

AN ABSTRACT OF THE THESIS OF

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Title: Post-Eruption Recovery and Secondary Production of Grazing Insects in Two Streams Near Mt. St. Helens.

Abstract approved:


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The eruption of Mt. St. Helens provided the opportunity to study secondary production of grazing insects in the context of disturbance. Two stream sites were chosen that significantly differed in how their watersheds were impacted by the eruption. Clearwater Creek was catastrophically disturbed (physical alteration of habitat, loss of riparian vegetation, and abundant ashfall); Elk Creek was disturbed only by heavy ashfall. Secondary production of the insect community was estimated for 1985 and 1986. The relative importance of disturbance history and between-site habitat differences in determining secondary production was assessed by placing results in the context of ten years (1980-1989) of summer data from both streams.

Few insects were found in Clearwater Creek four months after the eruption. In contrast, the community at Elk Creek was diverse and dominated by long-lived

taxa. From 1980 to 1989 at Clearwater Creek there was a gradual shift from dominance by Chironomidae to an increasingly diverse community with an abundance of mayflies, stoneflies, and caddisflies. Disturbance from ash scour during the 1980-81 winter reset the benthos of Elk Creek. However, the recovery process in that stream after 1982 was rapid.

The annual production of insects in 1985 was 9.7 g dry wt/m² at Elk Creek and 8.6 g/m² at Clearwater Creek. In 1986, production was higher at Clearwater Creek (27.4 g/m²) than at Elk Creek (16.3 g/m²). Aufwuchs grazers were the most important insects (ca. 75% of total insect production) of both streams in both years. After differences in assimilation efficiencies of food types were considered, it was found that 84.3% of grazer production at Clearwater Creek depended on algae as compared to 74.3% at Elk Creek.

The disturbance history of each site was an important factor determining the insect community structure and the importance of grazers at each site. Consequently, secondary production in 1985-1986 was influenced to a large degree by the 1980 eruption. However, between-site differences in basin dimensions, substrate size, and riparian vegetation likely controlled the productive capacity of each stream.

Post-Eruption Recovery and Secondary Production of
Grazing Insects in Two Streams Near Mt. St. Helens

by

Richard Dietrich Meyerhoff

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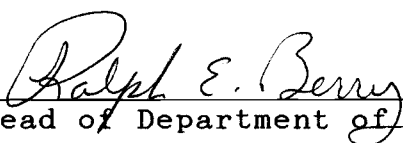
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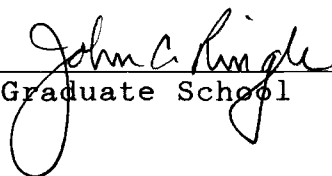
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POST-ERUPTION RECOVERY AND SECONDARY PRODUCTION OF GRAZING INSECTS IN TWO STREAMS NEAR MT. ST. HELENS

Chapter 1

INTRODUCTION

On May 18, 1980, the eruption of Mt. St. Helens devastated more than 600 km² north and east of the volcano in southwest Washington state. In addition ash was spread over a much wider area. For example, up to 7 cm was deposited at Ritzville, WA, 300 km ENE of Mt. St. Helens. This catastrophic disturbance modified the physical structure and eliminated the riparian vegetation of stream systems in the Mt. St. Helens area. Ashfall deposits changed rainfall-runoff relationships (Swanson et al. 1983), channel geometry (Janda et al. 1981, Lisle et al. 1983) and the amount of sediment available for transport in stream channels (Martinson et al. 1982). Much, if not all, of the flora and fauna was eliminated. Given the extent of devastation the recovery of the biota to pre-eruption conditions would be a long-term process.

By September 1980 researchers began charting the recolonization of organisms in various streams and lakes near the mountain. It is clear from their data that while many aquatic habitats had few surviving organisms, invertebrates and algae were quickly recolonizing (Fuste

1981, Ward et al. 1983, Wilzbach et al. 1983, Rushforth et al. 1986, Anderson and Wisseman 1987, Larson and Glass 1987, N.H. Anderson unpublished, C.P. Hawkins unpublished).

Research funded by a cooperative agreement between the U.S. Forest Service and Oregon State University and grants from the National Science Foundation allowed comparisons of the effects of the eruption on several streams. The research for this thesis focused on Clearwater Creek, which received major impacts from the eruption (physical alteration of habitat, loss of riparian vegetation, and abundant ashfall), and on Elk Creek which was only affected by ash deposition (Table 1.1).

The loss of riparian zones destabilized stream banks thereby increasing the sediment load in streams (Swanson et al. 1982). Ash is easily transported even at low current velocities, which results in substrate instability. Furthermore, the abrasive nature of the material is detrimental to surface-feeding invertebrates and to algae. It is assumed that the effects on the benthos were more severe in Clearwater Creek than in Elk Creek because more ash was deposited in the former watershed and there was no riparian vegetation to retard its transport into the stream channel.

Table 1.1. Effects of the May 18, 1980 eruption of Mt. St. Helens on watersheds of study streams.

| Parameter | Clearwater Cr. | Elk Cr. |
|-------------------|--|--|
| Blast | timber destroyed | timber left intact |
| Ashfall | | |
| Depth* | 10 cm | 5 cm |
| Type** | high density fines and coarse particles | low density fines; some coarse particles |
| Erosion | immediate and extensive | minor initially; heavy during winter of 1980-81*** |
| Long-Term Effects | unstable banks, shifting channel and substrates; ash scour | decreasing impact of ash scour in successive years |

* - Waite and Dzuring (1981)

** - Density of ash (g/cm^2) decreased markedly with distance from eruption (Sarna-Wojcicki et al. 1982, Waite and Dzuring 1981).

*** - Antos (1984)

Ash accumulation affected the melting of the winter snowpack in forested watersheds north and east of Mt. St. Helens (Antos and Zobel 1982). At high elevations (e.g. > 1200 m) patches of snow from the 1979-1980 winter still remained under the ash in the fall of 1980. The likely effect of delayed snowmelt was cooler water temperatures during the summer of 1980 and this could have been a factor at Elk Creek as the upper portion of its watershed is above 1200 m.

Given the above description of habitat conditions, it may be assumed that the stream bed of Clearwater Creek was highly unstable which would limit colonization by aquatic insects. Data collected from 1980-1983 showed that the insect community of Clearwater Creek had been affected by the eruption to a greater degree than that at Elk Creek. For example, in 1980 density was ca. 300/m² at Clearwater Creek, but ca. 4200/m² at Elk Creek, and biomass (g dry wt/m²) was 0.1 and 1.9, respectively. Long-lived taxa, especially Trichoptera, contributed most of the biomass at Elk Creek. By 1982 both density and biomass had greatly increased at Clearwater Creek (16,500 organisms/m² and 1.4 g dry wt/m²), while at Elk Creek, even though density had doubled to 10,000/m², biomass had declined 50% to 0.9 g dry wt/m². Chironomid midges and Baetis spp. mayflies were the dominant taxa at both sites in 1982. These are

opportunistic taxa that are capable of exploiting disturbed habitats (Oliver 1971, Brittain 1982).

Research was expanded at Clearwater Creek in 1983-1984 to determine how large woody debris influenced channel morphology and the development of the benthic community. This was done by removing large woody debris from parts of the stream channel. Four stream segments were divided into reaches with wood (Leave section), and without large woody debris (Take section). The importance of woody debris as a contributor to habitat structure and stability has been well documented (Swanson et al. 1976, Anderson et al. 1978, Swanson and Lienkaemper 1978, Anderson and Sedell 1979, Triska and Cromack 1980, Franklin et al. 1981, Sedell et al. 1982, Maser and Trappe 1984, Sedell and Froggatt 1984). Large debris helps shape a channel by modifying flow patterns creating pools and meanders. These structural modifications alter the habitat resulting in increased diversity of both invertebrates and vertebrates.

Recovery patterns of the stream biota were studied in the context of the presence or absence of large woody debris in 1985 and 1986. As part of this research, I conducted an intensive sampling program to compare the secondary production of aquatic insects in a Take and Leave section of one reach at Clearwater Creek. Quantifying secondary production provides information on

both the source and flow of energy resources in the benthic community. Coupled with this research at Clearwater Creek I chose to expand the study by including the site at Elk Creek. This provided a comparison of sites that differed not only in the amount of large woody debris, but also in regard to the condition of the riparian zone and the type of substrate.

As discussed above, there is a significant link between riparian vegetation and channel stability. However, an important link also exists between riparian vegetation and trophic structure of the benthic community (Hynes 1975, Vannote et al. 1980). For example, reduced canopy allows more solar radiation to reach the stream which affects both water temperature and primary production (Minshall 1978, Naiman and Sedell 1980, Minshall et al. 1983, Barton et al. 1985). Changes in primary production can influence production at higher trophic levels (Warren et al. 1964, Gregory 1980). Riparian vegetation also influences trophic structure as a source of food input to streams. In low-order streams of the Pacific Northwest allochthonous material normally constitutes the primary food for benthic insects (Chapman and Demory 1963, Mundie 1974).

Objectives - This study will focus on the secondary production of one guild of aquatic insects exposed to

the varying habitat conditions described above. For the purposes of this study, a guild is defined as a group of animals that use the same resource regardless of the manner in which it is acquired or used (MacMahon et al. 1981). Work done from 1980 to 1985 showed that both Clearwater and Elk Creeks had similar species in the grazer guild. These are consumers of the aufwuchs film (substrate-attached algae and its associated microbes, microscopic invertebrates, and fine detritus). Aquatic insects have been classified into functional feeding groups based upon food gathering mechanisms rather than on the type of food consumed (Cummins 1973). Based upon this classification, insects belonging to both the scraper and collector-gatherer functional feeding groups may be considered aufwuchs grazers. Thus, these two groups will be combined and considered the grazer guild for this study.

This study has the following objectives:

- 1). To compare the short and long-term effects of the eruption on Clearwater and Elk Creeks by:
 - a) describing habitat characteristics
 - b) monitoring changes in the benthic community for ten years after the 1980 eruption.
- 2). To determine the dominant grazer insects at each site and to compare their life histories and secondary production.
- 3). In terms of secondary production, to determine the importance of the grazer guild to the total production of the aquatic insect community at each site.

- 4). To compare the relative contributions of algae and detritus to the annual production of the important grazer taxa by analyzing feeding habits.

The results of this study are intended to provide additional information on the links between the aquatic habitat and its associated riparian zone and the trophic organization of the benthic community. Using secondary production as the basic unit of comparison will furnish clues as to the importance of this link.

Chapter 2

STUDY AREA

General Description

Clearwater Creek is 13 km NE of Mt. St. Helens near the outer limit of the blast zone (area in which all vegetation was destroyed or blown down) (Table 2.1, Fig. 2.1). Riparian vegetation along the mainstem channel was destroyed and at least 10 cm of ash was deposited throughout the watershed (Martinson et al. 1984). Mainstem tributaries were differentially affected. Those streams which have their headwaters nearest Mt. St. Helens were also catastrophically disturbed, while those with headwaters farthest from the volcano generally retained some forested reaches, especially in their headwaters.

The sample location for the Take and Leave sites is between 100 and 400 m downstream from the bridge at the northern end of the Clearwater Valley on Forest Service Road 2560. The Leave site (length ca. 100 m) on Clearwater Creek has large woody debris that was blown down during the eruption. This has resulted in a stair-step stream bed with numerous pools (pool/riffle ratio = 1.3). The Take site (length ca. 200 m) had its large woody debris first removed with bulldozers in 1983. However, after high water during the winter of 1983-1984

Table 2.1 Watershed characteristics of the study streams.

| Characteristic | Clearwater Cr. | Elk Cr. |
|-----------------------------------|----------------|----------|
| Watershed Area (km ²) | 21.9 | 10.4 |
| Orientation | NW to SE | NE to SW |
| Stream Order | Third | Second |
| Elevation Change* | 55 | 250 |
| Elevation (m) | 744 | 975 |
| Discharge (cu m/sec) - 1986 | | |
| May 3 | 0.89 | 0.31 |
| July 4 | 0.1 | 0.05 |
| September 5 | 0.06 | 0.02 |
| Stream Power (kw) | | |
| May 3 | 490 | 775 |
| July 4 | 55 | 125 |
| September 5 | 33 | 50 |
| Water Temperature (C) - Mean | | |
| Degree Days, May-Oct (1986-87) | 1818 | 1643 |
| By month: | | |
| May | 212 | 134 |
| June | 321 | 295 |
| July | 367 | 347 |
| August | 427 | 406 |
| September | 338 | 309 |
| October | 153 | 152 |

* - change in elevation between 500 m upstream and 500 m downstream of study site.

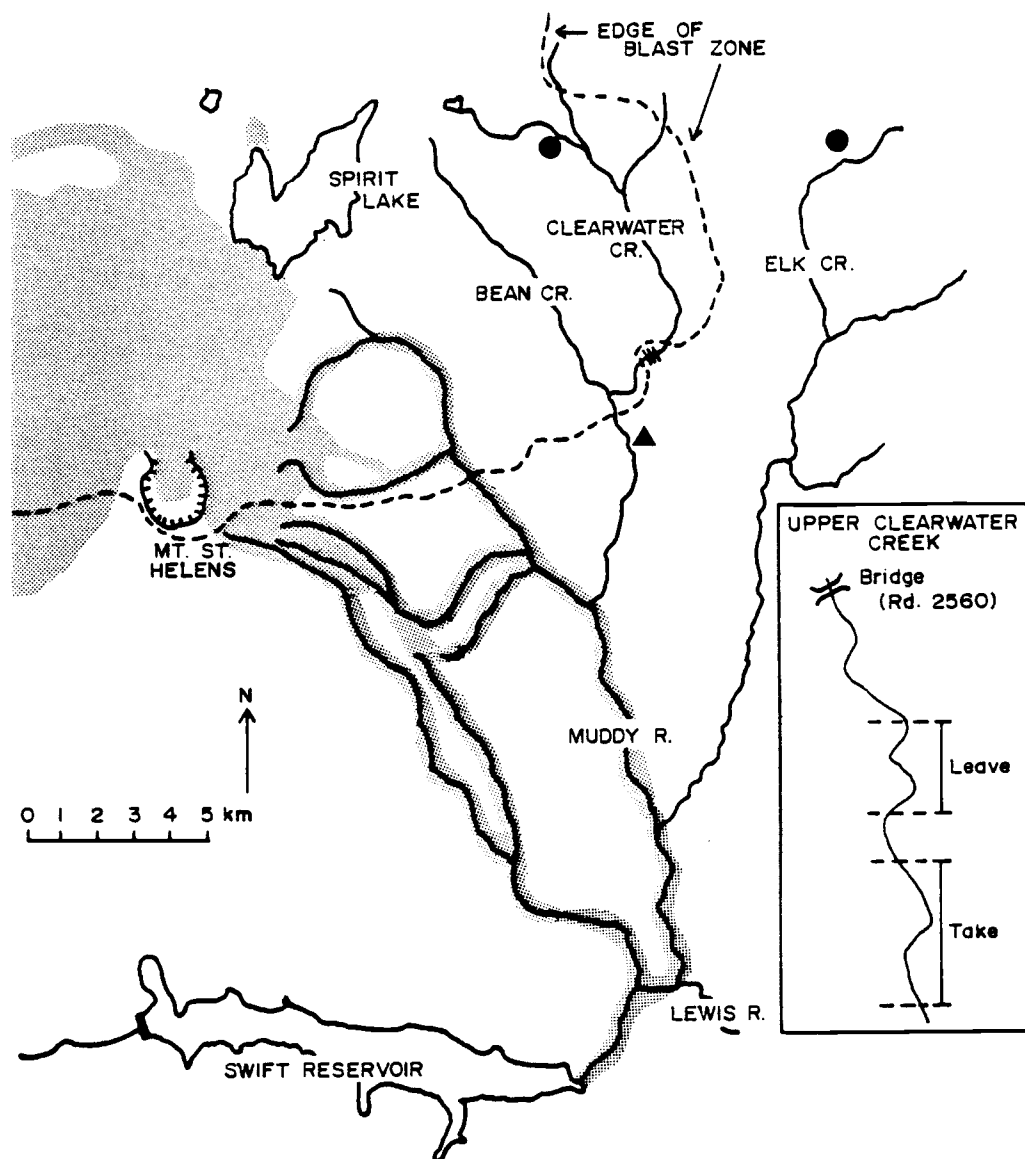


Figure 2.1. Location of study sites near Mt. St. Helens, Washington. Inset shows location of Take and Leave sites. ● = Clearwater and Elk Creek sites. ▲ = Location of gauging station on Lower Clearwater Creek.

redistributed the substrate and excavated buried logs more large woody debris had to be removed from the Take site in 1984. By the time this study was initiated in 1985, little evidence remained of the mechanical disturbance. The lack of woody debris in the channel reduced bed stability which was evidenced by shifts in flow patterns around bars. Pools were less common in this reach than at the Leave site (pool/riffle ratio ca. 0.7).

The Elk Creek site, located at the end of Forest Service Rd 2559, is ca. 7 km east of the Clearwater site and 18 km ENE of Mt. St. Helens. This locality is outside of the blast zone, but received ca. 5 cm of ash during the eruption. The reach of the stream that was sampled (length ca. 100 m) bordered a 15-20 year clearcut. However, above the study site the creek flowed through old-growth Douglas Fir (*Pseudotsuga menziesii*) and Western Hemlock (*Tsuga heterophylla*).

Several naturally occurring pieces of large woody debris in the upstream section of this site have clearly modified the substrate. The wood not only caused the formation of several pools with fine sediments in an otherwise moderately uniform large cobble/boulder substrate (pool/riffle ratio ca. 0.4), but also trapped smaller cobble substrates upstream of the wood.

Physical Comparisons of the Study Sites

Methods

Temperature - A battery-operated Omnidata datapod was placed at the Upper Bridge of Clearwater Creek in May 1985. It collected data at preset intervals and recorded these on a computer chip for later reading and processing. We recorded maximum/minimum water and air temperatures daily almost continuously until October 1986, and again from May to October of 1987. In addition, U.S. Forest Service temperature records were available for 1983 and 1984, so temperature data for the study interval could be placed in the context of a 5-year average from 1983-1987.

A Ryan pen recorder at Elk Creek logged daily air and water temperatures on a paper chart from June to October 1986. This recorder was calibrated with the datapod before its installation. The Ryan recorder was replaced by a second Omnidata datapod from May until October of 1987.

Discharge - The U.S. Geological Survey had a gauging station on lower Clearwater Creek just upstream of the Muddy River (see Fig. 2.1) from 1981-1989. A regression relationship was developed between discharge at this station and measurements made at the Upper Clearwater Creek sites (Fig. 2.2). Another regression

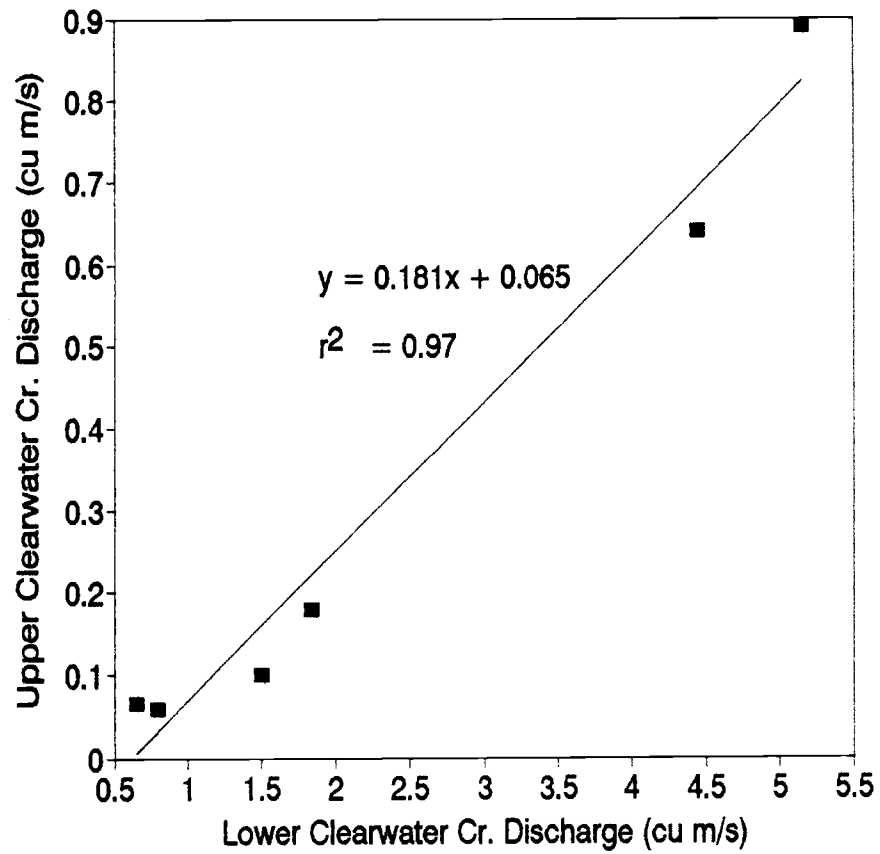


Figure 2.2 Relationship between discharge (cu m/sec) of Upper and Lower Clearwater Creek.

was developed between the Clearwater and Elk Creek sites.

Discharge at Clearwater and Elk Creeks was calculated from measurements of water depth and velocity at cross sections that were established in May and monitored regularly into the fall. Discharge data were gathered at both high and low flows thus yielding a wide range of values for the development of regressions between sites. Depth was measured with a meter stick and water velocity measured at 0.6 of total depth with a Montidoro-Whitney current meter. Two cross sections were monitored on each stream and the values were averaged to yield discharge.

Stream power is a measure of the effect of flow and channel characteristics on the stream bed, and incorporates discharge and slope. Stream Power (P) = $10Qh$, where Q = discharge (cu m/sec) and h = change in elevation (m).

Substrate - Twenty-seven random core samples were collected from each site for comparisons of mean particle size. A 15-cm dia. corer was pushed into the substrate and ten scoops of substrate removed. This material was wet-sieved in the field (sieve sizes = 16, 4, 1, 0.5, 0.25, 0.1, and 0.05 mm), and the volumes were measured in a graduated cylinder by displacement. Particles, < 0.1 mm, were not considered as this size

class was always $< 0.1\%$ of the total displaced volume. Estimates of volume displacement by particle sizes > 16 mm were made with a graduated bucket.

The substrate data from core samples were analyzed by the method of Morgans (1956) which converts particle sizes into phi values [particle diameter (\log_2 transformed)]. This method converts the uneven class intervals of the Wentworth scale (Wentworth 1922) into equal intervals, thereby allowing statistical comparisons of samples. The cumulative frequency of each size class is plotted against phi values and a median particle size (50th percentile) is derived from the resulting graph (e.g., Fig. 2.3).

Channel surveys were conducted twice (May/June and September of 1986) to make comparisons of stream bed characteristics. A cross-section of the stream was surveyed at ca. 5-meter intervals along the length of each study site. Substrate type was based on visual estimates of particle size diameter (sand, < 2 mm; gravel, 2-20 mm; small cobble, 20-60 mm; large cobble, 60-250 mm; small boulder, > 250 mm; bedrock). Water depth was recorded at 30-cm intervals along the transect.

A frequency tabulation was made of the different types of substrate present in each stream. Upon coding each substrate type (e.g., Sand = 0 to Bedrock = 5), a

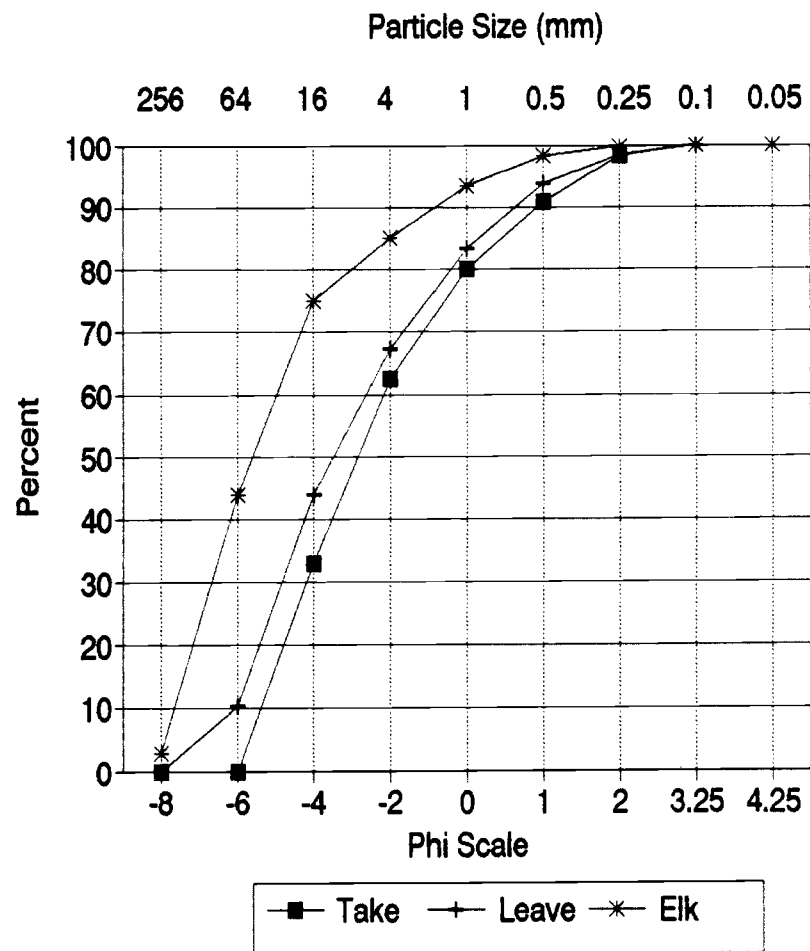


Figure 2.3 Cumulative frequency of substrate size classes (by volume) of three sites plotted against the phi scale and particle size (mm).

mean substrate code value could be calculated and compared among sites.

Results

Temperature - The average daily water temperature at Upper Clearwater Creek was warmer in 1986-1987 than the 5-yr average from 1983 to 1987 (Fig. 2.4). This difference was most pronounced in August. Average daily water temperature in May was 3° C lower at Elk Creek than at Clearwater Creek for 1986 and 1987. However, from June to October this difference was generally < 1°C. The difference in spring temperature was likely due to more shade at Elk Creek, which delayed snowmelt, as well as to higher altitude. Considering the lack of vegetation at Clearwater Creek the similarity of temperature regimes between the two sites was surprising. From May through October, Clearwater Creek only accumulated 175 degree days more than Elk Creek (Table 2.1).

Discharge - The magnitude of winter discharge declined markedly between 1982 and 1985 and then was similar for the winters of 1985-1988. In all years, there is a period of very low flow from July to September (Fig. 2.5, S), as is typical for the Pacific Northwest. However, the winter pattern varied from one year to the next and this variation likely was important

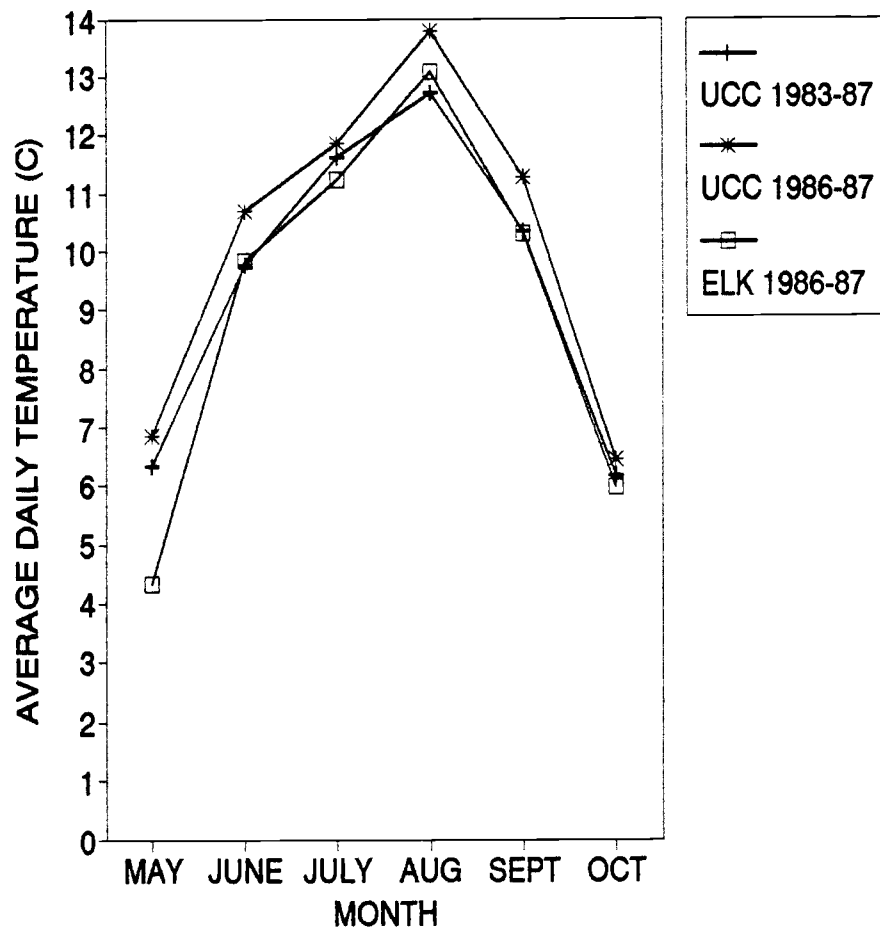


Figure 2.4 Mean daily temperature from May to October for 1986 and 1987 at Clearwater and Elk Creeks compared to a five-year average at Clearwater Creek (1983-1987).

for the colonization of insects. For some years discharge was high throughout the winter (Fig. 2.5, W1), while in others high flows were interspersed with periods of low flow (Fig. 2.5, W2). These mid-winter low flows could occur either from low precipitation or from exceptionally cold weather. The latter led to deep snowpack at low elevations, and increased spring flows when the snowpack melted. Both winter patterns occurred during this study (Fig. 2.6). In the winter of 1984-85 (December-March), discharge was only one-third of that in the spring (April-June, 1985). In contrast, discharge in winter 1985-86 was double that of the spring (Fig. 2.6).

For Elk Creek, data gathered in 1986 (Table 2.1) suggested that: 1) discharge was only about half of that for Clearwater Creek, and 2) the pattern was similar to that in Clearwater Creek for much of the year (at least for 1986). However, it is likely that high flows due to snowmelt lasted for several weeks longer than at Clearwater Creek. Although discharge was greater at Clearwater than at Elk Creek, between-site differences in slope resulted in greater stream power at Elk Creek than at Clearwater Creek (Table 2.1).

Substrate - Mean substrate size at Elk Creek was significantly greater than that at both Clearwater sites (Table 2.2). Almost 80% of the substrate was > 16 mm at

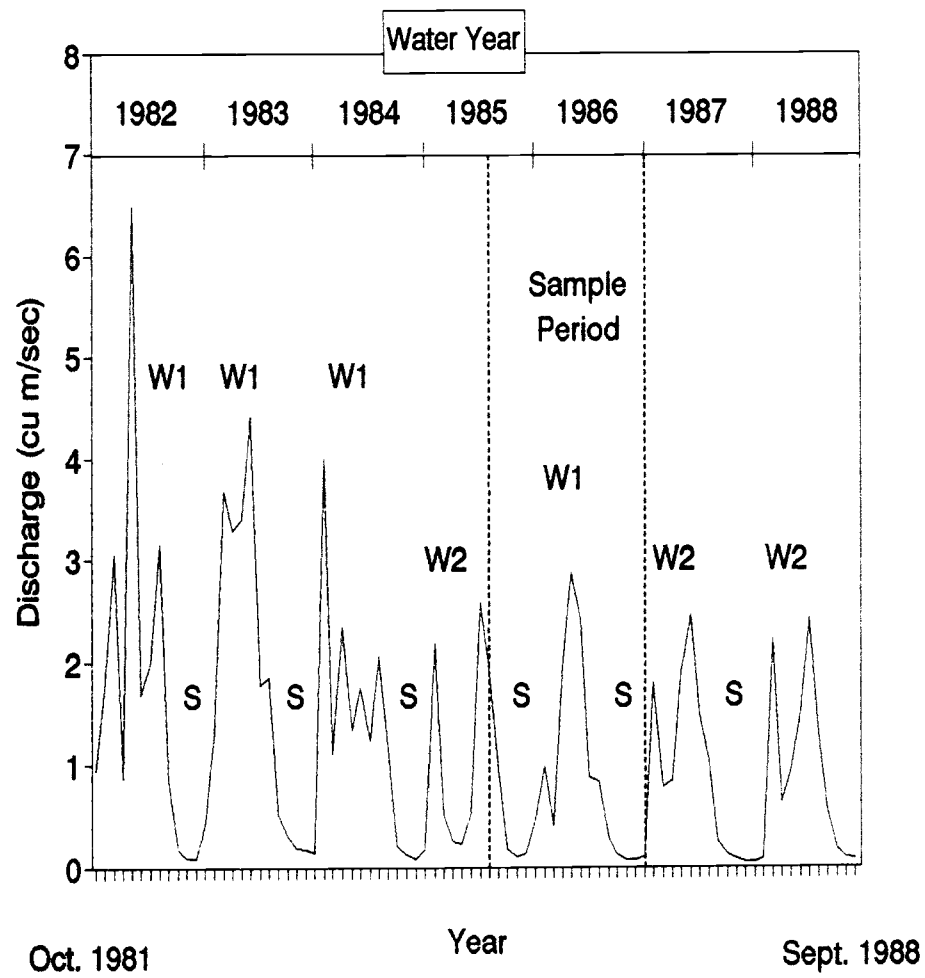


Figure 2.5 Discharge (cu m/sec) at Upper Clearwater Creek for water years 1982-1988 (S = summer; W1 and W2 indicate different winter patterns, see text for explanation).

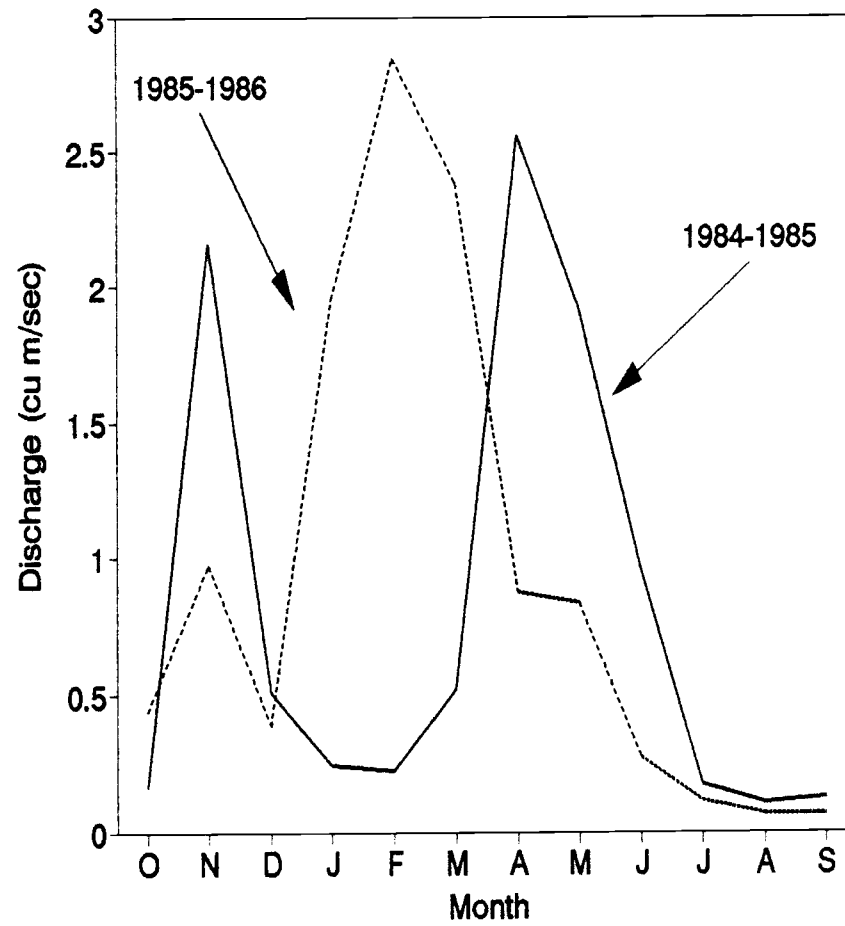


Figure 2.6 Comparison of discharge patterns of the winter season prior to sample years 1985 and 1986.

Elk Creek, while at both the Take and Leave sites < 50% of the substrate was > 16 mm (Fig. 2.7). No significant differences were found between the Leave and Take sites for mean substrate size even though mean particle size was larger at the Leave site (Table 2.2).

Based on the cross-sectional surveys both the Leave and Take sections had similar substrate distributions with a mean value of near one (Leave = 1.0, Take = 0.9) indicating the surface substrate was generally made up of gravel (Fig. 2.8). Elk Creek had a mean index value of 2.5 (Table 2.3) which is a substrate primarily comprised of small to large cobble (Fig. 2.8).

Stream depth dropped by a factor of 3-4 between May and September at Clearwater Creek (Table 2.4). The average depth of the Leave site was 1.5-2 times greater than at the Take site because the wood left at this site increased the frequency of pools. Elk Creek was initially surveyed in June rather than in May and stream depths had probably already declined significantly from spring levels. Still, average depth declined by 50% between June and September and was similar to that of the Take section of Clearwater Creek at that time.

Discussion

The Clearwater and Elk Creek basins differed in the following ways: 1) the Clearwater basin was twice the

Table 2.2 Results of one-way analysis of variance of the median diameter (ϕ) of substrate particles among sample sites. Random core samples were sieved into seven particle size classes during the 1986 sample season. $\phi(-4) = 16$ mm; $\phi(0) = 1$ mm particle. Letters refer to groups which were not significantly different.

| Site | n | Mean | +/- 95% C.I. | Homogeneous Groups |
|-------|----|-------|--------------|--------------------|
| Take | 27 | -2.79 | 0.63 | a |
| Leave | 27 | -3.57 | 0.64 | a |
| Elk | 27 | -5.75 | 0.63 | b |

F-ratio = 23.199 $p = < 0.001$

Table 2.3 Results of one-way analysis of variance of the mean substrate type among sample sites, where 0 = sand; 1 = gravel; 2 = cobble; 3 = large cobble; 4 = boulder; 5 = bedrock. Letters refer to groups which were not significantly different.

| Site | n | Mean | +/- 95% C.I. | Homogeneous Groups |
|-------|-----|------|--------------|--------------------|
| Take | 654 | 0.85 | 0.07 | a |
| Leave | 345 | 1.01 | 0.09 | a |
| Elk | 518 | 2.49 | 0.09 | b |

F-ratio = 445.11 p = < 0.001

Table 2.4 Comparison of mean depth (cm) among sites in May/June and September of 1986.

| Site | n | May/June | September |
|-------|-----|----------|-----------|
| Take | 441 | 21.5 | 6.0 |
| Leave | 217 | 30.5 | 10.0 |
| Elk | 329 | 9.9 | 4.2 |

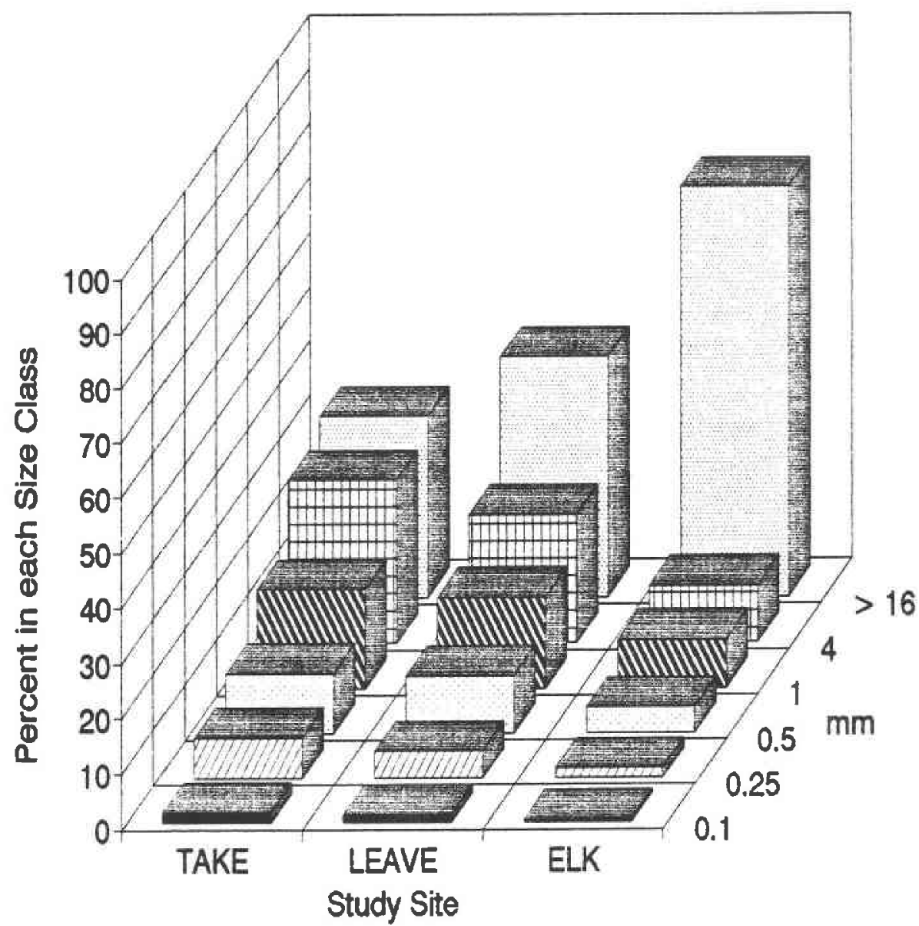


Figure 2.7 Comparison of the relative importance (percent of total volume) of substrate size classes among sample sites. Data based on core samples collected in 1986.

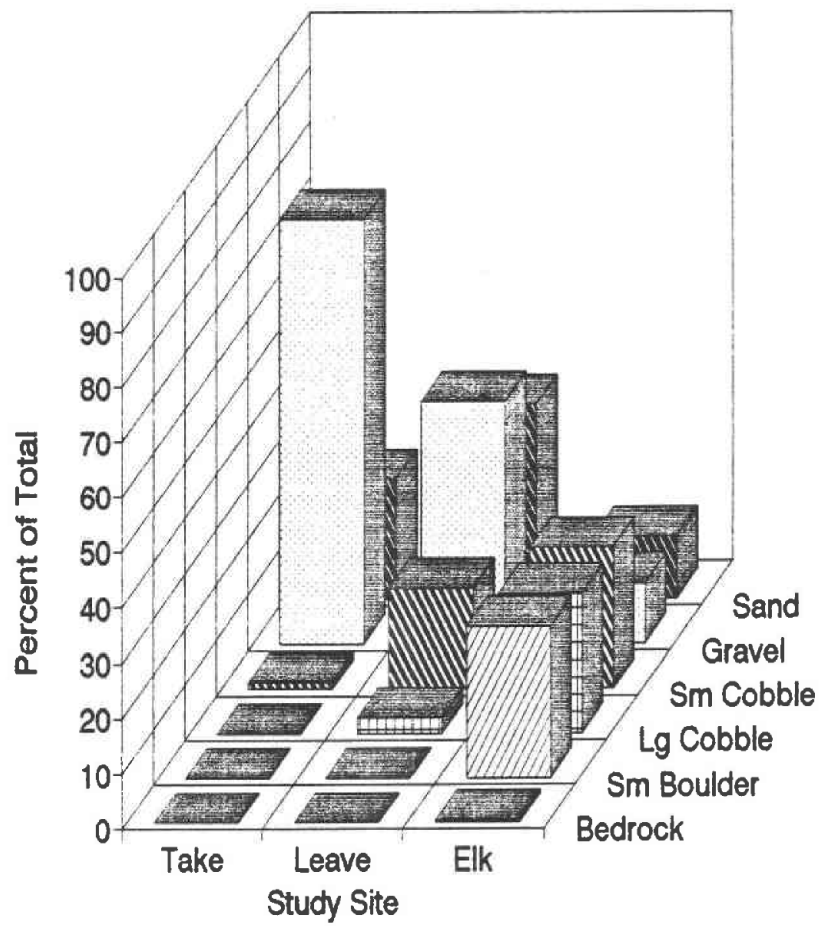


Figure 2.8 Comparison of the frequency of surface substrate types among sample sites. Data based on cross-sectional surveys in 1986.

size of the Elk Creek basin, and thus the potential for high discharge events was greater at the former; 2) elevation at the Clearwater site was ca. 220 m lower than that of the Elk site which likely led to more variation in the snowpack and thus differences in the timing and magnitude of runoff from snowmelt; 3) smaller substrates coupled with unstable banks resulted in a less stable habitat for insects at Clearwater than at Elk Creek. However, because stream power was greater at Elk Creek than Clearwater Creek, high flows could have affected insect populations there as well.

The eruption of Mt. St. Helens set the stage on which annual events, e.g., winter rains or summer low flows, were superimposed. High flows from winter rains and snowmelt are normal events in the Pacific Northwest. However annual variation in the timing and magnitude of these flows combined with the effects of the eruption determined the success of insect populations. This boom or bust scenario was further influenced by between-site differences in substrate stability.

Substrate stability, defined in terms of particle size, refers to the degree of resistance to movement. Smaller particles are less stable than are larger ones because they will be overturned or disturbed with greater frequency (see Minshall 1984 for review). The importance of substrate size and how it affects

invertebrate abundance and distribution has been well-documented (Thorup 1964, Chutter 1969, Luedtke and Brusven 1976, Malmqvist et al., 1978, Reice 1980, Petts and Greenwood 1985).

An example of how annual variation in high flows could affect insect populations was seen in the difference in the timing of high flow in the spring of 1985 and 1986. This event occurred ca. two months earlier (see Figure 2.6) in 1986 than in 1985. As many insect populations emerge and oviposit in the spring in Cascade Range streams, the timing of spring high flows can have an effect on the survivorship of insect populations. Late season high flows should have affected insects in Elk as well as Clearwater Creek as stream power was greater at the former. However, bank instability coupled with small substrates at Clearwater Creek likely was more detrimental than increased stream power due to the negative effects of shifting substrates on insects.

Chapter 3

LONG-TERM PATTERNS OF THE AQUATIC INSECT COMMUNITIES OF CLEARWATER AND ELK CREEKS

Introduction

This chapter presents a summary of changes in the riffle communities of Clearwater and Elk Creeks over a ten-year period after the eruption of Mt. St. Helens. While this thesis primarily deals with secondary production during years 1985 and 1986, placing those data in the context of the recovery process from the 1980 eruption is helpful to the overall interpretation. Furthermore, density and biomass in 1985 and 1986 were substantially different (see Chapter Four). Whether this between-year variation was part of the recovery process or a result of specific environmental conditions can be evaluated by looking at long term trends.

Methods

Field - Quantitative benthic samples were collected from riffles in late summer, i.e. August-September, for most years between 1980 and 1989. A modified Hess sampler (0.021 m^2) fitted with a 250 μm mesh screen was used for sampling. Samples were washed through a 250 μm mesh sieve, placed in Whirlpak bags, and preserved with Kahle's fluid.

Laboratory - Samples were washed in the laboratory to remove the Kahle's preservative and mineral sediment. Large samples were split to a level of 300-500 animals/sample. In the few instances when chironomids were very abundant relative to other taxa the sample was first sorted for non-chironomid taxa and then subsampled for the chironomids.

Insects were identified to genus or species under a stereo-microscope using available taxonomic keys (Allen and Edmunds 1962, Wiggins 1977, Merritt and Cummins 1984, Stewart and Stark 1988, Lehmkuhl unpublished). For chironomid identification a subsample of ca. 100 individuals was slide-mounted, examined with a compound microscope (10x eyepiece and 40x lens), and identified to genus using available keys (Bode 1983, Wiederholm 1983, Merritt and Cummins 1984).

Insect biomass was calculated from length/weight regression equations developed from personal data, unpublished data from C.P. Hawkins, and from Smock (1980). If no specific equation was available, then the length/weight regression for a taxon with similar body shape and life history was used.

Metrics - The Shannon-Wiener index was chosen for comparisons of diversity as it 1) includes both evenness and richness components (Peet 1974), and 2) it is commonly used in the literature and therefore is useful

for between-site comparisons (Wilhm 1968). Diversity was expressed as \log_2 and was calculated for both density and biomass.

Dominance-diversity curves (see Southwood 1978) were developed for density and biomass data for each year and site. Comparison of these curves indicates whether density and biomass become more evenly distributed among taxa with time.

Ordination - This technique summarizes community patterns by producing an ordination space in which similar species and samples are close together and dissimilar elements are far apart (Gauch 1982). Ordinations were done by Detrended Correspondence Analysis (DCA) (Hill 1974) with the DECORANA program (Hill 1979, Hill and Gauch 1980). While numerous methods for community ordination are available (see Gauch 1982), DCA was chosen because of its availability and relative ease in use for ecological interpretations of results. Data for analysis by this technique were entered as mean abundance or biomass of each taxon at each site in a given year.

Results

Tabulations of density and biomass for all taxa at Clearwater and Elk Creeks for each sample date are given

in Appendices A and B. The following is a summary of those data.

Density/Biomass - In September 1980 insect density was only 300/m² and biomass 0.1 g/m² at Clearwater Creek. These were primarily Diptera, especially Chironomidae (Table 3.1, Fig. 3.1). In contrast, the insects of Elk Creek were abundant and diverse (Table 3.2, Fig. 3.2). Both density and biomass were significantly greater at Elk Creek than at Clearwater Creek (Table 3.3) with caddisflies contributing over 50% of the biomass.

Insect abundance was relatively constant at Clearwater Creek from 1982 to 1985; density ranged from ca. 13,000-16,000/m² and biomass from 0.7-1.4 g/m² (Table 3.1). Comparable data were available from Elk Creek only for 1982 and 1985; density (ca. 9,700-14,700/m²) and biomass (0.9-1.0 g/m²) values were not significantly different from those at Clearwater Creek (Tables 3.2 and 3.3). Biomass at Elk Creek in 1982 had declined significantly from that in 1980 (Table 3.5).

The proportions of density and biomass contributed by various taxonomic groups had changed considerably at both Clearwater and Elk Creeks by 1982. Mayflies (primarily Baetis spp.) increased, while the number of Diptera declined at Clearwater Creek (Fig. 3.3). Most groups declined at Elk Creek and chironomid numbers

Table 3.1. Mean density (No./m²) and biomass (g dry wt/m²) of major taxonomic groups at Upper Clearwater Creek, late summer 1980-1989. No comparable samples were collected in 1981 or 1984. T = < 0.5 animals/m² or < 0.05 g/m².

| TAXON | | SAMPLE YEAR (n) | | | | | | | |
|------------------------|-----|--------------------|-------------|-------------|--------------|--------------|--------------|-------------|--------------|
| | | 1980 (5) | 1982 (8) | 1983 (9) | 1985 (10) | 1986 (14) | 1987 (13) | 1988 (6) | 1989 (10) |
| Ephemeroptera | No. | 0 | 7596 | 8211 | 3158 | 50590 | 33114 | 56270 | 19441 |
| | g | 0.0 | 0.4 | 0.1 | 0.2 | 1.1 | 0.9 | 1.5 | 0.7 |
| Plecoptera | No. | 0 | 111 | 695 | 4171 | 5865 | 3970 | 9794 | 4540 |
| | g | 0.0 | 0.1 | 0.1 | 0.2 | 0.4 | 0.7 | 2.1 | 0.4 |
| Trichoptera | No. | 28 | 0 | 42 | 98 | 257 | 1060 | 2156 | 551 |
| | g | T | 0.0 | T | T | T | 0.5 | 0.5 | 0.8 |
| Coleoptera | No. | 0 | 64 | 99 | 9 | 13 | 115 | 31 | 35 |
| | g | 0.0 | 0.1 | T | T | T | 0.1 | T | 0.1 |
| Diptera (non-midge) | No. | 103 | 3527 | 405 | 1668 | 2109 | 1391 | 2024 | 5063 |
| | g | T | 0.5 | 0.2 | 0.2 | 0.3 | 0.2 | 0.5 | 0.6 |
| Diptera (midge) | No. | 168 | 5260 | 6613 | 3994 | 48000 | 15052 | 14535 | 7199 |
| | g | T | 0.3 | 0.4 | 0.1 | 1.1 | 0.6 | 0.6 | 0.3 |
| Non-insects | No. | 0 | 1004 | 690 | 1004 | 3723 | 5102 | 4297 | 1999 |
| | g | 0.0 | 0.1 | 0.1 | 0.1 | 0.2 | 0.4 | 0.3 | 0.1 |
| Totals (insects) | No. | 299 | 16558 | 16064 | 13097 | 106835 | 54702 | 84810 | 36860 |
| | g | 0.1 | 1.4 | 0.9 | 0.7 | 3.0 | 3.1 | 5.1 | 3.0 |
| (all taxa) | No. | 299 | 17562 | 16754 | 14102 | 110558 | 59804 | 89107 | 38859 |
| | g | 0.1 | 1.5 | 0.9 | 0.8 | 3.2 | 3.5 | 5.4 | 3.2 |

Table 3.2. Mean density (No./m²) and biomass (g dry wt/m²) of major taxonomic groups at Elk Creek, late summer 1980-1989. No comparable samples collected in 1981, 1983-84, or 1988. T = < 0.5 animals/m² or < 0.05 g dry wt/m².

| TAXON | | SAMPLE YEAR (n) | | | | | |
|------------------------|-----|--------------------|-------------|-------------|-------------|-------------|-------------|
| | | 1980 (5) | 1982 (8) | 1985 (4) | 1986 (7) | 1987 (7) | 1989 (5) |
| Ephemeroptera | No. | 504 | 1191 | 3176 | 15608 | 11898 | 7679 |
| | g | 0.1 | 0.3 | 0.4 | 0.4 | 0.6 | 0.7 |
| Plecoptera | No. | 738 | 385 | 7941 | 15835 | 11704 | 14312 |
| | g | 0.4 | 0.1 | 0.3 | 0.5 | 0.4 | 0.4 |
| Trichoptera | No. | 617 | 238 | 712 | 1348 | 2095 | 1196 |
| | g | 1.1 | 0.2 | 0.1 | 0.5 | 0.4 | 0.4 |
| Coleoptera | No. | 0 | 12 | 0 | 0 | 0 | 0 |
| | g | 0.0 | T | 0.0 | 0.0 | 0.0 | 0.0 |
| Diptera (non-midge) | No. | 430 | 286 | 350 | 400 | 467 | 1074 |
| | g | 0.2 | 0.1 | 0.1 | 0.1 | 0.1 | 0.1 |
| Diptera (midge) | No. | 1626 | 7602 | 2557 | 7357 | 4190 | 5456 |
| | g | 0.1 | 0.2 | 0.1 | 0.2 | 0.1 | 0.1 |
| Non-insects | No. | 262 | 298 | 1611 | 1401 | 1028 | 1252 |
| | g | T | T | 0.1 | 0.1 | T | 0.1 |
| Totals (insects) | No. | 3914 | 9715 | 14737 | 40548 | 30355 | 29717 |
| | g | 1.9 | 0.9 | 1.0 | 1.6 | 1.6 | 1.7 |
| (all taxa) | No. | 4176 | 10012 | 16349 | 41949 | 31382 | 30969 |
| | g | 1.9 | 0.9 | 1.1 | 1.7 | 1.7 | 1.8 |

Table 3.3. Results of t-test comparing density and biomass of Clearwater and Elk Creeks for years in which comparisons were possible. Data were transformed $\text{Log}(x+1)$ before statistical tests were performed (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = no significant difference). C or E in parentheses indicates site which had significantly greater density or biomass.

| Year | Clearwater Creek (n) | Elk Creek (n) | Density | Biomass |
|------|----------------------------|---------------------|---------|---------|
| 1980 | 5 | 5 | ** (E) | *** (E) |
| 1982 | 8 | 8 | ns | ns |
| 1985 | 10 | 4 | ns | ns |
| 1986 | 14 | 7 | *** (C) | ** (C) |
| 1987 | 13 | 7 | * (C) | ** (C) |
| 1989 | 10 | 5 | ns | ns |

Table 3.4. Results of one-way analysis of variance comparing insect density and biomass between years at Clearwater Creek. Data were transformed $\text{Log}(x+1)$ before analysis. Mean values are the means of the log-transformed data. Letters refer to groups which were not significantly different ($p < 0.05$).

| DENSITY | | | | |
|---------|----|------|--------------|-------------------|
| Year | n | Mean | +/- 95% C.I. | Homogenous Groups |
| 1980 | 5 | 0.73 | 0.24 | a |
| 1982 | 8 | 2.46 | 0.20 | b |
| 1983 | 9 | 2.45 | 0.18 | b |
| 1985 | 10 | 2.38 | 0.17 | b |
| 1986 | 14 | 3.33 | 0.15 | d |
| 1987 | 13 | 3.00 | 0.15 | c |
| 1988 | 6 | 3.24 | 0.22 | c d |
| 1989 | 10 | 2.85 | 0.17 | c |

d.f. = 74 F-ratio = 53.35 $p = 0.000$

| BIOMASS | | | | |
|---------|----|------|--------------|-------------------|
| Year | n | Mean | +/- 95% C.I. | Homogenous Groups |
| 1980 | 5 | 0.39 | 0.23 | a |
| 1982 | 8 | 1.41 | 0.18 | b |
| 1983 | 9 | 1.22 | 0.17 | b |
| 1985 | 10 | 1.16 | 0.16 | b |
| 1986 | 14 | 1.79 | 0.14 | c |
| 1987 | 13 | 1.80 | 0.15 | c |
| 1988 | 6 | 2.03 | 0.21 | c |
| 1989 | 10 | 1.76 | 0.16 | c |

d.f. = 74 F-ratio = 33.50 $p = 0.000$

Table 3.5. Results of one-way analysis of variance comparing insect density and biomass between years at Elk Creek. Data were transformed $\text{Log}(x+1)$ before analysis. Mean values are the means of the log-transformed data. Letters refer to groups which were not significantly different ($p < 0.05$).

| DENSITY | | | | |
|---------|---|------|--------------|-------------------|
| Year | n | Mean | +/- 95% C.I. | Homogenous Groups |
| 1980 | 5 | 1.88 | 0.25 | a |
| 1982 | 8 | 2.13 | 0.19 | a b |
| 1985 | 4 | 2.47 | 0.27 | b c |
| 1986 | 7 | 2.86 | 0.21 | c |
| 1987 | 7 | 2.77 | 0.21 | c |
| 1989 | 5 | 2.75 | 0.24 | c |

d.f. = 35 F-ratio = 14.24 p = 0.000

| BIOMASS | | | | |
|---------|---|------|--------------|-------------------|
| Year | n | Mean | +/- 95% C.I. | Homogenous Groups |
| 1980 | 5 | 1.58 | 0.22 | b |
| 1982 | 8 | 1.05 | 0.18 | a |
| 1985 | 4 | 1.31 | 0.26 | a b |
| 1986 | 7 | 1.52 | 0.19 | b |
| 1987 | 7 | 1.54 | 0.19 | b |
| 1989 | 5 | 1.52 | 0.23 | a b |

d.f. = 35 F-ratio = 3.22 p = 0.000

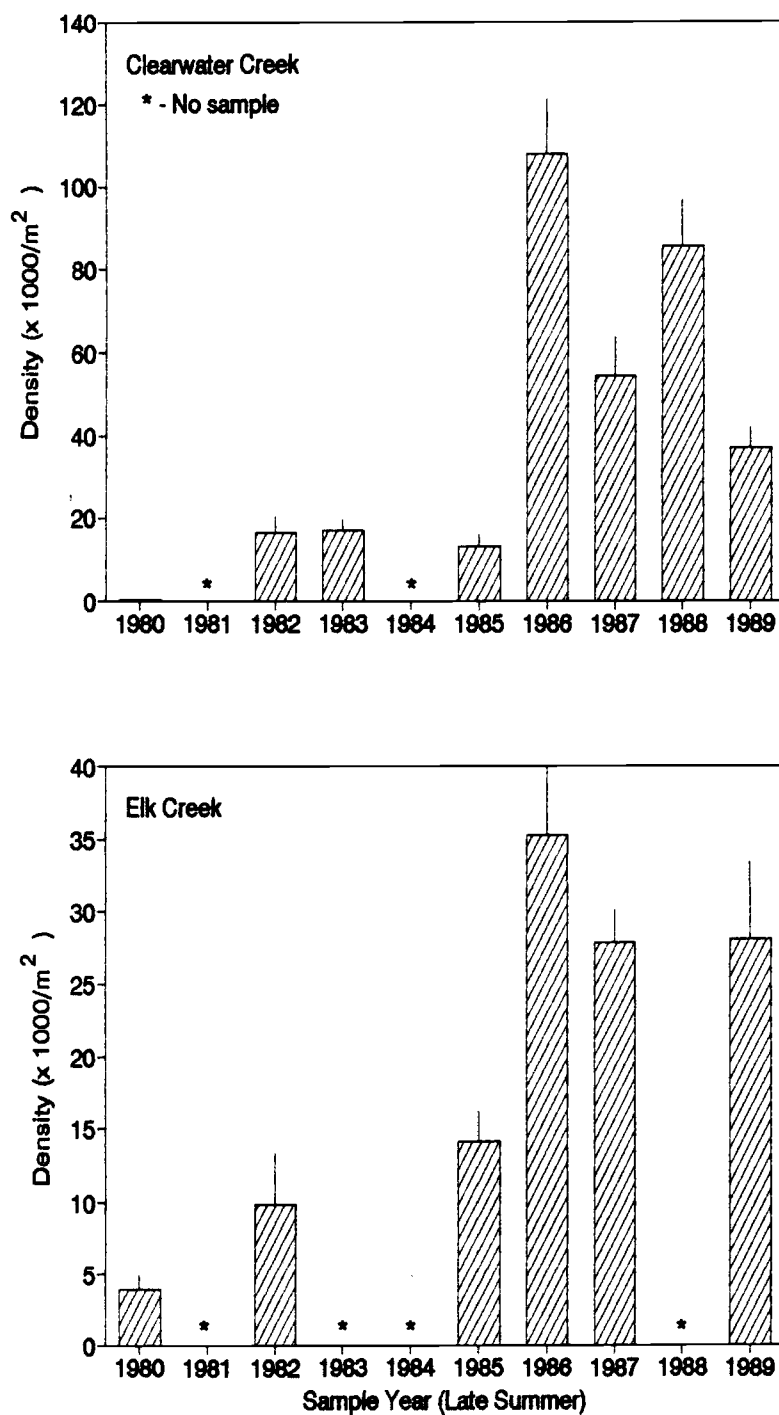


Figure 3.1. Insect density at Clearwater and Elk Creeks from 1980 to 1989. Error bars equal 1 S.E.

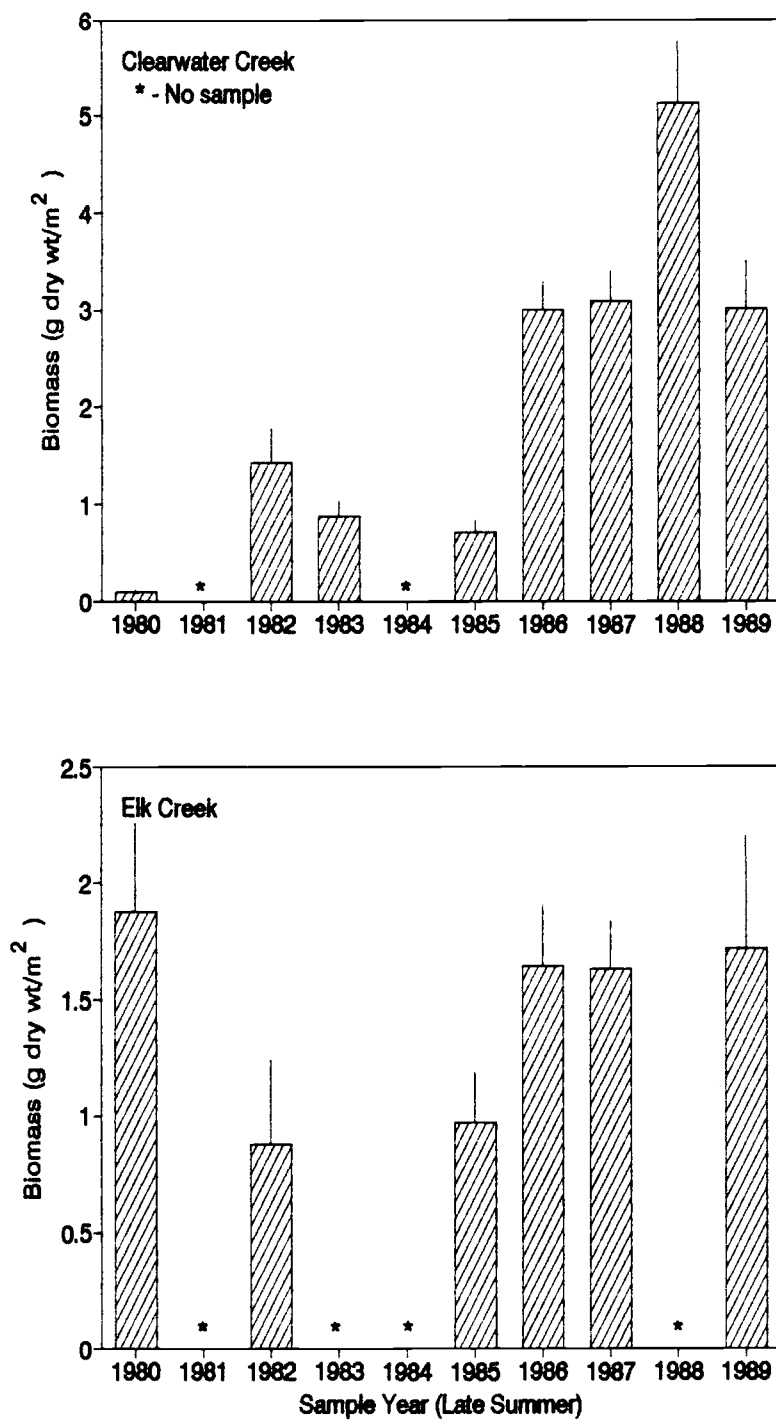


Figure 3.2. Insect biomass at Clearwater and Elk Creeks from 1980 to 1989. Error bars equal 1 S.E.

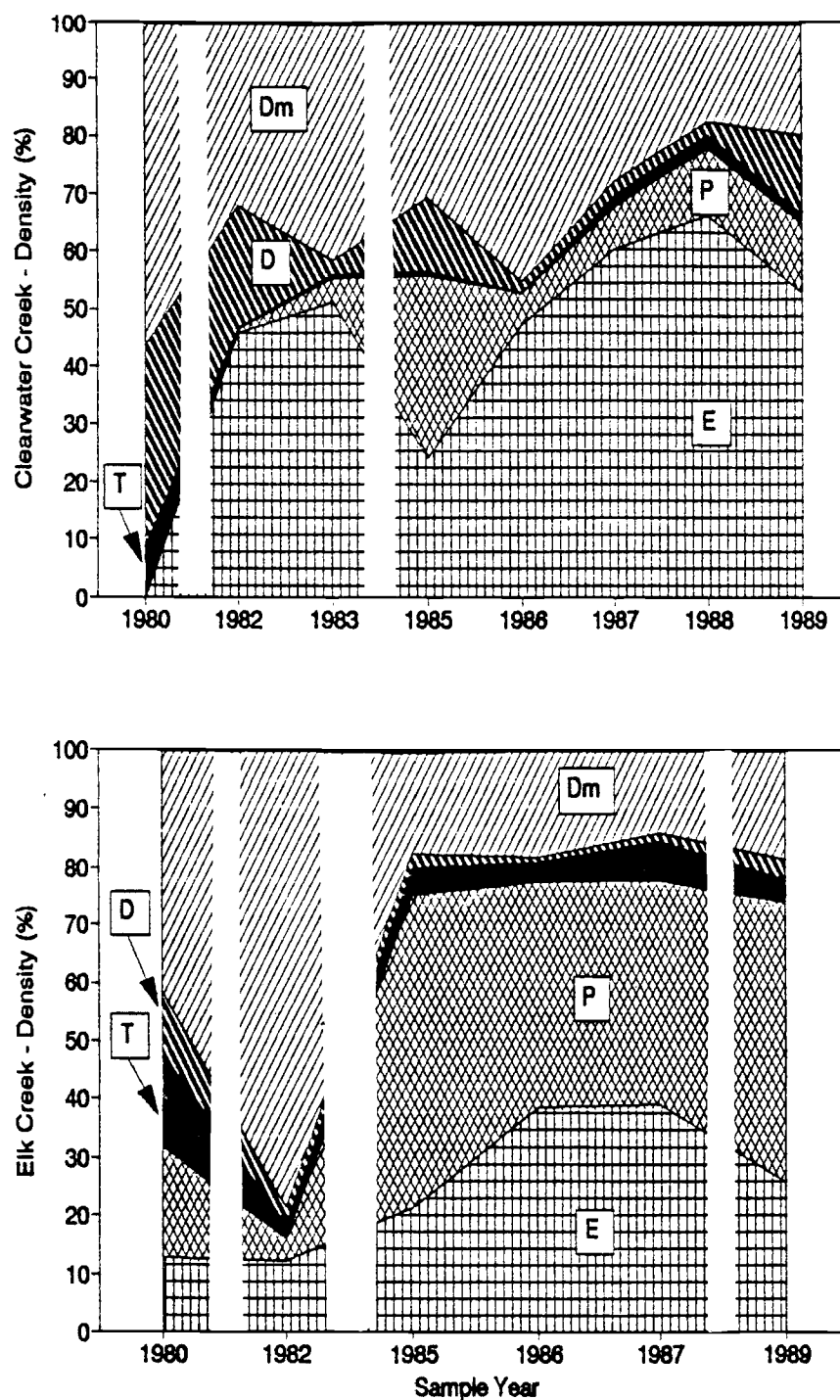


Figure 3.3. Changes in density contributed by taxonomic groups at Clearwater and Elk Creeks from 1980 to 1989. Note missing years. E = Ephemeroptera; P = Plecoptera; T = Trichoptera; C = Coleoptera; D = Diptera (non-chironomid); Dm = Diptera (Chironomidae).

increased sharply (Fig. 3.4). Trichoptera biomass declined at Elk Creek while chironomid biomass increased (Fig. 3.4). Except for an increase in stoneflies, the relative proportions of taxonomic groups at Clearwater Creek generally remained the same until 1985. Because data from 1983 and 1984 were not available at Elk Creek it is difficult to follow any trend for the years 1982-1985. However, changes in the relative importance of taxonomic groups between 1982 and 1985 were substantial (Fig. 3.4). The numerical abundance of Chironomidae declined sharply while stoneflies increased. Stonefly and mayfly biomass increased while Chironomidae biomass decreased.

The insect community of Clearwater Creek experienced large increases in both density and biomass in the latter half of the 1980's (Table 3.1, Fig. 3.1). Between 1985 and 1986 an eight-fold increase in density (to over 100,000/m²) and a four-fold increase in biomass (to > 3 g/m²) took place. Not surprisingly both values were significantly greater than for previous years (Table 3.4). A downward trend occurred for density from 1987 to 1989 to ca. one third the 1986 level. Biomass peaked at ca. 5.5 g/m² in 1988, but declined to about 3 g/m² in 1989.

Invertebrate density and biomass also increased at Elk Creek in 1986 but not to the degree that occurred at

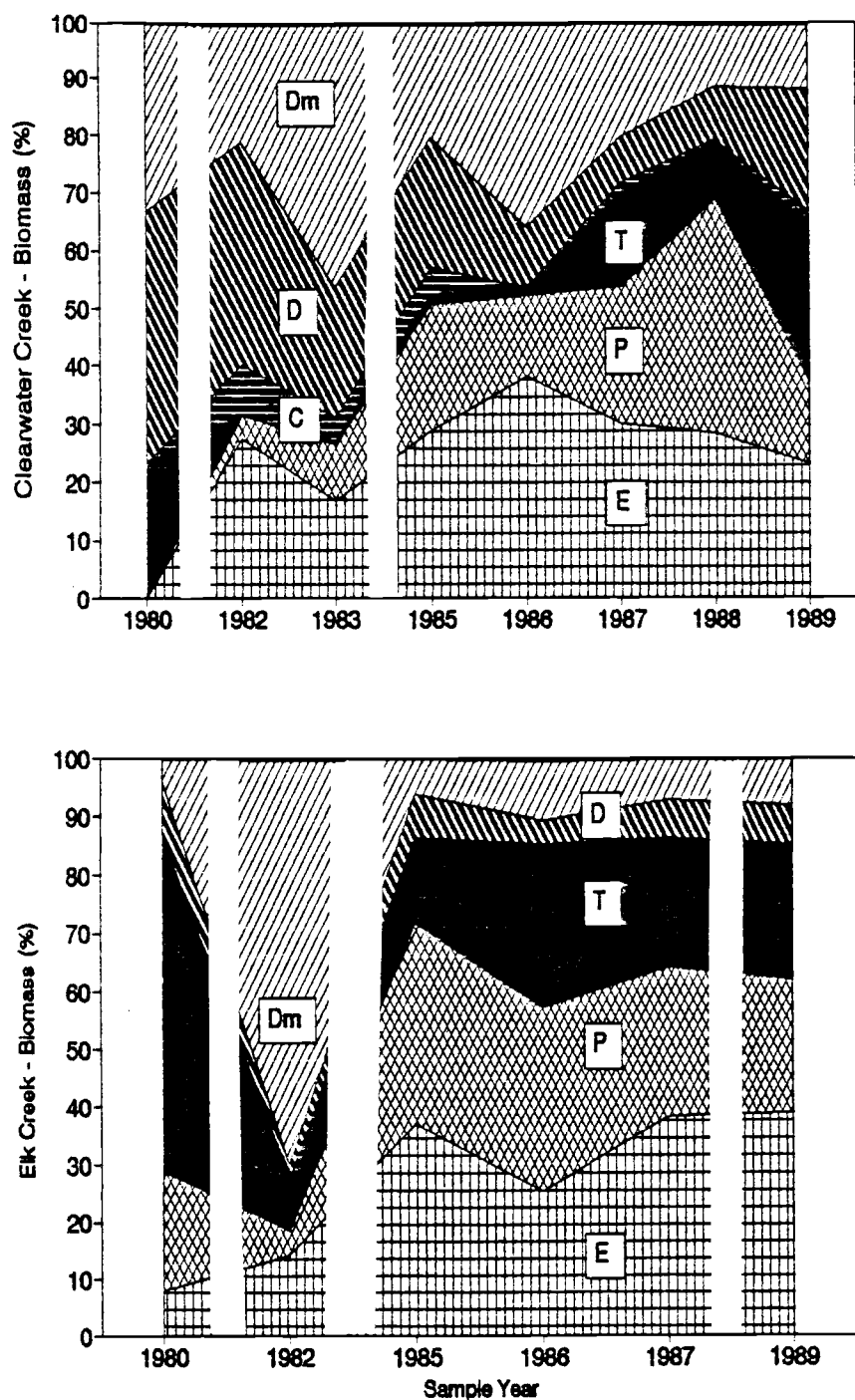


Figure 3.4. Changes in biomass contributed by taxonomic groups at Clearwater and Elk Creeks from 1980 to 1989. Note missing years. E = Ephemeroptera; P = Plecoptera; T = Trichoptera; C = Coleoptera; D = Diptera (non-chironomid); Dm = Diptera (Chironomidae).

Clearwater Creek (Table 3.2, Fig. 3.2). These values declined by ca. 25% between 1987 and 1989, while biomass remained relatively constant (1.6-1.7 g/m²).

The proportions of taxonomic groups continued to change between 1986 and 1989 at Clearwater Creek while remaining relatively constant at Elk Creek (Figs. 3.3 and 3.4). This change at Clearwater Creek was caused by increased numbers of mayflies (especially *Baetis* spp., *Cinygmula* sp., and *Paraleptophlebia temporalis*) and a decrease in chironomids. The overall trend for biomass was more Trichoptera (primarily *Parapsyche elsis* and *Arctopsyche grandis*) and fewer Chironomidae. A marked increase of perlodid stoneflies (*Megarcys* sp. and *Skwala* sp.) occurred in 1988, but these taxa declined in 1989. The importance of taxonomic groups changed little at Elk Creek from 1986 to 1989 (Fig. 3.4). Mayflies and stoneflies were especially abundant and any variations in density and biomass generally occurred within these two groups.

Long-term trends in the benthic community structure of Clearwater Creek were best exemplified by changes in the diversity of the Ephemeroptera, Plecoptera, and Trichoptera (E-P-T) taxa. It has already been shown that chironomid midges declined in importance (Figs. 3.3 and 3.4) from 1980 to 1989. Also the richness and diversity of chironomid taxa changed little over the

same period (Fig. 3.5). Consequently, the E-P-T taxa will be the focus of community analyses.

Sample size can affect the interpretation of various community indices. Species area curves showed that Shannon-Wiener diversity was a better measure than species richness for between-site and between-year comparisons (Figures 3.6 and 3.7). Sample sizes of greater than five showed only small changes in diversity while the number of taxa continued to increase even with ten or more samples. Because sample sizes were small at Elk Creek species richness could not be used for annual and site comparisons.

Diversity - Diversity of the E-P-T taxa rose markedly at Clearwater Creek during the ten-year sample period. H' (density), which was < 1.0 in 1980, remained low in 1983 (< 1.5) and then gradually increased to over 3.0 between 1985 and 1989 (Fig. 3.8). A similar pattern was found for H' (biomass) - although the index value recovered more rapidly and was higher than for H' (density) (3.6 in 1985 vs. 4.3 in 1989) (Fig. 3.8).

Diversity (density) was similar (ca. 4.0) for both 1980 and 1982 at Elk Creek (Fig. 3.8). However, H' declined in 1985 to ca. 3.0 and varied around that value from 1985-1989. H' (biomass) remained fairly high for the entire study period, ranging from a low of 3.4 in 1985 to a high of 4.3 in 1987 (Fig. 3.8).

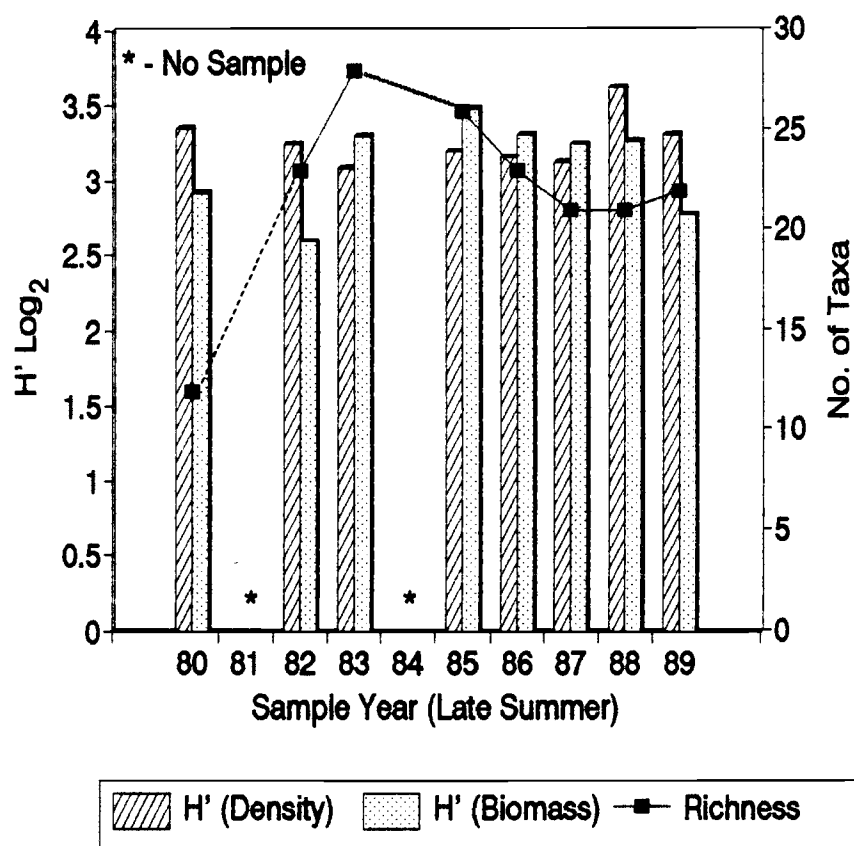


Figure 3.5. Diversity and richness of the chironomid community of Clearwater Creek from 1980 to 1989.

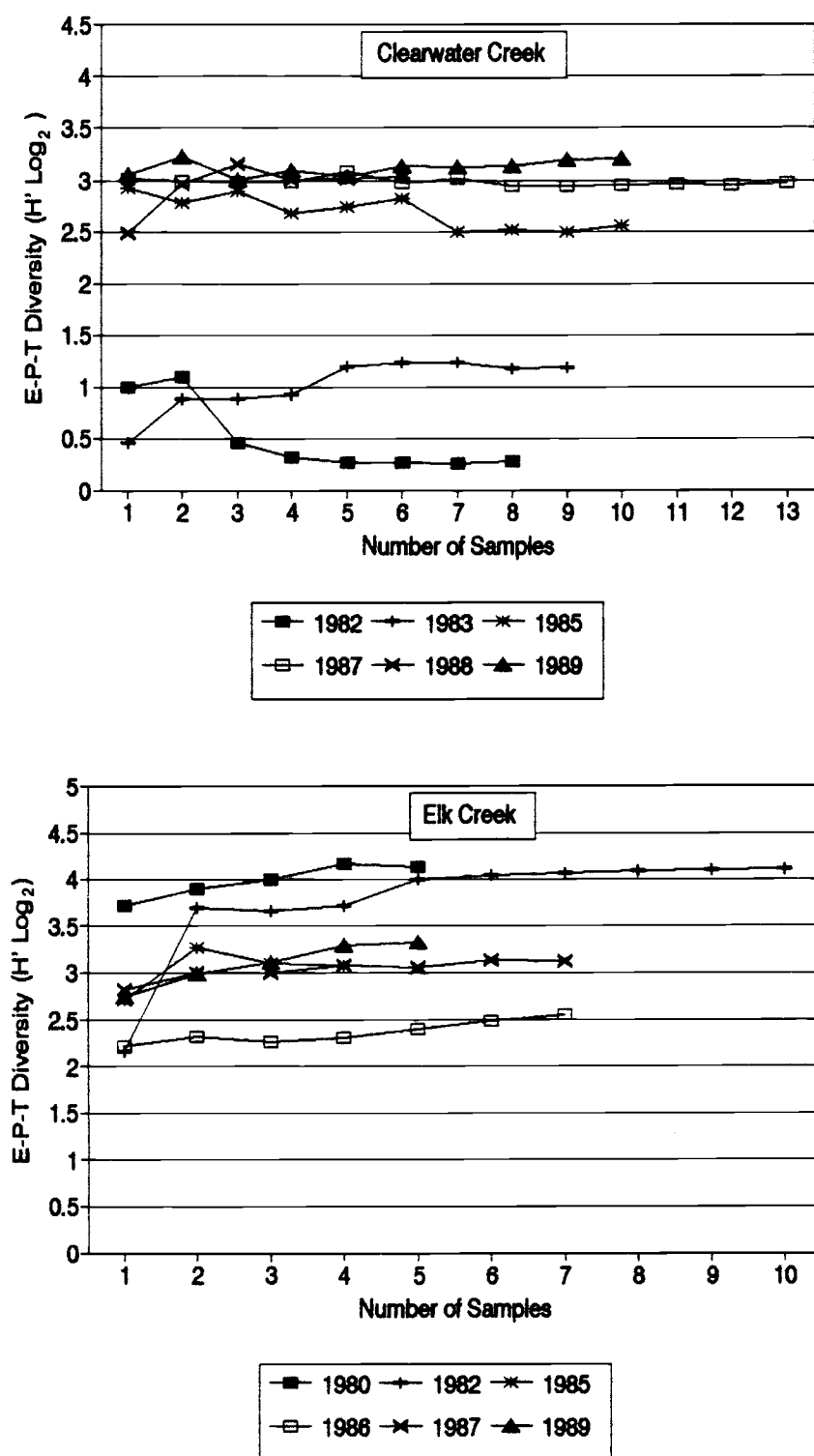


Figure 3.6. Species-area curves for Shannon-Wiener diversity (E-P-T density) at Clearwater and Elk Creek. Modified Hess sampler used for sample collection. Each sample equals 0.02 m^2 .

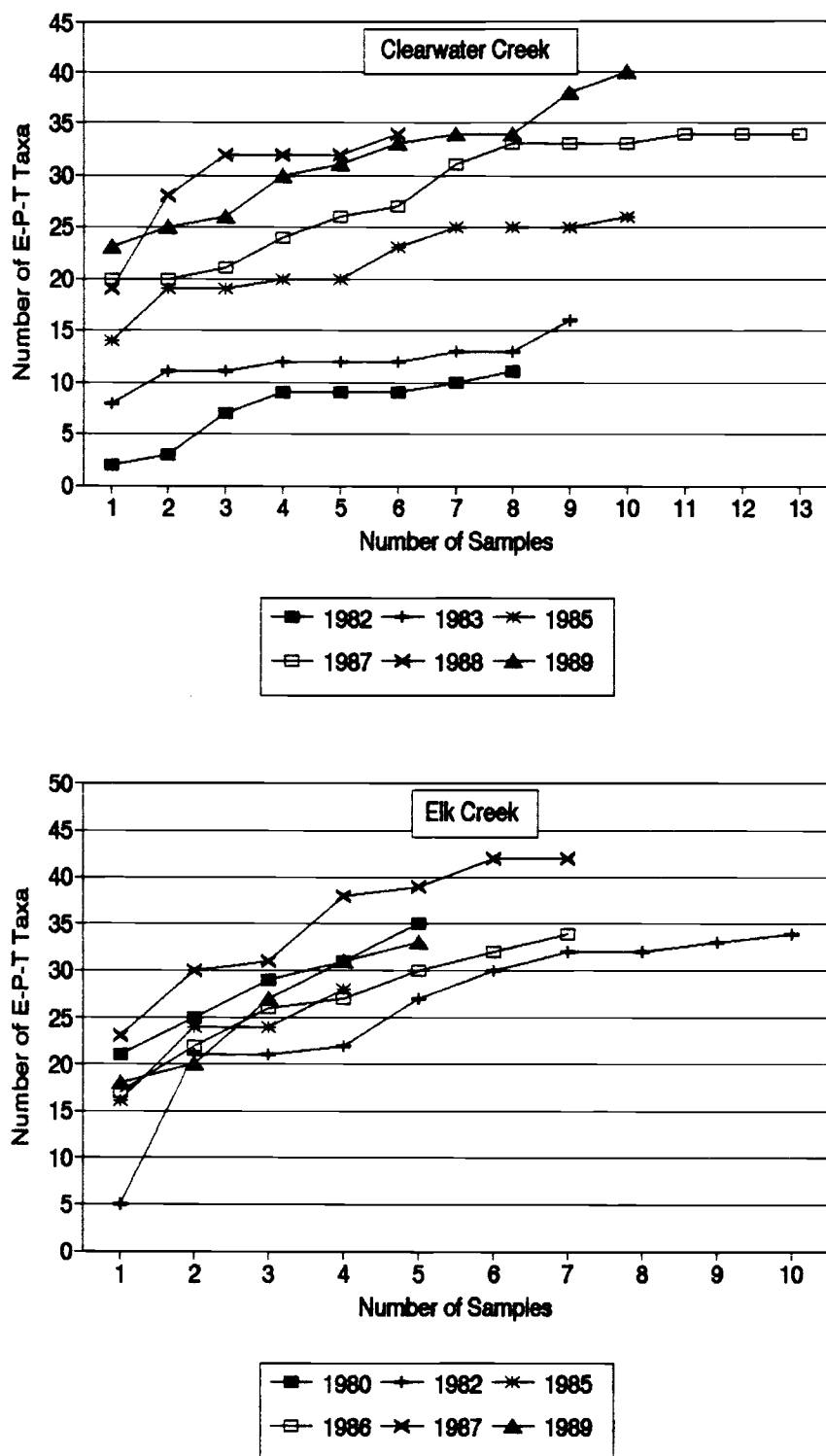


Figure 3.7. Species-area curves for E-P-T species richness at Clearwater and Elk Creek. Modified Hess sampler used for sample collection. Each sample equals 0.02 m².

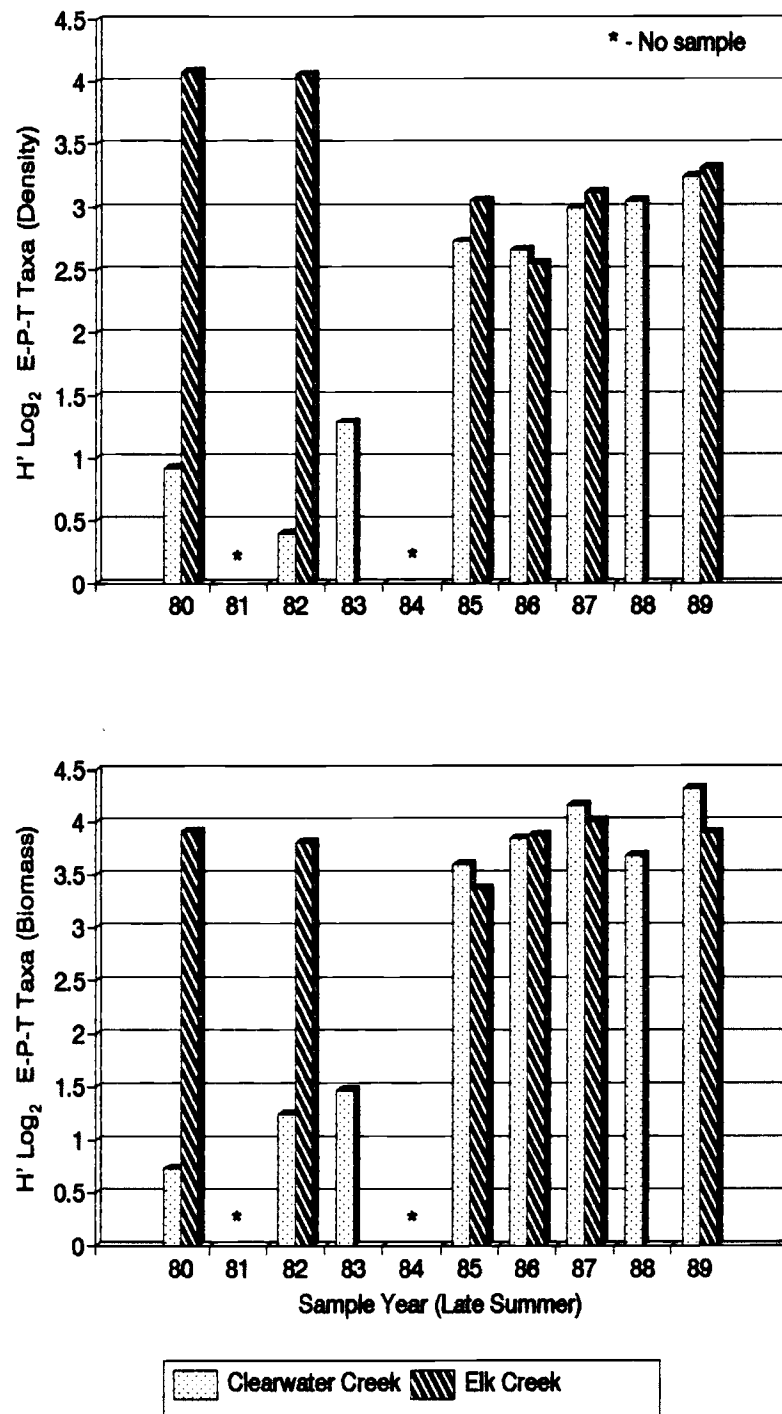


Figure 3.8. Shannon-Wiener diversity (density and biomass) of E-P-T taxa at Clearwater and Elk Creeks.

Dominance - Dominance-diversity curves for Clearwater Creek showed similar patterns for both numerical abundance and biomass (Figs. 3.9 and 3.10). A gradual flattening of the curves occurred between 1982 and 1985 indicating that the evenness of E-P-T species increased with time since the eruption. This pattern was generally maintained until 1989. While little change occurred in the shape of the curves from 1985-1989, a shift in the dominant species took place, especially for biomass (see Appendix A). For example, in 1986 no Trichoptera were among the ten taxa that contributed the greatest biomass but by 1989 five caddisflies were among this group.

The pattern of the dominance-diversity curves for Elk Creek differed between abundance and biomass (Figs. 3.11 and 3.12). The shape of the curves for biomass was essentially unchanged between 1980 and 1989 while abundance curves in 1980 and 1982 were relatively flat compared to those for 1985-1989. The dominance curve for 1986 was the steepest for this latter period. The important taxa for both density and biomass shifted greatly between 1980 and 1982 (see Appendix B). The result of this shift was fewer caddisfly and more mayfly taxa. After 1982 the number of Trichoptera taxa never recovered to 1980 levels.

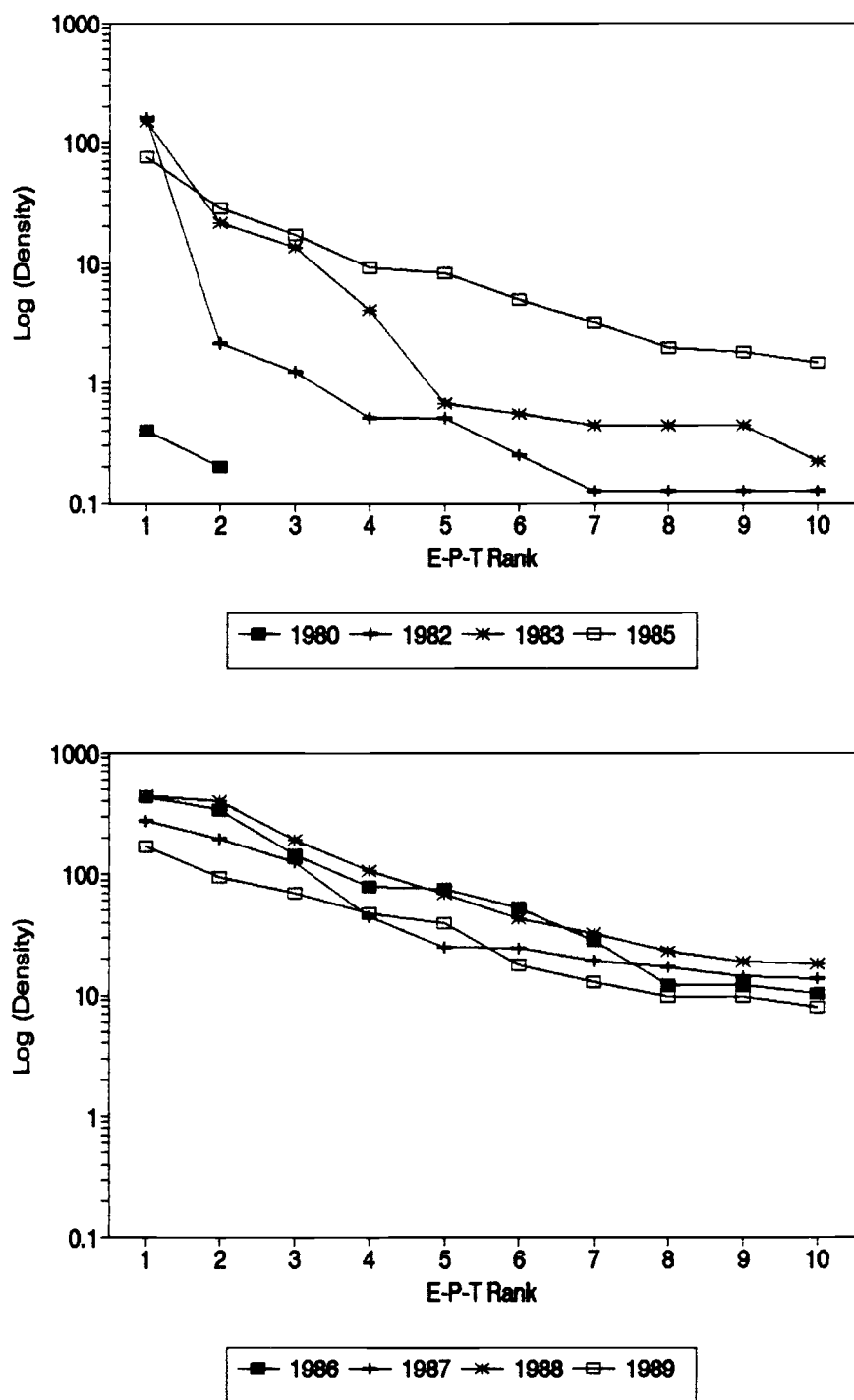


Figure 3.9. Dominance-diversity curves for the ten most abundant taxa at Clearwater Creek.

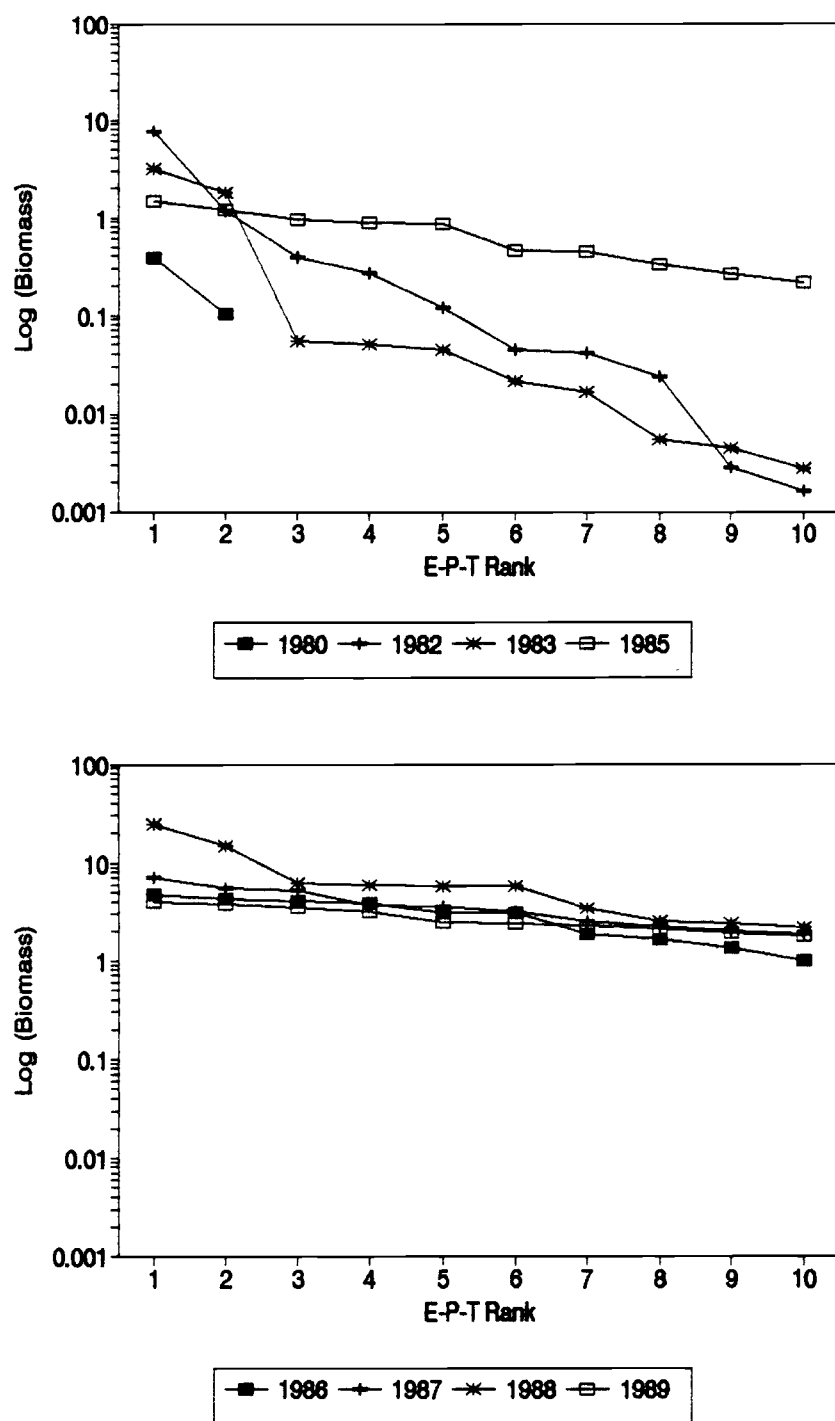


Figure 3.10. Dominance-diversity curves for the ten taxa with the most biomass at Clearwater Creek.

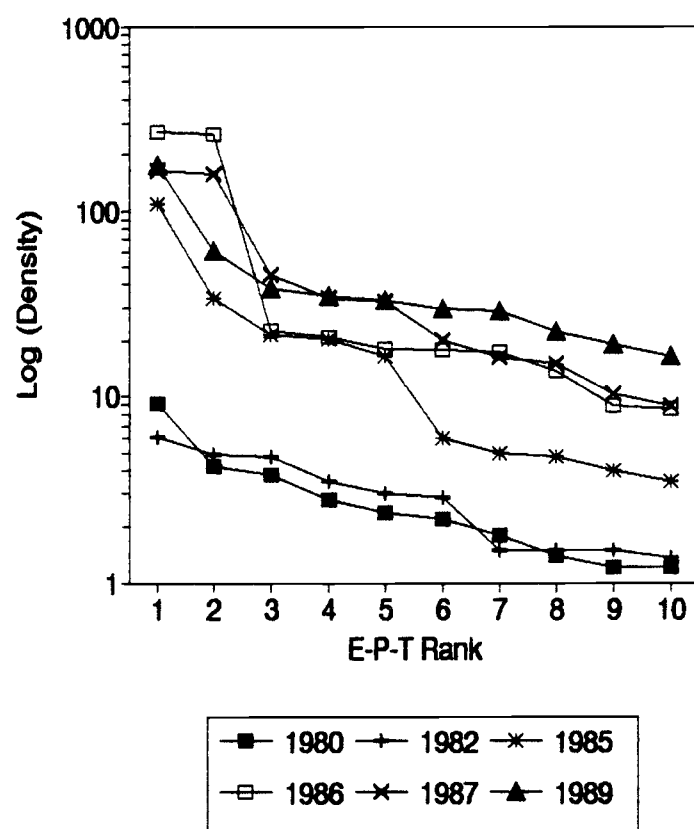


Figure 3.11. Dominance-diversity curves for the ten most abundant taxa at Elk Creek.

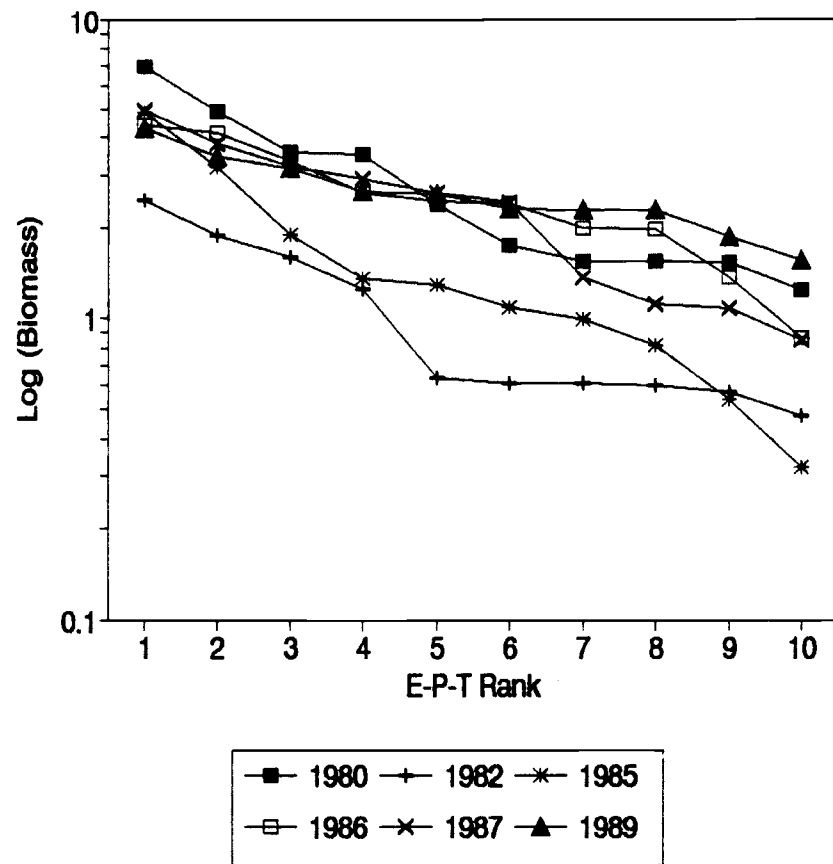


Figure 3.12. Dominance-diversity curves for the ten taxa with the most biomass at Elk Creek.

Voltinism - All taxa were considered in the analysis of voltinism at each site. Appendices A and B give the type of voltinism for each taxon.

A shift from a community dominated by multivoltine taxa to one dominated by univoltine taxa has occurred at Clearwater Creek since 1980 (Fig. 3.13). During the same period semivoltine taxa also increased in importance. Multivoltine taxa contributed more than 50% of the biomass from 1980-1983. However, other than in 1989 when large numbers of black fly larvae caused multivoltine taxa to dominate, univoltine taxa provided at least 50% of the biomass. Semivoltine taxa, which contributed only 5% of the biomass in 1986 supplied ca. 20% of the biomass in 1989.

Approximately 80% of the biomass at Elk Creek was comprised of semivoltine species in 1980 (Fig. 3.13). This dominance by long-lived taxa shifted to relatively even proportions of all types of life cycles in 1982. Univoltine taxa generally provided at least 50% of the biomass between 1985 and 1989.

Community Ordination - The results of the density and biomass analyses showed that distinct separation existed between the Clearwater and Elk insect communities along Axis 1 (Fig. 3.14). The trajectory for numerical abundance at Clearwater Creek followed no obvious pattern suggesting that the distribution of

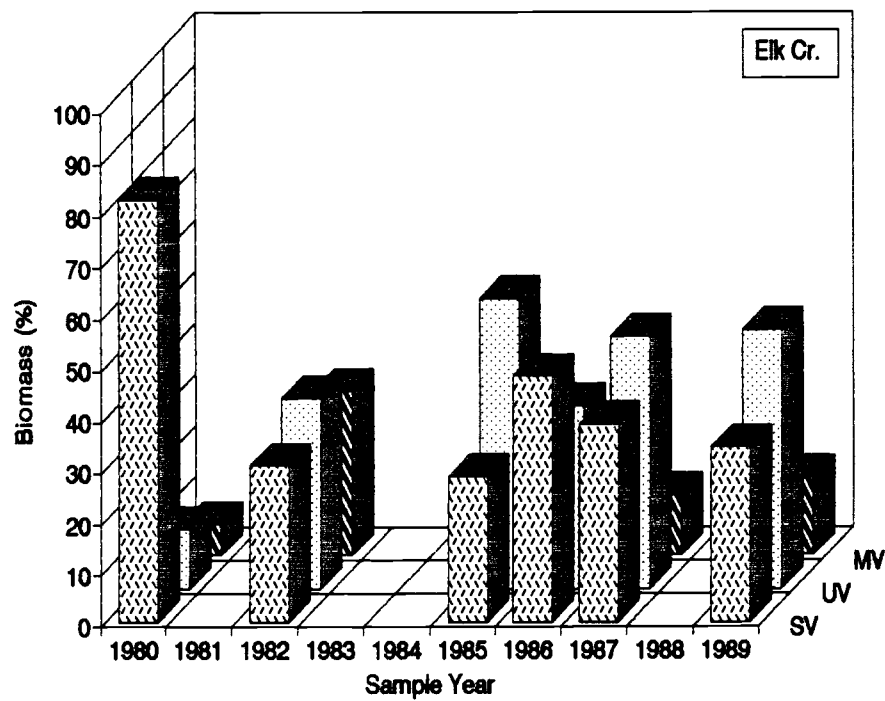
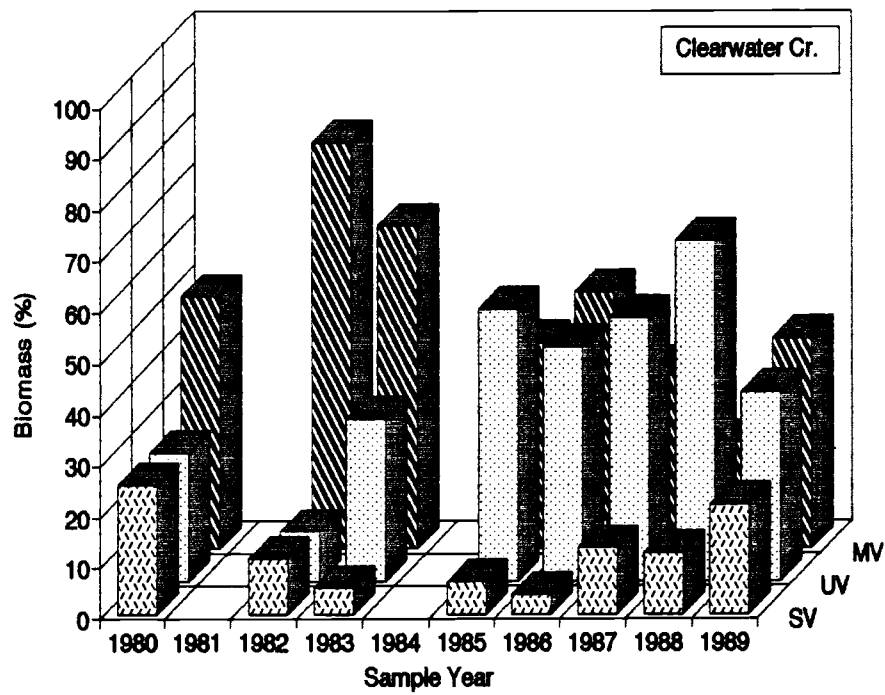


Figure 3.13. Percent of biomass contributed by insects with differing types of voltinism. MV = multivoltine; UV = univoltine; SV = semivoltine.

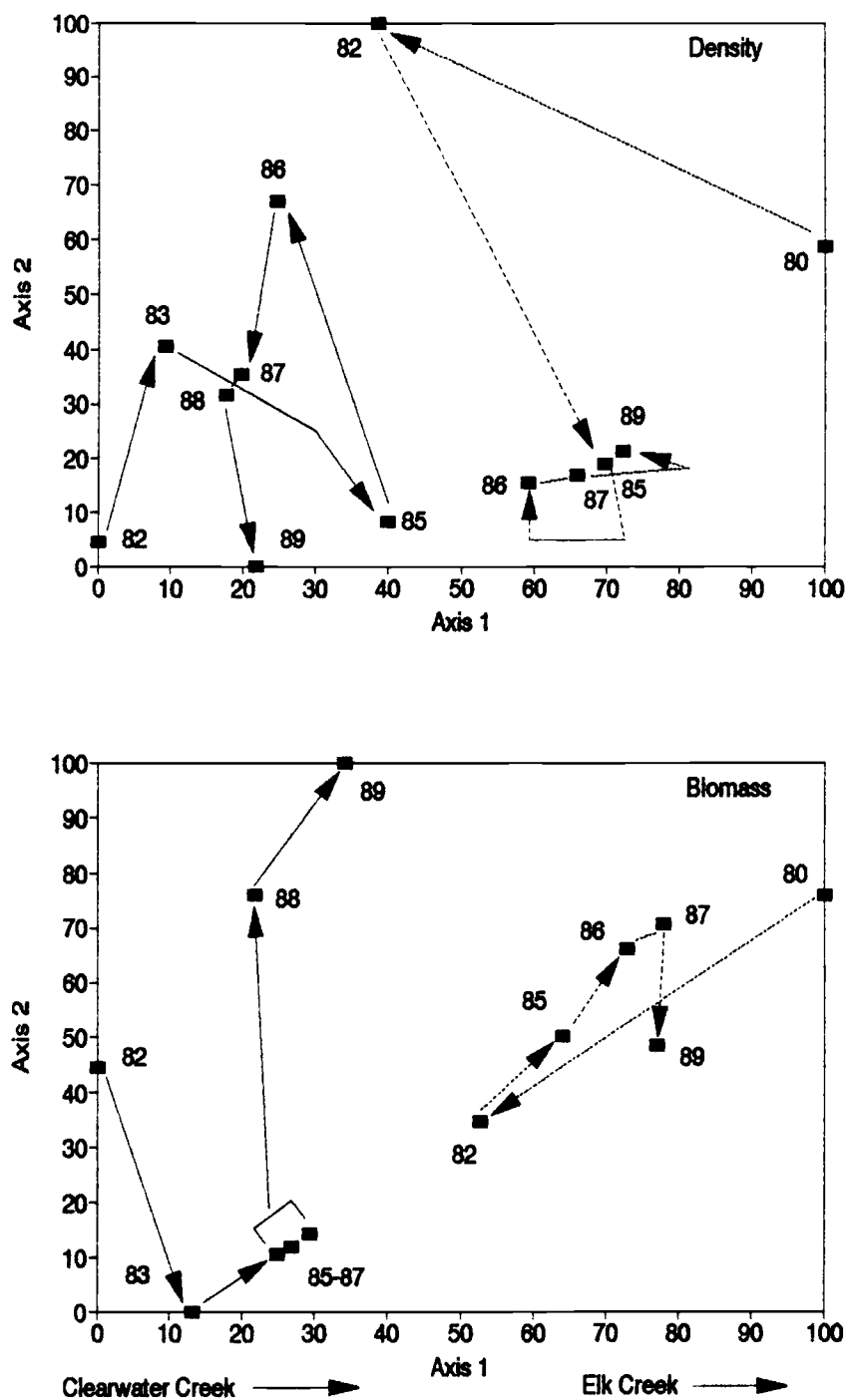


Figure 3.14. Ordination (DCA) of benthic communities of Clearwater (solid line) and Elk (dashed line) Creeks based on density and biomass. Numbered labels correspond to year of sample. Lines connecting subsequent years at each site suggest a successional trajectory.

abundance among taxa changed little. The pattern for biomass was fairly directional along axis 2. This trajectory is associated with the increased amount of biomass contributed by Trichoptera.

The displacement between data points for 1980 and 1982 at Elk Creek indicated that substantial changes occurred in the benthic community for both biomass and abundance. However, the trajectory for both parameters since 1982 suggested that the composition of the community was becoming more like the 1980 community. This pattern was more pronounced for biomass.

Discussion

Aquatic insect recovery at Clearwater Creek has been steady and somewhat predictable. Short-lived, opportunistic taxa were the early colonizers. This was followed by a gradual shift towards longer-lived taxa. This change was evidenced by 1) the increased diversity of E-P-T taxa, and 2) the gradual shift in the biomass from primarily Diptera to E-P-T. Figure 3.3 shows this shift in biomass best. The ratio Diptera:E-P-T taxa was 1.5:1 in 1982; by 1988 it had changed to about 0.3:1.

Increased numbers and biomass of E-P-T taxa are evidence of habitat stabilization (although a few mayfly taxa may be considered opportunistic, e.g. *Baetis* spp.). A benthic community dominated by chironomids is

indicative of unstable habitat conditions as these taxa are usually short-lived, opportunistic insects that can survive under a variety of difficult circumstances from poor substrates to low oxygen conditions (Oliver 1971). As the habitat improves, slow-growing species that require a year or more to complete their life cycles will colonize and eventually out-compete the opportunistic taxa. Since 1986 the increase in E-P-T biomass has come in the Plecoptera and Trichoptera, some of which are semivoltine. Further evidence of habitat stabilization may be found with the pattern of E-P-T dominance. The shape of the curves has changed from curvilinear in 1982 to almost linear by 1985. This change was primarily due to reduced dominance by Baetis spp.

The immediate effects of the eruption on the benthic community of Elk Creek are unclear from the data. On the surface the impact appeared minor as the biomass of long-lived taxa and diversity of E-P-T taxa were high in 1980 only four months after the eruption. Only a portion of the benthic community may have been affected initially (e.g., the insect community was dominated by predators while grazers were poorly represented, see Figure 7.1). More significant changes occurred during the 1980-1981 winter when much ash from the Elk Creek watershed was flushed into the stream

during winter storms and spring snowmelt (N.H. Anderson, personal communication). The 1982 data, which showed a considerable shift in community composition, suggest that scour from this ash was detrimental to the entire insect community.

DECORANA showed that the Clearwater and Elk Creek insect communities were distinctly separated in ordination space. The segregation of the communities along axis 1 likely resulted from differences in habitat stability (see Chapter Two). Elk Creek with its intact riparian zone and large substrates should have been more stable for insects than Clearwater Creek, especially in the years immediately following the eruption. If axis 1 does represent differences in habitat stability, then as the Clearwater Creek habitat stabilizes, e.g., through regrowth of riparian vegetation and streambed changes, the Clearwater Creek community should ordinate more closely to those of Elk Creek. Since 1982 this has been the general trend for the ordination of the Clearwater Creek sites.

A significant shift occurred between the ordination of the 1980 and 1982 communities at Elk Creek. Since 1982 the change in the ordination of the Elk Creek communities back towards the 1980 point suggests that the 1980 community was similar to the pre-eruption community at that site. However, as discussed above it

is likely that by fall 1980 the Elk Creek insect community had already experienced some impacts from the eruption, and we do not know what the pre-eruption community was like.

Data showed that considerable changes occurred in density and biomass between 1985 and 1986. Without a long-term context one could easily assume that the increase was part of the recovery process. However, because Elk Creek was similarly affected (although not to the same degree) it is likely the increased biomass and density reflect ideal environmental conditions in 1986 rather than an effect of disturbance. The following chapters will focus on these two years by making between-year and between-site comparisons of the benthic community structure and secondary production at each stream.

Chapter 4

BENTHIC COMMUNITY STRUCTURE OF CLEARWATER AND ELK CREEKS

Introduction

Intensive sampling at Clearwater and Elk Creeks was conducted in 1985 and 1986 to determine the benthic community structure. These samples also provided data on the relative importance of grazers in the benthic community. In this chapter I will compare the benthic communities between sites and between years..

Methods

Sample Schedule - Insect production was the primary focus of this research so a schedule was devised to maximize sampling when water temperature was high and insects were growing rapidly. This was based on sampling at equal degree-day intervals during the period when the sites were accessible. Nine samples were collected in 1985 between May 19 and October 19. Degree-days, based on temperature data for 1983-84, were used to determine the sampling schedule. In 1986, 12 samples were gathered between March 29 and October 13. The temperature data from 1985 were incorporated along with the 1983-84 data in determining the sampling schedule for that year. Figure 4.1 shows the sample schedule for 1986 that was based on the average accumulated degree days for 1983-85, and the actual

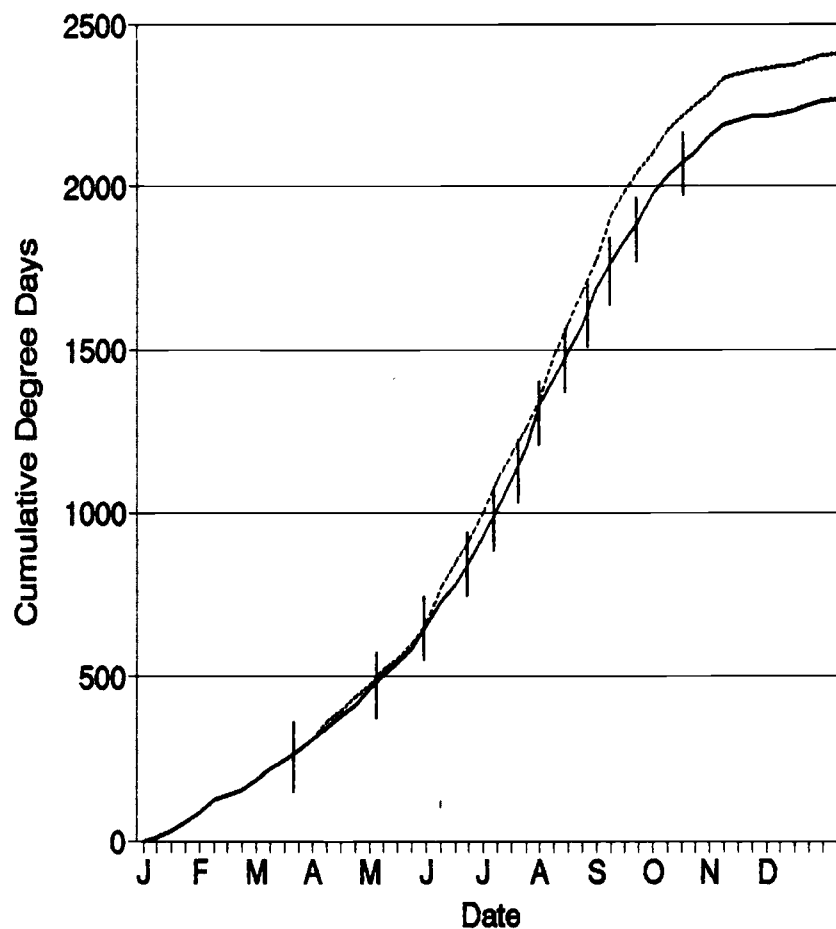


Figure 4.1. Estimated and actual cumulative degree-days at Clearwater Cr. for 1986. Solid line based on 1983-1985 data. Dashed line indicates actual 1986 values. Vertical lines indicate 1986 sample dates with each date separated by an equal number of degree days (see text).

degree days accumulated in 1986. The number of samples collected during each season and thus the number of degree-days between samples, was determined by available funding.

Sampling Procedure - Both qualitative and quantitative samples were collected on all sample dates. Qualitative kick-net samples and wood washings helped determine total species composition and provided information on life histories. A modified Hess sampler (0.021 m^2) fitted with a 250 μm mesh screen was used for quantitative samples. These were collected from both riffle and pool habitats but only where the surface was gravel or larger substrates. Ten quantitative samples were randomly collected from the Take, Leave, and Elk sites on each sample date. Equal numbers of samples were collected from riffles and pools in the middle part of the stream part. All other field and laboratory methods for sample processing, insect identification, and enumeration are discussed in Chapter Three.

Data Analysis - For site comparisons, a mean annual density or biomass for each taxon was calculated by averaging the mean values for all sample dates. This method did not provide a true annual mean since samples were not collected from November to April. However, the lack of winter dates should not be significant to this analysis as all sites were equally affected. Density

and biomass data were transformed ($\log [x+1]$) before statistical analyses were performed. A t-test was used to test for between-year differences ($p < 0.05$) for both biomass and density, and a one-way analysis of variance tested for differences between sites in either year.

Dominance-diversity curves were developed for each site by graphing \log_{10} density or biomass against species rank (Southwood 1978). Species richness (number of taxa) and Shannon-Wiener diversity (\log_2) also were used for community comparisons (Peet 1974).

Similar analyses were done for the grazer community as defined in Chapter One. The scraper and collector-gatherer functional feeding groups comprised the grazer community. Functional feeding group designations were available from data in Merritt and Cummins (1984). Because the focus of this thesis is secondary production, analysis of the grazer community focused on biomass rather than numerical abundance.

Results

Density/Biomass - Insect density and biomass of the Take and Leave sites did not significantly differ in either 1985 or 1986 (Table 4.1). Consequently, data from these two sites was pooled for subsequent analyses. Appendix C contains a list of the mean annual density

Table 4.1. Results of one-way analysis of variance comparing mean annual density and biomass among sites and between years. Data were transformed $\text{Log}(x+1)$ before analysis. Mean values are the means of the log-transformed data. Letters refer to groups which were not significantly different ($p < 0.05$).

| DENSITY | | | | |
|------------|----|------|--------------|-------------------|
| Site/Year | n | Mean | +/- 95% C.I. | Homogenous Groups |
| Take/1985 | 9 | 3.79 | 0.32 | a b |
| Leave/1985 | 9 | 3.70 | 0.32 | a |
| Elk/1985 | 8 | 4.12 | 0.35 | a b c |
| Take/1986 | 11 | 4.59 | 0.29 | c |
| Leave/1986 | 11 | 4.55 | 0.30 | c |
| Elk/1986 | 10 | 4.38 | 0.32 | b c |

d.f. = 57 F-ratio = 6.01 $p = 0.0002$

| BIOMASS | | | | |
|------------|----|------|--------------|-------------------|
| Year | n | Mean | +/- 95% C.I. | Homogenous Groups |
| Take/1985 | 9 | 2.60 | 0.25 | a |
| Leave/1985 | 9 | 2.71 | 0.26 | a |
| Elk/1985 | 8 | 2.95 | 0.27 | a b |
| Take/1986 | 11 | 3.38 | 0.25 | b |
| Leave/1986 | 11 | 3.26 | 0.23 | b |
| Elk/1986 | 10 | 3.27 | 0.24 | b |

d.f. = 57 F-ratio = 7.27 $p = 0.000$

and biomass for each taxon at Clearwater and Elk Creeks in both 1985 and 1986.

Insect density and biomass were higher at Elk Creek than at Clearwater Creek in 1985 (Fig. 4.2) although the between-site differences were not significant (Table 4.1). While density at Elk Creek increased by a factor of about two in 1986 (Fig. 4.2), this change was not significantly greater than the values for 1985 (Table 4.1). Biomass did increase significantly between years, with the greatest increases occurring in the stoneflies and chironomid Diptera (Table 4.2).

Significant increases occurred at Clearwater Creek in 1986 for both density and biomass (Table 4.2). Density increased by almost six-fold while biomass increased by a factor of about four (Fig. 4.2). Most taxonomic groups had significant increases in density and/or biomass with the greatest increases occurring in the mayflies and chironomid midges (Table 4.2).

Ephemeroptera, Plecoptera, and chironomid Diptera made up > 90% of the abundance of aquatic insects at all sites in 1985 (Table 4.2). Mayfly and midge density increased at Clearwater Creek in 1986 to the degree that these two groups alone contributed > 90% of the total density. In contrast, Plecoptera continued to be an important component of the community at Elk Creek in 1986 (Table 4.2).

Table 4.2. Mean annual density (No./m²) and biomass (g/m²) of taxonomic groups in 1985 and 1986. Proportions in parentheses. Asterisks indicate significant between-year differences. (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$). T = < 0.005 g/m².

| 1985 TAXONOMIC GROUP | CLEARWATER CREEK | | | | ELK CREEK | | | |
|----------------------------|------------------|--------|---------|--------|-----------|--------|---------|--------|
| | Density | | Biomass | | Density | | Biomass | |
| | No. | % | g | % | No. | % | g | % |
| Ephemeroptera | 3102 | (31.0) | 0.22 | (31.4) | 3455 | (22.1) | 0.37 | (32.4) |
| Plecoptera | 2725 | (27.2) | 0.08 | (11.4) | 5367 | (34.3) | 0.14 | (14.0) |
| Trichoptera | 57 | (0.6) | 0.06 | (8.8) | 538 | (3.4) | 0.22 | (22.2) |
| Coleoptera | 52 | (0.5) | 0.03 | (4.7) | 11 | (0.1) | 0.01 | (1.0) |
| Diptera | | | | | | | | |
| Chironomidae | 3609 | (36.0) | 0.13 | (18.2) | 5585 | (35.7) | 0.11 | (11.1) |
| Other families | 479 | (4.8) | 0.18 | (25.4) | 675 | (4.3) | 0.14 | (14.1) |
| GRAND TOTAL | 10024 | | 0.70 | | 15631 | | 0.99 | |

| 1986 TAXONOMIC GROUP | CLEARWATER CREEK | | | | ELK CREEK | | | |
|----------------------------|------------------|--------|----------|--------|-----------|--------|----------|--------|
| | Density | | Biomass | | Density | | Biomass | |
| | No. | % | g | % | No. | % | g | % |
| Ephemeroptera | ** 23537 | (41.0) | *** 1.17 | (47.3) | 9242 | (29.6) | ** 0.85 | (45.1) |
| Plecoptera | 3413 | (5.9) | ** 0.34 | (13.9) | 8156 | (26.2) | ** 0.34 | (18.1) |
| Trichoptera | ** 168 | (0.3) | 0.09 | (3.8) | 710 | (2.3) | 0.26 | (13.7) |
| Coleoptera | 45 | (0.1) | 0.03 | (1.0) | 4 | (0.0) | T | (0.2) |
| Diptera | | | | | | | | |
| Chironomidae | *** 29437 | (51.3) | *** 0.61 | (24.8) | 12378 | (39.7) | *** 0.29 | (15.4) |
| Other families | * 843 | (1.5) | 0.23 | (9.3) | 694 | (2.2) | 0.14 | (7.5) |
| GRAND TOTAL | *** 57443 | | *** 2.47 | | 31184 | | ** 1.88 | |

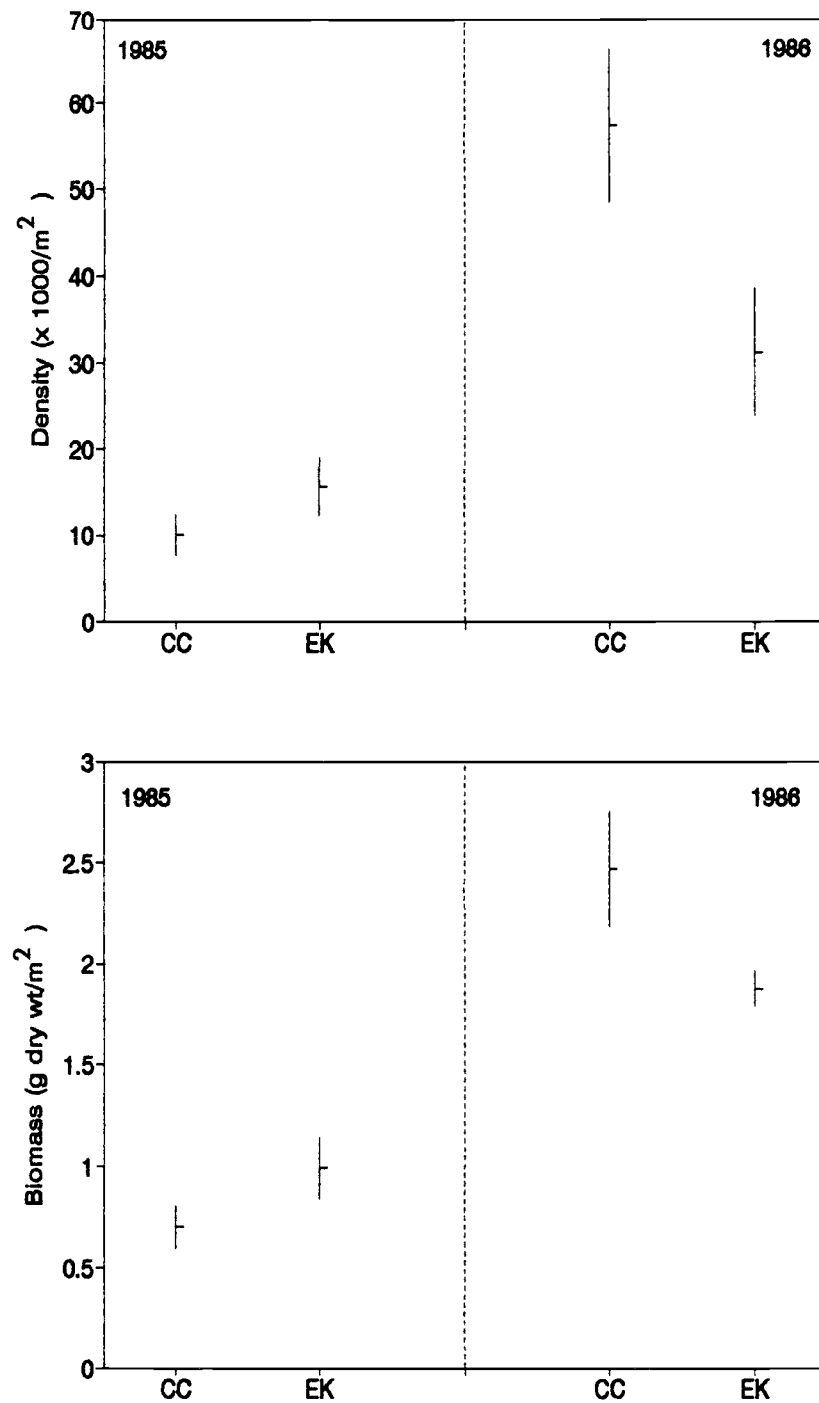


Figure 4.2. Insect density (No. of animals/m²) and biomass (g dry wt/m²) of Clearwater (CC) and Elk (EK) Creeks in 1985 and 1986. Error bars equal 1 S.E.

The biomass at Clearwater Creek in 1985 was ca. 50% Ephemeroptera and chironomid midges (Table 4.2). Mayflies and caddisflies were most important at Elk Creek contributing ca. 40% and 20% of the biomass, respectively (Table 4.2).

Dominance - Between-year within-site comparisons showed that similar taxa made up the most numerically abundant insects each year at the Clearwater Creek sites; nine of ten taxa were common to both 1985 and 1986 (Table 4.3). Chironomid, mayfly and stonefly species had the highest numerical abundance.

Generally, the ten dominant taxa at Clearwater Creek in terms of biomass were different from those that were numerically dominant (Table 4.3). Only two species were common to the lists of dominant taxa for 1985 and 1986. While various taxonomic groups were represented in the 1985 dominants, seven of the top ten taxa in 1986 were mayflies.

At Elk Creek a change of three taxa occurred in the ten most abundant taxa between 1985 and 1986 (Table 4.3). Five of the top ten taxa at Elk Creek were included in the list at Clearwater Creek for both years. Chironomid, mayfly, and stonefly taxa were the dominant groups.

As at Clearwater Creek, the taxa that contributed the greatest to density at Elk Creek were generally

Table 4.3. Ten dominant taxa of each site in 1985 and 1986 ranked in order of decreasing density and biomass. Rankings based on mean annual values. Percentages are cumulative for the entire insect community.

| 1985 | | 1986 | | 1985 | | 1986 | |
|-----------------------------|------|-----------------------------|------|---------------------------------|------|--------------------------------|------|
| TAXON | % | TAXON | % | TAXON | % | TAXON | % |
| CLEARWATER CREEK - DENSITY | | | | CLEARWATER CREEK - BIOMASS | | | |
| <i>Taenionema</i> sp. | 15.3 | <i>Micropectra</i> spp. | 16.0 | <i>Erioptera</i> sp. | 11.8 | <i>Baetis tricaudatus</i> | 6.8 |
| <i>Baetis bicaudatus</i> | 25.9 | <i>Paraleptophlebia</i> sp. | 31.7 | <i>Hesperoconopa</i> sp. | 20.1 | <i>Drunella coloradensis</i> | 13.5 |
| <i>Prostoia</i> sp. | 35.9 | <i>Tanytarsus</i> sp. | 42.7 | <i>Baetis bicaudatus</i> | 28.2 | <i>Paraleptophlebia</i> sp. | 20.2 |
| <i>Micropectra</i> spp. | 42.6 | <i>Cinygmula</i> sp. | 51.4 | <i>Rhyacophila Angelita</i> Gr. | 33.3 | <i>D. spinifera</i> | 26.8 |
| <i>Orthocladius</i> | | <i>Baetis tricaudatus</i> | 57.4 | <i>Ameletus</i> spp. | 37.5 | <i>Cinygmula</i> sp. | 33.3 |
| (<i>Euorthocladius</i>) B | 49.3 | <i>Orthocladius</i> | | <i>Megarcys</i> sp. | 41.5 | <i>Micropectra</i> spp. | 38.8 |
| <i>Ephemerella</i> sp. | 55.3 | (<i>Euorthocladius</i>) B | 62.6 | <i>Orthocladius</i> - | | <i>Serratella tibialis</i> | 44.2 |
| <i>Tanytarsus</i> sp. | 60.6 | <i>Orthocladius</i> - | | <i>Cricotopus</i> A | 45.4 | <i>Skwala</i> sp. | 49.5 |
| <i>Paraleptophlebia</i> sp. | 65.7 | <i>Cricotopus</i> A | 67.6 | Dytiscidae larvae | 48.9 | <i>Tanytarsus</i> sp. | 53.8 |
| <i>Orthocladius</i> - | | <i>Ephemerella</i> sp. | 71.7 | <i>Orthocladius</i> | | <i>Megarcys</i> sp. | 57.7 |
| <i>Cricotopus</i> A | 70.2 | <i>B. bicaudatus</i> | 75.5 | (<i>Euorthocladius</i>) B | 52.4 | | |
| <i>Cinygmula</i> sp. | 73.7 | <i>Taenionema</i> sp. | 78.6 | <i>Serratella tibialis</i> | 55.7 | | |
| ELK CREEK - DENSITY | | | | ELK CREEK - BIOMASS | | | |
| <i>Taenionema</i> sp. | 20.6 | <i>Taenionema</i> sp. | 17.8 | <i>Cinygmula</i> sp. | 12.8 | <i>Cinygmula</i> sp. | 11.7 |
| <i>Cinygmula</i> sp. | 30.7 | <i>Cinygmula</i> sp. | 34.5 | <i>Ameletus</i> spp. | 25.0 | <i>Rhithrogena</i> sp. | 21.3 |
| <i>Micropectra</i> spp. | 38.4 | <i>Tanytarsus</i> sp. | 47.4 | <i>Rhyacophila Betteni</i> Gr. | 29.2 | <i>Drunella coloradensis</i> | 29.7 |
| <i>Rheosmittia</i> sp. | 44.5 | <i>Micropectra</i> spp. | 54.4 | <i>Rhithrogena</i> sp. | 33.3 | <i>Megarcys</i> sp. | 35.4 |
| Capniidae | 50.6 | <i>StemPELLINELLA</i> sp. | 60.6 | <i>Ecclisocosmoecus</i> sp. | 37.2 | <i>Yoraperla</i> sp. | 40.8 |
| <i>StemPELLINELLA</i> sp. | 56.0 | <i>Paraleptophlebia</i> sp. | 64.5 | <i>Taenionema</i> sp. | 40.8 | <i>Diamesa</i> sp. | 45.6 |
| <i>Yoraperla</i> sp. | 59.8 | <i>Yoraperla</i> sp. | 67.3 | <i>Erioptera</i> sp. | 43.9 | <i>Ameletus</i> spp. | 49.6 |
| <i>Ephemerella</i> sp. | 63.6 | Capniidae | 69.8 | <i>Hexatoma</i> sp. A | 47.1 | <i>Rhyacophila Betteni</i> Gr. | 52.7 |
| <i>Thienemannimyia</i> sp. | 66.5 | <i>Epeorus</i> spp. | 72.0 | Ceratopogonidae | 50.2 | <i>R. verrula</i> | 55.6 |
| <i>Paraleptophlebia</i> sp. | 69.0 | <i>Tvetenia bavarica</i> | 73.7 | <i>Drunella coloradensis</i> | 53.2 | <i>Epeorus</i> sp. A | 58.4 |

different from those that contributed most to biomass (Table 4.3). Mayflies, stoneflies, and caddisflies were all part of the dominant taxa list. Depending on the year, only one to three taxa were common to the dominant taxa lists for both Clearwater and Elk Creeks.

A comparison of the shape of dominance-diversity curves for density and biomass showed few differences between sites and years (Fig. 4.3). This result indicated that: 1) the pattern of dominance was similar among sites; and 2) the high levels of density and biomass during 1986 were community increases, rather than a population explosion by one or two species.

Diversity - The number of taxa was similar between streams for both years, although 3 to 8 more taxa were collected from Elk Creek than from Clearwater Creek (Table 4.4). Clearwater Creek had fewer E-P-T taxa and more chironomid taxa than Elk Creek. This difference was more pronounced in 1985 than in 1986.

Shannon-Wiener diversity (density) was > 4.0 at all sites in 1985-86 (Table 4.4). H' (biomass) was even greater than H' (density) with values > 5.0 . Diversity was greatest at Elk Creek in both 1985 and 1986.

Grazer Community - Over 60 grazer taxa were collected from the three sites (see Appendix C). Approximately 50% of the total insect taxa could be

Table 4.4. Characteristics of benthic community structure for Clearwater (C) and Elk (E) Creeks in 1985 and 1986. Results based on mean annual values.

| Parameter | 1985 | | 1986 | |
|------------------------|------|------|------|------|
| | C | E | C | E |
| No. of Taxa | 99 | 102 | 99 | 107 |
| No. of E-P-T Taxa | 44 | 51 | 49 | 55 |
| No. of chironomid Taxa | 40 | 32 | 35 | 33 |
| H' (Density) | 4.5 | 4.67 | 4.22 | 4.37 |
| H' (Biomass) | 5.03 | 5.18 | 5.05 | 5.1 |

Figure 4.3. Dominance-diversity curves for the ten most abundant taxa (density and biomass) of Clearwater and Elk Creeks in 1985 and 1986.

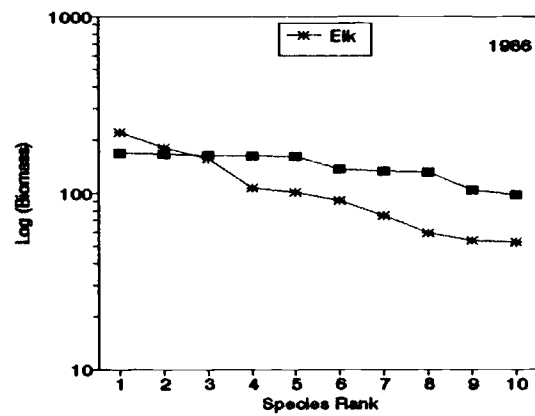
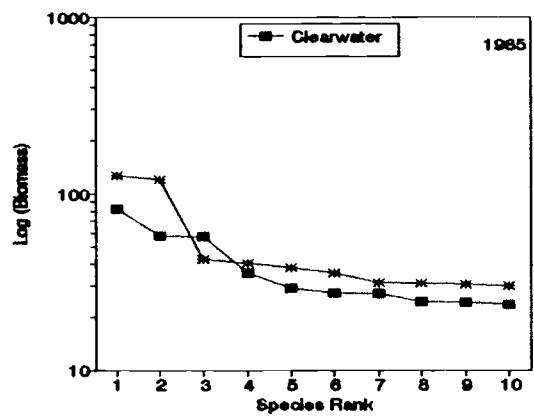
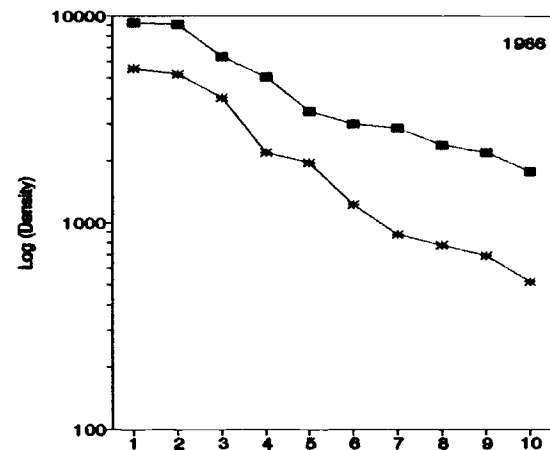
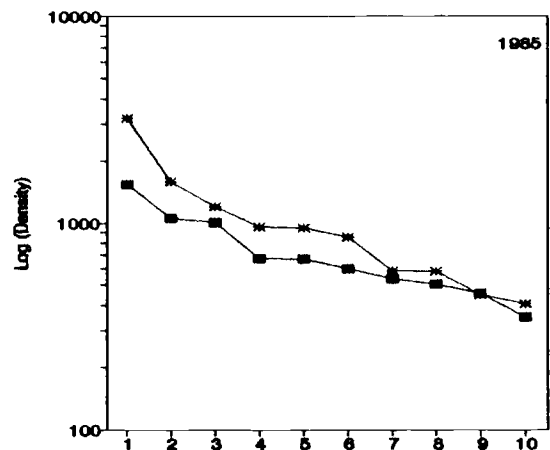


Figure 4.3

classified as grazers in both years; about half were chironomids and most of the others were mayflies.

The density of scrapers and collector-gatherers, and therefore the grazers, greatly exceeded that of all other feeding groups (Table 4.5). They accounted for 60-70% of the individuals at each site and in both years (Table 4.5). Grazer biomass was also greater than that of other groups although percentages were not as high as for density.

The two streams had similar grazer biomass in 1985. Significant increases occurred in 1986 at both sites (Fig. 4.4, Table 4.6). The greatest increase occurred at Clearwater Creek, although no significant differences were found between sites in either year.

For further analysis I have defined the dominant grazer taxa as those taxa that comprised at least 1% of total grazer biomass (Table 4.7). An average of four taxa made up 50% of the grazer biomass at each site and 14 taxa accounted for 90% of the biomass (Fig. 4.5). In order to include 95% of the biomass about seven taxa would have to be added to the list of dominant taxa. Adding this many taxa for only a 5% gain in cumulative biomass quickly diluted the idea of dominance.

The majority of aufwuchs grazers at Clearwater Creek had significantly greater biomass in 1986 than in 1985 (Table 4.7). However, few taxa had significant

Table 4.5. Mean annual density (No./m²) and biomass (g/m²) of functional groups in 1985 and 1986. Proportions in parentheses. T = < 0.005 g/m².

| 1985 FUNCTIONAL GROUP | CLEARWATER CREEK | | | | ELK CREEK | | | |
|-----------------------------|------------------|--------|---------|--------|-----------|--------|---------|--------|
| | Density | | Biomass | | Density | | Biomass | |
| | No. | % | g | % | No. | % | g | % |
| Grazer | 7331 | (73.1) | 0.49 | (70.0) | 11439 | (73.2) | 0.53 | (53.5) |
| Scraper | 3839 | (38.3) | 0.20 | (28.6) | 5551 | (35.5) | 0.25 | (25.3) |
| Collector-Gatherer | 3492 | (34.8) | 0.29 | (41.4) | 5888 | (37.7) | 0.28 | (28.3) |
| Filter-feeder | 619 | (6.2) | 0.01 | (1.4) | 98 | (0.6) | T | (0.3) |
| Predator | 406 | (4.2) | 0.18 | (25.7) | 1594 | (10.2) | 0.35 | (35.4) |
| Shredder | 1657 | (16.5) | 0.02 | (2.9) | 2499 | (16.0) | 0.12 | (12.1) |

| 1986 FUNCTIONAL GROUP | CLEARWATER CREEK | | | | ELK CREEK | | | |
|-----------------------------|------------------|--------|---------|--------|-----------|--------|---------|--------|
| | Density | | Biomass | | Density | | Biomass | |
| | No. | % | g | % | No. | % | g | % |
| Grazer | 38599 | (67.2) | 1.46 | (58.9) | 21440 | (68.8) | 1.08 | (57.2) |
| Scraper | 15833 | (27.6) | 0.67 | (27.4) | 13189 | (42.3) | 0.74 | (39.3) |
| Collector-Gatherer | 22765 | (39.6) | 0.78 | (31.5) | 8250 | (26.5) | 0.34 | (17.9) |
| Filter-feeder | 6644 | (11.6) | 0.13 | (5.3) | 4039 | (13.0) | 0.03 | (1.5) |
| Predator | 2333 | (4.1) | 0.69 | (28.0) | 1729 | (5.5) | 0.59 | (31.6) |
| Shredder | 9865 | (17.2) | 0.20 | (8.1) | 3975 | (12.8) | 0.18 | (9.7) |

Table 4.6. Results of one-way analysis of variance comparing mean annual grazer biomass between sites and years. Data were transformed $\text{Log}(x+1)$ before analysis. Mean values are the means of the log-transformed data. Letters refer to groups which were not significantly different ($p < 0.05$).

| Site/Year | n | Mean | +/- 95% C.I. | Homogenous Groups |
|-------------------------------------|----|------|--------------|----------------------|
| Clearwater/1985 | 18 | 2.52 | 0.15 | a |
| Clearwater/1986 | 22 | 3.12 | 0.14 | c |
| Elk/1985 | 8 | 2.68 | 0.24 | a b |
| Elk/1986 | 10 | 3.02 | 0.21 | b c |
| d.f. = 57 F-ratio = 12.43 p = 0.000 | | | | |

Table 4.7. Comparison of dominant grazer taxa (those which comprise at least 1% of the biomass) of Clearwater and Elk Creeks, 1985-1986. Asterisks indicate between-year significant differences (* = $p < 0.05$; ** = $p < 0.01$; *** $p < 0.001$).

| TAXON | BIOMASS (mg/m ²) | CUMUL. % | TAXON | BIOMASS (mg/m ²) | CUMUL. % |
|--|---------------------------------|-------------|--|---------------------------------|-------------|
| CLEARWATER CR. - 1985 | | | CLEARWATER CR. - 1986 | | |
| <i>Erioptera</i> sp. | 82.5 | 16.8 | <i>Baetis tricaudatus</i> | 167.9 ** | 11.5 |
| <i>Hesperoconopa</i> sp. | 57.9 | 28.6 | <i>Drunella coloradensis</i> | 165.8 ** | 22.9 |
| <i>Baetis bicaudatus</i> | 57.0 | 40.2 | <i>Cinygmula</i> sp. | 160.6 ** | 33.9 |
| <i>Ameletus</i> spp. | 29.4 | 46.2 | <i>Micropectra</i> spp. | 137.1 ** | 43.2 |
| <i>Orthocladius</i> - <i>Cricotopus</i> A | 26.8 | 51.7 | <i>Serratella tibialis</i> | 133.7 * | 52.4 |
| <i>Orthocladius</i> (<i>Euorthocladius</i>) A | 24.2 | 56.7 | <i>Erioptera</i> sp. | 90.5 | 58.6 |
| <i>Serratella tibialis</i> | 23.6 | 61.5 | <i>Parametriocnemus</i> sp. | 73.0 ** | 63.6 |
| <i>B. tricaudatus</i> | 22.9 | 66.1 | <i>Baetis bicaudatus</i> | 68.7 * | 68.3 |
| <i>Taenionema</i> sp. | 21.3 | 70.5 | <i>Ameletus</i> spp. | 68.6 ** | 73.0 |
| <i>Rhithrogena</i> sp. | 21.2 | 74.8 | <i>Orthocladius</i> - <i>Cricotopus</i> A | 45.1 ** | 76.1 |
| <i>Drunella coloradensis</i> | 17.9 | 78.5 | <i>Orthocladius</i> (<i>Euorthocladius</i>) B | 43.9 | 79.1 |
| <i>Cinygmula</i> sp. | 17.3 | 82.0 | <i>Hesperoconopa</i> sp. | 42.5 | 82.0 |
| <i>Micropectra</i> spp. | 13.6 | 84.8 | <i>Pagastia</i> sp. | 40.4 ** | 84.8 |
| <i>Orthocladius</i> (<i>Euorthocladius</i>) B | 10.2 | 86.9 | <i>Orthocladius</i> (<i>Euorthocladius</i>) A | 32.7 ** | 87.0 |
| <i>Krenosmittia</i> sp. | 7.9 * | 88.5 | <i>Ephemerella</i> sp. | 28.7 * | 89.0 |
| <i>Epeorus albertae</i> | 6.4 * | 89.8 | <i>Rhithrogena</i> sp. | 24.0 | 90.6 |
| <i>Ephemerella</i> sp. | 6.1 | 91.0 | <i>Taenionema</i> sp. | 18.7 | 91.9 |
| <i>Epeorus longimanus</i> | 6.1 | 92.3 | | | |
| <i>Eukiefferiella gracei</i> | 5.7 | 93.4 | | | |
| <i>Diamesa</i> sp. | 5.1 * | 94.5 | | | |
| ELK CR. - 1985 | | | ELK CR. - 1986 | | |
| <i>Cinygmula</i> sp. | 126.7 | 23.9 | <i>Cinygmula</i> sp. | 220.7 | 20.4 |
| <i>Ameletus</i> spp. | 120.8 | 46.7 | <i>Rhithrogena</i> sp. | 180.3 | 37.1 |
| <i>Rhithrogena</i> sp. | 40.6 ** | 54.4 | <i>Drunella coloradensis</i> | 157.4 | 51.7 |
| <i>Taenionema</i> sp. | 35.7 | 61.1 | <i>Diamesa</i> sp. | 91.0 ** | 60.1 |
| <i>Erioptera</i> sp. | 31.4 * | 67.0 | <i>Ameletus</i> spp. | 74.5 | 67.0 |
| <i>Drunella coloradensis</i> | 30.0 | 72.7 | <i>Epeorus</i> sp. A | 52.9 | 71.9 |
| <i>Micropectra</i> spp. | 16.4 | 75.8 | <i>Taenionema</i> sp. | 42.3 | 75.8 |
| <i>Baetis bicaudatus</i> | 16.1 | 78.8 | <i>Baetis bicaudatus</i> | 35.5 | 79.1 |
| <i>Rheosmittia</i> sp. | 13.3 | 81.3 | <i>Micropectra</i> spp. | 34.6 | 82.3 |
| <i>Ecclisomyia</i> sp. | 10.5 | 83.3 | <i>Baetis tricaudatus</i> | 20.8 ** | 84.3 |
| <i>Hesperoconopa</i> sp. | 8.7 | 84.9 | <i>StemPELLINella</i> sp. | 15.4 | 85.7 |
| <i>Tvetenia bavarica</i> | 6.5 | 86.2 | <i>Ecclisomyia</i> sp. | 13.2 | 86.9 |
| <i>Eukiefferiella gracei</i> | 5.2 | 87.2 | <i>Hesperoconopa</i> sp. | 11.1 | 87.9 |

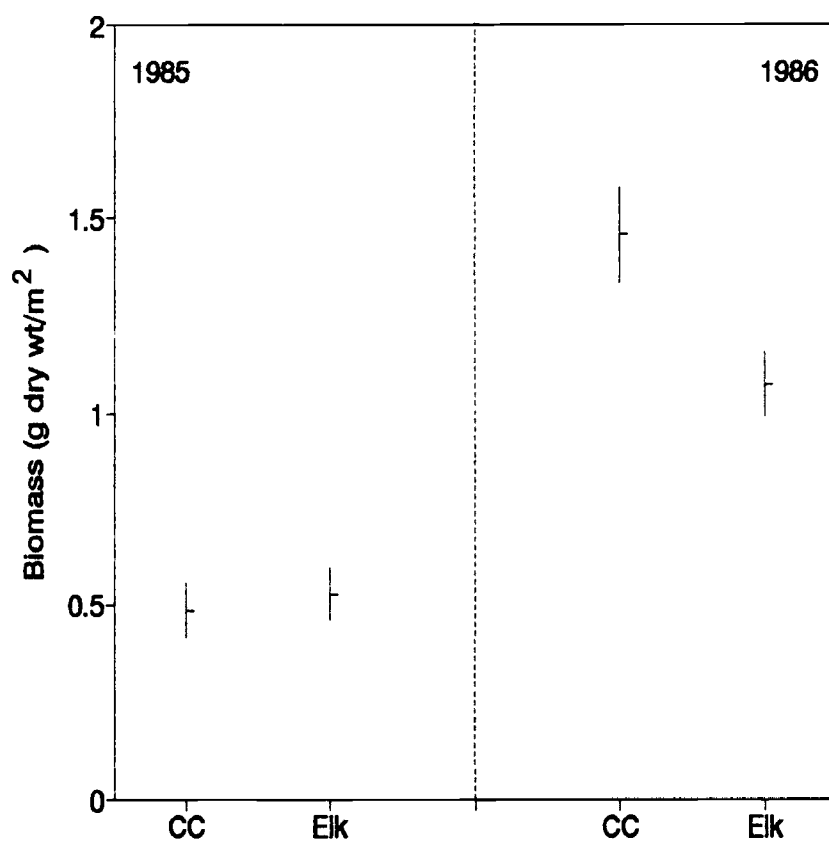


Figure 4.4. Biomass (g dry wt/m²) of aufwuchs grazers at Clearwater (CC) and Elk (EK) Creeks in 1985 and 1986. Error bars equal 1 S.E.

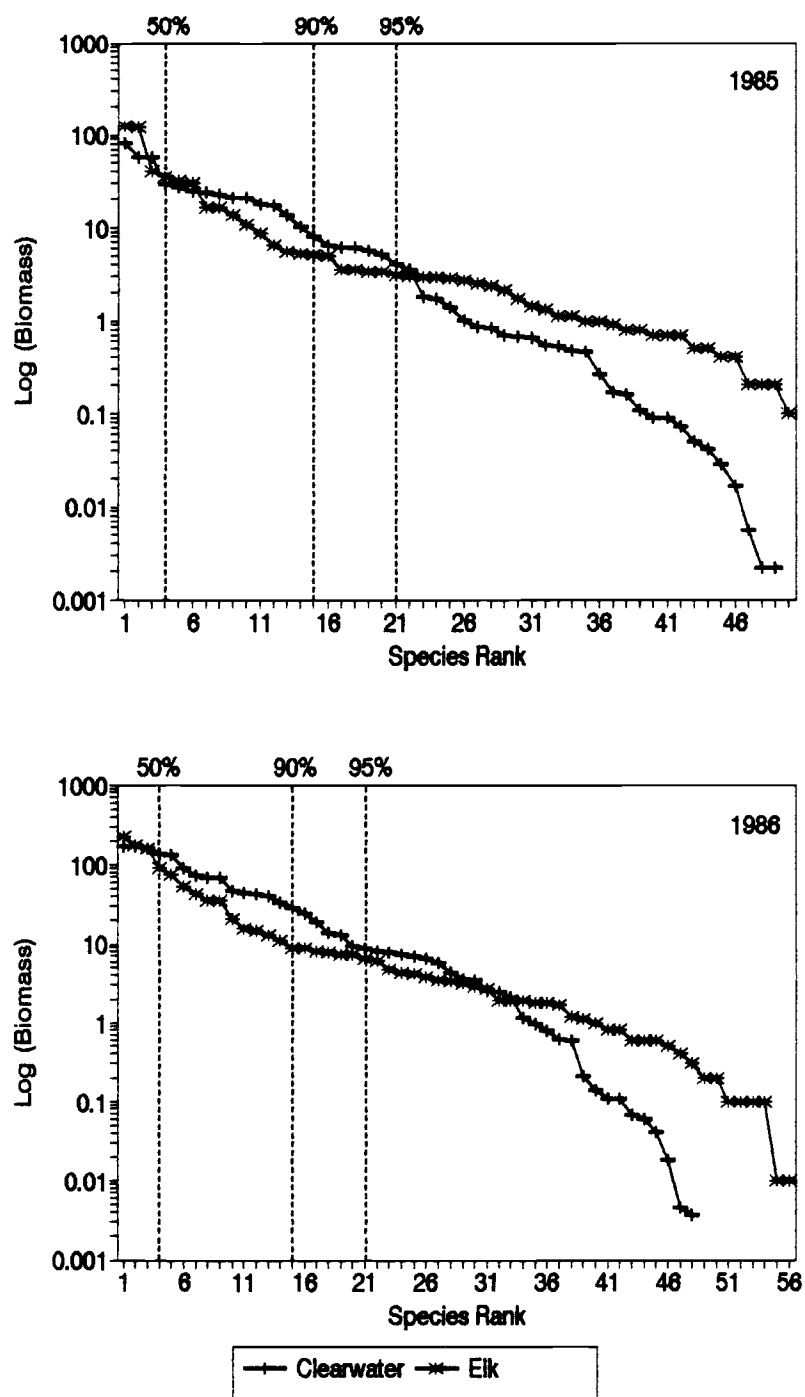


Figure 4.5. Dominance-diversity curves (biomass) for grazer taxa at Clearwater and Elk Creeks in 1985 and 1986. Vertical lines indicate the number of taxa which comprised 50, 90, and 95% of the grazer biomass.

between-year differences in biomass at Elk Creek (Table 4.7).

Discussion

Benthic Community (1985 vs 1986) - The most striking result was the greatly increased insect density and biomass in 1986 over that of 1985 in both Clearwater and Elk Creeks. A possible explanation may be the contrasting discharge patterns between years (see Fig. 2.6). Peak discharge occurred almost two months later in the spring in 1985 than in 1986. Most insect emergence from Mt. St. Helens streams occurs in May and June. If this period is marked by high water from rain and/or snowmelt, it could affect insect emergence, mating, oviposition, and larval establishment. This would result in reduced benthic populations for the following generation. McElravy et al. (1989) found that year-to-year variation in the spring benthic community in a northern California stream could be explained by variation in the frequency and intensity of winter storms. Reduced insect populations were found after severe winters, whereas the benthic community prospered after mild winters. However, no relationship was found between winter severity and late summer benthic community structure. Rosillon (1989) found that most between-year variation was related to flood events which

lowered the densities of many taxa. Wright et al. (1981) suggested that weather conditions during the flight period of an ephemerid mayfly could affect recruitment for the next generation. High water at Clearwater Creek lasted well into this emergence/egg-laying period in 1985 (see Table 5.2). In contrast, 1986 water levels had declined markedly by April, leaving relatively benign conditions for invertebrates in May.

High stream flows coupled with unstable substrates can be detrimental to benthic insect populations (see Minshall 1984 for review). Previously, it was shown that Clearwater Creek has smaller substrates than Elk Creek (see Table 2.2 and Fig. 2.7). Consequently, any effects of high water on emergence and egg-laying will be compounded in a stream where the substrate has less resistance to movement. Furthermore, the earlier in the season that water levels stabilize the sooner the aufwuchs can become established. The low-water conditions that were experienced earlier in 1986 than in 1985 likely enhanced the growth of the aufwuchs, providing an increased food base for larger than normal populations of insects.

Trophic Organization - Aufwuchs grazers clearly were the important component to both streams. An autochthonous-based food web was expected at Clearwater

Creek as it lacked a canopy but this result was unexpected for Elk Creek. The food web in low-order mountain streams has been shown to be allochthonous-based (Anderson and Sedell 1979, Vannote et al. 1980). The Elk Creek site had a relatively open canopy as a result of past logging. However, the time since logging was considerable (15-20 years), and the site was immediately downstream from old growth forest. These two factors should have ameliorated the effects of logging, and the food-web should still have been allochthonous-based. The dominance of grazers rather than shredders at Elk Creek may have been a result of the relative openness of the site as compared to the unlogged parts of the stream. The potential for grazers to aggregate in open stream reaches has been documented (Thorup 1964, Hughes 1966), and this factor will be more fully discussed in Chapter Seven.

The results from Clearwater Creek showed a benthic community well along in its recovery. The richness and diversity of taxa were high and similar to the less-disturbed Elk Creek. The grazer community, while varying in which taxa were dominant, contributed similar proportions to the overall community of each stream. Thus, even though distinct habitat differences were apparent, the similarities in the benthic community structure between sites is striking.

Chapter 5

SECONDARY PRODUCTION OF AUFWUCHS GRAZERS

Introduction

Aufwuchs grazers dominated the biomass of the benthic communities of both Clearwater and Elk Creeks in 1985 and 1986. However, to what degree grazers dominated the secondary production of each stream remains to be seen. In Chapter Four it was shown that the Chironomidae played a more important role in the grazer community of Clearwater than of Elk Creek. Rapid turnover rates, for which chironomid Diptera are noted (e.g., Mackey 1977), can greatly influence secondary production. How differences in benthic community composition influenced secondary production, and how the production of grazers varied between sites and years is the focus of this chapter.

Methods

Production Calculations - Four methods were used for calculating secondary production: (1) Size-frequency with sample data; (2) Size-frequency with estimated mortality schedules; (3) Removal-summation; (4) P/B ratio. An appropriate method was chosen for each taxon on the basis of life cycle, sampling, and taxonomic considerations.

The size-frequency method, developed by Hynes and Coleman (1968) and modified by Hamilton (1969), was used with most of the dominant taxa as it is especially useful when cohorts are asynchronous. Production for a taxon is estimated from an "average cohort", and then is corrected for the amount of time the insect actually spent in the larval phase of its life cycle.

The size-frequency method was also used for some taxa with relatively synchronous cohorts. For these taxa, the period of sampling (May to October) resulted in the collection of individuals from two different generations. For example, *Cinygmula* sp. required almost one year to complete its larval development. Eggs hatched in June/July, and adults emerged the following May/June. Therefore, late instars collected in May or June were from the previous summer's egg hatch, while early instars collected from July to October came from the following generation. By using the size-frequency method this generation difference could be ignored, and all samples were used to define an "average cohort" for that sample year.

The correction factor for converting cohort production into annual production is $365/\text{CPI}$, where CPI (or Cohort Production Interval) equals the number of days that the species spends in the larval stage (Benke 1979). I used a correction factor that was equivalent

to the number of generations per year. This was necessary as cohorts overlapped and correction factors could not be applied to individual generations.

The size-frequency method was used for all taxa with a mean standing crop of at least 100 animals/m². If densities of size classes (especially smaller ones) were lower than subsequent size classes, then the negative values obtained for production between these size classes were ignored. Negative values are often obtained for early size classes as these groups may be poorly represented due to sampling procedures (Benke and Wallace 1980). I consistently removed negative values from the final production calculation whether they occurred with small or large-sized instars.

Confidence intervals were estimated by the method of Krueger and Martin (1980). The reliability of confidence intervals has been questioned. Based on computer simulations, Morin et al. (1987) found that error estimates are only reliable under ideal sampling conditions, e.g. a high sampling effort throughout an entire life cycle and for species that were only weakly aggregated. These conditions were not necessarily always met in this study and the possibility of very large confidence intervals could result (Morin et al. 1987). However, although there are problems associated with the estimation of confidence intervals, these

values are useful because they show which of the dominant taxa are likely to have significantly different between-site or between-year production values.

The lack of winter collections meant that a major portion of the life cycle of four dominant species (*Drunella coloradensis*, *Ephemerella* sp., *Prostoia* sp. and *Taenionema* sp.) was poorly sampled. Abundance and survivorship during the winter had to be calculated before production could be estimated with the size-frequency method. High rates of mortality are likely in these overwintering populations given the nature of the effects of high water during winter storms. *D. coloradensis* hatches in late November/early December (Hawkins 1982), thus the first part of the life cycle of was not sampled. Using mortality estimates of 50% for each size class, I was able to obtain late-instar densities similar to those actually collected in 1985 and 1986. For the other three taxa, I chose 50% mortality rates for early instars, but 75% estimates for middle and late instars. Again the use of these estimates resulted in population sizes similar to those actually collected.

The removal-summation method of calculating production was used for *Serratella tibialis*. It hatched and emerged within the time-frame of the May-October sampling. This method, which mathematically estimates

the area under an Allen curve (number of individuals vs individual biomass) (Allen 1951), sums the loss of biomass over time. The causes of biomass loss, e.g. predation, are irrelevant, and the sum of the losses equals production. No CPI correction is required for this method.

Production for taxa that were collected only in small numbers was estimated from production/biomass ratios (P/B). Based on the studies of Waters (1969, 1979, 1987), the following P/B ratios were used for different types of insects: Univoltine hemimetabolous taxa - 5; univoltine holometabolous taxa - 3.5; semivoltine taxa - 2.5; multivoltine taxa - 10.

Because the Chironomidae may have rapid growth rates, additional samples were collected at Clearwater Creek in July and August of 1986 during the time of greatest degree-day accumulation. These samples were intended to help with production estimates by providing additional information on the voltinism of the important midge grazers. No additional collections were made from Elk Creek since, based on 1985 data, midges were not expected to be as important to the production of the insect community of that stream.

The sampling methodology was designed to emphasize midge collection without modifying the insect's environment using the techniques of Kimerle and Anderson

(1971) in their study of chironomid production in a sewage lagoon. They used plexiglass tubes as microcosms to prevent emigration and immigration of larvae and to estimate growth over short periods of time. Over a series of sample dates individual cohorts could be followed and production estimated.

Plexiglass tubes (15.2 cm I.D.) were placed in a pool with sandy/gravel substrate between the Take and Leave sites. Beginning and end samples were taken at 7-10 day intervals for nine weeks. Seven replicate samples were collected for each date. Based on changes in the size distribution of a taxon, cohorts were distinguished and production estimated. Kimerle and Anderson (1971) may be consulted for specific details about the sampling methodology.

Determination of Voltinism - Voltinism for the dominant taxa was determined from field data. This information was necessary for determining the appropriate CPI correction factor for the size-frequency production estimates. Generally, only 1986 data were used for determining life histories as sampling was more intense than in 1985. However, 1985 data were used when a particular species was more common in that year than in 1986. Body length (in mm) was measured with an ocular micrometer when insects were identified and enumerated (see Chapters Three and Four). The

distribution of individuals among size classes was plotted against sample date, and the interpretation of the changes in size distribution over time provided information on the timing of egg hatch and emergence.

The basic terminology of multi-, uni-, or semivoltine does not distinguish differences that can occur within each type of life cycle. Thus, the classification system of Landa (1968) with modifications by Clifford (1982) helped distinguish subtypes of voltinism that were found at Clearwater and Elk Creeks (Table 5.1).

Voltinism and Production - Production values of a taxon will vary depending on the number of generations completed per year. For some taxa (primarily midges), it was difficult to determine the number of generations from the size-frequency distributions. The presence of early instars throughout the entire sample period could result either from numerous generations or a few generations with continuous recruitment. Given that continuous recruitment is a common occurrence in certain taxa (especially midges, Oliver 1971), the final presentation of annual production results will be conservative. That is, given two choices for the number of generations completed in a year, I chose the lower number for between-site comparisons.

Table 5.1. Subtypes of major categories of voltinism (from Clifford 1982).

Univoltine

- Uw - seasonal univoltine winter cycle, the population overwinters in the larval stage.
- Us - seasonal univoltine summer cycle, the population overwinters in the egg stage.

Multivoltine

- MBws - seasonal bivoltine winter-summer cycle. One summer generation and an overwintering generation in the larval stage.
- MP - seasonal polyvoltine cycles with three or more generations/year, often with two or more summer generations and an overwintering generation in the larval stage.

Results

Voltinism - Generally, more of the dominant grazer taxa at Clearwater Creek were multivoltine (MBws and MP, Table 5.1) than those at Elk Creek (Table 5.2). This between-site difference was due primarily to the greater importance of midges to grazer production at Clearwater Creek than at Elk Creek. Micropsectra spp. was multivoltine at both sites, but had more generations per year at Clearwater Creek than at Elk Creek (Fig. 5.1). One overwintering generation occurred at each site, but only one summer generation occurred at Elk Creek, while two or three summer generations occurred at Clearwater Creek. Weekly samples from the plexiglass tubes helped clarify the number of summer generations for Micropsectra spp. and Parametriocnemus sp. The other important midges that were common in the Hess samples were not common in the tube samples.

Most mayfly grazers completed just one generation per year. However two types of univoltine life-history patterns were found. Cinygmula sp. illustrated a species with a Uw life history type, and Serratella tibialis with a Us type (Fig. 5.2). No between-site differences in voltinism were found (Table 5.2) for mayflies. However, the timing of egg hatch and adult emergence often differed. For example, for Cinygmula

Table 5.2. Comparison of the life cycles of important grazer insects (production) of Clearwater (CC) and Elk (EK) Creeks. See Table 5.1 for types of voltinism. Asterisks indicate that a species was not an important grazer. w = winter generation; s = summer generation(s). Numbers under Hatch Period indicate estimated number of summer generations.

| TAXON | VOLTINISM | | HATCH PERIOD | | EMERGENCE PERIOD | | CPI (Days) | |
|------------------------------|-----------|------|--------------|---------|------------------|---------|------------|-----|
| | CC | EK | CC | EK | CC | EK | CC | EK |
| Ephemeroptera | | | | | | | | |
| <i>Baetis bicaudatus</i> | Uw | Uw | | Aug-Sep | May-Jul | May-Jul | 300 | 300 |
| <i>B. tricaudatus</i> | MP | MP | (w) | Sep-Oct | May-Jun | Jun | 240 | 240 |
| | | | (s) | Jun-Aug | Jul-Oct | Jul-Oct | 120 | 120 |
| <i>Drunella coloradensis</i> | Uw | Uw | | Nov-Dec | Jul-Aug | Jul-Aug | 240 | 240 |
| <i>Serratella tibialis</i> | Us | ** | | May-Jun | Aug-Sep | *** | 75 | *** |
| <i>Cinygmula sp.</i> | Uw | Uw | | May-Aug | May-Jul | Jun-Aug | 300 | 300 |
| <i>Epeorus sp. A</i> | ** | Uw | | *** | *** | Jun-Jul | *** | ??? |
| <i>Rhithrogena sp.</i> | Uw | Uw | | Jun-Jul | Apr-May | May-Jun | 330 | 330 |
| <i>Ameletus sp.</i> | MBws | MBws | (w) | Aug-Sep | May-Jun | Jun-Jul | 240 | 300 |
| | | | (s) | May-Jun | Aug-Sep | Sep-Oct | 120 | 120 |
| Plecoptera | | | | | | | | |
| <i>Taenionema sp.</i> | Uw | Uw | | Jun-Aug | Apr-May | May-Jun | 300 | 300 |
| Trichoptera | | | | | | | | |
| <i>Ecclisomyia sp.</i> | ** | Uw | | *** | Jun-Jul | Apr-May | *** | 240 |
| Diptera (non-midge) | | | | | | | | |
| <i>Erioptera sp.</i> | Uw | Uw | | Sep | May-Jul | Jun-Aug | 275 | 365 |
| <i>Hesperoconopa sp.</i> | Uw | Uw | | Aug | Jul-Aug | Jul-Sep | 365 | 390 |

Table 5.2 (cont.). Comparison of the life cycles of important grazer insects (production) of Clearwater (CC) and Elk (EK) Creeks. See Table 5.1 for types of voltinism. Asterisks indicate that a species was not an important grazer. w = winter generation; s = summer generation(s). Numbers under Hatch Period indicate estimated number of summer generations.

| TAXON | VOLTINISM | | HATCH PERIOD | | EMERGENCE PERIOD | | CPI (Days) | |
|--|-----------|------|--------------------------------|--------------------|--------------------|--------------------|------------|-----------|
| | CC | EK | CC | EK | CC | EK | CC | EK |
| Diptera (midge) | | | | | | | | |
| <i>Diamesa sp.</i> | ** | Uw? | *** | ??? | *** | ??? | *** | ??? |
| <i>Pagastia sp.</i> | MBws | ** | (w) Aug (s) Jun-Jul | *** | Jun Aug-Sep | *** | 300 60 | *** |
| <i>Corynoneura sp.</i> | MP | ** | (w) Sep-Oct (s) May-Aug (2) | *** | May-Jun Jul-Sep | *** | 240 60 | *** |
| <i>Eukiefferiella gracei</i> | MBws | Uw | (w) Aug-Sep (s) Jun-Jul | Jun-Jul | Jun Aug-Sep | May-Jun | 240 90 | 330 |
| <i>Orthocladius- Cricotopus A</i> | MP | ** | (w) Oct? (s) May-Sep (2) | *** | May-Jun Jun-Oct | *** | 180 60 | *** |
| <i>Orthocladius (Euorthocladius) A</i> | MBws | ** | (w) Aug-Sep (s) Apr? | *** | Apr-Jul Aug? | *** | 240 150 | *** |
| <i>Orthocladius (Euorthocladius) B</i> | MBws | ** | (w) Sep-Oct (s) May-Aug | *** | Apr-May Jul-Oct | *** | 240 90 | *** |
| <i>Parametriocnemus sp.</i> | MBws | ** | (w) Aug (s) Jun | *** | Jul-Aug Oct-Nov | *** | 330 100 | *** |
| <i>Microspectra sp.</i> | MP | MBws | (w) Sep-Oct (s) Jun-Aug (2) | Aug-Oct Jun-Jul | May-Jun Jul-Oct | Jun-Aug Sep-Oct | 240 60 | 300 60 |
| <i>Stem Pellinella sp.</i> | ** | MBws | (w) *** (s) | Aug-Sep May-Jun | *** Aug-Sep | May-Jun Aug-Sep | *** 60 | 240 60 |

Figure 5.1. Comparison of the size-frequency (%) distribution of *Micropsectra* spp. at Clearwater Creek (Hess and Tube samples) and Elk Creek in 1986. Width of bar indicates proportion of population in each size class on sample date. Dashed lines indicate hypothesized cohorts - at least two summer generations at Clearwater Creek; one summer generation at Elk Creek.

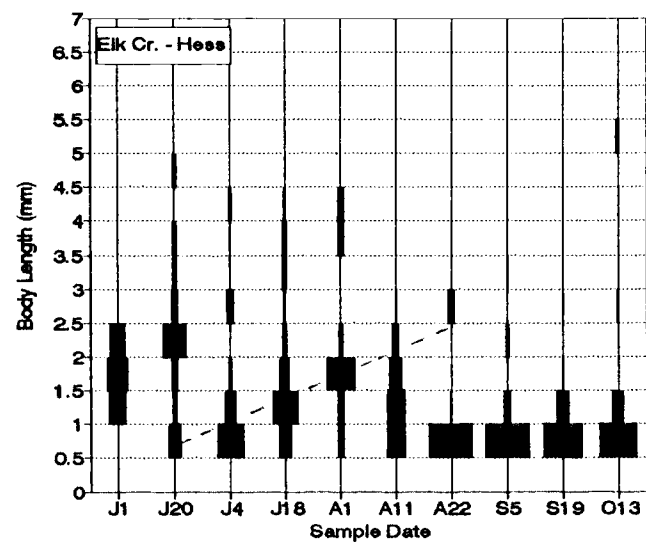
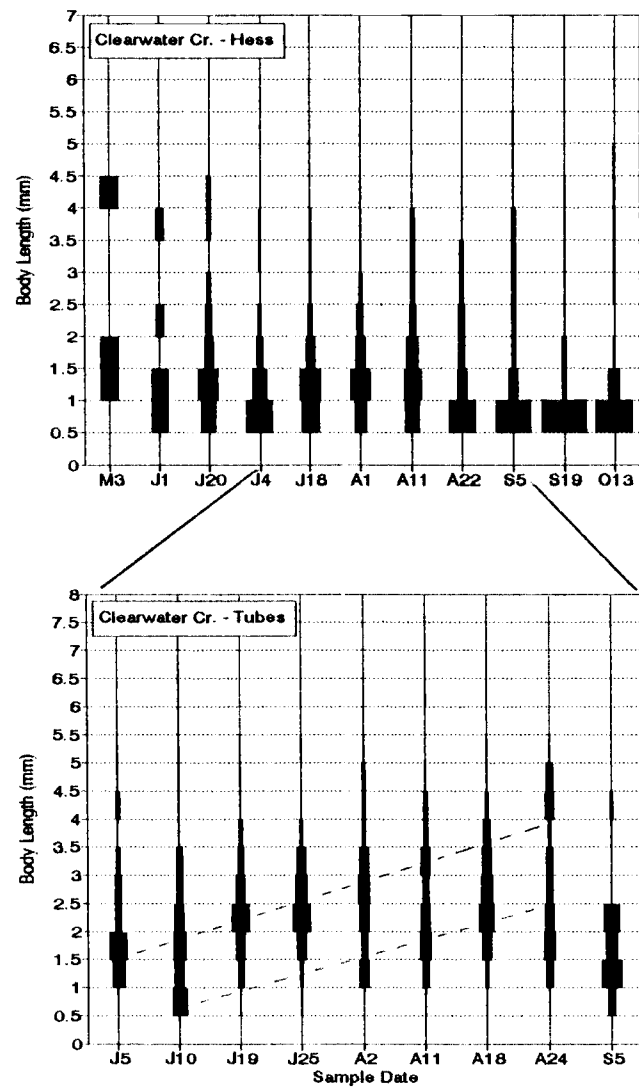


Figure 5.1

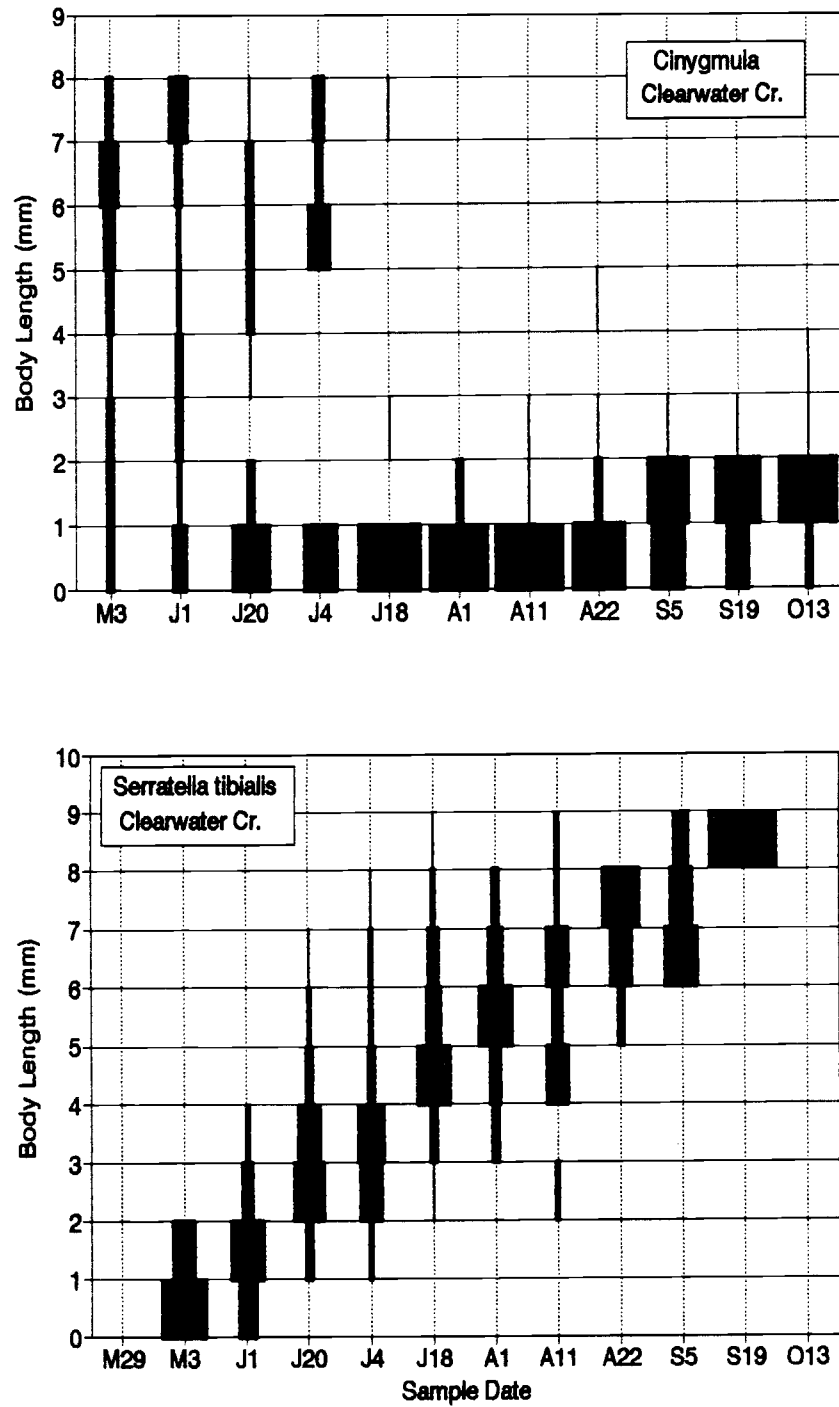


Figure 5.2. Size-frequency (%) distribution of *Cinygmula* sp. (Uw) and *Serratella tibialis* (Us) at Clearwater Creek in 1986. Width of bar indicates proportion of population in each size class on sample date.

sp. these events occurred about one month later at Elk Creek than at Clearwater Creek. Two mayfly taxa appeared to be multivoltine in both streams. Baetis tricaudatus had one summer and one winter generation, and Ameletus spp., which appeared to have a winter and summer generation, more likely consisted of two or more species (N.H. Anderson, personal communication).

Benthic Insect Production - Tables 5.3 and 5.4 list the annual production values of the dominant taxa of Clearwater and Elk Creeks. Total insect production in 1985 was ca. 1 g greater at Elk Creek (9.7 g/m^2) than at Clearwater Creek (8.6 g/m^2) (Table 5.5). E-P-T taxa contributed ca. 80% of the production at Elk Creek, but only 60% at Clearwater Creek. The balance of the production at Clearwater Creek was provided by Diptera, especially Chironomidae.

The great increase in density and biomass at both streams in 1986 (see Chapter Four) resulted in a sharp rise in production. Production increased more than 3-fold at Clearwater Creek to 27.4 g/m^2 , and 1.7 times at Elk Creek to 16.3 g/m^2 in 1986 (Table 5.5). The mayflies and Chironomidae contributed a disproportionate amount of the increase with a ca. 4.5-fold increase in production for both groups. At Elk Creek production rose by 1.7 X for mayflies and 3.4 X for Chironomidae.

Table 5.3. Annual production estimates (g/m^2) of benthic insects at Clearwater Creek in 1985 and 1986. Taxa accounting for > 90% of the total ranked in order of decreasing importance. Asterisk indicates taxa which are aufwuchs grazers. D = Diptera (non-midge); Dm = Diptera (midge); E = Ephemeroptera; P = Plecoptera; T = Trichoptera.

| TAXON | ORDER | METHOD | PROD. | CUMUL. (%) | TAXON | ORDER | METHOD | PROD. | CUMUL. (%) |
|---------------------------------|-------|--------|-------|---------------|------------------------------|-------|--------|-------|---------------|
| CLEARWATER CREEK - 1985 | | | | | CLEARWATER CREEK - 1986 | | | | |
| <i>Taenionema sp.</i> | P* | SF | 1.61 | 18.7 | <i>Baetis tricaudatus</i> | E* | SF | 2.62 | 9.6 |
| <i>Orthocladius</i> | | | | | <i>Ephemerella sp.</i> | E* | SF | 2.52 | 18.8 |
| <i>Cricotopus A</i> | Dm* | SF | 0.67 | 26.5 | <i>Micro psestra spp.</i> | Dm* | SF | 2.42 | 27.6 |
| <i>Erioptera sp.</i> | D* | SF | 0.66 | 34.2 | <i>Cinygmula sp.</i> | E* | SF | 2.09 | 35.2 |
| <i>Ephemerella sp.</i> | E* | SF | 0.64 | 41.6 | <i>Paralepto phlebia sp.</i> | E | SF | 1.89 | 42.1 |
| <i>Drunella coloradensis</i> | E* | SF | 0.50 | 47.4 | <i>Drunella coloradensis</i> | E* | SF | 1.61 | 48.0 |
| <i>Baetis bicaudatus</i> | E* | SF | 0.47 | 52.9 | <i>Tanytarsus spp.</i> | Dm | SF | 1.21 | 52.4 |
| <i>Ameletus spp.</i> | E* | SF | 0.38 | 57.3 | <i>Taenionema sp.</i> | P* | SF | 1.15 | 56.6 |
| <i>Micro psestra spp.</i> | Dm* | SF | 0.33 | 61.2 | <i>Thienemannimyia sp.</i> | Dm | SF | 1.00 | 60.3 |
| <i>Baetis tricaudatus</i> | E* | SF | 0.30 | 64.6 | <i>Parametriocnemus sp.</i> | Dm* | SF | 0.98 | 63.8 |
| <i>Hesperoconopa sp.</i> | D* | SF | 0.29 | 68.0 | <i>Erioptera sp.</i> | D* | SF | 0.85 | 66.9 |
| <i>Orthocladius</i> | | | | | <i>Baetis bicaudatus</i> | E* | SF | 0.85 | 70.1 |
| <i>(Euorthocladius) B</i> | Dm* | SF | 0.28 | 71.3 | <i>Ameletus spp.</i> | E* | SF | 0.80 | 73.0 |
| <i>Rhythrogena sp.</i> | E* | SF | 0.24 | 74.1 | <i>Orthocladius</i> | | | | |
| <i>Cinygmula sp.</i> | E* | SF | 0.23 | 76.7 | <i>Cricotopus A</i> | Dm* | SF | 0.74 | 75.7 |
| <i>Prostoia sp.</i> | P | SF | 0.17 | 78.7 | <i>Pagastia sp.</i> | Dm* | SF | 0.72 | 78.3 |
| <i>Paralepto phlebia sp.</i> | E | SF | 0.17 | 80.7 | <i>Megarcys sp.</i> | P | PB | 0.65 | 80.7 |
| <i>Rhyacophila Angelita Gr.</i> | T | PB | 0.13 | 82.2 | <i>Serratella tibialis</i> | E* | RS | 0.63 | 83.0 |
| <i>Megarcys sp.</i> | P | PB | 0.13 | 83.7 | <i>Orthocladius</i> | | | | |
| <i>Serratella tibialis</i> | E* | RS | 0.13 | 85.3 | <i>(Euorthocladius) B</i> | Dm* | SF | 0.54 | 85.0 |
| <i>Orthocladius</i> | | | | | <i>Orthocladius</i> | | | | |
| <i>(Euorthocladius) A</i> | Dm* | SF | 0.12 | 86.7 | <i>(Euorthocladius) A</i> | Dm* | SF | 0.32 | 86.1 |
| <i>Tanytarsus spp.</i> | Dm | SF | 0.11 | 87.9 | <i>Skwala sp.</i> | P | PB | 0.27 | 87.1 |
| <i>Cricotopus tremulus</i> | Dm | PB | 0.09 | 89.0 | <i>Cultus sp.</i> | P | PB | 0.27 | 88.1 |
| <i>Eukiefferella graciei</i> | Dm* | SF | 0.08 | 90.0 | <i>Drunella spinifera</i> | E | PB | 0.25 | 89.0 |
| Other taxa (74) | | | 0.86 | 100.0 | <i>Rhythrogena sp.</i> | E* | SF | 0.24 | 89.9 |
| | | | | | <i>Corynoneura sp.</i> | Dm* | SF | 0.21 | 90.6 |
| | | | | | Other taxa (74) | | | 2.57 | 100.0 |
| TOTAL | | | 8.60 | | TOTAL | | | 27.40 | |

Table 5.4. Annual production estimates (g/m^2) of benthic insects at Elk Creek in 1985 and 1986. Taxa accounting for > 90% of the total ranked in order of decreasing importance. Asterisk indicates taxa which are aufwuchs grazers. D = Diptera (non-midge); Dm = Diptera (midge); E = Ephemeroptera; P = Plecoptera; T = Trichoptera.

| TAXON | ORDER | METHOD | PROD. | CUMUL. (%) | TAXON | ORDER | METHOD | PROD. | CUMUL. (%) |
|--------------------------------|-------|--------|-------|---------------|--------------------------------|-------|--------|-------|---------------|
| ELK CREEK - 1985 | | | | | ELK CREEK - 1986 | | | | |
| <i>Taenionema sp.</i> | P* | SF | 1.74 | 17.9 | <i>Cinygmula sp.</i> | E* | SF | 2.47 | 15.2 |
| <i>Ameletus spp.</i> | E* | SF | 1.73 | 35.7 | <i>Taenionema sp.</i> | P* | SF | 2.18 | 28.6 |
| <i>Cinygmula sp.</i> | E* | SF | 1.07 | 46.7 | <i>Rhythrogena sp.</i> | E* | SF | 1.56 | 38.2 |
| <i>Drunella coloradensis</i> | E* | SF | 0.72 | 54.1 | <i>Drunella coloradensis</i> | E* | SF | 1.50 | 47.4 |
| <i>Rhythrogena sp.</i> | E* | SF | 0.39 | 58.1 | <i>Ameletus spp.</i> | E* | SF | 1.11 | 54.3 |
| <i>Caeniidae</i> | P | SF | 0.31 | 61.3 | <i>Megarcys sp.</i> | P* | PB | 0.54 | 57.6 |
| <i>Ceratopogonidae</i> | D | SF | 0.28 | 64.1 | <i>Micropectra spp.</i> | Dm* | SF | 0.48 | 60.5 |
| <i>Ephemerella sp.</i> | E* | SF | 0.28 | 67.0 | <i>Diamesa sp.</i> | Dm* | PB | 0.46 | 63.3 |
| <i>Paraleptophlebia sp.</i> | E | SF | 0.26 | 69.6 | <i>Tanytarsus spp.</i> | Dm | SF | 0.45 | 66.1 |
| <i>Erioptera sp.</i> | D* | SF | 0.20 | 71.7 | <i>Thienemannimyia sp.</i> | Dm | SF | 0.40 | 68.6 |
| <i>Hexatoma sp. A</i> | D | PB | 0.16 | 73.3 | <i>Ceratopogonidae</i> | D | SF | 0.39 | 71.0 |
| <i>Rhyacophila Bettini Gr.</i> | T | PB | 0.15 | 74.8 | <i>Baetis tricaudatus</i> | E* | SF | 0.30 | 72.8 |
| <i>Thienemannimyia sp.</i> | Dm | SF | 0.14 | 76.3 | <i>Epeorus sp. A</i> | E* | PB | 0.26 | 74.4 |
| <i>Ecclisocosmoecus sp.</i> | T | PB | 0.13 | 77.6 | <i>Paraleptophlebia sp.</i> | E | SF | 0.25 | 76.0 |
| <i>Megarcys sp.</i> | P | PB | 0.13 | 79.0 | <i>Baetis bicaudatus</i> | E* | SF | 0.25 | 77.5 |
| <i>Yora perla sp.</i> | P | SF | 0.13 | 80.4 | <i>Yora perla sp.</i> | P | SF | 0.23 | 78.9 |
| <i>Dicranota sp.</i> | D | SF | 0.12 | 81.6 | <i>Drunella doddsi</i> | E | PB | 0.21 | 80.2 |
| <i>Micropectra spp.</i> | Dm* | SF | 0.11 | 82.7 | <i>Rhyacophila Bettini Gr.</i> | T | PB | 0.21 | 81.5 |
| <i>R. Hyalinata Gr.</i> | T | PB | 0.10 | 83.8 | <i>Rhyacophila verrula</i> | T | PB | 0.19 | 82.7 |
| <i>Ecclisomyia sp.</i> | T* | SF | 0.10 | 84.8 | <i>Skwala sp.</i> | P | PB | 0.18 | 83.8 |
| <i>Hesperoconopa sp.</i> | D | SF | 0.09 | 85.7 | <i>Dicranota sp.</i> | D | SF | 0.16 | 84.7 |
| <i>Rhyacophila narvae</i> | T | PB | 0.08 | 86.5 | <i>Hexatoma sp. A</i> | D | PB | 0.15 | 85.6 |
| <i>Rhyacophila verrula</i> | T | PB | 0.07 | 87.3 | <i>Pseudorthocladus sp.</i> | Dm* | PB | 0.15 | 86.5 |
| <i>Baetis bicaudatus</i> | E* | SF | 0.07 | 88.0 | <i>Hesperoconopa sp.</i> | D* | SF | 0.14 | 87.4 |
| <i>Baetis tricaudatus</i> | E* | SF | 0.06 | 88.6 | <i>Stem Pellinella sp.</i> | Dm* | SF | 0.14 | 88.3 |
| <i>R. Brunnea Gr.</i> | T | PB | 0.05 | 89.2 | <i>Ephemerella sp.</i> | E* | SF | 0.11 | 88.9 |
| <i>Hexatoma sp. B</i> | D | PB | 0.05 | 89.7 | <i>Parapsyche elsis</i> | T | PB | 0.10 | 89.6 |
| <i>Stem Pellinella sp.</i> | Dm* | SF | 0.05 | 90.2 | <i>Parametriocnemus sp.</i> | Dm* | SF | 0.10 | 90.2 |
| Other taxa (74) | | | 0.82 | 100.0 | Other taxa (78) | | | 1.64 | 100.0 |
| TOTAL | | | 9.70 | | TOTAL | | | 16.30 | |

Table 5.5 Annual production (g/m^2) of taxonomic groups at Clearwater and Elk Creeks, 1985 and 1986.

| Taxonomic Group | Clearwater Creek | | Elk Creek | |
|------------------|------------------|------|-----------|------|
| | 1985 | 1986 | 1985 | 1986 |
| Ephemeroptera | 3.1 | 13.6 | 4.6 | 8.1 |
| Plecoptera | 2.0 | 2.6 | 2.5 | 3.4 |
| Trichoptera | 0.2 | 0.3 | 0.8 | 0.9 |
| Coleoptera | 0.1 | 0.1 | 0.0 | 0.0 |
| Diptera | | | | |
| Chironomidae | 1.9 | 8.9 | 0.8 | 2.7 |
| Other families | 1.2 | 1.9 | 1.0 | 1.0 |
| Total Production | 8.6 | 27.4 | 9.7 | 16.3 |

Grazer Production - Over 70% of the production was by grazers (scrapers and collector-gatherers) at both sites in 1985 and 1986. The proportion contributed by grazers declined by 10% between 1985 and 1986 at Clearwater Creek (Fig. 5.3). This small decline was made up by increases in predators and filter feeders (esp. the midge, Tanytarsus spp.). Few changes in relative production occurred between years for any of the feeding groups at Elk Creek (Fig. 5.3).

Although grazers provided a similar proportion of production in each stream in both years, the source of this production varied. At Clearwater Creek the Chironomidae contributed ca. 15% more to production in both years than they did at Elk Creek (Fig. 5.3).

In both years, three taxa at Elk Creek and five at Clearwater Creek produced 50% of the total grazer biomass (Table 5.6). Numerous taxa contributed to the increased production values in 1986, especially the mayflies Baetis tricaudatus, Ephemerella sp., and Cinygmula sp. and the chironomids Micropsectra spp. Seven of the ten most important taxa, in terms of production, were common to both sites in each year. Differences between sites were generally associated with chironomid midges (especially Orthocladius (Euorthocladius) B and Orthocladius-Cricotopus spp.),

Table 5.6. Annual production (P) (g/m²) of aufwuchs grazers at Clearwater and Elk Creeks in 1985 and 1986, ranked in decreasing order of their contribution to total grazer production. E = Ephemeroptera; P = Plecoptera; T = Trichoptera; D = Diptera (non-midge); Dm = Diptera (midge).

| TAXON | ORDER | ANNUAL P | CUMUL. % | 95% Conf. Int. | TAXON | ORDER | ANNUAL P | CUMUL. % | 95% Conf. Int. |
|--|-------|-------------|-------------|-------------------|--|-------|-------------|-------------|-------------------|
| CLEARWATER CREEK - 1985 | | | | | CLEARWATER CREEK - 1986 | | | | |
| <i>Taenionema</i> sp. | P | 1.61 | 22.2 | | <i>Baetis tricaudatus</i> | E | 2.62 | 12.8 | 2.00-3.24 |
| <i>Orthocladius</i> - <i>Cricotopus</i> A | Dm | 0.67 | 31.5 | 0.40-0.94 | <i>Ephemerella</i> sp. | E | 2.52 | 25.1 | |
| <i>Erioptera</i> sp. | D | 0.66 | 40.6 | 0.40-0.92 | <i>Micropectra</i> spp. | Dm | 2.42 | 36.9 | 1.54-3.30 |
| <i>Ephemerella</i> sp. | E | 0.64 | 49.5 | | <i>Cinygmula</i> sp. | E | 2.09 | 47.2 | 1.79-2.37 |
| <i>Drunella coloradensis</i> | E | 0.50 | 56.4 | | <i>Drunella coloradensis</i> | E | 1.61 | 55.0 | |
| <i>Baetis bicaudatus</i> | E | 0.47 | 62.9 | 0.39-0.55 | <i>Taenionema</i> sp. | P | 1.15 | 60.7 | |
| <i>Ameletus</i> spp. | E | 0.38 | 68.1 | 0.22-0.54 | <i>Parametriocnemus</i> | Dm | 0.98 | 65.5 | 0.60-1.26 |
| <i>Micropectra</i> spp. | Dm | 0.33 | 72.7 | 0.15-0.51 | <i>Erioptera</i> sp. | D | 0.85 | 69.6 | 0.67-1.03 |
| <i>Baetis tricaudatus</i> | E | 0.30 | 76.8 | 0.21-0.39 | <i>Baetis bicaudatus</i> | E | 0.85 | 73.8 | 0.59-1.11 |
| <i>Hesperoconopa</i> sp. | D | 0.29 | 80.8 | 0.14-0.44 | <i>Ameletus</i> spp. | E | 0.80 | 77.7 | 0.51-1.09 |
| <i>Orthocladius</i> (<i>Euorthocladius</i>) B | Dm | 0.28 | 84.7 | 0.18-0.38 | <i>Orthocladius</i> - <i>Cricotopus</i> A | Dm | 0.74 | 81.3 | 0.59-0.89 |
| <i>Rhithrogena</i> sp. | E | 0.24 | 88.0 | 0.19-0.29 | <i>Pagastia</i> sp. | Dm | 0.72 | 84.8 | 0.34-1.10 |
| <i>Cinygmula</i> sp. | E | 0.23 | 91.2 | 0.16-0.30 | <i>Serratella tibialis</i> | E | 0.63 | 87.9 | |
| | | | | | <i>Orthocladius</i> (<i>Euorthocladius</i>) B | Dm | 0.54 | 90.5 | 0.37-0.71 |
| ELK CREEK - 1985 | | | | | ELK CREEK - 1986 | | | | |
| <i>Taenionema</i> sp. | P | 1.74 | 24.0 | | <i>Cinygmula</i> sp. | E | 2.47 | 20.5 | 1.68-3.26 |
| <i>Ameletus</i> spp. | E | 1.73 | 48.7 | 0.64-2.42 | <i>Taenionema</i> sp. | P | 2.18 | 38.6 | |
| <i>Cinygmula</i> sp. | E | 1.07 | 63.7 | 0.63-1.01 | <i>Rhithrogena</i> sp. | E | 1.56 | 51.6 | 1.34-1.88 |
| <i>Drunella coloradensis</i> | E | 0.72 | 73.8 | | <i>Drunella coloradensis</i> | E | 1.50 | 64.0 | |
| <i>Rhithrogena</i> sp. | E | 0.39 | 79.3 | 0.20-0.46 | <i>Ameletus</i> spp. | E | 1.11 | 73.2 | 0.66-1.56 |
| <i>Ephemerella</i> sp. | E | 0.28 | 83.2 | | <i>Micropectra</i> spp. | Dm | 0.48 | 77.2 | 0.34-0.62 |
| <i>Erioptera</i> sp. | D | 0.20 | 86.0 | 0.03-0.14 | <i>Diamesa</i> sp. | Dm | 0.46 | 81.0 | |
| <i>Micropectra</i> spp. | Dm | 0.11 | 87.5 | 0.05-0.17 | <i>Baetis tricaudatus</i> | E | 0.30 | 83.5 | 0.17-0.43 |
| <i>Ecclisomyia</i> sp. | T | 0.10 | 88.9 | 0.00-0.12 | <i>Epeorus</i> sp. A | E | 0.26 | 85.7 | |
| <i>Hesperoconopa</i> sp. | D | 0.09 | 90.2 | 0.07-0.11 | <i>Baetis bicaudatus</i> | E | 0.25 | 87.8 | 0.17-0.33 |
| | | | | | <i>Stem Pellinella</i> sp. | Dm | 0.14 | 88.9 | 0.07-0.21 |
| | | | | | <i>Hesperoconopa</i> sp. | D | 0.14 | 90.1 | 0.12-0.16 |

Figure 5.3. Between-site and between-year comparisons of grazer production. Top = Grazer production as a proportion of total insect production. GR = grazers; PR = predators; FF = filter-feeders; SH = shredders. Bottom = Taxonomic contributions to grazer production. E = Ephemeroptera; Dm = Diptera (midge); P = Plecoptera; D = Diptera (non-midge); T/C = Trichoptera and Coleoptera.

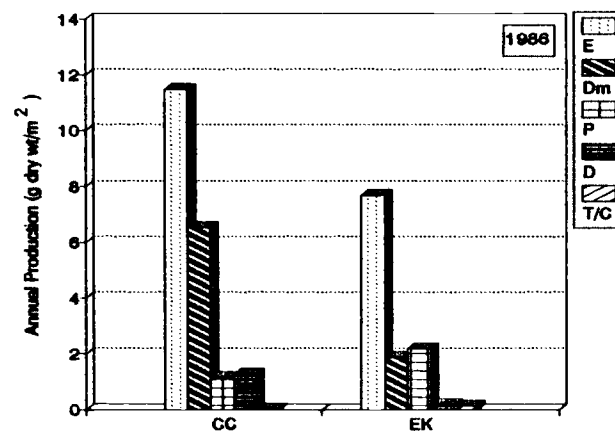
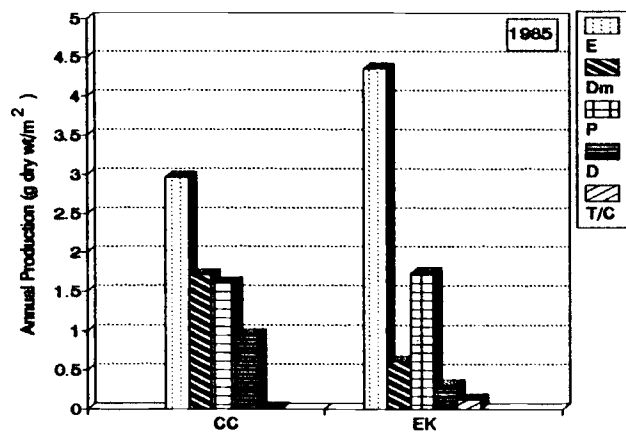
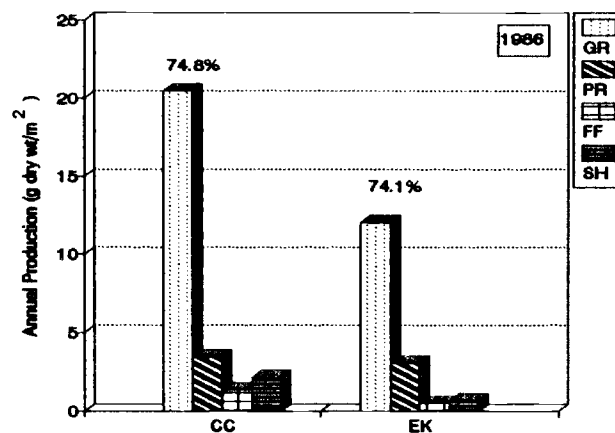
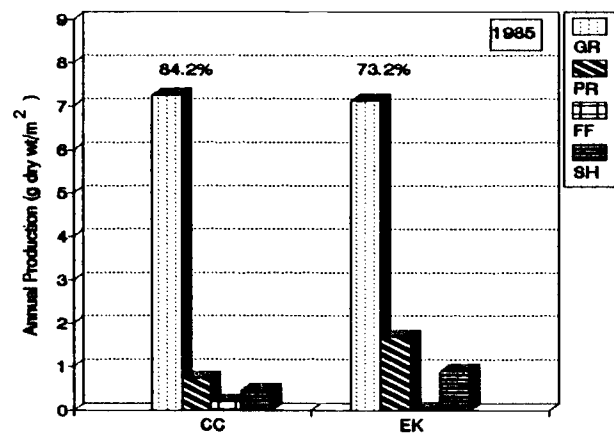


Figure 5.3

which were important to grazer production at Clearwater Creek.

Differences occurred in the shape of dominance-diversity curves for grazer production at each stream. This was most pronounced in 1986 when greater evenness was found among the top ten biomass producers at Clearwater Creek than at Elk Creek (Fig. 5.4).

Study Site Production vs. Total Stream Production - Secondary production can differ among habitat types (see Benke 1984, for review). If production rates are calculated according to habitat type and weighted according to the proportional occurrence of the habitat types in the stream (e.g., substrate type or pool vs riffle), then site production could differ from total stream production.

The production estimates reported in this chapter are based on samples collected from substrates of gravel or larger particle sizes; sandy substrates were not considered. Sandy substrates (particle sizes of 1 mm or less) comprised about 30% of the Clearwater sites and 10% of the Elk Creek site (Fig. 2.7).

Data collected in 1985 from Clearwater Creek (ten samples on each sample date) provided an estimate of the importance of the sand habitat to total stream production. Annual insect production was ca. 20% less in the sandy habitat than in large-substrate habitats

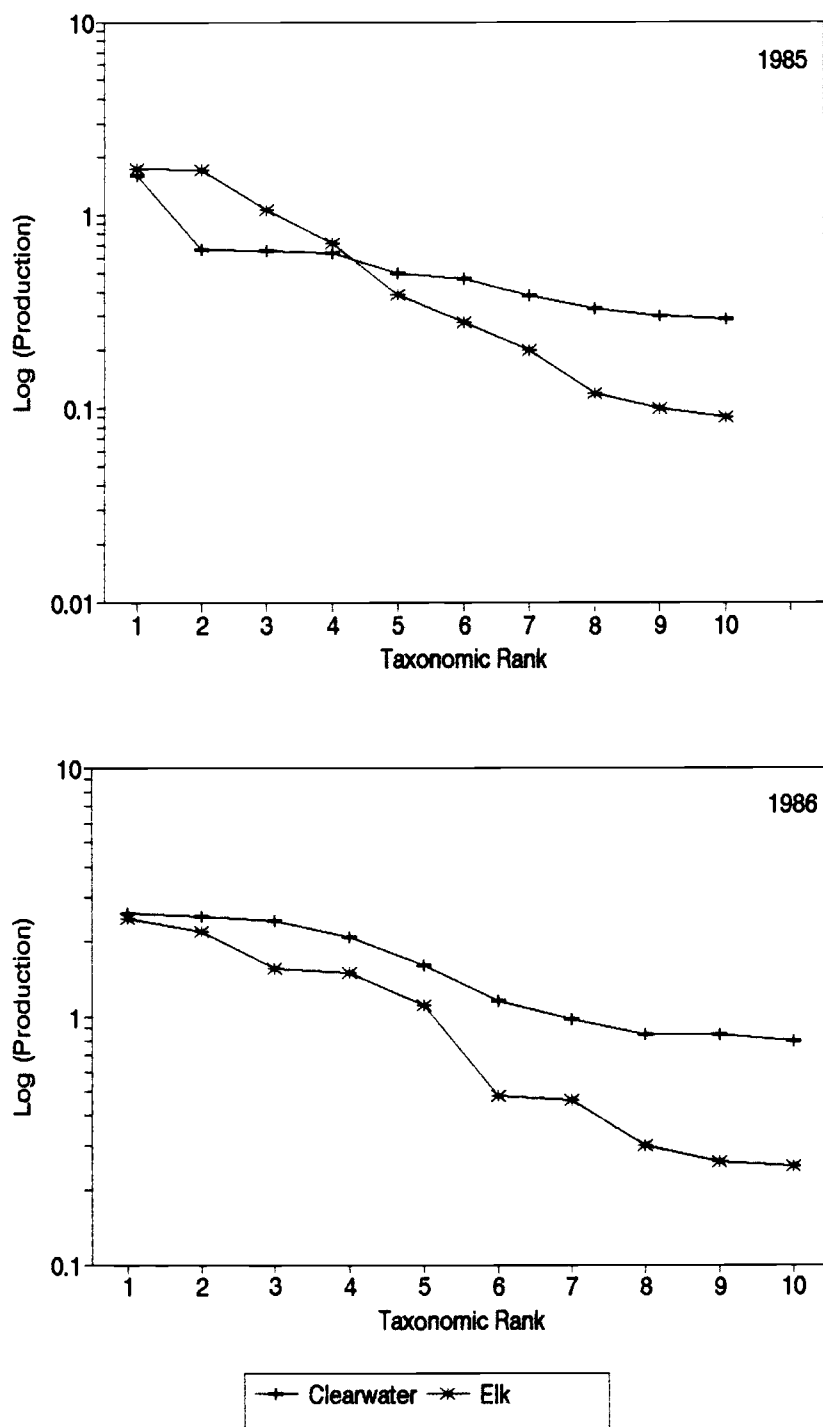


Figure 5.4. Dominance-diversity curves for grazer production at Clearwater and Elk Creeks in 1985 and 1986.

(Table 5.7). However, because sandy substrates were less common than other substrates total stream production was only 6% less when all habitats are considered in production estimates. It should be noted that the distribution of secondary production among taxonomic groups differed considerably between habitat types in 1985, i.e., > 70% of the insect production in sandy habitats was Chironomidae. In contrast, only 22% of the insect production was contributed by the Chironomidae in the large-sized substrates.

No comparable data were available from Elk Creek. However, since only about 10% of the habitat of that stream was comprised of sandy substrates, total stream production should be even more similar to the production estimated from large substrates than the 6% between-substrate difference that was found at Clearwater Creek.

The pool/riffle ratio differed between streams with pool habitat more common at the Clearwater Creek sites than the Elk Creek site. Specifically, pools comprised ca. 46% of the habitat at Clearwater Creek (Take and Leave sites combined) and ca. 30% of the Elk Creek habitat. Because pools and riffles were found in approximately equal proportions and equal numbers of samples were collected from these habitats, potential differences in production between pools and riffles should not affect estimates of total stream production

Table 5.7 Estimate of total annual stream production (g/m^2) at Clearwater Creek in 1985. Total stream production weighted by the proportion that the substrate type was found in each stream. Large = 70%; Sandy = 30% of stream area. $T = < 0.05 \text{ g/m}^2$.

| Taxonomic Group | Production by Substrate Type | | Total Annual Stream Production |
|-----------------|------------------------------|-------|--------------------------------|
| | Large | Sandy | |
| Ephemeroptera | 3.1 | 0.2 | 2.2 |
| Plecoptera | 2.0 | T | 1.4 |
| Trichoptera | 0.2 | 0.1 | 0.2 |
| Coleoptera | 0.1 | 0.3 | 0.2 |
| Diptera | | | |
| Chironomidae | 1.9 | 5.1 | 2.9 |
| Other families | 1.2 | 1.3 | 1.2 |
| Grand Total | 8.6 | 7.0 | 8.1 |

at Clearwater Creek. However, at Elk Creek equal numbers of samples were collected from pools and riffles even though pools represented only about one-third of the stream habitat. Insect production in pools was approximately half of insect production in riffles. The potential effect of the over-weighting of the pool habitat during sample collection was to slightly underestimate (ca. 10%) total stream production at Elk Creek.

Discussion

Reliability of Production Values - Many factors can affect the reliability of annual production estimates (see Benke 1984). Probably foremost of these factors is voltinism. Actual annual production values could be greater than those reported here as I chose to be conservative in the interpretation of voltinism. The effects of increased numbers of generations per year were confined to the Diptera (primarily Chironomidae) of Clearwater Creek. While cumulative degree days were similar at each stream (1818 at Clearwater Creek; 1643 at Elk Creek), temperatures warmed earlier in the spring at Clearwater Creek than at Elk Creek (see Chapter Two), and could have influenced the number of generations/year for midge taxa in that stream. If one additional generation was added to each dominant midge taxon and to

the tipulids Erioptera sp. and Hesperoconopa sp., there would be a 20-30% increase in Diptera production. However, that liberal interpretation of numbers of generations only increased total secondary production by 10% (Table 5.8).

Because the Chironomidae were so much more dominant at Clearwater than at Elk Creek, accurate estimates of their production were especially important. Data from the 1986 tube samples provided a separate production estimate for Micropsectra spp. to compare with the 1986 Hess samples. Although mean density was ca. 50% greater in the Hess samples than in the tube samples, mean biomass was ca. 80% and production ca. 50% greater in the tube samples (Table 5.9). The higher biomass resulted from the presence of more large individuals (5-6 mm in length) in the tube samples than in the Hess samples. These data suggest that, at least for Micropsectra spp., the Hess samples underestimated secondary production. However, this may not be the case. The tube samples were collected from pool rather than riffle habitat, and thus increased survivorship and frequencies of large-sized individuals are likely in the more benign environment. Given this consideration the production values obtained from the Hess samples are likely a reasonably good estimate of Micropsectra spp. production in the riffle habitat in the summer of 1986.

Table 5.8. Comparison of annual production estimates at Clearwater Creek if the interpretation of the numbers of generations/year is varied. C = conservative
L = liberal.

| Taxonomic Group | 1985 | | Change (%) | 1986 | | Change (%) |
|------------------|------|-----|---------------|------|------|---------------|
| | C | L | | C | L | |
| Ephemeroptera | 3.1 | 3.1 | 0 | 13.6 | 13.6 | 0 |
| Plecoptera | 2.0 | 2.0 | 0 | 2.6 | 2.6 | 0 |
| Trichoptera | 0.2 | 0.2 | 0 | 0.3 | 0.3 | 0 |
| Coleoptera | 0.1 | 0.1 | 0 | 0.1 | 0.1 | 0 |
| Diptera | | | | | | |
| Chironomidae | 1.9 | 2.5 | +32 | 8.9 | 10.9 | +23 |
| Other families | 1.2 | 1.5 | +25 | 1.9 | 2.3 | +21 |
| Total Production | 8.6 | 9.5 | +10 | 27.4 | 29.8 | +9 |

Table 5.9. Secondary production of *Micropsectra* spp. at Clearwater Creek from July 5 - Sept 5, 1986 based on data from Hess and Tube samples.

| Sample Method | Mean Density (No./m ²) | Mean Biomass (g/m ²) | Production (g/m ²) | P/B Ratio |
|------------------|--|--|-----------------------------------|-----------|
| Hess | 12585 | 0.22 | 1.32 | 6.1 |
| Tubes | 8281 | 0.39 | 1.93 | 5.0 |

The accuracy of production estimates for other taxa may depend on when most of their growth and development occurs. The sampling program was designed to emphasize sampling during the period of greatest degree-day accumulation (see Chapter Four). The midges with summer generations would have most growth during warm periods, and thus the sampling effort likely resulted in fairly good estimates of production. However, some species (e.g., *Cinygmula* sp., *Rhithrogena* sp.) overwintered as mid-instar larvae and completed their growth in late spring/early summer when the sampling effort was not intense. Production may have been underestimated for these taxa. Both Elk and Clearwater Creeks were equally affected by these underestimates, so comparisons between these sites are valid. However, comparisons with other sites for these taxa need to be kept in proper perspective.

I have treated the production data as if they were collected over an entire year. Appropriate correction factors were applied to express the results as annual production rather than as cohort production. However, data were only collected for half a year at best. The effect of this discrepancy on production values depends on the life-cycle pattern of a particular species and the method employed for estimating production. For those taxa which completed most of their growth, or

began their development during unsampled months, I have simulated a mortality schedule to arrive at what should be reasonable production values. Underestimates of production will occur for those taxa in which the middle portion of their life cycles were unsampled, e.g., Cinygmula sp. If the P/B ratio was used for estimating production, then the problems are two-fold. First, the choice of a ratio was based on literature values rather than actual values, and second, because no sampling was conducted during part of the year, actual standing stock biomass values could have been either over- or underestimated.

Again, these various considerations about the reliability of production estimates generally apply to comparisons made with other stream benthic communities. Other than problems with voltinism, comparisons between Clearwater and Elk Creek should be dependable given that the problems associated with sampling affected production estimates of the same dominant taxa of both streams.

Clearwater vs. Elk Creeks - Secondary production can vary greatly from one place to another depending on various environmental conditions or on benthic community composition. Large species, such as stoneflies, have high standing-stock biomass and thus high production. But production also may be increased by the presence of

numerous short-lived species, e.g. Chironomidae, with high turnover rates.

While it is tempting to separate taxonomic and ecological factors as the causes of site differences in production, they are interrelated. The fact that Chironomidae dominated the grazers of Clearwater Creek, as compared to Elk Creek, has resulted in a grazer community that should be able to respond quickly to changes in environmental conditions and food availability. Consequently, while the production of grazers increased at both streams in 1986, the greater change at Clearwater Creek than at Elk Creek reflects, to a certain degree, differences in benthic community structure. Furthermore, between-site differences in the benthic community structure found at each site in 1985 and 1986 were a direct result of differences in the degree to which the 1980 eruption disturbed each site (see Chapters One and Three). Thus, differences in secondary production related to community composition were primarily a result of past disturbance history.

Secondary Production of Lotic Systems - Primary consumer production at Clearwater and Elk Creeks in 1985 and 1986 is compared with that of other streams in Table 5.10. The range of 1.5 g AFDW/m² to ca. 121.5 g AFDW/m² illustrates how broadly annual production can vary depending on local conditions. While specific habitat

Table 5.10. Comparison of biomass, production, and P/B ratios of primary consumers of lotic systems. Conversion to ash-free dry weight (AFDW) = 0.9 of dry weight (Waters 1977). NA = information not available. Data for Clearwater and Elk Creeks based on large substrates only and include Oligochaete biomass and production (see text).

| Location | Watershed Characteristics | Annual Production (g AFDW/m ²) | Mean Annual Biomass (g AFDW/m ²) | Annual P/B | Reference |
|---------------------------|---------------------------|--|--|------------|-------------------------------|
| Cedar Cr., NC | Deciduous forest | 1.5 | 0.15 | 10.0 | Smock and Roeding (1986) |
| Cedar Cr., NC | Deciduous forest | 2.9 | 0.34 | 8.5 | Smock and Roeding (1986) |
| Factory Brook, MA - 1975 | Mixed hardwood forest | 3.4 | 0.44 | 7.7 | Neves (1979) |
| Factory Brook, MA - 1974 | Mixed hardwood forest | 3.8 | 0.47 | 8.1 | Neves (1979) |
| Caribou R., MN | Deciduous forest | 4.1 | 1.00 | 4.1 | Krueger and Waters (1983) |
| Blackhoof R., MN | Deciduous forest | 5.6 | 1.30 | 4.3 | Krueger and Waters (1983) |
| Hinau Cr., New Zealand | Canopied | 6.8 | 0.86 | 7.9 | Hopkins (1976) |
| Upper Ball Cr., NC | Mixed hardwood forest | 7.2 | 2.70 | 2.7 | Huryn and Wallace (1987) |
| Clearwater Cr., WA - 1985 | Open, mountain | 7.7 | 0.59 | 13.1 | This study |
| Elk Cr., WA - 1985 | Conifer, partly open | 8.2 | 0.78 | 10.5 | This study |
| Rold Kilde, Denmark | Old Beech forest | 8.7 | 3.20 | 2.7 | Iversen (1988) |
| Elk Cr., WA - 1986 | Conifer, partly open | 12.4 | 1.24 | 10.0 | This study |
| Horokiwi Cr., New Zealand | Wooded area | 17.2 | 2.89 | 6.0 | Hopkins (1976) |
| N. Branch Cr., MN | Agriculture, partly open | 18.0 | 3.60 | 5.0 | Krueger and Waters (1983) |
| Bisballe Baek, Denmark | Generally open | 21.4 | 5.69 | 3.8 | Mortensen and Simonsen (1983) |
| Clearwater Cr., WA - 1986 | Open, mountain | 22.4 | 1.79 | 12.5 | This study |
| Hinau Cr., New Zealand | Pasture, some trees | 27.8 | 3.72 | 7.5 | Hopkins (1976) |
| Horokiwi Cr., New Zealand | Open pasture | 30.0 | 4.71 | 6.4 | Hopkins (1976) |
| Horokiwi Cr., New Zealand | Open pasture | 40.0 | 7.57 | 5.3 | Hopkins (1976) |
| Middle Oconee R., GA | 5th-6th order, open | 50.4 | NA | NA | Nelson and Scott (1962) |
| Hinau Cr., New Zealand | Organic enrichment, open | *64.9 | 8.87 | 7.3 | Hopkins (1976) |
| Sycamore Cr., AZ | Open, arid | **121.5 | 2.68 | 45.3 | Fisher and Gray (1983) |

* - Oligochaetes comprised ca. 60% of this production.

** - Collectors only, but this group = > 90% of primary consumer biomass (Fisher et al. 1982).

comparisons are not possible among sites, it is apparent that production generally increased with reduced canopy. Converted to ash-free dry weight (AFDW = 0.9 of dry weight, (Waters 1977)), production of primary consumers was 7.1 and 21.5 g/m² at Clearwater Creek in 1985 and 1986, respectively. The comparable figures for Elk Creek were 7.2 and 11.9 g/m².

The values for Clearwater and Elk Creeks generally fall in the middle of the chart but the comparison is not exact since the other studies include non-insects in their production calculations. Oligochaeta and Amphipoda contributed most of this production. Amphipoda were not part of the fauna of either Clearwater or Elk Creeks. Oligochaete biomass at Clearwater Creek was 0.13 g/m² in 1985 and 0.20 g/m² in 1986. At Elk Creek it was 0.22 g/m² and 0.09 g/m² for the two years. Conversion of these values to production (P/B ratio = 5) results in values of 0.6 and 0.9 g AFDW at Clearwater Creek and 0.4 and 1.0 g AFDW at Elk Creek in 1985 and 1986, respectively. Even if these corrections are made to the data the positions of Elk and Clearwater Creeks remain in about the middle of the table (Table 5.10).

The values for Elk Creek were similar to other forested streams. Production at Clearwater Creek in 1985 was low compared to the other open streams. But

the increased production of primary consumers at Clearwater Creek in 1986 led to a value comparable to other open streams (e.g., Hopkins 1976, Mortenesen and Simonsen 1983), although certainly well below the highest values reported in the literature. For example, Hynes and Coleman (1968) reported benthic annual production of 180 g AFDW/m² in the Speed River, Ontario and Sycamore Creek, AZ, has values > 100 g AFDW/m² (Table 5.10). These sites had elevated invertebrate production levels due to high standing stock biomass in the former and warm temperatures coupled with a community dominated by multivoltine species in the latter. Invertebrate production may also be increased because of nutrient enrichment. For example, the 65 g AFDW/m² value reported by Hopkins (1976) was from a reach of stream that had been organically enriched. More than 60% of that production was by silt-feeding oligochaetes.

Secondary Production of Grazers in Lotic Systems -

For comparative purposes, what is of interest to this study is not grazer production *per se*, but the proportion of total insect production contributed by grazing insects. Table 5.11 shows that compared to other sites (excluding Sycamore Cr., which has elevated grazer production due to high turnover rates for insects and algae) grazers contributed relatively high amounts

Table 5.11. Comparison of annual production of grazer insects among sites and as a proportion of total insect production. Conversion to AFDW = 0.9 of dry weight (Waters 1977).

| Location | Grazer Production (g AFDW/m ²) | Proportion of Total Production | Reference |
|----------------------------------|--|--------------------------------------|---------------------------|
| Cedar Cr., NC | 0.9 | 38 | Smock and Roeding (1985) |
| Rold Kilde, Denmark | 1.3 | 16 | Iversen (1988) |
| Blackhoof R., MN | 1.4 | 22 | Krueger and Waters (1983) |
| Caribou R., MN | 1.4 | 44 | Krueger and Waters (1983) |
| Cedar Cr., NC | 1.5 | 41 | Smock and Roeding (1985) |
| Factory Brook, MA - 1975 | 2.6 | 67 | Neves (1979) |
| Factory Brook, MA - 1974 | 3.0 | 69 | Neves (1979) |
| <i>Elk Cr., WA - 1985</i> | <i>6.4</i> | <i>73</i> | <i>This study</i> |
| <i>Clearwater Cr., WA - 1985</i> | <i>6.5</i> | <i>84</i> | <i>This study</i> |
| N. Branch Cr., MN | 9.4 | 56 | Krueger and Waters (1983) |
| <i>Elk Cr., WA - 1986</i> | <i>10.8</i> | <i>74</i> | <i>This study</i> |
| <i>Clearwater Cr., WA - 1986</i> | <i>18.4</i> | <i>75</i> | <i>This study</i> |
| Sycamore Cr., AZ | > 120.0 | 90+ | Fisher and Gray (1983) |

of the total production at Clearwater and Elk Creeks. The only site with similar proportions was Factory Brook, MA (Neves 1979). At all other sites, grazers contributed ca. 20% less to insect production than they did at Clearwater and Elk Creeks, and of these sites the highest value (56%) was obtained in N. Branch Cr. (Krueger and Waters 1983). This stream flows through an agricultural area and receives nutrient inputs - factors which could lead to elevated algal biomass and therefore production of grazers. All other low values occurred in shaded low-order streams.

Annual Variation in Production Estimates - How much insect production varies from year-to-year at a given location is essentially unknown. Due to the intensive sampling required for estimating production, most studies are restricted to one year. Although between-year differences were greater at Clearwater Creek, production at Elk Creek in 1986 also increased substantially over 1985. Neves (1979) estimated production for two consecutive years and found very little difference (4.8 vs 4.3 g dry wt/m²). Illies (1975) monitored adult emergence from a small stream in Germany from 1969-1973. The biomass of emerged adults, which can be an index of benthic production (Speir and Anderson 1974), was similar for four of five years (2.7 - 3.3 g/m²). However, in one year biomass increased to

6.3 g/m². These results show that substantial between-year variation in production is possible. Fluctuations also occurred in the relative proportions of taxonomic groups contributing to this production. Illies (1975) suggested that much of the year-to-year variation was related to environmental conditions, especially water levels.

Summary - Differences in the effects of the Mt. St. Helens eruption on the Clearwater and Elk Creek watersheds influenced benthic community composition and thus the major contributors to secondary production. However, because production increased substantially at both Clearwater and Elk Creeks in 1986, the cause of this year-to-year variation was likely due to environmental conditions rather than to some factor related to the eruption. In Chapter Two I showed that stream discharge declined earlier in 1986 than in 1985, and in Chapter Four I showed that insect density and biomass increased dramatically in 1986. Benign conditions early in the season likely led to the early establishment of the aufwuchs and to increased food availability for grazing insects. The result was a 3.5-fold and 1.9-fold increase in standing stock biomass of grazers in 1986 at Clearwater and Elk Creeks, respectively. Production increased by about the same proportions in 1986 (Clearwater Creek = 3.2-fold; Elk

Creek = 1.7-fold). Because both streams experienced increased insect production in 1986, it is a reasonable assumption that both communities were responding to the same environmental conditions. However, the large difference in the response of each stream (ca. a factor of 2) suggests that there are differences in the capacity of each stream's benthic community to respond to these ideal conditions.

Between-site differences likely were caused by a variety of factors including effective habitat and food availability. Because Elk Creek drains a smaller watershed than does Clearwater Creek, discharge was generally one-third that of Clearwater Creek. By August many large cobbles or small boulders were exposed at Elk Creek reducing the area for insect colonization (personal observation). So although conditions were good for aufwuchs development at both streams, habitat conditions may have prevented development of the aufwuchs at Elk Creek to the same degree as occurred at Clearwater Creek. On the other hand, Clearwater Creek with its predominance of multivoltine midge taxa would have the capacity to respond to ideal conditions with larger than normal populations and possibly additional generations.

Part of the ability of insect populations to respond to changes in environmental conditions depends

on the insect's diet. Taxonomic comparisons showed that some taxa increased their production in 1986 to a much greater degree at Clearwater than at Elk Creek. For example, between 1985 and 1986 the production of *Cinygmula* sp. increased almost 10-fold at Clearwater Creek, but only 2.5-fold at Elk Creek. Diet can be important to the growth and development of insects. How diet was important to the production of the dominant grazers of each stream and how this may have affected total insect production will be the focus of the next chapter.

Chapter 6

THE INFLUENCE OF DIET ON THE SECONDARY PRODUCTION OF GRAZING INSECTS

Introduction

Grazer production was similar between sites in 1985. Production increased at both sites in 1986, but to a much greater degree at Clearwater Creek than at Elk Creek. Studies have shown that algae is a much higher quality food source than is detritus (e.g., see Lamberti and Moore 1984), and differences in the relative proportions of algae and detritus consumed in the diet can affect the growth, development, and thus production of insects. This chapter will focus on the diets of the dominant grazers and how their feeding ecology may have influenced their production at each site.

Methods

The diet of the important grazers was determined by examination of gut contents. Insects were collected from kick samples from June to October, 1986 and killed in 95% ethyl alcohol rather than Kahle's fluid; the latter often causes insects to regurgitate (Coffman et al. 1971). Formalin (15%) was added soon after killing to preserve food particles in the gut. The alcohol/formalin solution was rinsed from the sample in

the laboratory, and the insects were stored in 95% alcohol. Only those insects which were part of the dominant aufwuchs grazing insects were sorted from the samples. Because body size can influence food consumption, insects were grouped into small, medium, and large size classes; the actual range of body lengths for each group depended on the taxon in question.

Except for Chironomidae, the gut contents were analyzed according to the methods of Coffman et al. (1971). Guts of large insects (10-12 mm body length) were analyzed individually, but for small individuals (ca. 2 mm) up to eight specimens were pooled to obtain enough material. The foregut was removed to distilled water under a dissecting microscope. The contents were separated from the body wall, stirred to disperse the food contents, and filtered at low vacuum in a 15 ml Millipore funnel fitted with a 0.45 μ m gridded filter paper. The filter was then placed on a microscope slide and cleared with immersion oil in a covered chamber for about 24 hours. A few drops of immersion oil were placed on the filter and a coverslip applied before viewing the gut contents with a compound microscope.

Food particles were divided into four classes: animal, detritus, diatoms, and filamentous algae. No attempt was made to determine whether the detritus was derived from algae or leaf litter as this could not be

done consistently. The entire slide was scanned at 10x power for animal parts. Most prey items could be identified to the family or order level. Size and weight of prey were estimated from head-capsule width (measured at 40x power) and the head width/weight relationships of Smock (1980). Random grids were selected for analysis at 40x power for all other food types. Diatoms were counted and the area of detritus and filamentous algae was estimated with an ocular micrometer. These numerical estimates of diatoms and detritus were converted to biomass according to methods published by Coffman et al. (1971).

The gut contents of Chironomidae were analyzed from the same slide mounts that were used for taxonomic identification. Because of their small size, foreguts could not be dissected and food material dispersed for scoring of individual food particles. Instead, feeding habits were compared on the basis of the percent areal coverage of animal, diatoms, detritus, and filamentous algae in the gut. All estimates were made with an ocular micrometer at 40x power.

For statistical analyses, the percentages of each food type were transformed with $\arcsin(\sqrt{p})$, where p = the mean proportion of the food type found in the foregut. Comparisons were made between taxa that were common to the dominant grazers of both sites, and the

mean values for taxonomic groups, e.g. mayflies or Chironomidae.

Not all foods are converted to biomass with the same efficiency (Benke and Wallace 1980). Food particle biomass can be converted into secondary production by using food-specific assimilation efficiency ($\text{assimilation/ingestion} = \text{AE}$) and net production efficiency ($\text{production/assimilation} = \text{NPE}$) values. Estimates of NPE generally fall around 50% for freshwater invertebrates (Edington and Hildrew 1973, Otto 1974, McCullough 1975). Assimilation efficiency varies with food type. Appropriate conversion values were taken from the literature: Animal material, 70% (Lawton 1970, Brown 1974, Heiman and Knight 1976, Benke and Wallace 1980); algae, 30% (Cummins 1975, McCullough 1975, McCullough et al. 1979); detritus, 10% although literature values ranged from 10-25% (McDiffett 1970, Ladle et al. 1972, Anderson and Grafius 1975, McCullough 1975, Winterbourn and Davis 1976, McCullough et al. 1979).

Multiplying the gross production efficiency ($\text{AE} \times \text{NPE} = \text{production/ingestion}$) of each food type by the percent found in the gut yields the relative contribution of each food type towards production. And finally, multiplying these results by the annual production for each taxon quantifies the relative

importance of each food type towards that species annual production. Table 6.1 illustrates an example of this process.

Results

Insect guts initially were analyzed on the basis of body size. However, statistical analysis showed no significant correlations ($p < 0.05$) between body size and relative proportions of any food type. There was a trend towards less detritus and either increased animal material (e.g. *Drunella coloradensis*) or more diatoms (e.g. *Baetis* spp.) with increased body size, but the trends were not significant, at least for these sample sizes. Therefore, the data for all size classes are pooled in this analysis.

Diatoms were more common in the diet of the mayfly and midge grazers of Clearwater (84 and 59%, respectively) than at Elk Creek (58 and 24%, respectively) (Fig. 6.1). These differences were significant ($p < 0.001$) for both groups. Almost exactly opposite percentages were found for detritus as detritus and diatoms comprised most of the biomass of food found in the foregut.

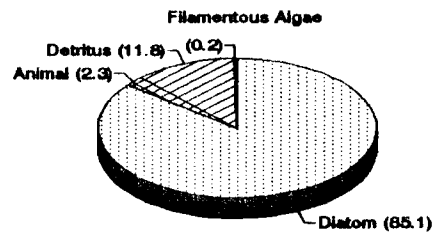
Between-site comparisons of those taxa which were at both sites showed shifts in proportions of food types in the gut. *Baetis* spp. and *Micropsectra* spp. had the

Table 6.1 Production attributed to food types consumed by *Serratella tibialis*. Secondary production in 1986 at Clearwater Creek was 0.63 g/m^2 . AE = assimilation efficiency (assimilation/ingestion); NPE = net production efficiency (production/assimilation). Figures for AE and NPE obtained from the literature (see text).

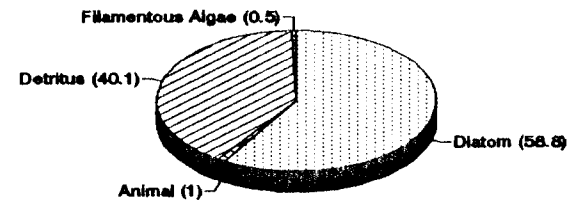
| Food Type | Percent in Foregut (1) | AE (2) | NPE (3) | Relative Production (1) x (2) x (3) | Percent of Production | Production attributed to food type (g/m^2) |
|--------------|------------------------|--------|---------|-------------------------------------|-----------------------|---|
| Diatom | 73.0 | 0.3 | 0.5 | 10.95 | 74.2 | 0.47 |
| Detritus | 18.8 | 0.1 | 0.5 | 0.94 | 6.4 | 0.04 |
| Animal | 8.2 | 0.7 | 0.5 | 2.87 | 19.4 | 0.12 |
| Filam. Algae | 0.0 | 0.3 | 0.5 | 0.00 | 0.0 | 0.00 |
| Totals = | | | | 14.76 | 100.0 | 0.63 |

Figure 6.1. Mean proportions of the foregut contents of important mayfly and chironomid grazers examined at Clearwater and Elk Creeks in 1986.

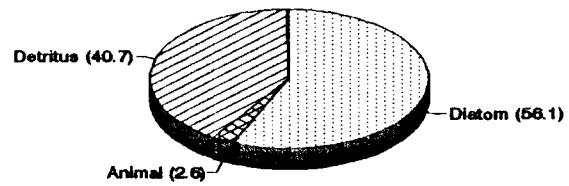
Clearwater Creek - Mayflies



Clearwater Creek - Chironomidae



Elk Creek - Mayflies



Elk Creek - Chironomidae

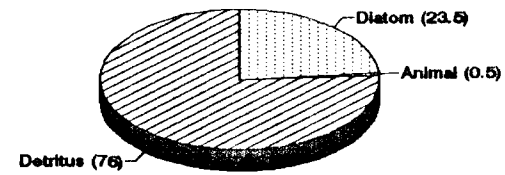


Figure 6.1

greatest differences ($p < 0.001$) with diatoms more prevalent in guts at Clearwater Creek than at Elk Creek (Table 6.2). Small, but significant ($p < 0.05$), between-site differences were found for the other important mayfly grazers, i.e. Ameletus spp., Cinygmula sp., and D. coloradensis.

Animal parts were found only occasionally in the guts of grazer taxa (Fig. 6.1). D. coloradensis and Pagastia sp. had the greatest percentages of animal parts (15.5 and 12%, respectively) at Clearwater Creek. D. coloradensis and Epeorus sp. A consumed the most animal material (13.1 and 7.8%, respectively) at Elk Creek.

No filamentous algae was found in the guts of any grazers at Elk Creek. Several important grazers consumed this algae at Clearwater Creek, e.g. Baetis spp., but it was never more than ca. 2% of the diet.

Based on gut contents alone, diatoms were more important to the diet of the grazers at Clearwater than those at Elk Creek (Table 6.3). However, because of the higher assimilation efficiency for algae than for detritus, diatoms were almost as important to the production of grazers at Elk (74.3%) as they were at Clearwater Creek (84.3%). This was true because mayflies made up a much greater proportion of the grazer production at Elk than they did at Clearwater Creek.

Table 6.2 Foregut contents (Mean percent \pm 1 S.E.) of dominant grazer taxa of Clearwater and Elk Creeks in 1986. Significant between-site differences indicated by asterisks. Data transformed [$\arcsin(\sqrt{p})$] before analysis (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

| TAXON | n | DIATOM | DETRITUS | ANIMAL | FILAMENTOUS ALGAE |
|--|----|--------------------|--------------------|-----------------|-------------------|
| CLEARWATER CREEK - 1986 | | | | | |
| <i>Bactis</i> spp. | 13 | 94.4 \pm 6.4*** | 5.5 \pm 6.3*** | 0.0 | 0.1 \pm 0.9 |
| <i>Ameletus</i> spp. | 6 | 79.7 \pm 16.4* | 20.3 \pm 16.4* | 0.0 | 0.0 |
| <i>Cinygmula</i> sp. | 4 | 90.3 \pm 14.8* | 8.0 \pm 13.6* | 0.0 | 1.8 \pm 6.6 |
| <i>Drunella coloradensis</i> | 3 | 80.1 \pm 23.1* | 4.5 \pm 12.0** | 15.5 \pm 20.9 | 0.0 |
| <i>Ephemerella</i> sp. | 3 | 78.4 \pm 14.5 | 20.6 \pm 14.3 | 0.0 | 0.0 |
| <i>Serratella tibialis</i> | 6 | 73.0 \pm 18.1 | 18.8 \pm 16.0 | 8.2 \pm 11.2 | 0.0 |
| <i>Taenionema</i> sp. | 10 | 92.1 \pm 8.5 | 7.9 \pm 8.5 | 0.0 | 0.0 |
| <i>Erioptera</i> sp. | 5 | 33.5 \pm 21.1 | 66.5 \pm 21.1 | 0.0 | 0.0 |
| <i>Pagastia</i> sp. | 7 | 65.7 \pm 17.9 | 22.9 \pm 15.9 | 12.0 \pm 11.4 | 0.0 |
| <i>Orthocladus</i> - <i>Cricotopus</i> A | 49 | 74.4 \pm 6.2 | 23.5 \pm 6.1 | 0.9 \pm 1.4 | 1.4 \pm 1.7 |
| <i>Orthocladus</i> (<i>Euorthocladus</i>) B | 11 | 92.7 \pm 7.8 | 7.3 \pm 7.8 | 0.0 | 0.0 |
| <i>Parametriocnemus</i> sp. | 27 | 28.3 \pm 8.7 | 70.7 \pm 8.8 | 0.6 \pm 1.4 | 0.2 \pm 0.8 |
| <i>Micropectra</i> spp. | 50 | 50.6 \pm 7.1*** | 49.4 \pm 7.1*** | 0.0 | 0.0 |
| ELK CREEK - 1986 | | | | | |
| <i>Bactis</i> spp. | 7 | 70.6 \pm 17.2*** | 29.4 \pm 17.2*** | 0.0 | 0.0 |
| <i>Ameletus</i> spp. | 5 | 55.1 \pm 22.2* | 44.2 \pm 22.2* | 0.7 \pm 3.6 | 0.0 |
| <i>Cinygmula</i> sp. | 3 | 66.3 \pm 27.3* | 33.7 \pm 27.3* | 0.0 | 0.0 |
| <i>Epeorus</i> sp. A | 4 | 36.2 \pm 27.7 | 56.0 \pm 28.7 | 7.8 \pm 15.5 | 0.0 |
| <i>Rhithrogena</i> sp. | 4 | 61.2 \pm 24.4 | 36.4 \pm 24.1 | 2.4 \pm 7.7 | 0.0 |
| <i>Drunella coloradensis</i> | 3 | 33.1 \pm 27.2* | 53.8 \pm 28.8** | 13.1 \pm 19.5 | 0.0 |
| <i>Taenionema</i> sp. | 10 | 88.5 \pm 10.1 | 11.5 \pm 10.1 | 0.0 | 0.0 |
| <i>Hesperoconopa</i> sp. | 7 | 22.5 \pm 15.8 | 77.5 \pm 15.8 | 0.0 | 0.0 |
| <i>Diamesa</i> sp. | 8 | 22.5 \pm 14.8 | 77.5 \pm 14.8 | 0.0 | 0.0 |
| <i>Micropectra</i> spp. | 20 | 23.5 \pm 9.5*** | 75.5 \pm 9.6*** | 1.0 \pm 2.2 | 0.0 |
| <i>Stem Pellinella</i> sp. | 12 | 24.2 \pm 12.4 | 75.8 \pm 12.4 | 0.0 | 0.0 |

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Even though the Diptera of Clearwater Creek had greater proportions of diatoms in their guts than those of Elk Creek, enough of their production came from detritus to dampen the contribution by algae to the overall production of the dominant grazers in that stream.

Discussion

Feeding Habits of Mayfly Grazers - Environmental and habitat conditions play an important role in determining food availability in streams. Consequently, opportunism is often seen in the feeding habits of aquatic insects, e.g. mayflies (Brown 1961, Moore 1977, Clifford 1979). Because the aufwuchs film consists of both algae and detritus (generally algal-derived) the food obtained by scraping or gathering will likely depend on local conditions and thus availability of either food type. It should not be surprising then to find considerable variation in the stomach contents of mayflies sampled from different localities under varying conditions. Table 6.4 compares the proportion of diatoms found in mayflies of Clearwater and Elk Creeks with those at other sites in the Pacific Northwest. The mayflies of Clearwater Creek consumed much greater quantities of diatoms (and thus less detritus) than did other populations. Most mayflies at Elk Creek also consumed more diatoms than those at other locations,

Table 6.4. The importance of diatoms to the diet of mayflies at Clearwater and Elk Creeks as compared to the same mayflies at other sites. CC = Clearwater Creek; EK = Elk Creek; (1) = St. Maries River, N. Idaho (Gilpin and Brusven, 1970); (2) and (3) = Oregon Coast Range (Chapman and Demory, 1963); (4) = Oregon Cascades streams (Hawkins, 1985).

| TAXON | CC | EK | (1) | (2) | (3) | (4) |
|------------------------------|----|----|------|-----|-----|-----|
| <i>Baetis spp.</i> | 94 | 71 | 34 | 70 | 55 | -- |
| <i>Ameletus spp.</i> | 80 | 55 | 32 | -- | -- | -- |
| <i>Drunella coloradensis</i> | 80 | 33 | 28 | -- | -- | 53 |
| <i>D. doddsi</i> | -- | 44 | 30 | -- | -- | 57 |
| <i>D. spinifera</i> | 60 | -- | 5 | -- | -- | 21 |
| <i>Ephemerella sp.</i> | 78 | -- | 25 | 60 | -- | 18 |
| <i>Serratella tibialis</i> | 73 | -- | 29 | -- | -- | 32 |
| <i>Cinygmula sp.</i> | 90 | 66 | 33 | 40 | 35 | -- |
| <i>Epeorus sp. A</i> | -- | 36 | 28* | 60* | 25* | -- |
| <i>E. longimanus</i> | 97 | 30 | 31 | -- | -- | -- |
| <i>Rhythrogena sp.</i> | 77 | 61 | 30 | -- | -- | -- |
| <i>Paraleptophlebia sp.</i> | 44 | 31 | 26** | 5 | 5 | -- |

(1) * - value based on mean of three *Epeorus* species.

** - value based on mean of five *Paraleptophlebia* species

(2) * - no species for *Epeorus* specified.

(3) * - no species for *Epeorus* specified.

(4) Values varied considerable among sites:

D. coloradensis (32-86%); *D. spinifera* (0-35%); *D. doddsi* (0-96%)

although the differences were not as great as between Clearwater Creek and those other sites.

An example of mayfly opportunism is their exploitation of habitat changes following disturbance. Gurtz and Wallace (1984) found increased abundances of *Baetis* spp. and *Ephemerella* spp. after logging. Comparing *Baetis* spp. populations of an undisturbed watershed with those of a logged area they found that *Baetis* spp. in the clearcut consumed 1.2-2.0 times more diatoms than those in the undisturbed site. Moreover, they also had 17.6 times the production as those of the undisturbed watershed (Wallace and Gurtz 1986).

The availability of diatoms at Clearwater Creek was likely enhanced by the mats of filamentous algae that were considerably more abundant at Clearwater than at Elk Creek. Epiphytic diatoms grow abundantly on filaments of *Cladophora* sp. (Moore 1975, Towns 1981, Iversen et al. 1985). Dudley et al. (1986) recently reported an association between *Baetis* spp. densities and the presence of macroalgae. It was assumed that the large surface area of algal filaments provided more substrate for epiphytic diatoms and thus abundant food for grazing insects.

Diatoms are a higher quality food resource than is detritus. Insects reared on diets enriched with algae have increased growth rates (Fuller and Mackay 1981).

This can lead to shorter life cycles and thus an increased number of generations and production (Wallace and Gurtz 1986). Fuller et al. (1986) recently showed that *B. tricaudatus*, a multivoltine mayfly, responded positively to increased levels of algal production. Those individuals that colonized a patch with greater algal production than one with less production consumed increased amounts of algae and grew to larger sizes.

The response to changes in food availability and quality may be expressed in other ways for univoltine mayflies, including increased survivorship, fecundity, and production. Hawkins (1982) found that laboratory populations of *Ephemerella infrequens* raised on algae had much higher growth rates than did field populations that fed on a variety of food types. He suggested that food limitation reduces populations because densities are lowest in detritus-based streams, and greatest in those with more algae. *E. infrequens* was one of several mayfly taxa at Clearwater Creek that had a large increase in density in 1986 over 1985 (see Appendix C). In contrast, it declined at Elk Creek in 1986. Increased availability of algae in 1986 could have increased survivorship and production of this species at Clearwater Creek in 1986.

Feeding Habits of Chironomid Grazers - Taxon-specific information on the feeding ecology of

Chironomidae is not as readily available as it is for mayflies. Orthoclaadiinae are generally considered either algal (primarily diatoms) or algal-detrital feeders, while Diamesinae primarily consume diatoms (Oliver 1971). Smock and Roeding (1986) found a predominance of fine detritus in the guts of Orthoclaadiinae and Tanytarsini midges. Coffman (1967) reported that the orthoclad midges Eukiefferiella spp. were generally algal feeders, while Walshe (1951) found Micropsectra spp. primarily to consume detritus. Gray and Ward (1979) found similar proportions of diatoms and detritus in the guts of Diamesa sp., and primarily diatoms and detritus in the guts of Eukiefferiella sp. and Orthocladus sp, respectively. These varied results suggest that, as with the mayflies, the diet of Chironomidae depends to a great extent on the availability of food types. This interpretation is supported by the midge gut contents analyzed for this study. While detritus was more common in the guts of midges than of mayflies for both Clearwater and Elk Creeks, the dominant midge grazers of Clearwater Creek had more diatoms in their guts than did the those of Elk Creek.

Micropsectra spp. were the only dominant midge grazers common to both Clearwater and Elk Creeks whose diets could be compared. The difference in food

composition between populations was highly significant with over twice the amount of diatoms in the guts of Microsectra spp. at Clearwater than those at Elk Creek. This taxon had at least two and possibly three summer generations at Clearwater Creek, but only one at Elk Creek (see Chapter Five). Temperature and food quality may have caused this difference. Although the cumulative degree days were similar between sites, water temperature warmed earlier in the spring at Clearwater Creek than it did at Elk Creek (see Chapter Two). This difference alone could have allowed Microsectra spp. to complete at least one additional summer generation at Clearwater Creek. However, increased food quality of the diet of Microsectra spp. at Clearwater could also have enhanced growth rates enough that additional generation(s) could be completed in the summer. Mackey (1977) showed that the growth rates of midges were enhanced when raised on food with higher quality. Ward and Cummins (1978) found that although under ideal conditions Paratendipes albimanus was capable of completing more than one generation per year, a low quality detritus diet normally prevented this from occurring.

Importance of Algae to Grazer Production - Although algae contributed less to grazer production at Elk Creek than at Clearwater Creek, algae was still of primary

importance to the production of grazers in that stream. Furthermore, because grazers comprised > 70% of benthic insect production in both streams in 1985 and 1986 it can be concluded that autochthonous food resources were more important than allochthonous inputs at both streams. Given the lack of riparian vegetation at Clearwater Creek this result was anticipated. However at Elk Creek this outcome contrasts with what would be expected in a low-order mountain stream (Vannote et al. 1980).

Differences in algal biomass were not measured between sites. However, results from studies on first and second-order streams in the same area showed that canopied streams had about 50% of the algal standing crop of that of open streams (1 and 2 g/m², respectively) in 1986 (G.A. Lamberti, personal communication). The site at Elk Creek was partially open, and, although it is possible that algal standing crop was greater than the 1 g/m² value found for other forested streams, it was likely less than what was found for completely open streams. The fact that grazers at Elk Creek consumed more detritus in their diet than those at Clearwater Creek suggests that algal biomass was less than was found at Clearwater Creek. Detritus was also likely to be more available at Elk than Clearwater Creek due to greater allochthonous inputs

from riparian vegetation and greater channel roughness which leads to better retention of detritus (see Minshall 1984, for review). Whether or not food was limiting to grazers at Elk Creek is unknown. But results that show greater grazer production at Elk Creek than at Clearwater Creek in 1985 and a substantial increase in grazer production at Elk in 1986 suggests that food may not have been a limiting factor to secondary production at that site.

The results presented in this chapter showed that while diatoms were the primary food source for the dominant grazers at both sites, they were significantly more important to most grazers at Clearwater Creek. Diet was supplemented with detritus at Elk Creek. These contrasts in diet could have been a factor in between-site differences in grazer production. However, other site characteristics including past disturbance history and habitat may have also had important roles in determining production at each site. These factors will be considered in the final chapter.

Chapter 7

BENTHIC COMMUNITY RECOVERY AND SECONDARY PRODUCTION

Introduction - This study was intended to provide information about the interrelationship between habitat and the production of aufwuchs grazers. Based on the appearance of Clearwater and Elk Creeks, it was assumed that their benthic communities would differ significantly, especially in the proportion of grazers. However, grazers proved to be almost equally important at both sites. The reasons for this contradiction are likely to be complex, and without further experimental data, can only be speculative.

The purpose of this final chapter is: 1) to look at the patterns of recovery at each stream in the context of their disturbance history; 2) to analyze how this recovery pattern may have influenced secondary production in 1985 and 1986; 3) to discuss how differences in habitat may have enhanced or limited secondary production at each site.

Disturbance and Succession - As disturbance has been increasingly recognized as an important organizing force in community structure, its definition has changed from one which assumes communities exist under near-equilibrium conditions to one which recognizes that equilibrium conditions are likely the exception rather

than the rule (see Sousa 1984, Pickett and White 1985, for reviews). Pickett and White (1985) defined disturbance as any relatively discrete event in time that disrupts ecosystem, community, or population structure, and that changes resources, availability of substratum, or the physical environment. Resh et al. (1988) modified this definition to include only unpredictable events, i.e., they occur so infrequently that organisms are unable to adapt to their occurrence. How unpredictable an event is will be highly subjective and depends on a region's climate, geography, and geomorphology. For example, in regions where elevated stream flows are common from winter rains and spring snowmelt, increased discharge may not be considered a disturbance because the benthos has evolved and adapted to this type of event (Minshall et al. 1985). Similarly, in desert streams the benthic community has the capacity to quickly recover from catastrophic flash floods because it is dominated by short-lived, rapidly colonizing insects (Fisher et al. 1982).

Gore and Milner (1990) categorized different levels of disturbance on the basis of areal extent and severity. A major disturbance event would result in primary succession, whereas a lesser one could lead to secondary succession. Succession is simply defined as changes in the community that occur after a discrete,

often unpredictable, disturbance at that site (Fisher 1990). Patterns of primary succession should be fairly predictable with changes in the benthic community dependent on habitat stabilization (including aspects of sedimentation and riparian zone development) and food availability (Odum 1969, Fisher 1983, 1990). Secondary succession can lead to changes in the organization of the benthic community which are caused by the removal of a dominant taxon (i.e., keystone species) or shifts in abundances of dominant taxa.

Fisher (1990) suggested that the complete disturbance of 1000-10,000 m of stream length is necessary before primary succession can be observed in streams. The almost complete destruction in the Clearwater Creek watershed certainly fits this criterion for primary succession to occur. The time required for recovery to occur will vary regionally and may depend on the magnitude of the disturbance. Because the mature community of low-order Cascades Mountain watersheds is conifer forest, at least 80-100 years will be required for the stream habitat to return to pre-disturbance conditions.

The disturbance at Elk Creek differed from that of Clearwater Creek in both areal extent and severity. When the streams were first sampled four months after the eruption, the benthos of Clearwater Creek obviously

had been devastated, while that of Elk Creek appeared to have suffered minimal damage (see Chapter Three). Thus, it seemed that the eruption did not immediately disturb the benthic community of Elk Creek. However, at some point between fall 1980 and summer 1982 the insect community experienced a disturbance event (see Figs. 3.3-3.4, note shift in proportions of the different orders).

No quantitative benthic data were available for late summer at Elk Creek in 1981, but collections from January and May 1981 showed that the richness and density of E-P-T taxa had declined markedly (September 1980 - 34 taxa, 1850/m²; January 1981 - 18 taxa, 460/m²; May 1981 - 20 taxa, 900/m²). The most likely explanation for this population decline is the detrimental effect of large amounts of ash washed into the channel by rain and snow meltwater during the winter of 1980-81. Prior to this period substantial amounts of ash were present in the watershed (N.H. Anderson, personal communication). Given the change in the benthic community structure of Elk Creek between the 1980 and 1982 sample dates, it is likely that the disturbance event was not a "normal" occurrence, and could have led to secondary succession.

In summary, both study sites experienced a disturbance prior to the 1985-86 interval of this

production study but the type of disturbance differed. At Clearwater Creek it was catastrophic, destroying the benthic fauna and riparian vegetation in much of the watershed, and initiating primary succession. Elk Creek experienced a disturbance of less severity; the watershed was left intact. However, after the winter of 1980-81, the density, biomass, and species richness of the benthic community were reduced. As a result, secondary succession was initiated.

Recovery Patterns at Clearwater Creek - The occurrence of primary succession in stream communities is an uncommon event because the removal of all organisms rarely occurs even under the most severe conditions. Aquatic invertebrates have a high degree of resilience to most kinds of disturbance (Fisher et al. 1982, Resh et al. 1988, Reice et al. 1990), and documented examples of primary succession in streams are not common in the literature. Fisher et al. (1982) studied succession in the desert stream, Sycamore Creek, following flash flooding. Recovery times were short (ca. two months) for most parameters, e.g. biomass and diversity. Studies of succession in streams that occurred over a much longer time period include Minshall et al. (1983), who followed the recolonization of the Teton River after dam failure completely scoured the downstream channel of all aquatic invertebrates, and

Milner (1987), who monitored the colonization of new stream channels following the retreat of glaciers in Alaska.

Data from Fisher et al. (1982), Minshall et al. (1983), and Clearwater Creek can be used to compare how differences in the magnitude of the disturbance can affect recovery time. At Sycamore Creek invertebrate density, richness, diversity, and trophic structure returned to pre-disturbance levels in less than three months. However, at the Teton River and Clearwater Creek these same parameters required considerably longer to recover (Table 7.1). The recovery time for richness and diversity was five to six years at Clearwater Creek (see Figs. 3.5-3.7), while invertebrate numbers and biomass continued to fluctuate. The trophic structure of the Teton River needed approximately four years to return to its pre-disturbance state. In contrast, as of 1989 the trophic structure of the insect community (predators vs primary consumers) of Clearwater Creek was still changing (Fig. 7.1).

The dissimilarity in recovery times among these studies probably has to do with differences in the amount of area disturbed. Insects can escape disturbance in space or time. For example, many taxa may survive flood events as eggs or as early-instar larvae in the hyporheic zone and in tributaries. Adults

Table 7.1 Estimates of the time (days) required for certain community parameters to recover from catastrophic disturbance. Values for Teton River from Minshall et al. (1983).

| Parameter | Teton River | Clearwater Creek |
|--------------------|-------------|------------------|
| Density | ~ 375 | > 3500 |
| Richness | ~ 440 | ~ 2100 |
| Diversity (H') | ~ 440 | ~ 1800 |
| Trophic Structure | > 1295 | Unknown |

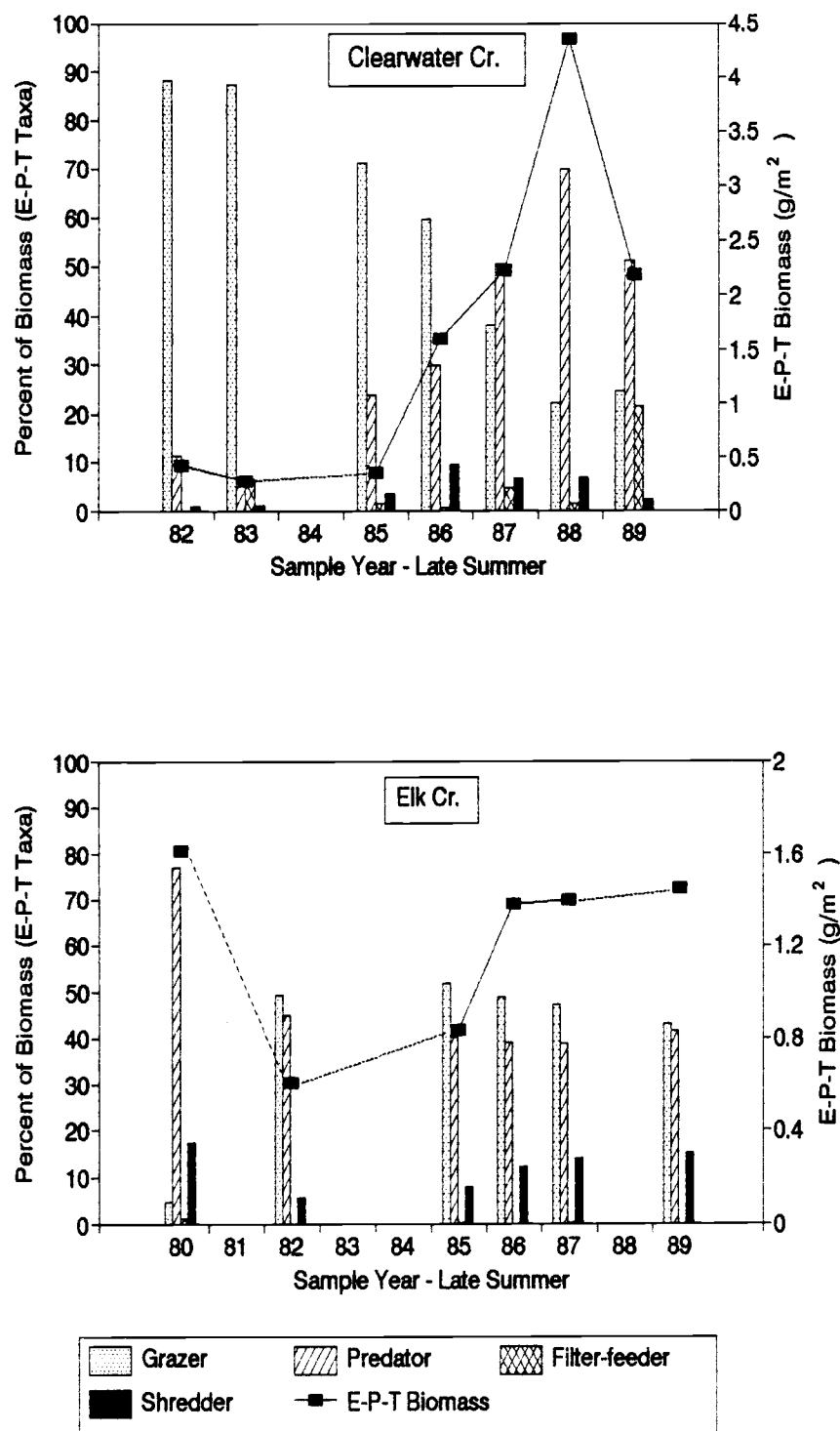


Figure 7.1. Change in the percent biomass of functional groups and total biomass for E-P-T taxa at Clearwater (1982-1989) and Elk Creeks (1980-1989).

may survive on nearby riparian vegetation. If the disturbance is confined to the stream channel, recolonization will occur quickly from these sources (e.g., Fisher et al. 1982). Other studies have reported that recovery to pre-disturbance levels generally requires less than a year (e.g., flooding, Siegfried and Knight 1977, Molles 1985; debris flow, Lamberti et al. 1991; coal strip-mining, Gore 1979). The Teton River flood was of much greater severity than any of these studies with a wall of water 15 to 23 m high sweeping through the channel. However, even the effects of that disturbance were less than those caused by the eruption of Mt. St. Helens which not only devastated the stream channel but also devastated nearby colonization sources such as tributaries, hyporheos (via ash deposition), and riparian zones. Furthermore, the timing of the disturbance may have delayed the beginning of the recovery at Clearwater Creek. Many taxa emerge from May to July. Because the eruption occurred in May, the late instars of these taxa were lost and along with them the possibility to escape the eruption in a more resistant life stage, e.g. as adults in nearby surviving forests.

Odum (1969) suggested trends that could be expected in an ecosystem developing from an immature to a mature state. Table 7.2 compares these trends with results from Sycamore Creek and Clearwater Creek. Appropriate

Table 7.2 Comparison of trends in post-disturbance recovery between Mt. St. Helens and Sycamore Creek (Fisher et al. 1982) and the predictions of Odum (1969) for changes that should occur as an ecosystem matures. Auto = Autochthonous; Allo = Allochthonous.

| Parameter | Clearwater Cr. | Sycamore Cr. | Odum's Prediction |
|---------------------|-----------------|------------------------|-------------------|
| Diversity (H') | Group dependent | Fluctuates | Increases |
| E-P-T Taxa | Increases | | |
| Chironomidae | Fairly stable | | |
| Organism Size | Increases | Remains small | Increases |
| Life Cycle Duration | Increases | Stable (short) | Increases |
| Habitat Stability | Improves | Remains low | Improves |
| Food Base | Auto | Allo --> Auto --> Allo | Auto --> Allo |

data were not available from the Teton River study for inclusion in this comparison. The results from Clearwater Creek more closely match Odum's suggested trends than do the results from the Sycamore Creek study. However, some differences with Odum's predictions also were found.

Odum (1969) hypothesized that diversity would increase with time but at Clearwater Creek, changes in diversity varied among taxonomic groups. This difference reflects the wide variation of life-history strategies found among insects. Because chironomids quickly colonize disturbed habitats, species richness increases rapidly and while richness may decline when other insects colonize, increased evenness among chironomid taxa helps maintain diversity. Thus overall, the Chironomidae maintained a relatively stable diversity. In contrast, many E-P-T taxa are slow colonizers and require a much longer period of time to increase in diversity. New taxa are still colonizing Clearwater Creek after ten years. Ide (1967) found a similar pattern of differential colonization in a stream disturbed by pesticides.

As the ecosystem matures the food base should shift from autochthonous to allochthonous-based (Odum 1969). In 1989 the composition of the Clearwater Creek community demonstrated that the energy base for aquatic

insects was still autochthonous-based (i.e., dependent on algae or detritus derived from algae). This result is not too surprising given the degree of disturbance. Until the riparian vegetation has recovered to the extent that the stream has a closed canopy, the energy base for Clearwater Creek probably will remain autochthonous.

Evidence that the recovery of the benthic community of Clearwater Creek is following an expected trajectory was seen in Figure 3.14. Changes in the late-summer benthic community showed a gradual increase in the biomass of long-lived taxa (Fig. 3.13), and in 1989 increased biomass of filter feeders (esp. hydropsychid and arctopsychid caddisflies). This shift in voltinism and taxonomic composition suggests that the substrate is stabilizing, especially the filter-feeding caddisflies which need stable substrates for net attachment.

The trend at Clearwater Creek has been for decreased biomass of grazers and increased biomass of predators (Fig. 7.1). This pattern also was found in two other studies which looked at long-term recovery of feeding groups in severely disturbed streams (Gore 1982, Minshall et al. 1983). Whether or not this pattern will continue or stabilize at Clearwater Creek remains to be seen.

Various models of stream ecosystem theory suggest that the relative abundance of functional feeding groups in the benthic community tracks available resource levels. Swanson et al. (1982) hypothesized how the source and rate of organic matter inputs would change over an 80-year period following clearcut logging (Fig. 7.2). They suggested that the importance of algae as a source of organic matter would begin to decline by the fifth year, while the rate of litter input from herbaceous plants and shrubs would increase rapidly. Except for one modification, this scenario should occur at Clearwater Creek. This change will be the increased inputs of deciduous leaf litter from planted alder, cottonwood, and willow. By 1989 many of these trees were over 6 m in height and beginning to shed a significant amount of leaves into the stream channel (personal observation).

Sheldon (1984) published a generalized resource-tracking model in which the densities of fast and slow colonizers were compared with their abilities to track their respective food resources (Fig. 7.3). From this model he predicted that the density of fast colonizers would peak early and then decline gradually to some equilibrium as they control their food supply. On the other hand, slow colonizers would overshoot their food supply and decline abruptly. The results of ten years

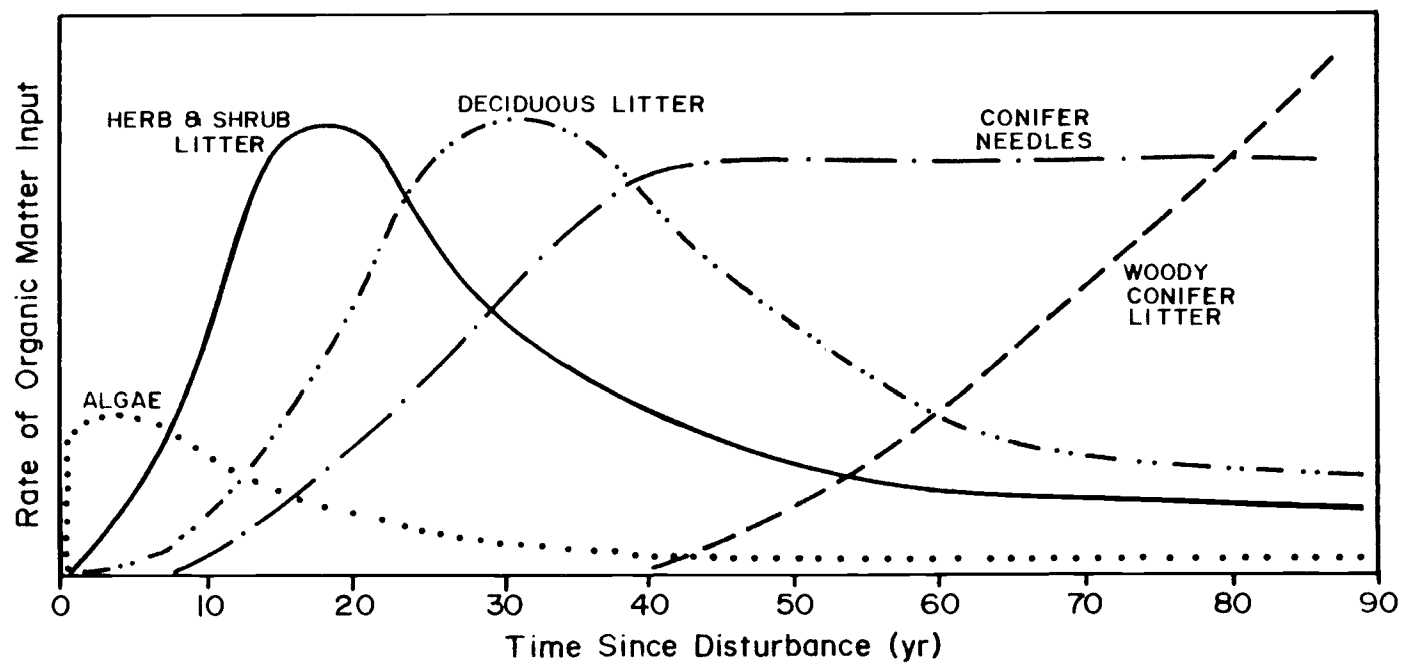


Figure 7.2. Changes in the source of organic matter inputs into a low-order Cascade mountain stream following a major disturbance (adapted from Swanson et al. 1982).

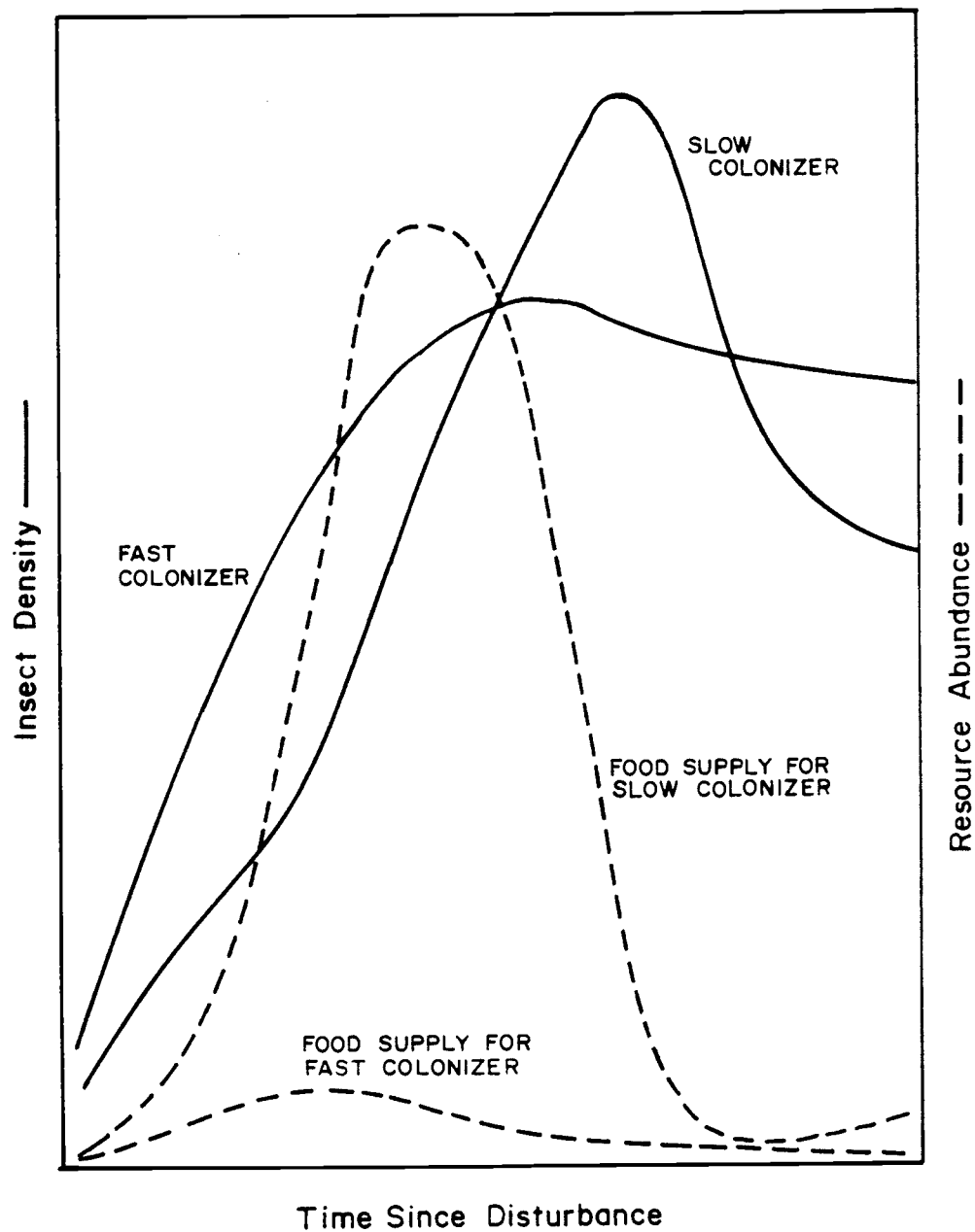


Figure 7.3. Resource-tracking model of colonizing insects following disturbance (adapted from Sheldon 1984).

of data from Clearwater Creek fit with this model with grazers as fast and predators as slow colonizers. Figure 7.1 showed that grazers peaked early and have since declined to what may be a stable level. Predators, responding to an abundance of prey (grazers), peaked later (i.e., 1988) but then because they overshot their food supply, subsequently declined sharply (i.e., 1989). Although these data suggest that predators responded to prey density and, therefore, support traditional predator-prey theory, good empirical evidence for this response is generally lacking in the literature (see Peckarsky 1984, for review). Preliminary data from 1990 showed a continuation of this pattern (i.e., proportions of E-P-T grazers and predators were similar to 1989 comprising 36 and 60% of E-P-T biomass, respectively; E-P-T biomass continued its decline to 1.72 g/m^2).

Recovery Patterns at Elk Creek - The recovery at Elk Creek is difficult to interpret given the lack of pre-eruption data. As was discussed in Chapter Three, even though the insect community at Elk Creek in fall 1980 was diverse and dominated by long-lived taxa, the lack of grazing insects suggests that the 1980 community had been at least partially affected by the eruption. Disruption of the entire community did not occur until the winter of 1980-1981 when runoff from rain and snowmelt flushed copious amounts of ash through the

stream channel. This disturbance event opened the door for colonization by opportunistic taxa, especially midges (see Figures 3.3 and 3.4, 1982 sample year).

Since 1982 the community has been returning to its pre-disturbance state through secondary succession processes. If the Elk Creek community is undergoing secondary succession, then there should be evidence that the insect community is on a trajectory towards some pre-disturbance state. Ordination of the late-summer benthic communities of 1980-1989 at Elk Creek suggest that in fact that is happening (see Fig. 3.14) although without pre-eruption data it is difficult to know what the endpoint or stable community at the end of this trajectory should be. However, while the relative proportions of individual taxa continue to change, Figures 3.3 and 3.4 show that a certain degree of stability existed in the composition of the benthic community by 1989 as there has been little change in the proportions of the major aquatic orders since 1985.

Recovery and Secondary Production - Although production was only measured for 1985 and 1986, a reasonable scenario of secondary production changes since 1986 can be inferred from the composition of the summer benthic community at Clearwater and Elk Creeks. Due to differences in biomass turnover rates there is not a one-to-one relationship between standing crop

biomass and production. However, if it is assumed that grazers (primarily mayflies and midges) have rapid turnover rates as compared to predators, then production trends can be estimated by comparing the relative contributions of these two groups to total biomass between 1980 and 1989.

Grazer production has likely declined at Clearwater Creek while the production of predators has increased. However, because of the difference between these two groups in biomass turnover rates the net result for the benthic insect community was probably production levels somewhere between the 1985-1986 values in 1987 and 1988, but a sharp drop in 1989 to a level near that found in 1985 as total biomass declined but predator biomass remained predominant. This pattern of change in production, if correct, closely follows Odum's predictions for secondary production as an ecosystem matures (Odum 1969).

The data from Elk Creek showed little change in the nature of the benthic community (including both functional group composition and total biomass) since 1986. Thus, it is likely that the secondary production of insects remained fairly close to the levels found in 1986.

Limitations on Production - Insect production, which was similar between sites in 1985, increased to a

much greater degree at Clearwater Creek in 1986 than at Elk Creek. Similar taxa were the primary contributors of production at each site. Yet why did production not increase to the same degree at Elk Creek in 1986?

Habitat factors can limit production (see Benke 1984 for review) and it is likely that habitat differences between Clearwater and Elk Creeks (see Chapter Two) contributed to between-site differences in the secondary production of grazers as well as the entire benthic community.

It was reported in Chapter Two that mean substrate size was significantly greater at Elk Creek than at Clearwater Creek suggesting that the substrate was more stable at Elk than Clearwater Creek. The relationship between substrate stability and particle size has been shown with models and experiments (Varoni 1964, Blatt et al. 1980, Reid and Frostick 1984). The fine sediments at Clearwater Creek are readily transported, and thus less stable than the large cobble substrates of Elk Creek. In addition, scour from ash transport would have a detrimental effect on benthic insects. Increased substrate stability at Elk Creek should promote constancy in insect populations. Consequently, all else being equal, year to year variation in insect production at Elk Creek should fluctuate less than at the less stable Clearwater Creek.

If stability was important to insect populations and production, then why was no significant difference found in the benthic populations between the Take and Leave sites in Clearwater Creek? It was assumed that these sites would differ in habitat stability because of differing amounts of woody debris. But upon finding no differences in mean density or biomass of insects the sites were subsequently combined for further analysis (see Chapter Four). Between-site differences were probably not found at Clearwater Creek as it is likely that insufficient time had passed for those differences to develop. However, the presence of woody debris should promote stability at the Leave site well before the Take site, and given enough time not only should the benthic community structures of the two sites diverge, but secondary production will also begin to differ. By 1989, evidence that the communities sites were beginning to diverge was becoming evident. Ordination of Take and Leave sites since 1985 shows that the distance between points gradually increased, especially in 1989 (Fig. 7.4). Also, preliminary data from qualitative kick samples indicate that over 10 additional E-P-T taxa were present at the Leave site as compared to the Take site in 1990. These between-site differences in the benthic community likely will lead to differences in secondary production between sites.

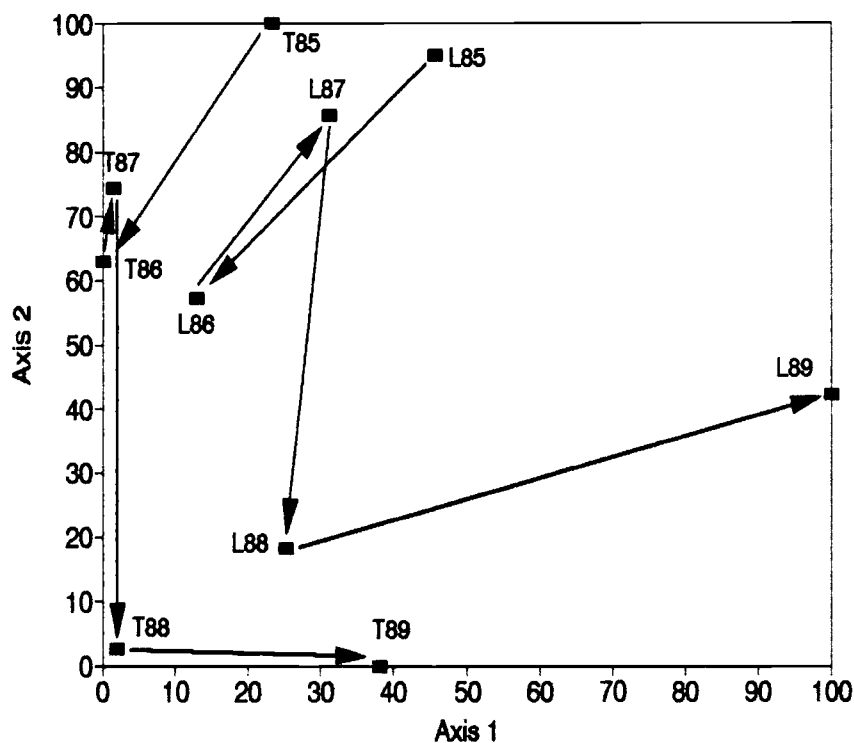


Figure 7.4. Ordination (DCA) of benthic communities of the Take (T) and Leave (L) sites from 1985 to 1989. Analysis based on mean biomass values from late summer collections. Labeled points correspond to site and year. Lines connecting labels are intended to suggest a successional trajectory.

Although the habitat may be stable for insect production, the amount of available habitat for insect colonization may limit production (Coleman and Hynes 1968, Mackey 1977, Menzie 1981, Cudney and Wallace 1980, Benke et al. 1984). Most of the dominant grazers were important to both streams and thus their preferred habitat was available. However, Clearwater and Elk Creek sites differed in size and discharge (see Table 2.1). Less discharge during summer months at Elk Creek coupled with larger substrates and a smaller stream channel than Clearwater Creek would have reduced available surface area for colonization by algae and grazers thus limiting standing-stock biomass and production.

The most obvious distinction between Clearwater and Elk Creeks was the development of the riparian zone. Yet riparian development appeared to have little affect on the production of each stream as: (1) the importance of grazers was similar at both streams; and (2) the cumulative degree days of each stream were similar in both sample years (1818 and 1643 for Clearwater and Elk Creeks, respectively). However, the presence or absence of the riparian zone can affect the benthic community in other ways.

Increased light intensity from a lack of riparian vegetation could enhance rates of primary production and

thus food availability for grazers. A corollary to the effect of more available food would be the aggregation of grazers. Because stream reaches both above and below the Elk Creek site had more shade, it is not unlikely that grazers aggregated in the relatively open study site. Thorup (1964) showed that Baetis rhodani consistently aggregated in open areas, and Hughes (1966) found similar patterns for other mayflies. It is possible that grazers were found at higher abundances in the study site than they occur in the more shaded areas of Elk Creek.

As long as food is not limiting, elevated water temperatures can enhance secondary production, and because of differences in the degree of shading of each stream it was assumed that water temperature would be a critical factor. This has been shown especially for midge species (e.g., Fisher and Gray 1983, Benke et al. 1984). Cumulative degree days were similar at both Clearwater and Elk Creeks. This result suggested that, contrary to initial assumptions, temperature was not a critical factor in causing between-stream differences in the production of grazers. However, for production the critical factor may not have been cumulative degree days, but the fact that temperatures warmed sooner at Clearwater Creek than at Elk Creek. This difference occurred because of the higher elevation and later

snowmelt at Elk Creek. Warmer spring temperatures could lead to the earlier emergence of overwintering species at Clearwater than at Elk Creek. Data suggest that at least for grazers this was a common occurrence (see Table 5.2). The sooner emergence occurred for multivoltine grazers, e.g. *Micropsectra* spp. or orthoclad midges, the greater the likelihood that an extra generation could be completed during the summer. In Chapter Six I suggested that food quality alone might have increased growth rates and allowed for additional generations. However, earlier emergence coupled with increased food quality might have been co-contributing factors.

Differences in the proportion of diatoms in the guts of some of the important grazers of Clearwater and Elk Creeks suggest that food quality may have influenced production at Elk Creek in 1986. But food availability can be influenced by a number of the characteristics of the stream channel. For example, temperature can affect primary production, and substrate characteristics can limit surface area for the development of the aufwuchs. Although it is likely algal biomass differed between sites (G.A. Lamberti, personal communication), whether food was limiting at either site cannot be deduced from this study. Based on personal observations of a well developed aufwuchs at Clearwater Creek in both years it

is doubtful that food was limiting in that stream. However, at Elk Creek, substrate surfaces appeared relatively "clean" as compared to rock surfaces at Clearwater Creek. In addition, little filamentous algal growth occurred on the substrate of Elk Creek. Although few insects consume much filamentous algae, it does provide additional surface area for aufwuchs development, especially epiphytic diatoms. Clearly, enough food was available to maintain a considerable grazer population at Elk Creek, but the lack of a similar production increase at Elk Creek in 1986 as was seen at Clearwater Creek could mean that food was limiting. Moreover, the fact that detritus was significantly more important in the diet of some grazers at Elk Creek than at Clearwater Creek, suggests the idea that high quality diatoms as a food source was limiting to those insects.

An important factor which could have affected algal biomass, and thus grazer insect production, at Elk Creek was the presence of the tailed frog, Ascaphus, a large herbivore common to many streams in the Pacific Northwest (Metter and Pauken 1969). Experimental studies with large herbivores have shown that not only can they influence the structure and biomass of algae, but they can also influence populations of consumers (Paine 1980, Gregory 1983, Lamberti and Moore 1984,

Hawkins and Furnish 1987, Furnish 1989). Although Ascaphus is sensitive to disturbance, including streambed scour by sediment (Noble and Putnam 1931, Metter 1964, 1968, Bury 1983), it was present in densities of 5 and 8 animals/m² in 1985 and 1986, respectively; levels that were similar to or greater than those found in other streams of the Mt. St. Helens area (Hawkins et al. 1988, C.P. Hawkins, personal communication).

Little is known about how Ascaphus interacts with other grazing invertebrates in streams. Unpublished studies from small streams near Mt. St. Helens showed that Ascaphus, at a density of 5 animals/m², can reduce aufwuchs biomass by 98%, and invertebrate density by 37% (S.V. Gregory, personal communication). The possibility that Ascaphus acts as a competitive dominant over other grazers and thus limits insect grazer production in Elk Creek cannot be ruled out.

Conclusions - Much has been written on factors that affect the benthic community and, therefore, secondary production of lotic systems. But before one can attribute differences in benthic community structure to habitat differences this study has shown the importance of knowing something about the disturbance history of the site(s) in question. If we had relied solely on data from 1985 and 1986, it would have appeared that the

similarities of the two sites in terms of the importance of grazers and their production (at least in 1985) outweighed the dissimilarities. However, production in the context of ten years of recovery indicated that central to the performance of each stream in 1985-1986 was the effect of the 1980 eruption on each site. While it is likely that habitat characteristics such as substrate, flow, and temperature played a major role in determining the productive capacity, these habitat differences were superimposed on the disturbance history and recovery patterns of each site.

Between-year differences in secondary production, especially at Clearwater Creek, indicate the need for long-term studies of production. The three-fold difference in production at Clearwater Creek between 1985 and 1986 shows that stream communities have the capacity to respond to ideal conditions for production. However, what remains unknown is whether Clearwater Creek will continue to experience wide variations in secondary production, or as Odum (1969) predicts, production (total as well as variability) will decline as the stream ecosystem matures.

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APPENDICES

Appendix A. Density (No./m²) and biomass (mg dry wt/m²) for each taxon collected at Clearwater Creek, late summer 1980-1989. VLT = Type of voltinism (MV = multivoltine; UV = univoltine; SV = semivoltine). T = < 0.5 animals/m² or 0.05 mg/m². Sample dates and sample sizes: September 8, 1980 - 5; August 11, 1982 - 8; September 20, 1983 - 9; August 29, 1985 - 10; August 22, 1986 - 14; August 22, 1987 - 13; September 9, 1988 - 6; August 24, 1989 - 10. No samples collected in 1981 or 1984. Note: Taeniopterygidae includes both Taenionema sp. and Doddsia sp.

| TAXON | VLT | SAMPLE YEAR | | | | | | | | |
|------------------------------|-----|-------------|------|-------|-------|------|-------|-------|-------|------|
| | | | 1980 | 1982 | 1983 | 1985 | 1986 | 1987 | 1988 | 1989 |
| Baetidae | | | | | | | | | | |
| <i>Baetis spp.</i> | MV | No. | 0 | 7462 | 6949 | 799 | 6860 | 5950 | 8999 | 4428 |
| | | mg | 0.0 | 350.2 | 145.9 | 21.2 | 182.3 | 119.7 | 83.2 | 71.1 |
| <i>B. bicaudatus</i> | UV | No. | 0 | 99 | 0 | 51 | 53 | 790 | 498 | 262 |
| | | mg | 0.0 | 12.8 | 0.0 | 9.9 | 14.5 | 86.1 | 64.5 | 31.4 |
| <i>B. tricaudatus</i> | MV | No. | 0 | 0 | 0 | 149 | 2429 | 478 | 623 | 448 |
| | | mg | 0.0 | 0.0 | 0.0 | 39.9 | 201.5 | 167.5 | 159.4 | 83.6 |
| <i>Dipheter hageni</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 905 | 3207 | 448 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 35.3 | 102.8 | 8.0 |
| Ephemerellidae | | | | | | | | | | |
| <i>Attenella sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 93 | 29 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 1.7 | 0.5 | 0.0 | 0.0 |
| <i>Drunella coloradensis</i> | UV | No. | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 45.4 | 0.0 | 0.0 | 0.0 |
| <i>D. doddsi</i> | UV | No. | 0 | 0 | 0 | 0 | 13 | 0 | 31 | 9 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 2.4 | 0.0 | 3.6 | 0.4 |
| <i>D. spinifera</i> | SV | No. | 0 | 0 | 0 | 0 | 53 | 61 | 311 | 177 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 40.4 | 42.3 | 281.9 | 83.0 |
| <i>Ephemerella spp.</i> | UV | No. | 0 | 0 | 5 | 388 | 3550 | 1164 | 1993 | 224 |
| | | mg | 0.0 | 0.0 | T | 0.9 | 7.8 | 3.3 | 8.3 | 1.2 |
| <i>Serratella tibialis</i> | UV | No. | 0 | 6 | 0 | 9 | 97 | 19 | 16 | 0 |
| | | mg | 0.0 | 18.1 | 0.0 | 41.1 | 219.5 | 75.5 | 57.8 | 0.0 |
| <i>Serratella sp. A</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 57.0 |
| Heptageniidae | | | | | | | | | | |
| <i>Cinygmula sp.</i> | UV | No. | 0 | 23 | 1012 | 1336 | 15961 | 12863 | 18559 | 7931 |
| | | mg | 0.0 | 1.1 | 1.0 | 15.4 | 143.1 | 95.5 | 274.7 | 76.0 |
| <i>Epeorus spp.</i> | UV | No. | 0 | 0 | 0 | 0 | 307 | 359 | 561 | 224 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 9.4 | 25.7 | 3.6 | 11.7 |
| <i>E. albertae</i> | UV | No. | 0 | 0 | 0 | 9 | 0 | 4 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.4 | 0.0 | T | 0.0 | 0.0 |
| <i>E. deceptivus</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 4 | 93 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.7 | 7.2 | 0.0 |
| <i>E. grandis</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 29 | 0 | 19 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 13.7 | 0.0 | 2.8 |
| <i>E. longimanus</i> | UV | No. | 0 | 0 | 31 | 9 | 13 | 0 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 2.4 | 4.7 | 1.0 | 0.0 | 0.0 | 0.0 |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | | |
|------------------------|-----|-------------|------|-------|-------|-------|--------|-------|--------|-------|--|
| | | 1980 | 1982 | 1983 | 1985 | 1986 | 1987 | 1988 | 1989 | | |
| <i>Epeorus sp. A</i> | UV | No. | 0 | 0 | 0 | 93 | 0 | 40 | 0 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 12.1 | 0.0 | 6.7 | 0.0 | 0.0 | |
| <i>Ironodes sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 32.7 | |
| <i>Rhithrogena sp.</i> | UV | No. | 0 | 6 | 0 | 234 | 561 | 1135 | 623 | 1868 | |
| | | mg | 0.0 | 5.6 | 0.0 | 57.2 | 87.4 | 148.9 | 112.0 | 188.5 | |
| Leptophlebiidae | | | | | | | | | | | |
| <i>P. temporalis</i> | UV | No. | 0 | 0 | 192 | 9 | 20032 | 9112 | 20584 | 3242 | |
| | | mg | 0.0 | 0.0 | 0.3 | 0.1 | 147.5 | 105.0 | 269.8 | 43.3 | |
| Siphonuridae | | | | | | | | | | | |
| <i>Ameletus spp.</i> | UV | No. | 0 | 0 | 21 | 70 | 564 | 172 | 171 | 131 | |
| | | mg | 0.0 | 0.0 | 0.1 | 1.3 | 46.1 | 3.8 | 35.4 | 12.2 | |
| EPHEMEROPTERA | | No. | 0 | 7596 | 8211 | 3158 | 50590 | 33114 | 56270 | 19441 | |
| | | mg | 0.0 | 387.9 | 149.7 | 204.2 | 1149.9 | 934.1 | 1464.3 | 703.0 | |
| Capniidae | UV | No. | 0 | 23 | 21 | 0 | 40 | 29 | 62 | 9 | |
| | | mg | 0.0 | 1.9 | 0.1 | 0.0 | 0.0 | 18.3 | 0.1 | 0.1 | |
| Chloroperlidae | | | | | | | | | | | |
| <i>Sweltsa sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 40 | 244 | 319 | 931 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 32.3 | 42.4 | 86.7 | 99.4 | |
| Leuctridae | UV | No. | 0 | 0 | 0 | 28 | 0 | 0 | 0 | 19 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.0 | T | |
| <i>Paraleuctra sp.</i> | UV | No. | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 4.9 | 0.0 | 0.0 | 0.0 | 0.0 | |
| Nemouridae | UV | No. | 0 | 6 | 10 | 0 | 0 | 0 | 0 | 0 | |
| | | mg | 0.0 | T | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| <i>Malenka sp.</i> | UV | No. | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 | 0.0 | 0.0 | |
| <i>Zapada spp.</i> | UV | No. | 0 | 0 | 0 | 0 | 480 | 0 | 0 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 3.6 | 0.0 | 0.0 | 0.0 | |
| <i>Z. cinctipes</i> | UV | No. | 0 | 0 | 0 | 5 | 0 | 388 | 1526 | 598 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 6.0 | 19.2 | 6.2 | |
| <i>Z. columbiana</i> | UV | No. | 0 | 0 | 0 | 19 | 80 | 0 | 0 | 103 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.4 | 0.7 | 0.0 | 0.0 | 1.3 | |
| Peltoperlidae | | | | | | | | | | | |
| <i>Yora perla sp.</i> | SV | No. | 0 | 12 | 5 | 9 | 0 | 0 | 31 | 0 | |
| | | mg | 0.0 | 0.1 | 0.1 | 0.1 | 0.0 | 0.0 | 1.2 | 0.0 | |

| TAXON | VLT | | SAMPLE YEAR | | | | | | | | |
|-----------------------------|-----|-----|-------------|------|------|-------|-------|-------|--------|-------|--|
| | | | 1980 | 1982 | 1983 | 1985 | 1986 | 1987 | 1988 | 1989 | |
| Perlidae | SV | No. | 0 | 6 | 0 | 0 | 13 | 57 | 31 | 19 | |
| | | mg | 0.0 | 2.1 | 0.0 | 0.0 | 4.8 | 1.1 | 2.6 | 4.8 | |
| <i>Calineuria sp.</i> | SV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| Perlodidae | UV | No. | 0 | 58 | 10 | 430 | 13 | 86 | 841 | 0 | |
| | | mg | 0.0 | 0.1 | 0.1 | 0.3 | T | 0.2 | 2.1 | 0.0 | |
| <i>Cultus sp.</i> | UV | No. | 0 | 0 | 0 | 84 | 1308 | 632 | 1090 | 364 | |
| | | mg | 0.0 | 0.0 | 0.0 | 6.0 | 63.0 | 29.1 | 62.3 | 16.2 | |
| <i>Megarcys sp.</i> | UV | No. | 0 | 6 | 21 | 19 | 17 | 57 | 156 | 14 | |
| | | mg | 0.0 | 55.9 | 85.3 | 21.6 | 76.1 | 259.4 | 691.3 | 105.6 | |
| <i>Skwala sp.</i> | UV | No. | 0 | 0 | 0 | 65 | 150 | 377 | 755 | 355 | |
| | | mg | 0.0 | 0.0 | 0.0 | 45.5 | 192.0 | 329.8 | 1152.2 | 174.2 | |
| Taeniopterygidae | UV | No. | 0 | 0 | 628 | 3503 | 3723 | 2098 | 7982 | 2228 | |
| | | mg | 0.0 | 0.0 | 2.6 | 69.1 | 43.8 | 36.6 | 53.5 | 28.2 | |
| PLECOPTERA | | No. | 0 | 111 | 695 | 4171 | 5865 | 3970 | 9794 | 4540 | |
| | | mg | 0.0 | 60.2 | 88.3 | 151.7 | 416.4 | 722.9 | 2071.2 | 436.1 | |
| Brachycentridae | | | | | | | | | | | |
| <i>Brachycentrus sp.</i> | SV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 31 | 19 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.2 | |
| Glossosomatidae | | | | | | | | | | | |
| <i>Glossosoma sp.</i> | MV | No. | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 19 | |
| | | mg | 0.0 | 0.0 | T | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | |
| Arctopsychidae | SV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 374 | 140 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 19.2 | 13.7 | |
| <i>Arcto psyche grandis</i> | SV | No. | 0 | 0 | 0 | 0 | 0 | 18 | 47 | 47 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 60.7 | 292.6 | 163.0 | |
| <i>Parapsyche elsis</i> | SV | No. | 0 | 0 | 0 | 0 | 3 | 4 | 31 | 9 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 11.3 | 31.3 | 7.8 | 67.3 | |
| Hydropsychidae | MV | No. | 0 | 0 | 26 | 19 | 0 | 661 | 0 | 0 | |
| | | mg | 0.0 | 0.0 | 2.1 | 5.1 | 0.0 | 242.8 | 0.0 | 0.0 | |
| <i>Hydro psyche sp. A</i> | MV | No. | 0 | 0 | 5 | 0 | 80 | 0 | 872 | 65 | |
| | | mg | 0.0 | 0.0 | 0.8 | 0.0 | 7.9 | 0.0 | 68.5 | 150.2 | |
| <i>Hydro psyche oslari</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 111.6 | |
| Hydroptilidae | UV | No. | 0 | 0 | 5 | 23 | 27 | 144 | 529 | 84 | |
| | | mg | 0.0 | 0.0 | 0.1 | 0.7 | T | 0.6 | 0.1 | 0.6 | |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | | |
|----------------------------|-----|-------------|------|------|------|------|------|-------|-------|-------|--|
| | | | 1980 | 1982 | 1983 | 1985 | 1986 | 1987 | 1988 | 1989 | |
| <i>Agraylea sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 7 | 156 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.7 | 2.5 | 0.0 | |
| <i>Hydroptila sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 13 | 101 | 31 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 2.3 | 0.2 | 0.0 | |
| Lepidostomatidae | | | | | | | | | | | |
| <i>Lepidostoma sp.</i> | UV | No. | 0 | 0 | 0 | 19 | 0 | 29 | 0 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 | 0.0 | 0.0 | |
| Limnephilidae | | | | | | | | | | | |
| <i>Ecclisomyia sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 62 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 12.5 | 0.0 | |
| <i>Neophylax sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | |
| <i>Pedomoecus sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 80 | 0 | 0 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | T | 0.0 | 0.0 | 0.0 | |
| Rhyacophilidae | | | | | | | | | | | |
| <i>Rhyacophila sp.</i> | SV | No. | 0 | 0 | 0 | 37 | 27 | 83 | 0 | 9 | |
| | | mg | 0.0 | 0.0 | 0.0 | 10.0 | 3.2 | 172.6 | 0.0 | 2.3 | |
| <i>R. arnaudi</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 37 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 81.3 | |
| <i>R. Betteni Gr.</i> | SV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 28 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 89.7 | |
| <i>R. Brunnea Gr.</i> | SV | No. | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 37 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 20.0 | 0.0 | 0.0 | 114.9 | |
| <i>R. Coloradensis Gr.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 23 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 118.2 | 0.0 | |
| <i>R. Hyalinata Gr.</i> | SV | No. | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 19 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 1.1 | 0.0 | 0.0 | 22.2 | |
| <i>R. narvae</i> | SV | No. | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | |
| | | mg | 4.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 13.2 | |
| <i>R. valuma</i> | SV | No. | 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | | mg | 19.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| Uenoidae | | | | | | | | | | | |
| <i>Neothremma sp.</i> | SV | No. | 0 | 0 | 0 | 0 | 0 | 14 | 0 | 0 | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | T | 0.0 | 0.0 | |
| TRICHOPTERA | | No. | 28 | 0 | 42 | 98 | 257 | 1060 | 2156 | 551 | |
| | | mg | 22.9 | 0.0 | 2.9 | 15.9 | 44.2 | 511.1 | 521.9 | 830.6 | |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | |
|------------------------|-----|-------------|------|-------|------|------|------|------|-------|-------|
| | | | 1980 | 1982 | 1983 | 1985 | 1986 | 1987 | 1988 | 1989 |
| Dytiscidae | SV | No. | 0 | 64 | 93 | 0 | 13 | 115 | 31 | 19 |
| | | mg | 0.0 | 124.4 | 34.6 | 0.0 | 0.1 | 52.8 | 19.0 | 7.2 |
| Hydrophilidae | SV | No. | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 9 |
| | | mg | 0.0 | 0.0 | 0.0 | 34.1 | 0.0 | 0.0 | 0.0 | 9.3 |
| Elmidae | SV | No. | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 28 |
| | | mg | 0.0 | 0.0 | 3.6 | 0.0 | 0.0 | 0.0 | 0.0 | 4.8 |
| <i>Narpus concolor</i> | SV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 41.1 |
| COLEOPTERA | | No. | 0 | 64 | 99 | 9 | 13 | 115 | 31 | 65 |
| | | mg | 0.0 | 124.4 | 38.1 | 34.1 | 0.1 | 52.8 | 19.0 | 62.4 |
| Ceratopogonidae | UV | No. | 0 | 128 | 21 | 23 | 294 | 14 | 249 | 112 |
| | | mg | 0.0 | 9.1 | 3.1 | 0.6 | 66.6 | 0.1 | 16.8 | 35.0 |
| Dolichopodidae | UV | No. | 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 5.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Empididae | UV | No. | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Chelifera sp.</i> | UV | No. | 0 | 0 | 21 | 0 | 0 | 0 | 93 | 65 |
| | | mg | 0.0 | 0.0 | 1.7 | 0.0 | 0.0 | 0.0 | 0.9 | 1.6 |
| <i>Clinocera sp.</i> | UV | No. | 0 | 169 | 78 | 19 | 147 | 86 | 125 | 9 |
| | | mg | 0.0 | 15.8 | 8.8 | 1.1 | 17.8 | 7.5 | 11.5 | 0.5 |
| <i>Oreogeton sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 31 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 |
| Muscidae | UV | No. | 9 | 18 | 5 | 5 | 27 | 29 | 0 | 28 |
| | | mg | 14.9 | 6.6 | 1.8 | 1.0 | 12.5 | 12.0 | 0.0 | 23.1 |
| Psychodidae | UV | No. | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Simuliidae | MV | No. | 56 | 3141 | 36 | 1462 | 1308 | 1006 | 779 | 4447 |
| | | mg | 17.0 | 471.3 | 0.7 | 76.9 | 43.7 | 52.2 | 78.9 | 467.2 |
| Tipulidae | UV | No. | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 28 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 2.8 |
| <i>Antocha sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 73 | 0 | 9 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 16.2 | 0.0 | 0.9 |
| <i>Dicranota sp.</i> | UV | No. | 0 | 29 | 156 | 33 | 227 | 75 | 654 | 262 |
| | | mg | 0.0 | 12.1 | 37.4 | 1.0 | 74.5 | 2.5 | 293.5 | 26.3 |
| <i>Erioptera sp.</i> | UV | No. | 0 | 0 | 5 | 65 | 53 | 43 | 62 | 9 |
| | | mg | 0.0 | 0.0 | 3.7 | 59.7 | 36.0 | 45.5 | 63.2 | 9.5 |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | |
|--------------------------|-----|-------------|------|-------|-------|-------|-------|-------|-------|-------|
| | | | 1980 | 1982 | 1983 | 1985 | 1986 | 1987 | 1988 | 1989 |
| <i>Hesperoconopa sp.</i> | UV | No. | 0 | 0 | 73 | 47 | 27 | 72 | 31 | 56 |
| | | mg | 0.0 | 0.0 | 133.0 | 17.1 | 38.4 | 93.5 | 8.7 | 50.0 |
| <i>Hexatoma sp. A</i> | UV | No. | 0 | 29 | 5 | 5 | 27 | 7 | 0 | 28 |
| | | mg | 0.0 | 17.4 | 6.6 | 1.3 | 31.7 | 12.7 | 0.0 | 13.4 |
| <i>Hexatoma sp. B</i> | UV | No. | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 9 |
| | | mg | 0.0 | 12.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 6.1 |
| <i>Ormosia sp.</i> | UV | No. | 0 | 0 | 5 | 5 | 0 | 14 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 0.4 | T | 0.0 | 2.5 | 0.0 | 0.0 |
| DIPTERA (non-midge) | | No. | 103 | 3527 | 405 | 1668 | 2109 | 1391 | 2024 | 5063 |
| | | mg | 39.6 | 545.2 | 197.2 | 158.9 | 321.5 | 244.8 | 474.0 | 636.3 |
| Chironomidae | | | | | | | | | | |
| <i>Brillia</i> | MV | No. | 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 4.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Chaetocladius</i> | MV | No. | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 35 |
| | | mg | 5.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.9 |
| Chironomini | MV | No. | 0 | 47 | 27 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 0.0 | 1.4 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Corynoneura</i> | MV | No. | 0 | 9 | 33 | 35 | 3264 | 689 | 70 | 245 |
| | | mg | 0.0 | 0.2 | 1.3 | 0.8 | 25.9 | 8.3 | 0.9 | 3.0 |
| <i>Cricotopus</i> | MV | No. | 9 | 0 | 0 | 18 | 0 | 0 | 0 | 0 |
| | | mg | 0.5 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>C. bicinctus</i> | MV | No. | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>C. tremulus</i> | MV | No. | 0 | 0 | 0 | 88 | 105 | 76 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 5.6 | 5.6 | 5.6 | 0.0 | 0.0 |
| <i>Diamesa</i> | UV | No. | 37 | 47 | 0 | 128 | 0 | 0 | 0 | 0 |
| | | mg | 3.6 | 2.1 | 0.0 | 4.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Eukiefferiella</i> | MV | No. | 0 | 0 | 47 | 47 | 163 | 158 | 163 | 58 |
| | | mg | 0.0 | 0.0 | 0.3 | 0.2 | 1.1 | 0.9 | 0.6 | 0.4 |
| <i>E. clari pennis</i> | MV | No. | 0 | 729 | 327 | 70 | 263 | 946 | 911 | 204 |
| | | mg | 0.0 | 27.1 | 7.1 | 2.0 | 7.4 | 16.0 | 18.1 | 3.9 |
| <i>E. coerulescens</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>E. cyanea</i> | MV | No. | 0 | 19 | 0 | 6 | 0 | 53 | 0 | 0 |
| | | mg | 0.0 | 2.7 | 0.0 | 0.3 | 0.0 | 3.4 | 0.0 | 0.0 |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | |
|--|-----|-------------|------|-------|-------|------|-------|-------|-------|-------|
| | | | 1980 | 1982 | 1983 | 1985 | 1986 | 1987 | 1988 | 1989 |
| <i>E. devonica</i> | MV | No. | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 0.0 | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>E. gracei</i> | MV | No. | 9 | 1523 | 641 | 636 | 3340 | 333 | 856 | 543 |
| | | mg | T | 38.6 | 23.6 | 14.2 | 28.4 | 7.6 | 36.0 | 154.4 |
| <i>Heleniella</i> | MV | No. | 0 | 9 | 13 | 0 | 111 | 0 | 0 | 82 |
| | | mg | 0.0 | T | 0.9 | 0.0 | 3.2 | 0.0 | 0.0 | 2.5 |
| <i>Krenosmittia</i> | MV | No. | 0 | 0 | 7 | 18 | 274 | 228 | 0 | 304 |
| | | mg | 0.0 | 0.0 | 0.6 | 0.9 | 11.6 | 3.4 | 0.0 | 12.9 |
| <i>Micropsectra</i> | MV | No. | 9 | 542 | 2609 | 601 | 17008 | 5086 | 3386 | 2446 |
| | | mg | 1.0 | 23.3 | 155.5 | 33.0 | 289.3 | 110.9 | 193.8 | 73.5 |
| <i>Odontomesa</i> | MV | No. | 0 | 0 | 40 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 1.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Orthocladius-Cricotopus A</i> | MV | No. | 9 | 252 | 534 | 298 | 2972 | 461 | 2437 | 181 |
| | | mg | T | 4.2 | 23.2 | 8.2 | 89.0 | 7.7 | 76.6 | 10.3 |
| <i>Orthocladius-Cricotopus B</i> | MV | No. | 0 | 0 | 0 | 41 | 1868 | 339 | 452 | 41 |
| | | mg | 0.0 | 0.0 | 0.0 | 2.1 | 34.1 | 15.9 | 21.9 | 1.1 |
| <i>Orthocladius (Euorthocladius) A</i> | MV | No. | 0 | 0 | 0 | 175 | 3486 | 368 | 654 | 193 |
| | | mg | 0.0 | 0.0 | 0.0 | 6.3 | 21.0 | 9.5 | 16.4 | 11.2 |
| <i>Orthocladius (Euorthocladius) B</i> | MV | No. | 9 | 392 | 827 | 1325 | 2277 | 251 | 1121 | 193 |
| | | mg | 2.2 | 7.9 | 19.2 | 28.6 | 49.6 | 2.2 | 20.1 | 3.0 |
| <i>Pagastia</i> | MV | No. | 0 | 972 | 334 | 18 | 852 | 385 | 257 | 70 |
| | | mg | 0.0 | 183.1 | 105.2 | 9.6 | 90.7 | 25.5 | 29.5 | 1.7 |
| <i>Paracladopelma</i> | MV | No. | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 3.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Parakiefferiella</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Parametriocnemus</i> | MV | No. | 9 | 177 | 20 | 70 | 1290 | 269 | 249 | 169 |
| | | mg | 2.5 | 9.0 | 5.6 | 5.9 | 88.7 | 13.3 | 43.0 | 7.3 |
| <i>Paraphaenocladus</i> | MV | No. | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 12 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 2.8 |
| <i>Parochlus</i> | MV | No. | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 3.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

| TAXON | VLT | | SAMPLE YEAR | | | | | | | | | |
|------------------------|-----|-----|-------------|-------|-------|-------|--------|-------|--------|-------|--|--|
| | | | 1980 | 1982 | 1983 | 1985 | 1986 | 1987 | 1988 | 1989 | | |
| <i>Parorthocladius</i> | MV | No. | 0 | 243 | 801 | 0 | 29 | 0 | 0 | 0 | | |
| | | mg | 0.0 | 4.8 | 31.6 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | | |
| <i>Polypedilum</i> | MV | No. | 0 | 19 | 53 | 6 | 134 | 286 | 31 | 23 | | |
| | | mg | 0.0 | 0.4 | 12.8 | 0.5 | 1.0 | 32.5 | 5.8 | 2.9 | | |
| <i>Psectrocladius</i> | MV | No. | 9 | 19 | 0 | 0 | 251 | 0 | 70 | 128 | | |
| | | mg | 3.6 | 0.4 | 0.0 | 0.0 | 4.6 | 0.0 | 0.6 | 3.3 | | |
| <i>Pseudodiamesa</i> | MV | No. | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | | |
| <i>Rheocricotopus</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 202 | 292 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 10.2 | 7.5 | | |
| <i>Rheotanytarsus</i> | MV | No. | 0 | 187 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | | mg | 0.0 | 2.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | |
| <i>Stempellina</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 148 | 0 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.8 | 0.0 | | |
| <i>Stempellinella</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 29 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | | |
| <i>Tanytarsus</i> | MV | No. | 0 | 0 | 13 | 292 | 8256 | 4005 | 965 | 1466 | | |
| | | mg | 0.0 | 0.0 | 3.0 | 15.1 | 240.0 | 97.8 | 41.5 | 32.6 | | |
| <i>Thienemaniella</i> | MV | No. | 0 | 9 | 180 | 58 | 975 | 309 | 459 | 0 | | |
| | | mg | 0.0 | 0.3 | 5.1 | 1.4 | 18.1 | 7.4 | 5.5 | 0.0 | | |
| <i>Thienemannimyia</i> | MV | No. | 0 | 0 | 27 | 23 | 461 | 280 | 825 | 169 | | |
| | | mg | 0.0 | 0.0 | 0.2 | 0.5 | 46.1 | 3.6 | 9.7 | 3.9 | | |
| <i>T. bavarica</i> | MV | No. | 0 | 0 | 13 | 18 | 485 | 485 | 1090 | 315 | | |
| | | mg | 0.0 | 0.0 | 2.6 | 0.4 | 10.3 | 16.9 | 33.8 | 8.5 | | |
| <i>T. discoloripes</i> | MV | No. | 0 | 0 | 53 | 6 | 134 | 0 | 187 | 0 | | |
| | | mg | 0.0 | 0.0 | 4.0 | 0.6 | 6.5 | 0.0 | 9.3 | 0.0 | | |
| <i>Zavreliomyia</i> | MV | No. | 9 | 0 | 0 | 0 | 0 | 47 | 0 | 0 | | |
| | | mg | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.8 | 0.0 | 0.0 | | |
| DIPTERA (midge) | | No. | 168 | 5260 | 6613 | 3994 | 48000 | 15052 | 14535 | 7199 | | |
| | | mg | 27.1 | 293.2 | 406.8 | 140.8 | 1072.2 | 629.3 | 574.1 | 348.5 | | |
| ALL DIPTERA | | No. | 271 | 8786 | 7018 | 5661 | 50109 | 16443 | 16559 | 12263 | | |
| | | mg | 66.8 | 854.6 | 604.0 | 299.7 | 1393.7 | 869.2 | 1048.2 | 984.8 | | |
| Acari | | No. | 0 | 93 | 26 | 126 | 948 | 618 | 1246 | 336 | | |
| | | mg | 0.0 | 1.9 | 0.5 | 2.5 | 19.0 | 12.4 | 24.9 | 6.7 | | |

| TAXON | VLT | SAMPLE YEAR | | | | | | | |
|------------------------------------|-----|-------------|--------|-------|-------|--------|--------|--------|--------|
| | | 1980 | 1982 | 1983 | 1985 | 1986 | 1987 | 1988 | 1989 |
| Oligochaetae | No. | 0 | 911 | 664 | 878 | 2776 | 4484 | 3052 | 1663 |
| | mg | 0.0 | 71.1 | 51.8 | 68.5 | 216.5 | 349.8 | 238.0 | 129.7 |
| MISCELLANEOUS | No. | 0 | 1004 | 690 | 1004 | 3723 | 5102 | 4297 | 1999 |
| | mg | 0.0 | 72.9 | 52.3 | 71.0 | 235.5 | 362.1 | 262.9 | 136.4 |
| GRAND TOTAL (Insects only) | No. | 299 | 16558 | 16064 | 13097 | 106835 | 54702 | 84810 | 36860 |
| | mg | 89.6 | 1427.1 | 883.1 | 705.6 | 3004.3 | 3090.1 | 5124.5 | 3016.9 |
| GRAND TOTAL (All invertebrates) | No. | 299 | 17562 | 16754 | 14102 | 110558 | 59804 | 89107 | 38859 |
| | mg | 89.6 | 1500.0 | 935.4 | 776.7 | 3239.8 | 3452.2 | 5387.5 | 3153.3 |

Appendix B. Density (No./m²) and biomass (mg dry wt/m²) for each taxon collected at Elk Creek, late summer 1980-1989. VLT = Type of voltinism (MV = multivoltine; UV = univoltine; SV = semivoltine). T = < 0.5 animals/m² or 0.05 mg/m². Sample sizes: September 10, 1980 - 5; August 9, 1982 - 10; August 29, 1985 - 4; August 22, 1986 - 7; August 22, 1987 - 7; August 24, 1989 - 5. No samples collected in 1981, 1983-1984, or 1988. Note: Taeniopterygidae includes both Taenionema sp. and Doddsia sp.

| TAXON | VLT | SAMPLE YEAR | | | | | | | | | | | |
|------------------------------|-----|-------------|------|------|-------|-------|--|-------|--|-------|--|-------|--|
| | | 1980 | | 1982 | | 1985 | | 1986 | | 1987 | | 1989 | |
| Baetidae | | | | | | | | | | | | | |
| <i>Baetis</i> spp. | MV | No. | 0 | | 286 | 47 | | 814 | | 707 | | 149 | |
| | | mg | 0.0 | | 28.1 | 0.2 | | 12.7 | | 8.2 | | 2.1 | |
| <i>B. bicaudatus</i> | UV | No. | 0 | | 222 | 0 | | 0 | | 40 | | 0 | |
| | | mg | 0.0 | | 115.3 | 0.0 | | 0.0 | | 4.8 | | 0.0 | |
| <i>B. tricaudatus</i> | MV | No. | 0 | | 70 | 23 | | 133 | | 40 | | 168 | |
| | | mg | 0.0 | | 26.6 | 38.0 | | 40.0 | | 24.4 | | 87.3 | |
| <i>Di phetor hageni</i> | MV | No. | 0 | | 0 | 0 | | 0 | | 53 | | 37 | |
| | | mg | 0.0 | | 0.0 | 0.0 | | 0.0 | | 0.7 | | 1.3 | |
| Ephemerellidae | | | | | | | | | | | | | |
| <i>Attenella</i> sp. | UV | No. | 0 | | 0 | 0 | | 0 | | 0 | | 0 | |
| | | mg | 0.0 | | 0.0 | 0.0 | | 0.0 | | 0.0 | | 0.0 | |
| <i>Caudatella</i> sp. | UV | No. | 196 | | 29 | 0 | | 0 | | 0 | | 0 | |
| | | mg | 23.2 | | 0.5 | 0.0 | | 0.0 | | 0.0 | | 0.0 | |
| <i>Drunella coloradensis</i> | UV | No. | 0 | | 0 | 0 | | 0 | | 7 | | 19 | |
| | | mg | 0.0 | | 0.0 | 0.0 | | 0.0 | | 38.4 | | 147.7 | |
| <i>D. doddsi</i> | UV | No. | 28 | | 0 | 93 | | 33 | | 93 | | 112 | |
| | | mg | 26.0 | | 0.0 | 3.9 | | 7.4 | | 3.9 | | 3.9 | |
| <i>D. spinifera</i> | SV | No. | 177 | | 0 | 47 | | 0 | | 0 | | 0 | |
| | | mg | 81.3 | | 0.0 | 2.0 | | 0.0 | | 0.0 | | 0.0 | |
| <i>Ephemerella</i> sp. | UV | No. | 103 | | 134 | 771 | | 414 | | 1581 | | 1626 | |
| | | mg | 18.1 | | 4.8 | 0.8 | | 0.7 | | 3.1 | | 1.5 | |
| <i>Serratella tibialis</i> | UV | No. | 0 | | 0 | 0 | | 0 | | 0 | | 0 | |
| | | mg | 0.0 | | 0.0 | 0.0 | | 0.0 | | 0.0 | | 0.0 | |
| <i>Serratella</i> sp. A | UV | No. | 0 | | 0 | 23 | | 27 | | 40 | | 168 | |
| | | mg | 0.0 | | 0.0 | 3.0 | | 9.0 | | 7.9 | | 8.6 | |
| Heptageniidae | | | | | | | | | | | | | |
| <i>Cinygmula</i> sp. | UV | No. | 0 | | 70 | 1588 | | 12238 | | 7414 | | 2840 | |
| | | mg | 0.0 | | 3.9 | 226.4 | | 122.3 | | 231.5 | | 200.7 | |
| <i>Epeorus</i> spp. | UV | No. | 0 | | 35 | 0 | | 387 | | 67 | | 19 | |
| | | mg | 0.0 | | 22.4 | 0.0 | | 2.7 | | 0.5 | | 1.4 | |
| <i>E. albertae</i> | UV | No. | 0 | | 0 | 0 | | 0 | | 33 | | 0 | |
| | | mg | 0.0 | | 0.0 | 0.0 | | 0.0 | | 52.0 | | 0.0 | |
| <i>E. deceptivus</i> | UV | No. | 0 | | 0 | 0 | | 13 | | 0 | | 0 | |
| | | mg | 0.0 | | 0.0 | 0.0 | | 24.8 | | 0.0 | | 0.0 | |
| <i>E. grandis</i> | UV | No. | 0 | | 0 | 0 | | 0 | | 0 | | 0 | |
| | | mg | 0.0 | | 0.0 | 0.0 | | 0.0 | | 0.0 | | 0.0 | |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | | |
|------------------------|-----|-------------|-------|-------|-------|-------|-------|-------|-----|-----|-----|
| | | | 1980 | 1982 | 1985 | 1986 | 1987 | 1989 | | | |
| <i>E. longimanus</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Ironodes sp.</i> | UV | No. | 0 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 0.0 | 9.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Rhithrogena sp.</i> | UV | No. | 0 | 18 | 163 | 400 | 754 | 1383 | | | |
| | | mg | 0.0 | 9.5 | 15.1 | 156.2 | 178.3 | 212.0 | | | |
| Leptophlebiidae | | | | | | | | | | | |
| <i>P. temporalis</i> | UV | No. | 0 | 163 | 280 | 841 | 948 | 1046 | | | |
| | | mg | 0.0 | 13.8 | 4.2 | 31.0 | 39.8 | 23.8 | | | |
| Siphonuridae | | | | | | | | | | | |
| <i>Ameletus spp.</i> | UV | No. | 0 | 140 | 140 | 307 | 120 | 112 | | | |
| | | mg | 0.0 | 75.1 | 60.1 | 8.5 | 27.6 | 64.9 | | | |
| EPHEMEROPTERA | | No. | 504 | 1191 | 3176 | 15608 | 11898 | 7679 | | | |
| | | mg | 148.5 | 310.0 | 353.7 | 415.2 | 621.0 | 664.2 | | | |
| Capniidae | UV | No. | 0 | 29 | 1004 | 974 | 414 | 1345 | | | |
| | | mg | 0.0 | 6.2 | 12.0 | 7.7 | 3.7 | 5.2 | | | |
| Chloroperlidae | | | | | | | | | | | |
| <i>Sweltsa sp.</i> | UV | No. | 131 | 228 | 93 | 827 | 480 | 1775 | | | |
| | | mg | 33.4 | 28.6 | 10.4 | 92.1 | 50.5 | 124.2 | | | |
| Leuctridae | UV | No. | 19 | 0 | 93 | 120 | 160 | 112 | | | |
| | | mg | 4.1 | 0.0 | 3.6 | 16.0 | 7.6 | 10.3 | | | |
| <i>Despaxia sp.</i> | UV | No. | 9 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 3.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Paraleuctra sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| Nemouridae | UV | No. | 37 | 0 | 152 | 294 | 133 | 0 | | | |
| | | mg | 1.5 | 0.0 | 1.1 | 0.2 | 0.1 | 0.0 | | | |
| <i>Malenka sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Visoka sp.</i> | UV | No. | 9 | 0 | 0 | 13 | 53 | 0 | | | |
| | | mg | 3.5 | 0.0 | 0.0 | 0.1 | 1.1 | 0.0 | | | |
| <i>Zapada spp.</i> | UV | No. | 0 | 29 | 0 | 0 | 214 | 897 | | | |
| | | mg | 0.0 | 0.3 | 0.0 | 0.0 | 2.2 | 0.3 | | | |
| <i>Z. cinctipes</i> | UV | No. | 0 | 0 | 0 | 0 | 13 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | | | |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | | |
|--------------------------|-----|-------------|-------|------|-------|-------|-------|-------|--|--|--|
| | | | 1980 | 1982 | 1985 | 1986 | 1987 | 1989 | | | |
| <i>Z. columbiana</i> | UV | No. | 9 | 0 | 23 | 0 | 80 | 0 | | | |
| | | mg | 3.5 | 0.0 | 0.2 | 0.0 | 2.9 | 0.0 | | | |
| <i>Z. oregonensis</i> | UV | No. | 56 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 22.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| Peltoperlidae | | | | | | | | | | | |
| <i>Yoraperla sp.</i> | SV | No. | 430 | 35 | 958 | 1068 | 2122 | 1532 | | | |
| | | mg | 166.9 | 0.4 | 46.1 | 114.6 | 135.5 | 107.5 | | | |
| Perlidae | SV | No. | 9 | 6 | 47 | 80 | 147 | 93 | | | |
| | | mg | 72.2 | 0.2 | 7.0 | 16.6 | 22.3 | 12.1 | | | |
| <i>Calineuria sp.</i> | SV | No. | 0 | 0 | 0 | 0 | 7 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 64.1 | 0.0 | | | |
| <i>Doroneuria sp.</i> | SV | No. | 0 | 35 | 0 | 7 | 0 | 0 | | | |
| | | mg | 0.0 | 58.4 | 0.0 | 64.1 | 0.0 | 0.0 | | | |
| Perlodidae | UV | No. | 0 | 18 | 152 | 13 | 0 | 224 | | | |
| | | mg | 0.0 | 0.3 | 3.0 | 0.0 | 0.5 | 0.5 | | | |
| <i>Cultus sp.</i> | UV | No. | 9 | 0 | 70 | 27 | 13 | 56 | | | |
| | | mg | 1.4 | 0.0 | 2.8 | 1.1 | 0.5 | 2.2 | | | |
| <i>Kogotus sp.</i> | UV | No. | 9 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 6.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Megarcys sp.</i> | UV | No. | 9 | 6 | 187 | 27 | 7 | 19 | | | |
| | | mg | 72.2 | 4.0 | 149.5 | 93.4 | 11.9 | 21.6 | | | |
| <i>Skwala sp.</i> | UV | No. | 0 | 0 | 47 | 27 | 13 | 19 | | | |
| | | mg | 0.0 | 0.0 | 11.9 | 4.1 | 9.2 | 2.8 | | | |
| Taeniopterygidae | UV | No. | 0 | 0 | 5115 | 12358 | 7834 | 8240 | | | |
| | | mg | 0.0 | 0.0 | 88.7 | 112.8 | 113.9 | 107.3 | | | |
| PLECOPTERA | | No. | 738 | 385 | 7941 | 15835 | 11704 | 14312 | | | |
| | | mg | 391.4 | 98.4 | 336.4 | 522.7 | 426.2 | 394.0 | | | |
| Brachycentridae | | | | | | | | | | | |
| <i>Brachycentrus sp.</i> | SV | No. | 0 | 0 | 23 | 0 | 13 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 | 0.0 | | | |
| <i>Micrasema sp.</i> | SV | No. | 65 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 10.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| Glossosomatidae | | | | | | | | | | | |
| <i>Agapetus sp.</i> | UV | No. | 19 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | | |
|-----------------------------|-----|-------------|-------|------|------|------|-------|-------|--|--|--|
| | | | 1980 | 1982 | 1985 | 1986 | 1987 | 1989 | | | |
| <i>Anagapetus sp.</i> | UV | No. | 112 | 0 | 93 | 641 | 1508 | 766 | | | |
| | | mg | 3.0 | 0.0 | 0.2 | 2.5 | 5.7 | 2.0 | | | |
| <i>Glossosoma sp.</i> | UV | No. | 9 | 64 | 0 | 13 | 40 | 19 | | | |
| | | mg | 6.1 | 0.1 | 0.0 | 1.3 | 4.1 | 0.7 | | | |
| Arctopsychidae | SV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Arctopsyche grandis</i> | SV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Parapsyche elsis</i> | SV | No. | 28 | 0 | 0 | 27 | 67 | 19 | | | |
| | | mg | 229.8 | 0.0 | 0.0 | 6.7 | 122.0 | 162.0 | | | |
| Hydropsychidae | MV | No. | 9 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 4.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Hydropsyche sp. A</i> | MV | No. | 9 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 13.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Hydropsyche oslari</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| Hydroptilidae | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Agraylea sp.</i> | UV | No. | 37 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 12.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Hydroptila sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| Lepidostomatidae | | | | | | | | | | | |
| <i>Lepidostoma sp.</i> | UV | No. | 0 | 12 | 0 | 0 | 107 | 0 | | | |
| | | mg | 0.0 | 8.8 | 0.0 | 0.0 | 0.1 | 0.0 | | | |
| Limnephilidae | | | | | | | | | | | |
| <i>Apatania sp.</i> | UV | No. | 28 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 7.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Ecclisocosmoecus sp.</i> | SV | No. | 19 | 0 | 0 | 0 | 0 | 37 | | | |
| | | mg | 57.9 | 0.0 | 0.0 | 0.0 | 0.0 | 73.1 | | | |
| <i>Ecclisomyia sp.</i> | UV | No. | 9 | 29 | 0 | 0 | 40 | 0 | | | |
| | | mg | 21.5 | 2.0 | 0.0 | 0.0 | 4.0 | 0.0 | | | |
| <i>Neophylax sp.</i> | UV | No. | 0 | 6 | 0 | 400 | 120 | 93 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 7.0 | 2.1 | 31.9 | | | |
| <i>Pedomoecus sp.</i> | UV | No. | 9 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 9.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Psychoglypha sp.</i> | SV | No. | 0 | 70 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 | | | |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | | |
|----------------------------|-----|-------------|--------|-------|-------|-------|-------|-------|--|--|--|
| | | | 1980 | 1982 | 1985 | 1986 | 1987 | 1989 | | | |
| Rhyacophilidae | | | | | | | | | | | |
| <i>Rhyacophila sp.</i> | SV | No. | 56 | 6 | 0 | 13 | 27 | 0 | | | |
| | | mg | 111.8 | 17.1 | 0.0 | 0.1 | 0.2 | 0.0 | | | |
| <i>R. arnaudi</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>R. Angelita Gr.</i> | UV | No. | 0 | 0 | 234 | 53 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 50.9 | 31.8 | 0.0 | 0.0 | | | |
| <i>R. Betteri Gr.</i> | SV | No. | 28 | 5 | 117 | 120 | 107 | 131 | | | |
| | | mg | 71.5 | 87.6 | 25.2 | 206.5 | 150.9 | 108.8 | | | |
| <i>R. Brunnea Gr.</i> | SV | No. | 84 | 6 | 23 | 0 | 27 | 19 | | | |
| | | mg | 326.0 | 3.0 | 2.3 | 0.0 | 22.0 | 9.7 | | | |
| <i>R. Coloradensis Gr.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>R. Hyalinata Gr.</i> | SV | No. | 37 | 12 | 222 | 27 | 0 | 19 | | | |
| | | mg | 164.4 | 29.8 | 63.2 | 14.0 | 0.0 | 1.5 | | | |
| <i>R. Rotunda Gr.</i> | SV | No. | 0 | 12 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 28.7 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>R. narvae</i> | SV | No. | 9 | 6 | 0 | 0 | 27 | 0 | | | |
| | | mg | 13.1 | 8.2 | 0.0 | 0.0 | 24.2 | 0.0 | | | |
| <i>R. valuma</i> | SV | No. | 28 | 6 | 0 | 0 | 0 | 75 | | | |
| | | mg | 26.5 | 1.5 | 0.0 | 0.0 | 0.0 | 10.8 | | | |
| <i>R. verrula</i> | SV | No. | 0 | 0 | 0 | 27 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 194.4 | 0.0 | 0.0 | | | |
| <i>R. vagrita</i> | UV | No. | 0 | 0 | 0 | 0 | 13 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 27.4 | 0.0 | | | |
| Uenoidae | | | | | | | | | | | |
| <i>Neothremma sp.</i> | SV | No. | 19 | 6 | 0 | 27 | 0 | 19 | | | |
| | | mg | 1.7 | 0.2 | 0.0 | 0.9 | 0.0 | 0.7 | | | |
| TRICHOPTERA | | No. | 617 | 238 | 712 | 1348 | 2095 | 1196 | | | |
| | | mg | 1092.0 | 187.5 | 141.9 | 465.1 | 362.9 | 401.1 | | | |
| Dytiscidae | SV | No. | 0 | 12 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 11.9 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| Hydrophilidae | SV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |

| TAXON | VLT | | SAMPLE YEAR | | | | | | | | | | | |
|------------------------|-----|-----|-------------|--|------|--|------|--|------|--|------|--|------|--|
| | | | 1980 | | 1982 | | 1985 | | 1986 | | 1987 | | 1989 | |
| Elmidae | | | | | | | | | | | | | | |
| <i>Narpus concolor</i> | SV | No. | 0 | | 0 | | 0 | | 0 | | 0 | | 0 | |
| | | mg | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | |
| COLEOPTERA | | No. | 0 | | 12 | | 0 | | 0 | | 0 | | 0 | |
| | | mg | 0.0 | | 11.9 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | |
| Ceratopogonidae | UV | No. | 131 | | 117 | | 140 | | 67 | | 160 | | 112 | |
| | | mg | 47.8 | | 9.5 | | 33.5 | | 23.8 | | 41.9 | | 32.1 | |
| Blephariceridae | UV | No. | 0 | | 0 | | 0 | | 0 | | 13 | | 0 | |
| | | mg | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | |
| Dixidae | | | | | | | | | | | | | | |
| <i>Dixa sp.</i> | UV | No. | 9 | | 6 | | 0 | | 27 | | 0 | | 56 | |
| | | mg | 12.1 | | 0.1 | | 0.0 | | 0.7 | | 0.0 | | 8.1 | |
| Empididae | UV | No. | 19 | | 0 | | 0 | | 0 | | 0 | | 0 | |
| | | mg | 3.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | |
| <i>Chelifera sp.</i> | UV | No. | 9 | | 12 | | 0 | | 0 | | 0 | | 19 | |
| | | mg | 1.0 | | 2.6 | | 0.0 | | 0.0 | | 0.0 | | 6.4 | |
| <i>Clinocera sp.</i> | UV | No. | 37 | | 35 | | 23 | | 0 | | 13 | | 0 | |
| | | mg | 8.1 | | 2.0 | | 0.4 | | 0.0 | | T | | 0.0 | |
| <i>Oreogeton sp.</i> | UV | No. | 47 | | 41 | | 0 | | 80 | | 53 | | 224 | |
| | | mg | 24.7 | | 4.3 | | 0.0 | | 1.8 | | 1.7 | | 18.8 | |
| Muscidae | UV | No. | 0 | | 0 | | 0 | | 0 | | 13 | | 0 | |
| | | mg | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 4.5 | | 0.0 | |
| Pelecorhynchidae | UV | No. | 0 | | 6 | | 0 | | 0 | | 0 | | 0 | |
| | | mg | 0.0 | | 3.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | |
| Psychodidae | | | | | | | | | | | | | | |
| <i>Pericoma sp.</i> | UV | No. | 28 | | 6 | | 23 | | 0 | | 13 | | 206 | |
| | | mg | 1.4 | | 0.1 | | 0.4 | | 0.0 | | 0.2 | | 1.8 | |
| Simuliidae | MV | No. | 47 | | 6 | | 0 | | 53 | | 40 | | 112 | |
| | | mg | 5.8 | | 1.3 | | 0.0 | | 1.2 | | 15.9 | | 4.0 | |
| Thaumaleidae | UV | No. | 9 | | 0 | | 0 | | 0 | | 0 | | 0 | |
| | | mg | 14.9 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | |
| Tipulidae | UV | No. | 0 | | 0 | | 0 | | 0 | | 0 | | 37 | |
| | | mg | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 3.5 | |
| <i>Antocha sp.</i> | UV | No. | 28 | | 18 | | 0 | | 0 | | 27 | | 0 | |
| | | mg | 1.8 | | 2.9 | | 0.0 | | 0.0 | | 26.7 | | 0.0 | |
| <i>Dicranota sp.</i> | UV | No. | 28 | | 6 | | 70 | | 80 | | 93 | | 187 | |
| | | mg | 4.1 | | 0.1 | | 1.1 | | 1.1 | | 4.5 | | 8.9 | |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | | |
|--------------------------|-----|-------------|-------|------|------|------|-------|-------|--|--|-----|
| | | | 1980 | 1982 | 1985 | 1986 | 1987 | 1989 | | | |
| <i>Erioptera sp.</i> | UV | No. | 0 | 12 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 17.3 | 0.0 | 0.0 | 0.0 | 0.0 | | | 0.0 |
| <i>Hesperoconopa sp.</i> | UV | No. | 0 | 0 | 47 | 13 | 27 | 56 | | | |
| | | mg | 0.0 | 0.0 | 0.7 | 0.2 | 5.7 | 5.3 | | | |
| <i>Hexatoma sp. A</i> | SV | No. | 19 | 18 | 47 | 53 | 13 | 9 | | | |
| | | mg | 27.7 | 6.0 | 36.4 | 31.0 | 5.5 | 18.1 | | | |
| <i>Hexatoma sp. B</i> | SV | No. | 0 | 6 | 0 | 27 | 0 | 37 | | | |
| | | mg | 0.0 | 3.8 | 0.0 | 11.3 | 0.0 | 8.6 | | | |
| <i>Ormosia sp.</i> | UV | No. | 0 | 0 | 0 | 0 | 0 | 19 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.3 | | | |
| <i>Rhabdomastix sp.</i> | UV | No. | 19 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 14.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| DIPTERA (non-midge) | | No. | 430 | 286 | 350 | 400 | 467 | 1074 | | | |
| | | mg | 167.4 | 52.7 | 72.5 | 71.1 | 106.9 | 118.9 | | | |
| Chironomidae | | | | | | | | | | | |
| <i>Brillia</i> | MV | No. | 65 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 2.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Chaetocladius</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| Chironomini | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Corynoneura</i> | MV | No. | 19 | 0 | 152 | 128 | 0 | 0 | | | |
| | | mg | 0.4 | 0.0 | 1.8 | 1.0 | 0.0 | 0.0 | | | |
| <i>Cricotopus</i> | MV | No. | 93 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 6.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>C. bicinctus</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>C. nostocicola</i> | MV | No. | 140 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 8.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>C. tremulus</i> | MV | No. | 121 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 6.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>C. triannulatus</i> | MV | No. | 37 | 0 | 0 | 0 | 0 | 0 | | | |
| | | mg | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | | | |
| <i>Diamesa</i> | UV | No. | 9 | 0 | 0 | 70 | 0 | 0 | | | |
| | | mg | 0.4 | 0.0 | 0.0 | 40.5 | 0.0 | 0.0 | | | |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | | |
|--|-----|-------------|------|------|------|------|------|------|-----|-----|-----|
| | | | 1980 | 1982 | 1985 | 1986 | 1987 | 1989 | | | |
| <i>Eukiefferiella</i> | MV | No. | 75 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | | mg | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>E. clari pennis</i> | MV | No. | 56 | 0 | 58 | 280 | 0 | 0 | 0 | | |
| | | mg | 0.8 | 0.0 | 0.5 | 1.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>E. coerulescens</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>E. cyanea</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>E. devonica</i> | MV | No. | 9 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | | mg | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>E. gracei</i> | MV | No. | 383 | 0 | 117 | 140 | 0 | 0 | 0 | | |
| | | mg | 6.4 | 0.0 | 0.4 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Heleniella</i> | MV | No. | 0 | 0 | 0 | 280 | 0 | 0 | 0 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Hydrobaenus</i> | MV | No. | 9 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | | mg | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Krenosmittia</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Micropectra</i> | MV | No. | 9 | 0 | 93 | 1074 | 0 | 0 | 0 | | |
| | | mg | 1.0 | 0.0 | 1.1 | 5.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Odontomesa</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Orthocladus-Cricotopus A</i> | MV | No. | 140 | 0 | 152 | 163 | 0 | 0 | 0 | | |
| | | mg | 4.8 | 0.0 | 7.2 | 2.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Orthocladus-Cricotopus B</i> | MV | No. | 0 | 0 | 0 | 23 | 0 | 0 | 0 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Orthocladus</i> (<i>Euorthocladus</i>) A | MV | No. | 0 | 0 | 0 | 23 | 0 | 0 | 0 | | |
| | | mg | 0.0 | 0.0 | 0.0 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Orthocladus</i> (<i>Euorthocladus</i>) B | MV | No. | 19 | 0 | 0 | 199 | 0 | 0 | 0 | | |
| | | mg | 2.1 | 0.0 | 0.0 | 4.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Pagastia</i> | MV | No. | 9 | 0 | 35 | 175 | 0 | 0 | 0 | | |
| | | mg | 1.5 | 0.0 | 4.3 | 24.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Parachaetocladus</i> | MV | No. | 9 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| | | mg | 1.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

| TAXON | VLT | SAMPLE YEAR | | | | | | | | | | | |
|--------------------------|-----|-------------|------|--|------|--|------|--|------|--|------|--|------|
| | | | 1980 | | 1982 | | 1985 | | 1986 | | 1987 | | 1989 |
| <i>Paracladopelma</i> | MV | No. | 0 | | 0 | | 0 | | 0 | | 0 | | 0 |
| | | mg | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 |
| <i>Parakiefferiella</i> | MV | No. | 56 | | 0 | | 0 | | 0 | | 0 | | 0 |
| | | mg | 0.7 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 |
| <i>Parametriocnemus</i> | MV | No. | 9 | | 0 | | 35 | | 47 | | 0 | | 0 |
| | | mg | 0.2 | | 0.0 | | 2.8 | | 0.3 | | 0.0 | | 0.0 |
| <i>Paraphaenocladus</i> | MV | No. | 0 | | 0 | | 35 | | 0 | | 0 | | 0 |
| | | mg | 0.0 | | 0.0 | | 1.9 | | 0.0 | | 0.0 | | 0.0 |
| <i>Parochlus</i> | MV | No. | 0 | | 0 | | 0 | | 0 | | 0 | | 0 |
| | | mg | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 |
| <i>Parorthocladus</i> | MV | No. | 0 | | 0 | | 23 | | 0 | | 0 | | 0 |
| | | mg | 0.0 | | 0.0 | | 0.8 | | 0.0 | | 0.0 | | 0.0 |
| <i>Polypeditum</i> | MV | No. | 0 | | 0 | | 0 | | 35 | | 0 | | 0 |
| | | mg | 0.0 | | 0.0 | | 0.0 | | 0.1 | | 0.0 | | 0.0 |
| <i>Psectrocladius</i> | MV | No. | 0 | | 0 | | 0 | | 0 | | 0 | | 0 |
| | | mg | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 |
| <i>Pseudodiamesa</i> | MV | No. | 0 | | 0 | | 0 | | 0 | | 0 | | 0 |
| | | mg | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 |
| <i>Rheocricotopus</i> | MV | No. | 0 | | 0 | | 0 | | 35 | | 0 | | 0 |
| | | mg | 0.0 | | 0.0 | | 0.0 | | 1.9 | | 0.0 | | 0.0 |
| <i>Rheotanytarsus</i> | MV | No. | 9 | | 0 | | 0 | | 0 | | 0 | | 0 |
| | | mg | 0.2 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 |
| <i>Stempellina</i> | MV | No. | 0 | | 0 | | 23 | | 514 | | 0 | | 0 |
| | | mg | 0.0 | | 0.0 | | 0.2 | | 1.4 | | 0.0 | | 0.0 |
| <i>Stempellinella</i> | MV | No. | 19 | | 0 | | 759 | | 479 | | 0 | | 0 |
| | | mg | 0.3 | | 0.0 | | 5.6 | | 1.4 | | 0.0 | | 0.0 |
| <i>Synorthocladus</i> | MV | No. | 19 | | 0 | | 0 | | 0 | | 0 | | 0 |
| | | mg | 1.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 | | 0.0 |
| <i>Tanytarsus</i> | MV | No. | 37 | | 0 | | 0 | | 2406 | | 0 | | 0 |
| | | mg | 0.2 | | 0.0 | | 0.0 | | 16.5 | | 0.0 | | 0.0 |
| <i>Thienemaniella</i> | MV | No. | 9 | | 0 | | 152 | | 58 | | 0 | | 0 |
| | | mg | 0.0 | | 0.0 | | 3.7 | | 1.1 | | 0.0 | | 0.0 |
| <i>Thienemannimyia</i> | MV | No. | 19 | | 0 | | 747 | | 701 | | 0 | | 0 |
| | | mg | 1.7 | | 0.0 | | 25.4 | | 47.3 | | 0.0 | | 0.0 |
| <i>Tveteria bavarica</i> | MV | No. | 243 | | 0 | | 152 | | 479 | | 0 | | 0 |
| | | mg | 6.7 | | 0.0 | | 3.4 | | 13.4 | | 0.0 | | 0.0 |

| TAXON | VLT | SAMPLE YEAR | | | | | | |
|------------------------------------|-----|-------------|--------|-------|--------|--------|--------|--------|
| | | | 1980 | 1982 | 1985 | 1986 | 1987 | 1989 |
| <i>T. discoloripes</i> | MV | No. | 0 | 0 | 23 | 47 | 0 | 0 |
| | | mg | 16.4 | 0.0 | 0.2 | 0.9 | 0.0 | 0.0 |
| <i>Zavreliomyia</i> | MV | No. | 0 | 0 | 0 | 0 | 0 | 0 |
| | | mg | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| DIPTERA (midge) | | No. | 1626 | 7602 | 2557 | 7357 | 4190 | 5456 |
| | | mg | 72.2 | 213.5 | 59.3 | 168.9 | 115.1 | 134.5 |
| ALL DIPTERA | | No. | 2055 | 7888 | 2908 | 7757 | 4657 | 6530 |
| | | mg | 239.6 | 266.2 | 131.8 | 240.0 | 221.9 | 253.4 |
| Acari | | No. | 243 | 111 | 397 | 948 | 841 | 504 |
| | | mg | 4.9 | 2.2 | 7.9 | 19.0 | 16.8 | 10.1 |
| Oligochaete | | No. | 19 | 187 | 1214 | 454 | 187 | 747 |
| | | mg | 1.5 | 14.5 | 94.7 | 35.4 | 14.7 | 58.3 |
| MISCELLANEOUS | | No. | 262 | 298 | 1611 | 1401 | 1028 | 1252 |
| | | mg | 6.4 | 16.8 | 102.6 | 54.4 | 34.5 | 68.4 |
| GRAND TOTAL (Insects only) | | No. | 3914 | 9715 | 14737 | 40548 | 30355 | 29717 |
| | | mg | 1871.6 | 874.0 | 963.7 | 1643.0 | 1632.0 | 1712.8 |
| GRAND TOTAL (All invertebrates) | | No. | 4176 | 10012 | 16349 | 41949 | 31382 | 30969 |
| | | mg | 1925.8 | 890.8 | 1099.9 | 1721.1 | 1705.4 | 1813.3 |

Appendix C. Mean annual density (No./m²) and biomass (mg dry wt/m²) for each taxon at Clearwater and Elk Creeks in 1985 and 1986. CC = Clearwater Creek; EK = Elk Creek. * - indicates grazer taxa. T = 0.5 < animals/m² or < 0.05 mg/m². unk = unidentifiable early instars. Note: Taeniopterygidae includes both Taenionema sp. and Doddsia sp.

| TAXON | | | 1985 | | 1986 | |
|------------------------------|---|-----|------|-------|-------|-------|
| | | | CC | ELK | CC | ELK |
| Baetidae | | | | | | |
| <i>Baetis bicaudatus</i> | * | No. | 1059 | 73 | 2187 | 311 |
| | | mg | 57.0 | 16.1 | 68.7 | 35.5 |
| <i>B. tricaudatus</i> | * | No. | 300 | 40 | 3453 | 368 |
| | | mg | 22.9 | 3.5 | 167.9 | 20.8 |
| Ephemerellidae | | | | | | |
| <i>Drunella coloradensis</i> | * | No. | 2 | 9 | 25 | 25 |
| | | mg | 17.9 | 30.0 | 165.8 | 157.4 |
| <i>D. doddsi</i> | | No. | 0 | 27 | 4 | 21 |
| | | mg | 0.0 | 1.5 | 0.7 | 42.6 |
| <i>D. spinifera</i> | | No. | 0 | 4 | 173 | 1 |
| | | mg | 0.0 | 0.2 | 162.2 | T |
| <i>Ephemerella</i> | | No. | 600 | 586 | 2377 | 362 |
| | | mg | 6.1 | 4.0 | 28.7 | 1.9 |
| <i>Serratella sp. A</i> | * | No. | 0 | 7 | 0 | 33 |
| | | mg | 0.0 | 0.7 | 0.0 | 6.5 |
| <i>S. tibialis</i> | * | No. | 31 | 0 | 171 | 0 |
| | | mg | 23.6 | 0.0 | 133.7 | 0.0 |
| Heptageniidae | | | | | | |
| <i>Cinygmula sp.</i> | * | No. | 347 | 1589 | 5038 | 5196 |
| | | mg | 17.3 | 126.7 | 160.6 | 220.7 |
| <i>Epeorus spp.</i> | * | No. | 0 | 185 | 347 | 691 |
| | | mg | 0.0 | 5.4 | 7.8 | 4.7 |
| <i>Epeorus albertae</i> | * | No. | 15 | 0 | 0 | 0 |
| | | mg | 6.4 | 0.0 | 0.0 | 0.0 |
| <i>E. deceptivus</i> | * | No. | 0 | 19 | 2 | 10 |
| | | mg | 0.0 | 3.0 | 0.8 | 7.8 |
| <i>E. grandis</i> | * | No. | 10 | 0 | 0 | 0 |
| | | mg | 0.2 | 0.0 | 0.0 | 0.0 |
| <i>E. longimanus</i> | * | No. | 16 | 9 | 14 | 15 |
| | | mg | 6.1 | 0.7 | 8.1 | 4.1 |
| <i>E. sp. A</i> | * | No. | 1 | 5 | 6 | 48 |
| | | mg | 0.7 | 0.8 | 4.3 | 52.9 |
| <i>Rhythrogena</i> | * | No. | 96 | 139 | 209 | 464 |
| | | mg | 21.2 | 40.6 | 24.0 | 180.3 |
| Leptophlebiidae | | | | | | |
| <i>P. temporalis</i> | | No. | 506 | 405 | 9062 | 1221 |
| | | mg | 10.7 | 20.8 | 164.8 | 38.3 |
| Siphonuridae | | | | | | |
| <i>Ameletus spp.</i> | * | No. | 120 | 358 | 470 | 479 |
| | | mg | 29.4 | 120.8 | 68.6 | 74.5 |

| TAXON | | 1985 | | 1986 | |
|-----------------------|-----|-------|-------|--------|-------|
| | | CC | ELK | CC | ELK |
| EPHEMEROPTERA | No. | 3102 | 3454 | 23763 | 9242 |
| | mg | 219.5 | 374.7 | 1166.7 | 847.9 |
| Capniidae | No. | 1 | 945 | 107 | 974 |
| | mg | 0.4 | 14.4 | 14.5 | 9.5 |
| Chloroperlidae | | | | | |
| <i>Sweltsa</i> | No. | 4 | 0 | 57 | 0 |
| | mg | 1.5 | 0.0 | 17.3 | 0.0 |
| Leuctridae | No. | 26 | 64 | 5 | 88 |
| | mg | 0.9 | 2.3 | 0.5 | 6.2 |
| Nemouridae (unk.) | No. | 0 | 205 | 1 | 338 |
| | mg | 0.0 | 0.2 | T | 0.3 |
| <i>Malenka</i> | No. | 0 | 0 | 0 | 0 |
| | mg | 0.2 | 0.0 | 0.0 | 0.0 |
| <i>Prostoia</i> | No. | 1005 | 0 | 133 | 0 |
| | mg | 0.2 | 0.0 | T | 0.0 |
| <i>Visoka</i> | No. | 0 | 59 | 0 | 40 |
| | mg | 0.0 | 3.2 | 0.0 | 2.2 |
| <i>Zapada spp.</i> | No. | 1 | 29 | 198 | 82 |
| | mg | T | 0.2 | 1.7 | 0.6 |
| <i>Z. cinctipes</i> | No. | 4 | 7 | 45 | 4 |
| | mg | T | 0.2 | 1.1 | T |
| <i>Z. columbiana</i> | No. | 10.0 | 47 | 9.0 | 40 |
| | mg | 0 | 2.7 | 0 | 3.3 |
| Peltoperlidae | | | | | |
| <i>Yora perla sp.</i> | No. | 3 | 589 | 8 | 874 |
| | mg | 0.1 | 29.1 | 0.4 | 101.3 |
| Perlidae (unk.) | No. | 0 | 45 | 0 | 116 |
| | mg | 0.0 | 5.7 | 0.0 | 16.8 |
| <i>Calineuria sp.</i> | No. | 1 | 2 | 8 | 6 |
| | mg | 0.1 | 8.0 | 0.7 | 6.5 |
| <i>Doroneuria sp.</i> | No. | 0 | 0 | 0 | 2 |
| | mg | 0.0 | 0.0 | 0.0 | 8.6 |
| Perlodidae (unk.) | No. | 6 | 6 | 150 | 9 |
| | mg | 3.7 | 0.2 | 4.5 | 0.2 |
| <i>Cultus sp.</i> | No. | 42 | 6 | 759 | 17 |
| | mg | 3.0 | 0.3 | 53.0 | 0.8 |
| <i>Megarcys sp.</i> | No. | 11 | 103 | 37 | 123 |
| | mg | 27.5 | 26.6 | 98.2 | 107.4 |

| TAXON | | 1985 | | 1986 | |
|-----------------------------|-----|------|-------|-------|-------|
| | | CC | ELK | CC | ELK |
| <i>Skwala sp.</i> | No. | 82 | 43 | 137 | 84 |
| | mg | 21.0 | 7.9 | 130.9 | 35.0 |
| Taeniopterygidae | No. | 1538 | 3216 | 1759 | 5548 |
| | mg | 21.3 | 35.7 | 18.7 | 42.3 |
| PLECOPTERA | No. | 2725 | 5367 | 3413 | 8156 |
| | mg | 80.0 | 136.7 | 341.8 | 340.9 |
| Brachycentridae | | | | | |
| <i>Brachycentrus sp.</i> | No. | 0 | 6 | 15 | 0 |
| | mg | 0.0 | T | T | 0.0 |
| <i>Micrasema sp.</i> | No. | 0 | 0 | 0 | 2 |
| | mg | 0.0 | 0.0 | 0.0 | T |
| Glossosomatidae | | | | | |
| <i>Anaga petus sp.</i> | No. | 1 | 56 | 3 | 150 |
| | mg | T | 0.7 | T | 1.1 |
| <i>Glossosoma sp.</i> | No. | 0 | 7 | 2 | 6 |
| | mg | T | 1.1 | T | 0.8 |
| Arctopsychidae | | | | | |
| <i>Arctopsyche grandis</i> | No. | 2 | 3 | 1 | 0 |
| | mg | 0.1 | 0.5 | 10.5 | 0.0 |
| <i>Parapsyche elsis</i> | No. | 0 | 2 | 1 | 23 |
| | mg | 0.0 | 9.3 | 7.1 | 29.1 |
| Hydropsychidae | | | | | |
| <i>Hydropsyche sp.</i> | No. | 7 | 1 | 37 | 1 |
| | mg | 1.3 | 0.4 | 15.8 | 0.6 |
| Hydroptilidae (unk.) | No. | 1 | 0 | 21 | 1 |
| | mg | T | 0.0 | 0.4 | 0.6 |
| <i>Agraylea sp.</i> | No. | 2 | 0 | 3 | 0 |
| | mg | T | 0.0 | T | 0.0 |
| <i>Hydroptila sp.</i> | No. | 2 | 0 | 9 | 0 |
| | mg | T | 0.0 | 0.2 | 0.0 |
| Lepidostomatidae | | | | | |
| <i>Lepidostoma sp.</i> | No. | 6 | 43 | 19 | 67 |
| | mg | T | 0.1 | 0.9 | 1.1 |
| Limnephilidae | | | | | |
| <i>Apatania sp.</i> | No. | 0 | 0 | 1 | 2 |
| | mg | 0.0 | 0.0 | 0.1 | 0.2 |
| <i>Ecclisocosmoecus sp.</i> | No. | 0 | 6 | 0 | 2 |
| | mg | 0.0 | 38.4 | 0.0 | 6.3 |

| TAXON | | | 1985 | | 1986 | |
|---------------------------|---|-----|------|-------|------|-------|
| | | | CC | ELK | CC | ELK |
| <i>Ecclisomyia</i> sp. | * | No. | 4 | 90 | 13 | 161 |
| | | mg | 1.8 | 10.5 | 3.5 | 13.2 |
| <i>Neophylax</i> sp. | * | No. | 2 | 18 | 4 | 98 |
| | | mg | 0.3 | 0.2 | 0.6 | 1.9 |
| <i>Oligophlebodes</i> sp. | * | No. | 1 | 10 | 0 | 2 |
| | | mg | 0.1 | 1.0 | 0.0 | 0.4 |
| <i>Pedomoecus</i> sp. | * | No. | 0 | 19 | 5 | 8 |
| | | mg | 0.0 | 1.0 | T | 1.8 |
| <i>Psychoglypha</i> sp. | * | No. | 0 | 0 | 0 | 4 |
| | | mg | 0.0 | 0.0 | 0.0 | 3.8 |
| <i>Rhyacophilidae</i> | | | | | | |
| <i>R. Alberta</i> Gr. | | No. | 1 | 0 | 0 | 0 |
| | | mg | 1.5 | 0.0 | 0.0 | 0.0 |
| <i>R. Angelita</i> Gr. | | No. | 11 | 53 | 16 | 30 |
| | | mg | 35.8 | 9.2 | 38.2 | 13.1 |
| <i>R. Betteni</i> Gr. | | No. | 4 | 55 | 5 | 60 |
| | | mg | 1.8 | 42.5 | 2.7 | 59.5 |
| <i>R. Brunnea</i> Gr. | | No. | 3 | 47 | 5 | 4 |
| | | mg | 0.8 | 15.3 | 6.4 | 5.1 |
| <i>R. Hyalinata</i> Gr. | | No. | 3 | 68 | 4 | 16 |
| | | mg | 4.0 | 29.9 | 0.3 | 10.7 |
| <i>R. Iranda</i> Gr. | | No. | 0 | 6 | 0 | 7 |
| | | mg | 0.0 | 7.7 | 0.0 | 13.5 |
| <i>R. Nevadensis</i> Gr. | | No. | 0 | 0 | T | 4 |
| | | mg | 0.0 | 0.0 | 1.3 | 16.4 |
| <i>R. Rotunda</i> Gr. | | No. | 1 | 0 | 0 | 0 |
| | | mg | 1.0 | 0.0 | 0.0 | 0.0 |
| <i>R. narvae</i> | | No. | 0 | 34 | 0 | 17 |
| | | mg | 0.0 | 22.6 | 0.0 | 14.1 |
| <i>R. verrula</i> | | No. | 1 | 4 | 0 | 7 |
| | | mg | 4.6 | 20.8 | 0.0 | 53.8 |
| <i>R. vagrita</i> | | No. | 8 | 3 | 4 | 25 |
| | | mg | 8.5 | 6.8 | 6.1 | 9.2 |
| <i>Uenoidae</i> | | | | | | |
| <i>Neothremma</i> sp. | * | No. | 0 | 6 | 0 | 15 |
| | | mg | 0.0 | 0.4 | 0.0 | 0.5 |
| TRICHOPTERA | | | | | | |
| | | No. | 57 | 538 | 168 | 710 |
| | | mg | 61.7 | 218.5 | 94.1 | 256.9 |

| TAXON | | 1985 | | 1986 | |
|------------------|-----|------|------|------|------|
| | | CC | ELK | CC | ELK |
| Dytiscidae | | | | | |
| Adult | No. | 2 | 10 | 5 | 0 |
| | mg | 0.9 | 6.2 | 1.8 | 0.3 |
| Larvae | No. | 42 | 0 | 34 | 1 |
| | mg | 24.6 | 0.0 | 16.0 | 0.2 |
| Hydrophilidae | | | | | |
| Adult | No. | 4 | 0 | 0 | 0 |
| | mg | 5.7 | 0.0 | 0.0 | 0.0 |
| Larvae | No. | 3 | 0 | 1 | 1 |
| | mg | 2.0 | 0.0 | 0.1 | 0.1 |
| Elmidae | | | | | |
| Adult | No. | 0 | 0 | 4 | 2 |
| | mg | 0.0 | 0.0 | 7.5 | 2.7 |
| Larvae | No. | 0 | 0 | 0 | T |
| | mg | 0.0 | 0.0 | 0.0 | 0.1 |
| COLEOPTERA | No. | 52 | 10 | 45 | 4 |
| | mg | 33.2 | 6.2 | 25.5 | 3.3 |
| Ceratopogonidae | No. | 35 | 200 | 56 | 216 |
| | mg | 1.9 | 30.7 | 3.7 | 44.2 |
| Blephariceridae | No. | 0 | 4 | 0 | 3 |
| | mg | 0.0 | 0.2 | 0.0 | 0.6 |
| Empididae | | | | | |
| <i>Chelifera</i> | No. | 5 | 5 | 1 | 3 |
| | mg | 0.5 | 0.4 | T | T |
| <i>Clinocera</i> | No. | 49 | 17 | 232 | 23 |
| | mg | 6.5 | 0.6 | 14.5 | 1.8 |
| <i>Oreogeton</i> | No. | 1 | 68 | 2 | 43 |
| | mg | T | 4.8 | 0.2 | 2.2 |
| Muscidae | No. | 21 | 1 | 14 | 0 |
| | mg | 14.8 | T | 4.2 | 0.0 |
| Pelecorhynchidae | No. | 0 | 4 | 0 | 5 |
| | mg | 0.0 | 4.3 | 0.0 | 5.8 |
| Psychodidae | | | | | |
| <i>Pericoma</i> | No. | 0 | 9 | 0 | 5 |
| | mg | 0.0 | 1.1 | 0.0 | 0.1 |
| Simuliidae | No. | 74 | 14 | 261 | 15 |
| | mg | 6.8 | 0.3 | 7.6 | 4.1 |

| TAXON | | | 1985 | | 1986 | |
|--------------------------|---|-----|-------|-------|-------|-------|
| | | | CC | ELK | CC | ELK |
| Tipulidae | | | | | | |
| <i>Antocha sp.</i> | * | No. | 0 | 2 | 0 | 0 |
| | | mg | 0.0 | 0.5 | 0.0 | 0.1 |
| <i>Dicranota sp.</i> | | No. | 28 | 144 | 90 | 219 |
| | | mg | 1.7 | 18.1 | 37.7 | 32.3 |
| <i>Erioptera sp.</i> | * | No. | 104 | 34 | 90 | 9 |
| | | mg | 82.5 | 31.4 | 90.5 | 8.0 |
| <i>Hesperoconopa sp.</i> | * | No. | 146 | 64 | 66 | 82 |
| | | mg | 57.9 | 8.7 | 42.5 | 11.1 |
| <i>Hexatoma sp. A</i> | | No. | 11 | 59 | 28 | 69 |
| | | mg | 5.2 | 31.2 | 21.7 | 29.2 |
| <i>Hexatoma sp. B</i> | | No. | 0 | 36 | 3 | 3 |
| | | mg | 0.0 | 10.3 | 6.0 | 0.8 |
| <i>Limonia sp.</i> | | No. | 0 | 4 | 0 | 0 |
| | | mg | 0.0 | 0.1 | 0.0 | 0.0 |
| <i>Ormosia sp.</i> | | No. | 4 | 4 | 0 | 0 |
| | | mg | 0.2 | 0.4 | 0.0 | 0 |
| <i>Rhabdomastix sp.</i> | | No. | 0 | 4 | 0 | 0 |
| | | mg | 0.0 | 0.7 | 0.0 | 0.0 |
| DIPTERA (non-midge) | | No. | 479 | 675 | 842 | 694 |
| | | mg | 177.9 | 143.9 | 228.4 | 140.2 |
| Chironomidae | | | | | | |
| <i>Brillia</i> | | No. | 1 | 4 | 1 | 4 |
| | | mg | T | 0.3 | T | 0.4 |
| <i>Chaetocladius</i> | * | No. | 9 | 0 | 0 | 0 |
| | | mg | 0.5 | 0.0 | 0.0 | 0.0 |
| <i>Corynoneura</i> | * | No. | 114 | 319 | 1244 | 319 |
| | | mg | 1.4 | 2.9 | 13.8 | 2.9 |
| <i>Cricotopus</i> | | No. | 1 | 0 | 1 | 8 |
| | | mg | T | 0.0 | T | 0.4 |
| <i>C. bicinctus</i> | | No. | 1 | 0 | 0 | 0 |
| | | mg | T | 0.0 | 0.0 | 0.0 |
| <i>C. tremulus</i> | | No. | 69 | 13 | 167 | 22 |
| | | mg | 9.3 | 1.4 | 10.9 | 1.4 |
| <i>Diamesa</i> | * | No. | 105 | 18 | 38 | 158 |
| | | mg | 5.1 | 3.3 | 2.4 | 91.0 |
| <i>Eukiefferiella</i> | * | No. | 4 | 0 | 98 | 26 |
| | | mg | T | 0.0 | 0.6 | 0.1 |

| TAXON | | | 1985 | | 1986 | |
|--|---|-----|------|------|-------|------|
| | | | CC | ELK | CC | ELK |
| <i>E. claripennis</i> | * | No. | 65 | 210 | 596 | 79 |
| | | mg | 0.9 | 1.3 | 6.8 | 0.8 |
| <i>E. cyanea</i> | * | No. | 1 | 0 | 0 | 0 |
| | | mg | T | 0.0 | 0.0 | 0.0 |
| <i>E. devonica</i> | * | No. | 2 | 9 | 0 | 0 |
| | | mg | 0.1 | 0.5 | 0.0 | 0.0 |
| <i>E. gracei</i> | * | No. | 248 | 324 | 787 | 412 |
| | | mg | 5.7 | 5.2 | 8.9 | 8.7 |
| <i>Euryhapsis</i> | | No. | 1 | 0 | 0 | 0 |
| | | mg | 0.1 | 0.0 | 0.0 | 0.0 |
| <i>Heleniella</i> | | No. | 6 | 89 | 38 | 356 |
| | | mg | 0.3 | 1.7 | 0.6 | 8.5 |
| <i>Hydrobaenus</i> | * | No. | 1 | 0 | 0 | 11 |
| | | mg | T | 0.0 | 0.0 | 0.2 |
| <i>Krenosmittia</i> | * | No. | 141 | 83 | 133 | 62 |
| | | mg | 7.9 | 2.7 | 5.8 | 3.1 |
| <i>Lopescladius</i> | * | No. | 0 | 0 | 3 | 0 |
| | | mg | 0.0 | 0.0 | T | 0.0 |
| <i>Micropectra</i> | * | No. | 676 | 1198 | 9250 | 2188 |
| | | mg | 13.6 | 16.4 | 137.1 | 34.6 |
| <i>Odontomesa</i> | * | No. | 0 | 0 | 3 | 0 |
| | | mg | 0.0 | 0.0 | 0.1 | 0.0 |
| <i>Orthocladus- Cricotopus A</i> | * | No. | 454 | 148 | 2869 | 223 |
| | | mg | 27.4 | 5.0 | 48.1 | 3.5 |
| <i>Orthocladus- Cricotopus B</i> | * | No. | 13 | 19 | 554 | 15 |
| | | mg | 0.7 | 0.9 | 9.6 | 1.2 |
| <i>Orthocladus (Euorthocladus) A</i> | * | No. | 196 | 0 | 1272 | 11 |
| | | mg | 10.2 | 0.0 | 32.7 | 0.3 |
| <i>Orthocladus (Euorthocladus) B</i> | * | No. | 668 | 73 | 2999 | 125 |
| | | mg | 24.2 | 0.8 | 43.9 | 7.3 |
| <i>Pagastia</i> | * | No. | 29 | 16 | 287 | 82 |
| | | mg | 3.5 | 2.5 | 40.4 | 4.4 |
| <i>Parakiefferiella</i> | * | No. | 10 | 0 | 0 | 0 |
| | | mg | 0.6 | 0.0 | 0.0 | 0.0 |
| <i>Parametriocnemus</i> | * | No. | 49 | 63 | 962 | 128 |
| | | mg | 4.0 | 3.1 | 73.0 | 7.2 |

| TAXON | | | 1985 | | 1986 | |
|--------------------------|---|-----|------|------|-------|------|
| | | | CC | ELK | CC | ELK |
| <i>Paraphaenocladus</i> | * | No. | 6 | 31 | 0 | 0 |
| | | mg | 0.8 | 2.8 | 0.0 | 0.0 |
| <i>Parorthocladus</i> | * | No. | 14 | 63 | 51 | 91 |
| | | mg | 0.5 | 3.3 | 2.1 | 3.3 |
| <i>Polypedilum</i> | | No. | 34 | 18 | 62 | 25 |
| | | mg | 0.4 | 0.1 | 0.6 | 0.1 |
| <i>Psectrocladus</i> | * | No. | 2 | 3 | 36 | 0 |
| | | mg | T | 0.1 | 1.0 | 0.0 |
| <i>Pseudodiamesa</i> | * | No. | 2 | 8 | 8 | 0 |
| | | mg | 0.2 | 0.2 | 0.2 | 0.0 |
| <i>Pseudoorthocladus</i> | * | No. | 0 | 3 | 0 | 25 |
| | | mg | 0.0 | 2.1 | 0.0 | 14.5 |
| <i>Rheocricotopus</i> | * | No. | 4 | 26 | 287 | 95 |
| | | mg | T | 1.4 | 3.6 | 1.9 |
| <i>Rheosmitia</i> | * | No. | 2 | 958 | 3 | 307 |
| | | mg | 0.1 | 13.3 | 0.1 | 6.2 |
| <i>Rheotanytarsus</i> | | No. | 2 | 15 | 0 | 0 |
| | | mg | T | 0.7 | 0.0 | 0.0 |
| <i>Smitia</i> | * | No. | 1 | 0 | 0 | 0 |
| | | mg | 0.1 | 0.0 | 0.0 | 0.0 |
| <i>StemPELLina</i> | * | No. | 0 | 3 | 0 | 397 |
| | | mg | 0.0 | 2.9 | 0.0 | 1.9 |
| <i>StemPELLinella</i> | * | No. | 21 | 854 | 153 | 1949 |
| | | mg | 0.5 | 5.1 | 1.1 | 15.4 |
| <i>Symposiocladius</i> | | No. | 0 | 0 | 10 | 0 |
| | | mg | 0.0 | 0.0 | T | 0.2 |
| <i>Synorthocladus</i> | * | No. | 0 | 0 | 13 | 14 |
| | | mg | 0.0 | 0.0 | 0.1 | 1.0 |
| <i>Tanytarsus</i> | | No. | 536 | 61 | 6332 | 4023 |
| | | mg | 4.6 | 1.6 | 104.3 | 23.4 |
| <i>Thienemaniella</i> | * | No. | 29 | 135 | 345 | 111 |
| | | mg | 0.7 | 2.4 | 6.4 | 1.8 |
| <i>Thienemannimyia</i> | | No. | 25 | 452 | 420 | 489 |
| | | mg | 0.8 | 19.9 | 40.1 | 31.7 |
| <i>Tvetenia</i> | * | No. | 0 | 0 | 7 | 0 |
| | | mg | 0.0 | 0.0 | 0.1 | T |
| <i>T. bavarica</i> | * | No. | 46 | 286 | 278 | 516 |
| | | mg | 1.7 | 6.5 | 13.1 | 8.8 |

| TAXON | | 1985 | | 1986 | | |
|------------------------|---|------|-------|-------|--------|--------|
| | | CC | ELK | CC | ELK | |
| <i>T. discoloripes</i> | * | No. | 18 | 10 | 43 | 34 |
| | | mg | 1.0 | 0.4 | 2.5 | 0.6 |
| <i>Zavrelimya</i> | | No. | 6 | 72 | 87 | 75 |
| | | mg | 0.5 | 3.5 | 2.2 | 3.2 |
| DIPTERA (midge) | | No. | 3608 | 5385 | 29437 | 12378 |
| | | mg | 127.4 | 114.2 | 612.4 | 289.8 |
| GRAND TOTALS | | No. | 10024 | 15631 | 57667 | 31184 |
| | | mg | 699.7 | 993.6 | 2469.0 | 1879.7 |