extensively canopied. RC3 was located at the lower end of a 1.3 km reach intermittently shaded by alders and with a narrow riparian area subject to grazing by cattle. RC2 was situated below a heavily grazed 3.4 km section of Rock Creek that flowed through open pasture and lacked riparian vegetation. The lowest Rock Creek reach, RC1, occupied the downstream end of a 2.25 km basalt canyon that was heavily shaded by alder. No grazing occurred here. The MTC reach, located immediately upstream from the confluence of Mountain Creek with Rock Creek, had no canopy due to livestock grazing and was denuded of streambank vegetation for 27.5 km upstream. In contrast, Fields Creek (FDC) was densely shaded with Douglas-fir from the study reach to its source, 12 km upstream. Murderers Creek (MUR) was unshaded over most of its length, but owing to good livestock management had intact bank vegetation of grasses, sedges, and shrubs, a condition that extended 5 km upstream. All reaches but Fields Creek were subject to decreases in summer discharge due to irrigation.

Methods

On 12-18 July 1988, standard physical inventories of stream characteristics (Platts et al. 1983), including discharge, area, and volume of stream units, were conducted in each study reach. In addition, mean accumulated solar input (Megajoules/ m^2) for June, July, and August was measured for each site with a Solar Pathfinder™ (Platts et al. 1987). This device measures the proportion of solar radiation reaching the stream surface by recording the vegetation or topographic features that cast shade, thus quantifying relative density of riparian cover. Because it integrates the effects of azimuth, topographic altitude, height of vegetation, aspect, latitude, hour angle, and time of year, the Solar Pathfinder™ gives a realistic estimate of solar energy inputs to the water surface of a given stream. Readings were taken by placing the instrument in the center of the stream on a tripod and tracing the outline of shading objects impinging on a transparent dome. Measurements were made at a number of sites per reach and averaged. Turbidity, which would influence the amount of light reaching the substrate, was not a factor; it varied little between reaches and streams were shallow. Weekly maximum-minimum temperatures were recorded with maximum-minimum thermometers placed in each study site (Table 1.1).

Biological variables measured at all study sites included periphyton biomass, macroinvertebrate species composition, numbers, and biomass, and fish numbers. To assess periphyton standing crops, five flat, symmetrical rocks were removed from riffle habitats in mid-July. Periphyton was removed from each rock with a stiff brush and diluted to a 1-L slurry. Subsamples of the slurry were filtered onto glass fiber filters (Whatman

GF/C; .45 μm pore size) and frozen in the field. To determine total periphyton biomass as ash-free dry mass (AFDM), the filters were dried at 55° C for 24 h, weighed, then combusted at 500° C for 16 h and reweighed. AFDM was the difference between the two weights. Surface area for the sampled rocks was estimated by molding aluminium foil around each rock, weighing the foil, and converting foil weight to surface area using a known foil weight/area ratio. Estimated surface areas were halved to represent the upper portion of the rocks where most periphyton growth occurs. Because AFDM is a combination of nonphotosynthetic components of the periphyton (bacteria, fungi, detritus) as well as living algae, it is the actual diet of most grazers and is a good measure of resources available to consumers (Lamberti and Moore 1984).

Abundances of invertebrates were measured in mid-July by taking five 0.1 m² Hess samples (250 μm mesh) from riffle habitats randomly selected in each study reach. Sampling sites were all approximately 0.3 m deep with rubble substrates. Invertebrates were preserved in 95% ethanol, identified to genus (except Chironomidae), and enumerated. Taxa were later assigned to functional feeding groups (Merritt and Cummins 1984). Scrapers and other invertebrates that commonly feed on living algal cells were together designated grazers. These included the mayflies Baetis and Ameletus which are known to forage on the algal components of periphyton (Dudley et al. 1986; Hill and Knight 1987; Richards and Minshall 1988). Collector-gatherers and filterers were combined and designated collectors. Shredders and predators were also recognized. Site-specific biomasses of individual taxa were determined by drying and weighing the preserved specimens in each sample. No corrections were made for weight loss in

preservative, but all specimens were preserved for the same length of time before processing.

Fishes at each site were inventoried in mid-July by snorkelling (Pearsons et al. 1992; Li et al. 1994); divers counted fishes by species and made age/size class distinctions for some species. Three to 15 habitat units (e.g. riffles, pools) representative of the stream reach were snorkelled at each study site, and all counts were conducted between 1000 and 1600 h. Two divers entered the sampling site from the lower end and moved in parallel lanes upstream, recording fish counts on plexiglass slates. Although snorkelling may not be as accurate as electrofishing for estimating fish densities in small streams (Rodgers et al. 1992), it is nevertheless an effective census technique for relative fish counts in streams with high water clarity and moderate velocity (Griffith 1981). Precision of the snorkelling technique was determined by repeated counts in some reaches. Numbers of fish estimated in the second pass ranged between 91-99% of the original counts. Fish densities were calculated as numbers/m^2 of stream reach. Biomass estimates were not possible due to lack of length/weight data for some species.

Data were analyzed with Pearson's product-moment correlations with t-tests for significance. Possible confounding effects of autocorrelated variables were examined with partial correlation analysis. $Log_{10}(x + 1)$ transformations were used to control non-normality and heteroscedastisity in the data.

Results

Physical characteristics

The upstream extent and density of riparian canopy had a profound influence on water temperatures in the study reaches (Table 1.1). Sites with considerable upstream vegetative cover, such as RC4 and Fields Creek, maintained cooler summer temperatures than unshaded reaches (MTC, RC2) or canopied sites with limited extent of upstream riparian vegetation (RC1). Elevation also influenced temperature: Murderers Creek, at 927 m, had cooler mean July temperatures than lower elevation sites with more canopy (RC1, RC3, MTC). Because water temperatures were influenced by the longitudinal extent of upstream cover and elevation as well as overhead canopy density, temperature and site-specific solar input were positively but not significantly correlated (r = 0.64; $\underline{p}$ = 0.13).

Relationship between canopy and periphyton abundance

Canopy density and the consequent amount of solar input reaching the streambed strongly influenced periphyton abundance. Thick growths of a filamentous green alga, <u>Cladophora</u>, encrusted with epiphytic diatoms (principally <u>Cocconeis</u>, <u>Gomphonema</u>, and <u>Epithemia</u>) occurred in open areas, whereas low amounts of epilithic diatoms and cyanobacteria dominated shaded sites. Periphyton biomass increased with site-specific incident light (r = 0.89; $\underline{p}$ = .007). Mean biomass ranged from 9.2 g AFDM/m^2 at FDC (solar input = 300 Mj/m^2) to 57.9 g AFDM/m^2 at MUR (solar input = 1994 Mj/m^2). Although periphyton biomass closely tracked solar input, other factors probably also influenced biomass. For example,

periphyton standing crop at the site with the highest level of insolation, RC2 (solar input = 2230 Mj/m^2), was 35% lower than at the more shaded MUR.

Relationship between canopy and macroinvertebrate community structure

Macroinvertebrate assemblages at all sites were dominated by three insect families. On average, more than half of the invertebrates at the seven study sites were chironomid midge larvae (26%) and larval and adult elmid beetles (27%). Baetid mayflies accounted for about 10% of the community. No distinct patterns in absolute abundance of these groups occurred over the gradient in solar input or periphyton standing crop. Other taxa usually made up <10% of all invertebrates at any site with the exceptions of the caddisflies Hydropsyche (29% at shaded RC1) and Dicosmoecus (19% at open MTC).

Macroinvertebrate densities for total invertebrates (Table 1.2) were not related statistically to light level or quantity of periphyton (Table 1.3). Neither density nor biomass of total invertebrates was related to light levels, although invertebrate biomass was positively correlated with quantity of periphyton (Fig 1.2a). In contrast, grazer biomass increased significantly with both solar input and periphyton AFDM (Table 1.3; Fig. 1.2b). However, when the effect of AFDM was removed through partial correlation, the relationship between grazer biomass and solar input was insignificant (r = 0.15).

Shredder numbers decreased significantly with solar input and AFDM (Table 1.3). However, collector and predator densities and biomasses were not correlated with solar input, AFDM, or abundances of other functional groups.

Table 1.2. Mean (±1 SE) abundance and biomass (as dry weight) of invertebrates from John Day Basin tributaries.

	RC1	RC2	RC3	RC4	MTC	MUR	FDC
Total Invertebrates							
Number/m²	16744 ±4261	14357 ±3702	14715 ±4361	10335 ±1673	4021 ±1406	11338 ±3508	9619 ±3187
Biomass (g/m²)	3.796 ±1.24	7.489 ±2.61	6.377 ±1.46	6.561 ±1.99	29.29 ±5.67	17.68 ±4.78	3.364 ±1.12
Grazers							
Number/m²	4742 ±752	6146 ±1245	2884 ±750	2607 ±452	1683 ±460	4090 ±746	3108 ±991
Biomass (g/m²)	0.830 ±0.09	5.380 ±2.29	2.902 ±1.37	0.690 ±0.12	28.749 ±5.51	13.200 ±4.75	0.451 ±0.19
Collectors							
Number/m²	10892 ±3334	6975 ±2100	9686 ±2869	6500 ±1067	2019 ±858	5453 ±2064	5154 ±1754
Biomass (g/m²)	2.422 ±0.88	1.972 ±0.38	2.878 ±1.10	0.793 ±0.08	0.330 ±0.12	2.220 ±1.23	2.439 ±0.91

Table 1.2 (Continued)

	RC1	RC2	RC3	RC4	MTC	MUR	FDC
Shredders							
Number/m²	53	4	20	94	8	12	240
	±48	±4	±16	±31	±8	±8	±235
Biomass	0.265	0.001	0.120	4.671	0.003	0.421	0.022
(g/m²)	±0.24	±0.001	±0.15	±2.03	±0.003	±0.28	0.020
Predators							
Number/m²	573	1022	1941	918	228	1233	1051
	±153	±428	±815	±243	±86	±446	±427
Biomass	0.258	0.136	0.313	0.300	0.171	1.845	0.448
(g/m²)	±0.11	±0.04	±0.10	±0.15	±0.12	±1.02	±0.14

Table 1.3. Correlation matrix of invertebrate densities (LOG number/m²) and invertebrate biomasses (LOG g DW/m²) vs solar radiation and periphyton biomass (AFDM); values are Pearson correlation coefficients; ** = $p < 0.01$, * = $p < 0.05$.

	Invertebrate Density		Invertebrate Biomass	
	Solar radiation	AFDM	Solar radiation	AFDM
All invertebrates	-0.22	-0.26	0.73	0.83*
Grazers	0.18	0.05	0.87**	0.94**
Collectors	-0.39	-0.40	-0.16	-0.16
Shredders	-0.91**	-0.83*	-0.56	-0.33
Predators	-0.06	-0.14	0.03	0.31
Dicosmoecus	0.90**	0.91**	0.85*	0.92**
All invertebrates without Dicosmoecus	-0.24	-0.29	-0.31	-0.30
Grazers without Dicosmoecus	0.02	-0.11	0.71	0.60

a

b
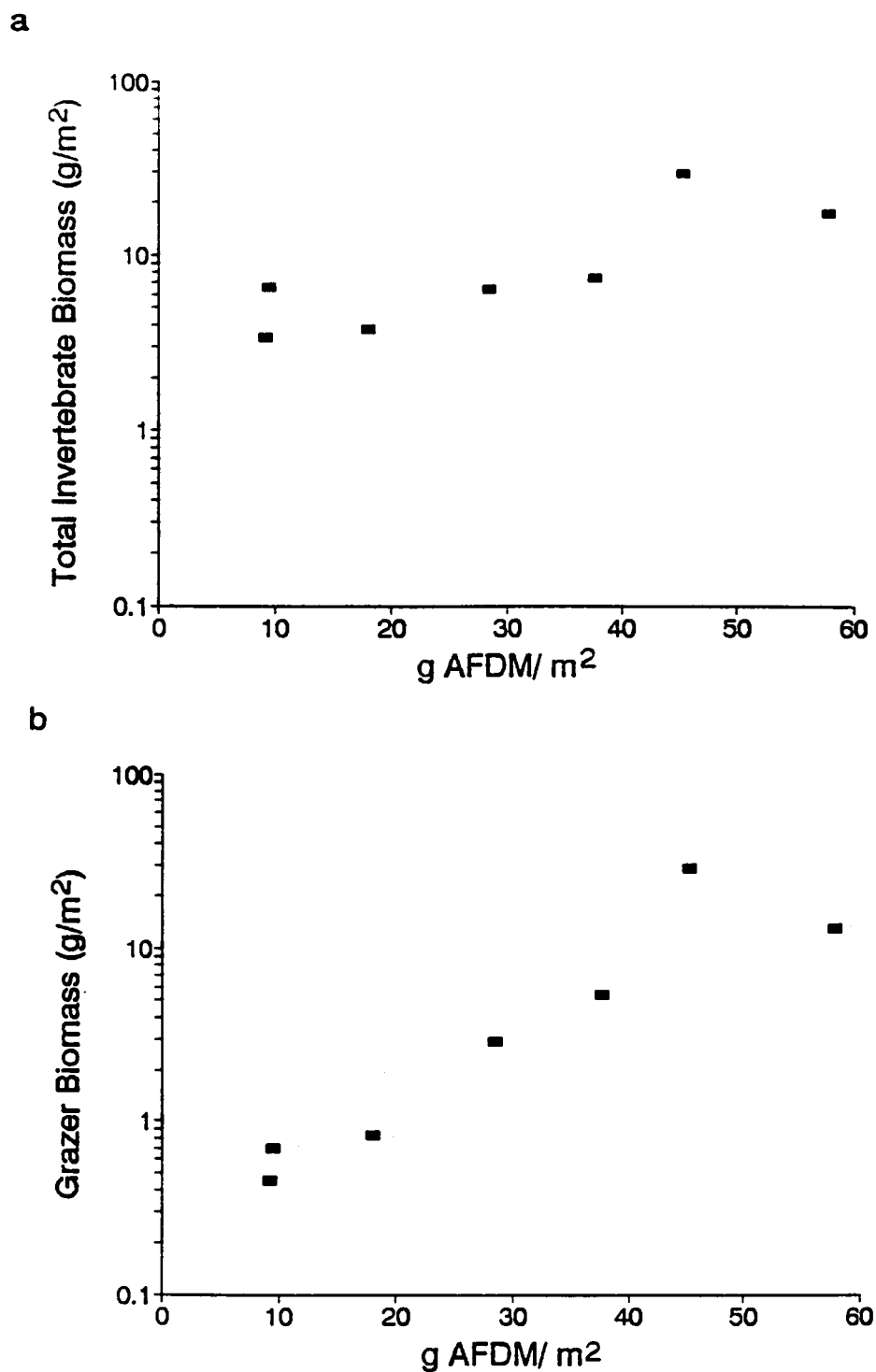
Fig. 1.2. Correlations of log-transformed invertebrate biomasses with periphyton biomass for all study reaches: (a) total invertebrate biomass vs periphyton biomass; (b) grazer biomass vs periphyton biomass.

Differences in relative abundances and biomasses of invertebrate functional feeding groups were detectable with changing riparian cover (Table 1.4). Although grazer density did not vary significantly with solar input, the relative abundance of grazers increased from about 25% at shaded sites to 45% at open sites. In shadier reaches, collectors and shredders made up a greater proportion of the fauna. The relative abundance of predators (about 10%) was unaffected by the amount of canopy.

The relative biomasses of these feeding groups followed similar patterns. Grazer relative biomass increased markedly with insolation, primarily because of higher numbers of large-bodied Dicosmoecus caddisfly larvae (Fig. 1.3; Table 1.4). Collectors and shredders were negatively but not significantly correlated with solar input and predator relative biomass did not vary with light regimes.

The presence of the large-bodied algivore Dicosmoecus gilvipes at open sites accounted for much of the increase in total invertebrate biomass observed at unshaded sites. The biomass of Dicosmoecus increased with both periphyton biomass and solar input (Table 1.3), though partial correlation of Dicosmoecus biomass with AFDM and solar input indicates only a weak association (r = 0.17) with solar input. Dicosmoecus composed 55-96% of the total invertebrate biomass in open reaches but only 0-1.35% in the three most shaded sites (Fig. 1.3). When Dicosmoecus was excluded from the analyses, weak correlations occurred between the remaining invertebrates and solar input or AFDM (Table 1.3). No relationship was evident between the biomass of other grazers and Dicosmoecus biomass (r = 0.45; p = 0.31).

Table 1.4. Correlation matrix of relative abundances (individuals/m^2) and biomasses (g DW/m^2) of invertebrate guilds vs solar radiation; values are Pearson correlation coefficients; ** = $p < 0.01$, * = $p < 0.05$.

	Relative abundance	Relative biomass
Grazers	0.71	0.90**
Collectors	-0.78*	-0.62
Shredders	-0.83*	-0.70
Predators	0.14	-0.49
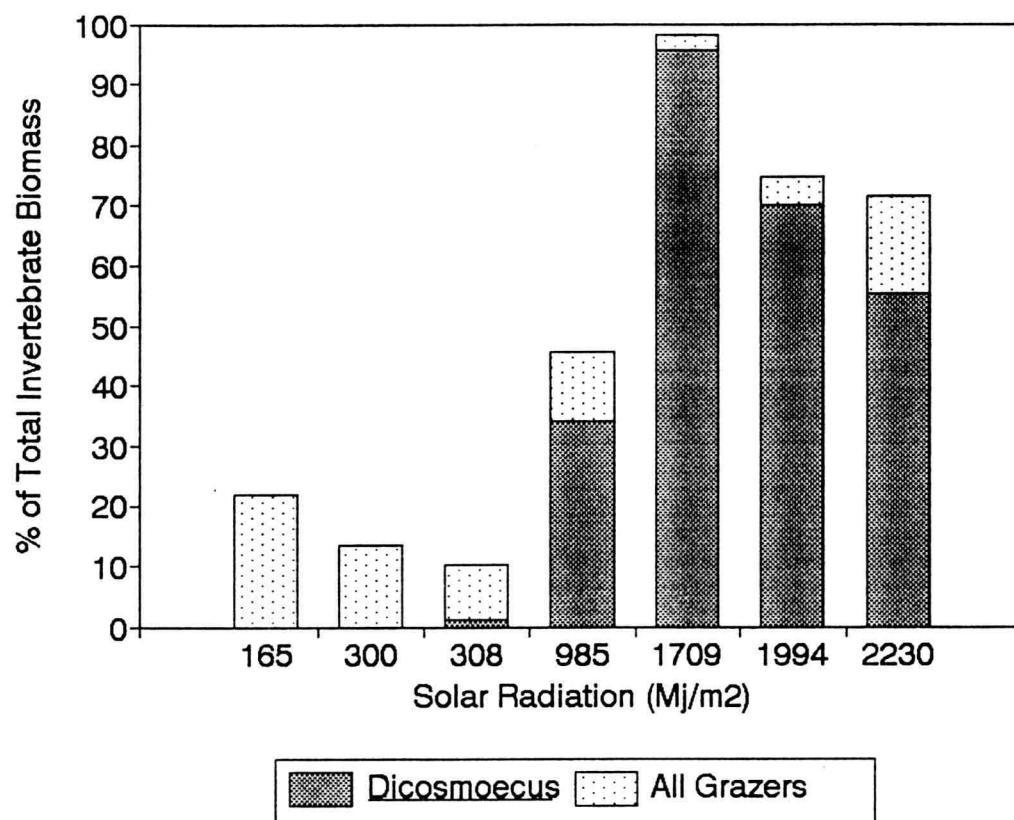
Fig. 1.3. Dicosmoecus biomass as a proportion of total invertebrate and grazer biomasses. Dicosmoecus biomass is shown as a subset of grazer biomass.

Relationship between canopy and fish communities

Total fish density, including both cool stenothermal and eurythermal species, showed a positive but insignificant correlation with solar input and temperature. When warm-adapted species (redside shiners (Richardsonius balteatus), bridgelip suckers (Catostomus columbianus), northern squawfish (Ptychocheilus oregonensis), and chiselmouth chub (Acrocheilus alutaceus)) were considered separately, this group was positively related to solar input ($r = 0.82$; $p = .025$; Fig. 1.4) but unrelated to temperature ($r = 0.63$; $p = 0.13$). In contrast, cool-adapted rainbow trout (Oncorhynchus mykiss) and Paiute sculpin (Cottus beldingi) showed a strong negative correlation ($r = -0.97$; $p = 0.0004$) with temperature (Fig. 1.5) and a negative but insignificant correlation ($r = -0.47$; $p = 0.29$) with incident light.

Discussion

Relationship between canopy and macroinvertebrate structure

In John Day Basin tributaries, macroinvertebrate densities (numbers/ m^2) generally did not change with greater light levels or increases in periphyton, although invertebrate biomass did increase. These results contrasted with many studies in coolwater streams (Towns 1979; Newbold et al. 1980; Murphy et al. 1981; Murphy & Hall 1981; Hawkins et al. 1982; Triska et al. 1983; Carlson et al. 1990; Weatherley and Ormerod 1990) and in one warmwater Arizona stream (Bruns and Minckley 1980), which reported increases in total invertebrate and herbivore densities, as well as their biomasses, with declining canopy cover. Much of this increase was
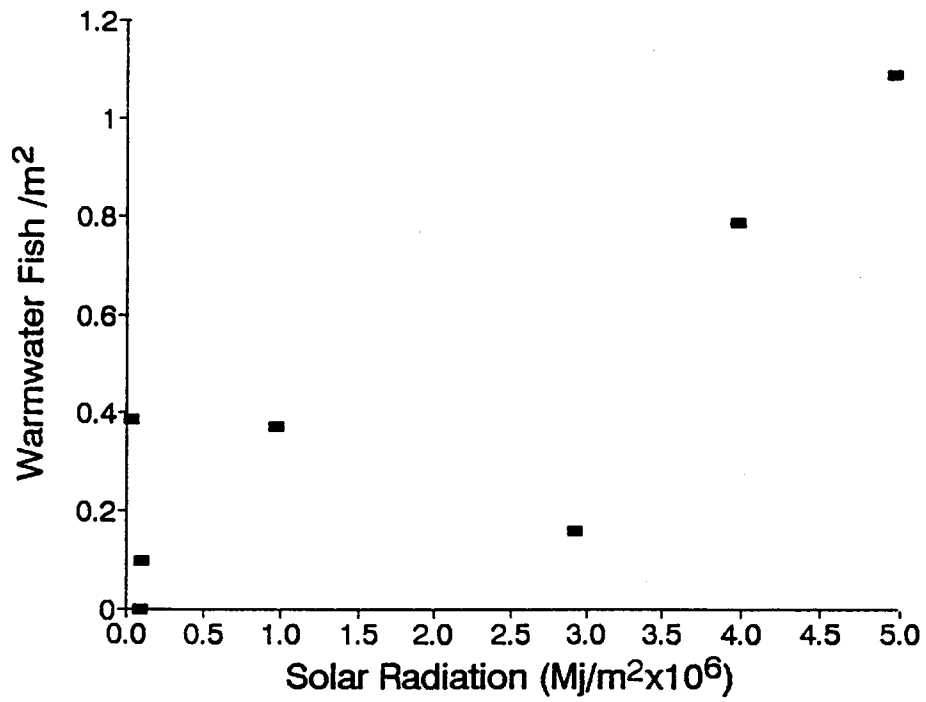
Fig. 1.4. Correlation between warmwater fish density and solar radiation at all study sites. Solar radiation values are Megajoules/m².
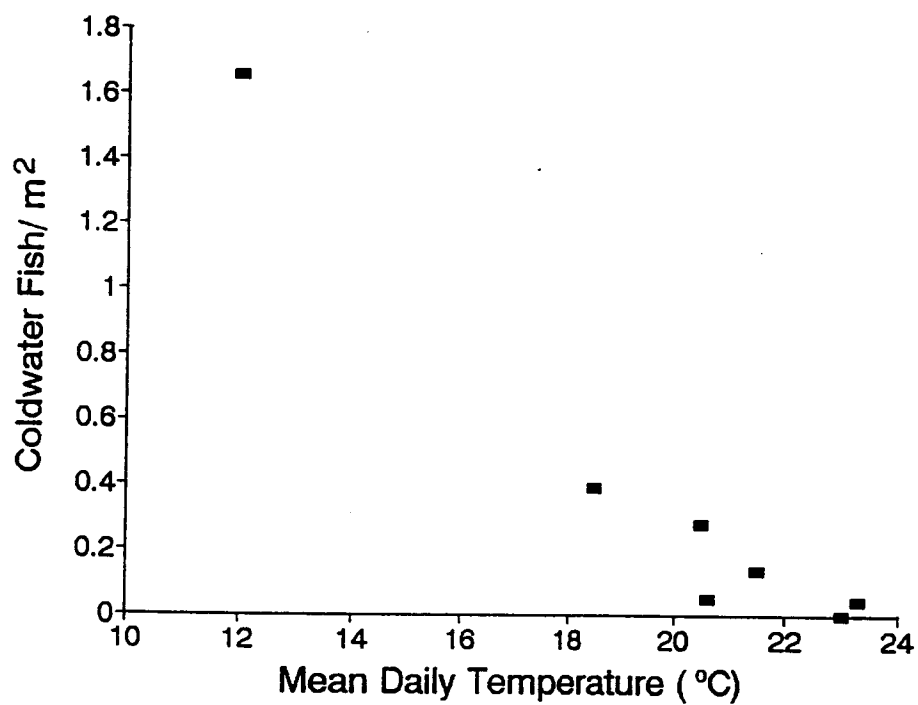
Fig. 1.5. Correlation of cold stenothermal fish densities (rainbow trout and Paiute sculpin) and mean daily temperature for July 1988 in all study sites.

attributable to increases in chironomids and baetids in open riffles (Newbold et al. 1980; Hawkins et al. 1982, 1983). This is consistent with studies that show that chironomid and baetid abundance generally increases with intensity of incident radiation and concomitant algal growth (Triska et al. 1983; Behmer and Hawkins 1986; Dudley et al. 1986; Hawkins and Furnish 1987; Richards and Minshall 1988). Although chironomids and baetids were dominant taxa in our study streams in mid-July, we detected no change in their abundances either with increasing light levels or periphyton resources.

In our study, the increase in invertebrate biomass observed at higher light levels was not due to increased biomasses of chironomids, baetids, elmids, or other small drifting prey, but rather to increased biomass of Dicosmoecus larvae. The large size, robust mandibles and curved tarsal claws of these larvae enable them to exploit thick growths of filamentous algae (Li 1990) which are used less by smaller scraping taxa (Hawkins et al. 1982). The large size and mineral case of Dicosmoecus may allow it to escape predation by many of the fishes found in the study reaches, especially warmwater species (Johansson 1991). Young trout have been shown to prefer drifting insects, such as mayflies, and rarely consume cased trichopterans which rarely drift (Elliot 1973; Allan 1981; Moore and Gregory 1988). Tippets and Moyle (1978) reported a preferential selection of Dicosmoecus by McCloud River (California) rainbow trout, but their fish were much larger than those found in our study reaches and drift feeding was reduced by high water turbidity. Dicosmoecus larvae that occurred at high densities were absent from stomachs of juvenile trout and adult and juvenile speckled dace (Rhinichthys osculus) sampled from a nearby drainage (see Chapter 2). Most other species at these sites were probably

too small (redside shiners, juvenile squawfish, suckers) or lacked appropriate mouthparts (chiselmouth, suckers) to ingest Dicosmoecus.

Dicosmoecus larvae can reduce algal abundance, both in coolwater stream systems (Hart 1981; Lamberti et al. 1992) and in artificial streams (Lamberti et al. 1987; DeNicola et al. 1990). Through competitive exploitation of food resources Dicosmoecus may exert negative indirect effects on other benthic herbivores (Lamberti et al. 1992). Because of their large size and mobility, Dicosmoecus probably are able to track food resources in unshaded stream patches in a manner similar to the caddisfly Gumaga in California (Feminella et al. 1989). Competition from Dicosmoecus may in part regulate numbers of baetids and chironomid midges in uncanopied study reaches. However, no negative relationships occurred between abundance of other grazers and Dicosmoecus and algal resources did not appear to be limiting at any open site.

Dicosmoecus may, however, indirectly affect higher trophic levels by sequestering a significant portion of the energy entering the stream that would otherwise be transferred to predators. Because large-bodied Dicosmoecus can escape predation from the fishes present in small John Day tributaries, these caddisflies may function as a trophic "shunt", diverting energy from direct transfer to higher consumers in the aquatic food chain. Hawkins and Furnish (1987) found that the large snail Juga dominated the invertebrate biomass (up to 97%) of an Oregon stream and expropriated energy potentially available to higher trophic levels. Efficient herbivores that are well-defended from their predators, such as armored catfish of small Panamanian streams, may sustain aquatic communities as two-trophic level systems (Power 1984, 1992). Opening the canopy and

stimulating autotrophic production increases the food resource base for herbivores, but the benefits to higher trophic levels may be limited.

Relationship between canopy and fish assemblages

Canopy removal in coolwater streams often has been associated with increased salmonid abundance or biomass (Aho 1976; Murphy and Hall 1981; Murphy et al. 1981; Hawkins et al. 1983; Weatherley and Ormerod 1990). Increased fish numbers are usually attributed to higher autotrophic production and consequent greater densities of invertebrate prey. Aho (1976) associated a doubling of trout numbers in unshaded reaches to increases in insect biomass at open vs. shaded sites. Hawkins et al. (1983) reported that canopy removal increased riffle-dwelling chironomids and baetids which constituted important food items for drift-feeding fish. Stream temperatures in these studies remained well below incipient lethal limits for salmonids, even in unshaded sites. For three studies in western Oregon, maximum stream temperature ranged between 20° and 22° (Murphy et al. 1981; Hawkins et al. 1982, 1983). In contrast, maximum stream temperatures at open reaches in our research area commonly exceeded 30°, well beyond the normal range of tolerance for most trout (Bidgood and Berst 1969; Carlander 1969). As a consequence, trout numbers declined with reduction in stream canopy and increases in temperature, a phenomenon previously noted by Barton et al. (1985) in Ontario, Canada, Platts and Nelson (1989) in the Great Basin, and Li et al. (1994) in many of the same sites as this study.

In our study streams, reaches with open canopies not only had high periphyton standing crops and biomasses of some macroinvertebrate taxa,

but also had high abundances of eurythermal fish. Substantial numbers of warm-adapted bridgelip suckers, northern squawfish, redside shiners, and chiselmouth, not present in coolwater streams (Newbold et al. 1980; Murphy et al. 1981; Hawkins et al. 1983) were most numerous at open sites. Speckled dace, a temperature generalist, was abundant in all but our coldest reach. Redside shiner, speckled dace, and juvenile squawfish feed on small aquatic insects from either the drift or the benthos (Wydoski and Whitney 1979; Reeves et al. 1987). Herbivorous suckers and chiselmouths also consume a large proportion of animal prey as juveniles (Moodie and Lindsey 1972; Wydoski and Whitney 1979) and certainly are able to disrupt or dislodge small invertebrate grazers in the periphyton. We speculate that disruption or predation by eurythermal fishes on small-bodied invertebrates such as chironomids and baetids may explain the low population densities of these taxa in open reaches. Schlosser and Ebel (1989) observed that cyprinid predators were able to reduce invertebrate abundance in stream pools, but not in riffles, and other workers (Gilliam et al. 1989; Power 1990) have reported that non-salmonid fishes can reduce abundances of benthic invertebrates in streams.

Implications for high desert streams

It is probable that before European settlement many small streams of the John Day basin were canopied, cool, and inhabited primarily by cold stenothermic salmonids and sculpins. If this was the case, extensive destruction of riparian stream cover by human activity has dramatically affected the structure of these ecosystems by increasing incident radiation and altering water temperature regimes. Open areas supported greater

periphyton abundance and increased macroinvertebrate standing crops, but in our study streams a large proportion of this energy was sequestered as herbivore biomass (Dicosmoecus) unavailable to higher trophic levels. Water temperatures often exceeded the upper lethal limits for salmonids and cottids, but provided suitable conditions for many eurythermic species which would otherwise not enter tributaries of this size.

Acknowledgments

References

Aho, R. S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of a stream. M.S. Thesis, Oregon State University., Corvallis.

Allan, J. D. 1981. Determinants of the diet of brook trout (Salvelinus fontinalis) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 38:184-192.

Barton, D. R., W. D. Taylor, and R. M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. North American Journal of Fisheries Management 5:364-378.

Behmer, D. J., and C. P. Hawkins. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. Freshwater Biology 16:287-300.

Benke, A. C., Henry, R. L., Gillespie, D. M., and R. J. Hunter. 1985. Importance of snag habitat for animal production in southeastern streams. Fisheries 10:8-13.

Bidgood, B.F., and A. H. Berst. 1969. Lethal temperatures for Great Lakes rainbow trout. Journal of the Fisheries Research Board of Canada 26:456-459.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540-551.

Bisson, P. A., Bilby, R. E., Bryant, M. D., Dolloff, C. A., Grette, G. B., House, R. A., Murphy, M. L., Koski, K. V., and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. Pages 143-190 in E. O. Salo and T. W. Cundy (editors). Streamside management: forestry and fishery interactions. Institute of Forest Resources, University of Washington, Seattle.

Bott, T. L. 1983. Primary productivity in streams. Pages 29-53 in T. D. Fontaine and S. M. Bartell (editors). Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, MI.

Bruns, D. A., and W. L. Minckley. 1980. Distribution and abundance of benthic invertebrates in a Sonoran desert stream. Journal of Arid Environments 3:117-131.

Carlander, K. D. 1969. Handbook of freshwater fishery biology. Iowa State University Press, Ames.

Carlson, J. Y., C. W. Andrus, and H. A. Froehlich. 1990. Woody debris, channel features, and macroinvertebrates of streams with logged and

undisturbed riparian timber in northeastern Oregon, USA. Canadian Journal of Fisheries and Aquatic Sciences 47:1103-1111.

Cummins, K. W., M. A. Wilzbach, D. W. Gates, J. A. Perry, and W. Taliaferro. 1989. Shredders and riparian vegetation. BioScience 39 :24-30.

DeNicola, D. M., C. D. McIntire, G. A. Lamberti, and L. R. Ashkenas. 1990. Temporal patterns of grazer-periphyton interactions in laboratory streams. Freshwater Biology 23:475-489.

Dudley T. L., S. D. Cooper, and N. Hemphill. 1986. Effects of macroalgae on a stream invertebrate community. Journal of the North American Benthological Society 5:93-106.

Elliot, J. M. 1973. Food of brown and rainbow trout in relation to the abundance of drifting invertebrates in a mountain stream. Oecologia 12:329-347.

Feminella, J. W., M. E. Power, and V. H. Resh. 1989. Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. Freshwater Biology 22:445-457.

Gilliam, J. F., D. F. Fraser, and A. M. Sabat. 1989. Strong effects of foraging minnows on a stream benthic invertebrate community. Ecology 70:445-452.

Grafius, E. 1976. The conversion of allochthonous material by stream detritivores. M.S. Thesis, Oregon State University, Corvallis.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. Bioscience 41:540-551.

Griffith, J. S. 1981. Estimation of the age-frequency distribution of stream-dwelling trout by underwater observation. Progressive Fish-Culturalist 43:51-53.

Hart, D. D. 1981. Foraging and resource patchiness: field experiments with a grazing insect. Oikos 37:46-52.

Hawkins, C. P., and J. Furnish. 1987. Are snails important competitors in stream ecosystems? Oikos 49:209-220.

Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in the Cascade Range streams of Oregon. Ecology 63:1840-56.

Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173-85.

Hill, W. R., and A. W. Knight. 1987. Experimental analysis of the grazing interaction between a mayfly and stream algae. Ecology 68:1955-1965.

Johansson, A. 1991. Caddis larvae cases (Trichoptera, Limnephilidae) as anti-predatory devices against brown trout and sculpin. Hydrobiologia 211:185-194.

Lamberti, G. A., L. R. Ashkenas, S. V. Gregory, and A. D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. Journal of the North American Benthological Society 6:92-104.

Lamberti, G. A., S. V. Gregory, C. P. Hawkins, R. C. Wildman, L. R. Ashkenas, and D. M. DeNicola. 1992. Plant-herbivore interactions in streams near Mt. St. Helens. Freshwater Biology 27:237-247.

Lamberti, G. A., and J. W. Moore. 1984. Aquatic insects as primary consumers. Pages 164-195 in V. H. Resh and D. M. Rosenberg (editors). The ecology of aquatic insects. Praeger Publishers, New York.

Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, J. L. Li, and J. C. Buckhouse. 1994. Cumulative impact of riparian disturbances on high desert trout streams of the John Day Basin. Transactions of the American Fisheries Society 123:627-640.

Li, J. L. 1990. Foraging behavior of the limnephilid caddisfly Dicosmoecus gilvipes and co-occurring herbivores in streams of the Pacific Northwest. Ph.D. Dissertation, Oregon State University, Corvallis.

Lyford, J. H., and S. V. Gregory. 1975. The dynamics and structure of periphyton communities in three Cascade Mountain streams. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 19:1610-1616.

Merritt, R. W., and K. W. Cummins. 1984. An introduction to the aquatic insects of North America. Kendall Hunt Publishers, Dubuque, Iowa.

Moodie, G. E. E., and C. C. Lindsey. 1972. Life-history of a unique cyprinid fish, the chiselmouth (Acrocheilus alutaceus), in British Columbia. Syesis 5:55-61.

Moore, K., and S. V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat fry in Cascade Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 45:1921-1930.

Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137-145.

Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modifications and accumulated sediment on stream

communities. Transactions of the American Fisheries Society 110:469-478.

Newbold, J. D., D. C. Erman, and K. B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Canadian Journal of Fisheries and Aquatic Sciences 37:1076-85.

Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance and resilience of stream fish assemblages to flooding. Transactions of American Fisheries Society 121:85-119.

Platts, W. S., C. Armour, G. D. Booth, D. Gordon, M. Bryant, J. L. Bufford, P. Cuplin, S. Jensen, G. W. Lienkaemper, G. W. Minshall, S. B. Monsen, R. L. Nelson, J. R. Sedell, J. S. Tuhy. 1987. Methods for evaluating riparian habitats with applications to management. General Technical Report INT-221. Ogden, Utah: USDA Forest Service, Intermountain Research Station.

Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. USDA Forest Service INT-138.

Platts, W. S., and R. L. Nelson. 1989. Stream canopy and its relationship to salmonid biomass in the intermountain west. North American Journal of Fisheries Management 9:446-457.

Power, M. E. 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. Journal of Animal Ecology 53:357-374.

---. 1990. Effects of fish in river food webs. Science 250:811-814.

---. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733-746.

Prochazka, K., Stewart, B. A., and B. R. Davies. 1991. Leaf litter retention and its implications for shredder distribution in two headwater streams. Archiv für Hydrobiologie 120:315-325.

Reeves, G. H., F. H. Everest, and J. D. Hall. 1987. Interactions between the redside shiner (Richardsonius balteatus) and the steelhead trout (Salmo gairdneri) in western Oregon: the influence of water temperature. Canadian Journal of Fisheries and Aquatic Sciences 44: 1603-1613.

Richards, C., and G. W. Minshall. 1988. The influence of periphyton abundance on Baetis bicaudatus distribution and colonization in a small stream. Journal of the North American Benthological Society 7:77-86.

Rodgers, J.D., M. F. Solazzi, S. L. Johnson, and M. A. Buckman. 1992. Comparison of three techniques to estimate juvenile coho salmon populations in small streams. North American Journal of Fisheries Management 12:79-86.

Schlosser, I. J., and K. K. Ebel. 1989. Effects of flow regime and cyprinid predation on a headwater stream. Ecological Monographs 59:41-57.

Speaker, R., K. Moore, and S. V. Gregory. 1984. Analysis of the process of retention of organic matter in stream ecosystems. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22:1835-1841.

Tippets, W. E., and P. B. Moyle. 1978. Epibenthic feeding by rainbow trout (Salmo gairdneri) in the McCloud River, California. Journal of Animal Ecology 47:549-559.

Towns, D. R. 1979. Composition and zonation of benthic invertebrate communities in a New Zealand kauri forest stream. Freshwater Biology 9:251-262.

Towns, D. R. 1981. Effects of artificial shading on periphyton and invertebrates in a New Zealand stream. New Zealand Journal of Marine and Freshwater Research 15:185-192.

Triska, F. J., V. C. Kennedy, R. J. Avanzino, and B. N. Reilly. 1983. Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. Pages 129-159 in T. D. Fontaine and S. M. Bartell (editors). Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Michigan.

Tschaplinski, P.J., and G. F. Hartman. 1983. Winter distribution of juvenile coho salmon (Oncorhynchus kisutch) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Canadian Journal of Fisheries and Aquatic Sciences 40:452-461.

Weatherley, N. S., and S. J. Ormerod. 1990. Forests and the temperature of upland streams in Wales: a modelling exploration of the biological effects. Freshwater Biology 24:109-122.

Wydoski, R. S., and R. R. Whitney. 1979. Inland fishes of Washington. University of Washington Press, Seattle.

Chapter 2

The Importance of Primary and Secondary Consumers to Benthic
Community Regulation in a High Desert Stream

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Abstract

The relative importance of predation and resource availability to benthic community structure is one of the fundamental issues of community ecology. In some ecosystems, multiple controlling factors may influence trophic processes. The objective of this study was to determine the impacts of a stream fish assemblage and dominant invertebrate grazers on benthic communities in a stream where irradiance levels were high. The study was conducted in Camp Creek, a productive high desert stream in the John Day Basin, Oregon. Plastic mesh was used to completely enclose 18 replicate log weir pools, which were stocked with varying densities of native fishes (rainbow trout, speckled dace, largescale suckers, and torrent sculpin) for 32 days in mid-summer. During this interval, periphyton biomass and invertebrate densities and biomasses were periodically measured. Fish density had no negative effects on densities of total invertebrates and was unrelated to the abundance of mayflies, a highly selected prey. Although top-down impacts of fish predators on invertebrates were not detected, the grazing caddisfly _Dicosmoecus gilvipes_ exerted direct downward control on periphyton standing crops and, indirectly, on invertebrate densities and biomasses. Because _Dicosmoecus_' large case protected them from consumption by resident fishes, their presence limited energy available for top trophic levels. _Dicosmoecus_ acted as a keystone species and an "intermediate regulator" in the benthic food web of Camp Creek by simultaneously influencing trophic levels both below and above its own.

Introduction

The relative importance of abiotic and biotic influences on community structure and function is one of the fundamental issues of community ecology. Several syntheses have addressed the effects of multiple controlling factors on trophic processes in both terrestrial and aquatic systems (Menge and Sutherland 1976, 1987; Fretwell 1987; Oksanen 1988; Hunter and Price 1992; Power 1992b; Strong 1992; Lamberti 1996), with much debate on the relative roles of predation and competition (initiated by Hairston et al. 1960). In lakes, researchers have established fairly repeatable and predictable patterns of trophic regulation (Brett and Goldman 1996), but a consistent and unifying mechanism for benthic community regulation in streams has been elusive. Primary productivity is fundamental to all ecosystems, and provides a "bottom-up template" that dictates the number of trophic levels in a food web and thereby constrains the intensity of top-down predator control (Hunter and Price 1992). But whether the community is ultimately regulated by top-down predator limitation, by bottom-up resource limitation at every level, or both, depends on many biotic and abiotic factors (Power 1992b). Lotic environments are notoriously heterogeneous both within and between streams (Hynes 1970; Pringle et al. 1988), so that identifying the factors that affect the relative strengths of predation and resource limitation is daunting.

In community ecology, predation has long been considered an important regulator of lower trophic levels (Paine 1966; Carpenter et al. 1985; Sih et al. 1985; Menge and Sutherland 1987), but stream ecosystems do not clearly follow this pattern. Fish are top consumers in most streams, but studies show variable impacts of fish predation. No prey response has been observed to predation by brook trout (Allan 1982; Reice

and Edwards 1986), coho (Culp 1986), steelhead and roach (on gravel substrates, Power 1992a) and sunfishes (Holomuzki and Stevenson 1992). Some studies have reported significant predator effects, usually for specific prey taxa or habitats, with trout (Hemphill and Cooper 1984; Bowlby and Roff 1986; Bechara et al. 1992; Power 1992a; Forrester 1994), minnows (Gilliam et al. 1989; Schlosser and Ebel 1989), and sunfishes (Crowder and Cooper 1982; Power et al. 1985). Factors that influence the strength of fish predation effects include the experimental design (Cooper et al. 1990; Wooster 1994), feeding strategies of the fishes (Gerking 1994), habitat structural complexity (Gilinsky 1984), and productivity of the community (McQueen et al. 1989). Trophic cascades, which are seldom documented in streams (but see Power 1984, 1992a; Power et al. 1985; Lamberti 1996 for review), are well known in lakes with homogeneous pelagic habitats and clearly defined plankivorous and piscivorous feeding guilds (Carpenter et al. 1985). Trophic cascades are more frequently observed in oligotrophic lakes, as fish predation appears less effective at regulating lower trophic levels when productivity is high (McQueen et al. 1989).

Resource limitation, or bottom-up community regulation, is often documented for lotic systems. In many stream studies, grazer abundance and growth were strongly affected by periphyton abundance (reviewed by Feminella and Hawkins 1995). Benthic fauna respond not only to increased food resources but also to greater structural complexity for retreats, attachment sites, and refuges (Dudley et al. 1986; Lamberti 1996). Mobile grazers have the ability to track rich food patches and numerical responses can be rapid (Kohler 1985; Lamberti and Resh 1983; Richards and Minshall 1988; Feminella et al. 1989). In lower John Day Basin tributaries (Chapter 1), grazers were regulated by algal standing crops which were, in turn,

limited by irradiance. In some communities, higher herbivore and fish densities have been documented in nutrient-enriched or high-light environments, suggesting bottom-up control of all trophic levels (Aho 1976; Hawkins et al. 1983; Bisson and Sedell 1984; Peterson et al. 1993). However, most studies that demonstrate upward control reaching to the level of fish predators take place in cool-water, resource-limited streams where productivity is low.

Bottom-up and top-down regulation of aquatic communities may occur simultaneously and be dynamically linked. With higher primary productivity, consumer biomasses may increase so that impacts on lower trophic levels can become more intense (Menge 1992). McQueen et al. (1989) suggested that control of biomass at a particular trophic level is determined by the combined impacts of predation and energy availability, and that in lakes these two influences often commingle at the plant-herbivore interface. In stream studies where both nutrient/light levels and grazing intensity were manipulated, upward control of herbivore populations by periphyton production had primacy but occurred in conjunction with strong downward control of periphyton by herbivores (Steinman 1992; Rosemond et al. 1993; Hill et al. 1992, 1995). Benthic community dynamics are frequently dominated by robust midlevel consumers such as Juga (Hawkins and Furnish 1987; Lamberti et al. 1989), Elimia (Hill et al. 1995), cased caddisflies (Lamberti and Resh 1983; McAuliffe 1984; Lamberti et al. 1987) or Campostoma (Power et al. 1985). Lamberti (1996) suggested the designation "intermediate regulators" for those species whose influences can extend laterally and upward as well as to lower trophic levels. These dominant consumers with an intermediate position in

the trophic community can exert substantial control over the entire food web.

Light was limiting in stream reaches of the John Day Basin investigated in Chapter 1, and both periphyton and grazers increased in uncanopied sites with higher irradiance. No top-down effects were apparent at any trophic level. Potential trout predation was confounded, however, by near-lethal water temperatures in the most productive, unshaded sites (Li et al. 1994). In this study we selected a tributary higher in the basin that, although warm, had less extreme temperature regimes. This stream had little canopy, with higher mean summer irradiance than the lower John Day basin sites, and therefore we could contrast community regulation in a well-illuminated system with one constrained by low light. The purpose of the study was to evaluate the importance of top-down regulation of benthic communities in a productive system where light was not limiting. Our specific objectives were to determine the influences of a stream fish assemblage (secondary or tertiary consumers) as well as those of dominant herbivores (primary consumers) on the abundances and species composition of the benthic community.

Study Area

The study was conducted in Camp Creek (44°39' latitude; 118°49' longitude), a third-order stream within the John Day River Basin in northcentral Oregon. Camp Creek flows northwest and ranges in elevation from 1719 m to 1055 m. The study area receives about 60 cm of precipitation annually, mostly falling from November to May. Summer low flows occur in August and September and summer water temperatures are

warm due to lack of overhanging canopy. Although no irrigation diversions or other agricultural uses are present at or above the research area, intense livestock grazing occurs throughout the watershed and limits canopy development. Typical streamside vegetation includes grasses (Phalaris spp.), sedges (Carex spp.), white alder (Alnus rhombifolia), and black cottonwood (Populus trichocarpa). Willows (Salix spp.) are rare. Ponderosa pine (Pinus ponderosa) and Douglas-fir (Pseudotsuga menziesii) dominate the hillslopes, but most riparian conifers were logged in the 1920's.

Historically, Camp Creek provided spawning habitat for steelhead and resident rainbow trout (Oncorhynchus mykiss) and for spring chinook (Oncorhynchus tschawytsha). While both species still occur in the stream, conditions are no longer favorable for chinook spawning. Other fishes frequently observed in Camp Creek include speckled dace (Rhinichthys osculus), redside shiners (Richardsonius balteatus), largescale suckers (Catostomus macrocheilus), torrent sculpin (Cottus rhotheus), and Paiute sculpin (Cottus beldingi). Juvenile rainbow trout and juvenile and adult speckled dace were numerically dominant. In an effort to increase pool:riffle ratios and improve fish habitat in Camp Creek, the Bonneville Power Administration installed 256 log weirs along 19 km of stream in the 1970's. The log weirs formed pools of fairly uniform size and morphology which were used as experimental units.

The log weir experimental pools were located within a mid-basin reach of Camp Creek and varied little in elevation, solar input, stream temperature, or volume (Table 2.1). Average summer solar input in the pools ranged from 950 to 2174 Mj/m^2 and was comparable to unshaded reaches of the lower John Day Basin study sites (Table 1.1). Mean

Table 2.1. Physical characteristics of 3.3 km Camp Creek reach where 18 experimental pools were located. Solar radiation is the cumulative summer average (June, July, and August); discharge and stream temperatures are for July-August 1990; standard errors are in parentheses.

Elevation (m)	1253-1318
Discharge (m^3/s)	0.11
Mean solar radiation (Mj/m^2)	1491 ($\pm$83.6)
Mean stream width (m)	7.2 ($\pm$0.5)
Mean pool volume (m^3)	9.9 ($\pm$0.9)
Stream temperature (^{o}C)	
Mean daily	20.3
Mean maximum	28.1
Mean minimum	13.0
Maximum	29.5

daily summer stream temperatures (20.3° C) in Camp Creek in 1990 were lower than the unshaded John Day Basin sites in 1988, probably due to higher elevation rather than climatic differences between years. Maximum Camp Creek temperatures (29.5° C) were comparable to temperature maxima recorded at the uncanopied John Day sites, despite elevational differences.

Methods

Field experiments were conducted July-August 1990 along a 3.3 km reach of lower Camp Creek to determine possible effects of varying densities of fishes on the abundance and species composition of lower trophic levels. We selected 18 log weir pools that were separated by at least 2 channel units (approximately 50 m). Mean accumulated solar input (Megajoules/m^2) for June, July, and August was determined for each pool with a Solar Pathfinder (see Chapter 1). Turbidity that could affect the amount of light reaching the substrate was low. Pools were ranked from lowest to highest in solar input and were assigned to three irradiance groups: low (950-1332 Mj/m^2), intermediate (1355-1671 Mj/m^2), and high (1672-2174 Mj/m^2). Pools from each group were randomly assigned to the 6 experimental treatments to provide a range of light intensities per treatment. Pool volumes were determined at the beginning and end of the experiment. Weekly maximum and minimum stream temperatures were recorded mid-reach with maximum-minimum thermometers.

Six treatments of varying fish densities and species assemblages were used: (1) no fish; (2) low fish density (insectivores); (3) high fish density (insectivores); (4) high fish density (insectivores) plus piscivorous fish; (5)

low fish density (insectivores) plus piscivorous fish; and (6) low fish density (insectivores) plus herbivorous fish. Fishes were removed from each experimental pool with 8 passes of an electroshocker over a period of 4 days. Fishes were held in net pens and used to stock the experimental pools at appropriate densities. Whereas numbers of fishes captured in each pool prior to the experiment were recorded, only fish to be stocked were weighed and measured. The fish species stocked were the following: rainbow trout juveniles (age 1+ and young-of-the-year (YOY); insectivores), speckled dace juveniles and adults (insectivores), largescale sucker juveniles (herbivore), and torrent sculpin (piscivore). Stocking levels were based on the range of natural fish densities observed during field sampling in previous years (T. Pearsons, unpubl. data). High fish treatments all received 10 fish/m^3 divided among four species/age groups: YOY rainbow trout, 1+ rainbow trout, juvenile speckled dace, and adult speckled dace. Low fish treatments all received 1 fish/m^3 divided equally among the same four species/age groups. Piscivores and herbivores were stocked at 1 sculpin/m^3 and 3.33 suckers/m^3, respectively.

The experimental log weir pools were enclosed with plastic mesh (4 mm X 16 mm apertures) that would confine fishes but permit flow through of invertebrate drift. The screening was installed at the upper and lower pool margins, buried in the substrate and tied to rebar for support. A minnow emigration trap was spliced into the rear barrier in order to capture fish attempting to swim downstream. Emigration traps were checked and screens were cleaned daily. Fish in the traps were released back into the pool, and any dead fish were recorded and replaced by live fish in order to maintain target densities. Wandering garter snakes (Thamnophis elegans

vagrans), belted kingfishers (Megaceryle alcyon), and dippers (Cinclus mexicanus) observed near the pools were counted.

The fishes were confined for 32 days (14 July-14 August). However, because the enclosures proved to be imperfect barriers to fish movement we were not able to control the absolute fish densities within the pools. Nevertheless, the relative densities of fishes at the end of the experiment were in accord with our desired treatments such that the 18 pools represented a gradient of fish densities. The "no fish" pools were ultimately regarded as "low fish density" pools (Table 2.2).

Sampling of benthic communities in each pool occurred prior to fish stocking, and at days 10, 17, and 32. For qualitative identification of epilithic algal taxa present, rock surfaces were scraped with a scalpel and the algae obtained preserved in Lugol's solution. Algal standing crops were estimated visually by recording the relative cover of prominent algal growth forms (filamentous algae, diatom mats, and cyanobacteria) within six, 0.25 m^2 quadrats in each experimental pool. Quadrats were delimited by a 0.5 m x 0.5 m metal frame placed in a regular pattern throughout the pool. A glass-bottomed viewing scope was used to scan the substrate. In addition, periphyton biomass (g ash-free dry mass/ m^2 (AFDM)) and chlorophyll a concentration (mg/m^2) were determined using methods described in Chapter 1 for other John Day Basin sites. Although both chlorophyll a and AFDM are useful measures of periphyton abundance, AFDM may be a more accurate and less variable estimator of food resources available for consumers than chlorophyll a (Feminella and Hawkins 1995). Consequently, AFDM was primarily used in the analysis. In order to assess the potential impact of macroinvertebrate grazing on periphyton abundance in experimental pools, nine rocks were selected at random from the

Table 2.2. Mean total fish densities (number/m^3) and mean relative proportion of each species at the end of the experiment in Camp Creek; infrequently occurring species are not included; standard errors are in parentheses. n = number of pools per treatment, SPD = speckled dace, RBT = rainbow trout, TSC = torrent sculpin, LSS = largescale sucker.

Treatment	Total Density	Relative density of each species			
		SPD	RBT	TSC	LSS
Low fish (n = 5)					
	6.8 (±0.5)	0.77 (±0.08)	0.16 (±0.11)	0.05 (±0.02)	0
Low fish with piscivore (n = 3)					
	8.3 (±1.1)	0.68 (±0.10)	0.23 (±0.09)	0.09 (±0.01)	0
High fish (n = 4)					
	24.0 (±3.1)	0.78 (±0.04)	0.17 (±0.03)	0	0.01 (±0.01)
High fish with piscivores (n = 3)					
	19.6 (±2.0)	0.79 (±0.06)	0.14 (±0.06)	0.08 (±0.01)	0
Largescale suckers (n = 3)					
	11.3 (±0.6)	0.58 (±0.17)	0.13 (±0.05)	0.10 (±0.07)	0.18 (±0.05)

substrate and were protected from invertebrate grazing by placement on platforms suspended over, but not touching, the pool bottom (as per Lamberti and Resh 1983). While platforms excluded most heavy-bodied, crawling grazers such as caddisflies and snails, they were easily colonized by drifting mayflies and midges, and therefore grazing was decreased but not completely eliminated. These reduced grazing treatments were assigned to the three "no fish" experimental pools where herbivorous fishes were absent. At each sampling period, periphyton from three platform rocks was removed, pooled, and measured with the same methods used to obtain substrate AFDM and chlorophyll a.

Macroinvertebrate abundances were estimated in each pool by scooping 5 nonembedded, cobble-sized rocks from the substrate into a 250μm mesh net, removing all invertebrates, and pooling the organisms into one sample (Wrona et al. 1986). Rock surface area was estimated by molding the rocks with aluminum foil, weighing the foil, and converting foil weight to surface area using a known surface area/weight ratio. All invertebrates retained by a 250μm sieve were preserved in 95% ethanol, identified to genus (except chironomids to family), enumerated, and measured. Taxa were later assigned to functional feeding groups (Merritt and Cummins 1984). Scrapers and other invertebrates that commonly feed on living algal cells were together designated grazers (see Chapter 1). Collector-gatherers, filterers, shredders, and predators were also recognized. Biomasses were estimated by using known length-weight relationships for preserved material (Smock 1980). Snails were removed from shells, dried at 55°C for 24 h, and weighed. In addition, population estimates were made of the large caddisfly Dicosmoecus gilvipes visible with a viewing scope on substrate surfaces within the 6 sample quadrats where algal cover was also

estimated. There was a close correlation between destructive samples and visual counts for <u>Dicosmoecus</u> in July, but by mid-August destructive sampling tended to overestimate the number of caddisflies capable of feeding by incorporating recently diapaused animals. Visual counts of <u>Dicosmoecus</u> were used for these later population estimates.

On 3 August, unusual densities of <u>Dicosmoecus gilvipes</u> were discovered in two adjacent, non-experimental log weir pools. Movement of caddisflies from the lower to the upper pool was restricted by lack of stream flow over the log dividing the pools, and <u>Dicosmoecus</u> could not traverse the dry wood. Consequently, <u>Dicosmoecus</u> were aggregated in the lower pool and occurred at normal densities in the upper pool. This "natural" but unreplicated experiment was an opportunity to compare intra- and interspecific effects of two <u>Dicosmoecus</u> densities under unmanipulated conditions.

Physical and biological measurements similar to those used to assess experimental pools were made for the two adjacent pools. Pool volumes, solar inputs, and temperatures were recorded. Fish densities and species composition were determined by snorkeling the pools. Periphyton AFDM, chlorophyll <u>a</u>, and filamentous algal cover were measured to estimate algal abundance. <u>Dicosmoecus</u> larvae were counted with a viewing scope on substrate surfaces within the 6 sample quadrats where algal cover was also estimated. To assess the possiblility of intraspecific competition, 25 <u>Dicosmoecus</u> were collected from each pool and mean individual masses determined from dry weights obtained after preservation.

To determine if herbivorous largescale suckers affected periphyton, observations on sucker microhabitat use and feeding behavior were made in the 3 herbivorous fish treatment pools. Diurnal and nocturnal behaviors

were recorded during 5 observation sessions over 4 days. Substrate composition, aquatic vegetation, and depths were mapped for each pool. Observations were made either from the bank or by snorkeling. The observer selected individuals and followed each for 3 min, noting activity (e.g. resting, swimming, feeding) and location in pool. A total of 21 fish were observed. If feeding occurred, the foraging methods and browsing locations were recorded. On two occasions, rock surfaces where feeding was concentrated were scraped with a scalpel and the algae obtained preserved in Lugol's solution for later identification.

After 32 days, the experiment was terminated. On 14-16 August 1990, final periphyton and macroinvertebrate sampling was performed and fishes were removed from each of the 18 pools using 6-pass electroshocking. Fishes were counted, weighed, and measured. In order to determine feeding preferences of the numerically dominant fishes in Camp Creek, rainbow trout and speckled dace were collected from 6 experimental pools for gut contents analysis. Thirty-six juvenile rainbow trout and 31 juvenile and adult speckled dace were preserved in formalin. Stomachs were dissected and food items were identified to genus when possible and enumerated. Food selection was quantified using Jacob's (1974) electivity index which compares the proportional use and availability of a food item, but is independent of the relative abundance of that food item. The electivity (D) is

$$D = (r-p)/(r+p)-2rp$$

where r is the proportion of the food item used by a species and p is the proportion available in the environment. The index varies continuously between -1 (strong avoidance) and +1 (strong selection), and was interpreted using Moyle and Baltz's (1985) range of selection intensities.

Data were analyzed with linear regression and Pearson's product-moment correlations, with t-tests for significance. Log_{10} (x + 1) and arcsine square-root transformations were used to control for non-normality and heteroscedastisity in the data.

Results

Benthic community structure at Day 0 (14 July 1990)

Periphyton

In Camp Creek logweir pools in July, periphyton was dominated by the filamentous green alga Cladophora that, in some pools, overgrew other algal forms to completely blanket the substrate. During midsummer Cladophora hosted dense epiphytic diatom growth (principally Cocconeis, Gomphonema, and Epithemia), which is readily consumed by herbivorous invertebrates (Gregory 1983). Cladophora filaments were short (1-5 cm) relative to growth forms observed in other warm streams (e.g. Power 1990). Mean algal standing crop for the 18 experimental pools was 11.5 g $AFDM/m^2$ (SE = 1.07), with means of 9.8 g $AFDM/m^2$ (SE = 2.0) for the low irradiance pools, 12.8 g $AFDM/m^2$ (SE = 1.8) for intermediate irradiance pools, and 11.8 g $AFDM/m^2$ (SE = 1.9) for high irradiance pools. Chlorophyll a concentrations averaged 30.1 mg/m^2 (SE = 3.1) and were highly correlated (r = 0.92; p < 0.001) with periphyton biomass. Neither chlorophyll a, periphyton AFDM, nor filamentous algal cover were correlated with solar input, suggesting that irradiance was not the limiting factor for algal standing crops in the study pools. Other algae present in pools included the green alga Chaetophora, cyanobacteria (Oscillatoria and

Nostoc), and epilithic diatoms such as Epithemia, Cymbella, Synedra, and Navicula.

Macroinvertebrates

Macroinvertebrate assemblages at Day 0 were dominated by grazers, collectors, and predators (Fig. 2.1; Table 2.3). Shredders and filterers together made up less than 4% of the community by either abundance or biomass. Grazers that were prominent numerically included heptageniid mayflies (12.1%), pulmonate snails (16.5%), and chironomids (13.8%) (Table 2.4). Although the caddisfly Dicosmoecus gilvipes occurred at relatively low densities (0.4% of total invertebrate abundance), this grazer comprised 37.5% of benthic invertebrate biomass. The most numerous collectors were the mayflies Tricorythodes and Paraleptophlebia (25.6% together) and chironomids (17%), but collectors only accounted for 14% of total invertebrate biomass. Predators contributed significantly to both total invertebrate number and biomass. Although the perlid stoneflies Hesperoperla and Calineuria occurred at low densities, they made up almost 15% of benthic community biomass. Over half of predator numbers consisted of Hydracarina, but mites accounted for little biomass.

Relationships between solar input, periphyton, macroinvertebrates, and fish

At the onset of the experiment, solar input appeared to have no impact on most invertebrate groups although grazer biomass was positively but non-significantly correlated with light levels ($r = 0.41$; $p = 0.10$). Among
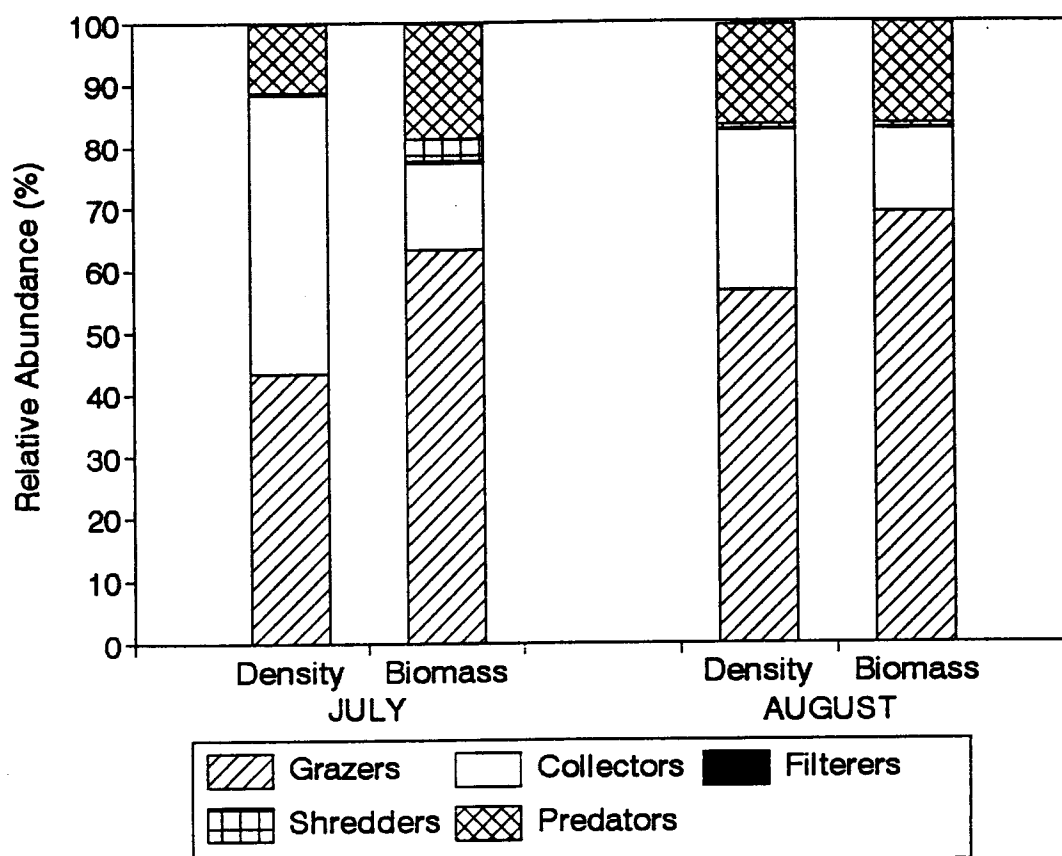
Fig. 2.1. Relative densities and biomasses of invertebrate feeding guilds in mid-July and mid-August for 18 experimental pools in Camp Creek.

Table 2.3. Mean (± 1 SE) density (number/m^2) and biomass (g dry weight/m^2) of invertebrate guilds in Camp Creek study pools at onset and at termination of fish enclosure experiment. Probability values are based on paired t-tests on log-transformed data.

	Day 0 (14 July)		Day 32 (14 Aug)		p-value	
	Density	Biomass	Density	Biomass	Density	Biomass
Total invertebrates	2382 (± 469)	0.75 (± 0.09)	3602 (± 605)	1.35 (± 0.13)	0.07	0.001
Grazers	1040 (± 221)	0.47 (± 0.09)	2040 (± 342)	0.94 (± 0.14)	0.003	0.001
Collectors	1067 (± 238)	0.10 (± 0.02)	928 (± 217)	0.18 (± 0.05)	0.19	0.16
Shredders	9 (± 3)	0.03 (± 0.01)	31 (± 16)	0.01 (± 0.01)	0.46	0.18
Predators	265 (± 37)	0.14 (± 0.03)	590 (± 95)	0.22 (± 0.04)	0.001	0.10

Table 2.4. Average relative densities and biomasses of dominant invertebrate taxa in study pools at onset and at termination of fish enclosure experiment. Standard errors are in parentheses.

	14 July		14 August	
	Density	Biomass	Density	Biomass
Baetis	0.04 (±0.01)	0.01 (±0.003)	0.02 (±0.003)	0.01 (±0.002)
Heptageniidae	0.12 (±0.02)	0.10 (±0.02)	0.03 (±0.001)	0.06 (±0.01)
Tricorythodes	0.23 (±0.07)	0.03 (±0.01)	0.08 (±0.03)	0.03 (±0.01)
Perlidae	0.005 (±0.002)	0.15 (±0.04)	0.004 (±0.001)	0.14 (±0.04)
Dicosmoecus	0.004 (±0.001)	0.38 (±0.10)	0.003 (±0.001)	0.24 (±0.08)
Helicopsyche	0.02 (±0.005)	0.03 (±0.01)	0.13 (±0.05)	0.002 (±0.001)
Chironomidae	0.35 (±0.08)	0.13 (±0.03)	0.21 (±0.05)	0.06 (±0.01)
Physa	0.005 (±0.002)	0.02 (±0.001)	0.007 (±0.002)	0.12 (±0.03)
Fossaria	0.005 (±0.001)	0.01 (±0.001)	0.05 (±0.01)	0.13 (±0.04)
Gyraulus	0.16 (±0.03)	0.04 (±0.01)	0.20 (±0.05)	0.08 (±0.02)
Hydracarina	0.07 (±0.01)	0.01 (±0.002)	0.12 (±0.01)	0.02 (±0.001)

individual grazer taxa, only Helicopsyche biomass was significantly, correlated with light (r = 0.54; p = 0.03) although Helicopsyche comprised a minor proportion of the benthic community. Dicosmoecus, which dominated grazer biomass, demonstrated a weak positive association with solar input (r = 0.32; p = 0.21). However, 14 days later, Dicosmoecus densities were significantly associated with solar input (r = 0.57; p = 0.01).

Densities of total invertebrates and all invertebrate guilds except shredders were positively correlated with percent filamentous algal cover (Table 2.5). However, invertebrate biomasses varied in their relation to algal cover. Predator and total invertebrate biomasses were not correlated with filamentous algal cover. Collector biomass increased and grazer biomass decreased with algal cover. This inverse relationship of grazers and algal cover was linked to a strong negative correlation between larval Dicosmoecus, which made up two-thirds of grazer biomass, and filamentous algal cover (Fig. 2.2). In contrast to algal cover, periphyton AFDM was not significantly correlated with invertebrate densities or biomasses. This may be because AFDM was not correlated with algal cover (r = 0.07; p = 0.79).

Before experimental pools were stocked with fishes at treatment densities, all fishes were counted, weighed, and removed. No significant correlations were found between original fish densities or biomasses and algal or invertebrate communities (Table 2.5; Table 2.6).

Table 2.5. (a) Correlation matrix of log-transformed invertebrate densities (number/m^2) and invertebrate biomasses (g DW/m^2) vs. periphyton biomass (g AFDM/m^2) and percent filamentous algal cover; (b) correlation matrix of of log-transformed fish densities (number/m^3) and biomasses (g/m^3) vs. periphyton biomass (g AFDM/m^2) and percent filamentous algal cover. Day 0 fish densities and biomasses are those that were present in pools before fish were removed and restocked. Values are Pearson correlation coefficients; ** = $p < 0.01$, * = $p < 0.05$.

(a)	Periphyton		% Algal Cover	
	Invert Density	Invert Biomass	Invert Density	Invert Biomass
Day 0 (14 July)				
Total invertebrates	0.23	-0.23	0.61**	-0.26
Grazers	0.14	-0.33	0.48*	-0.50*
Collectors	0.34	0.24	0.57*	0.54*
Shredders	-0.22	-0.09	0.24	0.22
Predators	0.05	-0.26	0.56*	0.04
Day 32 (14 Aug)				
Total invertebrates	0.81**	0.23	0.69**	-0.27
Grazers	0.73**	0.04	0.51*	-0.55*
Collectors	0.75**	0.57*	0.73**	0.75**
Shredders	0.53*	-0.04	0.60*	-0.01
Predators	0.68**	-0.15	0.75**	0.14

Table 2.5 (Continued)

(b)

	Periphyton		% Algal Cover	
	Fish Density	Fish Biomass	Fish Density	Fish Biomass
Day 0 (14 July)				
Fishes	0.11	0.23	-0.13	0.21
Day 32 (14 Aug)				
Fishes	0.55*	0.21	0.40	0.04
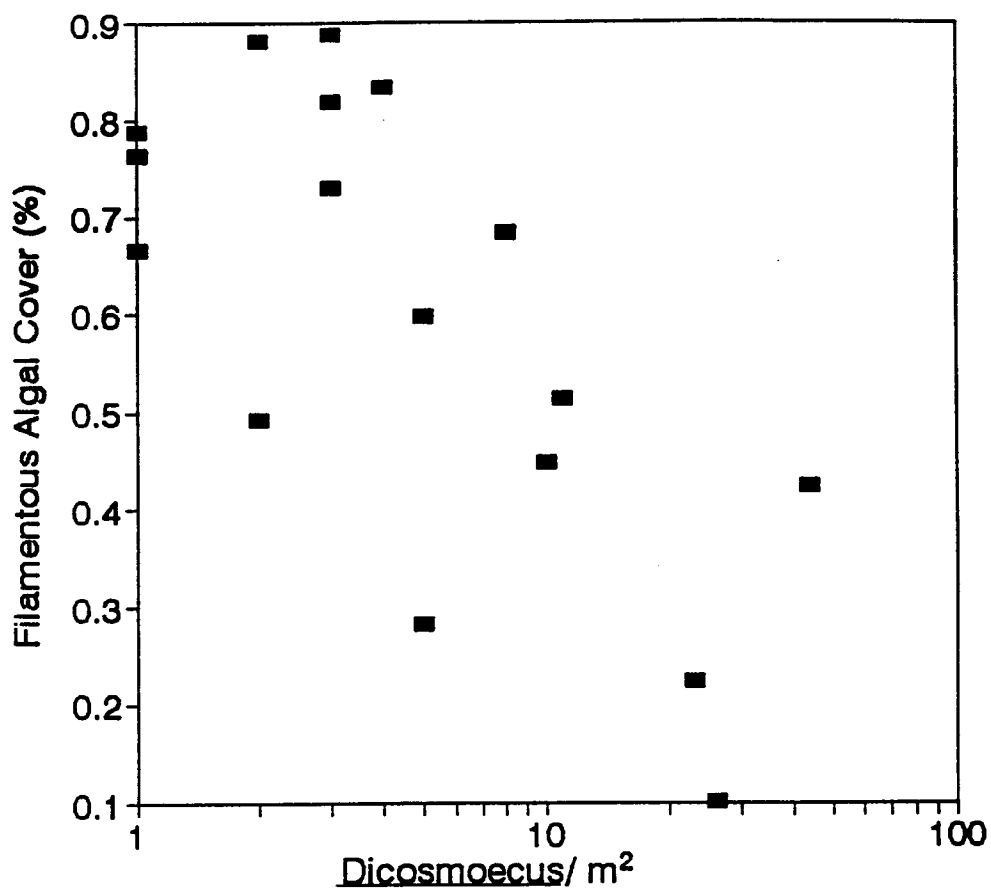
Fig. 2.2. Correlation of % filamentous algal cover (arcsine square-root transformed) and log-transformed Dicosmoecus densities in mid-July ($r = -0.72$; $p < 0.001$, $n = 18$).

Table 2.6. Correlation matrix of invertebrate densities (number/m^2) and invertebrate biomasses (g DW/m^2) vs. fish density (number/m^3) for experimental pools. Values are Pearson correlation coefficients; * = $p < 0.05$.

Day 0 (14 July)

	Fish density	
	Invertebrate Density	Invertebrate Biomass
Total invertebrates	0.32	0.03
Grazers	0.20	0.13
Collectors	0.41	0.14
Shredders	-0.35	-0.17
Predators	0.31	-0.40

Day 32 (14 Aug)

	Fish density	
	Invertebrate Density	Invertebrate Biomass
Total invertebrates	0.41	-0.10
Grazers	0.27	-0.21
Collectors	0.46	-0.29
Shredders	0.35	0.27
Predators	0.50*	0.17
All mayflies	-0.12	-0.19
Pulmonate snails	-0.18	-0.29
Chironomidae	0.60*	0.56*

Benthic community structure at Day 32 (14 August 1990)

Periphyton

Mean periphyton biomass increased during the experiment but had decreased in a few pools by Day 32, probably due to senescence and sloughing (Fig. 2.3). Nevertheless, final algal standing crops averaged 19.0 g AFDM/m^2 (SE = 1.9) and were significantly higher ($p < 0.001$) than Day 0 levels (11.5 g/m^2; SE = 1.1). AFDM was highly correlated (r = 0.94; $p < 0.001$) with chlorophyll a concentrations (mean = 47.9 mg/m^2; SE = 6.2). Because percent filamentous algal cover correlated significantly (r = 0.64; $p < 0.01$) with total algal biomass measured concurrently, percent Cladophora cover was deemed a reasonable estimator of algal standing crops by Day 32 in experimental pools. Filamentous algal cover averaged 43% (SE = 6.5) and ranged from 12 to 88%. Mean filamentous algal cover for all pools did not change between Day 17 (mean = 40%; SE = 5.4) and the end of the experiment.

Macroinvertebrates

Mean densities and biomasses of benthic invertebrates across all pools increased by about 50% during the experiment (Table 2.3). Relative abundances of most functional groups remained fairly constant, although relative density of collectors declined from 45% to 26% (Table 2.4; Fig. 2.1). Among the grazers, heptageniid mayflies and Dicosmoecus were relatively less important components of the community than on Day 0, while pulmonate snails increased in dominance, accounting for 25% of the numbers and 32% of the biomass of all macroinvertebrates (Table 2.4). The
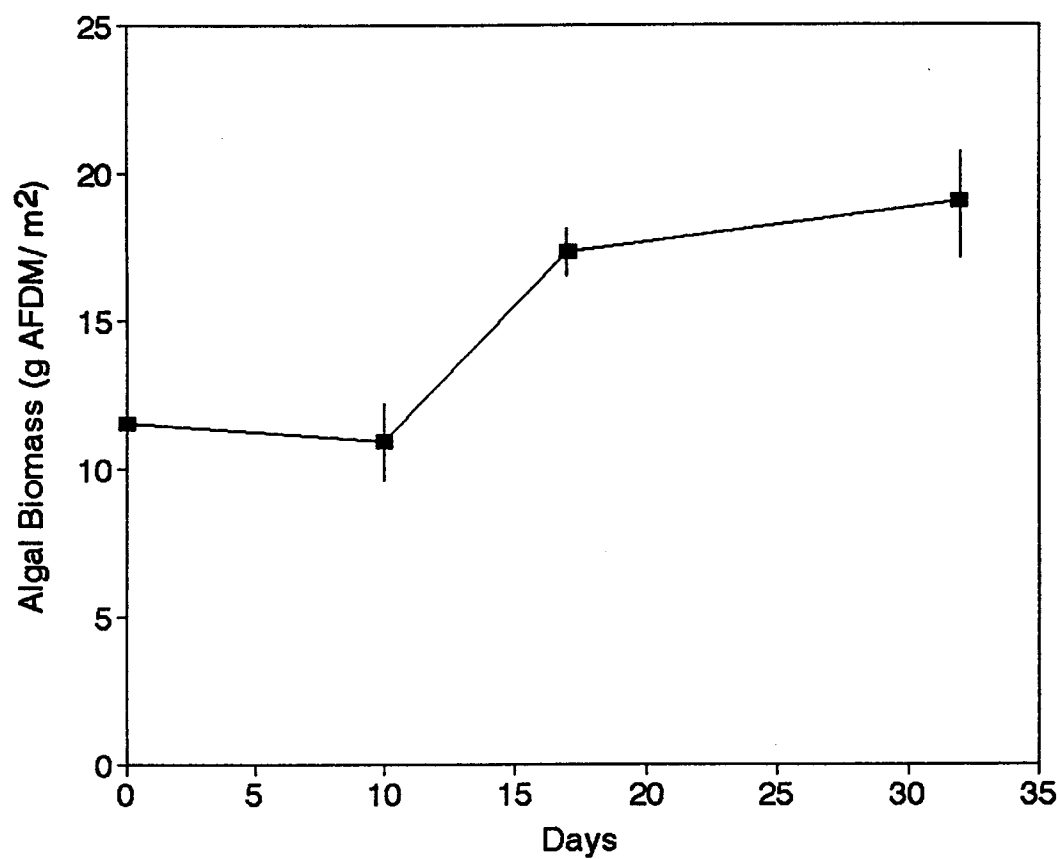
Fig. 2.3. Average algal biomass accrual in 18 log weir pools during the experimental period in Camp Creek. Bars represent ± 1 standard error.

grazing caddisfly Helicopsyche borealis also increased in relative abundance, contributing 10.3% to total invertebrate density by Day 32 but <1% to biomass. The collector mayflies Paraleptophlebia and Tricorythodes declined by 50% in relative density but increased in relative biomass. The relative abundance of shredders remained low, comprised primarily of the caddisflies Lepidostoma and Psychoglypha. The relative abundance of the predator guild, principally perlid stoneflies, was fairly constant during the experiment, although relative density of Hydracarina increased.

Significant changes in absolute abundances of some taxa occurred during the experimental period. Mean densities of active Dicosmoecus were lower in August ($4.1/m^2$) than in July ($10/m^2$; $p < 0.001$) due to the onset of diapause and pupation. Fifty percent of Dicosmoecus collected at this time were in diapause. Pulmonate snails proliferated, however, with densities two-fold greater and biomasses ten-fold greater in August than in July. Helicopsyche larval densities increased 8X but with a proportional decrease in biomass caused by Helicopsyche emergence during the experimental period. Consequently, Day 0 Helicopsyche populations consisted of relatively few, large larvae and many pupae, whereas by Day 32 numerous young larvae and no pupae were present. Among the mayflies, densities of heptageniids, Paraleptophlebia, and Tricorythodes all declined by half, while biomasses increased, indicating cycles of growth and emergence.

In experimental pools with high Dicosmoecus numbers, abundances of total benthic invertebrates were relatively low (Table 2.7; Fig. 2.4), with particularly strong declines in collectors ($r = -0.67$ and -0.65 in July and August, respectively; $p < 0.01$). Chironomids appeared to be particularly affected by Dicosmoecus presence in July ($r = -0.75$; $p < 0.001$).

Table 2.7. Correlation matrix of densities (number/m^2) of two dominant
Camp Creek grazers vs. total invertebrate density. Snails include the genera
Gyraulus, Fossaria, and Physa. Values are Pearson correlation coefficients;
* = p<0.05.

	Total Invertebrates
Day 0 (14 July)	
Dicosmoecus	-0.55*
Pulmonate snails	0.08
Day 32 (14 August)	
Dicosmoecus	-0.57*
Pulmonate snails	-0.09
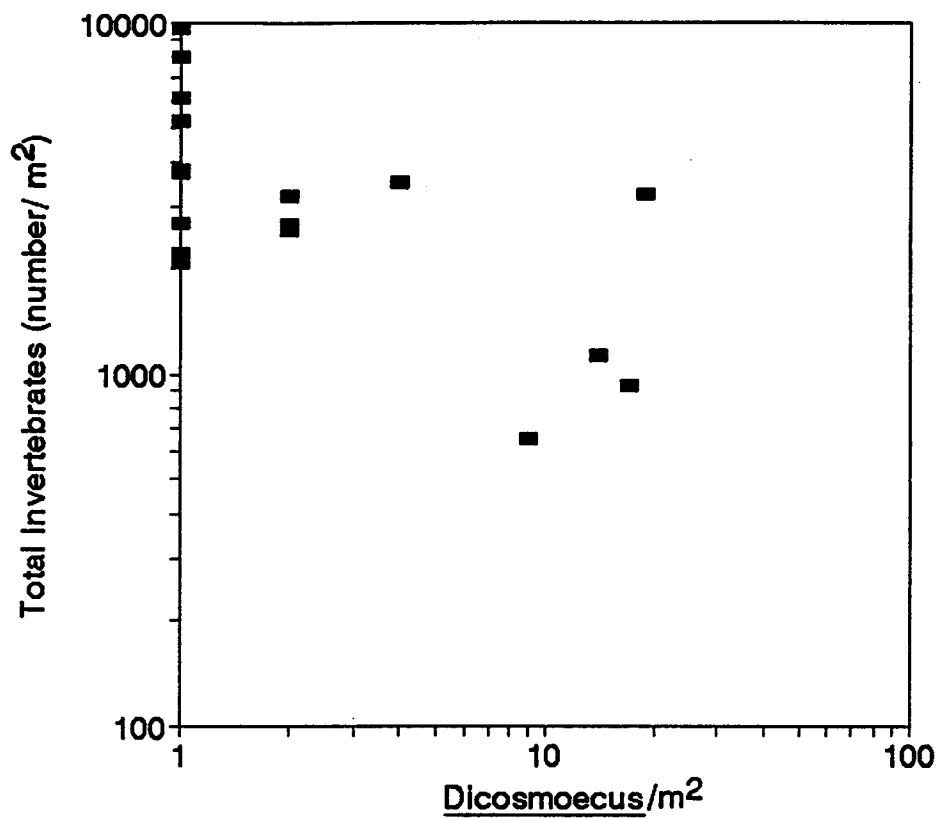
Fig. 2.4. Correlation of log-transformed total invertebrate density with Dicosmoecus density in mid-August pools ($r = -0.57$; $p < 0.05$, $n = 18$).

The lepidopteran <u>Petrophila</u> and hydroptilid caddisflies, sessile taxa that colonize bare rock surfaces and would be expected to benefit from algal removal, were not significantly correlated with <u>Dicosmoecus</u> abundance. Although pulmonate snails also reduced algal biomass in experimental pools (see below), their abundance showed no relationship to abundances of other invertebrates (Table 2.7).

Relationship between macroinvertebrates and periphyton

Grazer exclusion

Platforms installed in three of the experimental pools isolated the impacts of grazers and collectors on periphyton by generally reducing invertebrate densities relative to densities on surrounding substrates. Primarily mayflies (baetids, heptageniids, leptophlebiids, and <u>Tricorythodes</u>) and chironomids occurred on platform rocks. Baetids and leptophlebiids appeared to colonize platform rocks at higher than ambient densities, whereas heptageniids occurred at densities similar to those on the streambed. Snails were found on platform rocks at about 10% and chironomids at 50% of their streambed abundances. No caddisflies were found on platforms.

Algae accrued at a higher rate on platforms than on grazed substrates (Fig 2.5). At Day 10, platform periphyton biomass averaged 3X greater than biomass on control substrates. By Day 32 variability in periphyton abundance had increased, but platform AFDM (mean $= 32.6$ g/m^2; SE $= 9.7$) was still significantly greater ($p < 0.01$) than substrate AFDM (mean $= 14.1$ g/m^2; SE $= 3.4$).
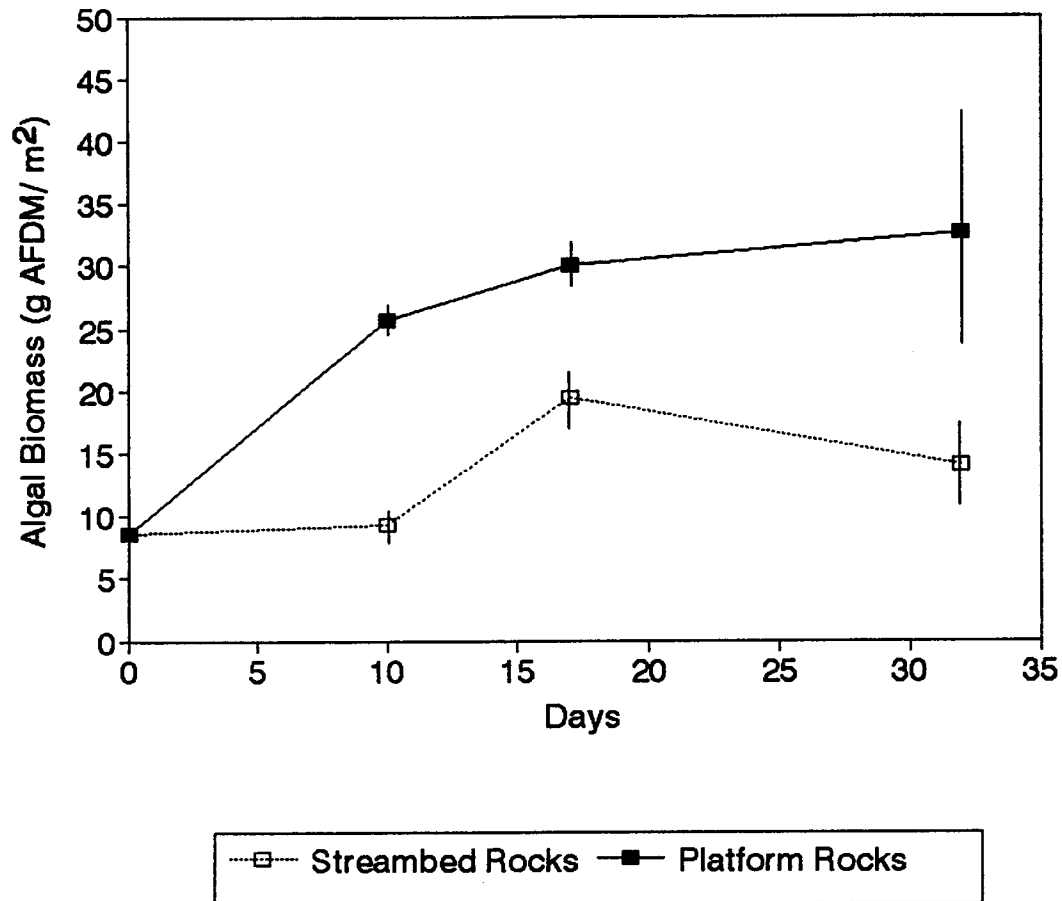
Fig. 2.5. Comparison of mean algal biomass accrual between two grazing treatments in three log weir pools. Grazing is reduced on platform treatments; streambed rocks are controls. Bars represent ± 1 standard error.

Because algivorous mayflies and chironomids had access to periphyton both on platforms and surrounding substrates, differences in algal biomass between grazed and grazing-reduced surfaces were not likely attributable to these organisms. However, the platforms completely excluded Dicosmoecus and reduced snail densities by 90%. These two grazers accounted for 39% and 34%, respectively, of total invertebrate biomass in the three platform pools, and one or both could potentially reduce algal standing crops (Jacoby 1987; Lamberti et al. 1989; Barnese et al. 1990). In the three platform pools, the largest grazing effect (D), calculated as the simple absolute difference between AFDM on grazed and ungrazed surfaces (Feminella and Hawkins 1995), occurred where Dicosmoecus biomass was high (Fig 2.6), suggesting that high biomasses of this caddisfly reduced periphyton to levels significantly below its potential abundance. In a Cascade Range stream, densities of Dicosmoecus were higher and stream temperatures, elevations, and probably irradiance were lower than Camp Creek, but grazed and ungrazed periphyton AFDM (5 and 25 g AFDM/m^2, respectively) were remarkably similar to mid-July levels in our study (Jacoby 1987). In contrast, the grazing effect decreased in the Camp Creek pools where snail biomasses were relatively higher than Dicosmoecus biomasses (Fig. 2.6), suggesting that snails were not as effective as Dicosmoecus in reducing periphyton. The inverse relationship between these two grazer abundances may suggest interspecific competition or exclusion, but there were no significant relationships between Dicosmoecus and snail densities or biomasses among the experimental pools.
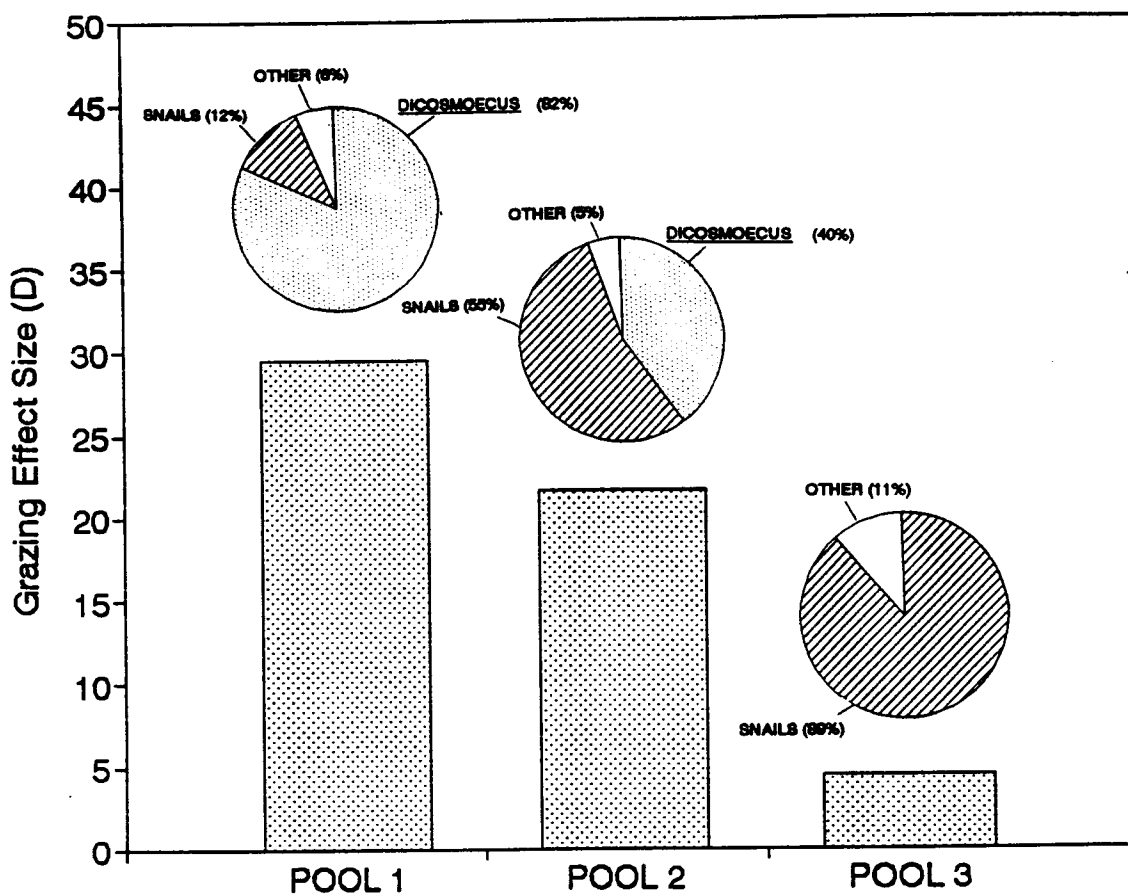
Fig. 2.6. Relative biomasses of grazers on streambed rocks in three log weir pools. Bars represent grazing effect size (D), the simple absolute difference in g AFDM/m² between grazed and grazing-reduced treatments.

Impacts of Dicosmoecus densities in nonexperimental pools

In the two adjacent, unmanipulated log weir pools, caddisfly and periphyton abundances differed sharply (Table 2.8). In the lower pool where upstream movement of larvae was blocked by an exposed log weir, Dicosmoecus reached densities of $78.5/m^2$. Density of Dicosmoecus in the upper pool was $3.5/m^2$ and comparable to average August densities in the 18 experimental pools nearby. Upper pool periphyton biomass was 2X higher and filamentous algal cover 20X greater than in the lower pool where Dicosmoecus were abundant. Dicosmoecus grazing appeared to have a disproportionately greater effect on surface area coverage than on mass per unit area for periphyton.

Competition for limited food resources was suggested in the lower pool, where average individual masses for caddisfly larvae were significantly lower ($p < 0.001$) than in the pool above. When a Cladophora-covered rock (44 cm X 22 cm) from the upper pool was placed in the lower pool, 65 Dicosmoecus larvae were grazing its surface within 24 h. Algal filaments 30 mm in length were cropped to <5 mm or removed entirely, and 20% of the rock surface was bare after 42 h.

Macroinvertebrate abundance and periphyton

In the experimental pools, by Day 32 filamentous algal cover and periphyton AFDM were positively and significantly correlated with total invertebrate density as well as densities of all individual invertebrate guilds (Table 2.5). As on Day 0, invertebrate biomasses varied in their associations with algae. Total invertebrate, shredder, and predator biomasses did not correlate with either measure of algal abundance.

Table 2.8. Comparison of two adjacent log weir pools with differing densities of larval Dicosmoecus gilvipes. Pools were not among the 18 experimental pools. Sampling occurred 3 August 1990. Standard errors are in parentheses.

	Lower pool	Upper pool
Dicosmoecus density (number/m^2)	78.5 (±18.4)	3.5 (±0.4)
Mean individual mass (mg DW/Dicosmoecus)	35.8 (±0.2)	56.7 (±0.4)
% Filamentous algae	3.0 (±0.7)	57.0 (±7.2)
Periphyton biomass (g AFDM/m^2)	6.8	15.2
Fish density (number/m^3)	3.0	5.8
Pool volume (m^3)	11.7	5.4
Solar input (Mj/m^2)	1725	1437

Collector biomass (predominantly mayflies and chironomids) was positively associated with both filamentous algal cover and periphyton AFDM. Grazer biomass was not related to AFDM but was negatively correlated to filamentous algal cover. This inverse relationship was driven by the dominance of Dicosmoecus and pulmonate snails (Table 2.9; Fig. 2.2). Where filamentous algal cover was low, both taxa were more abundant, but AFDM did not appear to be related to these grazers. Biomasses of other individual grazers, such as heptageniid mayflies and Helicopsyche, were positively correlated ($p = <0.01$) with both measures of algal standing crop.

Relationship between fish density and benthic communities

Fish diet analysis

Analysis of stomach contents from speckled dace and rainbow trout collected from six experimental pools on Day 32 (Fig. 2.7) indicated that grazers and collectors made up the majority of their diet by number. The only filterer present in stomachs was the caddisfly Hydropsyche, which rarely occurred in benthic samples. Apparently fishes foraged for Hydropsyche at the head of pools on weir logs which were not sampled for invertebrates. Predators consumed were primarily water striders, mites, and the caddisfly Oecetis.

The diets of both fish species were dominated by mayflies, primarily baetids, heptageniids, Paraleptophlebia, and Tricorythodes. Among mayflies, electivity indices showed strong election of Baetis, a frequent drifter (Waters 1972), and Tricorythodes over their availability, whereas election for heptageniids, a group less likely to drift, was weak (Table 2.10).

Table 2.9. Correlation matrix of densities (number/m^2), and biomasses (mg DW/m^2) of two dominant Camp Creek grazers vs. periphyton biomass (g AFDM/m^2) and percent filamentous algal cover. Snails include the genera Gyraulus, Fossaria, and Physa. Values are Pearson correlation coefficients; ** = p<0.01, * = p<0.05.

	Periphyton		% Algal Cover	
	Density	Biomass	Density	Biomass
Day 0 (14 July)				
Dicosmoecus	-0.54*	-0.59*	-0.72**	-0.57*
Pulmonate snails	-0.19	-0.35	-0.16	-0.31
Day 32 (14 Aug)				
Dicosmoecus	-0.09	-0.24	-0.70**	-0.48*
Pulmonate snails	-0.06	-0.07	-0.47	-0.50*

RAINBOW TROUT
(juveniles)

Terrestrials (7.0%)
Filterers (5.5%)
Predators (8.2%)
Other (4.9%)
Grazers (40.0%)
Collectors (34.4%)

SPECKLED DACE
(adults and juveniles)

Filterers (6.0%)
Predators (5.0%)
Other (2.5%)
Grazers (40.0%)
Collectors (46.5%)
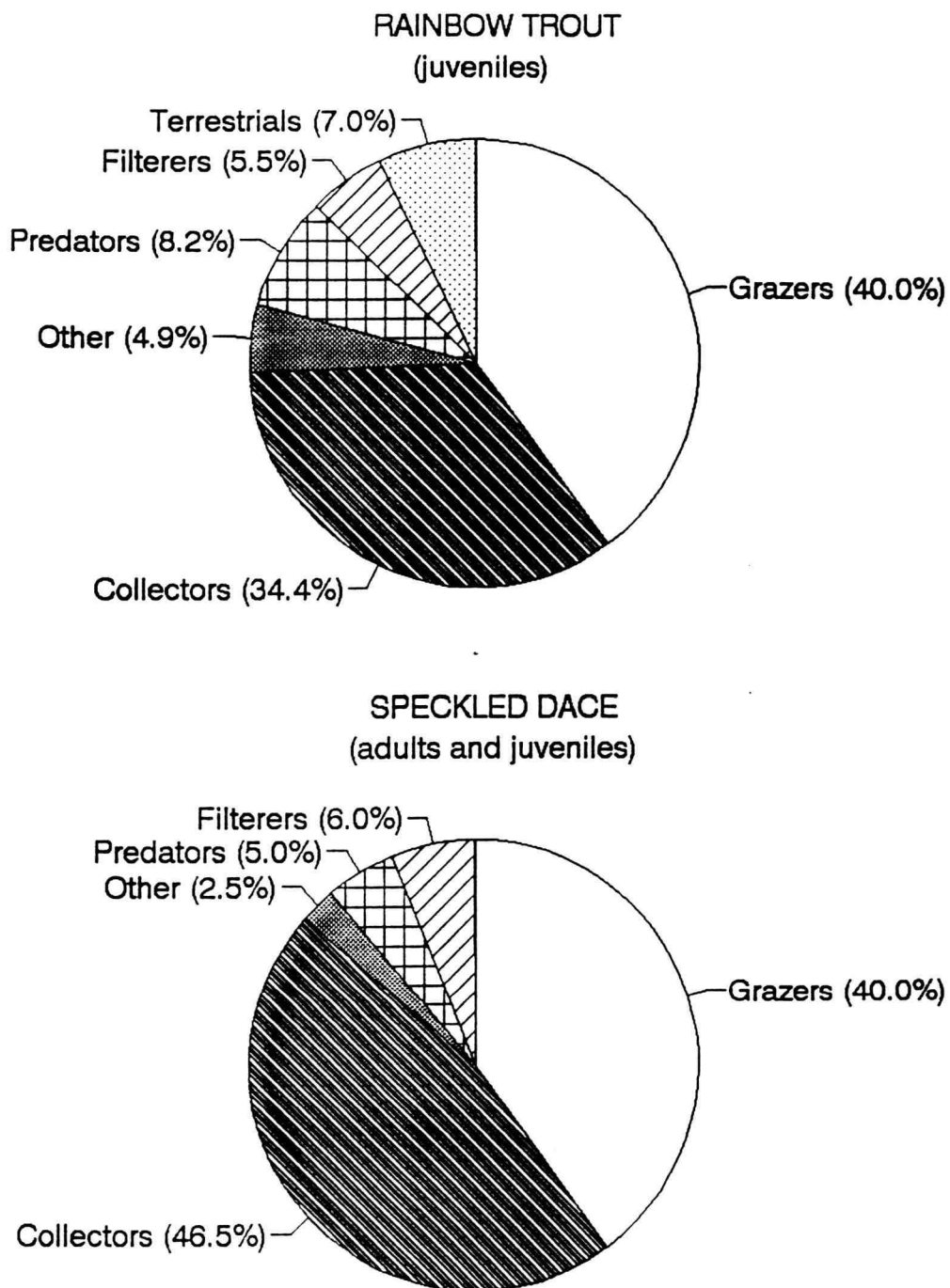
Fig. 2.7. Fish diets based on percent composition of invertebrate functional feeding groups. Juvenile rainbow trout (n = 36) and juvenile and adult speckled dace (n = 31) were collected at the end of the experiment.

Table 2.10. Percent composition (%) of fish stomach contents by number of most common prey taxa. $\underline{D}$ = Electivity Index; $\underline{D}$ values of -1.00 to -0.50 indicate strong avoidance of that prey; -0.49 to -0.26, moderate avoidance; -0.25 to +0.25, neutral selection; +0.26 to +0.49, moderate selection; and +0.50 to +1.00, strong selection (Moyle and Baltz 1985). SPD = speckled dace; RBT = rainbow trout; juv = juvenile; yoy = young-of-the-year.

	Mayflies (all taxa)		Helicopsyche		Chironomids		Snails	
	%	D	%	D	%	D	%	D
SPD adult	46.3	0.66	2.6	-0.66	17.0	-0.13	22.0	-0.08
SPD juv	66.6	0.84	0	-1.00	3.5	-0.73	0	-1.00
RBT juv	46.8	0.67	1.8	-0.76	5.7	-0.61	2.7	-0.85
RBT yoy	73.5	0.88	3.5	-0.56	0	-1.00	3.6	-0.80

Pulmonate snails, although comprising 22% of adult speckled dace diets and about 3% of trout diets, were only neutrally or negatively selected relative to abundance. Chironomids also had low electivities despite their high densities in pools, probably because foraging for them was difficult where algal growth was thick.

Torrent sculpins generally occurred at lower densities than speckled dace or trout (Table 2.2) and were primarily piscivorous. Out of seven stomachs analyzed, 3 had one mayfly, 1 had 2 mayflies, and five had fish.

Largescale suckers

Largescale suckers were stocked in three experimental pools at densities of 3.33 fish/m^3. No other fishes were placed in these pools, but by Day 32 combined densities of speckled dace, rainbow trout, and torrent sculpin exceeded sucker numbers. In addition, some suckers disappeared from pools during the experiment (one pool lost 75% of its fish), either through escapement or predation by kingfishers or other terrestrial predators. Consequently, any potential benthic responses to sucker presence were confounded by decreases in sucker density and invasion by other fish species. Not unexpectedly, by Day 32 sucker pools did not differ in macroinvertebrate or periphyton abundances from other experimental pools with similar total fish densities. Observations of foraging behavior of largescale suckers indicated that feeding time was equally split between hovering over epilithic biofilms (consisting of Cladophora basal cells, Oscillatoria, and the diatoms Epithemia, Cocconeis, Cymbella, Synedra, and Navicula) and picking at algal filaments.

Fish density and macroinvertebrates

The presence of varying densities of rainbow trout, speckled dace, and torrent sculpin had no significant negative effects on numbers or biomasses of macroinvertebrate guilds in the experimental pools (Table 2.6). The abundances of mayflies, a highly preferred prey, and snails, a non-preferred prey, were unrelated to fish density, with the probability of Type II error less than 0.10. A positive correlation between fish density and predator and chironomid densities, and the positive, nearly significant relation of fish with collector and total invertebrate densities, were linked to partial correlations of these groups with periphyton AFDM (Table 2.11).

Fish density and periphyton

Fish densities at the end of the experiment were positively correlated with periphyton biomass and filamentous algal cover (Table 2.5; Fig. 2.8), though the association with algal cover was not significant. Because no negative effects of fish on any invertebrate guild were detected, higher algal abundance with higher densities of fish was not attributable to a reduction of herbivorous invertebrates and subsequent increase in algal production. No associations were apparent ($r = 0.17$; $p = 0.52$) between periphyton biomass and the natural fish densities present in study pools before the start of the experiment.

Table 2.11. Partial correlations of selected invertebrate densities (number/m^2) vs. fish density (number/m^3), with the variable periphyton (g AFDM/m^2) held constant. None were significant.

Day 32 (14 Aug)

	<u>Fish Density</u>
Total invertebrates	0.13
Collectors	0.21
Predators	0.27
Chironomidae	0.42
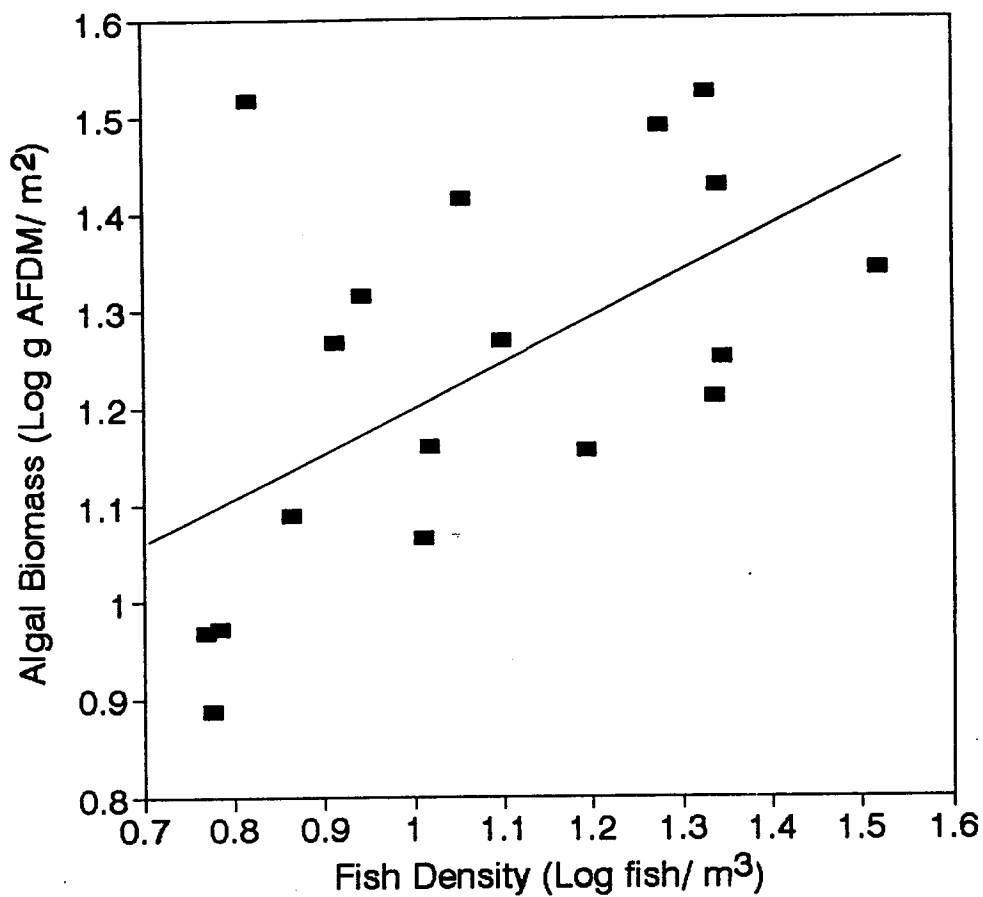
Fig. 2.8. Regression of fish density vs. periphyton biomass in mid-August experimental pools. Best fit to line is $\log_{10} y = 0.45 \log_{10} x + 0.76$; $R^2 = 0.30$; $p < .05$.

Discussion

Effects of fish on benthic communities

The presence of predaceous fishes had no detectable negative effects on densities or biomasses of invertebrate guilds in the Camp Creek experimental pools. Although both speckled dace and rainbow trout fed heavily on mayflies and snails, neither of these invertebrate groups were significantly impacted. Whereas some studies in streams have demonstrated that vertebrate predators have significant top-down effects on their prey (Crowder and Cooper 1982; Gilliam et al. 1989; Powers 1990), other studies in freshwater habitats have shown predaceous vertebrates to have little or no effect on other trophic levels (Allan 1982; Reice and Edwards 1986; Culp 1986). The lack of a measurable decline in prey abundance in this study may be attributable to several factors, including prey exchange, habitat complexity, and abundance of algal resources.

The magnitude of prey exchange (immigration/recruitment or emigration) between habitat patches has a strong influence on the detectable effects of predators on prey in stream studies (Cooper et al. 1990). Predator impacts are governed by the rates of prey depletion relative to prey immigration through drift or recruitment, and by factors such as sufficient upstream habitat to provide a continuous supply of prey (Power 1992a). Large mesh sizes on enclosure cages and high flow rates also facilitate movement of prey. A recent meta-analysis of predator impact studies on stream benthic prey (Cooper et al. 1990) indicated that large-meshed cages (>4mm), which freely allow prey drift and recolonization, may show fewer predator effects than small-meshed cages, especially when placed in habitats with fast flow. Camp Creek enclosure meshes of 4mm X

16mm were large and should not have impeded prey immigration or emigration. Although velocities in the pools were relatively slow, drift rates of incoming mayfly nymphs from continuous riffle habitat upstream were high (J. Li, unpublished data) and may have swamped prey reductions by fish. Power (1992a) found fish predator impacts to be strong in Cladophora on bedrock "islands" isolated from potential sources of invertebrate drift, whereas impacts were weak in enclosures set up on long gravel bars where invertebrate production constantly replenished the prey.

Fish may also be less effective in structuring lower trophic levels in ecosystems where primary production is high. Power et al. (1996) postulated that in mesotrophic systems, rapid growth of aquatic vegetation allows faster recruitment and more refuges for prey than oligotrophic systems, and fish predation is unable to deplete prey. Because Camp Creek pools were warm and unshaded, algal standing crop was high and may have weakened top-down consumer impacts on lower trophic levels.

Although fish in Camp Creek did not reduce prey abundance in experimental pools, there was significantly more periphyton in pools with higher fish densities (Fig. 2.8). Increases in periphyton could occur if fish predation reduced the abundance of herbivores (Bechara et al. 1992), but there was no evidence of this in our study. Alternatively, predators can indirectly increase algal abundance by altering herbivore behavior without reducing their numbers. In an Oklahoma stream, the presence of tethered smallmouth bass restricted foraging by algivorous chubs and caused localized algal blooms (Power et al. 1985). In a tropical stream, avoidance of avian predators by herbivorous armored catfish allowed algae to grow uncropped in nearshore shallows (Power 1984). Foraging behaviors of macroinvertebrate grazers are also affected by the presence of predators.

Peckarsky et al. (1993) reported that for Baetis mayflies, algal consumption rates and, consequently, Baetis growth and fecundity, were reduced in the presence of predaceous stoneflies. In another study, the presence of sculpin similarly reduced Baetis foraging; the mayflies were restricted to suboptimal algal patches in unexposed crevices (Kohler and McPeek 1989). A direct link between fish-induced reduction in macroinvertebrate grazing and increased algal biomass was demonstrated in a New Zealand stream (McIntosh and Townsend 1996). In enclosures with brown trout, a visual feeder, and tactile-foraging common river galaxias, foraging times of a dominant leptophlebiid mayfly on rock surfaces were greatly reduced, though mayfly densities were unaffected. In treatments with fish, algal AFDM was 2X greater than in treatments without fish where mayflies could feed freely. This suggests that the presence of trout produced a trophic cascade driven by changes in the behavior of the primary consumer rather than by its removal. In Camp Creek pools, both visual (trout) and tactile foragers (dace) were present at high densities and their combined activities may have reduced feeding rates of small invertebrate grazers, especially mayflies, causing a subsequent increase in periphyton levels.

Another explanation for higher periphyton AFDM in high density fish treatments may be nutrient enhancement in the enclosures. An increase in nutrient availability due to nitrogenous waste from fish concentrated in pools can stimulate algal growth (Threlkeld 1987). Because cage screens were cleaned daily and mesh sizes were large enough to permit nearly natural flows, the probability of nutrient accumulations was reduced. However, no water chemistry data that compare nutrient concentrations inside and outside enclosures were obtained.

Lack of predator impacts can occur when prey increase as predators increase. These "unexpected results" often arise through higher-order interactions where predators reduce the densities of the enemies (competitors or intermediate predators) of their prey (Sih and Wooster 1994). In Camp Creek, negative predator effects occurred with chironomids and invertebrate predators. Density of invertebrate predators and density and biomass of chironomids were positively correlated with fish density. Although increases in chironomid abundance were observed in studies where fish predation depleted numbers of intermediate invertebrate predators (Crowder and Cooper 1982; Power 1990; Bechara et al. 1992; Diehl 1992), there was no evidence in this study, either correlative or dietary, that fish predation impacted abundance of invertebrate predators. A more likely mechanism for lack of predator effects is that benefits to invertebrates caused by the periphyton increase associated with higher fish densities outweighed the deleterious effects of predation. With higher algal resources, not only is the food base greater for herbivores but more detritus and prey are available for collectors and predators (Dudley et al. 1986). In addition, thicker growths of periphyton provide more complex and heterogeneous spatial refuges for invertebrates, and decrease foraging efficiencies of fish (Crowder and Cooper 1982; Gilinsky 1984; Sih et al. 1985).

The role of Dicosmoecus gilvipes in the regulation of benthic communities

The caddisfly Dicosmoecus gilvipes was a dominant and effective herbivore in Camp Creek. Although frequently consumed by terrestrial vertebrates such as dippers (Teague et al. 1985), late-instar Dicosmoecus

larvae escaped predation by speckled dace and juvenile trout because of their large size and heavy case. Dicosmoecus played a key role in the regulation of benthic algal abundance and composition in Camp Creek, especially during late-instar stages in mid-summer. Fifth instars, which were most abundant in late July, have much higher nutritional demands and foraging rates than younger instars, resulting in intense algal consumption (Li and Gregory 1989; Lamberti et al. 1992). In artificial stream studies, fifth-instar Dicosmoecus at natural densities reduced periphyton to lower levels than did Baetis or Juga by removing filamentous overstory algae and thick understory mats of diatoms (Lamberti et al. 1987; DeNicola et al. 1990). Jacoby (1987) observed in situ that Dicosmoecus removed almost all overstory and filamentous algal species from cobbles, leaving only smaller adnate cells.

Although late-instar Dicosmoecus larvae are capable of rapid depletion of periphyton, their window of peak consumptive demand is narrow. In mid-July on Camp Creek, 60% of Dicosmoecus were fourth instars and 5% were fifth instars. By the first week of August, 98% were fifth instars, but half the population had entered diapause, sealing their cases to the underside of cobbles. By September all larvae were in diapause. John Day Basin streams that are exposed to high daily solar input lack a diversity of benthic grazers able to restrict periphyton abundance. When diapause is complete and fifth-instar Dicosmoecus are no longer feeding, periphyton is released from grazer control despite a high relative biomass of herbivorous snails in late summer. Although September periphyton abundance was not measured in Camp Creek, comparisons were possible between mid-July and September algal biomasses at stream sites in lower John Day Basin. In four low canopy or partially canopied stream reaches (Chapter 1, Table 1.1),

algal AFDM levels were 1.5 to 2.5 times higher in mid-September (after Dicosmoecus diapause) than in mid-July (when Dicosmoecus were active) (Table 2.12).

Although Jacoby (1987) reported that the period of highest nutritional needs for fifth-instar larvae coincided with peak periphyton production in a western Washington stream, Dicosmoecus appeared to be decoupled from temporal cycles of food availability in unshaded eastern Oregon streams. In John Day Basin streams the period of high algal abundance extends into autumn, and algal standing crops are reduced, but not eliminated, by Dicosmoecus for only a few weeks.

The potential for exploitative competition is high with an organism that can rapidly deplete algal resources. Intraspecific exploitative competition was suggested in the non-experimental log weir pool where Dicosmoecus density was high. Because filamentous algae provide food, cover, and structure for many invertebrates (Dudley et al. 1986; Power 1990; Hart 1992), grazing by Dicosmoecus can also have deleterious effects on other benthic species. Densities of other benthic invertebrates were negatively correlated with Dicosmoecus abundance on Camp Creek as well as in a Cascade Range stream with low canopy cover (Lamberti et al. 1992). At both sites, small invertebrates may be subject to direct interference by Dicosmoecus through bulldozing or predation. Small invertebrates may also be responding to periphyton abundance and thus indirectly to algal removal by Dicosmoecus. Algal overstory removal can benefit some benthic invertebrates by providing specific epilithic habitats unavailable with dense algal growth. Where crayfish consumption eliminated Cladophora from pools of a Michigan stream, density of sessile grazers such as Leucotrichia and Psychomyia increased (Creed 1994).

Table 2.12. Comparison of periphyton biomasses (g AFDM/m^2) measured in lower John Day Basin study reaches in mid-July and mid-September, 1988. See Table 1.1 for reach physical characteristics.

Site	July	September	Sept/July
RC2	29.1	57.9	2.0
MUR	43.3	106.1	2.5
MTC	27.2	39.2	1.4
RC3	23.4	35.1	1.5

In this study, the silk cases of hydroptilid caddisflies and Petrophila were more apparent on cobbles where filamentous algal cover was low, but there were no positive associations between Dicosmoecus numbers and these species. It may be that the interval for active feeding and control of algal cover by the caddisfly is too brief, whereas crayfish influence lasts several months in Michigan and allows considerable time for colonization and completion of sessile invertebrate life cycles.

Dicosmoecus not only impacts its immediate community by depleting periphyton, but may also influence downstream communities by dislodging algal material and possibly small invertebrates (Lamberti et al. 1992). In artificial streams, Dicosmoecus hastened export of undigested algae downstream by dislodging filaments with their tarsal claws and heavy mineral cases (Lamberti et al. 1987; DeNicola et al. 1990). Algal food resources entrained in the current would benefit collectors, filterers, and, indirectly, predators downstream from the site of entrainment.

Because of its ability to regulate algal abundance and composition, and to influence benthic community structure through direct and indirect effects on algae and invertebrates, Dicosmoecus acts as a keystone species in this stream. Elaborating from Paine (1969), Power et al. (1996) defined a keystone species as one whose impact on its community is disproportionately large relative to its abundance. To quantify this impact, Power et al. (1996) suggested estimating "community importance" (CI), a measure similar to interaction strength (Paine 1992), where a species' impact on a community is estimated by removing that species and comparing a particular community trait, such as diversity or nutrient availability, with and without the species. CI is calculated as

$$CI = [(t_N - t_D)/t_N](1/p_i)$$

where t_N is the quantitative measure of a trait in the intact community and t_D is the trait without species i. In our study, Dicosmoecus was species i and the community trait was periphyton AFDM on stream substrates (t_N) and on Dicosmoecus-excluded platforms (t_D) of three experimental pools. P_i is the proportional abundance of species i, in this case Dicosmoecus biomass (g/m^2) on pool substrates. A CI with an absolute value much greater than 1 indicates that species i is a keystone organism. Average CI for Dicosmoecus was -52, which suggests keystone status for this species in Camp Creek.

Many keystone species are context dependent, and are not necessarily controlling agents in all parts of their range or at all times (Menge et al. 1994; Power et al. 1996). The impacts Dicosmoecus has on algal community structure changes seasonally in tandem with ontogenetic development (Li and Gregory 1989), and were at maximal strength in Camp Creek for only one month in mid-summer. Periphyton in uncanopied streams recovers quickly when released from intense herbivory, but long-term indirect effects of Dicosmoecus on other benthic organisms are unknown. Although the interval of peak feeding activity of Dicosmoecus is brief, even a temporary depletion of algae that provide food and cover may negatively affect multivoltine invertebrates with life cycles of days or weeks.

Conclusions

In Camp Creek, experimental pools with high fish densities had more periphyton than pools with less fish, and invertebrate abundances closely tracked algal standing crops. An increase in invertebrate abundance with increasing periphyton indicates a community structure controlled from the

bottom up by resource availability. Although top-down impacts of fish predation were not detected, a direct downward control was exerted by the primary consumer Dicosmoecus on algal standing crops and, indirectly, on invertebrate densities and biomasses.

Plants, through their productivity, provide fundamental control of food webs by determining the number of trophic levels possible. Ultimately, plants influence the top-down forces that, in turn, regulate their standing crops (Fretwell 1987; Oksanen et al. 1981; Power 1992b). A keystone herbivore can alter composition and abundance of plant communities in the trophic level below, and these changes can transfer up the food web beyond the herbivore level (Hunter and Price 1992). Dicosmoecus appears to act as an "intermediate regulator" (sensu Lamberti 1996) in the benthic food web of Camp Creek by simultaneously influencing trophic levels both below and above its own. Like the prosobranch snail Juga, an intermediate regulator in northwest streams (Hawkins and Furnish 1987; Lamberti et al. 1989; Lamberti 1996), Dicosmoecus directly reduces periphyton and indirectly reduces abundance of other invertebrates. At the same time, Dicosmoecus may limit top trophic levels. Because its large size and heavy case precludes consumption by the small predaceous fish inhabiting Camp Creek, high abundances of the caddisfly may inhibit fish growth and viability.

Acknowledgments

References

Aho, R. S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of stream. M.S. Thesis. Oregon State University, Corvallis.

Allan, J. D. 1982. The effects of reduction in trout density on the invertebrate community of a mountain stream. Ecology 63:1444-1455.

Barnese, L. E., R. L. Lowe, and R. D. Hunter. 1990. Comparative grazing efficiency of pulmonate and prosobranch snails. Journal of the North American Benthological Society 9:35-44.

Bechara, J. A., G. Moreau, and D. Planas. 1992. Top-down effects of brook trout (Salvelinus fontinalis) in a boreal forest stream. Canadian Journal of Fisheries and Aquatic Sciences 49:2093-2103.

Bisson, P. A., and J. R. Sedell. 1984. Salmonid populations in streams in clearcut vs. old-growth forests of western Washington. Pages 121-129 in W. R. Meehan, T. R. Merrell and T. A. Hanley (editors). Fish and wildlife relationships in old-growth forests: proceedings of a symposium held in Juneau, Alaska, 12-15 April 1982. American Institute of Fishery Research Biologists, Asheville, N. C.

Bowlby, J. N., and J. C. Roff. 1986. Trophic structure in southern Ontario streams. Ecology 67:1670-1679.

Brett, M. T., and C. R. Goldman. 1996. A meta-analysis of the freshwater trophic cascade. Proceedings of the National Academy of Sciences 93:7723-7726.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634-639.

Cooper, S. D., S. J. Walde, and B. L. Peckarsky. 1990. Prey exchange rates and the impact of predators on prey populations in streams. Ecology 71:1503-1514.

Creed, R. P. 1994. Direct and indirect effects of crayfish grazing in a stream community. Ecology 75:2091-2103.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802-1813.

Culp, J. M. 1986. Experimental evidence that stream macroinvertebrate community structure is unaffected by different densities of coho salmon fry. Journal of the North American Benthological Society 5:140-149.

DeNicola, D. M., C. D. McIntire, G. A. Lamberti, and L. R. Ashkenas. 1990. Temporal patterns of grazer-periphyton interactions in laboratory streams. Freshwater Biology 23:475-489.

Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73:1646-1661.

Dudley, T. L., S. D. Cooper, and N. Hemphill. 1986. Effects of macroalgae on a stream invertebrate community. Journal of the North American Benthological Society 5:93-106.

Feminella, J. W., and C. P. Hawkins. 1995. Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. Journal of the North American Benthological Society 14:465-509.

Feminella, J. W., M. E. Power, and V. H. Resh. 1989. Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. Freshwater Biology 22:445-457.

Forrester, G. E. 1994. Influences of predatory fish on the drift dispersal and local density of stream insects. Ecology 75:1208-1218.

Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? Oikos 50:291-301.

Gerking, S. D. 1994. Feeding ecology of fish. Academic Press, San Diego.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65:455-468.

Gilliam, J. F., D. F. Fraser, and A. M. Sabat. 1989. Strong effects of foraging minnows on a stream benthic invertebrate community. Ecology 70:445-452.

Gregory, S. V. 1983. Plant-herbivore interactions in stream systems. Pages 157-189 in J. R. Barnes and G. W. Minshall (editors). Stream ecology: application and testing of general ecological theory. Plenum Press, New York.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421-425.

Hart, D. D. 1992. Community organization in streams: the importance of species interactions, physical factors, and chance. Oecologia 91:220-228.

Hawkins, C. P., and J. K. Furnish. 1987. Are snails important competitors in stream ecosystems? Oikos 49:209-220.

Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and

physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173-1185.

Hemphill, N., and S. D. Cooper. 1984. Differences in the community structure of stream pools containing or lacking trout. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22:1858-1861.

Hill, W. R., H. L. Boston, and A. D. Steinman. 1992. Grazers and nutrients simultaneously limit lotic primary productivity. Canadian Journal of Fisheries and Aquatic Sciences 49:504-512.

Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology 76:1297-1309.

Holomuzki, J. R., and R. J. Stevenson. 1992. Role of predatory fish in community dynamics of an ephemeral stream. Canadian Journal of Fisheries and Aquatic Sciences 49:2322-2330.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724-732.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto.

Jacobs, J. 1974. Quantitative measurement of food selection. Oecologia 14:413-417.

Jacoby, J. M. 1987. Alterations in periphyton characteristics due to grazing in a Cascade foothill stream. Freshwater Biology 18:495-508.

Kohler, S. L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. Ecology 66:1749-1761.

Kohler, S. L., and M. A. McPeek. 1989. Predation risk and the foraging behavior of competing stream insects. Ecology 70:1811-1825.

Lamberti, G. A. 1996. The role of periphyton in benthic food webs. Pages 533-572 in R. J. Stevenson, M. L. Bothwell and R. L. Lowe (editors). Algal ecology. Academic Press, San Diego.

Lamberti, G. A., L. R. Ashkenas, S. V. Gregory, and A. D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. Journal of the North American Benthological Society 6:92-104.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, A. D. Steinman, and C. D. McIntire. 1989. Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. Ecology 70:1840-1856.

Lamberti, G. A., S. V. Gregory, C. P. Hawkins, R. C. Wildman, L. R. Ashkenas, and D. M. DeNicola. 1992. Plant-herbivore interactions in streams near Mount St Helens. Freshwater Biology 27:237-247.

Lamberti, G. A., and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64:1124-1135.

Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, and J. L. Li. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Transactions of the American Fisheries Society 123:627-640.

Li, J. L., and S. V. Gregory. 1989. Behavioral changes in the herbivorous caddisfly Dicosmoecus gilvipes (Limnephilidae). Journal of the North American Benthological Society 8:250-259.

McAuliffe, J. R. 1984. Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. Oikos 42:327-333.

McIntosh, A. R., and C. R. Townsend. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? Oecologia 108:174-181.

McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs 59:289-309.

Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? Ecology 73:755-765.

Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs 64:249-287.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110:351-369.

---. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730-757.

Merritt, R. W., and K. W. Cummins. 1984. An introduction to the aquatic insects of North America. Kendall Hunt Publishers, Dubuque, Iowa.

Moyle, P. B., and D. M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Transactions of the American Fisheries Society 114:695-704.

Oksanen, L. 1988. Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for existence? American Naturalist 131:424-444.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240-261.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65-75.

---. 1969. A note on trophic complexity and community stability. American Naturalist 103:91-93.

---. 1992. Food web analysis through field measurement of per capita interaction strength. Nature 355:73-75.

Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology 74:1836-1846.

Peterson, B. J., L. Deegan, J. Helfrich, J. E. Hobbie, M. Hullar, B. Moller, T. E. Ford, A. Hershey, A. Hiltner, G. Kipphut, M. A. Lock, D. M. Fiebig, V. McKinley, M. C. Miller, J. R. Vestal, R. Ventullo, and G. Volk. 1993. Biological responses of a tundra river to fertilization. Ecology 74:653-672.

Power, M. E. 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. Journal of Animal Ecology 53:357-374.

---. 1990. Effects of fish in river food webs. Science 250:811-814.

---. 1992a. Hydrologic and trophic controls of seasonal algal blooms in northern California rivers. Archiv für Hydrobiologie 125:385-410.

---. 1992b. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733-746.

Power, M. E., W. J. Matthews, and A. J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. Ecology 66:1448-1456.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. BioScience 46:609-620.

Pringle, C. M., R. J. Naiman, G. Bretschko, J. R. Karr, M. W. Oswood, J. R. Webster, R. L. Welcomme, and M. J. Winterbourn. 1988. Patch dynamics in lotic systems: the stream as a mosaic. Journal of the North American Benthological Society 7:503-524.

Reice, S. R., and R. L. Edwards. 1986. The effect of vertebrate predation on lotic macroinvertebrate communities in Quebec, Canada. Canadian Journal of Zoology 64:1930-1936.

Richards, C., and G. W. Minshall. 1988. The influence of periphyton abundance on Baetis bicaudatus distribution and colonization in a small stream. Journal of the North American Benthological Society 7:77-86.

Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton effects of nutrients and herbivores. Ecology 74:1264-1280.

Schlosser, I. J., and K. K. Ebel. 1989. Effects of flow regime and cyprinid predation on a headwater stream. Ecological Monographs 59:41-57.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16:269-311.

Sih, A., and D. E. Wooster. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. Ecology 75:1199-1207.

Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10:375-383.

Steinman, A. D. 1992. Does an increase in irradiance influence periphyton in a heavily-grazed woodland stream? Oecologia 91:163-170.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73:747-754.

Teague, S. A., A. W. Knight, and B. N. Teague. 1985. Stream microhabitat selectivity, resource partitioning, and niche shifts in grazing caddisfly larvae. Hydrobiologia 128:3-12.

Threlkeld, S. T. 1987. Experimental evaluation of trophic cascade and nutrient-mediated effects of planktivorous fish on plankton community structure. Pages 161-173 in C. W. Kerfoot and A. Sih (editors). Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH.

Waters, T. F. 1972. The drift of stream insects. Annual Review of Entomology 17:253-272.

Wooster, D. 1994. Predator impacts on stream benthic prey. Oecologia 99:7-15.

Wrona, F. J., P. Calow, I. Ford, D. J. Baird, and L. Maltby. 1986. Estimating the abundance of stone-dwelling organisms: a new method. Canadian Journal of Fisheries and Aquatic Sciences 43:2025-2035.

Chapter 3

Artificial Shading of a Benthic Community Modifies Trophic Interactions in a
High Desert Stream

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Abstract

In temperate streams, the effects of canopy removal on benthic community processes are well known but the potential effects of canopy restoration on streams that have lacked natural canopy for decades have not been addressed. Our study examined the effects of artificial shade on a stream system that has experienced 100 years of high light and water temperature regimes. In Camp Creek, a third-order tributary of the John Day River in eastern Oregon, riparian canopy had been removed by logging and heavy grazing. Summer solar inputs for the study sites were high, averaging 1572 Megajoules/m^2. We artificially shaded 3 randomly selected pools with plastic tarps for 4 wks and compared periphyton biomasses, invertebrate densities and biomasses, and fish densities between these shaded pools and 3 open control pools. Although the tarps reduced irradiance on treatment pools to 5% of original light levels, periphyton biomasses did not vary between shaded and open pools, averaging 10 g AFDM/m^2 in both treatments. However, densities of total invertebrates in open pools were 2X and biomasses were 3X those in shaded pools. Specific taxa more abundant in open pools were pulmonate snails, chironomids, stoneflies, and the predaceous caddisfly Oecetis. Mayflies, such as Baetis and heptageniids, and the algivorous caddisflies Helicopsyche and Dicosmoecus gilvipes, did not differ between canopy treatments. Canopy had no effect on fish abundances. In many streams, increased light is associated with higher photosynthetic rates and algal growth, and light-stimulated primary production in open pools of Camp Creek apparently was converted to grazer biomass rather than periphyton standing crop. This study demonstrated top-down regulation of periphyton by herbivory and concurrent bottom-up control imposed by reduction in incident radiation. Shading altered the

productive capacity of periphyton and subsequently reduced the density and biomass of invertebrates the periphyton could support, but shading had little influence on periphyton standing crop, which was maintained at uniformly low levels by grazers.

Introduction

In many temperate streams, much research has focused on the effects of deforestation on benthic community processes. Removal of riparian vegetation increases the amount of incident solar radiation reaching stream substrates, triggering biotic responses at all trophic levels. Several studies in the Cascade and Coast Ranges of the Pacific Northwest have documented that canopy removal stimulates periphyton growth and accrual and, subsequently, increases in macroinvertebrate and salmon abundances occur (Aho 1976; Newbold et al. 1980; Murphy et al. 1981; Murphy and Hall 1981; Hawkins et al. 1982,1983; Bilby and Bisson 1992). In other studies, increases in incident radiation did not enhance periphyton accrual because heavy invertebrate grazing cropped algae to low and uniform levels regardless of canopy density (Hawkins and Furnish 1987; Feminella et al. 1989; Steinman 1992; Hill et al. 1995). In streams, especially those in lower elevation rangeland, where canopy removal caused both higher irradiance and marked increases in water temperature, periphyton and invertebrate abundances increased. However, the higher water temperatures proved deleterious to salmonids (Barton et al. 1985; Platts and Nelson 1989; Tait et al. 1994). High stream temperatures induce greater metabolic demands in trout than can be offset by increased food supply, exacerbated by an inhibition of feeding behavior at high temperatures (Li et

al. 1994). Increases in water temperature can also disrupt timing of salmon life history patterns that leads to reduced population viability (Holtby 1988).

It is likely that before European settlement, many small streams in the high desert region of the intermontane west were canopied, cool, and inhabited primarily by cold stenothermic salmonids and sculpins. However, livestock grazing, logging, and agricultural development during the last 150 years have removed extensive tracts of riparian vegetation from many streams (Kauffman and Krueger 1984; Meehan 1991). In Chapter 2, we examined trophic interactions on Camp Creek, a third-order rangeland stream whose sparsely canopied streambanks allowed high solar inputs and elevated summer temperatures. Periphyton accrual was not limited by irradiance but was controlled primarily by Dicosmoecus gilvipes, a robust, grazing caddisfly that acted, in mid-summer, as an intermediate regulator influencing multiple trophic levels. Speckled dace, a generalist species tolerant of warm water, was 6X more abundant than rainbow trout and sculpins in Camp Creek. The fish community as a whole appeared to have minimal impact on lower trophic levels.

It is unlikely that streams such as Camp Creek will return to a pristine state with fully restored riparian canopy and cold groundwater recharge. However, current land management philosophies support careful riparian stewardship to increase streamside vegetation (Interior Columbia Basin Ecosystem Management Project 1997). If riparian management is improved, eventually heavier canopy cover should exist on Camp Creek. In this study we examined the influence of canopy restoration, rather than canopy removal, on a stream system that has experienced decades of high light and temperature conditions. We artificially shaded randomly selected pools and compared periphyton biomasses, invertebrate densities and biomasses, and

fish densities between these shaded pools and open control pools. In addition, we compared Camp Creek to a heavily-canopied, relatively pristine reference stream, Deardorff Creek, with regard to benthic community structure and processes in the two systems.

Study Areas

Camp Creek

The study was conducted in Camp Creek (44°39' latitude; 118°49' longitude) within the John Day River Basin of northcentral Oregon. Camp Creek is a third-order stream that flows northwest and ranges in elevation from 1719 m to 1055 m. The study area receives about 60 cm of precipitation annually, mostly falling from November to May. Summer low flows (0.11 m³/s in 1991) occur mid-July through September and summer stream temperatures are warm due to lack of overhanging canopy. Intense livestock grazing occurs throughout the watershed. Typical streamside vegetation includes grasses (Phalaris spp.), sedges (Carex spp.), white alder (Alnus rhombifolia), and black cottonwood (Populus trichocarpa). Willows (Salix spp.) are rare. Ponderosa pine (Pinus ponderosa) and Douglas-fir (Pseudotsuga menziesii) dominate the hillslopes, but most riparian conifers were logged in the 1920's.

Historically, Camp Creek provided spawning habitat for steelhead and resident rainbow trout (Oncorhynchus mykiss) and spring chinook (Oncorhynchus tschawytsha). While both species presently occur in the stream, conditions are no longer favorable for chinook to spawn. Presently juvenile rainbow trout and juvenile and adult speckled dace (Rhinichthys osculus) are numerically dominant, although redside shiners (Richardsonius

balteatus), largescale suckers (Catostomus macrocheilus), and sculpins
(Cottus spp.) also occur. In an effort to improve fish habitat in Camp Creek,
the Bonneville Power Administration installed 256 log weirs along 19 km of
stream in the 1970's. The log weirs formed pools of fairly uniform size and
morphology which were used for experimental units.

The log weir experimental pools were located within a mid-basin
reach of Camp Creek (length = 3.3 km) and varied little in elevation (1253-
1318 m), solar input, stream temperature, or volume. The six study pools
received similar levels of solar input prior to installation of artificial canopies,
averaging 1572 Mj/m^2 (CV = 15.6%). The canopies reduced irradiance on
treatment pools to 5% of original light levels on average (mean = 84 Mj/m^2
± 4.5). Daily summer stream temperatures averaged 20° C, with mean
maximum and mean minimum temperatures of 24.5° C and 12.3° C,
respectively. Maximum summer water temperature was 26° C. Because of
cooler, wetter weather in summer 1991, average daily summer stream
temperatures and maximum temperatures were lower and August stream
flows higher than the previous year.

Deardorff Creek

Deardorff Creek was selected as a reference stream for this study
based on cluster analysis of 26 John Day Basin watersheds (Li et al. 1994).
Watersheds were analyzed based on physical characteristics, such as mean
annual precipitation, watershed area, compass aspect, elevation, and mean

Table 3.1. Some physical characteristics of paired Camp Creek and Deardorff Creek watersheds in the John Day Basin, OR.

Watershed	Area (km²)	Cumulative Mean Annual Precip (cm)	Compass Aspect	High Elev	Low Elev
Camp Creek	168	63.5	1.75	1719	1055
Deardorff Creek	53	69.9	2.75	2030	1213

annual runoff, and Deardorff Creek was most closely associated with Camp Creek (Table 3.1). Deardorff Creek ($44^\circ23'$ latitude; $118^\circ37'$ longitude) is a forested, third-order stream that flows northwest from the Blue Mountains. Summer low flows (0.03 m^3/s in 1991) occur in August and September. Deardorff Creek is cold (average daily = 12.0° C; average summer maximum = 13.5° C; average minimum = 7.0° C) and densely canopied through much of its length with mixed conifers (Douglas-fir and ponderosa pine) and herbaceous shrubs. Although the Deardorff Creek watershed is grazed periodically, the effects of livestock on riparian canopy have been minor.

Deardorff Creek provides spawning habitat for steelhead and resident rainbow trout, cutthroat trout (Oncorhynchus clarki), and bull trout (Salvelinus confluentus). As in Camp Creek, log weir structures were installed at frequent intervals in an effort to improve fish habitat. Six log weir pools along a 2 km reach (elev. 1320-1345 m) were chosen as sampling sites and were similar in volume (mean = 12.4 m^3; SE = 1.2). Average summer solar input in the pools ranged from 273 to 980 Mj/m^2 (mean = 605 Mj/m^2; SE = 162).

Methods

Camp Creek artificial canopy experiment

Field experiments were conducted in mid-summer 1991 along a 3.3 km reach of lower Camp Creek in order to determine the impacts of artificial shading on the abundance and species composition of benthic communities. For study units, we reused six of the 18 log weir pools selected the previous year for a fish enclosure experiment (see Chapter 2). The six pools

were chosen at random. Mean accumulated solar input (Megajoules/m^2) for June, July, and August was measured in each pool using a Solar Pathfinder (see Chapter 1). Because of high water clarity, turbidity did not affect the amount of light reaching the substrate. Pool volumes were determined at the beginning and end of the experiment. Weekly maximum and minimum water temperatures were recorded with maximum-minimum thermometers.

Three of the six pools were selected at random to be canopied. Each pool was covered on 15 July with an opaque plastic tent fly (2.5 m X 4 m) suspended 1 m over the water surface. The tents may have interfered with some terrestrial inputs of leafy debris and insects, but lack of overhanging vegetation in these pools made a significant decrease in allochthonous input unlikely. Solar Pathfinder readings under the canopies showed a 95% reduction in solar input, and only angled light from near the horizon reached the streambed. The tent flies were left in place for 4 wks, whereas the remaining three pools were not covered and served as controls. Sampling of benthic communities in each pool occurred prior to canopy installation and again at the end of the experiment. Algal standing crops were estimated visually by recording relative cover of prominent algal growth forms (see Chapter 2), and by direct sampling of periphyton biomass (g/m^2 ash-free dry mass (AFDM)) and chlorophyll a concentration (mg/m^2) using methods described in Chapter 1 for other John Day Basin sites. In addition, allochthonous debris, such as leaf and woody litter, was collected from the streambed of each pool by vacuuming the substrate surface inside a Hess sampler with a backpack pump. Debris was separated from mineral material, dried at 55° C for 24h, and weighed.

In order to assess the potential impact of macroinvertebrate grazing on periphyton abundance in experimental pools, three rocks with typical

accumulations of periphyton were selected from the substrate and were protected from invertebrate grazing by placement on platforms suspended over, but not touching, the pool substrate. While platforms excluded most large, crawling grazers such as caddisflies and snails, they were easily colonized by drifting mayflies and midges, and therefore grazing was decreased but not completely eliminated. After 4 wks, periphyton from the three platform rocks and from three control rocks was removed, pooled, and measured using the same methods as for substrate AFDM and chlorophyll a.

Invertebrates were collected in each pool by scooping 5 nonembedded, cobble-sized rocks from the substrate into a net, removing all invertebrates, and pooling the organisms into a single sample (Wrona et al. 1986). Total rock surface area was estimated by wrapping with aluminum foil. All organisms retained by a 250μm mesh sieve were preserved in 95% ethanol, identified to genus, enumerated, and measured. Taxa were later assigned to functional feeding groups sensu Merritt and Cummings (1984). Scrapers and other invertebrates that commonly feed on living algal cells were designated grazers. Gatherers and filterers were combined into collectors. Shredders and predators also were recognized. Biomasses were estimated by using known length-weight relationships for preserved material (Smock 1980). Snails were removed from shells, dried at 55° C for 24 h, and weighed. In addition, population estimates were made of the large caddisfly Dicosmoecus gilvipes visible with a viewing scope on substrate surfaces within the 6 sample quadrats where algal cover was also estimated.

Fishes in each pool and in the adjacent upstream riffle were inventoried before and after the experiment by snorkeling; divers counted fishes by species and age class. Methods were similar to snorkeling counts

described in Chapter 1, except that three divers were used instead of two. Fish densities were calculated as numbers/m^3.

Differences between treatments were analyzed with t-tests; data were transformed with $\log_{10}(x + 1)$ or squareroot arcsine when necessary to control heteroscedastisity and nonnormality. Percent change in invertebrate densities and biomasses, calculated as the density or biomass of an invertebrate group on Day 30 divided by the same parameter on Day 0, was used to compare the magnitude of changes in invertebrates over time for each treatment.

Deardorff Creek sampling

No experiments were conducted on Deardorff Creek, but most of the physical and biological measurements and analysis done in Camp Creek were repeated in Deardorff Creek. Sampling units were six, nonadjacent log weir pools of similar size and volume. Maximum and minimum stream temperatures were monitored from mid-July to mid-August. Sampling of periphyton, allochthonous debris, macroinvertebrates, and fish occurred 12-13 August 1991 immediately after the termination of the Camp Creek experiment.

Results

Camp Creek artificial canopy experiment

<u>Periphyton Abundance</u>

No differences in periphyton biomass (g AFDM/m^2) between July and August ($p=0.35$ for open pools; $p=0.78$ for shaded pools) or between open and shaded treatments ($p=0.71$) were found (Fig. 3.1). Although algal accrual would be expected in control pools during the period of peak summer growth, only a modest, nonsignificant increase occurred. AFDM for different times and treatments was remarkably consistent, with values similar (≤ 10 g/m^2) to those found in other grazed streams under diverse nutrient and irradiance regimes (Feminella and Hawkins 1995). Percent filamentous algal cover ranged from 0% to 70% among experimental pools in August, but no significant differences were detected among treatments. Ratios of g algal biomass to mg chlorophyll <u>a</u> were marginally lower in shaded pools (mean$=0.23 \pm 0.05$) than open pools (mean$=0.52 \pm 0.38$; $p=0.08$). Lamberti et al. (1989) observed similar trends in artificial streams where biomass/chlorophyll of periphyton decreased with decreasing light intensities. Shade-adapted plants commonly have higher photosynthetic pigment concentrations (McIntire and Phinney 1965; Hill 1996) in order to capture light more efficiently.

Effects of experimentally reduced grazing on periphyton accrual were ambiguous. Although no heavy grazers such as snails or <u>Dicosmoecus</u> were found on platforms, these platforms in both open and shaded pools were colonized by large numbers of heptageniid, baetid, and leptophlebiid
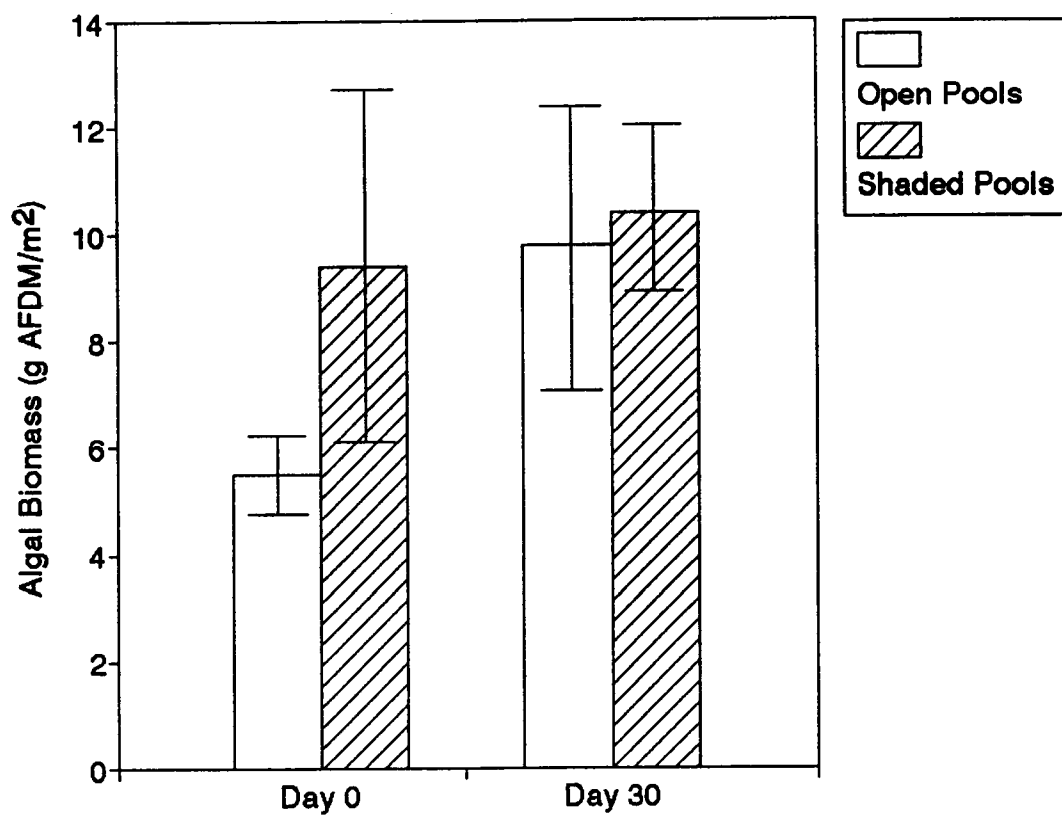
Fig. 3.1. Average algal biomasses in Camp Creek pools at onset and end of artificial canopy experiment. Bars represent ± 1 standard error.

mayflies, frequently at greater than ambient densities. Periphyton biomass accumulations did not differ between platforms and substrates for either canopy treatment. Small sample sizes (the platform in one pool was lost during a spate) and low frequency of sampling considerably reduced the probability of detecting effects of grazing if they were present.

Benthic Invertebrates

By the end of the 4 wk experiment, total densities of invertebrates in open pools were about 2X those of shaded pool densities (Table 3.2; Fig. 3.2). Densities of all guilds except shredders were higher in open pools, although grazer densities were not significantly so. Shredder densities increased by 100X in both treatments, primarily due to recruitment of the caddisfly Lepidostoma. Total invertebrate biomass was 3X higher in open pools, with especially large differences in predator biomasses between open and shaded sites (Table 3.2). Biomasses of collectors and grazers were also higher in open pools, though grazer biomass was not significant. Specific invertebrates that were more abundant in open pools included pulmonate snails (Physa, Fossaria, and Gyraulus); the collectors Tricorythodes, elmid larvae, and annelids; and the predators Calineuria and Oecetis. Chironomids also occurred in greater numbers in open sites. Some grazer taxa that showed no response to the treatment included the mayflies Baetis, Paraleptoplebia, and Leucrocuta, and the caddisflies Helicopsyche and Dicosmoecus. The dipterans Atherix and Antocha occurred in low numbers and only in shaded pools.

Percent change in densities and biomasses of invertebrate groups during the 4 wk experiment showed few significant differences between

Table 3.2. Mean densities (number/m^2) and biomasses (g dry weight/m^2) of benthic invertebrates in artificially shaded and open pools of Camp Creek. standard errors are in parentheses; P-values were calculated using two-sample t-test on log transformed means.

|	Open Pools		Shaded Pools		P-Value	
	Density	Biomass	Density	Biomass	Density	Biomass
Total Invertebrates	3870 (±405)	0.89 (±0.70)	1915 (±102)	0.29 (±0.03)	.004	.001
Grazers	1320 (±93)	0.43 (±0.16)	920 (±116)	0.20 (±0.09)	.071	.081
Collectors	1574 (±444)	0.30 (±0.08)	560 (±106)	0.07 (±0.01)	.047	.019
Shredders	246 (±120)	0.001 (±0.001)	133 (±81)	0.002 (±.002)	.45	.92
Predators	719 (±117)	0.17 (±0.02)	290 (±28)	0.02 (±0.003)	.009	.001
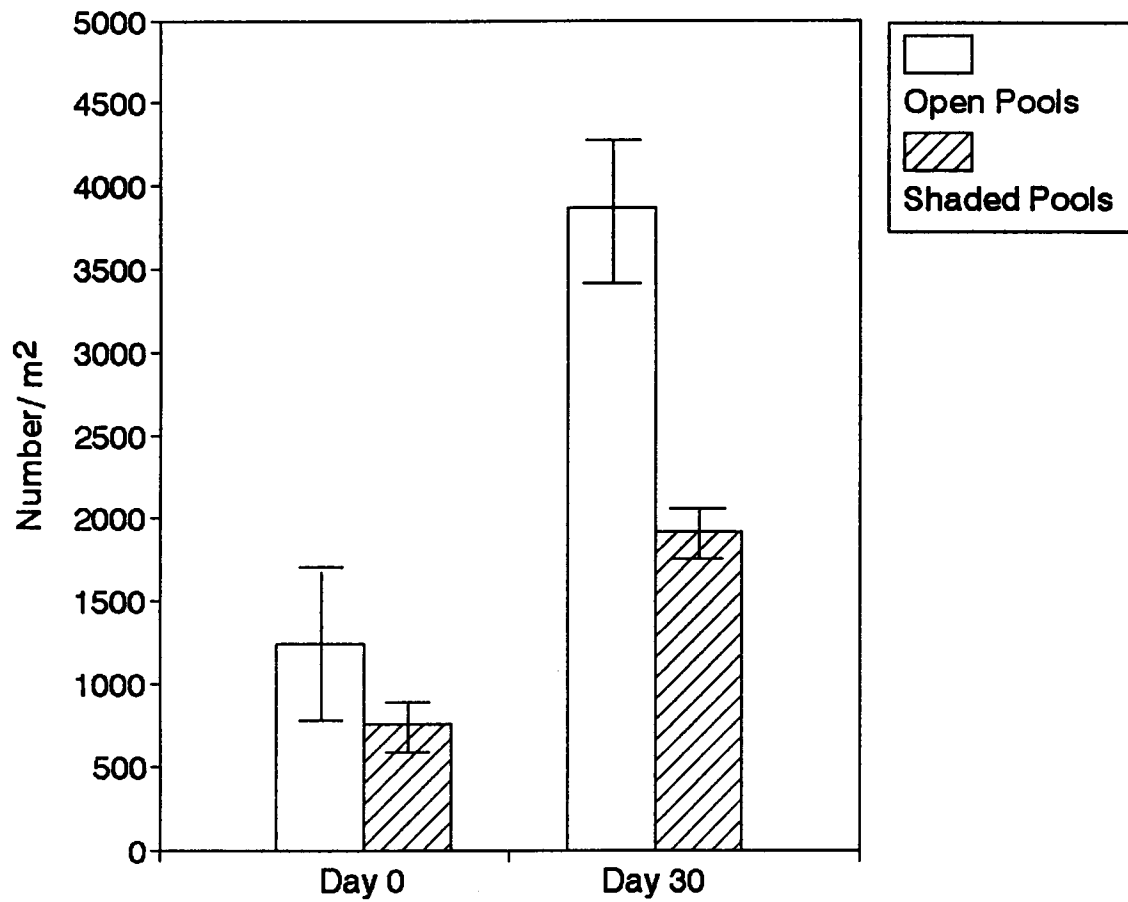
Fig. 3.2. Average total invertebrate density in Camp Creek pools at onset and end of artificial canopy experiment. Bars represent ± 1 standard error.

open and shaded treatments (Table 3.3). Percent changes between July and August in densities and biomasses of total invertebrates, collectors, grazers, and predators in open pools were greater than in shaded pools, but were not significant because of high variability. Changes in shredder density and biomass were greater in shaded pools, but were also not significant.

For two specific taxa, percent change in density or biomass was significantly greater in the open than in the shaded treatment. Increase in pulmonate snail biomass in open pools was 4.2X greater than the increase in shaded pools. Although percent change in snail density in open pools was 2X that in shaded pools, large sample variances precluded significance ($p = 0.18$). Change in density of the predaceous caddisfly Oecetis was significantly greater (by 4.8X) in open treatments.

Changes of abundances for other taxa revealed no canopy effects. Baetis densities increased similarly in both treatments over time, although Baetis biomasses appeared to increase more in open pools than in shaded pools (but not significantly so). No significant changes occurred in Paraleptophlebia and Leucrocuta densities, but Helicopsyche numbers decreased by 30% in both treatments, probably due to emergence. Dicosmoecus densities and biomasses also declined in both open and shaded pools as larvae entered diapause and ceased feeding.

The relative abundances (for densities and biomasses) of invertebrates at the onset and termination of the experiment were compared between open and shaded pools (Fig. 3.3). For most guilds, changes in relative abundances were similar in both treatments, and appeared related to ontogeny rather than canopy effects. Grazers, the dominant guild in both

Table 3.3. Percent change in invertebrate densities and biomasses after 4 wks in open pools and pools under artificial canopy in Camp Creek. Standard errors are in parentheses. No differences between treatments were significant.

	Open Pools	Shaded Pools
Total invertebrates		
Density	402 ($\pm$103)	279 ($\pm$63)
Biomass	382 ($\pm$198)	92 ($\pm$41)
Grazers		
Density	288 ($\pm$61)	243 ($\pm$69)
Biomass	408 ($\pm$171)	99 ($\pm$21)
Collectors		
Density	385 ($\pm$107)	223 ($\pm$19)
Biomass	761 ($\pm$353)	242 ($\pm$39)
Shredders		
Density	3830 ($\pm$1294)	9933 ($\pm$7583)
Biomass	59 ($\pm$37)	116 ($\pm$63)
Predators		
Density	943 ($\pm$331)	531 ($\pm$206)
Biomass	279 ($\pm$167)	148 ($\pm$138)
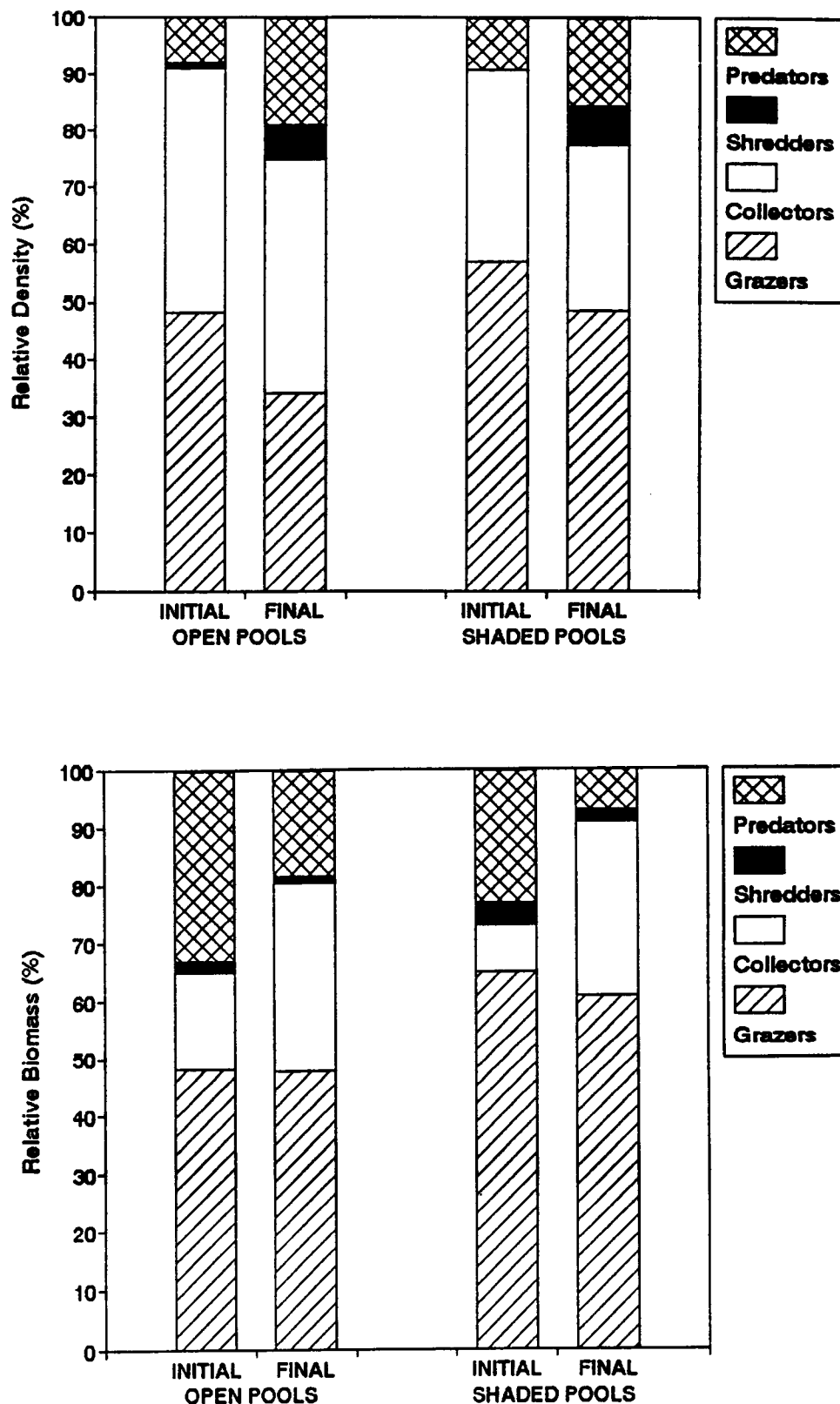
Fig. 3.3. (a) Relative densities and (b) relative biomasses of invertebrate functional feeding groups in open pools and pools with artificial canopy in Camp Creek. Initial and final values were measured before start of experiment in mid-July and at experiment end in mid-August, respectively.

open and shaded sites, declined in relative density but did not change appreciably in relative biomass. Relative densities of collectors remained similar over time while biomasses increased with time. Shredder relative abundance increased in both treatments because of greater numbers of hatching and developing Lepidostoma. Predators increased in relative density in both treatments as population size of the small-bodied Oecetis grew, and decreased in relative biomass with the emergence of Calineuria and the dragonfly Ophiogomphus.

Relative abundances of some dominant invertebrate taxa also changed between experiment onset and termination (Table 3.4). Pulmonate snails (both density and biomass) comprised less than 9% of the invertebrate community in all pools initially. After 4 wks, snail relative abundance in shaded pools was unchanged, but snails accounted for 33% of the biomass and 13% of total invertebrate density in open treatments. Baetis relative densities were also similar in all pools initially (5%), but tripled in shaded pools by the end of the experiment. Dicosmoecus biomass was relatively more important at the outset in pools to be canopied (32%) than pools to be left open (15%) but had declined by 10% in both treatments after 4 wks.

Fish Abundance

The canopy treatment had no apparent effect on densities of juvenile and adult speckled dace or rainbow trout (Table 3.5). Although fish densities (except young-of-the-year) generally decreased in all pools over time, there were no significant differences in fish numbers or in

Table 3.4. Average relative densities (number/m²) and biomasses (g dry weight/m²) of invertebrates in study pools at onset and at end of canopy treatment. Snails are pooled abundances of Gyraulus, Fossaria, and Physa. Standard errors are in parentheses.

	Open pools		Shaded pools	
	Initial	Final	Initial	Final
Snails				
Density	0.03 (±0.01)	0.13 (±0.04)	0.05 (±0.03)	0.06 (±0.02)
Biomass	0.02 (±0.01)	0.32 (±0.24)	0.09 (±0.08)	0.09 (±0.03)
Baetis				
Density	0.04 (±0.02)	0.07 (±0.01)	0.05 (±0.02)	0.16 (±0.04)
Biomass	0.01 (±0.01)	0.02 (±0.001)	0.03 (±0.02)	0.05 (±0.02)
Dicosmoecus				
Density	0.02 (±0.01)	0.0004 (±0.0004)	0.01 (±0.003)	0.001 (±0.001)
Biomass	0.13 (±0.06)	0.05 (±0.05)	0.32 (±0.10)	0.21 (±0.20)

Table 3.5. Fish densities (number/m³) at onset and end of canopy experiment. Standard errors are in parentheses. Differences in final densities between treatments are not significant.

	Open pools		Shaded pools	
	Initial	Final	Initial	Final
Rainbow trout (age 1 + to 3 +)	0.23 (±0.06)	0.05 (±0.03)	0.56 (±0.18)	0.26 (±0.12)
Speckled dace (juveniles, adults)	5.7 (±1.8)	3.1 (±1.2)	8.6 (±3.5)	5.1 (±2.9)
Young-of-the-year (all species)	2.8 (±1.6)	8.0 (±0.5)	2.3 (±2.2)	6.5 (±1.7)

the rate of population decline between open and shaded pools after 4 wks. Young-of-the-year fish increased throughout the experiment because of summer recruitment, but no canopy effects were detectable.

In adjacent upstream riffles, none of which were artificially shaded, rainbow trout densities were lower (mean = 0.03 trout/m^3; SE = 0.01) than densities in log weir pools, but the difference was not significant (p = 0.11). Speckled dace densities in riffles (mean = 6.17 fish/m^3; SE = 2.21) were similar to those in log weir pools.

Deardorff Creek--physical and biological characteristics

Periphyton Abundance

Periphyton in Deardorff Creek consisted mainly of thin biofilms, and most substrate surfaces appeared bare or covered with diatom mats. Filamentous green algae occurred along pool margins, covering about 15% of the streambed. Mean algal standing crop for the six pools was 8.9 g AFDM/m^2 (SE = 2.5). Chlorophyll a concentrations averaged 31.6 mg/m^2 (SE = 2.5) and were correlated with periphyton biomass (r = 0.73; p = .01). Allochthonous debris consisted principally of fir needles and small wood, and averaged 18.6 g/m^2 (SE = 7.5).

Benthic Invertebrates

Average densities and biomasses of invertebrate functional feeding groups in Deardorff Creek are shown in Table 3.6. Invertebrate densities were dominated by grazers and collectors (Fig. 3.4), with most of these

Table 3.6. Mean densities (number/m²) and biomasses (g dry weight/m²) of benthic invertebrates in 6 logweir pools of Deardorff Creek, John Day Basin, Oregon, in August 1991. Standard errors are in parentheses.

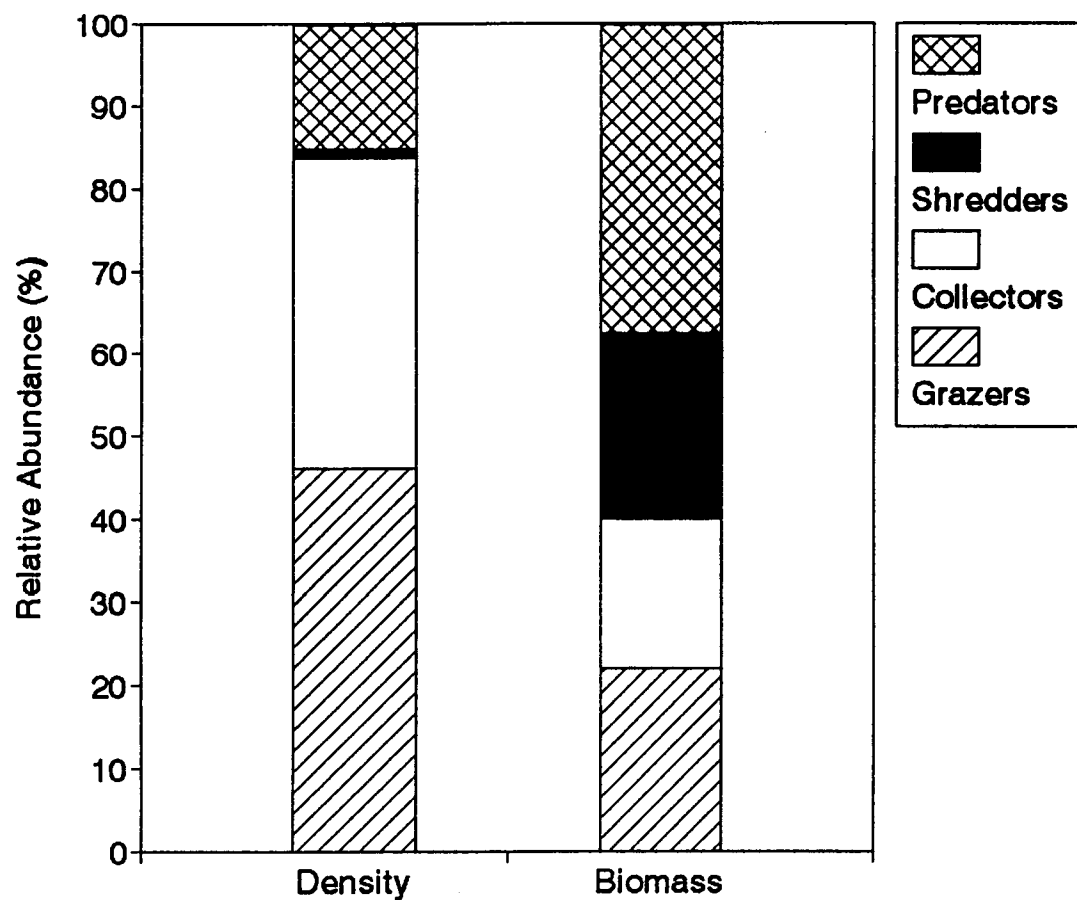|	Density	Biomass
Total invertebrates	1557 (±380)	0.80 (±0.27)
Grazers	711 (±193)	0.17 (±0.5)
Collectors	574 (±150)	0.14 (±0.05)
Shredders	18 (±9)	0.18 (±0.06)
Predators	235 (±58)	0.30 (±0.17)

Fig. 3.4. Relative densities and biomasses of invertebrate functional feeding groups in Deardorff Creek pools in mid-August.

being small taxa such as <u>Baetis</u>, <u>Cinygmula</u>, chironomids, and the elmids <u>Optioservus</u> and <u>Zaitzevia</u>. The larger grazer <u>Glossosoma</u> accounted for 6% of total invertebrate density and 1% of invertebrate biomass. Shredders, which comprised <2% of invertebrate density, were 22.5% of invertebrate biomass. The limnephilid caddisfly <u>Dicosmoecus atripes</u>, a congener of the keystone grazer <u>D. gilvipes</u> found in Camp Creek, was the dominant shredder, contributing over 95% to shredder biomass and making up 23% of total invertebrate biomass. <u>D. atripes</u> is also predaceous, with 30% of its diet consisting of animal prey (Gotceitas and Clifford 1983), and so is not readily assigned to a single functional feeding group. Predator biomass (38%), which was almost entirely comprised of the perlid stonefly <u>Doroneuria</u>, dominated the invertebrate assemblage.

<u>Fish Abundance</u>

Snorkeling surveys in the Deardorff Creek log weir pools recorded only 2 fish species, rainbow and cutthroat trout, at average densities of 0.19 trout/m^3 (SE=0.09). Trout were more abundant in adjacent riffles (mean=0.27 trout/m^3; SE=0.10) than in log weir pools, but the difference was not significant (p=0.54).

Discussion

Use of artificial canopy to simulate natural riparian cover is unrealistic in some respects, but instructive in others. The canopies in this study were in place for only 1 month beginning mid-summer, and were installed over pools with benthic communities already established under full light regimes. Only mobile species or species with short developmental times could

demonstrate detectable responses to canopy within that brief period. Nevertheless, some community responses occurred that provide insight to the nature of community regulation in Camp Creek and augment conclusions drawn from previous studies (Chapter 2).

Despite a 20-fold difference in light intensity between open and shaded pools, periphyton abundances did not vary with canopy treatment in Camp Creek (Fig. 3.1), averaging about 10 g AFDM/m^2 in both treatments and not differing significantly from pre-experiment AFDM levels. By contrast, many stream studies show that sites with high irradiance frequently develop high periphyton standing crops. Periphyton is often positively correlated with irradiance, and AFDM can be 4-5 times higher in open than in shaded sites (Lowe et al. 1986; Hill and Knight 1988; Tait et al. 1994). However, these high periphyton biomasses are usually found in streams where grazing pressure is low relative to primary production. In studies such as this one, where periphyton biomass was not correlated with light, high grazing pressure may be a factor (Hill et al. 1995; Hill 1996). Grazing pressure was significant in Camp Creek (see Chapter 2) as demonstrated by 55% higher periphyton biomass in reduced-grazing treatments compared with controls. In a California stream with varying irradiance levels, Feminella et al. (1989) attributed uniformly low substrate periphyton (10 g AFDM/m^2) to differential grazing by caddisflies and mayflies. Although light is associated with faster algal growth and photosynthetic rates (Jasper and Bothwell 1986; Lamberti et al. 1989; Hill 1996), light-stimulated primary production can be converted to grazer biomass rather than periphyton standing crop (Behmer and Hawkins 1986; Lamberti et al. 1989; Hill et al. 1995). Standing crops of food resources in Camp Creek were similar between canopy treatments, but open pools

supported 3X the invertebrate biomass of shaded pools. Apparently, higher primary production in open pools was subsequently converted to higher secondary production rather than algal standing crop.

For specific invertebrates in Camp Creek, absolute abundances (densities and biomasses) and percent increases in abundance were significantly greater in open pools than in shaded pools. Pulmonate snail biomass was 10X greater and density was 4X greater in open pools after 4 wks. Snails became the dominant grazer in these pools, comprising 32% of the invertebrate biomass, compared with 9% of the biomass in shaded pools. Many studies demonstrate that prosobranch snails are able to track algal abundance and are capable of regulating algal communities. In western Oregon, Hawkins and Furnish (1987) found that Juga maintained low AFDM levels under a variety of canopy densities because snail numbers paralleled algal biomass. In Tennessee streams, Elimia grazed periphyton standing crops to low biomasses regardless of irradiance, and algal abundance increased with light only when snails were removed (Steinman 1992). Pulmonate snails are also capable of reducing algal standing crops, especially stalked diatom and filamentous overstories (Brönmark et al. 1992). In the pools used for this study, Dicosmoecus occurred in low numbers, and snails were likely the principle regulator of algal standing crops in open pools. The lower abundance of snails in shaded pools was probably due to avoidance of shaded sites or to reduced recruitment in shade.

Several mobile grazers that were expected to avoid shaded patches with lowered primary productivity demonstrated no changes in distribution with canopy treatment. Among the mayflies, Baetis, Paraleptophlebia, and Leucrocuta showed no significant differences in abundance between shaded

and open pools. By contrast, in a comparison of riffle sites in a Utah stream, Behmer and Hawkins (1986) reported that biomasses of two Baetis species were 5.7X and 2.3X higher, and biomass of Cinygmula was 1.6X higher, in open sites than in shaded sites. Fuller et al. (1986) reported a reduction of Baetis tricaudatus densities along with periphyton under artificial canopies. Others have documented that abundance of grazing mayflies generally increases with intensity of incident radiation and concomitant algal growth (Bruns and Minckley 1980; Newbold et al. 1980; Hawkins et al. 1982; Dudley et al. 1986; Richards and Minshall 1988). In all of these studies, shading was of long duration, in contrast to the short-term shading of the Camp Creek streambed. However, baetid drift rates increase when food is lacking (Kohler 1985) and Baetis is capable of rapid response to food abundance levels, colonizing rich patches or abandoning poor ones within hours (Richards and Minshall 1988). Periphyton biomass in Camp Creek was grazed to uniform levels in both canopy treatments, and baetids and other mayflies did not gather in pools with higher light levels.

Another mobile grazer that showed no difference in abundance with treatments was Helicopsyche, which at high densities can significantly affect periphyton abundance and spatial distribution. Lamberti and Resh (1983) found that Helicopsyche borealis in a northern California stream aggregated on rich periphyton patches but became randomly distributed once they reduced periphyton to background levels. Furthermore, Helicopsyche larvae competed intraspecifically for limited algal resources (Lamberti et al. 1987). Feminella et al. (1989) reported Helicopsyche numbers in the same stream to be unrelated to riparian canopy. Canopy had little influence on periphyton standing crop so that distribution of food-rich patches that could attract the caddisflies was not determined by

incident light levels. In Camp Creek, the algivore <u>Dicosmoecus</u> also appeared to be uninfluenced by canopy, occurring initially in moderate densities in open and shaded pools but decreasing by 80% in both treatments by the end of the experiment. Because <u>Dicosmoecus</u> was entering diapause during the experiment rather than actively dispersing, its life history stage may have had a greater effect on its distribution than canopy. However, late-instar <u>Dicosmoecus</u> spend 90% of their time foraging (Hart 1981), and concentrate their efforts on rich food patches in a manner reminiscent of <u>Helicopsyche</u> (Lamberti and Resh 1983). <u>Dicosmoecus</u>, then, were likely important grazers for part of the study and may have contributed significantly to the reduction of periphyton biomass to uniformly low levels.

Conclusions

The scarcity of riparian canopy on lower Camp Creek is not a natural condition and was caused by past logging and overgrazing by livestock. Improved land management practices may eventually restore some riparian canopy, and the benthic community should adjust to reduced irradiance. If canopy is restored to near complete closure, accompanied by a significant decrease in maximum stream temperature, an alteration in benthic species composition would be expected.

It is instructive to examine benthic community structure and processes on a relatively pristine reference stream, Deardorff Creek, in order to visualize the endpoint of complete canopy restoration on Camp Creek. Deardorff Creek is similar to Camp Creek in many physical respects (e.g., elevation, aspect, stream order) but the undisturbed riparian forest on

Deardorff Creek transmitted 50% less light than was measured on Camp Creek. In Deardorff Creek log weir pools, average maximum temperatures (13.5° C) were lower than in Camp Creek (24.5° C), but mean periphyton biomass (8.9 g $AFDM/m^2$) and total invertebrate biomass (0.80 g dry weight/m^2) were not significantly different than in open Camp Creek pools (9.8 g $AFDM/m^2$, $p = 0.75$; 0.89 g dry weight/m^2, $p = 0.92$). However, total invertebrate density in open Camp Creek pools (3870/m^2) was significantly greater than in Deardorff Creek pools (1557/m^2; $p = <0.05$), suggesting a greater abundance of small prey for fishes.

Relative abundances and composition of benthic invertebrates should shift to accommodate the changes in energy resources that occur when canopy density is altered. In Camp Creek, where higher overall light and temperature regimes likely stimulated photosynthetic rates, dominant grazers were large; snails and Dicosmoecus made up 75% of grazer biomass (Fig. 3.5a). In Deardorff Creek, with lower potential photosynthetic capacity but higher allochthonous inputs, the majority of grazer biomass (77%) was comprised of small baetid and heptageniid mayflies (Fig. 3.5b) that are adapted to harvest the thin biofilms that proliferate in shaded streams (DeNicola et al. 1990). Dicosmoecus gilvipes and snails, common in Camp Creek, were absent.

Along with reduced solar energy input, restored canopy on Camp Creek should increase allochthonous inputs from leaf litter and woody debris. Deardorff Creek displays the trophic characteristics expected of a low-order stream under the river continuum concept (Vannote et al. 1980), where inputs of coarse particulate organic matter provide a critical resource base for consumers. Mean dry weight of streambed litter from Deardorff Creek pools (18.6 g/m^2) was 2X the amount measured in Camp Creek

a)

Camp Creek

Chironomidae (3.5%)

mayflies (21.4%)

Dicosmoecus (28.8%)

Helicopsyche (0.3%)

snails (45.9%)

b)

Deardorff Creek

other (5.9%)

Glossosoma (5.3%)
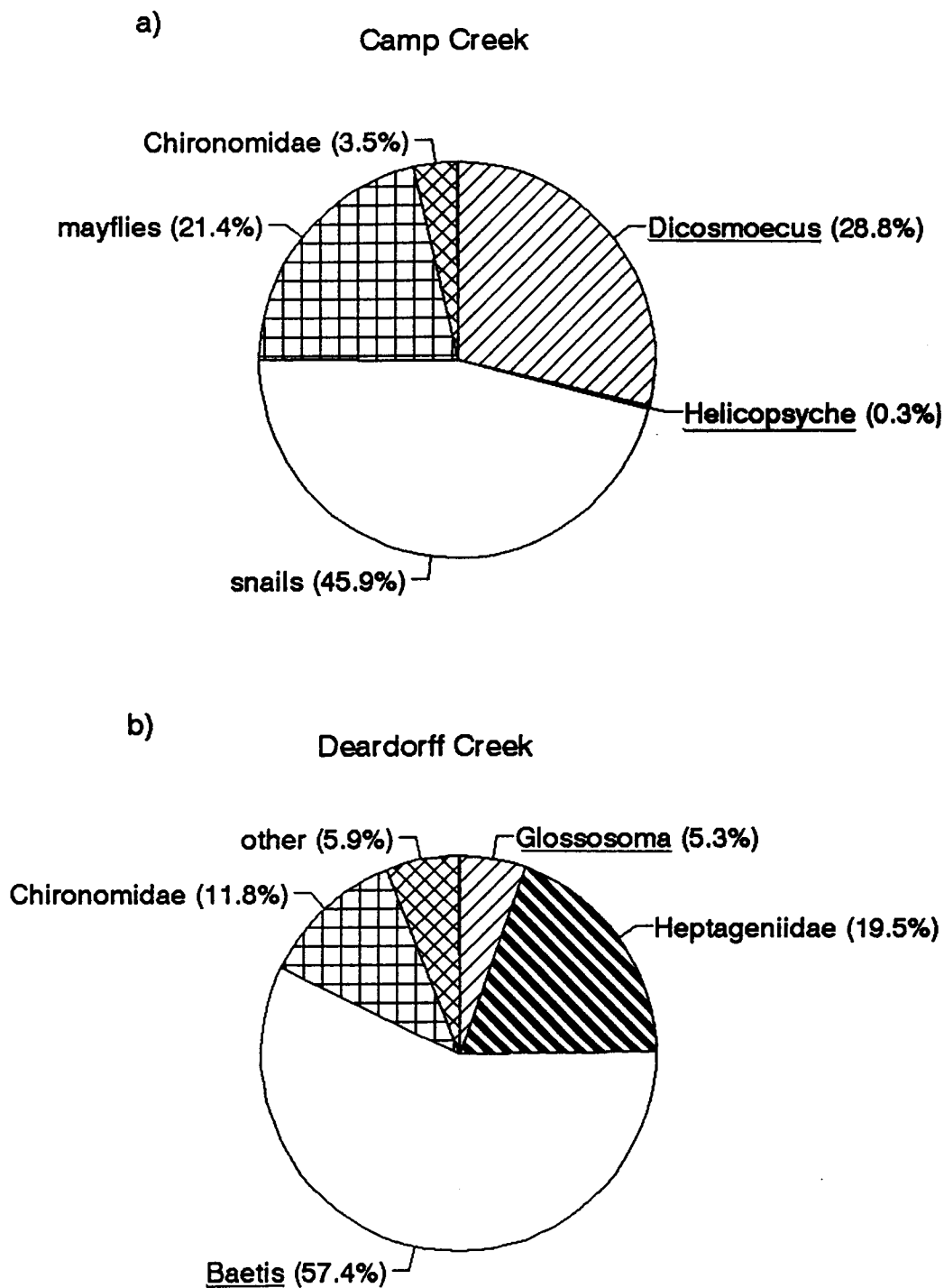
Chironomidae (11.8%)

Heptageniidae (19.5%)

Baetis (57.4%)

Fig. 3.5. Density of specific grazer taxa relative to total grazer density in (a) Camp Creek control pools and (b) Deardorff Creek pools.

(7.9 g/m^2). Consequently, shredders were large and dominant in Deardorff Creek, accounting for 22% of invertebrate biomass compared to <1% in Camp Creek (Figs. 3.3, 3.4). Although Camp Creek lies at about the same elevation as Deardorff Creek (study areas on both streams were at approx. 1300 m), canopy removal effectively displaces Camp Creek downstream in the river continuum, where ample sunlight reaches the streambed to support significant periphyton productivity, and heterotrophy declines.

The dominant shredder in Deardorff Creek was <u>Dicosmoecus</u> <u>atripes</u>, a large caddisfly closely related to <u>D</u>. <u>gilvipes</u>, the keystone grazer of Camp Creek (Chapter 2). Although the two species have broadly differing diets and life histories, they rarely coexist (Gotceitas and Clifford 1983; Wiggins and Richardson 1982). <u>D</u>. <u>atripes</u>' 2-year life cycle and extended diapauses enable it to inhabit cold, high elevation streams, whereas <u>D</u>. <u>gilvipes</u> requires warmer water to complete its 1-year developmental period. If canopy restoration on Camp Creek is sufficient to significantly lower water temperatures and increase allochthonous inputs, significant changes may occur in benthic species composition and processes. These changes may include the replacement of <u>D</u>. <u>gilvipes</u> with <u>D</u>. <u>atripes</u>, its locally abundant congener, and a shift from grazer-dominated to shredder-dominated benthic communities.

Along with the greater density of invertebrates in Camp Creek, total fish densities were 20X higher there than in Deardorff Creek. Trout densities in Camp Creek pools (0.15 trout/m^3) were not significantly different than densities in Deardorff Creek pools (0.19 trout/m^3; $p = 0.77$), despite greater food availability in Camp Creek. However, Deardorff Creek trout appear to underutilize log weir pools relative to other habitats, such as natural pools and riffles (Adams et al. 1990), and therefore trout densities

for log weir pools likely underestimate salmonid standing crop in Deardorff Creek. Only 3.5% of Camp Creek fishes were salmonids, whereas all fishes observed in cooler Deardorff Creek were salmonids (rainbow and cutthroat trout). Higher metabolic demands of trout at warmer water temperatures have been shown to negate the potential benefits of increased food supply (Li et al. 1994).

A more likely riparian restoration scenario on Camp Creek than complete canopy would be a mosaic of canopy densities, from heavy to completely open. Dominant benthic taxa likely would not change under this regime, but their local distributions may shift with the amount of light in their habitat. A biofilm similar to that described by Feminella et al. (1989) may occur, where periphyton is cropped to low and uniform levels regardless of irradiance by the combined action of grazers targeting different primary productivities. The impacts of fish predation on lower trophic levels should be minor. Lowered stream temperatures and improved bank conditions should increase the density of salmonids (Li et al. 1994; Platts and Nelson 1989; Hicks et al. 1991), but because salmonids have only infrequently been shown to impact lower trophic levels (Thorp 1986; Bechara et al. 1993; Sih and Wooster 1994), invertebrate grazers will likely remain the primary control agents of benthic community structure.

Acknowledgments

References

Adams, R. M., P. C. Klingeman, and H. W. Li. 1990. A bioeconomic analysis of water allocations and fish habitat enhancements, John Day Basin, Oregon. U. S. Geological Survey Grant Number 14-68-0001-G1479.

Aho, R. S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of stream. M.S. Thesis. Oregon State University, Corvallis.

Barton, D. R., W. D. Taylor, and R. M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. North American Journal of Fisheries Management 5:364-378.

Bechara, J., G. Moreau, and L. Hare. 1993. The impact of brook trout (Salvelinus fontinalis) on an experimental stream benthic community: the role of spatial and size refuge. Journal of Animal Ecology 62:451-464.

Behmer, D. J., and C. P. Hawkins. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. Freshwater Biology 16:287-300.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540-551.

Brönmark, C., S. P. Klosiewski, and R. A. Stein. 1992. Indirect effects of predation in a freshwater benthic food chain. Ecology 73:1662-1674.

Bruns, D. A., and W. L. Minckley. 1980. Distribution and abundance of benthic invertebrates in a Sonoran Desert stream. Journal of Arid Environments 3:117-131.

DeNicola, D. M., C. D. McIntire, G. A. Lamberti, and L. R. Ashkenas. 1990. Temporal patterns of grazer-periphyton interactions in laboratory streams. Freshwater Biology 23:475-489.

Dudley, T. L., S. D. Cooper, and N. Hemphill. 1986. Effects of macroalgae on a stream invertebrate community. Journal of the North American Benthological Society 5:93-106.

Feminella, J. W., and C. P. Hawkins. 1995. Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. Journal of the North American Benthological Society 14:465-509.

Feminella, J. W., M. E. Power, and V. H. Resh. 1989. Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. Freshwater Biology 22:445-457.

Fuller, R. L., J. L. Roelofs, and T. J. Fry. 1986. The importance of algae to stream invertebrates. Journal of the North American Benthological Society 5:290-296.

Gotceitas, V., and H. F. Clifford. 1983. The life history of Dicosmoecus atripes (Hagen) (Limnephilidae: Trichoptera) in a Rocky Mountain stream of Alberta, Canada. Canadian Journal of Fisheries and Aquatic Sciences 61:586-596.

Hart, D. D. 1981. Foraging and resource patchiness: field experiments with a grazing stream insect. Oikos 37:46-52.

Hawkins, C. P., and J. K. Furnish. 1987. Are snails important competitors in stream ecosystems? Oikos 49:209-220.

Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology 63:1840-1856.

Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173-1185.

Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. Responses of salmonids to habitat changes. Pages 483-518 in W. R. Meehan (editor). Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.

Hill, W. 1996. Effects of light. Pages 121-148 in R. J. Stevenson, M. L. Bothwell and R. L. Lowe (editors). Algal ecology. Academic Press, San Diego.

Hill, W., and A. W. Knight. 1988. Nutrient and light limitation of algae in two northern California streams. Journal of Phycology 24:125-132.

Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology 76:1297-1309.

Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (Oncorhynchus kisutch. Canadian Journal of Fisheries and Aquatic Sciences 45:502-515.

Interior Columbia Basin Ecosystem Management Project. 1997. Eastside draft environmental impact statement. U. S. Department of Agriculture.

Jasper, S., and M. L. Bothwell. 1986. Photosynthetic characteristics of lotic periphyton. Canadian Journal of Fisheries and Aquatic Sciences 43:1960-1969.

Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications...a review. Journal of Range Management 37:430-437.

Kohler, S. L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. Ecology 66:1749-1761.

Lamberti, G. A., J. W. Feminella, and V. H. Resh. 1987. Herbivory and intraspecific competition in a stream caddisfly population. Oecologia 73:75-81.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, A. D. Steinman, and C. D. McIntire. 1989. Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. Ecology 70:1840-1856.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman, and K. M. Moore. 1991. Stream ecosystem recovery following a catastrophic debris flow. Canadian Journal of Fisheries and Aquatic Sciences 48:196-208.

Lamberti, G. A., and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64:1124-1135.

Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, and J. L. Li. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Transactions of the American Fisheries Society 123:627-640.

Lowe, R. L., S. W. Golladay, and J. R. Webster. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. Journal of the North American Benthological Society 5:221-229.

McIntire, C. D., and H. K. Phinney. 1965. Laboratory studies of periphyton production and community metabolism in lotic environments. Ecological Monographs 35:237-258.

Meehan, W. R. (editor). 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.

Merritt, R. W., and K. W. Cummins. 1984. An introduction to the aquatic insects of North America. Kendall Hunt Publishers, Dubuque, Iowa.

Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137-145.

Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. Transactions of the American Fisheries Society 110:469-478.

Newbold, J. D., D. C. Erman, and K. B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Canadian Journal of Fisheries and Aquatic Sciences 37:1076-1085.

Platts, W. S., and R. L. Nelson. 1989. Stream canopy and its relationship to salmonid biomass in the intermountain West. North American Journal of Fisheries Management 9:446-457.

Richards, C., and G. W. Minshall. 1988. The influence of periphyton abundance on Baetis bicaudatus distribution and colonization in a small stream. Journal of the North American Benthological Society 7:77-86.

Sih, A., and D. E. Wooster. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. Ecology 75:1199-1207.

Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10:375-383.

Steinman, A. D. 1992. Does an increase in irradiance influence periphyton in a heavily-grazed woodland stream? Oecologia 91:163-170.

Tait, C. K., J. L. Li, G. A. Lamberti, T. N. Pearsons, and H. W. Li. 1994. Relationships between riparian cover and the community structure of high desert streams. Journal of the North American Benthological Society 13:45-56.

Thorp, J. H. 1986. Two distinct roles for predators in freshwater assemblages. Oikos 47:75-82.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Wiggins, G. B., and J. S. Richardson. 1982. Revision and synopsis of the caddisfly genus Dicosmoecus (Trichoptera: Limnephilidae; Dicosmoecinae). Aquatic Insects 4:181-217.

Wrona, F. J., P. Calow, I. Ford, D. J. Baird, and L. Maltby. 1986. Estimating the abundance of stone-dwelling organisms: a new method. Canadian Journal of Fisheries and Aquatic Sciences 43:2025-2035.

CONCLUSION

Summary of the three riparian studies

Riparian vegetation plays a crucial role in the productivity and trophic relationships of stream ecosystems, ultimately regulating physical stability and energy inputs, and affecting food web interactions of aquatic communities (Gregory et al. 1991). The preceding studies have addressed the influences of riparian canopy on benthic communities in streams that sustain beleaguered populations of anadromous salmonids. Because these streams were located in arid rangeland, the thermal loading and alterations of trophic relationships caused by canopy disturbance were potentially more severe than would be the case in streams of more mesic climates (Beschta 1997). The results of each study contribute to an assessment of the interdependence between riparian canopy, benthic community structure, and the carrying capacity of high desert streams for salmonid fishes.

In Chapter 1, benthic and fish communities were compared in stream reaches varying in density of riparian canopy. These lower John Day Basin sites received summer solar inputs ranging from dim (165 Mj/m^2) to bright (2230 Mj/m^2). Water temperatures varied with the density and upstream extent of canopy. Densely canopied sites were cool, but water temperatures increased as canopy decreased, and the sites with the highest irradiances had water temperatures that exceeded the upper lethal limit for salmonids. Periphyton standing crops and, concomitantly, biomasses of grazer invertebrates were greater in these well-lighted sites, but 90% of the biomass of these grazers consisted of Dicosmoecus gilvipes, a large, stone-cased caddisfly rarely consumed by juvenile trout and other resident fishes.

Increases in water temperature with the reduction of riparian canopy likely resulted in higher metabolic demands for salmonids, but the overwhelming dominance of <u>Dicosmoecus</u> in open sites and scarcity of edible mayflies shifted energy flow away from trout, shrinking their food base. High water temperatures in well-lighted sites eliminated salmonids and cottids, but provided suitable habitat for many warmwater fishes that would otherwise not enter tributaries of this size.

In Camp Creek, study sites were located at a higher elevation (approx. 1300 m), and light levels were high and less variable (mean = 1491 $\pm$ 83.6 Mj/m^2) than at the lower John Day Basin sites. Neither periphyton abundance nor invertebrate abundance was correlated with irradiance. Rather, periphyton standing crops were maintained at low, uniform levels by grazers, particularly <u>Dicosmoecus</u> and snails. In contrast, periphyton standing crops in well-lighted lower John Day basin sites (Chapter 1) were 3-4X higher than in Camp Creek, despite higher densities of <u>Dicosmoecus</u> (mean = 190 <u>Dicosmoecus</u>/m^2 in lower basin sites vs. 10 <u>Dicosmoecus</u>/m^2 in Camp Creek) and other invertebrates. The lower elevation, warmer water temperatures, and longer growing period in the lower John Day Basin streams may contribute to higher primary production and may account for the higher periphyton and invertebrate standing crops found there. In Chapter 2, manipulations of fish densities in enclosures showed that trout and speckled dace had no apparent negative effects on population sizes of invertebrate prey. On the contrary, periphyton and, subsequently, invertebrate abundances increased as fish densities increased. High fish numbers may have disturbed grazers and reduced their foraging rates, thereby increasing algal accrual. Regardless, grazers played a more prominent role in regulating lower trophic levels than did fish. <u>Dicosmoecus</u>,

in particular, appeared to act as an intermediate regulator in the benthic food web of Camp Creek by simultaneously influencing trophic levels both below and above its own. Dicosmoecus directly reduced periphyton and indirectly reduced abundances of other invertebrates. At the same time, Dicosmoecus' unavailability as a food resource for small predaceous fish may inhibit fish growth and viability.

When incident radiation was severely reduced on Camp Creek under artificial canopies (Chapter 3), periphyton standing crops were not different from those in open control pools after 4 wks. However, total invertebrate densities and abundances of specific taxa, such as snails, were greater in unshaded pools. The cropping of periphyton to low, uniform levels, despite a presumed disparity in the amount of primary production occurring in open sunlight and deep shade, suggests that mobile grazers targeted sites of varying productivities, as they may do in a naturally vegetated stream with a range of canopy densities. Comparisons of benthic communities in less canopied Camp Creek with densely canopied Deardorff Creek suggested that relative abundances and species compositions of benthic invertebrates shifted to accommodate changes in energy resources that occurred when canopy density was altered.

Implications for riparian management

The John Day River Basin has one of the few remaining wild anadromous fish runs in the Columbia River Basin (Oregon Water Resources Department [OWRD] 1986). Historically, the John Day Basin provided spawning and rearing habitat for fall and spring chinook, summer steelhead, and resident species such as bull trout. However, due to human

disturbance and activities, anadromous fish populations have declined by over 50% in the Columbia and John Day basins over the last 40 years (OWRD 1986), and fragmented bull trout populations are restricted to headwater refugia (Ratliff and Howell 1992). Some populations face extinction, leading to current or proposed listing of several salmon, steelhead, and bull trout stocks under the Endangered Species Act.

The most ubiquitous human disturbance in the John Day Basin is livestock grazing (OWRD 1986). Overgrazing impacts riparian environments by reducing vegetation, and may impact fish habitat through channel widening, channel aggradation, or lowering of the water table (Platts 1991). Removal of streambank vegetation reduces periodic inputs of organic matter (leaf and woody litter) and terrestrial insects, which represent important food resources for benthic organisms (Gregory et al. 1991). Elimination of riparian cover also leads to higher water temperatures that can negatively affect salmonids and change fundamental attributes of the aquatic ecosystem (Johnson et al. 1977; Kauffman and Krueger 1984; Platts and Nelson 1989; Beschta 1997). Overgrazing leading to stream canopy removal has been suggested as one of the principal factors contributing to the decline of native trout in the West (Behnke and Zarn 1976).

Restoration of riparian canopy, either in the lower John Day Basin streams or in Camp Creek, should alter the community structure and ecosystem processes that developed under disturbed conditions. If restored canopy is maintained as a mosaic of densities, and decreases in water temperatures are moderate, the existing invertebrate assemblage should not change significantly, but species compositions and distributions may adjust locally to the amount of light reaching the streambed. For example, mobile grazers, such as Dicosmoecus gilvipes or snails, should track areas with

higher irradiance and primary production, whereas other taxa, such as mayflies, may prefer less productive sites with thin biofilms. Periphyton would be cropped to low, uniform levels regardless of irradiance by the combined action of these grazers targeting different primary productivities. Under canopy, the relative abundance of <u>Dicosmoecus</u> would be reduced, and consequently the proportion of energy available to fishes would increase. Streamside vegetation would also increase numbers of terrestrial insects to augment benthic food resources for fishes (Gerking 1994). With higher allochthonous inputs, the shredder component of the benthic community would increase. Salmonids, then, would benefit from cooler water temperatures and higher prey availability, whereas warmwater fishes would encounter less optimal water temperatures and increased competition from salmonids (Reeves et al. 1987; Moyle and Cech 1988).

At higher elevations, as in Camp Creek, canopy restoration may lower water temperatures sufficiently to produce significant changes in benthic communities by affecting timing of life cycles, growth rates, and metabolism (Vannote and Sweeney 1980; DeNicola 1996). With low solar input and dense canopy, stream temperature fluctuations often are narrow, and species diversity may be low because only those species that function within a narrow temperature range would persist (Vannote et al. 1980). The warm water component of the fish community would thus be eliminated, and habitat would be optimal for cool stenothermic species that historically occupied these streams.

BIBLIOGRAPHY

Adams, R. M., P. C. Klingeman, and H. W. Li. 1990. A bioeconomic analysis of water allocations and fish habitat enhancements, John Day Basin, Oregon. U. S. Geological Survey Grant Number 14-68-0001-G1479.

Aho, R. S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of stream. M.S. Thesis. Oregon State University, Corvallis.

Allan, J. D. 1981. Determinants of the diet of brook trout (Salvelinus fontinalis) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 38:184-192.

---. 1982. The effects of reduction in trout density on the invertebrate community of a mountain stream. Ecology 63:1444-1455.

Barnese, L. E., R. L. Lowe, and R. D. Hunter. 1990. Comparative grazing efficiency of pulmonate and prosobranch snails. Journal of the North American Benthological Society 9:35-44.

Barton, D. R., W. D. Taylor, and R. M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. North American Journal of Fisheries Management 5:364-378.

Bechara, J., G. Moreau, and L. Hare. 1993. The impact of brook trout (Salvelinus fontinalis) on an experimental stream benthic community: the role of spatial and size refuge. Journal of Animal Ecology 62:451-464.

Bechara, J. A., G. Moreau, and D. Planas. 1992. Top-down effects of brook trout (Salvelinus fontinalis) in a boreal forest stream. Canadian Journal of Fisheries and Aquatic Sciences 49:2093-2103.

Behmer, D. J., and C. P. Hawkins. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. Freshwater Biology 16:287-300.

Behnke, R. J., and M. Zarn. 1976. Biology and management of threatened and endangered western trouts. U.S.Forest Service General Technical Report RM-28, .

Benke, A. C., Henry, R. L., Gillespie, D. M., and R. J. Hunter. 1985. Importance of snag habitat for animal production in southeastern streams. Fisheries 10:8-13.

Beschta, R. L. 1997. Riparian shade and stream temperatures: an alternative perspective. Rangelands 19: 25-28.

Bidgood, B.F., and A. H. Berst. 1969. Lethal temperatures for Great Lakes rainbow trout. Journal of the Fisheries Research Board of Canada 26:456-459.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540-551.

Bisson, P. A., Bilby, R. E., Bryant, M. D., Dolloff, C. A., Grette, G. B., House, R. A., Murphy, M. L., Koski, K. V., and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. Pages 143-190 in E. O. Salo and T. W. Cundy (editors). Streamside management: forestry and fishery interactions. Institute of Forest Resources, University of Washington, Seattle.

Bisson, P. A., and G. E. Davis. 1976. Production of juvenile chinook salmon, Oncorhynchus tshawytscha, in a heated model stream. Fishery Bulletin 74: 763-774.

Bisson, P. A., and J. R. Sedell. 1984. Salmonid populations in streams in clearcut vs. old-growth forests of western Washington. Pages 121-129 in W. R. Meehan, T. R. Merrell and T. A. Hanley (editors). Fish and wildlife relationships in old-growth forests: proceedings of a symposium held in Juneau, Alaska, 12-15 April 1982. American Institute of Fishery Research Biologists, Asheville, N. C.

Bott, T. L. 1983. Primary productivity in streams. Pages 29-53 in T. D. Fontaine and S. M. Bartell (editors). Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, MI.

Bowlby, J. N., and J. C. Roff. 1986. Trophic structure in southern Ontario streams. Ecology 67:1670-1679.

Brett, M. T., and C. R. Goldman. 1996. A meta-analysis of the freshwater trophic cascade. Proceedings of the National Academy of Sciences 93:7723-7726.

Brönmark, C., S. P. Klosiewski, and R. A. Stein. 1992. Indirect effects of predation in a freshwater benthic food chain. Ecology 73:1662-1674.

Bruns, D. A., and W. L. Minckley. 1980. Distribution and abundance of benthic invertebrates in a Sonoran Desert stream. Journal of Arid Environments 3:117-131.

Carlander, K. D. 1969. Handbook of freshwater fishery biology. Iowa State University Press, Ames.

Carlson, J. Y., C. W. Andrus, and H. A. Froehlich. 1990. Woody debris, channel features, and macroinvertebrates of streams with logged and undisturbed riparian timber in northeastern Oregon, USA. Canadian Journal of Fisheries and Aquatic Sciences 47:1103-1111.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634-639.

Cooper, S. D., S. J. Walde, and B. L. Peckarsky. 1990. Prey exchange rates and the impact of predators on prey populations in streams. Ecology 71:1503-1514.

Creed, R. P. 1994. Direct and indirect effects of crayfish grazing in a stream community. Ecology 75:2091-2103.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802-1813.

Culp, J. M. 1986. Experimental evidence that stream macroinvertebrate community structure is unaffected by different densities of coho salmon fry. Journal of the North American Benthological Society 5:140-149.

Cummins, K. W., M. A. Wilzbach, D. W. Gates, J. A. Perry, and W. Taliaferro. 1989. Shredders and riparian vegetation. BioScience 39:24-30.

DeNicola, D. M. 1996. Periphyton responses to temperature at different ecological levels. Pages 149-181 in R. J. Stevenson, M. L. Bothwell and R. L. Lowe (editors). Algal ecology. Academic Press, San Diego.

DeNicola, D. M., C. D. McIntire, G. A. Lamberti, and L. R. Ashkenas. 1990. Temporal patterns of grazer-periphyton interactions in laboratory streams. Freshwater Biology 23:475-489.

Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73:1646-1661.

Dudley, T. L., S. D. Cooper, and N. Hemphill. 1986. Effects of macroalgae on a stream invertebrate community. Journal of the North American Benthological Society 5:93-106.

Elliot, J. M. 1973. Food of brown and rainbow trout in relation to the abundance of drifting invertebrates in a mountain stream. Oecologia 12:329-347.

Feminella, J. W., and C. P. Hawkins. 1995. Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. Journal of the North American Benthological Society 14:465-509.

Feminella, J. W., M. E. Power, and V. H. Resh. 1989. Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. Freshwater Biology 22:445-457.

Forrester, G. E. 1994. Influences of predatory fish on the drift dispersal and local density of stream insects. Ecology 75:1208-1218.

Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? Oikos 50:291-301.

Fuller, R. L., J. L. Roelofs, and T. J. Fry. 1986. The importance of algae to stream invertebrates. Journal of the North American Benthological Society 5:290-296.

Gerking, S. D. 1994. Feeding ecology of fish. Academic Press, San Diego.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65:455-468.

Gilliam, J. F., D. F. Fraser, and A. M. Sabat. 1989. Strong effects of foraging minnows on a stream benthic invertebrate community. Ecology 70:445-452.

Gotceitas, V., and H. F. Clifford. 1983. The life history of Dicosmoecus atripes (Hagen) (Limnephilidae: Trichoptera) in a Rocky Mountain stream of Alberta, Canada. Canadian Journal of Fisheries and Aquatic Sciences 61: 586-596.

Grafius, E. 1976. The conversion of allochthonous material by stream detritivores. M.S. Thesis, Oregon State University, Corvallis.

Gregory, S. V. 1983. Plant-herbivore interactions in stream systems. Pages 157-189 in J. R. Barnes and G. W. Minshall (editors). Stream ecology: application and testing of general ecological theory. Plenum Press, New York.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540-551.

Griffith, J. S. 1981. Estimation of the age-frequency distribution of stream-dwelling trout by underwater observation. Progressive Fish-Culturalist 43:51-53.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421-425.

Hart, D. D. 1981. Foraging and resource patchiness: field experiments with a grazing stream insect. Oikos 37:46-52.

---. 1992. Community organization in streams: the importance of species interactions, physical factors, and chance. Oecologia 91:220-228.

Hawkins, C. P., and J. K. Furnish. 1987. Are snails important competitors in stream ecosystems? Oikos 49:209-220.

Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology 63:1840-1856.

Hawkins, C. P., M. L. Murphy, N. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173-1185.

Hemphill, N., and S. D. Cooper. 1984. Differences in the community structure of stream pools containing or lacking trout. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22:1858-1861.

Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. Responses of salmonids to habitat changes. Pages 483-518 in W. R. Meehan (editor). Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.

Hill, W. 1996. Effects of light. Pages 121-148 in R. J. Stevenson, M. L. Bothwell and R. L. Lowe (editors). Algal ecology. Academic Press, San Diego.

Hill, W. R., H. L. Boston, and A. D. Steinman. 1992. Grazers and nutrients simultaneously limit lotic primary productivity. Canadian Journal of Fisheries and Aquatic Sciences 49:504-512.

Hill, W. R., and A. W. Knight. 1987. Experimental analysis of the grazing interaction between a mayfly and stream algae. Ecology 68:1955-1965.

---. 1988. Nutrient and light limitation of algae in two northern California streams. Journal of Phycology 24:125-132.

Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology 76:1297-1309.

Holomuzki, J. R., and R. J. Stevenson. 1992. Role of predatory fish in community dynamics of an ephemeral stream. Canadian Journal of Fisheries and Aquatic Sciences 49:2322-2330.

Holtby, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (Oncorhynchus kisutch. Canadian Journal of Fisheries and Aquatic Sciences 45:502-515.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724-732.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto.

Interior Columbia Basin Ecosystem Management Project. 1997. Eastside draft environmental impact statement. U. S. Department of Agriculture.

Jacobs, J. 1974. Quantitative measurement of food selection. Oecologia 14:413-417.

Jacoby, J. M. 1987. Alterations in periphyton characteristics due to grazing in a Cascade foothill stream. Freshwater Biology 18:495-508.

Jasper, S., and M. L. Bothwell. 1986. Photosynthetic characteristics of lotic periphyton. Canadian Journal of Fisheries and Aquatic Sciences 43:1960-1969.

Johansson, A. 1991. Caddis larvae cases (Trichoptera, Limnephilidae) as anti-predatory devices against brown trout and sculpin. Hydrobiologia 211:185-194.

Johnson, R. R., L. T. Haight, and J. M. Simpson. 1977. Endangered species vs. endangered habitats: a concept. Pages 68-79 in Importance, preservation, and management of riparian habitats. USDA Forest Service General Technical Report RM-43.

Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications...a review. Journal of Range Management 37:430-437.

Kohler, S. L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. Ecology 66:1749-1761.

Kohler, S. L., and M. A. McPeek. 1989. Predation risk and the foraging behavior of competing stream insects. Ecology 70:1811-1825.

Lamberti, G. A. 1996. The role of periphyton in benthic food webs. Pages 533-572 in R. J. Stevenson, M. L. Bothwell and R. L. Lowe (editors). Algal ecology. Academic Press, San Diego.

Lamberti, G. A., L. R. Ashkenas, S. V. Gregory, and A. D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. Journal of the North American Benthological Society 6:92-104.

Lamberti, G. A., J. W. Feminella, and V. H. Resh. 1987. Herbivory and intraspecific competition in a stream caddisfly population. Oecologia 73:75-81.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, A. D. Steinman, and C. D. McIntire. 1989. Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. Ecology 70:1840-1856.

Lamberti, G. A., S. V. Gregory, C. P. Hawkins, R. C. Wildman, L. R. Ashkenas, and D. M. DeNicola. 1992. Plant-herbivore interactions in streams near Mount St Helens. Freshwater Biology 27:237-247.

Lamberti, G. A., and J. W. Moore. 1984. Aquatic insects as primary consumers. Pages 164-195 in V. H. Resh and D. M. Rosenberg

(editors). The ecology of aquatic insects. Praeger Publishers, New York.

Lamberti, G. A., and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64:1124-1135.

Li, H. W., G. A. Lamberti, T. N. Pearsons, C. K. Tait, and J. L. Li. 1994. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. Transactions of the American Fisheries Society 123:627-640.

Li, J. L. 1990. Foraging behavior of the limnephilid caddisfly Dicosmoecus gilvipes and co-occurring herbivores in streams of the Pacific Northwest. Ph.D. Dissertation, Oregon State University, Corvallis.

Li, J. L., and S. V. Gregory. 1989. Behavioral changes in the herbivorous caddisfly Dicosmoecus gilvipes (Limnephilidae). Journal of the North American Benthological Society 8:250-259.

Lowe, R. L., S. W. Golladay, and J. R. Webster. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. Journal of the North American Benthological Society 5:221-229.

Lyford, J. H., and S. V. Gregory. 1975. The dynamics and structure of periphyton communities in three Cascade Mountain streams. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 19:1610-1616.

McAuliffe, J. R. 1984. Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. Oikos 42:327-333.

McIntire, C. D., and H. K. Phinney. 1965. Laboratory studies of periphyton production and community metabolism in lotic environments. Ecological Monographs 35:237-258.

McIntosh, A. R., and C. R. Townsend. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? Oecologia 108:174-181.

McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs 59:289-309.

Meehan, W. R. (editor). 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.

Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? Ecology 73:755-765.

Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs 64:249-287.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110:351-369.

---. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730-757.

Merritt, R. W., and K. W. Cummins. 1984. An introduction to the aquatic insects of North America. Kendall Hunt Publishers, Dubuque, Iowa.

Moodie, G. E. E., and C. C. Lindsey. 1972. Life-history of a unique cyprinid fish, the chiselmouth (Acrocheilus alutaceus), in British Columbia. Syesis 5:55-61.

Moore, K., and S. V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat fry in Cascade Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 45:1921-1930.

Moyle, P. B., and D. M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Transactions of the American Fisheries Society 114:695-704.

Moyle, P. B., and J. J. Cech. 1988. Fishes: an introduction to ichthyology. Prentice Hall, Englewood Cliffs, NJ.

Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137-145.

Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. Transactions of the American Fisheries Society 110:469-478.

Newbold, J. D., D. C. Erman, and K. B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Canadian Journal of Fisheries and Aquatic Sciences 37:1076-1085.

Oksanen, L. 1988. Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for existence? American Naturalist 131:424-444.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240-261.

Oregon Water Resources Department. 1986. John Day River basin report. OWRD, Salem, Oregon.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65-75.

---. 1969. A note on trophic complexity and community stability. American Naturalist 103:91-93.

---. 1992. Food web analysis through field measurement of per capita interaction strength. Nature 355:73-75.

Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance and resilience of stream fish assemblages to flooding. Transactions of American Fisheries Society 121:85-119.

Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology 74:1836-1846.

Peterson, B. J., L. Deegan, J. Helfrich, J. E. Hobbie, M. Hullar, B. Moller, T. E. Ford, A. Hershey, A. Hiltner, G. Kipphut, M. A. Lock, D. M. Fiebig, V. McKinley, M. C. Miller, J. R. Vestal, R. Ventullo, and G. Volk. 1993. Biological responses of a tundra river to fertilization. Ecology 74:653-672.

Platts, W. S. 1991. Livestock grazing. Pages 389-423 in W. R. Meehan (editor). Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19.

Platts, W. S., C. Armour, G. D. Booth, D. Gordon, M. Bryant, J. L. Bufford, P. Cuplin, S. Jensen, G. W. Lienkaemper, G. W. Minshall, S. B. Monsen, R. L. Nelson, J. R. Sedell, J. S. Tuhy. 1987. Methods for evaluating riparian habitats with applications to management. General Technical Report INT-221. Ogden, Utah: USDA Forest Service, Intermountain Research Station.

Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. USDA Forest Service INT-138.

Platts, W. S., and R. L. Nelson. 1989. Stream canopy and its relationship to salmonid biomass in the intermountain West. North American Journal of Fisheries Management 9:446-457.

Power, M. E. 1984. Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. Journal of Animal Ecology 53:357-374.

---. 1990. Effects of fish in river food webs. Science 250:811-814.

---. 1992a. Hydrologic and trophic controls of seasonal algal blooms in northern California rivers. Archiv für Hydrobiologie 125:385-410.

---. 1992b. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73:733-746.

Power, M. E., W. J. Matthews, and A. J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. Ecology 66:1448-1456.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. BioScience 46:609-620.

Pringle, C. M., R. J. Naiman, G. Bretschko, J. R. Karr, M. W. Oswood, J. R. Webster, R. L. Welcomme, and M. J. Winterbourn. 1988. Patch dynamics in lotic systems: the stream as a mosaic. Journal of the North American Benthological Society 7:503-524.

Prochazka, K., Stewart, B. A., and B. R. Davies. 1991. Leaf litter retention and its implications for shredder distribution in two headwater streams. Archiv für Hydrobiologie 120:315-325.

Ratliff, D. E., and P. J. Howell. 1992. The status of bull trout populations in Oregon. Pages 10-17 in Howell, P. J. and D. V. Buchanan (editors). Proceedings of the Gearhart Mountain bull trout workshop. Oregon Chapter of the American Fisheries Society, Corvallis.

Reeves, G. H., F. H. Everest, and J. D. Hall. 1987. Interactions between the redside shiner (Richardsonius balteatus) and the steelhead trout (Salmo gairdneri) in western Oregon: the influence of water temperature. Canadian Journal of Fisheries and Aquatic Sciences 44: 1603-1613.

Reice, S. R., and R. L. Edwards. 1986. The effect of vertebrate predation on lotic macroinvertebrate communities in Quebec, Canada. Canadian Journal of Zoology 64:1930-1936.

Richards, C., and G. W. Minshall. 1988. The influence of periphyton abundance on Baetis bicaudatus distribution and colonization in a small stream. Journal of the North American Benthological Society 7:77-86.

Rodgers, J.D., M. F. Solazzi, S. L. Johnson, and M. A. Buckman. 1992. Comparison of three techniques to estimate juvenile coho salmon populations in small streams. North American Journal of Fisheries Management 12:79-86.

Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton effects of nutrients and herbivores. Ecology 74:1264-1280.

Schlosser, I. J., and K. K. Ebel. 1989. Effects of flow regime and cyprinid predation on a headwater stream. Ecological Monographs 59:41-57.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16:269-311.

Sih, A., and D. E. Wooster. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. Ecology 75:1199-1207.

Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10:375-383.

Speaker, R., K. Moore, and S. V. Gregory. 1984. Analysis of the process of retention of organic matter in stream ecosystems. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22:1835-1841.

Steinman, A. D. 1992. Does an increase in irradiance influence periphyton in a heavily-grazed woodland stream? Oecologia 91:163-170.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73:747-754.

Tait, C. K., J. L. Li, G. A. Lamberti, T. N. Pearsons, and H. W. Li. 1994. Relationships between riparian cover and the community structure of high desert streams. Journal of the North American Benthological Society 13:45-56.

Teague, S. A., A. W. Knight, and B. N. Teague. 1985. Stream microhabitat selectivity, resource partitioning, and niche shifts in grazing caddisfly larvae. Hydrobiologia 128:3-12.

Thorp, J. H. 1986. Two distinct roles for predators in freshwater assemblages. Oikos 47:75-82.

Threlkeld, S. T. 1987. Experimental evaluation of trophic cascade and nutrient-mediated effects of planktivorous fish on plankton community structure. Pages 161-173 in C. W. Kerfoot and A. Sih (editors). Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH.

Tippets, W. E., and P. B. Moyle. 1978. Epibenthic feeding by rainbow trout (Salmo gairdneri) in the McCloud River, California. Journal of Animal Ecology 47:549-559.

Towns, D. R. 1979. Composition and zonation of benthic invertebrate communities in a New Zealand kauri forest stream. Freshwater Biology 9:251-262.

Towns, D. R. 1981. Effects of artificial shading on periphyton and invertebrates in a New Zealand stream. New Zealand Journal of Marine and Freshwater Research 15:185-192.

Triska, F. J., V. C. Kennedy, R. J. Avanzino, and B. N. Reilly. 1983. Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. Pages 129-159 in T.

D. Fontaine and S. M. Bartell (editors). Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Michigan.

Tschaplinski, P.J., and G. F. Hartman. 1983. Winter distribution of juvenile coho salmon (Oncorhynchus kisutch) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Canadian Journal of Fisheries and Aquatic Sciences 40:452-461.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Vannote, R. L. and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. American Naturalist 115:667-695.

Waters, T. F. 1972. The drift of stream insects. Annual Review of Entomology 17:253-272.

Weatherley, N. S., and S. J. Ormerod. 1990. Forests and the temperature of upland streams in Wales: a modelling exploration of the biological effects. Freshwater Biology 24:109-122.

Wiggins, G. B., and J. S. Richardson. 1982. Revision and synopsis of the caddisfly genus Dicosmoecus (Trichoptera: Limnephilidae; Dicosmoecinae). Aquatic Insects 4:181-217.

Wooster, D. 1994. Predator impacts on stream benthic prey. Oecologia 99:7-15.

Wrona, F. J., P. Calow, I. Ford, D. J. Baird, and L. Maltby. 1986. Estimating the abundance of stone-dwelling organisms: a new method. Canadian Journal of Fisheries and Aquatic Sciences 43:2025-2035.

Wydoski, R. S., and R. R. Whitney. 1979. Inland fishes of Washington. University of Washington Press, Seattle.